The Annals of Applied Probability
1999, Vol. 9, No. 4, 1226–1259

AN EXPLICITLY SPATIAL VERSION OF THE LOTKA–VOLTERRA MODEL WITH INTERSPECIFIC COMPETITION

By Claudia Neuhauser[1] and Stephen W. Pacala[2]

University of Minnesota and Princeton University

We consider a spatial stochastic version of the classical Lotka–Volterra model with interspecific competition.

The classical model is described by a set of ordinary differential equations, one for each species. Mortality is density dependent, including both intraspecific and interspecific competition. Fecundity may depend on the type of species but is density independent. Depending on the relative strengths of interspecific and intraspecific competition and on the fecundities, the parameter space for the classical model is divided into regions where either coexistence, competitive exclusion or founder control occur.

The spatial version is a continuous time Markov process in which individuals are located on the d-dimensional integer lattice. Their dynamics are described by a set of local rules which have the same components as the classical model.

Our main results for the spatial stochastic version can be summarized as follows. Local competitive interactions between species result in (1) a reduction of the parameter region where coexistence occurs in the classical model, (2) a reduction of the parameter region where founder control occurs in the classical model, and (3) spatial segregation of the two species in parts of the parameter region where the classical model predicts coexistence.

1. Introduction. A fundamental problem faced by ecologists is that the spatial and temporal scales at which measurements are practical, are typically smaller than those at which the most important phenomena occur. For example in plant ecology, we can measure the growth, survivorship, fecundity and seed dispersal of individual plants, and we can predict those quantities using simple equations (see [25], [27]). But what is needed is a way to model changes in distribution and abundance of plant species at spatial scales from hectares to many square kilometers and at temporal scales from years to a century or more.

Because we lack an ecological statistical mechanics, ecologists rely on computer simulations of ensembles of individuals to predict the consequences of their observations and on phenomenological "mean-field" models to gain general insights (see [17]). These mean-field models are typically coupled systems of ordinary differential equations, with state variables giving the mean abundances of several interacting species. The mean-field models cannot generally be derived from observable individual-level rules, except in the special case where rapid movement and/or long-range interactions among individuals ef-

---

Received September 1998; revised December 1998.

[1] Supported in part by NSF Grant DMS-97-03694.

[2] Supported in part by grants from NASA, the Sloan foundation and the Mellon foundation.

AMS 1991 *subject classifications*. Primary 60K35; secondary 92B05.

Key words and phrases. Competiton, contact process, interacting particle system, voter model.

fectively mixes them completely. A considerable body of evidence demonstrates the importance of short-range interactions and dispersal, especially when organisms are sedentary (e.g., plants, marine invertebrates, [1], [26]).

In this paper we investigate a simple individual-level stochastic process that corresponds, in the long-range limit, to a classical model of competition between species, the Lotka–Volterra model, [34], [19]. This Lotka–Volterra model describes the competitive interaction between two species for which population growth is density dependent. We give a description of the model. Denote by N_1 and N_2 the number of individuals of species 1 and 2, respectively. Then

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1\left(1 - \frac{N_1}{K_1} - a_{12}\frac{N_2}{K_1}\right), \\ \frac{dN_2}{dt} &= r_2 N_2\left(1 - \frac{N_2}{K_2} - a_{21}\frac{N_1}{K_2}\right), \end{aligned} \tag{1.1}$$

where r_i is the intrinsic rate of growth of species i. The quantity K_i denotes the carrying capacity of species i, that is, K_i is the equilibrium density of species i in the absence of species j. Note that the dynamics of species i in the absence of species j is given by the logistic equation which incorporates inhibitory effects of species i on itself, the so-called *intraspecific competition*. The effect *of* species j *on* species i, the so-called *interspecific competition*, is described by a_{ij}. We assume a_{12}, $a_{21} \geq 0$.

It is easy to analyze the equilibria of (1.1) using phase plane analysis (i.e., zero isoclines). The following hold.

1. When interspecific competition is less important than intraspecific competition (i.e., $K_1 > K_2 a_{12}$ and $K_2 > K_1 a_{21}$), then *coexistence* is possible, that is, there exists a nontrivial stable equilibrium in which both species are present.
2. A strong interspecific competitor out-competes a weak interspecific competitor. That is, when $K_1 < K_2 a_{12}$ and $K_2 > K_1 a_{21}$, then species 2 takes over and species 1 dies out. (Likewise, species 1 takes over and species 2 dies out when the inequalities are reversed.) This is called *competitive exclusion*.
3. When interspecific competition is more important than intraspecific competition (i.e., $K_1 < K_2 a_{12}$ and $K_2 < K_1 a_{21}$), the two species cannot coexist. The outcome of the competition depends on the initial densities. This is referred to as *founder control*.

Note that the coexistence outcome requires that the strengths of interspecific competition (a_{12} and a_{21}) be sufficiently small. Classical explanations for the coexistence of species center on the idea that the a's are reduced by so-called niche-displacement, for example, differences in diet that reduce each species' tendency to deplete the other's food supply (i.e., [20]). The coexistence of plant species is particularly difficult to explain because plants must have similar diets; all green plants require light, water and a few mineral nutrients (see [1], [33]).

The model described in (1.1) assumes global interactions, that is, mortality depends on global densities and dispersal is infinite. This greatly facilitates the analysis but leaves out the critical short-distance interactions and dispersal. When individuals interact over short distances, demographic stochasticity may play an important role in determining the outcome of competition on a local scale.

To be able to study the effects of such short-range interactions on the outcome of competition, we extend the nonspatial deterministic Lotka–Volterra model (1.1) to an explicitly spatial stochastic model.

We model the spatial system as a continuous time Markov process on $\mathbf{Z}^d$, the d-dimensional integer lattice. The state at time t is denoted by η_t with $\eta_t \in \{1,2\}^{\mathbf{Z}^d}$. That is, $\eta_t(x) = 1$ if x is occupied by a particle of type 1, and $\eta_t(x) = 2$ if x is occupied by a particle of type 2. We assume that at all times every site on the lattice is occupied by exactly one particle, that is, there are never any vacant sites. To describe the dynamics, we define

$$f_i(x) = \frac{\left|\{y\colon \eta_t(y) = i\colon y \in \mathcal{N}_x\}\right|}{\left|\mathcal{N}_x\right|},$$

where $\mathcal{N}_x = x + \{y\colon 0 < \|y\|_\infty \le R\}$ and $\|\cdot\|_\infty$ denotes the supnorm [i.e., $\|y\|_\infty = \max_i y_i$ for $y = (y_1, y_2, \dots, y_d)$]. The evolution of the process is described by the following rules.

1. If $\eta_t(x) = 1$, it becomes a 2 at rate
$$\frac{\lambda f_2}{\lambda f_2 + f_1}(f_1 + \alpha_{12} f_2).$$
2. If $\eta_t(x) = 2$, it becomes a 1 at rate
$$\frac{f_1}{\lambda f_2 + f_1}(f_2 + \alpha_{21} f_1).$$

The rates can be interpreted as follows. A particle of type i dies at rate $f_i + \alpha_{ij} f_j$ and gets instantaneously replaced by an offspring of one of its neighbors chosen from its neighborhood according to the relative fecundities of the two species. We refer to this as the high-density limit. (The low-density limit, in which the replacement is not instantaneous and which therefore has vacant sites, will be analyzed elsewhere.)

The density-dependent mortality $f_i + \alpha_{ij} f_j$ has two components. The first one, f_i, describes the effect of intraspecific competition; the second one, $\alpha_{ij} f_j$, describes the effect of interspecific competition. We assume here that both species experience the same strength of intraspecific competition. It is easy to incorporate different strengths of intraspecific competition, but our model already has three parameters. Replacement after death is proportional to the respective *weighted* densities of the two species which is measured by the parameter λ. We assume $\lambda \ge 1$. If $\lambda = 1$, the two species contribute equally relative to their local frequencies. If $\lambda > 1$, then species 2 has a higher fecundity than species 1; that is, it contributes a proportionally higher fraction to the pool from which the offspring is chosen.

Although this stochastic process is simple, similar models already predict the dynamics of plant communities in the field (i.e., [29], [30], [32]). The assumption of large fecundity, ensuring complete occupancy of space, is appropriate for sites of moderate to high productivity, including most forests and many grasslands. Also, as in our model, competitive interactions in perennial vegetations primarily affect establishment and mortality, rather than adult fecundity, [27].

The first step in understanding the behavior of the system is to study its *mean-field* behavior. That is, we pretend that all sites are independent and investigate how the densities evolve under translation invariant initial conditions. We denote by u_i the fraction of sites in state i. Since $u_1 + u_2 = 1$, one ordinary differential equation suffices to describe the evolution.

$$\frac{du_1}{dt} = -u_1 \frac{\lambda u_2}{\lambda u_2 + u_1}(u_1 + \alpha_{12} u_2) + u_2 \frac{u_1}{\lambda u_2 + u_1}(u_2 + \alpha_{21} u_1).$$

Using $u_1 + u_2 = 1$, this simplifies to

$$\frac{du_1}{dt} = \frac{u_1(1-u_1)}{\lambda(1-u_1)+u_1}\big[1 - \lambda\alpha_{12} - u_1(1 + \lambda - \alpha_{21} - \lambda\alpha_{12})\big]. \tag{1.2}$$

Besides the two trivial equilibria 0 and 1, there is a nontrivial equilibrium at

$$u_1^* = \frac{1}{1 + (\lambda - \alpha_{21})/(1 - \lambda\alpha_{12})}$$

which is contained in $[0,1]$ for $(\alpha_{21}, \alpha_{12}) \in [0, \lambda] \times [0, 1/\lambda] \cup [\lambda, \infty) \times [1/\lambda, \infty)$. It is easy to analyze the stability of the nontrivial equilibrium and we obtain the following behavior.

1. If $0 \le \alpha_{21} < \lambda$ and $0 \le \alpha_{12} < 1/\lambda$, the nontrivial equilibrium is stable and coexistence is possible.
2. If $\alpha_{21} > \lambda$ and $0 \le \alpha_{12} < 1/\lambda$, species 1 outcompetes species 2. If $\alpha_{12} > 1/\lambda$ and $0 \le \alpha_{21} < \lambda$, species 2 outcompetes species 1.
3. If $\alpha_{21} > \lambda$ and $\alpha_{12} > 1/\lambda$, the nontrivial equilibrium is unstable and coexistence is not possible. The outcome of the competitive interactions depends on the initial densities, a situation referred to as founder control.

In this paper, we show that short-range interactions (finite R) alter the predictions of the mean-field model in three important ways. First, short-range interactions reduce the size of the region of parameter space in which coexistence is possible. This result amplifies the paradox of plant diversity by making it even more difficult to explain the coexistence of species such as plants, with necessarily similar resource requirements. Second, short-range interactions cause plant species to segregate spatially. This result has been obtained previously with approximate methods and is supported by a large experimental literature (see [26], [28]). The spatial segregation reduces the effective amount of competition simply by separating the species and may serve to increase a plant community's ability to recover following disturbance (see [26]). Third, the founder control region is reduced in size. We in fact believe that the possibility of founder control is completely eliminated by interactions of finite range.

2. Results. We begin with the *symmetric* case in which both species are identical, that is, we set $\lambda = 1$ and $\alpha \equiv \alpha_{12} = \alpha_{21}$. To identify the effects of space on the outcome of competition, we compare the results for the spatial model to the predictions of the mean-field model (1.2). The equilibria for the mean-field model in the symmetric case are 0, $\frac{1}{2}$ and 1. The stability of the nontrivial mean-field equilibrium $u_1^* = 1/2$ follows from the analysis above. If $\alpha \in [0, 1)$, the equilibrium $u_1^* = 1/2$ is stable which implies that coexistence is possible. If $\alpha > 1$, the equilibrium $u_1^* = 1/2$ is unstable which implies that there is no coexistence; the outcome of the competition depends on the initial densities. When $\alpha = 1$, then $du_1/dt \equiv 0$ regardless of the value of u_1. This suggests that any value of $u_1 \in [0, 1]$ constitutes a possible equilibrium and the behavior depends on the initial densities.

Before we state our results for the spatial system, we need a couple more definitions (see [4]). We say that *coexistence* occurs if for $\varepsilon > 0$ and large enough L, any given $L \times L$ square will possess both types of particles with probability at least $1 - \varepsilon$ at all large enough times. We say that an initial distribution or a stationary distribution is *nontrivial* if it concentrates on both types of particles.

We are now ready to state our results. We begin with coexistence results.

THEOREM 1. *Assume* $\lambda = 1$ *and* $d = 1$ *or* 2.

(a) *When* $\alpha = 0$, *then, except for the one-dimensional nearest neighbor case, product measure with density* 1/2 *is the limiting distribution starting from any nontrivial initial distribution.*

(b) *If* α *is sufficiently small* (*depending on* R), *then coexistence is possible except for the one-dimensional nearest neighbor case.*

Theorem 1 says that when α is small, then except for the one-dimensional nearest neighbor case, the explicitly spatial model behaves qualitatively similarly to the mean-field model: coexistence is possible in both cases. Theorem 1 can easily be extended to more than two dimensions using the same ideas. But since the one- and two-dimensional cases are the biologically most relevant ones and since the estimates in the proof get messy in higher dimensions, we omit the proof for $d \geq 3$.

The one-dimensional nearest neighbor case is a bit of an exception. To state the theorem in this case, we need to define the so-called boundary process β_t which lives on $1/2 + \mathbf{Z}$ with

$$\beta_t(x) = \begin{cases} 1, & \text{if } \eta_t(x - \frac{1}{2}) \neq \eta_t(x + \frac{1}{2}), \\ 0, & \text{otherwise.} \end{cases}$$

THEOREM 2. *Suppose* $d = 1$ *and* $\mathscr{N} = \{-1, 1\}$.

(a) *When* $\alpha = 0$, *there is a one-parameter family of stationary distributions* $\{\pi_\theta\colon 0 \le \theta \le 1\}$ *for which the boundary process* β_t *has product measure with density* θ.

(b) *When* $\alpha > 0$, *then clustering occurs starting from any translation invariant initial state* η_0. *That is, for any* $x, y \in \mathbf{Z}$, $P(\eta_t(x) \ne \eta_t(y)) \to 0$ *as* $t \to \infty$.

The proof of part (b) of Theorem 2 is identical to the proof of Theorem 5.1 in [7] and is omitted.

When $\lambda = 1$ and $\alpha = 1$, then since $f_1 + f_2 = 1$, the system reduces to the well-known voter model. The voter model was introduced independently by Holley and Liggett [15] and Clifford and Sudbury [5]. Its behavior is well understood. Starting from any translation invariant initial configuration in $d = 1$ or 2, clustering occurs, that is, for any $x, y \in \mathbf{Z}^d$, $d = 1$ or 2,

$$P\big(\eta_t(x) \ne \eta_t(y)\big) \to 0 \quad \text{as } t \to \infty.$$

In $d \ge 3$ coexistence is possible. Specifically, in $d \ge 3$, there exists a one-parameter family of ergodic measures $\{\nu_\theta\colon \theta \in [0,1]\}$ which are the limits of $\mu_\theta S(t)$ where μ_θ is product measure with density θ of 1's and $S(t)$ is the corresponding semigroup of the process. (For more on the voter model see [18].)

The next theorem shows that as $\alpha \to 1$ (from below), clusters form and the two types become spatially segregated, thus effectively reducing interspecific competition.

THEOREM 3. *Assume* $\lambda = 1$ *and* R *is fixed.*

(a) *Assume* $d = 1$ *and* $\alpha < 1$. *Fix* $\varepsilon > 0$. *If* $\alpha \to 1$ *and* $L \to \infty$ *so that* $(1-\alpha)L^{2+\varepsilon} \to 0$, *then*

$$P\big(\eta_{L^{2+\varepsilon}}(L) \ne \eta_{L^{2+\varepsilon}}(0)\big) \to 0.$$

(b) *Assume* $d = 2$ *and fix* x_0 *with* $\|x_0\| = L$. *Let* $\alpha < 1$. *If* $\alpha \to 1$ *and* $L \to \infty$ *so that* $(1-\alpha)L^{\log L} \to 0$, *then*

$$P\big(\eta_{L^{\log L}}(x_0) \ne \eta_{L^{\log L}}(0)\big) \to 0.$$

The spatial segregation stated in Theorem 3 is solely due to local interactions and the low dimensionality and cannot be deduced from the mean-field equation (1.2). However, if we fix α, the clusters will break up as we increase R, the range of interaction. Specifically, we will discuss below that the nontrivial stationary distribution will be close to product measure with density 1/2 for R sufficiently large. This is a by now well-known phenomenon in long-range models or models with fast stirring with two possible states for which the mean-field model has exactly one stable equilibrium (see, e.g., [7], [8], [9], [22]). In this case it is typically not too hard to show that the stationary distribution of the spatial model is close to product measure with density close to the mean-field equilibrium provided the range of interaction is sufficiently large.

Even though when $\alpha < 1$, spatial segregation does occur in $d \le 2$, we do not believe that these clusters continue to grow indefinitely as in the case $\alpha = 1$. Our belief is based on the behavior of the key ingredient in the proof of Theorems 1 and 3, namely the existence of a double branching annihilating dual process when $\alpha < 1$. We will explain this in Section 4. We conjecture the following.

CONJECTURE 1. *Assume* $\lambda = 1$ *and* $\alpha \equiv \alpha_{12} = \alpha_{21}$. *Except for the one-dimensional nearest neighbor case, coexistence is possible for any* $\alpha < 1$, *regardless of the spatial dimension.*

We leave the symmetric case now and describe the behavior of the spatial model when $\lambda \ge 1$ with the rates given above. We demonstrated above that in the nonspatial model coexistence is possible whenever $(\alpha_{21}, \alpha_{12}) \in [0, \lambda) \times [0, 1/\lambda)$. As mentioned above, in the long range limit the system behaves like the mean-field model when $\alpha < 1$. This can be extended to the entire mean-field coexistence region. The proof is a straightforward extension of [22] and will not be included here. The result is as follows.

(*) Assume $\lambda \ge 1$. Fix $(\alpha_{21}, \alpha_{12}) \in [0, \lambda) \times [0, 1/\lambda)$. The spatial model has a nontrivial stationary distribution in which the distribution of 1's is close to product measure with density

$$u_1^* = \frac{1}{1 + (\lambda - \alpha_{21})/(1 - \lambda\alpha_{12})}$$

for R sufficiently large.

In essence, such long-range limits imply that once the scale of interactions is sufficiently large compared to the amount of space each individual occupies, then space does not matter and a mean-field description is adequate when the mean-field equation has exactly one stable equilibrium. In some sense, by taking long-range limits, one throws out any effects that are solely due to local interactions since the long range allows individuals to interact on a global scale.

In the following we will focus on effects that are solely due to local interactions. An extension of Theorem 1 which follows readily from [24] shows that if $\alpha_{12} = \alpha_{21} = 0$, then product measures with density $1/(1 + \lambda)$ of 1's is an equilibrium. When $\lambda > 1$, we do not have a complete convergence result as in the case $\lambda = 1$ (Theorem 1), but we conjecture that except for the one-dimensional nearest neighbor case, product measure with density $1/(1 + \lambda)$ is always the limiting distribution when starting from a nontrivial initial distribution. This would then imply that changing R, the range of interaction, has no influence on the stationary distribution in the absence of interspecific competition.

We will now turn to situations where local interactions change the nature of the outcome of competitive interactions. The first such result shows that the coexistence region is smaller in the spatial setting.

THEOREM 4. *We assume* $\lambda \geq 1$ *and set* $N = |\mathscr{N}|$. *If initially there are infinitely many* 2*'s, then* 2*'s take over with probability* 1 *if*

$$\alpha_{12} > \begin{cases} \dfrac{N-1+\alpha_{21}}{\lambda(N-1)+1}, & \text{for } 0 \leq \alpha_{21} \leq \dfrac{1}{\lambda}, \\ \alpha_{21}, & \text{for } \dfrac{1}{\lambda} \leq \alpha_{21} \leq \lambda, \\ \dfrac{\lambda-1+N}{\lambda}\alpha_{21} - N + 1, & \text{for } \alpha_{21} \geq \lambda. \end{cases}$$

The boundary of the region described in Theorem 4, where 2's competitively exclude 1's, is a polygon (in particular, it is a continuous function of α_{21}). (A picture is provided in Section 5 where we prove Theorem 4.) We compare this region to the corresponding region in the mean-field model. There we showed that 2's outcompete 1's when $\alpha_{12} > 1/\lambda$ and $\alpha_{21} < \lambda$. Note that

$$\frac{N-1+\alpha_{21}}{\lambda(N-1)+1} = \begin{cases} \dfrac{1}{\lambda}\left[1 - \dfrac{1}{\lambda(N-1)+1}\right], & \text{for } \alpha_{21} = 0, \\ \dfrac{1}{\lambda}, & \text{for } \alpha_{21} = 1/\lambda. \end{cases}$$

That is, this boundary line is a straight line connecting the points $(0, [1 - 1/(\lambda(N-1)+1)]/\lambda)$ and $(1/\lambda, 1/\lambda)$. Since $[1 - 1/(\lambda(N-1)+1)]/\lambda < 1/\lambda$ for $\lambda \geq 1$, it follows that the boundary line for $0 \leq \alpha_{21} \leq 1/\lambda$ is entirely contained in the mean-field coexistence region. This implies that the effect of space is a reduction of the size of the coexistence region. Combining this with our results for the long-range case (*), it follows that this effect is more pronounced for smaller values of R.

Furthermore, since

$$\frac{\lambda-1+N}{\lambda}\alpha_{21} - N + 1 = \lambda \quad \text{for } \alpha_{21} = \lambda$$

and

$$\frac{\lambda-1+N}{\lambda} > 0 \quad \text{for } \lambda \geq 1,$$

the boundary line for $\alpha_{21} \geq \lambda$ is entirely contained in the founder control region of the mean field model. This implies that the effect of space is a reduction of the size of the founder control region.

In the symmetric case $\lambda = 1$, if we exchange the roles of 1's and 2's in Theorem 4, then we obtain a region where species 1 wins. The boundaries of both regions are given by two lines, both go through $(1, 1)$, one has slope $1/N$, the other has slope N. These two lines divide the parameter space into four regions. We designate the horizontal axis as the α_{21} axis and the vertical axis as the α_{12} axis. This is shown in Figure 1. We summarize our findings for the symmetric case in the following corollary.

COROLLARY 1. *Assume the symmetric case* $\lambda = 1$. *Species* 1 *competitively excludes species* 2 *if*

$$\alpha_{12} < \begin{cases} N\alpha_{21} - N + 1, & \text{for } \alpha_{21} \in \left(1 - \frac{1}{N}, 1\right], \\ \frac{1}{N}\alpha_{21} + 1 - \frac{1}{N}, & \text{for } \alpha_{21} > 1. \end{cases}$$

Species 2 *competitively excludes species* 1 *if*

$$\alpha_{12} > \begin{cases} \frac{1}{N}\alpha_{21} + 1 - \frac{1}{N}, & \text{for } \alpha_{21} \in (0, 1], \\ N\alpha_{21} - N + 1, & \text{for } \alpha_{21} > 1. \end{cases}$$

Corollary 1 shows that species 1 wins in the convex region bounded above by the two lines and species 2 wins in the convex region bounded below by the two lines. If we compare this with the predictions from the mean-field model, we see that both the coexistence region and the founder region is smaller.

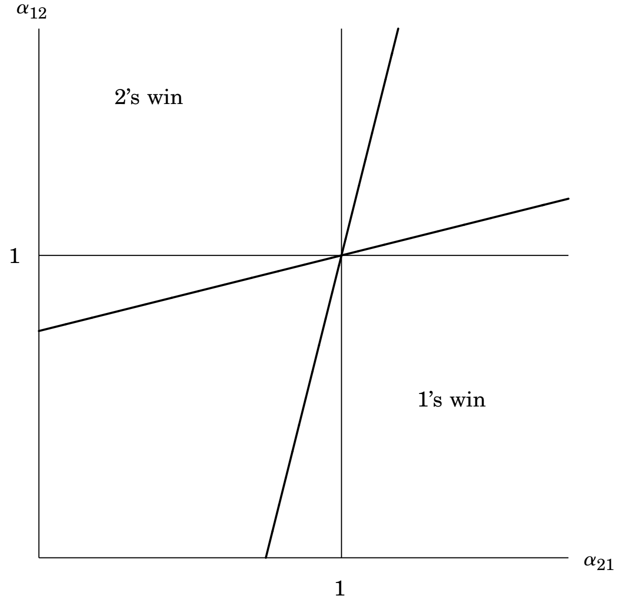

FIG. 1. *Regions of competitive exclusion in the symmetric case* ($\lambda = 1$). *The thick lines are the phase boundaries from Theorem* 4. *The thin lines are the mean field phase boundaries.*

The reason for the reduction of the coexistence region is as follows. (Because of symmetry, we only discuss the region in which species 1 wins.) Coexistence is not possible since a low density of 2's cannot be maintained. One 2 in a local neighborhood increases the relative frequency of 2's in the neighborhood enough so that the 1's experience a positive drift and drive the 2 out again.

The reason for the reduction of the founder control region is as follows. (Because of symmetry, we only discuss the region in which species 1 wins.) As soon as there is one 1 in the neighborhood, the relative frequency of 1's in the neighborhood rises above the threshold for invasion of 1's. This is caused by the discreteness of the neighborhood. No arbitrarily small densities can be experienced locally, the densities always change by discrete amounts of size $1/N$.

Since the region where one species drives the other to extinction in mean field is contained in the corresponding region in the spatial model, this region is therefore expanded in the spatial setting.

In the asymmetric case, when $\lambda > 1$, we can also obtain bounds on the competition parameters so that 1's competitively exclude 2's. This is contained in the following theorem.

THEOREM 5. *We assume* $\lambda > 1$ *and set* $N = |\mathcal{N}|$. *If initially there are infinitely many* 1*'s, then* 1*'s take over with probability* 1 *if*

$$\alpha_{12} < \begin{cases} \alpha_{12}^*(\alpha_{21}), & \textit{for } \dfrac{1}{\lambda} < \alpha_{21} \le \lambda + (N-1)(\lambda^2 - 1), \\ \alpha_{12}^{**}(\alpha_{21}), & \textit{for } \alpha_{21} \ge \lambda + (N-1)(\lambda^2 - 1), \end{cases}$$

with

$$\alpha_{12}^*(\alpha_{21}) = \frac{1}{\lambda}\frac{N+\lambda-1}{\lambda(N-1)+1}\alpha_{21} - \frac{1}{\lambda}\frac{(N-1)^2(\lambda^2-1)}{\lambda(N-1)+1},$$

$$\alpha_{12}^{**}(\alpha_{21}) = \frac{1}{\lambda(N-1)+1}\alpha_{21} + \frac{N-1}{\lambda(N-1)+1}.$$

Note that $\alpha_{12}^*(\alpha_{21}) = \alpha_{12}^{**}(\alpha_{21}) = \lambda$ for $\alpha_{21} = \lambda + (N-1)(\lambda^2 - 1)$. Two consequences of this theorem are contained in the following corollaries.

COROLLARY 2. *For each* $N > 2$ *there exist* $\lambda \in (1, \infty)$ *so that there are choices for* α_{21} *and* α_{12} *for which the mean-field model predicts coexistence, whereas in the explicitly spatial model the* 1*'s competitively exclude the* 2*'s.*

COROLLARY 3. *For each* $N > 2$ *there exist* $\lambda \in (1, \infty)$ *so that there are choices for* α_{21} *and* α_{12} *for which the mean-field model predicts founder control, whereas in the explicitly spatial model the* 1*'s competitively exclude the* 2*'s.*

Our discussion for the case $\lambda = 1$ (Corollary 1) shows that the founder control region is reduced in size. That is, the outcome of the competitive interaction does not depend on the initial densities as long as infinitely many sites are occupied by the superior type. We conjecture the following.

CONJECTURE 2. *Assume* $\lambda = 1$. *There is no founder control in the spatial model. If* $\alpha_{21} > \alpha_{12} > 1$ *and initially there are infinitely many* 1*'s, then the* 1*'s take over with probability* 1. *If* $\alpha_{12} > \alpha_{21} > 1$ *and initially there are infinitely many* 2*'s, then the* 2*'s take over with probability* 1.

Our conjecture is supported by the following modification of the model. It is convenient to define the model on the rescaled lattice $\varepsilon\mathbf{Z}^d$. In addition to the births and deaths, individuals are allowed to swap positions with their neighbors. That is, for each $x, y \in \varepsilon\mathbf{Z}^d$ with $\|x - y\|_1 = \varepsilon$, we exchange the values at x and y at rate $\varepsilon^{-2}/2$. Results in [10] show that the density of 1's in the limit $\varepsilon \to 0$ is given by the following reaction diffusion equation:

$$\frac{\partial u_1}{\partial t} = \tfrac{1}{2}\Delta u_1 + u_1(1-u_1)\big[1-\alpha_{12} - u_1(2-\alpha_{12}-\alpha_{21})\big].$$

This pde admits travelling wave solutions and one can show that, if initially

$$u_1(x,0) = \begin{cases} 1, & \text{for } x \le 0,\\ 0, & \text{for } x > 0,\end{cases}$$

then

$$\lim_{t\to\infty} u_1(x,t) = \begin{cases} 1, & \text{for } \alpha_{21} > \alpha_{12},\\ 0, & \text{for } \alpha_{21} < \alpha_{12}.\end{cases}$$

Since one of the conditions in [10] does not hold here (the configuration consisting of all 1's is a trap in our case), the argument in [10] needs to be slightly modified. The results are the same, however. Given α_{12} and α_{21} then, for ε small enough, the particle system follows the partial differential equation closely.

The paper is organized as follows. Section 3 introduces the dual process for the symmetric case when $0 \le \alpha \le 1$. This is the key ingredient of Theorems 1 and 3. Theorems 1 and 2 are proved in Section 4. Section 5 is devoted to the proof of Theorem 3. Theorem 4 is proved in Section 6 and Theorem 5 is proved in Section 7.

3. A dual process.

In this section we restrict ourselves to the symmetric case $\lambda = 1$ and $\alpha \equiv \alpha_{12} = \alpha_{21}$. That is, both species are identical. We will demonstrate that when $\alpha \le 1$, a dual process exists. This is the key ingredient in the proofs of Theorems 1, 2 and 3.

Duality ([31], [15], [16]) is a powerful tool in the study of interacting particle systems since it allows one to investigate the infinite system by tracing the ancestry of a *finite* number of particles *without* knowledge of the actual configuration in the past. That is, starting at time t with a finite number of sites, we go backwards in time and find the ancestral paths and hence the set of sites at time 0 which determine the states of the sites at time t.

It is important to note that if a dual process exists, then the history of the process is independent of the state of the system in the past. In particular, this allows one to find the state of a finite number of sites by knowing only the initial configuration and the history of the sites. (A dual process does not always exist or if it exists, it might be too complicated to be useful.)

The dual process for the symmetric case is an *annihilating dual process*. This is a continuous time Markov process on the set

$$Y = \{A\colon A \subset \mathbf{Z}^d,\, A \text{ finite}\}$$

with transition kernels $p(x, A)$, $A \in Y$. That is, the dual process is a set-valued process. Suppose at time t, the dual process consists of the set F for $F \in Y$. We refer to the elements in F as *dual particles*. Then at rate $c(x)$, $x \in F$, the dual particle at x is removed from the set F and with probability $p(x, A)$, all dual particles in the set A are added to the set $F - \{x\}$ and the following rule, which explains the name "annihilating dual process," is applied. If a dual particle lands on a site already contained in the dual process (i.e., in the set $F - \{x\}$), the two dual particles annihilate each other. For a dual process to exist, it is necessary that $p(x, A) \geq 0$ and $\sum_{A \in Y} p(x, A) \leq 1$.

The dual process for the symmetric case is given by a double branching annihilating random walk. To demonstrate this, it will be convenient to denote the possible states by 0 and 1 instead of 1 and 2. We denote this relabelled process by ζ. The symmetric process with state space $\{0, 1\}^{\mathbf{Z}^d}$ has transition rates

$$c(x, \zeta) = \begin{cases} f_0\big(1 - (1-\alpha) f_0\big), & \text{when } \zeta(x) = 1, \\ f_1\big(1 - (1-\alpha) f_1\big), & \text{when } \zeta(x) = 0, \end{cases} \tag{3.1}$$

where $f_0 = n_0/N$ with $n_0 = |\{y \in \mathcal{N}_x\colon \zeta(y) = 0\}|$ and $N = |\mathcal{N}_x|$. Recall that $\mathcal{N}_x = x + \{z\colon 0 < \|z\|_\infty \leq R\}$ denotes the set of neighbors of x. We set $f_1 = n_1/N$ with $n_1 = N - n_0$.

If the rates $c(x, \zeta)$ can be written in the following form (see Liggett [18], page 158, who based his representation on [16]):

$$c(x, \zeta) = \frac{c(x)}{2}\left\{1 - [2\zeta(x) - 1] \sum_{A \in Y} p(x, A) H(\zeta, A)\right\} \tag{3.2}$$

with

$$H(\zeta, A) = \prod_{y \in A} [2\zeta(y) - 1] \tag{3.3}$$

and $c(x) \geq 0$, $p(x, A) \geq 0$ for all $A \in Y$ and $\sum_{A \in Y} p(x, A) \leq 1$, then the process has an annihilating dual with the interpretation given above. We denote the dual process by $\hat{\zeta}$. In the following it will be convenient to consider the two processes ζ and $\hat{\zeta}$ as set-valued processes; that is, $x \in \zeta$ (or $\hat{\zeta}$) if and only if $\zeta(x) = 1$ [or $\hat{\zeta}(x) = 1$]. We write ζ_t^A for the process at time t if the initial configuration is the set A [i.e., $\zeta_0^A(x) = 1$ for all $x \in A$ and $\zeta_0^A(x) = 0$ for all $x \notin A$]. Similarly, $\hat{\zeta}_t^B$ denotes the dual process at time t when starting with the set B. The following *duality equation* relates the processes ζ and $\hat{\zeta}$:

$$P\bigl(|\hat{\zeta}_t^B \cap A| \text{ is odd}\bigr) = P\bigl(|\zeta_t^A \cap B| \text{ is odd}\bigr), \tag{3.4}$$

where $|\cdot|$ denotes the cardinality. The structure of the dual process $\hat{\zeta}$ is contained in the following proposition.

PROPOSITION 1. *Suppose the rates are given by* (3.1). *Then there exists an annihilating dual process with*

$$\begin{aligned} p_1 &\equiv p(x, y) = \frac{2\alpha}{2N - (N+1)(1-\alpha)}, \qquad y \in \mathcal{N}_x, \\ p_2 &\equiv p\bigl(x, \{x, y, z\}\bigr) = \frac{2(1-\alpha)}{N\bigl[2N - (N+1)(1-\alpha)\bigr]}, \qquad y, z \in \mathcal{N}_x, y \neq z, \\ c &\equiv c(x) = \frac{2N - (N+1)(1-\alpha)}{2N}. \end{aligned} \tag{3.5}$$

Before proving the proposition, we state its interpretation. The dual process, denoted by $\hat{\zeta}_t$, is a set-valued process which takes values in $Y = \{A \subset \mathbf{Z}^d\colon A \text{ finite}\}$. Suppose at time t, $\hat{\zeta}_t = F$; that is, the dual particles are located at the points of the set F. At rate $c|F|$, a particle in F is chosen at random. Suppose the particle is located at x. Two things can happen; either the particle jumps to a site chosen at random from the set $\mathcal{N}_x$, according to the transition kernel $p_1 = p(x, y)$, or the particle produces two offspring which are then sent to two different sites chosen at random from the set $\mathcal{N}_x$, according to the transition kernel $p_2 = p(x, \{x, y, z\})$. In either case, if a particle jumps to a site already contained in the dual process, annihilation occurs; that is, both the particle jumping to the already occupied site and the particle located at the landing site disappear. The random walk step occurs with probability Np_1, the double branching occurs with probability $\binom{N}{2}p_2$. Note that $Np_1 + \binom{N}{2}p_2 = 1$.

PROOF OF PROPOSITION 1. We begin with the following calculation:

$$\begin{aligned} &\frac{1}{2N} \sum_{\substack{y,z,\in\mathcal{N}_x \\ y\neq z}} [2\zeta(y) - 1][2\zeta(z) - 1] \\ &\quad = \frac{1}{2N}\left[\binom{n_0}{2} + \binom{n_1}{2} - n_0 n_1\right] \\ &\quad = \frac{1}{2N}\left[\frac{1}{2}n_0^2 - \frac{1}{2}n_0 + \frac{1}{2}(N - n_0)^2 \right. \\ &\qquad\qquad \left. - \frac{1}{2}(N - n_0) - n_0(N - n_0)\right] \\ &\quad = \frac{1}{2N}\left[2n_0^2 - 2Nn_0 + \frac{1}{2}N^2 - \frac{1}{2}N\right] \\ &\quad = \frac{1}{2N}\left[\frac{N(N-1)}{2} - 2n_0(N - n_0)\right]. \end{aligned} \tag{3.6}$$

We rewrite (3.2) using (3.3) and (3.5) to show that this results in the rates given in (3.1):

$$\begin{aligned} Nc(x,\zeta) = {} & \frac{2N-(N+1)(1-\alpha)}{4} \\ & \times \Biggl\{ 1 - [2\zeta(x)-1] \sum_{y\in\mathcal{N}_x} \frac{2\alpha}{2N-(N+1)(1-\alpha)}[2\zeta(y)-1] \\ & \quad - [2\zeta(x)-1] \sum_{\substack{y,\,z,\,\in\mathcal{N}_x \\ y\neq z}} \frac{2(1-\alpha)}{N\bigl(2N-(N+1)(1-\alpha)\bigr)} \\ & \qquad \times [2\zeta(x)-1][2\zeta(y)-1][2\zeta(z)-1] \Biggr\} \end{aligned}$$

Note that $[2\zeta(x)-1]^2 = 1$ regardless of whether $\zeta(x) = 0$ or 1 and that $\sum_{y\in\mathcal{N}_x}[2\zeta(y)-1] = n_1 - n_0$. Then using (3.6), we find

$$\begin{aligned} Nc(x,\zeta) = {} & \frac{2N-(N+1)(1-\alpha)}{4} - [2\zeta(x)-1]\frac{\alpha}{2}(n_1-n_0) \\ & - \frac{1-\alpha}{2N}\biggl[\frac{N(N-1)}{2} - 2n_0(N-n_0)\biggr]. \end{aligned} \tag{3.7}$$

We consider the two cases $\zeta(x) = 0$ and $\zeta(x) = 1$ separately. When $\zeta(x) = 0$, then (3.7) becomes

$$\begin{aligned} Nc(x,\zeta) &= \frac{N}{2} - \frac{(N+1)(1-\alpha)}{4} + \frac{\alpha}{2}(2n_1 - N) \\ & \quad - \frac{(N-1)(1-\alpha)}{4} + \frac{1-\alpha}{N}n_1(N-n_1) \\ &= n_1 - \frac{1-\alpha}{N}n_1^2 = N\bigl(f_1 - (1-\alpha)f_1^2\bigr). \end{aligned} \tag{3.8}$$

When $\zeta(x) = 1$, then (3.7) becomes

$$\begin{aligned} Nc(x,\zeta) &= \frac{N}{2} - \frac{(N+1)(1-\alpha)}{4} - \frac{\alpha}{2}(N - 2n_0) \\ & \quad - \frac{1-\alpha}{2N}\biggl[\frac{N(N-1)}{2} - 2n_0(N-n_0)\biggr] \\ &= n_0 - \frac{1-\alpha}{N}n_0^2 = N\bigl(f_0 - (1-\alpha)f_0^2\bigr). \end{aligned} \tag{3.9}$$

Comparing (3.8) and (3.9) with (3.1) proves the proposition. □

Having found the dual process we can now understand where the structure comes from. To do this we turn to the graphical representation of the process.

We rewrite the rates as

$$c(x,\zeta)=\begin{cases}\alpha f_0+(1-\alpha)f_0f_1, & \text{if } \zeta(x)=1,\\ \alpha f_1+(1-\alpha)f_1f_0, & \text{if } \zeta(x)=0.\end{cases} \tag{3.10}$$

Note that $Ncp_1=\alpha$ and $N^2cp_2=1-\alpha$. To construct this process we use the standard graphical representation [14]. For each $x\in\mathbf{Z}^d$ and $y\in x+\mathcal{N}$, let $\{T_n^{x,y}\colon n\geq 1\}$ be a Poisson process with rate $\alpha/|\mathcal{N}|$. For each $x\in\mathbf{Z}^d$ and $y,z\in x+\mathcal{N}$ (y and z are not necessarily different), let $\{S_n^{x,y,z}\colon n\geq 1\}$ be a Poisson process with rate $2(1-\alpha)/|\mathcal{N}|^2$. At times $T_n^{x,y}$ we draw an arrow from x to y to indicate that the particle at x imitates the type of the particle at y. At times $S_n^{x,y,z}$ we draw two arrows, one from x to y labelled as the crowding arrow, the other from x to z labelled as the imitating arrow. If the particle at x and the particle where the crowding arrow landed are of the same type, then the particle at x imitates the type of the particle where the imitating arrow landed. An idea of Harris [14] then allows us to construct the process starting from any initial configuration.

Comparing the rates in the dual process with the rates given in (3.10), the connection should be clear. At rate α, the particle at x sends out an arrow to one of the neighboring sites and imitates the "opinion" at that site. Note that a change in state only occurs if the arrow lands on a site of opposite type. This corresponds to the random walk steps in the dual process which occur at rate α.

At rate $1-\alpha$, the particle at x sends out two arrows into its neighborhood, which may land on the same site. If the arrows land on opposite types, the state of the particle at x changes. We changed the dynamics in the construction somewhat and sent out the two arrows at twice the rate while specifying which of the arrows checks whether the chosen site is occupied by the same type as the parent particle and which of the arrows would be used to imitate the opinion. This part corresponds to the double branching events. If we allow the two dual particles produced in the double branching event to land on the same site, then this occurs at rate $1-\alpha$. (When both dual particles land on the same site, they annihilate each other which reduces to the original dual.)

Note that α describes the strength of interspecific competition. That is, when $\alpha=0$, competition only occurs between particles of the same type. This is reflected in the fact that a change of state only occurs if the crowding arrow lands on a particle of the same type and there is no random walk component. The random walk component corresponds to imitating either particles of the same type or the other type indiscriminantly. As α increases, the random walk component becomes dominant. When $\alpha=1$, no branching occurs. When $\alpha=1$, intraspecific competition and interspecific competition are of equal strength, that is, death occurs at a rate which is independent of the respective densities of the two species. This case is the voter model we mentioned above.

The graphical representation thus allows for a different interpretation of the dual process, namely a double branching coalescing structure where the double arrows are labelled as defined above. To determine the state at x at time

t, one first needs to find the double branching coalescing structure. Given the configuration at time 0, one can then follow the paths on the double branching coalescing structure forward into the future and determine the state of x at time t. This interpretation can be generalized to more than two species. It is not clear at this point whether this interpretation is useful in the context of two-species competition. It has been successfully applied in finding the genealogy of samples in frequency-dependent selection [23], which has the same dual structure. When dealing with more than two species, the double branching coalescing structure is the only available dual process since it does not seem to be possible to generalize the annihilating dual process to more than two species.

4. Proofs of Theorems 1 and 2. We assume throughout this section that $\lambda = 1$ and $\alpha_{12} = \alpha_{21} = \alpha$. We first consider the case $\alpha = 0$ and give a complete characterization of the limiting behavior. This will prove part (a) of Theorem 1. Part (b) of Theorem 1 will then follow from a perturbation argument.

We showed in the previous section that a dual process exists in the symmetric case when $0 \le \alpha \le 1$. To show this we introduced the relabelled process ζ in which the states were labelled 0 and 1 instead of 1 and 2. The dual process was denoted by $\hat{\zeta}$. We will use this relabelled process and duality to prove our results when $\alpha = 0$.

When $\alpha = 0$, the dual process $\hat{\zeta}_t$ reduces to a double branching annihilating process without the random walk component ($p_1 = 0$). Each event in the dual process thus adds two new particles to the set of dual particles resulting in one of the following three outcomes: (1) Both dual particles survive, which increases the number of dual particles by 2. (2) One dual particle survives and the other is annihilated together with one of the dual particles already present in the dual resulting in no change in the number of dual particles. (3) Both dual particles are annihilated together with two dual particles already present in the dual; this decreases the number of dual particles by 2. Note that this last case can only occur when the number of particles in the dual particles exceeds 2.

We denote by $\hat{\zeta}_t^B$ the dual process at time t when starting from the set B (i.e., $\hat{\zeta}_0^B = B$). It follows immediately from considerations in the previous paragraph that $|\hat{\zeta}_t^B|$ is odd for all $t > 0$ if and only if $|B|$ is odd. ($|\cdot|$ denotes the cardinality of the set.) Furthermore, the dual process cannot die out. This follows from the fact that (1) the even–odd parity is preserved, (2) once the size of the dual process is 2, only two transitions are possible: either the size remains 2 or it increases by 2, and (3) an isolated particle cannot die.

Using the properties of the dual process when $\alpha = 0$ and the duality relationship (3.4) from the previous section, it is easy to show the following lemma.

LEMMA 1. *When $\alpha = 0$, product measure with density $1/2$ is an invariant measure.*

PROOF. If we denote by $\zeta_t^{1/2}$ the process starting from product measure with density 1/2, then the duality relation (3.4) implies

$$P\big(\big|\hat{\zeta}_t^B \cap \zeta_0^{1/2}\big| \text{ is odd}\big) = P\big(\big|\zeta_t^{1/2} \cap B\big| \text{ is odd}\big). \tag{4.1}$$

The left-hand side of (4.1) is equal to

$$\tfrac{1}{2} P\big(\hat{\zeta}_t^B \neq \varnothing\big). \tag{4.2}$$

Since the dual process does not die out, it follows immediately that

$$P\big(0 \in \zeta_t^{1/2}\big) = \tfrac{1}{2} \tag{4.3}$$

by setting $B = \{0\}$ in (4.1) and (4.2). Of course, (4.3) does not imply that $\zeta_\infty^{1/2}$ is nontrivial since $\zeta_\infty^{1/2}$ could still be a mixture of the pointmass at the all 1 state and the all 0 state. To show that the limiting distribution is nontrivial, we need to look at the two-point distribution. Setting $B = \{x, y\}$ for $x \neq y$ in (4.1) and using $P(\hat{\zeta}_t^{\{x,y\}} \neq \varnothing) = 1$, it follows that

$$P\big(\zeta_t^{1/2}(x) = \zeta_t^{1/2}(y)\big) = \tfrac{1}{2}.$$

In fact, more can be concluded (see, for instance, [13] or [2]). Since $P(|\zeta_t^{1/2} \cap B|$ is odd$) = \frac{1}{2}$ for all sets $B \in Y$, it follows that $\zeta_\infty^{1/2}$ is product measure with density 1/2. □

Lemma 1 shows that product measure with density 1/2 is a stationary distribution when $\alpha = 0$. This, however, does not imply that starting from any initial configuration, the limiting distribution is product measure with density 1/2. In fact, this is wrong in the one-dimensional nearest neighbor case. The following argument provides a proof of Theorem 2(a). To see what happens in this case, we look at the following configuration:

1111.00.1.0.11.00.1.000.11.0.1.000.

The dots indicate boundaries between 0's and 1's. These boundaries perform a simple exclusion process in the one-dimensional nearest neighbor case when $\alpha = 0$. (See Chapter VIII in [18] for results on the simple exclusion process.) It follows from Theorem VIII.1.47 in [18] that if the boundaries in the initial measure of the process ζ are distributed according to a translation invariant ergodic measure with density θ, then the limiting distribution of the boundaries is product measure with density θ and hence product measure with density 1/2 cannot be the limiting distribution for the process ζ. This argument proves part (a) of Theorem 2.

We will show in the following that the one-dimensional nearest neighbor case is the only exception. In all other cases, we will show that if $\alpha = 0$ and the initial configuration is nontrivial (i.e., contains both types of particles), then product measure with density 1/2 is the limiting distribution.

We begin with the one-dimensional case when $R \geq 2$ and $\alpha = 0$. Parts of the proof are identical to [2] and we will only present those arguments which are different. The proof uses a by now standard rescaling technique which is surveyed in [6]. The basic idea is to show that if $\varepsilon > 0$, then both ζ and $\hat{\zeta}$ dominate oriented site percolation with parameter $1-\varepsilon$. To explain this, we need to introduce oriented site percolation. Let $\mathscr{L} = \{(m,n) \in \mathbf{Z}^2\colon m+n \text{ even}\}$ and for $(m,n) \in \mathscr{L}$ let $\omega(m,n)$ be identically distributed with $P(\omega(m,n) = 1) = 1-\varepsilon$ and $P(\omega(m,n) = 0) = \varepsilon$. The sites may be j-dependent; that is, for any sequence (m_a, n_a), $a = 1, 2, \dots, h$ satisfying $|m_{a_1} - m_{a_2}| > 2j$ whenever both $a_1 \neq a_2$ and $n_{a_1} = n_{a_2}$, then

$$P\big(\omega(m_a, n_a) = 0 \text{ for } a = 1, 2, \dots, h\big) = \varepsilon^h.$$

We say that there is an open path from $(x,0)$ to (y,n) if there is a sequence of points $x_0 = x, x_1, \dots, x_n = y$ with $|x_k - x_{k-1}| = 1$ and $\omega(x_k, k) = 1$ for $1 \le k \le n$. We define

$$W_n^0 = \big\{y\colon \text{there is an open path from } (0,0) \text{ to } (y,n)\big\}$$

and think of W_n^0 as the set of wet sites at time n when the origin $(0,0)$ is wet. It is a well-known fact that if ε is close to 0, then percolation occurs; that is, if $(0,0)$ is wet at time 0, then there is a positive probability that there is an infinite open path starting at $(0,0)$.

To compare our two processes ζ and $\hat{\zeta}$ with oriented site percolation, we tile $\mathbf{Z} \times [0,\infty)$ into boxes; that is, for $(m,n) \in \mathscr{L}$ and L a positive integer, we set

$$\begin{aligned}\Phi(m,n) &= (mL, nT),\\ B &= [-L, L] \times [0, T],\\ B(m,n) &= \Phi(m,n) + B\end{aligned}$$

and

$$I = \left[-\frac{L}{2}, \frac{L}{2}\right] \quad \text{and} \quad I(m) = mL + I, m \in \mathbf{Z}.$$

We introduce the symbol $\mathscr{M}$ to denote a monochrome configuration; that is, for $A \subset \mathbf{Z}$, we set

$$\zeta_t \cap A = \mathscr{M}$$

if either $\zeta_t(x) = 1$ for all $x \in A$ or $\zeta_t(x) = 0$ for all $x \in A$. We then define

$$\chi_n^A = \big\{m\colon \zeta_{nT}^A \cap I_m \neq \mathscr{M}, (m,n) \in \mathscr{L}\big\},$$

$$\hat{\chi}_n^A = \big\{m\colon \hat{\zeta}_{nT}^A \cap I_m \neq \mathscr{M}, (m,n) \in \mathscr{L}\big\}.$$

The comparison which shows that both ζ and $\hat{\zeta}$ dominate oriented site percolation is contained in the following proposition.

PROPOSITION 2. *Let $\varepsilon > 0$. We can find L so that W_n^0 and χ_n^0 (W_n^0 and $\hat{\chi}_n^0$, respectively) can be defined on the same space with $\chi_n^0 \supset W_n^0$ ($\hat{\chi}_n^0 \supset W_n^0$, respectively) for all $n \ge 0$.*

If ε is small enough, percolation occurs which implies that both ζ and $\hat{\zeta}$ spread. The remaining steps are then identical to [2] and we will only provide a brief outline of this part of the proof. The main ingredient is a result of [12], which also holds for the processes ζ and $\hat{\zeta}$. Namely, if A is a finite set, then

$$P\big(\big|\zeta_{s+t} \cap A\big| \text{ is odd}\big) = P\big(\big|\zeta_s \cap \hat{\zeta}_t^A\big| \text{ is odd}\big). \tag{4.4}$$

It then follows from [2] that if $P(\zeta_0 \neq \mathscr{M}) = 1$ and $A \neq \varnothing$ is finite, then

$$P\big(\big|\zeta_t \cap \hat{\zeta}_t^A\big| \text{ is odd}\big) \to \tfrac{1}{2} \quad \text{as } t \to \infty. \tag{4.5}$$

The corresponding proof of (4.5) in [2] only uses the fact that their processes dominate oriented site percolation, which implies that if each the forward process starting at time 0 and the dual process starting at time $2t$ run for t units of time, then the number of sites that are contained in both the forward process and the dual process at time t (i.e., the set $\zeta_t \cap \hat{\zeta}_t^A$), goes to infinity as $t \to \infty$.

To prove Proposition 2 for the forward process, we show that 1's can invade clusters of 0's. Since 0's and 1's are symmetric, this will then also imply that 0's can invade clusters of 1's. To demonstrate that 1's can invade a cluster of 0's, we start with the origin occupied by a 1, an arbitrary configuration to the left of the origin and only 0's to the right of the origin. We then look at the rightmost 1 and show that it has a drift to the right. A similar argument will be employed in the proof of Proposition 2 for the dual process. There we will show that when starting with a finite number of dual particles, the rightmost dual particle has a drift to the right.

We begin with the forward process. We assume that the origin is occupied by a particle of type 1, there are no 1's to the right of the origin and there is an arbitrary but fixed configuration to the left of the origin. Denote by

$$-K = \max\{x < 0\colon \zeta(x) = 1\} \tag{4.6}$$

the gap between the 1 at the origin and the closest 1 to the left of the origin. If $K \le R$, the 1 at the origin flips at rate less than or equal to $(R-K+1)/2R$. Each 0 within distance $x \le R$ to the right of the origin flips at rate greater than or equal to $(1/2R)(1-1/2R)$. The expected displacement for $K \le R$ after one unit of time is thus greater than or equal to

$$\begin{aligned} &(-K)\frac{R-K+1}{2R} + \sum_{x=1}^{R} x \frac{1}{2R}\left(1-\frac{1}{2R}\right) \\ &= \frac{1}{2R}\left[-K(R-K+1) + \frac{(2R-1)(R+1)}{4}\right] \\ &\ge \frac{1}{2R}\left[-\left(\frac{R+1}{2}\right)^2 + \frac{(2R-1)(R+1)}{4}\right] = \frac{(R+1)(R-2)}{8R} > 0 \end{aligned} \tag{4.7}$$

for all $K \le R$ provided $R > 2$. When $R = 2$, we can still use the first line of (4.7) but calculate the result without further estimates. We find that the expected displacement after one unit of time is greater than or equal to

$$(-2)\tfrac{1}{4} + (1)\tfrac{3}{16} + (2)\tfrac{3}{16} = \tfrac{1}{16} > 0.$$

Since an isolated particle cannot die, it follows that the expected displacement after one unit of time for $K > R$ is positive as well. Combining the results for $K \le R$ and $K > R$ implies that the rightmost 1 has a positive drift.

We will now prove the analogous result for the dual process. The argument is similar. Given a configuration of dual particles with $\hat{\zeta}_0(0) = 1$, $\hat{\zeta}_0(x) = 0$ for $x > 0$ and an arbitrary but fixed configuration to the left of the origin with gap K, we find the expected displacement when $K \le R$ as follows. To obtain a lower bound on the positive displacement, we observe that the dual particle at 0 produces offspring that are placed at x and y ($x \ne y$, $x, y \ne 0$) at rate $cp_2 = 1/(2R)^2$. If the rightmost offspring lands at $x > 0$, then the other offspring can be chosen from $R+x-1$ sites and the displacement will be x. We ignore any contributions to the positive displacement by dual particles to the left of the dual particle at the origin. A lower bound on the expected positive displacement after one unit of time is thus

$$\begin{aligned}
&\sum_{x=1}^{R} x\frac{1}{(2R)^2}(R+x-1)\\
&\qquad = \frac{1}{(2R)^2}\left[(R-1)\frac{R(R+1)}{2} + \frac{R(R+1)(2R+1)}{6}\right] \qquad (4.8)\\
&\qquad = \frac{R(R+1)(5R-2)}{6(2R)^2}.
\end{aligned}$$

To find the negative displacement, we observe that if the gap is of size K, $K \le R$, then there is a dual particle at $-K$ and there might be dual particles to the left of $-K$. If the dual particle at $-K$ places one offspring at 0 and the other to the left of $-K$, then the displacement will be $-K$; if it places one at 0 and the other at $-l$ for $-K < -l < 0$, then the displacement will be $-l$. Similarly, a dual particle at $-K-x$, $1 \le x \le R-K$ can have the following effects: (1) if it produces one offspring at 0 and the other to the left of $-K-x$, the displacement is $-K$; (2) if it produces one offspring at 0 and the other at $-K$, the displacement is at most $-K-x$ and (3) if it produces one offspring at 0 and the other at $-l$, $-K < l < 0$, the displacement is $-l$. Summarizing this, we find the following lower bound on the expected negative displacement after one unit of time greater than or equal to

$$\begin{aligned}
&\frac{1}{(2R)^2}\Bigg[(-K)(R-K) + (-K)(R-K-1)(R-K)\\
&\qquad + (R-K+1)\sum_{l=1}^{K-1}(-l) + \sum_{x=1}^{R-K}(-K-x)\Bigg] \qquad (4.9)
\end{aligned}$$

$$= \frac{1}{(2R)^2}\left[-K(R-K)^2 - (R-K+1)\frac{K(K-1)}{2} \right.$$
$$\left. - (R-K)\frac{R+K+1}{2}\right]$$
$$\geq \frac{1}{(2R)^2}\left[-\frac{4R^3}{27} - (R+1)\frac{R(R-1)}{2} - \frac{R(R+1)}{2}\right].$$

Combining (4.8) and (4.9) and using MATHEMATICA to simplify, we find that the expected displacement after one unit of time is bounded below by

$$\big[\text{positive displacement} + \text{negative displacement}\big]$$
$$\geq \frac{1}{(2R)^2}\left[-\frac{R}{3} + \frac{5R^3}{27}\right] = \frac{1}{(2R)^2}\frac{R}{3}\left[\frac{5R^2}{9} - 1\right] > 0$$

if $R \geq 2$.

It is now straightforward to show Proposition 2. The basic idea is similar to estimates in [3] and [11]. We will show that for any $\varepsilon > 0$ we can choose L so that if I is occupied by a (dual) particle, then with probability at least $1 - \varepsilon$ both $I(1)$ and $I(-1)$ will be occupied by a (dual) particle at time T. The estimates are the same for the forward and the dual process. Note that 0's and 1's play a symmetric role in the forward process. We therefore call a particle in the forward process either a 0 or a 1.

We denote by r_t the rightmost particle in the interval $[-L, L]$. The following lemma shows that if I is occupied at time 0, then with probability close to 1, $r_t \in [\frac{3}{4}L - R, \frac{3}{4}L + R]$ at some time before time T. We can assume that none of the sites to the right of I are occupied.

LEMMA 2. *Assume* $r_0 \in I$ *and* $\zeta_0 \cap (L/2, \infty) = \varnothing$. *If* $T = \kappa L$, *then there exist constants* $C, \gamma > 0$ *so that*

$$P\big(r_t < \tfrac{3}{4}L \text{ for all } t \leq T\big) \leq Ce^{-\gamma T}$$

for L *and* κ *sufficiently large.*

PROOF. This follows from a simple large deviations estimate for Poisson processes. Observe that it follows from (4.7) that if $r_0 = 0$, then $Er_t \geq \lambda t$ for some $\lambda > 0$. If $T = \kappa L$ and both κ and L are sufficiently large, the estimate follows. □

Lemma 2 shows that we can move the rightmost particle close to $3L/4$. The next lemma shows that with high probability we can then keep a particle in $[L/2, L]$ for the remainder of the time so that there will be a particle in $[L/2, L]$ at time T with high probability.

LEMMA 3. *Let* $T = \kappa L$ *as in Lemma* 2. *If* $r_0 \in [\frac{3}{4}L - R, \frac{3}{4}L + R]$, *then there are constants* $C, \gamma > 0$ *so that*

$$P\left(\left[\frac{L}{2}, L\right] \cap \zeta_t = \varnothing \text{ for some } t \leq T\right) \leq Ce^{-\gamma T}.$$

PROOF. To keep a particle in $[L/2, L]$ for all times $t \in [0, T]$, we define a tagged particle with position z_t and use the following repositioning algorithm. We require z_t to satisfy the following three conditions:

(i) $\zeta_t(z_t) = 1$.
(ii) If $z_t > 3L/4$, then $\zeta_t \cap [3L/4, z_t) = \varnothing$.
(iii) If $z_t < 3L/4$, then $\zeta_t \cap (z_t, 3L/4] = \varnothing$.

If one of the three conditions (i)–(iii) is violated, we tag another particle so that the tagged particle is again the closest occupied site to $3L/4$.

Observe that $|z_t - 3L/4|$ has a negative drift if $|z_t - 3L/4| > R$. It therefore follows from a simple large deviations estimate for Poisson processes that if $T = \kappa L$, there are constants $C, \gamma > 0$ so that

$$P\big(|z_t - \tfrac{3}{4}L| \geq \tfrac{1}{4}L \text{ for some } t \leq T\big) \leq Ce^{-\gamma T}$$

for L sufficiently large and κ chosen as in Lemma 2. □

The estimates in Lemmas 2 and 3 are the same for the dual process $\hat{\zeta}$. Combining Lemmas 2 and 3 then proves Proposition 2 for both the forward and the dual process (see, e.g., [2]). This finishes the proof of Theorem 1(a) for the one-dimensional nonnearest neighbor case. Theorem 1(b) for the one-dimensional nonnearest neighbor case then follows from a simple perturbation argument in the rescaling step. Since the estimates in the rescaling step only involve finite space–time boxes, it is easy to show that for α sufficiently small, Proposition 2 holds with ε replaced by 2ε.

When $d \geq 2$, the argument becomes more involved. We only present the proof for $d = 2$; the argument is similar when $d > 2$. The basic idea is the same as in the one-dimensional case. We need to show that both the dual process and the forward process "spread out" and then use the analogue of (4.5) to prove that product measure with density 1/2 is the limiting measure. To do this we use the two-dimensional analogue of the rescaling argument employed in the one-dimensional case.

For both the forward and the dual process we define a tagged particle and show that the first coordinate of the tagged particle in either process has a positive drift. This will enable us to populate regions with the desired type of particle as in the one-dimensional case. The definition of the tagged particle is essentially the same in both processes. We denote the location of the tagged particle at time t by $r_t = (r_{t,1}, r_{t,2})$ and assume that at time $t = 0$, $r_0 = (0, 0)$, $\zeta_0(x) = 0$ for all $x = (x_1, x_2)$ with $x_1 > 0$. The tagged particle in the forward process has the following properties (this is similar to the definition in [2]):

1. $\zeta_t(r_t) = 1$.
2. $\zeta_t(r_{t,1} + x, r_{t,2} + y) = 0$ for $x = 1, 2, \dots, R$ and $-R \leq y \leq R$.
3. $\zeta_t(r_{t,1}, r_{t,2} + y) = 0$ for $-2|r_{t,2}| < y \leq -1$ if $r_{t,2} > 0$ and for $1 \leq y < 2|r_{t,2}|$ if $r_{t,2} < 0$.

If the rules are violated due to births or deaths of particles, we reposition the tagged particle so that again the tagged particle is the rightmost particle. If there is more than one rightmost particle, we choose the one whose second coordinate is closest to 0. If a particle to the right of r_t appears within range R, $r_{t,1}$ increases; if the particle at r_t gets killed, $r_{t,1}$ might decrease, but not by more than R since it must have been killed by a particle within range R. We will show that $r_{t,1}$ has a tendency to increase while at the same time the second coordinate $r_{t,2}$ stays close to 0. To define the tagged particle for the dual particle we simply replace ζ by $\hat{\zeta}$.

For the forward process we carry out the following calculation for the expected displacement. We assume that the position of the closest particle within range R to the left of r_t is $(r_{t,1} - L, y)$, $r_{t,2} - R \le y \le r_{t,2} + R$. As in the one-dimensional case, we need to find an upper bound on the rate at which the particle at $(r_{t,1}, r_{t,2})$ gets killed. There are $(2R+1)(R+L)$ sites in $[r_{t,1} - L + 1, r_{t,1} + R] \times [r_{t,2} - R, r_{t,2} + R]$ which are all vacant except for the particle at $(r_{t,1}, r_{t,2})$. The maximum rate is achieved if all sites in $[r_{t,1} - R, r_{t,1} - L] \times [r_{t,2} - R, r_{t,2} + R]$ are occupied. Hence this rate is bounded by

$$\frac{(2R+1)(R-L+1)}{(2R+1)^2-1}\,\frac{(2R+1)(R+2)-1}{(2R+1)^2-1}.$$

To estimate the rate at which particles to the right of $(r_{t,1}, r_{t,2})$ are born at distance x from $(r_{t,1}, r_{t,2})$, that is, in the strip $(r_{t,1} + x, r_{t,2} + y)$ for some y between $-R$ and R, note that there are $2R+1$ sites in the strip and for each site in the strip the rate is smallest if all sites in its neighborhood except for the particle at $(r_{t,1}, r_{t,2})$ are vacant. For each site in the strip, the rate is therefore at least

$$\frac{1}{(2R+1)^2-1}\,\frac{(2R+1)^2-2}{(2R+1)^2-1}$$

Putting things together, we find that the expected displacement after one unit of time is at least

$$\begin{aligned}(-L)&\frac{(2R+1)(R-L+1)}{(2R+1)^2-1}\,\frac{(2R+1)(R+L)-1}{(2R+1)^2-1}\\&+\sum_{x=1}^{R} x(2R+1)\frac{1}{(2R+1)^2-1}\,\frac{(2R+1)^2-2}{(2R+1)^2-1}.\end{aligned}$$

Using MATHEMATICA, it is easy to see that the expected displacement is positive for $1 \le L \le R$ and $R \ge 1$.

For the dual process we carry out the following estimates. For $1 \le x \le R$, we denote by "strip x" all sites with coordinates $(r_{t,1}+x, r_{t,2}+y)$ and $-R \le y \le R$. We assume that the rightmost dual particle is located at $(r_{t,1}, r_{t,2})$ and gives birth to two offspring which are placed within the neighborhood of $(r_{t,1}, r_{t,2})$. We denote by A_x the event that at least one offspring of $(r_{t,1}, r_{t,2})$ lands in the strip x (i.e., has coordinates $(r_{t,1}+x, r_{t,2}+y)$ for some y between $-R$ and

R) and no offspring land to the right of the strip x. Then

$$P(A_x) = \frac{\binom{2R+1}{2} + \binom{2R+1}{1}\binom{(R+x)(2R+1)-1}{1}}{\binom{4R(R+1)}{2}}.$$

Using MATHEMATICA we find for the expected positive displacement,

$$\sum_{x=1}^{R} xP(A_x) = \frac{(1+2R)(5R^2-2)}{6(4R^2+4R-1)}. \tag{4.10}$$

Next we calculate the negative displacement in the case when there are K dual particles at sites within distance R of r_t which are not automatically designated as vacant by the rules for the tagged particle. If $k(2R+1) < K \le (k+1)(2R+1)$, $k = 0, 1, \dots, R$, then the expected negative displacement after one unit of time is less than or equal to

$$(k+1)(2R+1)(R-k+1)\frac{R(2R+1)}{\binom{4R(R+1)}{2}}, \tag{4.11}$$

since there are at most $(k+1)(2R+1)$ dual particles within r_t. One of their offspring needs to land on the dual particle at r_t, the other one to the left (term $R(2R+1)/\binom{4R(R+1)}{2}$). The displacement to the left is then at most $R-k+1$.

Combining (4.10) and (4.11), MATHEMATICA finds that the expected displacement [i.e., (4.10) and (4.11)] is positive for $R \ge 3$.

The cases $R = 1$ and $R = 2$ can be dealt with as well. When $R = 1$, the expected displacement is at least

$$(1)\frac{(3)(5)}{\binom{8}{2}} - (1)(3)\frac{(1)(2)}{\binom{8}{2}} = \frac{9}{\binom{8}{2}} > 0.$$

When $R = 2$ the expected displacement is at least

$$\begin{aligned}&(1)\frac{(5)(14)}{\binom{24}{2}} + (2)\frac{(5)(19)}{\binom{24}{2}}\\ &\qquad - (1)\frac{(10)(1)(10)}{\binom{24}{2}} - (2)\frac{(5)(1)(1)}{\binom{24}{2}} = \frac{150}{\binom{24}{2}} > 0.\end{aligned}$$

The above calculations show that we can move a tagged particle into target regions as in the one-dimensional case. The remaining steps (including the perturbation argument) are very similar to the one-dimensional case and we omit the details.

5. Proof of Theorem 3.

Theorem 3 shows that in $d = 1$ and $d = 2$ the two types of particles become increasingly more spatially segregated as α approaches 1 from below, that is, as the strength of interspecific competition increases relative to the strength of intraspecific competition. When $\alpha = 1$, the model reduces to the voter model; in this case it is known that clustering occurs in $d = 1$ and 2, that is, clusters continue to grow indefinitely.

Theorem 3 provides a lower bound on the cluster size in $d \le 2$ when $\alpha < 1$. To show Conjecture 1, we would either need to give a corresponding upper bound on the cluster size or show that the dual process starting from two different sites has a positive probability of survival.

The proof of Theorem 3 uses some ideas and estimates from [21]. The strategy is to show that if α and L are chosen as in the assumptions of Theorem 3, then with probability close to 1, the dual process starting at two sites distance L apart, will die out (i.e., both dual particles will annihilate each other before either dual particle branches. This will then imply that the two sites where the dual process started from are occupied by the same type. Except for a difference in time scale, the proofs are the same in $d = 1$ and $d = 2$.

We begin with introducing some notation. Instead of following the movement of two dual particles, we look at the difference and estimate the amount of time it takes for the difference process to hit 0. It is convenient to look at the discrete time embedded random walk. We denote by $N(t)$ the number of steps the discrete time random walk takes by time t and denote by $M(t)$ the number of branching events in the dual process by time t. Then in $d = 1$,

$$\begin{aligned} &P\big(\eta_{L^{2+\varepsilon}}(0) \ne \eta_{L^{2+\varepsilon}}(L)\big) \\ &\quad \le P\big(\eta_{L^{2+\varepsilon}}(0) \ne \eta_{L^{2+\varepsilon}}(L); N(L^{2+\varepsilon}) \le 4L^{2+\varepsilon}; M(L^{2+\varepsilon}) = 0\big) \\ &\qquad + P\big(N(L^{2+\varepsilon}) > 4L^{2+\varepsilon}\big) + P\big(M(L^{2+\varepsilon}) > 0; N(L^{2+\varepsilon}) \le 4L^{2+\varepsilon}\big). \end{aligned} \tag{5.1}$$

Using a standard estimate for random walks, the first term on the right hand side of (5.1) is bounded by the probability that two random walks, starting distance L apart, have not met by time $L^{2+\varepsilon}$. This is a standard estimate and was used, for instance, in [21] in a similar context. We find the bound

$$\le C\frac{L}{\sqrt{L^{2+\varepsilon}}} \le CL^{-\varepsilon/2}. \tag{5.2}$$

The second term on the right-hand side of (5.1) can be estimated using a standard large deviations estimate for Poisson processes. Each dual particle jumps at rate at most 1 [see (3.5)]. Hence the difference jumps at rate less than or equal to 2. Therefore,

$$P\big(N(L^{2+\varepsilon}) > 4L^{2+\varepsilon}\big) \le C\exp(-\gamma L^{2+\varepsilon}) \tag{5.3}$$

for some $\gamma > 0$. To estimate the third term on the right-hand side of (5.1), note that by (3.5) the probability that a random walk step occurs before a branching event, is equal to

$$\frac{p_1}{p_1+p_2} = \frac{2\alpha}{2\alpha + 2(1-\alpha)/N} = \frac{1}{1+(1-\alpha)/N\alpha},$$

where p_1 and p_2 were defined in (3.5). Hence the third term is

$$\le 8L^{2+\varepsilon}\left(1 - \frac{1}{1+(1-\alpha)/N\alpha}\right) = 8L^{2+\varepsilon}(1-\alpha)\frac{1}{N\alpha + 1 - \alpha}. \tag{5.4}$$

Combining (5.2)–(5.4) implies the first part of Theorem 3.

It takes longer in $d = 2$ for two random walks to hit. We replace $L^{2+\varepsilon}$ in (5.1) by $L^{\log L}$. The estimate in (5.2) gets replaced by

$$\leq C \frac{\log L}{\log L^{\log L}} = \frac{C}{\log L}. \tag{5.5}$$

The estimate in (5.3) becomes

$$P\big(N(L^{\log L}) > 4L^{\log L}\big) \leq C \exp(-\gamma L^{\log L}) \tag{5.6}$$

and (5.4) becomes

$$\leq 8L^{\log L}(1-\alpha)\frac{1}{N\alpha + 1 - \alpha}. \tag{5.7}$$

Combining (5.5)–(5.7) then proves the second part of Theorem 3. □

6. Proof of Theorem 4. The proof of Theorem 4 uses a coupling argument. To demonstrate that 2's take over with probability 1 when starting with infinitely many 2's, we couple our process to a biased voter model in which the 2's are the favored type and then show that the 2's in our process dominate the 2's in the biased voter model. Since the 2's take over with probability 1 in a biased voter model in which the 2's are favored, this will prove Theorem 4. We define

$$h_1(x) = \frac{\lambda x}{\lambda x + (1-x)}\big(1 - x + \alpha_{12}x\big) \quad \text{for } x \in [0,1], \tag{6.1}$$

$$h_2(x) = \frac{x}{\lambda(1-x) + x}\big(1 - x + \alpha_{21}x\big) \quad \text{for } x \in [0,1]. \tag{6.2}$$

That is, $h_1(x)$, $0 \leq x \leq 1$, is the rate at which the transition $1 \to 2$ occurs if x denotes the density of 2's in the neighborhood, that is, $x = f_2$. The function $h_2(x)$ is the rate at which the transition $2 \to 1$ occurs if x denotes the density of 1's in the neighborhood, that is, $x = f_1$. Throughout this section we assume $\lambda \geq 1$.

We define a biased voter model whose configuration at time t is denoted by $\xi_t \in \{1,2\}^{\mathbf{Z}^d}$ and which has the same neighborhood structure $\{\mathcal{N}_x \colon x \in \mathbf{Z}^d\}$ as the process η. The dynamics for ξ are given by

$$1 \to 2 \quad \text{at rate } g_1(f_2) = \kappa_1 f_2, \tag{6.3}$$

$$2 \to 1 \quad \text{at rate } g_2(f_1) = \kappa_2 f_1, \tag{6.4}$$

where f_i denotes the relative frequency of species i in the corresponding neighborhood.

The following proposition provides the key ingredient to the proof of Theorem 4.

PROPOSITION 3. *Assume* (6.1)–(6.4). *If*

$$\kappa_1 > \kappa_2, \tag{6.5}$$

$$h_1(x) \geq g_1(x) \quad \textit{for } x \in \left[\frac{1}{N}, 1\right], \tag{6.6}$$

$$h_2(x) \leq g_2(x) \quad \textit{for } x \in \left[\frac{1}{N}, 1\right], \tag{6.7}$$

then 2*'s take over with probability* 1 *in the process* η *if initially there are infinitely many* 2*'s.*

PROOF. Since $h_1(0) = g_1(0) = 0$ and $h_2(0) = g_2(0) = 0$ and N is the neighborhood size, conditions (6.6) and (6.7) imply for $\xi \leq \eta$,

$$\text{if}\quad \xi(x) = \eta(x) = 1, \quad \text{then } c_1(x, \xi) \leq c_2(x, \eta);$$

$$\text{if}\quad \xi(x) = \eta(x) = 2, \quad \text{then } c_1(x, \xi) \geq c_2(x, \eta).$$

where $c_1(x, \xi)$ [respectively, $c_2(x, \eta)$] is the rate at which the state $\xi(x)$ [respectively, $\eta(x)$] changes to the other state. Theorem III.1.5 in [18] then allows us to couple the two processes so that if $\xi_0 \leq \eta_0$, then $\xi_t \leq \eta_t$ with probability 1 for all $t \geq 0$. Because of (6.5), 2's take over in the process ξ which completes the proof of the proposition. □

We will break up the region in the $\alpha_{21} - \alpha_{12}$ plane defined in Theorem 4 into subregions. This is shown in Figure 2. In each subregion we define a biased voter model which will allow us to employ the proposition. To check the conditions in the proposition, the following properties of $h_1(x)$ and $h_2(x)$ are useful.

$$h_1'(0) = \lambda \quad \text{and} \quad h_2'(0) = \frac{1}{\lambda} \tag{6.8}$$

and for $x \in [0, 1]$,

$$h_1''(x) = \frac{2\lambda(\alpha_{12} - \lambda)}{[(\lambda - 1)x + 1]^3}, \tag{6.9}$$

$$h_2''(x) = \frac{2\lambda(\lambda\alpha_{21} - 1)}{[\lambda - (\lambda - 1)x]^3}. \tag{6.10}$$

Assuming $\lambda \geq 1$, we find

$$h_1''(x) > 0 \quad \text{for } x \in [0, 1] \text{ if and only if } \alpha_{12} > \lambda, \tag{6.11}$$

$$h_2''(x) > 0 \quad \text{for } x \in [0, 1] \text{ if and only if } \alpha_{21} > \frac{1}{\lambda}. \tag{6.12}$$

CASE 1. We assume

$$\alpha_{12} > \lambda \quad \text{and} \quad \alpha_{21} < \frac{1}{\lambda}.$$

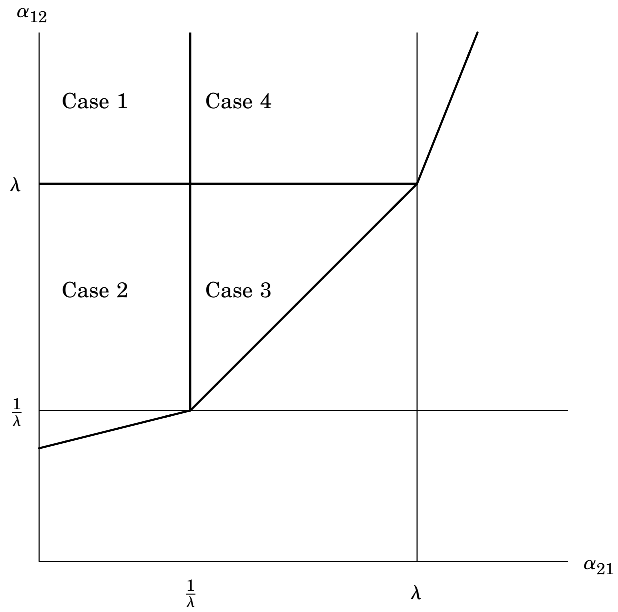

FIG. 2. *Subregions in the proof of Theorem* 4. *The thick lines are the phase boundaries from Theorem* 4. *The thin lines are the mean field phase boundaries.*

We define

$$g_1(x) = xNh_1\left(\frac{1}{N}\right) \quad \text{and} \quad g_2(x) = xNh_2\left(\frac{1}{N}\right).$$

Observe that $\lambda \geq 1$ implies $h_1'(0) \geq h_2'(0)$; $\alpha_{12} > \lambda$ implies $h_1''(x) > 0$ for $x \in [0, 1]$ and $\alpha_{21} < 1/\lambda$ implies $h_2''(x) < 0$ for $x \in [0, 1]$. Therefore, $h_1(1/N) > h_2(1/N)$ which shows that (6.5) holds.

Since $h_1(0) = g_1(0)$, $h_1(1/N) = g_1(1/N)$ and $h_1''(x) > 0$ for $x \in [0, 1]$, (6.6) holds. Since $h_2(0) = g_2(0)$, $h_2(1/N) = g_2(1/N)$ and $h_2''(x) < 0$ for $x \in [0, 1]$, (6.7) holds.

CASE 2. We assume

$$\frac{N - 1 + \alpha_{21}}{\lambda(N-1)+1} < \alpha_{12} \leq \lambda \quad \text{and} \quad \alpha_{21} \leq \frac{1}{\lambda}.$$

We define

$$g_1(x) = xh_1(1) \quad \text{and} \quad g_2(x) = xNh_2\left(\frac{1}{N}\right).$$

Since

$$h_1(1) = \alpha_{12} \quad \text{and} \quad Nh_2\left(\frac{1}{N}\right) = \frac{N - 1 + \alpha_{21}}{\lambda(N-1)+1},$$

condition (6.5) holds if

$$\alpha_{12} > \frac{N-1+\alpha_{21}}{\lambda(N-1)+1}.$$

To show that (6.6) holds, we observe that $h_1''(x) \le 0$ for $x \in [0,1]$ if $\alpha_{12} \le \lambda$. Since $g_1(0) = h_1(0)$ and $g_1(1) = h_1(1)$, it follows that $h_1(x) \ge g_1(x)$ for all $x \in [0,1]$, implying (6.6).

To show that (6.7) holds, we observe that $h_2(0) = g_2(0)$, $h_2(1/N) = g_2(1/N)$ and $h_2''(x) \le 0$ for $x \in [0,1]$ if $\alpha_{21} \le 1/\lambda$, which implies that $h_2(x) \le g_2(x)$ for all $x \in [1/N, 1]$. This is condition (6.7).

CASE 3. We assume

$$\frac{1}{\lambda} < \alpha_{21} < \lambda \quad \text{and} \quad \alpha_{21} < \alpha_{12} < \lambda.$$

We define

$$g_1(x) = xh_1(1) \quad \text{and} \quad g_2(x) = xh_2(1).$$

Since $h_1(1) = \alpha_{12}$ and $h_2(1) = \alpha_{21}$, (6.5) holds if $\alpha_{21} < \alpha_{12}$.

Since $h_1(0) = g_1(0)$, $h_1(1) = g_1(1)$ and $h_1''(x) < 0$ for $x \in [0,1]$ if $\alpha_{12} < \lambda$, (6.6) holds. Since $h_2(0) = g_2(0)$, $h_2(1) = g_2(1)$ and $h_2''(x) > 0$ for $x \in [0,1]$ if $\alpha_{21} > 1/\lambda$, (6.7) holds.

CASE 4. We assume

$$\alpha_{21} > \frac{1}{\lambda} \quad \text{and} \quad \alpha_{12} > \max\left\{\lambda, \frac{\lambda-1+N}{\lambda}\alpha_{21} - N + 1\right\}.$$

We define

$$g_1(x) = xNh_1\left(\frac{1}{N}\right) \quad \text{and} \quad g_2(x) = xh_2(1).$$

Condition (6.5) holds if $h_2(1) < Nh_1(1/N)$, that is, if

$$\alpha_{21} < \frac{\lambda}{\lambda+N-1}(N-1+\alpha_{12}).$$

Solving for α_{12} yields

$$\alpha_{12} > \frac{\lambda-1+N}{\lambda}\alpha_{21} - N + 1.$$

Since $h_1(0) = g_1(0)$, $h_1(1/N) = g_1(1/N)$ and $h_1''(x) \ge 0$ for $\alpha_{12} \ge \lambda$, (6.6) holds for $\alpha_{12} \ge \lambda$. Since $h_2(0) = g_2(0)$, $h_2(1) = g_2(1)$ and $h_2''(x) \ge 0$ for $\alpha_{21} \ge 1/\lambda$, (6.7) holds for $\alpha_{21} \ge 1/\lambda$.

7. Proof of Theorem 5. The proof of Theorem 5 uses the same basic idea as the proof of Theorem 4, namely, we couple the process η to a suitably chosen biased voter model ξ. This time, however, we need to show that the 1's in the process η dominate the 1's in the process ξ and that the 1's are the favored type in the biased voter model ξ. We will use Proposition 3 again, but reverse the roles of 1's and 2's. Recall

$$h_1(x) = \frac{\lambda x}{\lambda x + (1-x)}(1 - x + \alpha_{12} x) \quad \text{for } x \in [0,1], \tag{7.1}$$

$$h_2(x) = \frac{x}{\lambda(1-x) + x}(1 - x + \alpha_{21} x) \quad \text{for } x \in [0,1]. \tag{7.2}$$

We define

$$g_1(x) = xNh_1\left(\frac{1}{N}\right) \quad \text{and} \quad g_2(x) = xNh_2\left(\frac{1}{N}\right). \tag{7.3}$$

Recall (6.11) and (6.12), namely,

$$h_1''(x) < 0 \quad \text{for } x \in [0,1] \text{ if and only if } \alpha_{12} < \lambda, \tag{7.4}$$

$$h_2''(x) > 0 \quad \text{for } x \in [0,1] \text{ if and only if } \alpha_{21} > \frac{1}{\lambda}. \tag{7.5}$$

Since $h_1(0) = h_2(0) = 0$ and $h_1'(0) > h_2'(0)$ for $\lambda > 1$, if $h_1(1) < h_2(1)$ and if $\alpha_{12} < \lambda$ and $\alpha_{21} > 1/\lambda$, then (7.4) and (7.5) imply that the graphs of $h_1(x)$ and $h_2(x)$ have exactly one point of intersection whose x-coordinate is in $(0,1)$. If the x-coordinate of the point of intersection is less than $1/N$, it follows from the convexity properties (7.4) and (7.5) that $h_1(1/N) < h_2(1/N)$ and consequently, $g_1(x) < g_2(x)$ for all $x \in (0,1]$ with $g_1(0) = g_2(0) = 0$. If the biased voter model ξ has transitions

$$\begin{aligned} 1 &\to 2 \quad \text{at rate } g_1(f_2),\\ 2 &\to 1 \quad \text{at rate } g_2(f_1), \end{aligned}$$

then 1's are the favored type if $g_1(x) < g_2(x)$ for all $x \in (0,1]$ with $g_1(0) = g_2(0) = 0$.

Our first task will therefore be to determine the point of intersection of the graphs of $h_1(x) = h_2(x)$ whose x-coordinate is in $(0,1)$ and then to find conditions so that the x-coordinate is less than $1/N$. We need to solve $h_1(x) = h_2(x)$, that is,

$$\frac{\lambda x}{\lambda x + (1-x)}(1 - x + \alpha_{12} x) = \frac{x}{\lambda(1-x) + x}(1 - x + \alpha_{21} x)$$

The following discussion is illustrated in Figure 3. We first find the condition so that the curves intersect at $x = 1/N$. This yields

$$\alpha_{12}^*(\alpha_{21}) = \frac{1}{\lambda}\frac{N + \lambda - 1}{\lambda(N-1) + 1}\alpha_{21} - \frac{1}{\lambda}\frac{(N-1)^2(\lambda^2 - 1)}{\lambda(N-1) + 1}. \tag{7.6}$$

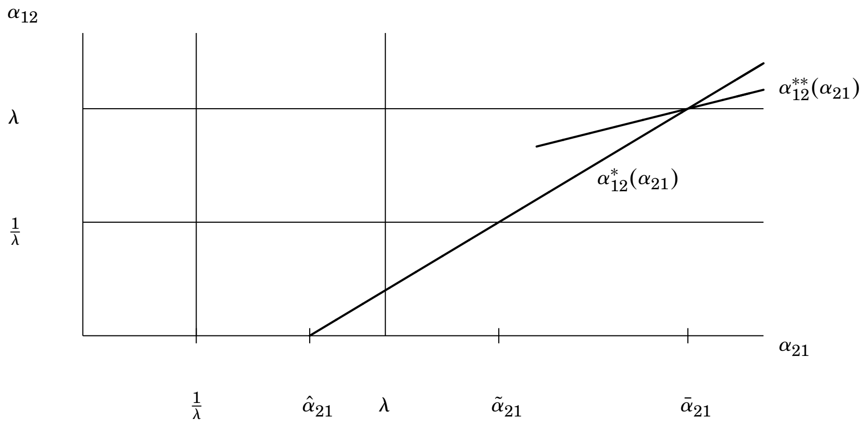

FIG. 3. *Quantities involved in the proof of Theorem* 5.

Since

$$\frac{\partial}{\partial \alpha_{12}} h_1(x, \alpha_{12})\bigg|_{x=1/N} = \frac{\lambda}{N(\lambda + N - 1)} > 0 \quad \text{for } N \geq 1,$$

it follows that the x-coordinate of the point of intersection is less that $1/N$ if $\alpha_{12} < \alpha_{12}^*(\alpha_{21})$.

We therefore conclude that if

$$\alpha_{21} > \frac{1}{\lambda} \quad \text{and} \quad 0 \leq \alpha_{12} < \min\bigl(\lambda, \alpha_{12}^*(\alpha_{21})\bigr), \tag{7.7}$$

then 1's take over with probability 1 if initially there are infinitely many 1's.

For $\alpha_{12} > \lambda$ we employ a different comparison. Note that if $\alpha_{12} > \lambda$, then $h_1''(x) > 0$ for $x \in [0,1]$, and if $\alpha_{21} > 1/\lambda$, then $h_2''(x) > 0$ for $x \in [0,1]$. If we set

$$g_1(x) = x h_1(1) \quad \text{and} \quad g_2(x) = x N h_2\left(\frac{1}{N}\right),$$

then $g_2(x) > g_1(x)$ for $x \in [0,1]$ if

$$N h_2\left(\frac{1}{N}\right) > \alpha_{12},$$

which implies

$$\alpha_{12} < \frac{1}{\lambda(N-1)+1}\alpha_{21} + \frac{N-1}{\lambda(N-1)+1}. \tag{7.8}$$

If we define

$$\alpha_{12}^{**}(\alpha_{21}) = \frac{1}{\lambda(N-1)+1}\alpha_{21} + \frac{N-1}{\lambda(N-1)+1} \tag{7.9}$$

and define $\bar{\alpha}_{21}$ through

$$\alpha_{12}^*(\bar{\alpha}_{21}) = \lambda,$$

we find $\bar{\alpha}_{21} = \lambda + (N-1)(\lambda^2 - 1)$ and we see that also

$$\alpha_{12}^{**}(\bar{\alpha}_{21}) = \lambda. \tag{7.10}$$

If we combine (7.7) with (7.8), we obtain Theorem 5; namely, 1's outcompete 2's if

$$\alpha_{12} < \begin{cases} \alpha_{12}^*(\alpha_{21}), & \text{for } \dfrac{1}{\lambda} < \alpha_{21} \le \lambda + (N-1)(\lambda^2 - 1), \\ \alpha_{12}^{**}(\alpha_{21}), & \text{for } \alpha_{21} \ge \lambda + (N-1)(\lambda^2 - 1). \end{cases} \tag{7.11}$$

In the following we will discuss the implications of the conditions in (7.11). First note that the slopes of the straight lines described in (7.6) and (7.9) are positive for $\lambda \ge 1$.

The mean-field region where 1's competitively exclude 2's is given by $\alpha_{21} > \lambda$ and $\alpha_{12} < 1/\lambda$. If we define $\tilde{\alpha}_{21}$ through

$$\alpha_{12}^*(\tilde{\alpha}_{21}) = \frac{1}{\lambda},$$

we find that

$$\tilde{\alpha}_{21} - \lambda = \frac{(\lambda^2 - 1)(N-2)N}{\lambda + N - 1} \ge 0$$

if $N \ge 2$ and $\lambda \ge 1$. That is, the boundary line described by (7.6) intersects the line $\alpha_{12} = 1/\lambda$ at a point $(\tilde{\alpha}_{21}, \alpha_{12}^*(\tilde{\alpha}_{21}))$ whose first coordinate is never outside of the mean-field region where 1's competitively exclude 2's.

To check whether the region given in (7.7) ever extends into the mean field coexistence region, we define $\hat{\alpha}_{21}$ through

$$\alpha_{12}^*(\hat{\alpha}_{21}) = 0;$$

that is, $\hat{\alpha}_{21}$ is the first coordinate of the point of intersection of the graph of $\alpha_{12}^*(\alpha_{21})$ and the line $\alpha_{12} = 0$. We find

$$\hat{\alpha}_{21}(N, \lambda) = \frac{(N-1)^2(\lambda^2 - 1)}{N + \lambda - 1}.$$

We find that for $\lambda > 1$ and $N > 2$,

$$\frac{\partial}{\partial \lambda}\hat{\alpha}_{21}(N, \lambda) > 0 \quad \text{and} \quad \frac{\partial^2}{\partial \lambda^2}\hat{\alpha}_{21}(N, \lambda) > 0$$

with $\hat{\alpha}_{21}(N, 1) = 0$. This implies that for each $N > 2$, there exists a nonempty open interval Λ_N (depending on N) so that

$$\frac{1}{\lambda} < \hat{\alpha}_{21}(N, \lambda) < \lambda \quad \text{for all } \lambda \in \Lambda_N \tag{7.12}$$

and $\Lambda_N \subset (1, \infty)$.

If we combine (7.7) and (7.12), it follows that for each $N > 2$, there exist values of $\lambda \in (1, \infty)$ so that the region given in (7.7) has a nonempty intersection with the mean-field coexistence region, implying that we can find λ, α_{21} and α_{12} so that the mean-field model predicts coexistence, whereas in the corresponding explicitly spatial model 1's competitively exclude 2's.

Since the mean-field founder control region is described by $\alpha_{21} > \lambda$ and $\alpha_{12} > 1/\lambda$, it follows from (7.8), (7.10) and the fact that the slope of the straight line given in (7.9) is positive, that the region where 1's competitively exclude 2's also extends into the mean-field founder control region, thus reducing this region.

Note that our discussion in this section does not improve the statements concerning the mean-field coexistence region obtained in the previous section. Condition (7.7) in the limit $\lambda \to 1$ merely recovers the mean-field region where 1's competitively exclude 2's. But we already showed this in the previous section. We do recover the region in the mean-field founder control region in the limit $\lambda \to 1$ where 1's competitively exclude 2's.

REFERENCES

[1] ANTONOVICS, J. and LEVIN, D. A. (1980). The ecological and genetic consequences of density dependent regulation in plants. *Annual Review of Ecology and Systematics* **11** 411–452.

[2] BRAMSON, M., WAN-DING, DING and DURRETT, R. (1991). Annihilating branching processes. *Stochastic. Process Appl.* **37** 1–17.

[3] BRAMSON, M. and NEUHAUSER, C. (1994). Survival of one-dimensional cellular automata under random perturbations. *Ann. Probab.* **22** 244–263.

[4] BRAMSON, M. and NEUHAUSER, C. (1997). Coexistence for a catalytic surface reaction model. *Ann. Appl. Probab.* **7** 565–614.

[5] CLIFFORD, P. and SUDBURY, A. (1973). A model for spatial conflict. *Biometrika* **60** 581–588.

[6] DURRETT, R. (1991). A new method for proving the existence of phase transitions. In *Spatial Stochastic Processes* (K. S. Alexander and J. S. Watkins, eds.) 141–170. Birkhäuser, Boston.

[7] DURRETT, R. (1995). Ten lectures on particle systems. *Lectures on Probability Theory, Ecole d'Eté de Probabilités de Saint-Flour XXIII–1993*. Springer, New York.

[8] DURRETT, R. (1998). Stochastic spatial models. Preprint.

[9] DURRETT, R. and LEVIN, S. A. (1994). The importance of being discrete (and spatial). *Theoret. Population Biol.* **46** 363–394.

[10] DURRETT, R. and NEUHAUSER, C. (1994). Particle systems and reaction diffusion equations. *Ann. Probab.* **22** 289–333.

[11] DURRETT, R. and NEUHAUSER, C. (1997). Coexistence results for some competition models. *Ann. Appl. Probab.* **7** 10–45.

[12] GRIFFEATH, D. (1978). Limit theorems for nonergodic set-valued Markov processes. *Ann. Probab.* **6** 379–387.

[13] GRIFFEATH, D. (1979). *Additive and Cancellative Interacting Particle Systems. Lecture Notes in Math*. **724**. Springer, Berlin.

[14] HARRIS, T. E. (1972). Nearest neighbor Markov interaction processes. *Adv. Math* **9** 66–89.

[15] HOLLEY, R. and LIGGETT, T. M. (1975). Ergodic theorems for weakly interacting particle systems and the voter model. *Ann. Probab.* **3** 643–663.

[16] HOLLEY, R. and STROOCK, D. (1979). Dual processes and their applications to infinite interacting systems. *Adv. Math.* **32** 149–174.

[17] LEVIN, S. A. and PACALA, S. W. (1997). Theories of simplification and scaling of spatially distributed processes. In *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (D. Tilman and P. Kareiva, eds.) 271–295. Princeton Univ. Press.

[18] LIGGETT, T. M. (1985). *Interacting Particle Systems*. Springer, New York.

[19] LOTKA, A. J. (1932). The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* **22** 461–469.

[20] MACARTHUR, R. H. (1972). *Geographical Ecology. Patterns in the Distribution of Species*. Harper and Row, New York.

[21] NEUHAUSER, C. (1992). Ergodic theorems for the multitype contact process. *Probab. Theory Related Fields* **91** 467–506.

[22] NEUHAUSER, C. (1994). A long range sexual reproduction process. *Stochastic Process Appl.* **53** 193–220.

[23] NEUHAUSER, C. (1999). The ancestral graph and gene genealogy under frequency-dependent selection. *Theoret. Population Biol.* To appear.

[24] NEUHAUSER, C. and SUDBURY, A. (1993). The biased annihilating branching process. *Adv. Appl. Probab.* **25** 24–38.

[25] PACALA, S. W. (1989). Plant population dynamic theory. In *Perspectives in Ecological Theory* (J. Roughgarden, R. M. May and S. A. Levin, eds.) 54–67. Princeton Univ. Press.

[26] PACALA, S. W. (1997). Dynamics of plant communities. In *Plant Ecology*, 2nd ed. (M. C. Crawley, ed.) 532–555. Blackwell, Oxford.

[27] PACALA, S. W., CANHAM, C. D., SAPONARA, J. SILANDER, J. A., KOBE, R. K. and RIBBENS, E. (1996). Forest models defined by field measurements II. Estimation, error analysis and dynamics. *Ecological Monographs* **66** 1–44.

[28] PACALA, S. W. and LEVIN, S. A. (1997). Biologically generated spatial pattern and the coexistence of competing species. In *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (D. Tilman and P. Kareiva, eds.) 204–232. Princeton Univ. Press.

[29] PACALA, S. W. and SILANDER, J. A. JR. (1990). Field tests of neighborhood population dynamic models of two annual weed species. *Ecological Monographs* **60** 113–134.

[30] REES, M. (1996). Evolutionary ecology of seed dormancy and seed size. *Philos. Trans. Roy. Soc. London Ser. B* **351** 1299–1308.

[31] SPITZER, F. (1970). Interaction of Markov processes. *Adv. Math.* **5** 246–290.

[32] THRALL, P. and ANTONOVICS, J. (1995). Theoretical and empirical studies of meta-populations: population and genetic dynamics of the *Silene–Ustilago* system. *Canadian Journal of Botany* **73** S1249–S1258.

[33] TILMAN, D. (1982). *Resource Competition and Community Structure*. Princeton Univ. Press.

[34] VOLTERRA, V. (1926). Variations and Fluctuations of the Number of Individuals in an Animal Species Living Together. In *Animal Ecology* (R. N. Chapman, ed.). (Reprinted in 1931. McGraw Hill, New York.)

SCHOOL OF MATHEMATICS
UNIVERSITY OF MINNESOTA
127 VINCENT HALL
206 CHURCH STREET S.E.
MINNEAPOLIS, MINNESOTA 55455
E-MAIL: nhauser@math.umn.edu

DEPARTMENT OF ECOLOGY
AND EVOLUTIONARY BIOLOGY
ENO HALL
PRINCETON UNIVERSITY
PRINCETON, NEW JERSEY 08544-1003
E-MAIL: steve@eno.princeton.edu