

Local Frequency Dependence and Global Coexistence

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In sessile organisms such as plants, interactions occur locally so that important ecological aspects like frequency dependence are manifest within local neighborhoods. Using probabilistic cellular automata models, we investigated how local frequency-dependent competition influenced whether two species could coexist. Individuals of the two species were randomly placed on a grid and allowed to interact according to local frequency-dependent rules. For four different frequency-dependent scenarios, the results indicated that over a broad parameter range the two species could coexist. Comparisons between explicit spatial simulations and the mean-field approximation indicate that coexistence occurs over a broader region in the explicit spatial simulation. © 1999 Academic Press

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1. INTRODUCTION

Interactions between species or genotypes, whether negative or positive, can be important in determining the diversity of species or genotypes within a community. Some, such as herbivory and disease spread, may convey

an advantage to rare species, leading to negative frequency dependence in the relative fitness of species. More generally, negative frequency dependence, an important mechanism for the maintenance of genetic diversity in natural populations, can arise in a number of ways: there is strong empirical evidence for such effects in both competition (if resource requirements differ among species,

e.g., Antonovics and Kareiva, 1988) and predation (e.g., through apostasis, Clarke, 1969, 1979). Similarly, negative frequency dependence may occur in parasite–host systems if parasites prefer the most common host type (May and Anderson, 1983). Other mechanisms, such as competition for pollinators or mycorrhizae or other mutualistic interactions, may lead to positive frequency dependence. For example, pollinators may prefer to specialize on the most common floral type and therefore be more likely to carry the common pollen on any given visit to a plant. This gives the common floral type an advantage. Finally, processes such as competition for resources may be either positively and negatively frequency dependent, depending on the relative strengths of interspecific and intraspecific interactions, or may exhibit mixed influences as frequencies change.

In concert, these influences may produce overall species interactions that are positive over some ranges of densities and negative over others. In the absence of spatial localization of effects, the predictions from models of simple frequency dependence are well known. In general, negative frequency dependence facilitates coexistence and positive frequency dependence does not. However, in sessile organisms such as terrestrial plants and marine invertebrates, and in any population in which movement is restricted, the strongest interactions among individuals take place locally (Harper, 1977; Antonovics and Levin, 1980). This means that frequency dependence is governed by local densities. In situations where individuals interact only within local subpopulations, there may be some subpopulations where interactions are primarily positive and others where interactions are primarily negative. Therefore, inclusion of spatially local interactions can confound our intuition about the outcome of positive and negative frequency dependence. Models that consider local interactions explicitly are needed, but these models are so complex that the results are difficult to interpret. In this paper, we analyze a simple spatial frequency-dependent model. As we shall show, novel results arise from incorporating spatially explicit interactions.

To investigate the effect of frequency-dependent interactions in a spatial environment, we constructed probabilistic cellular automata that retained the essential characteristics of competition, but simplified the details. By specifying very simple rules about the dynamics of an individual cell in response to its own state and that of its neighbors, one can explore how spatial structure influences the dynamics of populations. Recently, cellular automata have become increasingly popular in the ecological literature because they can be used to understand the consequences of spatial structure in populations in a simple but intuitive way (Crawley and May,

1987; Inghe, 1989; Green, 1989; Phipps, 1991; Hassell *et al.*, 1991; May and Nowak, 1992; Silvertown *et al.*, 1992; Molofsky, 1994).

Incorporating spatial structure into models can lead to qualitatively different results from non-spatial models (Kareiva, 1990). For example, Hassell *et al.* (1991) found that the dynamics of a host–parasite system varied depending on immigration rates among adjacent cells. Stochastic spatial models are advantageous for studying spatial structure, because in certain simplified scenarios analytical solutions are possible (Durrett, 1988; Durrett and Levin, 1994). These simplified cases can provide a jumping-off point for more complex, and hence realistic, ecological models. However, reference to the standard models provides an expectation about the behavior of more complex models. One example of a simplified model is the “voter” model (Durrett, 1988), so named because of its obvious analogy to human decision making. An ecological interpretation of the voter model is that each species or genotype occupies space strictly in proportion to its presence in the community. For the two-dimensional voter model, Holley and Liggett (1975) have shown that coexistence cannot occur.

In this paper, we expand upon the voter model to consider situations where the response of the species (or genotype) is not simply proportional to the species that are present, but where the species response is nonlinear (i.e., the common species is either enhanced or diminished as a function of its frequency in the surrounding population). From this expanded voter model, we show that a wide variety of spatially local, frequency-dependent interactions can lead to coexistence and that the exclusion of one species is relatively uncommon.

2. DEVELOPMENT OF THE MODEL

We consider competition between two species (species 0 and 1), for example, clonal plants, on a finite grid (although the model applies equally well for two non-mating genotypes). We assume that a site in the model receives seed input primarily from itself and its four nearest neighbors (Fig. 1). If a seed from a neighboring patch is as likely to capture a site as a seed from that site itself, then the probability that a site will be captured by a particular species, (say for the case of annual plants) is simply proportional to the frequency of that species in the neighborhood. Suppose, for example, that species compete equally and that each site contains exactly one adult plant; then the probability that a site will be occupied by species 1 is simply proportional to n , the

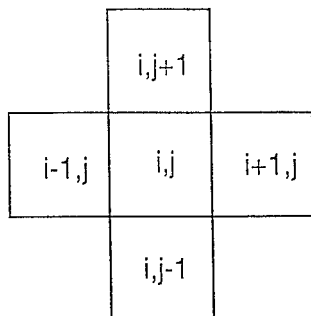


FIG. 1. The configuration of the neighborhood used in the model.

number of plants of species 1 in the five squares centered at the focal cell; that is,

$$P(\text{species 1}) = \frac{n}{5},$$

where n is the number of plant species 1 in the five-square neighborhood.

More generally, the probability of capturing a site may increase or decrease depending on the ecological situation. We treat four general cases based on the following assumptions.

First, we assume that each location or site contains a single individual of either species 0 or species 1; we do not allow empty cells. The dynamics are simple: the identity (0 or 1) of the individual at a particular location depends upon the identity of the individual at that location in the previous time step and the identity of its four neighbors (the von Neumann neighborhood). More general neighborhoods are considered in Durrett and Levin (1994). We assume that a propagule from a given cell has probability 0.2 of landing in any of the five cells in its neighborhood (including the donor cell), so that the probability a focal cell will be occupied in the next generation by a given species is determined by the number of cells in the neighborhood occupied by that type; such rule systems, based only on the sum, are sometimes termed totalistic (Wolfram, 1986). One may think of such systems as stating that the probability a site will be occupied by species 1 is a function only of the number of available propagules of species 1 in the neighborhood.

In the deterministic case, these probabilities are 0's and 1's. The possible "transition" rules then specify the state of a cell in the present generation, given the numbers in the neighborhood in the previous generation. This associates one of two states with each of the six possible sums, leading to 64 possible sets of rules. We reduce that set to 16 by requiring that in cases where only one species is present in a neighborhood (corresponding to a sum of

0 or a sum of 5), it maintains the site in the next generation; i.e., if the number of cells in the neighborhood occupied by species 1 is zero, species 0 always wins, whereas if the number of cells occupied by species 1 in the neighborhood is 5, species 1 always wins. We reduce the set further, to four possible cases, by assuming symmetry between the two species. Thus, the four general cases correspond to the following four scenarios. The probability of capturing a site may increase with the number of individuals of that species present in the neighborhood, but the increase may be nonlinear (Fig. 2A). Alternatively, the probability of success need not increase with frequency; for example, where pathogens are important, there is an advantage to being rare. The effects of disease may depress fitness (probability of site capture) as frequency increases from low densities (Fig. 2B). Ultimately, the probability of success must rise with local frequency, because if only one species is present in the neighborhood, it is the only candidate for capturing the site. The picture may become even more complicated if multiple processes interact. For example, the effects of disease may dominate when one species is rare, but be overshadowed if competition favors the common species at intermediate densities. In this case, species 1 loses when very rare but can capture the site when moderately rare, as might be the case in the presence of an Allee effect (Fig. 2C). In the final case, species 1 wins when very rare but loses when moderately rare (Fig. 2D).

These four basic cases (Table I) define the complete parameter space but are of limited interest because they do not admit stochasticity. In any realistic scenario,

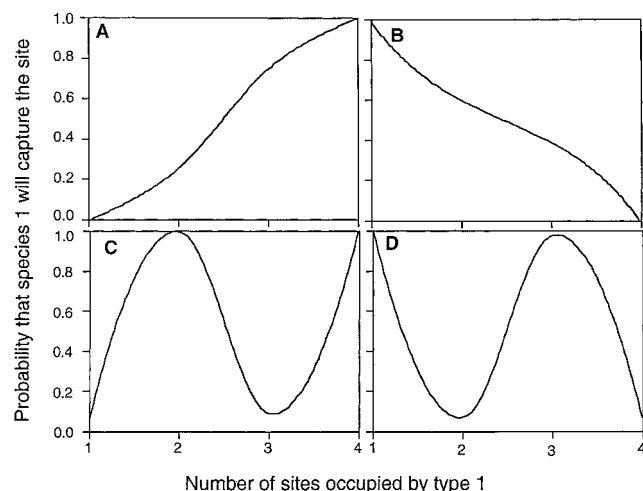


FIG. 2. The probability that species 1 will capture the target site for the four scenarios given in Table I. Rule 1 is represented in A, Rule 2 is represented in B, Rule 3 is represented in C, and Rule 4 is represented in D.

TABLE I

The Four Deterministic Rules Used in the Simulation Model

Rule systems	The sum of the neighbors			
	1	2	3	4
1. Positive	0	0	1	1
2. Negative	1	1	0	0
3. Allee effect	0	1	0	1
4. Modified Allee	1	0	1	0

Note. The deterministic cases delimit the extreme cases and form the boundary of the square of the parameter space.

stochasticity will be important. Hence we define the following:

p_1 = probability that the target cell becomes a 1 given that the neighborhood sum equals 1

p_2 = probability that the target cell becomes a 1 given that the neighborhood sum equals 2.

Because of the symmetry assumptions already mentioned, these two parameters totally characterize the set of possibilities because $p_3 = 1 - p_2$ and $p_4 = 1 - p_1$. Thus, p_1 and p_2 determine the dynamics of competition.

The purely deterministic cases ($p_1 = 0$ or $1, p_2 = 0$ or 1) form the boundaries of the feasible set of parameters. In particular, $p_1 = p_2 = 0$ represents absolute positive frequency dependence, in which the numerically dominant species always wins locally; $p_1 = p_2 = 1$ represents absolute negative frequency dependence. The other cases are intermediate, representing various degrees of positive or negative frequency dependence depending on the local state.

In this paper, we consider completely symmetric dynamics between the two species. If that assumption is relaxed, instability remains for mean field dynamics but not for the interacting particle system on the infinite grid (Durrett and Levin, 1994). Even under weak asymmetry, however, the analyses for the symmetric case provide insight into the dynamics on finite grids, or on finite regions of the infinite grid, and hence a first step toward understanding fast time scale dynamics on the infinite grid.

3. DETERMINATION OF THE REGION OF COEXISTENCE

Mean-Field Approximation

Much previous work has shown that the dynamics of systems with local interactions will differ fundamentally

from mean-field versions, but that the latter provide a point of departure in classifying outcomes and in guiding simulations (e.g., Durrett and Levin, 1994; Tainaka, 1994; Harada *et al.*, 1995; Kubo *et al.*, 1996; Nakamura *et al.*, 1997; Hiebeler, 1997). Thus, we first consider a mean-field approximation to the system, by considering an infinite lattice on which sites are mixed randomly after each time step. On such a lattice, the proportion of neighborhoods with a specified number of individuals of species 1 is given by the binomial expansion; and since the lattice is infinite, we can write a deterministic system describing x_t , the proportion of sites occupied by species 1:

$$x_{t+1} = 5p_1x_t(1-x_t)^4 + 10p_2x_t^2(1-x_t)^3 + 10(1-p_2) \times x_t^3(1-x_t)^2 + 5(1-p_1)x_t^4(1-x_t) + x_t^5. \quad (1)$$

The equilibrium equation $x_{t+1} = x_t$ is a quintic equation, with five possible equilibria.

By inspection, we verify that 0, 1/2, and 1 are all equilibria of the mean-field Eq. (1), as we would expect from the symmetry of the system. Factoring out these roots leaves us with a quadratic equation that determines the remaining two roots, which we will call the "quadratic" equilibria. Depending on parameter values, these two roots may or may not "exist" biologically as equilibria. To exist as equilibria for the system, they must be real and lie between 0 and 1.

The stability of solutions can be assessed by looking at the Jacobian: the derivative of x_{t+1} with respect to x_t . A

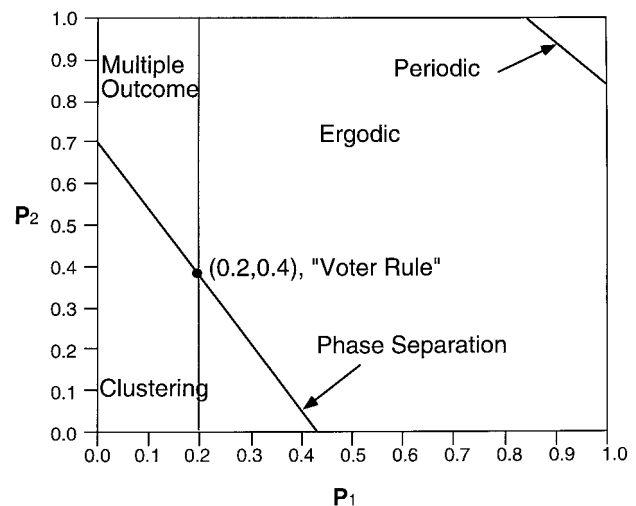


FIG. 3. Phase plot for the mean-field approximation of the local frequency-dependent model.

solution will be locally stable when $|J| < 1$. The Jacobian at the equilibria $x = 0$ and $x = 1$ is given by

$$J(0) = J(1) = 5p_1. \quad (2)$$

Hence the one-species equilibria will be stable when $p_1 < 1/5$ and unstable when $p_1 > 1/5$. In this non-spatial system, the ability of a rare species to invade does not depend at all on p_2 . This is to be expected, since without spatial correlations, an individual from a rare species will encounter other individuals of the same species negligibly often.

The Jacobian when $x = 1/2$ is given by

$$J(1/2) = (15 - 15p_1 - 10p_2)/8.$$

This equilibrium has $J > 1$ and thus “repels” solutions locally when $15p_1 + 10p_2 < 7$ (there is another way for

this equilibrium to become unstable, which we will discuss later).

These two criteria define four regions of parameter space. Intuitively, we might expect the two “quadratic” solutions to exist biologically, and be stable, when the equilibria at 0, 1/2, and 1 are all repulsive, and to exist and be repulsive when the equilibria at 0, 1/2, and 1 are attractive. Analysis of (1) indicates that this is in fact the case, and that in the larger regions where the one-species equilibria and the equilibrium at 1/2 are of different types, the quadratic equilibria do not exist biologically.

The resulting regions of phase space are shown in Fig. 3. The two largest domains of this system are the “ergodic” regime, where only the $x = 1/2$ equilibrium is stable, and the “clustering” regime, where only the equilibria at $x = 0$ and $x = 1$ are stable. In these two regimes, the two quadratic solutions do not exist biologically. In addition, there is a small “multiple outcome” regime

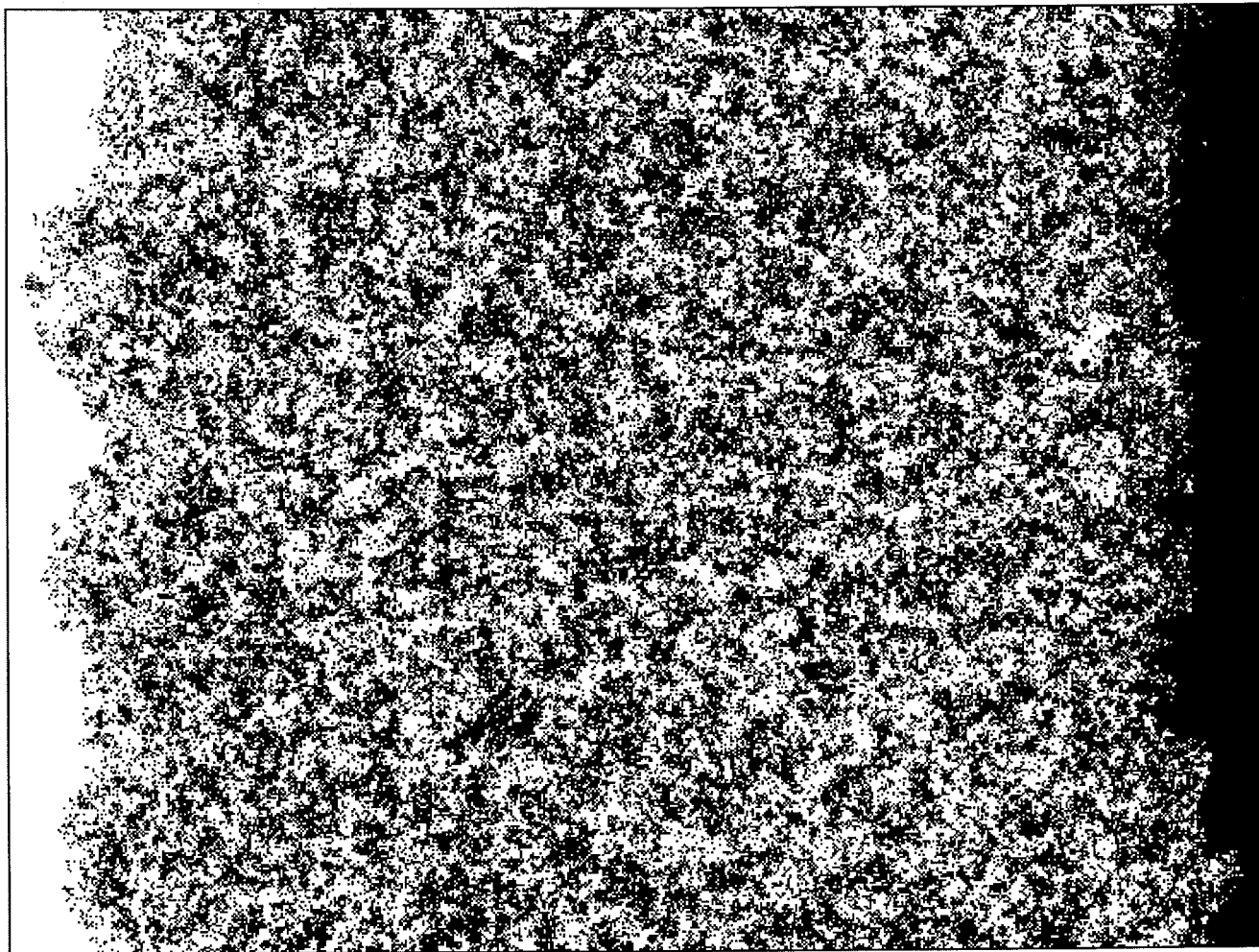


FIG. 4. The (0.35, 0) model from a vertical interface after 1000 updates.

where the equilibria at 0, 1/2, and 1 are stable and divided by unstable quadratic equilibria, and a “phase separation” regime where only the quadratic equilibria are stable. The small region in the upper right-hand corner will be discussed below.

Interpretation of these results is straightforward. Increasing either p_1 or p_2 generally tends to favor the rarer species. When both values are large enough, in the ergodic region, the rare species always tends to do better, and the species exist in a 50/50 balance. When both p_1 and p_2 are small, in the clustering regime, the common species always does better and whichever species gains an advantage will exclude the other one. If p_1 is moderately large and p_2 is very small, however, we have a situation where a very rare species is favored, whereas a moderately rare one is not. This is the phase separation region, where a rare species will invade, but not reach 50% prevalence, instead stopping at some intermediate

equilibrium. Similarly, in the multiple outcome regime p_1 is small while p_2 is very large. Here, a moderately rare species can increase to 50% prevalence, while a very rare species will go extinct, leading to three qualitatively different possible outcomes, depending on initial conditions. The results of the non-spatial model are summarized in Fig. 3.

There is another way for the equilibrium at $x = 1/2$ to become unstable. From (3), we see that $J < -1$ when $15p_1 + 10p_2 > 23$ (requiring both p_1 and p_2 to be quite close to 1). This corresponds to a “flip” bifurcation. The equilibrium attracts points that are far away, but is not stable, leading to cycles of period 2. As p_1 and p_2 increase even further, we would expect to find a period-doubling cascade. Note that the quadratic equilibria do not exist in this region of parameter space. From a biological point of view, the situation in which species 1 almost certainly wins a site if it has one or two individuals in the

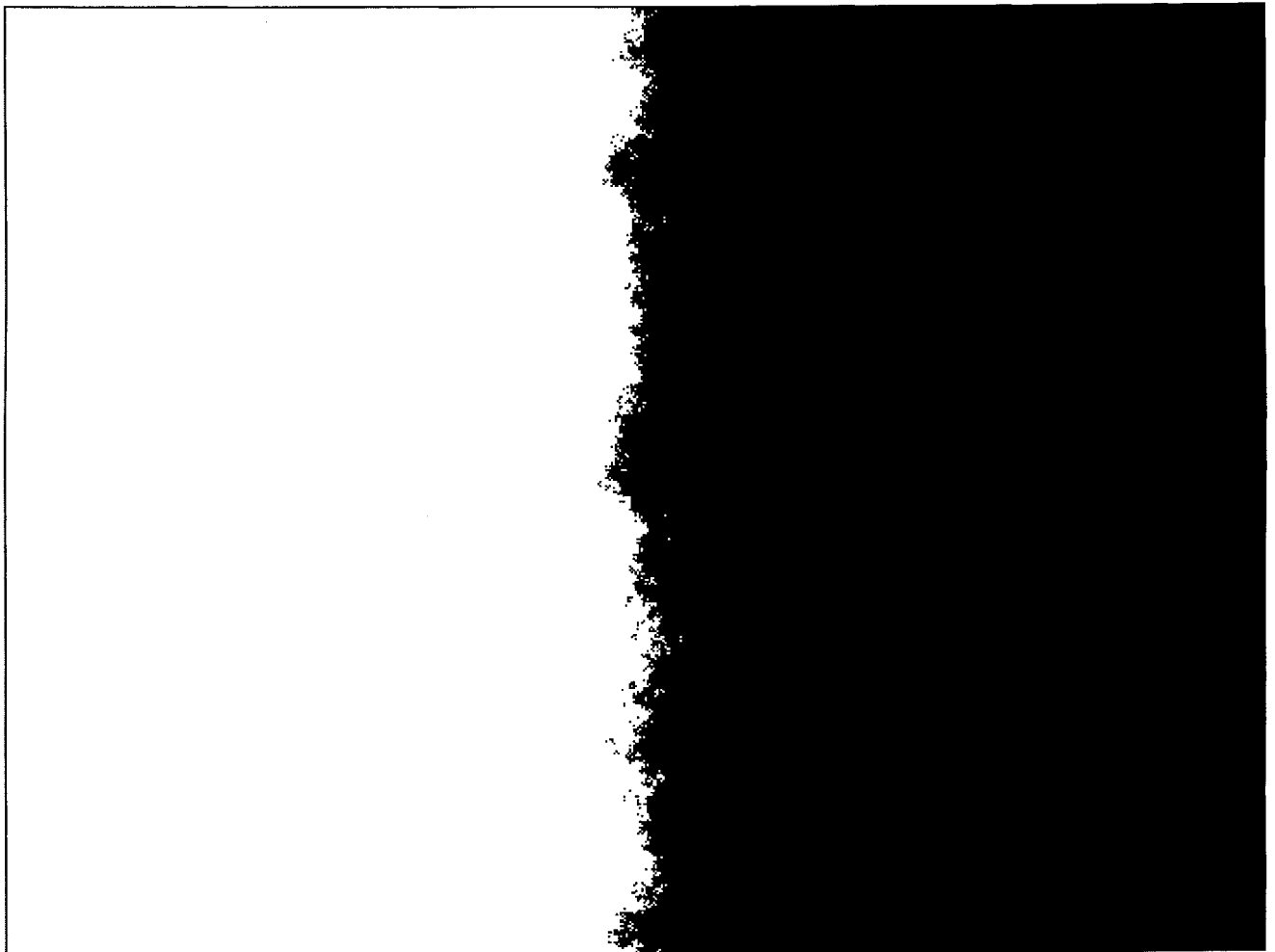


FIG. 5. The (0.27, 0) model from a vertical interface after 5000 updates.

neighborhood, and almost certainly loses if it has three or four, but certainly wins with five seems rather contrived; but it is of interest for mathematical completeness.

Simulation Results

Returning to the nearest-neighbor spatial version of our competition model, we investigate the various types of system behavior that can arise for different choices of the parameters p_1 and p_2 . In light of the preceding mean-field analysis, we should anticipate a similarly complex phase diagram, but the extent of correspondence is hard to predict. Unfortunately, rigorous mathematical analysis is impossible except in the linear voter case $(\frac{1}{5}, \frac{2}{5})$ (Holley and Liggett, 1975). Thus we resort to Monte Carlo simulation in order to compare and contrast the phase diagram of the spatial model with that of its non-spatial counterpart.

Figure 3 suggests that evidence of ergodicity, clustering, and phase separation may be most easily discernible with parameters on the “bottom edge” $\{p_2=0; 0 < p_1 < 1\}$. In order to test for qualitatively different spatial behaviors, we use the WinCA cellular automata modeling software to check how readily each species is able to invade the other’s terrain. Our experiments take place on a 640×480 array, with species 0 (white) initially on the left half, with species 1 (black) on the right half, and with a mixed boundary condition that wraps the top edge to the bottom, but disables interaction between the left and right edges. The “mixed” boundary condition allows us to simulate competitive interactions occurring along a discrete boundary as would be the case for an ecological border. By wrapping the top of the array to the bottom, but not the left to the right, interactions can propagate only from the initial interface rather than two “parallel” interfaces as would occur in a torus. This setup

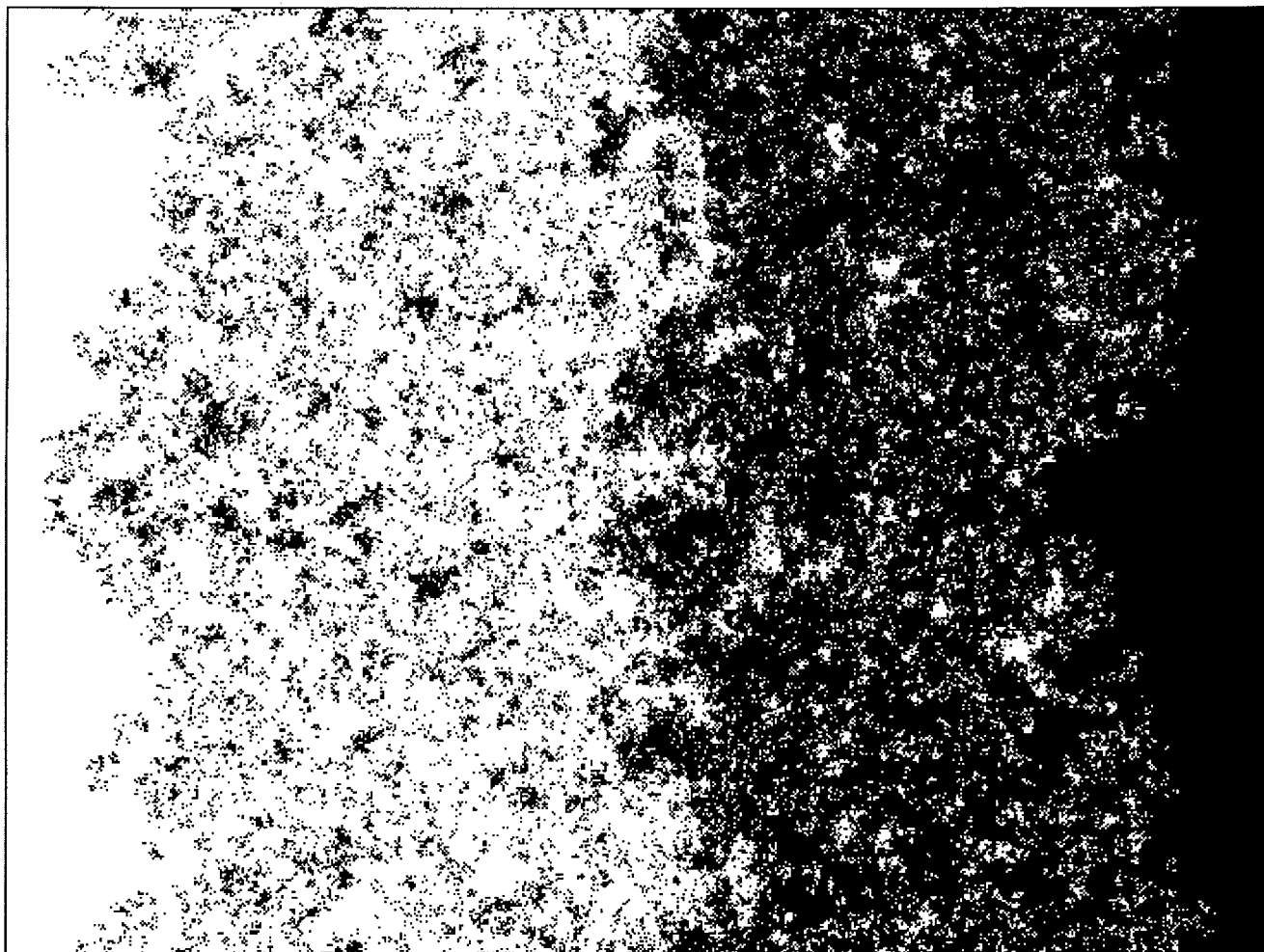


FIG. 6. The $(0.31, 0)$ model from a vertical interface after 2000 updates.

effectively emulates large-scale interface dynamics in an infinite system. We also analyze more conventional simulations, starting from random initial configurations with 0's and 1's randomly placed on the grid in a 50/50 mixture (i.e., $\phi \in (0, 1)$ (i.e., from Bernoulli product measures u_ϕ)) with wraparound at each edge. As it turns out, we encounter three distinct scenarios by varying p_1 , with p_2 fixed at 0.

If $p_1 = 0.35$, or for any larger value of the parameter, each species invades the other's territory at a linear rate; and between the two wave fronts the system rapidly reaches an equilibrium with density $\frac{1}{2}$. Figure 4 shows this process after 1000 updates. Starting from any random distribution (u_ϕ , $\phi \in (0, 1)$), the simulation appears to converge quickly to the same symmetric equilibrium with short length scale, i.e., a random pattern. This, then, is the ergodic case. One should note that our probabilistic automata, when restricted to a finite array, are finite Markov chains with only the trivial states “all

0's” and “all 1's” as traps. Therefore, strictly speaking, nontrivial invariant distributions do not exist for the finite systems. We are observing a metastable steady state that will persist for eons, but eventually will break down. Only in the infinite system should we expect to obtain a true stochastic equilibrium with this or any other choice of parameters.

For $p_1 = 0.27$ or smaller, on the other hand, neither species is able to make significant headway into the other's domain. Rather, the interface stays tight even after 5000 updates (Fig. 5). Starting from the symmetric random distribution $u_{1/2}$, this standoff allows solid regions of either species to consolidate. Pockets of one species that are completely surrounded by the other gradually disappear, by a kind of curvature-driven surface tension. In other words, because a neighborhood that spans a curved boundary will on average have unequal frequencies of the two species, the common type will continue to be favored albeit at an ever-decreasing

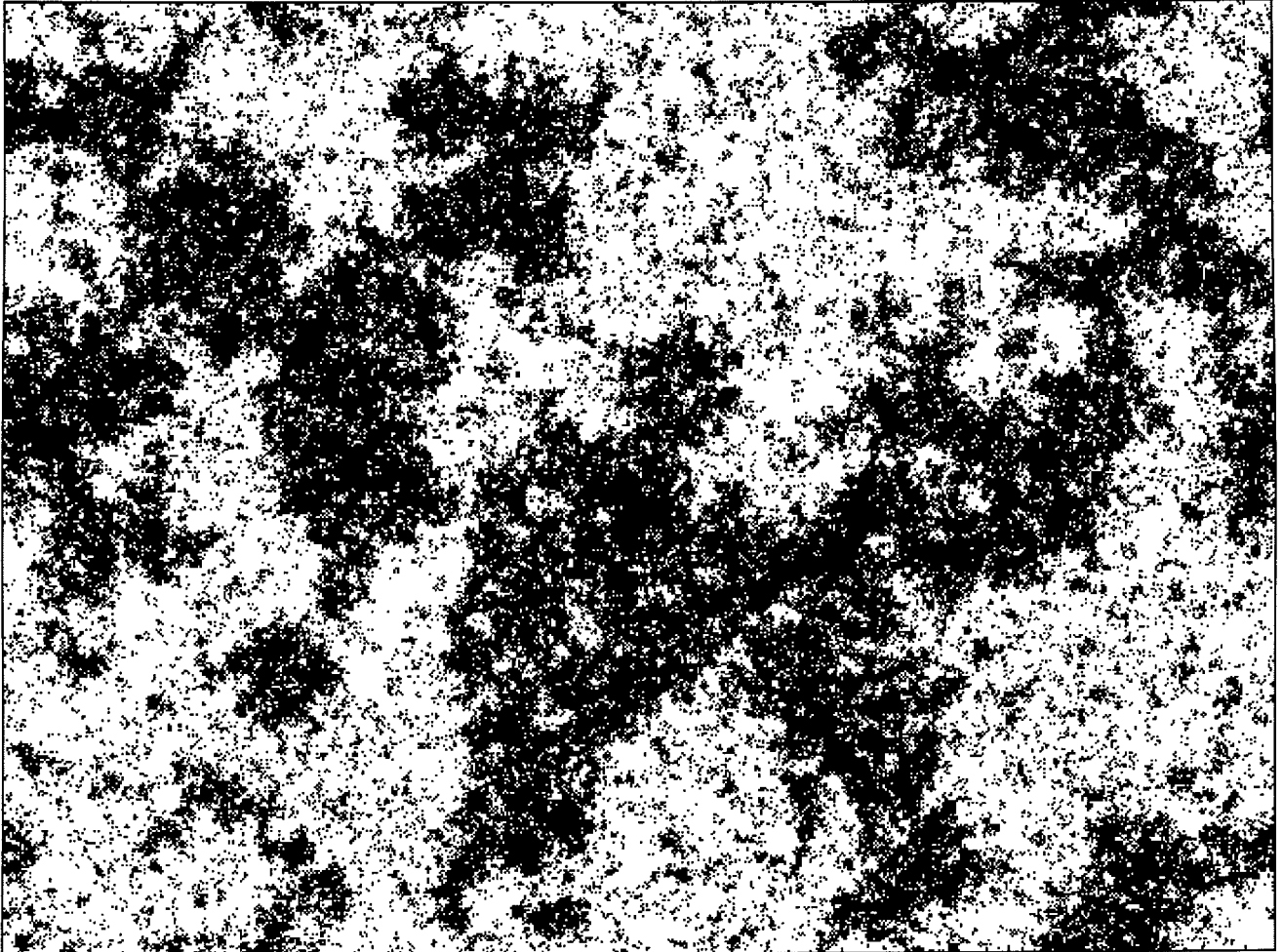


FIG. 7. The (0.31, 0) model from symmetric randomness after 5000 updates.

rate as the boundary curvature decreases. In our finite simulation, the species that acquires more territory by chance eventually takes over the entire array. This is the clustering regime. From random initial distributions with any density other than $\frac{1}{2}$, the consolidation process favors the predominant species, so that after a long time, in all likelihood, that species will take over the finite system.

The plot thickens when we investigate $p_1 = 0.31$, in which case each species is able to invade, but only as a minority faction. Waves of mixed populations advance steadily (at about half the speed of the ergodic instance above), as shown in Fig. 6 after 2000 updates. Now, however, there is evidently a predominance of species 0 emerging on the left, and a predominance of species 1 on the right. For instance, sample averages over moderate-sized windows within the predominantly species 0 region average about 0.2 and rarely exceed 0.25, whereas corresponding averages within the predominantly species 1 region average about 0.8 and are rarely lower than 0.75. This, then, is phase separation. The corresponding dynamics starting from a density of 0.5, $u_{1/2}$, create ever larger patches of the two nontrivial equilibria over time, with the changes in relative frequency being determined by interaction in neighborhoods at the patch interfaces; Fig. 7 shows that process at time 5000. For any other $\phi \in (0, 1)$ the evolution starting from u_ϕ apparently converges to nontrivial steady state with a higher density of the initially prevalent species. To summarize, the phase point $(0.31, 0)$ corresponds to a system in which “all 0’s” and “all 1’s” are unstable, yet there are two distinct stable mixed equilibria dominated by 0’s and 1’s, respectively.

The simulations provide an estimate of the qualitative patterns that develop. However, to quantify differences, we calculated mean time to extinction and clustering for two one-dimensional transects through the parameter space. For mean time to extinction, we selected a transect that contained the linear voter model $p_1 = 0$ to 2 at 0.1 intervals, $p_2 = 0.4$. We simulated 100 starting conditions, each containing a 50/50 mixture of the two species and recorded when one species excluded the other species. We set an upper limit of 10,000 generations so for cases where both species persisted at 10,000 generations, we underestimated the time to extinction. The mean time to extinction increases as we approach the boundary between clustering and ergodic (Fig. 8(top)).

To calculate the clustering index, we calculated the frequency each species was next to the same species versus the other species. The one-dimensional slice was chosen to encompass ergodic regions of varying distances from the clustering border. Thus, we chose $p_1 = 0.2$ and $p_2 = 0.5$ to 1.0. We averaged 20 simulations (each started at an initial frequency of 50/50). Clusters of each species

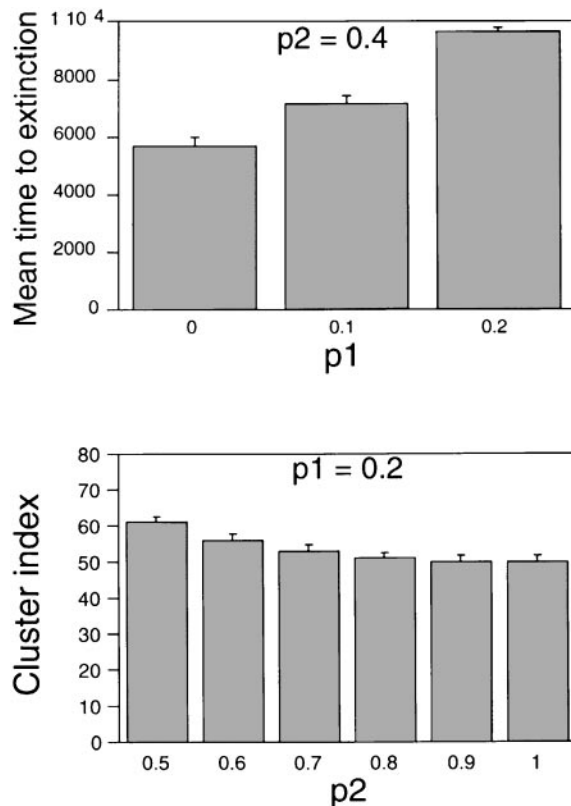


FIG. 8. (Top) Mean (+1 se) time to extinction ($p_1 = 0$ to 0.2, $p_2 = 0.4$) and (bottom) mean (+1 se) cluster index ($p_1 = 0.2$ and $p_2 = 0.5$ to 1.0) for the cluster region and ergodic region, respectively.

develop close to the clustering border, i.e., $p_1 = 0.2$ and $p_2 = 0.5$, but as we move farther away from the border ($p_2 = 0.6$ to 1.0), any association between the two species breaks down and we see only random patterns (Fig. 8(bottom)).

Our initial experiments indicate convincingly that the bottom edge of the spatial phase diagram agrees qualitatively with that of the mean-field model, exhibiting ergodicity, clustering, and phase separation, though this last phenomenon would seem to be rather rare. The next order of business is to obtain a good empirical estimate of the complete spatial phase diagram—in particular, searching for evidence of multiple outcome and periodic phases. To this end, we have enlisted the aid of CAM8, a dedicated cellular automata machine from MIT capable of simulating our model on a 512×512 array at several hundred updates per second. We conclude this section by summarizing our findings based on extensive, detailed simulation of the entire (p_1, p_2) parameter space using both WinCA and CAM8.

Motivated by Fig. 3, we have investigated barely ergodic systems for large sampling values of p_2 , especially

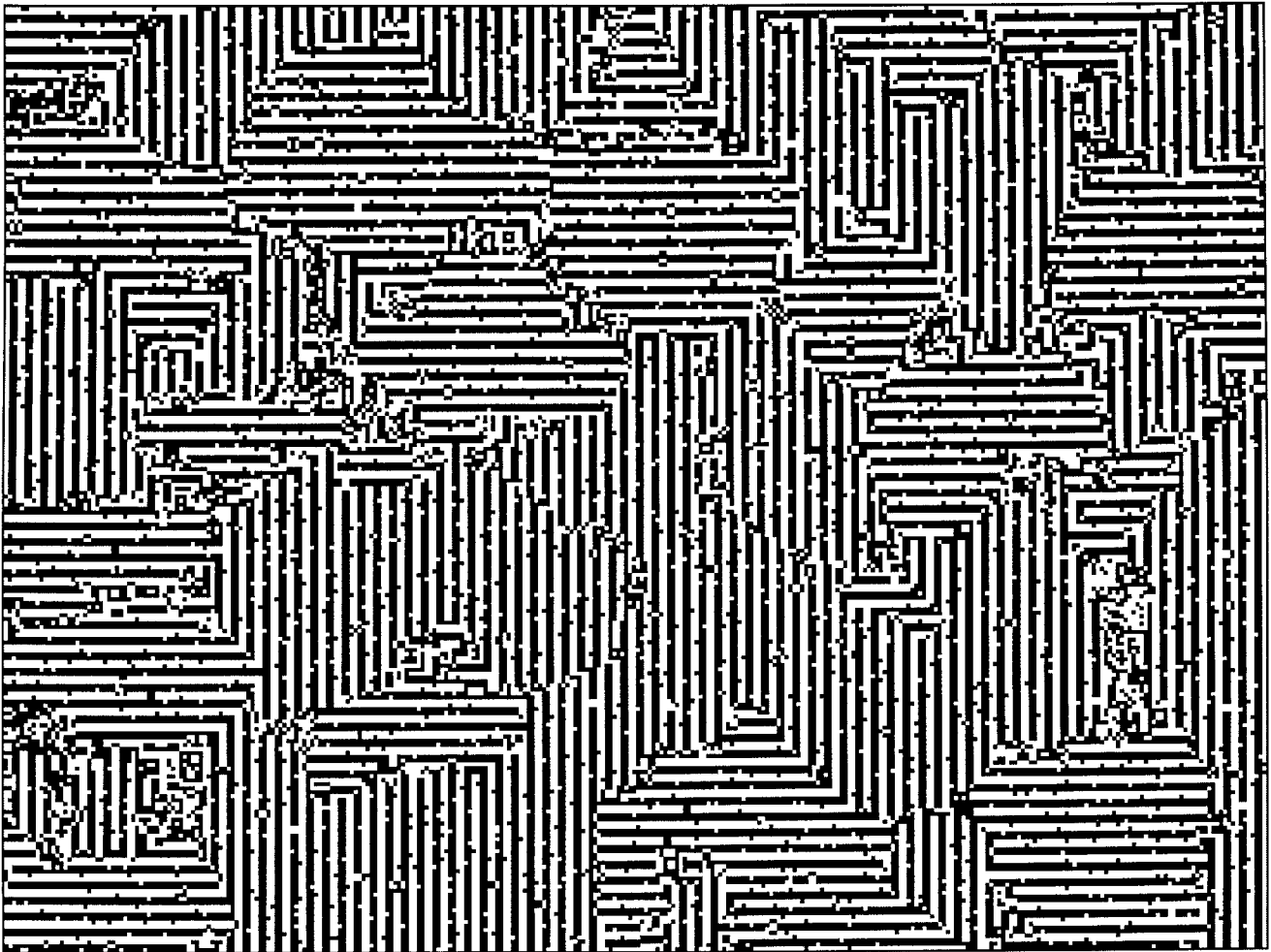


FIG. 9. The (0.998, 0.998) model from symmetric randomness after 5000 updates.

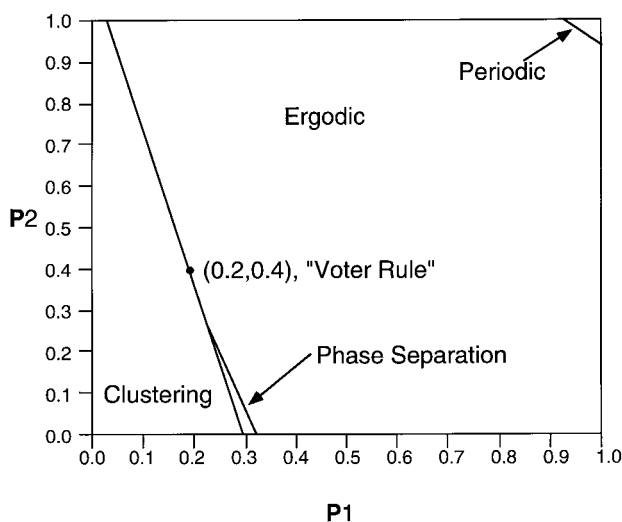


FIG. 10. Estimation of the phase diagram for the spatial model.

for p_2 between $\frac{2}{5}$ and 1, starting from random distributions with very small density of the rare type (e.g., from $u_{0.01}$). In multiple outcome cases, one would expect convergence to all 0's from sufficiently small initial densities of species 1. In every instance, however, small isolated configurations of species 1—such as the dyads described in the next section—have a propensity to nucleate linearly growing patches of the symmetric equilibrium. We conclude that, in contrast to the mean-field model, there is no multiple outcome regime of the spatial model.

To our surprise, careful inspection of a minuscule neighborhood of the upper right corner of the phase space does reveal a fourth regime for the spatial model corresponding to the mean-field periodic case. For instance, starting from $u_{1/2}$, on a 320×240 array with wraparound edges, parameter choices $p_1 = p_2 = 0.998$ lead to the highly clustered configuration of Fig. 9 after 5000 updates. What's going on here? The system is best viewed as a perturbation of the deterministic cellular

automaton at $(1, 1)$, which is locally periodic, meaning that the sequence of values at each site repeats from some time on, but the sequences at different sites can have different patterns and lengths. That rule subjected to very occasional random errors self-organizes into quasi-periodic configurations dominated by horizontal and vertical clusters of period 2 stripes. Over time stochastic fluctuations prevent fixation and, provided that the error is small enough, aligned clusters apparently grow to arbitrarily large length scale. This phase admits two totally aligned steady states: v_h and v_v , say. Starting from any u_ϕ with $\phi \in (0, 1)$, the dynamics converge to $\frac{1}{2}v_h + \frac{1}{2}v_v$. For cases in which the errors occur more than a few times in a thousand, however, the alignment process breaks down and ergodicity prevails. (A similar but more robust phenomenon takes place in the opposite corner of the square: rule $(0, 0)$, i.e., deterministic majority vote, is locally periodic with fixation at most sites, whereas any small or moderate random perturbation of $(0, 0)$ results in clusters.)

Finally, the results of our extensive CAM8 simulation are summarized in the estimated phase diagram of Fig. 10. Note that the boundary separating the clustering and ergodic regions runs from about $(0.024, 1)$ at the top edge, down through the linear voter point $(0.2, 0.4)$, before a bifurcation encloses the tiny phase separation.

4. DISCUSSION

Among the fundamental questions in ecology are determining under what conditions two species can coexist and understanding why we see the patterns of coexistence we do in nature. Simple spatial models have a role to play in answering both these questions. We have shown using a simple spatial model of local frequency-dependent competition between two species that coexistence of two species is possible for large regions of the parameter space. In the region of the parameter space corresponding to positive and negative frequency dependence, the conclusions from the mean-field model and the explicit spatial model are similar to conclusions from nonspatial models of frequency dependence, mainly that positive frequency dependence leads to exclusion and negative frequency dependence allows coexistence. Within the region of the parameter space corresponding to positive frequency dependence, the mean-field model and the explicit spatial model both predict exclusion of one species, but in the explicit spatial simulation, exclusion can take many generations. Choosing parameter combinations close to the border between positive and negative frequency dependence causes exclusion to occur

very slowly. In the proportional case ($p_1 = 0.2, p_2 = 0.4$) exclusion can take nearly 10,000 generations. In any reasonable ecological study, these long exclusion times would effectively appear as coexistence of the two species.

This simple spatial model has bearing on a second major question. What creates patterns in communities? One surprising result from this study is that stochastic rules can produce persistent spatial patterns that are maintained over long time intervals. Clusters or patches develop that have characteristic sizes but where the majority and the minority species coexist. In these cases, the majority patch type is infected with a small number of the minority species and this association is stable through time. In addition, different characteristic patch sizes occur at different regions of the grid. Larger clusters appear as one approaches the boundary between coexistence and exclusion. The presence of persistent spatial patterns in a relatively small area might lead a field ecologist to conclude that an underlying environmental factor could be structuring the community. As one moves farther into the coexistence region, the clustering breaks down into random associations. In the purely deterministic case, $p_1 = 1, p_2 = 1$, one gets a random or quasi-periodic arrangement of the two species in space. The presence of random patterns developing from deterministic rules might also lead a field ecologist to conclude that environmental noise rather than species interactions is responsible for the patterns. Purely deterministic rules leading to chaotic spatial patterns has been demonstrated in other studies (Hassell *et al.*, 1991; Molofsky, 1994) and such results are typical of cellular automata models (Wolfram, 1986). A more interesting result is that persistent patterning is possible for stochastic parameters.

The stochastic model allows us to assess how easy it is to move from the extinction region to the coexistence region. The region of the parameter space that corresponds to exclusion is relatively small, meaning that any combination of parameters resulting in extinction is close to the coexistence boundary so a change in the parameter values is more likely to promote coexistence. Therefore, we can ask, what ecological circumstances might allow a species to escape from the extinction region? There are ecological situations that will minimize the chance of extinction. First, if predominantly positive frequency dependence is occurring (i.e., at the $p_1 = 0, p_2 = 0$ border) then if stochasticity is high enough, the probability of coexistence increases. Alternatively, the sum of the two processes, say, for example, pollination and competition, leads one process to dominate at certain local frequencies and the other to dominate at other local frequencies.

The precise boundary for the region of coexistence differs when full mixing is assumed as in the mean-field approximation, rather than local mixing, as in the simulation. Specifically, the multiple outcome region (found when p_1 is small and p_2 is relatively large) disappears in the explicit spatial model, making coexistence possible under a wider range of conditions than is found in the mean-field approximation. Biologically, this is the region where the rare species “wins” only if the two species occur at approximately equal frequencies, as might be the case if pollinators limit reproduction at low frequencies, but competition for the same resource limits reproductive success at more moderate frequencies. The placement of the other four regimes (clustering, phase separation, ergodic, and periodic) are modified only slightly in the explicit spatial simulation.

Another analytical approximation for the spatial model can be found by considering the behavior of dyads (occupied pairs of cells). The dyad provides a more appropriate basis for considering establishment than does the monad (single cell), because an invading species occupying a cell must have come from some occupied neighbor; thus, it is more likely that a neighbor cell will be occupied than mean-field considerations would suggest. When dyads are considered, the boundary between coexistence and exclusion is in excellent agreement with the analytical criterion for a rare species of either species to spread. The remarkable success of this “rule of thumb” cannot be completely explained (Levin and Durrett, 1996), although it is consistent with approximations for pair approximations.

The dyad rule is easily derived. Consider a pair of cells occupied by species 1 and surrounded by six neighbors occupied by species 0. The probability that the rare dyadic type will increase in the population is found by comparing the expected number of daughter cells ($6p_1 + 2p_2$) that replace the two parent cells, and requiring therefore that for population growth

$$6p_1 + p_2 > 2;$$

that is,

$$3p_1 + p_2 > 1.$$

This condition makes intuitive sense. Large values of p_1 and p_2 accord with negative frequency dependence, promoting coexistence. The so-called neutral case, $p_1 = 0.2$, $p_2 = 0.4$, in which coexistence is impossible, sits on the boundary of this region. Increasing p_1 and decreasing p_2 equally from these values introduce

nonlinearities in which locally rare species do better than those with more similar neighbors (Levin and Durrett, 1996), and moves the parameters into the region of coexistence. The dyad rule does not predict the phase separation regime that appears in both the mean-field model and explicit spatial simulation.

Note that it may seem surprising that one does not need to impose the *monad* rule ($5p_1 > 1$) as a necessary condition for spread. The explanation lies in the stochastic nature of the process. On a large grid, if the monad rule is violated but the dyad rule is satisfied (e.g., if $p_1 = 0.1$ and $p_2 = 0.5$), most introductions will fail. A few isolated monads, however, stochastically will duplicate, getting beyond the initial threshold and allowing the dyad rule to become operational.

The results of this paper present a general analysis of spatially explicit frequency dependence, and a framework for embedding other results. Most notably, Hubbell (1979) showed that proportional frequency dependence can lead to long-term persistence of tree species in tropical forests, although the eventual outcome will be extinction. Bever *et al.* (1997) used a spatially explicit cellular automata model to show that positive feedback between soil microorganisms and the plant species they infect can lead to long-term persistence of two plant species. Our model expands upon this previous work to provide a more general framework for examining frequency-dependent interactions among species. We have shown that coexistence occurs for a large region of the parameter space and that the patterns that develop are random, even though interactions are not. In regions of the parameter space where exclusion occurs, long-term persistence is possible. Moreover, statistically recognizable patch structure can develop and be maintained over long time intervals. Effective long-term persistence with coherent patch structure may arise from underlying environmental variation, or from positive frequency dependence (see Levin, 1974). Distinguishing between these alternatives can come only from careful empirical work.

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