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Cellular Automaton Models for Competition in Patchy Environments: Facilitation, Inhibition, and Tolerance

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We have developed cellular automaton models for two species competing in a patchy environment. We have modeled three common types of competition: facilitation (in which the winning species can colonize only after the losing species has arrived) *inhibition* (in which either species is able to prevent the other from colonizing) and tolerance (in which the species most tolerant of reduced resource levels wins). The state of a patch is defined by the presence or absence of each species. State transition probabilities are determined by rates of disturbance, competitive exclusion, and colonization. Colonization is restricted to neighboring patches. In all three models, disturbance permits regional persistence of species that are excluded by competition locally. Persistence, and hence diversity, is maximized at intermediate disturbance frequencies. If disturbance and dispersal rates are sufficiently high, the inferior competitor need not have a dispersal advantage to persist. Using a new method for measuring the spatial patterns of nominal data, we show that none of these competition models generates patchiness at equilibrium. In the inhibition model, however, transient patchiness decays very slowly. We compare the cellular automaton models to the corresponding mean-field patch-occupancy models, in which colonization is not restricted to neighboring patches and depends on spatially averaged species frequencies. The patch-occupancy model does an excellent job of predicting the equilibrium frequencies of the species and the conditions required for coexistence, but not of predicting transient behavior.

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1. INTRODUCTION

The spatial distribution of populations can profoundly affect their dynamics. There is now a large amount of literature on spatial models [e.g., the recent books by Shigesada and Kawasaki (1997), Hanski and Gilpin (1997), Tilman and Kareiva

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(1997), and Turchin (1998)]. The models fall into two categories: *spatially-explicit models*, which describe (and thus, are sensitive to) the actual spatial arrangement of the populations and *spatially-averaged* or *mean-field models*, which depend only on the average properties of the spatial pattern. Mean-field models have been extensively studied as 'metapopulation' models, which describe the age-, size-, or occupancy-distributions of spatial patches [e.g., Cohen (1970), Levins (1970), Caswell (1978), Hastings (1978), Hanski (1983), Caswell and Cohen (1991a, b), (1993), (1995), Gilpin and Hanski (1991), Nee and May (1992), Czaran and Bartha (1993), Barradas and Cohen (1994), Barradas *et al.* (1996)]. These metapopulation models are usually presented without specifying the spatially explicit model to which they are mean-field approximations.

In this paper, we present a general method for constructing comparable meanfield and spatially-explicit models for interacting populations. These models are specified in terms of the spatial and temporal scales of the population interactions [cf. Levin (1992) for a review of scale in ecology]. Our approach permits the direct study of the effects of spatial arrangement *per se*. The mean-field models are nonlinear Markov chains. The spatially-explicit models are stochastic cellular automata.

We apply this framework to the study of competition and coexistence, building on mean-field models of competing species studied by Caswell and Cohen (1991a, b, 1995), Barradas and Cohen (1994), and Barradas *et al.* (1996). A central question is the extent to which disturbance and dispersal can mediate coexistence among species that cannot coexist in a single patch. That they can do so has long been apparent from simulations, and has been proven by Barradas and Cohen (1994) and Barradas *et al.* (1996) for some special cases.

We examine three models for competition, corresponding to the facilitation, inhibition and tolerance succession models of Connell and Slatyer (1977). The differences among these models correspond to observable features of competition and our results show that the consequences—in a spatially explicit model—can be significant. We examine equilibrium abundance, transient dynamics, local species diversity, and the existence of spatial structure. We identify which properties are satisfactorily predicted by the mean-field model and which are not.

2. CONSTRUCTING CELLULAR AUTOMATON MODELS

A cellular automaton (CA) is an array (usually a regular lattice) of finite-state, discrete-time dynamical systems. The dynamics at one site (a 'cell' or, in our usage, 'patch') depend on the state at that site and the states of sites in some neighborhood of that site. We will often refer to the entire CA array as a 'landscape', although no restriction to terrestrial ecosystems is intended.

2.1. *Patch states.* Cellular automaton are discrete-state systems, so the first step in their construction is defining a discrete state space. One way to do this (Hsu, 1987; Ermentrout and Edelstein-Keshet, 1993) is to divide a continuous state variable

(e.g., population density) into intervals and define discrete states in terms of these intervals. In this paper we carry this approach to its logical conclusion, dividing the abundance of each species into just two categories: *absent* and *present*. A system with N species is thus described in terms of 2^N states.

Presence vs absence is a biologically relevant distinction, and the processes (colonization, extinction, population growth, and interaction) that determine the transitions between these two states are biologically important. However, it is possible to construct CA models with more detailed state variables (absent, rare, and abundant, for example), and to include information in addition to the species densities, for example reflecting environmental conditions [e.g., Caswell and Etter (1993) and Caswell and Cohen (1995)].

2.2. Patch state dynamics. The within-patch dynamics are specified in terms of transition probabilities among the patch states. These probabilities can be expressed in terms of the characteristic time scales of the underlying processes (Caswell and Cohen, 1991a, b). We suppose, for example, that species become locally extinct due to disturbance. If the characteristic time between disturbances is τ_d , then the probability of disturbance in a unit of time is $p_d = 1/\tau_d$. We also suppose that an inferior competitor is excluded by a superior competitor in a characteristic time τ_c ; the probability of exclusion in a unit of time is $p_c = 1/\tau_c$. In general, the probability of a transition can be taken as the inverse of the corresponding characteristic time scale.

The colonization of unoccupied patches requires propagules that originate in occupied patches. We suppose that there is a characteristic dispersal radius; an empty patch can be colonized only from occupied patches within this radius. In the mean-field models, the dispersal radius includes the entire landscape; in our CA models, it is limited to the eight immediately adjacent patches.

The mean number of propagules arriving in an interval of time depends on the number of occupied patches within the dispersal radius and the production of propagules per unit time. Let $d_i \ge 0$ denote the mean number of propagules produced per occupied patch per unit time, and let $f_i \in [0, 1]$ be the proportion of patches within the dispersal radius that are occupied by S_i . If propagules are distributed randomly within the dispersal radius, the number arriving in a empty patch per unit time will be a Poisson random variable with mean $d_i f_i$. The colonization probability is the probability of the arrival of at least one propagule in the next time interval:

$$C_i = 1 - e^{-d_i f_i}.$$
 (1)

The transition probabilities form a nonlinear Markov transition matrix, whose structure depends on the biological details of the process being modeled.

This approach can be generalized to any set of interacting populations. For N species, there are 2^N patch states. The interactions among the N species define time scales for each each of the 2^{2N} inter-state transitions. The inverses of these time scales provide transition probabilities among the patch states. If a transition

does not occur, its characteristic time is infinite and its transition probability is zero. Transitions that involve colonization are described by equation (1); the result is a complete set of transition probabilities. In Section 3 we show examples for three models of interspecific competition; see Caswell and Cohen (1991a, b), Barradas and Cohen (1994), and Barradas *et al.* (1996) for additional examples.

2.3. *Cellular automata and patch occupancy models.* If the system is well mixed, so that every patch interacts equally with every other patch, then the state of the landscape is completely specified by the proportion of patches in each patch state. Because such a landscape can be described by the proportions of patches occupied by each species combination, we call these *patch-occupancy (PO) models*. Their dynamics can be written

$$\mathbf{x}(t+1) = \mathbf{A}_{x}\mathbf{x}(t),\tag{2}$$

where **x** is a vector of proportions $(0 \le x_i \le 1, \sum_i x_i = 1)$ and **A**_x is a columnstochastic transition matrix (i.e., $0 \le a_{ij} \le 1$ and $\sum_i a_{ij} = 1$ for all *j*) whose entries may depend on **x**.

A CA model, directly comparable to a PO model, can be constructed by applying the same transition matrix to a local neighborhood, instead of to the entire landscape.

Both PO and CA models are 'spatial', in the sense that they describe landscapes composed of sets of patches. Several sets of terms have been used to distinguish these two kinds of models. We will refer to them as 'implicitly' and 'explicitly' spatial models, because PO models are independent of the explicit spatial arrangement of the patches. The PO models are also called mean-field approximations to the corresponding CA model; they assume that each patch experiences the overall land-scape mean frequency of each species combination. Kareiva (1990) would classify PO models as 'island models' and CA models as 'stepping-stone' models. Hiebeler (1997) calls our PO models 'infinite-dispersal mean-field approximations".

3. THREE COMPETITION MODELS

We turn now to models for three types of competition: facilitation, inhibition, and tolerance. This terminology was introduced by Connell and Slatyer (1977) to describe ecological succession. Patch-occupancy models for the three types were developed and analysed by Caswell and Cohen (1991b).

Each model contains two species, S_1 and S_2 . Species S_1 is the winner in local competition; i.e., the 'late successional' species. Species S_2 is the loser in local competition; i.e., an early successional or fugitive species. A patch is in one of four states,

S_2	S_1	State
0	0	1
0	1	2
1	0	3
1	1	4

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where 0 denotes absence and 1 denotes presence.

The three models are:

- *Facilitation competition*. The winning competitor S_1 can colonize a patch only after the losing competitor S_2 has colonized and rendered the environmental conditions suitable. Once S_1 colonizes a patch, it eventually excludes S_2 .
- *Inhibition competition*. Both species can colonize empty patches, but each species can prevent invasion by the other (a priority effect). The two species co-occur locally only after colonizing a patch simultaneously; when they do so, S_1 eventually excludes S_2 .
- Tolerance competition. Both species can colonize empty patches. When the two species co-occur in a patch, the outcome of competition is determined by their relative abilities to tolerate reduced resource levels. The winning species can tolerate lower resource levels than the losing species; hence, S_1 can invade a patch containing S_2 , and when it does so, S_2 is eventually excluded. The losing competitor S_2 , however, cannot invade a patch containing S_1 .

The probability of competitive exclusion within a patch is p_c . The probability of disturbance is p_d . Disturbance is assumed to remove all species from a patch, and is assumed not to affect unoccupied cells. The probability of colonization during a unit time interval is given by equation (1), where the species frequencies are given by $f_1 = x_2 + x_4$ and $f_2 = x_3 + x_4$.

The transition structures implied by the three competition models are shown in Fig. 1. The corresponding transition matrices are:

$$\mathbf{A}_{\mathbf{x}}^{(F)} = \begin{pmatrix} 1 - C_2 & p_d & p_d & p_d \\ 0 & 1 - p_d & 0 & p_c(1 - p_d) \\ C_2 & 0 & (1 - C_1)(1 - p_d) & 0 \\ 0 & 0 & C_1(1 - p_d) & (1 - p_c)(1 - p_d) \end{pmatrix},$$
(4)

$$\mathbf{A}_{\mathbf{x}}^{(I)} = \begin{pmatrix} (1 - C_1)(1 - C_2) & p_a & p_a & p_a \\ C_1(1 - C_2) & 1 - p_d & 0 & p_c(1 - p_d) \\ C_2(1 - C_1) & 0 & 1 - p_d & 0 \\ C_1C_2 & 0 & 0 & (1 - p_c)(1 - p_d) \end{pmatrix},$$
(5)
$$\begin{pmatrix} (1 - C_1)(1 - C_2) & p_d & p_d & p_d \\ C_1(1 - C_2) & 1 & p_d & p_d & p_d \\ C_1(1 - C_2) & 1 & p_d & p_d & p_d \end{pmatrix}$$

$$\mathbf{A}_{\mathbf{x}}^{(T)} = \begin{pmatrix} C_1(1-C_2) & 1-p_d & 0 & p_c(1-p_d) \\ C_2(1-C_1) & 0 & (1-C_1)(1-p_d) & 0 \\ C_1C_2 & 0 & C_1(1-p_d) & (1-p_c)(1-p_d) \end{pmatrix}.$$
(6)

The properties of the PO version of these models have been investigated by Caswell and Cohen (1991b). In all three models, the persistence of the losing competitor, and hence local species diversity, is maximized at intermediate disturbance frequencies. At low disturbance frequencies, the losing competitor S_2 cannot



Figure 1. Transition graphs for the *facilitation* (top), *inhibition* (middle) and *toler*ance (bottom) models of competition. States as defined by equation (3). Parameters: p_d = probability of disturbance, p_c = probability of competitive exclusion, C_i = probability of colonization by species *i*, as given by equation (1).



Figure 2. A three-dimensional plot showing the development of a simulation of the facilitation model. Time proceeds from left to right; each vertical slice represents the landscape at one instant in time. Parameter values: $p_c = p_d = 0.1$, $d_1 = d_2 = 2$. Colors: white = empty, blue = S_1 , yellow = S_2 , red = both.

Figure 3. A three-dimensional plot of the development of the inhibition model. Parameters and colors as in Fig. 2.

Figure 4. A three-dimensional plot of the development of the tolerance model. Parameters and colors as in Fig. 2.

Figure 5. Equilibrium frequencies (\hat{f}_2) of the losing competitor (S_2) in the facilitation model, as a function of the disturbance rate p_d , the competitive exclusion rate p_c , and the dispersal coefficients d_1 and d_2 . Solid line = PO model, open circles = CA model. Baseline parameter values: $p_d = p_c = 0.1$, $d_1 = d_2 = 2$.

find enough empty patches to colonize. At high enough disturbance frequencies, both species are driven to extinction. At intermediate disturbance frequencies, both species may co-occur. Beta diversity (landscape heterogeneity) is also maximized at intermediate disturbance levels.

4. COMPARING CA AND PO MODELS FOR COMPETITION

We want to compare the spatially explicit CA and the spatially averaged PO versions of the three competition models. We will examine equilibrium frequencies, transient dynamics, conditions for coexistence, and spatial autocorrelation patterns.

The CA models were simulated on a 256×256 grid with periodic boundary conditions. The neighborhood of a cell was defined as the eight immediately adjacent cells (the 'Moore neighborhood'). Patches were updated in parallel; i.e., new patch states were computed for all patches in the landscape and the entire landscape was updated simultaneously. The simulations were stochastic. At each step of the simulation, neighborhood frequencies of both species were computed for each patch. A new patch state was drawn at random from the distribution given by the column

Figure 6. Equilibrium frequencies (\hat{f}_2) of the losing competitor (S_2) in the inhibition model, as a function of the disturbance rate p_d , the competitive exclusion rate p_c , and the dispersal coefficients d_1 and d_2 . Solid line = PO model, open circles = CA model. Baseline parameter values: $p_d = p_c = 0.1$, $d_1 = d_2 = 2$.

of the transition matrix [equations (4)–(6)] corresponding to the current patch state. The program was written in Pascal and run on Macintosh computers.

Typical results of starting the models in a largely empty landscape with a few scattered cells containing each of the two species are shown in Figs 2–4. The facilitation model produces a landscape that is rapidly filled by the losing competitor S_2 . Only then does the winning species begin to spread through the landscape, producing large regions where the two species are intermingled. Eventually, the entire landscape becomes an apparently random mixture of cells in all four states.

In the inhibition model, both species begin to spread through the largely empty landscape, producing large monospecific clumps of patches. These clumps persist for a long time, because the winning species S_1 can invade territory controlled by S_2 only when disturbance opens up a cell along the boundary of two adjacent patches. Thus, the landscape heterogeneity produced by the initial distribution decays more slowly than in either of the other two models.

In the tolerance model, the two species begin by spreading across the landscape. As they collide, the winning species S_1 invades the cells occupied by S_2 and rapidly produces an apparently homogeneous landscape.

Figure 7. Equilibrium frequencies (\hat{f}_2) of the losing competitor (S_2) in the inhibition model, as a function of the disturbance rate p_d , the competitive exclusion rate p_c , and the dispersal coefficients d_1 and d_2 . Solid line = PO model, open circles = CA model. Baseline parameter values: $p_d = p_c = 0.1$, $d_1 = d_2 = 2$.

4.1. *Equilibrium frequencies.* Since Hutchinson (1951) introduced the concept of 'fugitive' species, attention has focused on the regional persistence of species that are doomed to local exclusion. In our models, S_2 is a fugitive species. It is eventually eliminated by S_1 from any patch where they co-occur. In the PO models for facilitation and tolerance, this implies certain regional extinction in the absence of disturbance. Thus, in these models, regional persistence of S_2 depends on disturbance and re-colonization of empty patches.

The inhibition PO model has two absorbing states in the absence of disturbance (x_2 and x_3), so eventually only one species will remain in any patch. However, because neither species can invade a patch occupied by the other, regional persistence of S_2 is possible in the absence of disturbance, as long as the initial conditions include some patches in state x_3 . Again, the equilibrium regional abundance of S_2 depends on disturbance and re-colonization.

There is no *a priori* guarantee that the CA model will exhibit similar equilibrium frequencies or conditions for coexistence, because of the spatial variance in local state frequencies in the CA model. To compare the two types of models, we calculated equilibrium frequencies \hat{f}_2 of the fugitive species S_2 as a function of disturbance frequency, competitive exclusion rate, and the dispersal coefficients of the two species.

Figure 8. Transient dynamics for the PO (upper) and CA (lower) versions of the facilitation model. Parameter values: $p_d = p_c = 0.01$, $d_1 = d_2 = 2$.

Equilibria for the PO model were found numerically by solving for $\hat{\mathbf{x}}$ satisfying

$$\hat{\mathbf{x}} = \mathbf{A}_{\hat{x}}\hat{\mathbf{x}}.\tag{7}$$

Equilibria for the CA models were obtained from simulations. To decide when a simulation had reached equilibrium, we calculated a 100-point running average of the state frequencies. We calculated a linear regression of these running means against time for the most recent 400 iterations. When the sum of the absolute values of the slopes was less than 1.5×10^{-5} (i.e., the average frequency changes, over 400 time steps, were less than a single patch), we concluded that there was no consistent change in frequencies. The simulation was continued for 100 iterations and the equilibrium state frequencies calculated as the mean of the frequencies over the last 100 interactions. All equilibrium calculations began with initial conditions consisting of equal frequencies of the four states randomly distributed across the landscape.

Figures 5–7 show the equilibrium frequencies of S_2 under the three models, as functions of p_d , p_c , d_1 and d_2 . In each case, the parameters are varied around a baseline set of values $p_d = p_c = 0.1$ and $d_1 = d_2 = 2$. Similar patterns were found for other parameter values.

Figure 9. Transient dynamics for the PO (upper) and CA (lower) versions of the inhibition model. Parameter values: $p_d = p_c = 0.01$, $d_1 = d_2 = 3$.

In all three models, the frequency \hat{f}_2 of the losing competitor is maximized at intermediate disturbance frequencies, and declines as competitive exclusion becomes more rapid. It also declines as the dispersal abilities of the winning species S_1 improve, and increases with increases in d_2 .

The facilitation model differs from the inhibition and tolerance models, because in this model S_1 actually depends on S_2 for the ability to colonize new patches. Thus, S_2 can withstand lower disturbance rates and higher rates of competitive exclusion and dispersal of the winning species than in the other two models.

The results of the CA and PO models are qualitatively similar. The agreement is particularly close in the facilitation model. In the inhibition and tolerance models, \hat{f}_2 is generally lower in the CA than in the PO models. This translates into more stringent thresholds for persistence of S_2 (i.e., necessary conditions for $\hat{f}_2 > 0$). This pattern is investigated in more detail below. However, the explicit spatial arrangement of patches clearly has no qualitative effect on the equilibrium frequency of the losing competitor in any of these models.

4.2. *Approach to equilibrium.* Because of the finite speed of colonization in an explicitly spatial model, transient dynamics persist longer in the CA than in the

Figure 10. Transient dynamics for the PO (upper) and CA (lower) versions of the tolerance model. Parameter values: $p_d = p_c = 0.01$, $d_1 = d_2 = 2$.

PO models (Figs 8–10). Initial frequencies for both species were set at 0.001, randomly and independently distributed over the landscape (so that the initial frequency of patches with both species was about 1.0×10^{-6}). Results are shown for $p_d = p_c = 0.01$ and $d_1 = d_2 = 2$ (except for the inhibition model, where $d_1 = d_2 = 3$). These values were chosen to assure that S_2 would persist in both the PO and CA models (see Section 4.3). We found similar results for other parameter values.

In both the CA and PO models, the approach to equilibrium is smooth and nonoscillatory; it is much slower in the CA model than in the PO model. In the PO model, each patch type experiences the overall frequency of each of the other patch types. In the CA model, a patch experiences only its neighbors frequency. Thus, it takes longer for, e.g., a patch occupied by S_1 in the facilitation model to *find* and invade one of the relatively rare patches occupied by S_2 . The result is the longer persistence of transient conditions.

4.3. *Persistence and coexistence.* In spite of their ease of construction and simulation, analytical stability results for these PO models are difficult to come by. We know that the *single-species* versions admit at most a single nonzero equilibrium

Figure 11. Critical dispersal coefficients for persistence in the PO and CA models, for systems with slow ($p_d = p_c = 0.01$; left column) and fast ($p_d = p_c = 0.1$; right column) rates of dispersal and disturbance. In each graph, the asymptotically horizontal solid lines plot the critical value $d_2 = \Phi_2(d_1)$ for persistence of S_2 in the PO model. The open circles show the results for the CA model. The asymptotically vertical solid lines plot the critical value $d_1 = \Phi_1(d_2)$ for persistence of S_1 in the PO model. The filled circles show the results for the CA model.

frequency, which is globally stable (from all nonzero initial conditions) if it exists. For a slight generalization of the tolerance model, Barradas and Cohen (1994) and Barradas *et al.* (1996) have proven that in the two-species model possesses at most a single unique interior fixed point, and that this fixed point is globally stable (from all initial conditions with both species present) when it exists. Based on extensive numerical investigations, we believe (though we cannot prove) that the the facilitation, inhibition and tolerance models under investigation here have the same global stability properties.

Stability conditions for the PO models can be conveniently displayed in terms of the dispersal coefficients d_i . Consider the losing species, S_2 . For a given set of parameters (disturbance rate, exclusion rate, and dispersal of the winning species) there is a critical value of d_2 below which S_2 is unable to persist. Similarly, for given values of the other parameters, there is a critical value of the dispersal coefficient d_1 below which S_1 is unable to persist. Plotting these critical values in d_1-d_2 parameter space permits us to identify combinations that permit persistence of S_1 , S_2 , both, and neither.

For the PO models, the stability of the equilibrium can be determined by examining the invasibility of boundary equilibria[†]. We look for conditions under which each species is able to invade a landscape on which the other species has reached its equilibrium.

Invasibility depends on the values of the dispersal coefficients d_i . For fixed values of p_d and p_c , there exist two curves:

$$d_2 = \Phi_2(d_1),\tag{8}$$

$$d_1 = \Phi_1(d_2). \tag{9}$$

Species S_i can invade an equilibrium of the other species if and only if $d_i > \Phi_i$. That is, the functions Φ_i define the critical dispersal coefficients required for invasion. The intersection of the critical dispersal functions Φ_i divides the d_1-d_2 parameter space into four regions, corresponding to extinction of both species, persistence of one or the other species alone, and coexistence of both species.

To find Φ_2 for the PO model, we specify d_1 , p_d , and p_c , and solve numerically for the equilibrium frequency state $\hat{\mathbf{x}} = \begin{bmatrix} \hat{x}_1 & \hat{x}_2 & 0 & 0 \end{bmatrix}^T$. We calculate the Jacobian matrix for the model in the neighborhood of $\hat{\mathbf{x}}$. The submatrix describing x_3 and x_4 (the states involving the invading species) near this equilibrium is independent of the rest of the matrix, but depends on d_2 (and, of course, on the other parameters). We then solve numerically for the value of d_2 at which the dominant eigenvalue of this

[†]We are not certain that invasibility guarantees coexistence in these models. Such proofs are nontrivial (Hutson and Schmitt, 1992), and are not available for the models we are studying here. We know that invasibility implies coexistence in the models of Barradas and Cohen (1994) and Barradas *et al.* (1996), which are similar to the ones we examine here. Our numerical results also suggest that invasibility and coexistence go hand-in-hand.

submatrix equals 1; this value is the critical value of d_2 that makes the boundary equilibrium unstable and permits invasion of S_2 . Repeating the process for a range of values of d_1 gives the function $\Phi_2(d_1)$. Calculation of Φ_1 proceeds in a similar fashion.

No such simple analytic criterion is available for the CA models. Instead, we used repeated simulations to estimate the critical dispersal coefficient as the minimum value of d_i for which $\hat{f}_i > 0$. While it is possible in CA models for the equilibrium to depend on the initial configuration of patch states, we have never found such dependence in our simulations, and for this analysis we used initial conditions in which the two species were distributed independently with equal expected frequencies (0.5).

4.3.1. Dispersal and coexistence. The results are shown in Fig. 11. For each model, we examined a system with slow competition and low disturbance rates $(p_c = p_d = 0.01)$ and one with rapid competition and high disturbance rates $(p_c = p_c = 0.1)$. In both systems, an average of one disturbance occurs during the average time required for competitive exclusion.

In the facilitation model, coexistence is easy in both the PO and CA models. The winning species S_1 cannot drive S_2 to extinction, because as S_2 declines, sites available for colonization by S_1 become rarer and rarer. Thus, in both fast and slow communities, critical dispersal coefficients are determined by the necessity of dispersing fast enough to counteract losses due to disturbance.

In the inhibition model, the critical dispersal coefficients are higher than in the facilitation model. The critical values for the CA model are similar to those for the PO model. In slow communities, persistence is slightly easier in the CA than in the PO model. In faster communities, the persistence of S_1 is the same in the PO and CA models, but persistence of S_2 is slightly more difficult (requiring a slightly higher value of d_2). However, the differences are not dramatic.

Finally, in the tolerance model, there is good agreement between the PO and CA models (Fig. 11). Again, in the communities with slow competition, it is slightly easier for S_2 to persist in the CA model than in the PO model; the reverse is true in the communities with fast competition. The criteria for persistence of S_1 are the same for the PO and CA models.

We conjecture that these differences in persistence reflect, at least in part, the balance between disturbance, colonization, and competitive exclusion. Empty patches are harder to find in the CA model than in the PO model. The more quickly competition operates, the more critical the ability to find empty patches becomes. This does not, however, explain why the critical dispersal rates for S_2 are actually lower in the tolerance CA model when competition is slow.

4.4. *Spatial pattern.* Patch-occupancy models include exactly two spatial scales: the individual patch and the entire landscape. This is, of course, a major improvement over models which make no distinctions between different scales, and PO models have been studied as spatial models for precisely this reason. CA models,

Figure 12. Spatial association for the facilitation model after 20, 60, and 200 iterations. The left figure shows the landscape, with colors corresponding to patch states (white = 1, light grey = 2, dark grey = 3, black = 4). The right figure shows the spatial association index τ as a function of distance, for a random sample of 1000 pairs of cells. The horizontal dotted line is the critical value of τ that is just significantly different from zero at the 0.05 level. Parameter values: $p_d = p_c = 0.01$, $d_1 = d_2 = 4$.

in contrast, can include and generate spatial pattern on any scale between the single patch and the whole landscape.

Spatial autocorrelation is one way to quantify the scale of spatial pattern. It uses a correlation coefficient to measure the strength of the relationship between values at randomly selected pairs of points separated by a given distance. Ordinary correlation methods, however, are not applicable to our CA models, because they produce

Figure 13. Spatial association for the inhibition model after 20 and 500 iterations, and at equilibrium (several thousand iterations). The left figure shows the landscape (coded as in Fig. 12); the right figure shows the spatial association index τ as a function of distance, for a random sample of 1000 pairs of cells. The horizontal dotted line is the critical value of τ that is just significantly different from zero at the 0.05 level. Parameter values: $p_d = p_c = 0.01$, $d_1 = d_2 = 4$.

nominal rather than interval or ordinal output. Relationships among nominal variables can be quantified by association coefficients calculated from a contingency table [e.g., Liebetrau (1983)]. Therefore, we developed a spatial version of the Goodman–Kruskal τ (Goodman and Kruskal, 1954) association coefficient. For each distance δ , we randomly sampled 2000 pairs of points separated by δ . From these points we constructed a 4 × 4 contingency table relating the states of the pairs of patches. Let n_{ij} denote the frequency in the (i, j) cell of this table, and let n_{i+} ,

Figure 14. Spatial association for the tolerance model after 20, 100, and 500 iterations. The left figure shows the landscape (coded as in Fig. 12); the right figure shows the spatial association index τ as a function of distance, for a random sample of 1000 pairs of cells. The horizontal dotted line is the critical value of τ that is just significantly different from zero at the .05 level. Parameter values: $p_d = p_c = 0.01$, $d_1 = d_2 = 4$.

 n_{+j} , and *n* denote the row sums, column sums, and overall total, respectively. Let *r* and *c* denote the number of rows and columns in the table (r = c = 4 in our case). Then the spatial association coefficient $\tau(\delta)$ was estimated as:

$$\hat{\tau}(\delta) = \frac{n \sum_{j=1}^{c} \sum_{i=1}^{r} \frac{n_{ij}^2}{n_{+j}} - \sum_{i=1}^{r} n_{i+}^2}{n^2 - \sum_{i=1}^{r} n_{i+}^2}.$$
(10)

Under the null hypothesis $\tau(\delta) = 0$, the statistic,

$$U^{2} = (n-1)(r-1)\hat{\tau}(\delta), \qquad (11)$$

Figure 15. The correlation length (in cells) as a function of time for the simulations shown in Figs 12–14. Correlation length is defined as the distance at which the spatial association τ drops below 0.01 for the first time.

has a χ^2 distribution with (r - 1)(c - 1) degrees of freedom (Light and Margolin, 1971).

When $\tau(\delta) = 1$, the state at one location completely determines the state at a distance δ . If the two states are statistically independent, $\tau(\delta) = 0$. Between these two extremes, τ measures the information that the state of one patch provides about the state of another. Light and Margolin (1971) showed that τ is the discrete equivalent of the coefficient of determination R^2 ; it measures the proportion of the variance in the state of a distant patch explained by the state of the local patch. Thus, $\tau(\delta)$ is equivalent to the square of a spatial autocorrelation, or the complement of the semivariance.

Figures 12–14 show the creation and eventual decay of spatial pattern, starting from an initial condition of a few patches containing S_1 or S_2 scattered at random in an empty landscape. Initially, all three models generate patchiness as the initial populations spread over the landscape. Eventually, however, the pattern decays to a random arrangement, with a correlation length of zero. Knowledge of the state of a patch provides no information on the state of an adjacent patch.

The three competition models differ in the rate of decay of the transient spatial pattern (Fig. 15). Pattern decay occurs most rapidly in the facilitation model, more slowly in the tolerance model, and extremely slowly in the inhibition model, because the latter model produces patches occupied by one or the other species. These patches can be invaded only along the boundary between two different species. The transient patchiness shown here may be as important as possible permanent patchiness. A landscape colonized, after a large-scale disturbance, by species that follow the inhibition model is likely to display large-scale patchiness for a very long time.

5. **DISCUSSION**

The mean-field PO competition models provide a good approximation to the corresponding spatially explicit CA model.

In particular:

- (a) Equilibrium species frequencies at the landscape level are predicted very closely by the PO model; except when either dispersal or disturbance rates are low and persistence of the species is difficult.
- (b) In both the PO and CA models, coexistence can be mediated by disturbance. Landscape-level diversity is maximized at intermediate disturbance levels. These results do not require that the inferior competitor has an advantage in dispersal (Figs 5–7), provided that p_d is high enough and p_c is small enough; i.e., as long as disturbance is sufficiently rapid compared to the time scale of transient *within-patch* coexistence.

Of course, a dispersal advantage obviously helps, since the equilibrium frequency of the losing competitor is an increasing function of its dispersal coefficient. Nor is this to say that trade-offs between competitive ability and dispersal do not exist. Such trade-offs influence the potential for extinction resulting from habitat loss (Nee and May, 1992; Tilman and Kareiva, 1997).

- (c) There is no consistent difference between the PO and CA models in the conditions required for coexistence. If dispersal coefficients are too low, the species is driven extinct by the disturbance process. If both dispersal coefficients are high enough, both species coexist. There are regions of the parameter space in which each species may persist alone, if its competitor's dispersal coefficient is too low. The critical dispersal coefficients are similar in the two types of models.
- (d) Because of the finite speed of dispersal in the CA model, the approach to equilibrium is slower than in the PO model.

Spatially explicit models admit the possibility of spatial pattern formation, but none of the models examined here produced persistent spatial pattern. The spatial correlation length decays to zero as time increases. The three models differ in the rate of decay of transient spatial pattern. The inhibition model yields very longlasting transient patchiness, because regions occupied by one species can be invaded by the other only across their mutual boundary.

Transient does not imply trivial. A landscape colonized by inhibition competitors following a large-scale disturbance is likely to exhibit patchy distributions for a long time. This is particularly likely to be true of species that exhibit interference competition for space, in which the priority effects that give rise to the inhibition model are likely to occur.

Other comparisons of implicitly and explicitly spatial models have produced different results. Durrett and Levin (1994a, b) compared the equilibrium frequencies of spatial and nonspatial models for hawk–dove interactions with different payoff matrices. They found that qualitative differences between explicitly (reaction– diffusion and interacting particle systems) and implicitly (ordinary differential equation and patch occupancy) spatial models depended on the nature of the pay-off matrix of the the interaction. All models produced similar results for mutualistic pay-off matrices. For competitive interactions, spatial and nonspatial models did not agree. The outcome was dependent on the initial conditions for the nonspatial models, but not for the spatially explicit versions. When hawks always reproduced faster than doves, but pure hawks died out, there was no difference between the spatial and nonspatial models, however, the deterministic (reaction–diffusion and ordinary differential equations) and stochastic (patch occupancy and interacting particle systems) versions differed.

Dytham (1994) compared a spatially explicit CA model of competition to the nonspatial version of Nee and May (1992). These models are similar to our tolerance models, but with instantaneous exclusion of S_2 by S_1 when they simultaneously colonize a patch. Dytham found that the outcome of competition, as habitable area declines, differed between the spatial and nonspatial formulations. In particular, the persistence of the superior competitor with inferior dispersal was less sensitive to habitat loss in the spatially explicit version. However, Moilanen and Hanski (1995) have shown that a more biologically realistic spatial version of Nee and May's (1992) model produces results that do not differ greatly from the nonspatial results.

Thus far, the limited number of direct comparisons between spatial and nonspatial competition models make it difficult to draw any general conclusions. It seems that the effect of explicit spatial structure depends on the nature of the interaction.

In general, explicitly spatial models are expected to differ from implicitly spatial models because of: (i) the formation of spatial pattern, which changes the local interactions; and (ii) increased temporal and spatial variance due to local interactions. These two reasons are not independent; spatial pattern increases spatial variance in neighborhood frequencies. We have found that interspecific competition does not generate spatial pattern. We have also found, in results not shown here, that the temporal variance in species frequencies in these models is no greater than what would be expected on the basis of random sampling of 65 536 patches from the spatially implicit PO model. Thus, neither of the two conditions that would lead to a difference between the PO and CA models are satisfied for these models.

This suggests that two-species competition models, regardless of the mechanism, may be too simple to produce interesting spatial phenomena. In a review of spatial models (not cellular automata), Kareiva (1990) notes that two-species competition models cannot produce diffusive instabilities. Models of predator–prey interactions are known to be more prone to produce spatial patterns. We suppose that more complicated food web models might also do so. Intransitive competitive networks involving three or more species have, in PO models, effects on diversity similar to predator–prey interactions (Caswell and Cohen, 1991b). The CA version of such models would be interesting to examine, because they might produce enough spatial heterogeneity to differ from their spatially implicit counterparts.

Spatial pattern can, of course, be created by environmental heterogeneity. Largescale disturbance, for example, that produces large continguous blocks of empty patches, can produce spatial autocorrelation on the scale of the disturbance size. Spatial pattern may also be more common, or more long-lasting, when parameters are close to their critical values for persistence.

Finally, we note that there is an important distinction between ecological CA in which cells represent individual organisms [e.g., Inghe (1989), Iwasa *et al.* (1991), Wilson *et al.* (1993)] and those, such as the present paper and Schwinning and Parsons (1996), in which cells represent spatial patches that may be occupied by populations of one or more species. Individual and patch CA models obviously differ in the scales on which they describe biological processes, but they also differ in the ways in which biological processes relate to the CA framework. In individual CA models, the influence of a cell on its neighbors represents the processes of individual movement or growth, or ecological interactions such as competition or predation between adjacent individuals. In patch CA, cells influence each other through the processes of dispersal and colonization, but interspecific interactions take place within a cell.

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