



The effect of initial pattern on competitive exclusion

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Abstract: We used cellular automata models to investigate the effect of initial pattern geometry on competition. We measured the average proportion of sites with foreign neighbours to track interspecific segregation during pattern development. Our simulation results show that intraspecific aggregation can considerably slow down the extinction of the weaker competitor. A series of experiments was performed to estimate the expected time to extinction for the weaker species. The perimeter-to-area ratio of the initial configuration proved to be an adequate determinant of expected time-to-extinction. Furthermore, we demonstrated that the degree of aggregation is closely related to the local density dependence of the colonization functions.

Abbreviations: CA—Cellular Automata; IPS—Interacting Particle System; PDE—Partial Differential Equation.

Introduction

Spatial competition and species coexistence are among of the most fundamental issues in ecology. Although environmental heterogeneity offers an obvious explanation of species diversity, a large body of theory has been developed to demonstrate the possibility of species coexistence in physically homogeneous environment (Tilman and Kareiva 1997, Dieckman et al. 2000, Neuhauser 2001 and Silvertown 2004). Various spatially implicit and explicit models have been developed to investigate competition in homogeneous but subdivided habitats and to find out conditions for the coexistence of two or more species (Skellam 1951, Tilman 1994, Durrett and Levin 1998, Holmes and Wilson 1998, Doncaster et al. 2003, Amarasekare 2003). There is no intrinsic difference in homogeneous space so that, according to niche theory, coexistence requires some form of niche partitioning. This can occur in two basic ways (Amarasekare 2003): The first one is via life history trade-offs (Kneitel and Chase 2004) among them competition colonization trade-off has been investigated in most details with spatial models (Tilman 1994, Yu and Wilson 2001). The second setting for coexistence requires that intraspecific and interspecific competition act at different spatial scales (Neuhauser 1998, Murrell and Law 2003).

Spatially explicit models are reliable techniques to describe not only the overall behaviour of the system, but this approach is suitable for tracking pattern formation as well. Since plants and other sessile organisms generally show aggregated patterns and individuals interact mostly with their neighbours, intraspecific and interspecific competition within the neighbourhood highly determines the development of the community through pattern formation. Although many models handle space explicitly, only a few of them deal with the effect of spatial pattern on the interaction between species. Investigations of pattern development in deterministic cellular automata models (Molofsky 1994, Wolfram 2002) have proved that simple rules can lead to complex dynamics and initial conditions may be critical in determining the final pattern. For stochastic cellular automaton models, Molofsky et al. (1999, 2002) have found that the strength of frequency dependence is a considerable determinant of generated patterns. Using other types of spatial models (such as interacting particle systems [IPS] and partial differential equations) Gandhi et al. (1998, 1999) experienced sensitivity of time to extinction on the initial density of competing species.

Several authors investigated patterns of habitat destruction. They compared random, clustered and linear (Dytham 1995), checkerboard (Tilman and Lehman

1997) and other patterns (Neuhauser 1998) and found that in a community of hierarchically ordered competing species the order in which the species go extinct could be altered by the spatial geometry of habitat destruction.

The relative location of competing species can also modify the outcome of competition among several species (Silvertown et al. 1992, Silvertown and Wilson 2000). Recently, Korniss and Caraco (2005) have demonstrated that invasion success also depends on the initial spatial geometry.

Cluster formation can arise as a result of spatial dynamics (Murray 1989, Bolker and Pacala 1999, Molofsky et al. 2002), but it has manifold impact on the development of the system via increasing intraspecific competition relative to intraspecific competition, and restricting interspecific interactions to cluster borders (Chesson and Neuhauser 2002). Most models contain some additional factors in addition to neighbourhood competition such as life history trade-offs, different interaction neighbourhoods, density dependent mortality, etc. Therefore, the underlying reasons of aggregation and its effects on the dynamics of the system are scarcely perceivable.

In this paper, we focus on the spatial pattern of two competing species, and study the effect of the initial species pattern on the persistence of the competing populations on a relatively large timescale. Our models originate from a two species version of the Levins' model (Levins 1969), described by the following ordinary differential equations,

$$\begin{aligned} \frac{dp_1}{dt} &= c_1 p_1 (1 - p_1 - p_2) + v_1 p_1 p_2 - v_2 p_1 p_2 - e_1 p_1 \\ \frac{dp_2}{dt} &= c_2 p_2 (1 - p_1 - p_2) + v_1 p_1 p_2 - v_2 p_1 p_2 - e_2 p_2 \end{aligned} \quad (1)$$

The fraction of patches occupied by species 1 (p_1) or by species 2 (p_2) increases with the colonization of empty patches (i.e., patches that are currently not colonized by neither species 1 nor species 2) proportional to colonization rate c_1 and c_2 , respectively. Patch occupancy can further be increased by overcolonizing patches from the other species and decreased by losing patches through overcolonization by the other species. The overcolonization rate v_1 (v_2) describes how species 1 (2) can gain patches from species 2 (1). Independently of the presence of the other species, the species 1 and 2 experience local extinction proportional to extinction rate e_1 and e_2 , respectively.

By substituting $v_1 = 0$ and $v_2 = c_2$, we obtain the Nee-May model (1992) of asymmetric competition of a superior competitor (species 1) and an inferior competitor

(species 2). In this case, species 2 has no influence on the dynamics of species 1, but the superior one can overcolonize patches occupied by the inferior competitor. Stable coexistence is possible if the inferior species is a better disperser. Tilman (1994) showed that an infinite amount of hierarchically ordered species can coexist. In accordance with the competitive exclusion principle (Gause 1934), it is easy to prove that the system has no equilibrium of coexistence if $v_1 = v_2 = 0$, i.e., overcolonization is excluded (Neuhauser 1992).

In order to concentrate on the interdependence of local competition and spatial aggregation, we use very simple cellular automata (von Neumann 1966, Burks 1970, Gaylord and Nishidate 1996, Czárán 1998, Wolfram 1986, 2002, Kun and Oborny 2003, Itzész et al. 2005) models, which can be considered as spatially explicit analogues of the system described by eq. (1). To achieve our goals, we employ two families of cellular automata models. One of them describes strict dominance competition between the two species, i.e., only one of the species can overcolonize the other, similarly to the model of Nee and May (1992). The second one supposes preemptive competition (only empty sites can be colonized).

We have studied these models in respect to coexistence, testing it for robustness on initial density and initial configuration over a wide range of the parameter space of the model and different classes of initial configurations (Rácz and Karsai 2003). In this paper, reasons of clumping are investigated by measuring the degree of aggregation during pattern development. We reveal that overcolonization has a disintegrating effect strong enough to prevent cluster formation. On the other hand, in systems with preemptive competition local density dependence of colonization proved to be the primary cause of clumping. A series of simulations were performed to measure time to extinction of the declining species starting from several initial conditions differing only in spatial geometry. The importance of perimeter-to-area ratio of the initial pattern in the determination of extinction time was also investigated.

Methods

A general cellular automaton model of competition between two species

Cellular automata are discrete time models defined in discrete space (so-called cell space). Each cell can be in one of the finite number of predefined states. The change of the state of a given cell from a time step to the next depends on the actual state of the cell itself and the states

Table 1. Abbreviations and notations of functions and parameters used.

State of the site	
0	empty
1	occupied by species 1
2	occupied by species 2
Functions	
r_i	overcolonization function of species i
c_i	colonization function of species i
w_i	seedling competition function of species i
Parameters	
e_i	local extinction probability of species i
N_i	number of i -type neighbours in a given cells neighbourhood

of neighbouring cells, as specified by the transition (or update) function.

As cell space of the automaton, we consider a finite, sufficiently large square grid with periodic boundary conditions (i.e., torus topology), representing a landscape with habitable patches. Moore neighbourhood with eight adjacent neighbours (north, northeast, east, southeast, south, southwest, west and northwest) is applied. Two species are competing for space; hence the state of each cell can be empty (0) or occupied by the first (1) or the second (2) species, respectively. Table 1 summarises the parameters of the model.

Transition rules are the following (Table 2). Occupied patches can become vacant by local extinction (assumed to be neighbour-independent) described by the extinction probabilities e_1 and e_2 ; or can be overcolonized by the other species. The probability that a 1-type patch will be replaced by species 2 depends on the number of potential propagule sources (i.e., number of 2-stated cells in the actual cell's neighbourhood). The case for 2-type patches is analogous. Local extinction is considered as a one-time-step process, not an instantaneous action, therefore an empty site cannot be recolonized within one time step.

Empty patches can be colonized by propagula from neighbouring occupied patches. Colonisers (for example seeds) from each occupied neighbouring patch arrive at the focal patch, but only one individual can occupy it.

If there was only one species (i) in the system, the probability of colonization of an empty site could be described by the function $c_i(N_i)$ of the number of occupied cells in the given empty site's neighbourhood. We refer to this function as the colonization function of species i . If both species are present, a given empty site receives colonizers belonging to both species from its neighbourhood with the probability given by the individual colonization functions.

Table 2. Transition rules of the general cellular automaton model.

Probability of transition from state 1	
to	
0	e_1
2	$(1-e_1) r_2(N_2)$
1	otherwise
Probability of transition from state 2	
to	
0	e_2
1	$(1-e_2) r_1(N_1)$
2	otherwise
Probability of transition from state 0	
to	
0	$(1-c_1(N_1)) (1-c_2(N_2))$
1	$c_1(N_1) (1-c_2(N_2)) + c_1(N_1) c_2(N_2) w_1$
2	$c_2(N_2) (1-c_1(N_1)) + c_1(N_1) c_2(N_2) w_2$

The probabilities of species 1 or species 2 reaching an empty site given that the other species fails are $c_1(N_1)(1-c_2(N_2))$ and $c_2(N_2)(1-c_1(N_1))$, respectively. With probability $c_1(N_1) c_2(N_2)$ both species have viable seedlings on the given habitat patch and seedling competition decides about the winner. Seedling competition is described by the seedling competition weight functions $w_1(N_1, N_2)$ and $w_2(N_1, N_2)$ such that $w_1 + w_2 = 1$. Thus, for example, the probability of successful colonization by species 1 is $c_1(N_1) c_2(N_2) w_1(N_1, N_2)$.

Similarly to classical cellular automata models (von Neumann 1966, Burks 1970) we apply transition rules simultaneously to the entire cell space (synchronous updating), i.e., all sites are updated at the same time.

Model of displacement competition

In the case of displacement competition (also referred to as dominance competition, Amarasekare 2003), species 1 is a superior competitor and is able to over-

Table 3. Transition rules of the displacement competition model.

Probability of transition from state 1	
to	
0	e_1
1	otherwise

Probability of transition from state 2	
to	
0	e_2
1	$(1-e_2) r_1(N_1)$
2	otherwise

Probability of transition from state 0	
to	
0	$(1-c_1(N_1)) (1-c_2(N_2))$
1	$c_1(N_1) (1-c_2(N_2)) + c_1(N_1) c_2(N_2)$
2	$c_2(N_2) (1-c_1(N_1))$

colonize patches owned by the inferior competitor (species 2). Following Nee and May (1992), it is eligible to substitute $r_1 \equiv c_1$ and $r_2 \equiv 0$; $w_1 \equiv 1$ and $w_2 \equiv 0$ in Table 2, since the inferior competitor is not able to win the seedling competition. The transition rule of this model and its associated functions are summarised in Table 3.

Model of preemptive competition

Several invasive alien species have similar or even higher colonization ability than their native competitors, but superior competitors may not be able to overcolonize them (Pimentel et al. 2001). Therefore, a symmetrical model without overcolonization ($r_1 \equiv r_2 \equiv 0$ in Table 2) is also reasonable.

For simplicity, assume that the seedling competition weights are of the forms

$$w_1(N_1, N_2) = \frac{c_1(N_1)}{c_1(N_1) + c_2(N_2)}, \quad (2)$$

$$w_2(N_1, N_2) = \frac{c_2(N_2)}{c_1(N_1) + c_2(N_2)}.$$

This means that good colonizers (seed producers) are good in seedling competition as well. Update rules of the cellular automaton model of preemptive competition are given in Table 4.

Simulations

We compared the models of displacement and preemptive competition by computer simulations applying update functions defined in Tables 3 and 4, respec-

Table 4. Transition rules of the preemptive competition model.

Probability of transition from state 1	
to	
0	e_1
1	otherwise

Probability of transition from state 2	
to	
0	e_2
1	otherwise

Probability of transition from state 0	
to	
0	$(1-c_1(N_1)) (1-c_2(N_2))$
1	$c_1(N_1) (1-c_2(N_2)) + c_1(N_1) c_2(N_2) w_1$
2	$c_2(N_2) (1-c_1(N_1)) + c_1(N_1) c_2(N_2) w_2$

tively. A wide range of parameter values, different classes of colonization functions; and different initial species densities have been tested (see also Rácz and Karsai 2003). For the same initial density, several different initial configurations (Fig. 1) were evaluated.

To study aggregation, we measured the number of cells having foreign neighbours during pattern development. In each time step, we calculated what proportion of cells in state 1 has at least one empty, state 1 and state 2 neighbours, denoted by $A_1(1,0)$, $A_1(1,1)$ and $A_1(1,2)$, respectively. Analogously, we considered $A_2(2,0)$, $A_2(2,1)$ and $A_2(2,2)$, for cells occupied by species 2 and $A_1(0,0)$, $A_1(0,1)$ and $A_1(0,2)$, for empty sites. In a well-mixed cell space, the values of all these measures are close to 1 (unless the density of one of the species is extremely low).

As clumping seemed to help the weaker species to persist, we performed a series of simulations to examine the effect of aggregation. We considered each and every possible chessboard patterned initial configurations in a 128×128 cell space, with each species having the same (i.e., 50-50%) initial density. The patterns are named after the sizes of the smallest uniform areas (Figs 1.b, d, e show examples). In each case, 250 repetitions were made and the simulation run until the weaker species disappeared. Similarly, the corresponding striped initial patterns were investigated as well (Figs 1.e, f). A uniformly distributed random initial configuration was used as a control.

In order to verify the independence of extinction time from initial arrangement, we executed a shorter simulation series for constant colonization functions ($c_i=0.1$ if $N_i > 0$). We compared the most aggregated (64×64 cell

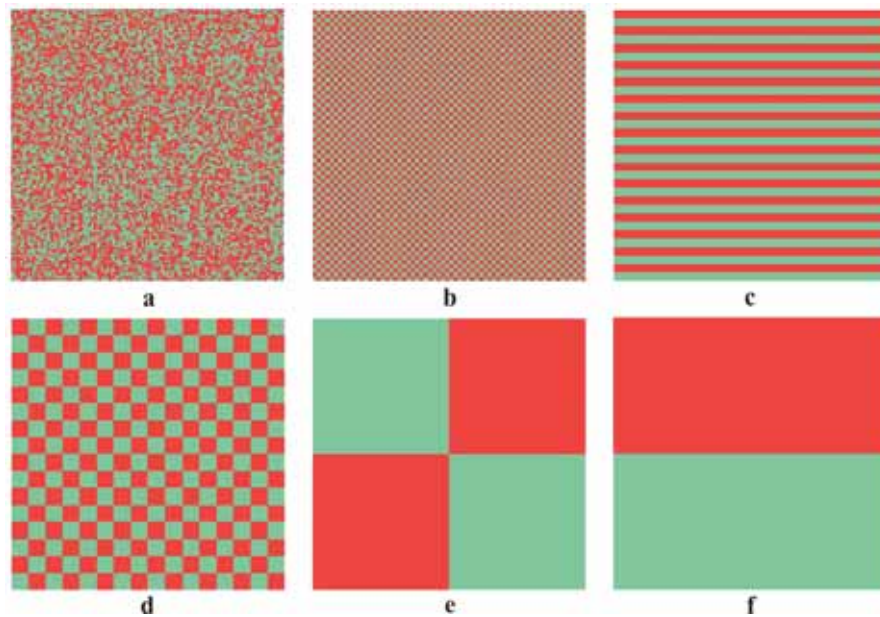


Figure 1. Examples of initial configurations for 50-50% initial species densities on a 128×128 sized cell space. **a)** random, **b)** checkerboard with fields of 2×2 cells, **c)** 4 cell wide stripes, **d)** checkerboard with fields of 8×8 cells, **e)** checkerboard with fields of 64×64 cells, **f)** 64 cell wide stripes. Dark and light grey shades indicate cells occupied by species 1 and 2, respectively.

based; see Fig. 1.e) and a moderately aggregated (8×8 cell based; see Fig. 1.d) checkerboard pattern to the same random initial configuration (Fig. 1.a) as used in the large simulation series. Results of 50 runs from each of the three initial arrangements were analysed.

Results

Spatial pattern dynamics

The overcolonization model is robust with respect to both initial densities and species patterns. In agreement with the corresponding mean field model with overcolonization (1), there exists a domain of coexistence (Rácz and Karsai 2003). Our simulations confirm that overcolonization has an essential role in stabilizing coexistence of two species since it attenuates intraspecific aggregation. To follow aggregation or mixing processes, we calculated the proportion of sites with at least one neighbour occupied by species 1, 2 or being empty in each time step for all the three types during the simulations. From this 3×3 data series for both species, the proportion of sites having foreign neighbours is an indicator of clumping (Fig. 2). Overcolonization increases or keeps the proportion of cells having foreign neighbours high, particularly for the superior competitor (species 1).

In the case of preemptive competition, clumping is determined by the local density dependence of the colonization functions (Figs 2.b and c). If the probability of colonization does not depend on the number of sources (occupied neighbours), i.e., the colonization functions are constant for $N_i > 0$, then the proportion of cells with foreign neighbours does not increase (Fig. 2.b) and intraspecific aggregation disappears (Fig. 3).

Contrarywise, linear local density dependence of the colonization function (in general $c_i(N_i) = \min(k N_i, c_{max})$, where k is a positive constant) is enough to generate clusters indicated by the decreasing proportion of occupied sites with foreign neighbours.

The proportion of sites having conspecific neighbour(s) is always high for both species, because spreading is limited to the neighbourhood. Note that similar results were obtained by applying other types of colonization functions (such as power and logistic) instead of linear colonization function. Comparison of cases presented in Figure 2 suggests that positive density dependence in colonization functions causes intraspecific aggregation, but overcolonization dissolves aggregated patterns.

In contrast to the overcolonization model, the preemptive competition model proved to be sensitive with respect to the initial pattern, the initial proportion of occupied sites and the form of the colonization function. There are colonization functions which can yield different results for different initial patterns with same initial density, i.e., either species 1 or species 2 can win depending on the initial configuration (Rácz and Karsai 2003). This agrees with the lack of coexistence in the equilibrium of the corresponding mean field model (1).

Even though the outcome is independent of the initial arrangement in cases shown in Fig. 2, the initial patterns have considerable influence on the timescale of the dynamics.

Extinction dynamics

In models with biologically more relevant colonization functions, there are remarkable differences with re-

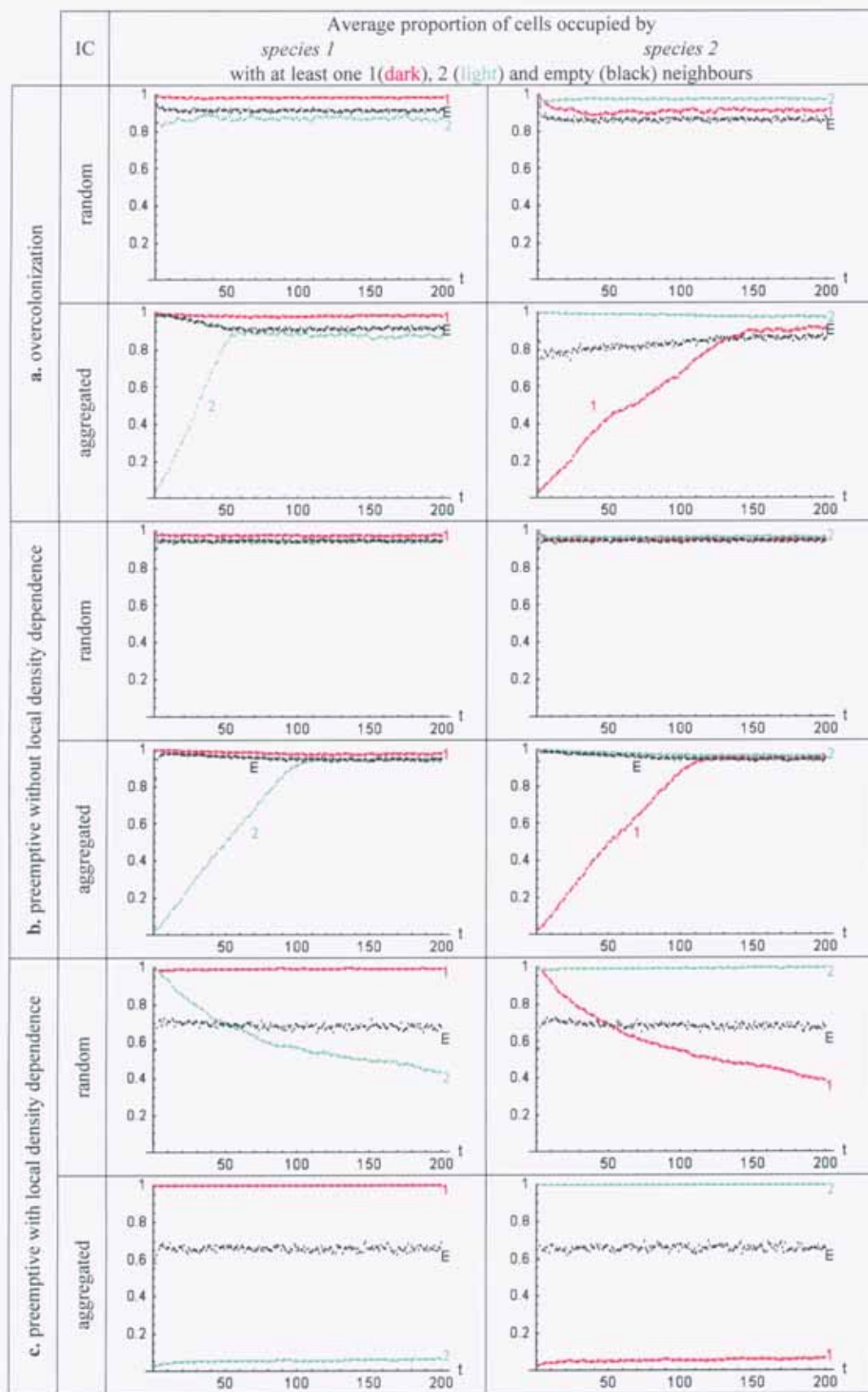


Figure 2. Clumping in the dominance competition model with overcolonization and in two different cases of the model of preemptive competition. Starting from a given random (Fig. 1.a) or ordered (Fig. 1.f) initial configuration, we counted the proportion of i state cells with j state neighbour(s) ($i=1,2$ and $j=1,2$, empty) in each time step of the simulation. **a:** During a run of the dominance competition model, the blending effect of overcolonization is visible in the increasing number of foreign neighbours for both species. The proportion of superior competitors having inferior neighbour(s) increases faster than the proportion of inferior competitors with superior neighbours ($e_1 = 0.4$, $c_1(N_1) = \min(0.1N_1, 0.7)$; $e_2 = 0.2$, $c_2(N_2) = \min(0.7N_2, 1)$). **b:** Preemptive competition (no overcolonization) and no local density dependence ($e_1 = 0.2$, $c_1(0) = 0$ and $c_1(N_1) = 0.3$; $e_2 = 0.3$, $c_2(0) = 0$ and $c_2(N_2) = 0.4$). Interspecific segregation decreases in time. **c:** Preemptive competition. The probability of occupation of an empty site depends on the number of seed sources. Intraspecific aggregation develops unless it is not present initially ($e_1 = 0.1$, $c_1(N_1) = 0.1N_1$; $e_2 = 0.1$, $c_2(N_2) = 0.1N_2$).

spect to the survival time of the weaker species. From an ecological point of view, long-lasting competition can be considered as quasi-coexistence, therefore extinction dynamics can have high importance. The duration of quasi-coexistence (the expected extinction time of the weaker species) proved to depend highly on explicit spatial patterns.

To support the conjecture that initial arrangement has great effect on the extinction time in case of local density dependent colonization, a series of computer simulations of the preemptive competition model was performed. The parameters for local extinction and colonization were fixed ($e_1 = 0.3$, $e_2 = 0.1$, $c_1(N_1) = 0.1N_1$ and $c_2(N_2) = 0.04N_2$). We tested the outcome of competition with different initial configurations with 50–50 percent densities.

We considered all the possible chessboard and striped initial configurations in a space of 128×128 cells. Results from 250–250 repetitions were statistically evaluated (Table 5).

The difference between the mean extinction times of one-cell chessboard pattern and the most aggregated initial pattern exceeds two orders of magnitude. Figure 4 shows the mean extinction times presented in Table 1 as a function of the perimeter-to-area (P/A) ratio of the initial configuration (of both species). All initial configurations can be coupled except for the most distributed (1×1 chessboard) and the most aggregated (64 cell wide stripes). The initial configuration with 2^n cell wide stripes has the same P/A ratio as a $2^{n+1} \times 2^{n+1}$ cell based chessboard pattern in the cell space with torus topology. Pe-

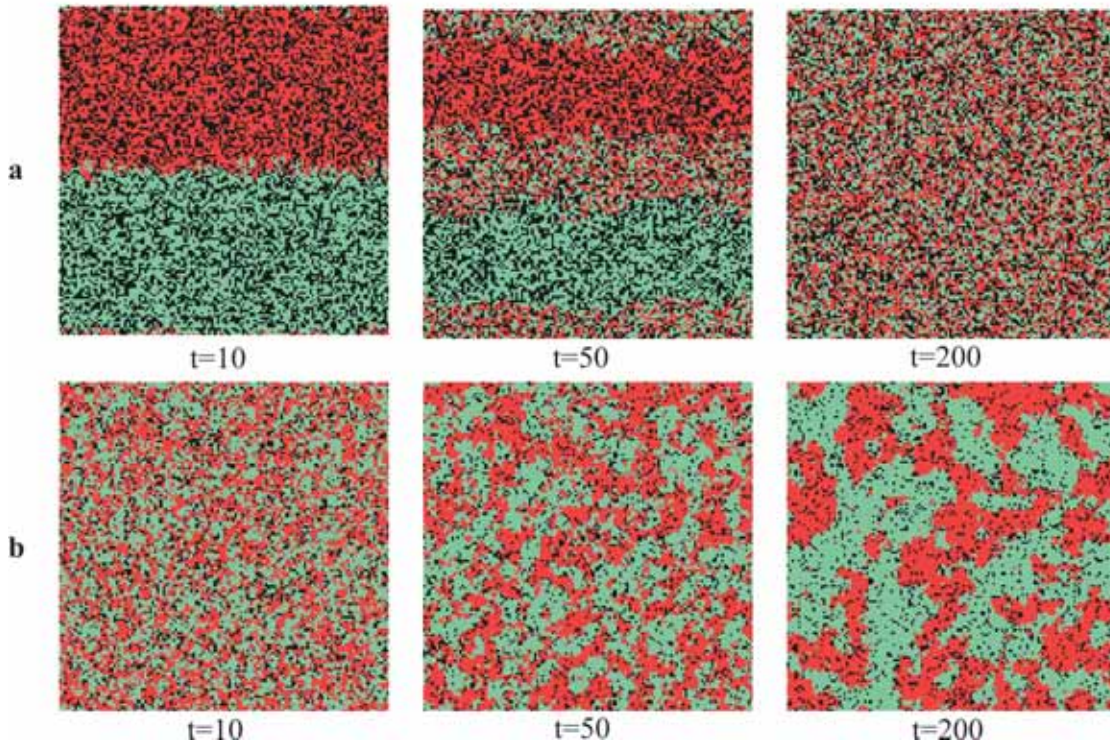
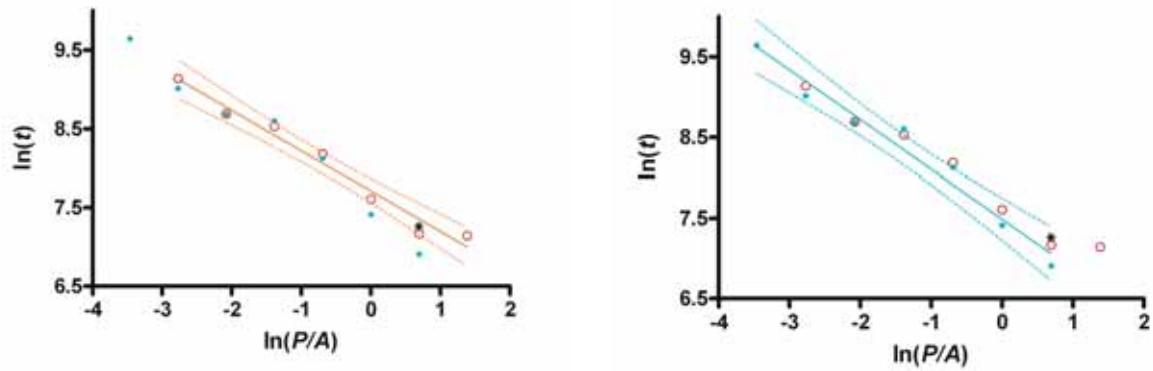


Figure 3. Snapshots from cellular automata simulations of the preemptive competition model. The states of the cells are colour-coded by the following shades: dark grey – occupied by species 1, light grey – species 2, black – empty. **a:** Preemptive competition without density dependence, time step t starting from the aggregated initial configuration Fig. 1.f. (Same run as shown in Figure 2.b lower row). **b:** Preemptive competition with density dependent colonization functions. A random initial configuration evolves to aggregation. (Same run as in Figure 2.c, upper row.)

Table 5. Summary of statistics from the simulation series (250 repetitions for each initial configuration).

Initial configuration	P/A	Extinction time of the weaker species			
		min	max	mean	standard error of mean
<i>random</i>	1.99	663	3905	1427	32
1×1 chessboard	4	615	3270	1263	25
1 cell wide stripes	2	464	4022	999	24
2×2 chessboard	2	619	2954	1296	28
2 cell wide stripes	1	839	4395	1652	38
4×4 chessboard	1	874	5257	2011	47
4 cell wide stripes	0.5	1226	8365	3369	80
8×8 chessboard	0.5	1359	9326	3587	85
8 cell wide stripes	0.25	1948	12665	5434	132
16×16 chessboard	0.25	2015	12380	5053	116
16 cell wide stripes	0.125	2166	13788	5906	121
32×32 chessboard	0.125	2445	19145	5931	126
32 cell wide stripes	0.0625	5199	12721	8200	101
64×64 chessboard	0.0625	5962	15352	9270	118
64 cell wide stripes	0.0313	9776	22204	15396	157

**Figure 4.** Logarithm of the mean extinction time of the weaker species as a function of the logarithm of perimeter-to-area ratio in the initial configuration. Each point represents the mean extinction time derived from 250 runs (Table 1). Items corresponding to checkerboard, striped and the random initial configurations are represented by dots, hollow circles and an asterisk, respectively. **a:** Lines fitted to the checkerboard data set with the corresponding 95% confidence interval. **b:** Lines fitted to the striped data set with the corresponding 95% confidence interval.

rimeter-to-area ratio of the (uniformly distributed) random pattern is very close to the P/A of the 1 cell wide stripes and 2×2 cell based checkerboard (Fig. 1.b). The respective statistics are also remarkably close to each other (Fig. 4).

Further statistical investigations were also performed comparing the line fitted to the seven $(\ln(P/A), \ln(\text{mean}))$ points from the checkerboard data set to the line fitted to the seven corresponding points from the data of striped initial configurations.

The slopes of the lines are significantly nonzero (both cases $p < 0.0001$; for checkerboards $r^2 = 0.9725$ and for striped patterns $r^2 = 0.9658$). Univariate analysis of variance (calculated by SPSS, SPSS Inc.) found no significant difference between the two lines nor in respect to the slopes ($p = 0.137$) or their constant ($p = 0.265$). The single mean value of the series with random initial configuration falls into the 95% confidence band around both of the two lines (Figs 4.a and b).

As a control experiment, a shorter simulation series was performed using density independent colonization functions [with $e_1 = 0.3$, $c_1 = 0.1$ (if $N_1 > 0$) and $e_2 = 0.1$, $c_2 = 0.05$ (if $N_2 > 0$) parameter values]. The mean time to extinction of species 1 was calculated from 50-50 runs starting from the 64 cell wide (Fig. 1f), the 8 cell wide striped configurations and the same random (Fig. 1a) initial configuration used in the original simulation series. The means calculated from the survival time of the weaker species are 2181, 2323, and 2276, respectively. Kruskal-Wallis test shows no significant difference among them ($p = 0.3551$).

Discussion

Dominance competition is an extensively investigated theory of competitive coexistence, especially in the context of habitat destruction. Our results are in agreement with previous findings that overcolonization can lead to coexistence both in spatially implicit and explicit models (Nee and May 1992, Dytham 1994), since the higher competitive ability of the superior species is capable of compensating for a relatively higher colonization ability of the inferior (fugitive, weed-like) species. In several ecosystems, weed-like species can quickly colonize empty patches, though slower but more stable species (superior competitor) overcolonize them sooner or later. As a trivial example, consider competition of annual and perennial plant species (Crawley and May 1987).

Although the role of endogenous spatial heterogeneity is well recognized (Durrett and Levin 1998, Bolker et al. 2003), the spatial arrangement of species and the effect

of initial spatial configuration on competition have seldom been discussed. Silvertown et al. (1992) emphasized that using only random initial configurations in spatial models overestimates the importance of interspecific competition in field communities, where intraspecific aggregation is prominent. They compared runs starting from random and aggregated (one species-one stripe) initial configurations in a cellular automata model of a community consisting of five species. They showed that changing the juxtaposition of species alters the order of species extinctions. Even though slow-down in the extinction dynamics of the competition of the last two species was recognized, the survival time of the weaker competitor has not been investigated as yet.

Bolker and Pacala (1999) pointed out that “spatial coexistence depends on the balance between intraspecific clustering or spacing and interspecific segregation”. Intraspecific aggregation is often attributed to local dispersal (Bolker and Pacala 1997, Murrell et al. 2001, Molofsky et al. 2002). In this paper, we gave examples of models with local dispersal but without any clumping for lack of local density dependence. On the other hand, aggregation emerged in our simple preemptive competition models with local density dependent colonization functions. Our results imply that local dispersal in itself is not sufficient to form aggregated patterns, so that local density dependent colonization functions are also necessary. The latter, very important condition is hidden in many models in the literature. Without local density dependence in the colonization function, even the most aggregated pattern would be dissolved (Fig. 3.a). Intraspecific aggregation was quantitatively studied in simulation models using the proportion of sites having foreign neighbours.

Overcolonization counteracts to clustering thereby enables the coexistence of two species in a homogeneous environment. If there is no spatial mixing process in the system, such as overcolonization, then local density dependent dispersal forms a forefront between the species, and the movement of the forefront determines the outcome of competition. The species with higher colonization rate relative to its extinction rate (at local densities at the front line) wins (Fig. 3.b). Random initial configuration is disadvantageous for the weaker species, because it may go extinct before an aggregated pattern could be developed. This effect is more expressed in the case of lower initial densities.

Furthermore, our results illustrate that the perimeter-to-area ratio (P/A) is in close connection with the expected lifetime of the declining species. Statistical investigations confirm that there is a power function relation

between P/A of the initial configuration and the expected lifetime of the weaker species, in accordance with the fact P/A is a widely used metric in landscape ecology and conservation biology (Turner et al. 1999).

We used a simple model for measuring the time to extinction so that the effect of spatial arrangement would be clear. All the initial configurations we used in our experiments contain equally large monospecific areas, therefore P/A is the same for any (large enough) part of the cell space. For initial configurations consisting of highly different sized patches, the expected extinction time may be somewhat different since smaller patches of the weaker competitor disappear quickly and larger patches have stronger influence on survivorship. Of course, we do not suggest that any of our checkerboard or striped initial configurations occur in real plant communities. However, several natural species patterns can hardly be considered more similar to any uniformly distributed random configuration than a relatively aggregated checkerboard pattern. Obviously, several plant and insect species exhibit highly aggregated spatial geometry in natural communities (Plotkin et al. 2000, Ives 1998), and species often have constant clump radius (Plotkin et al. 2000). Molofsky et al. (2002) argued that clumped and even sharply banded pattern can appear in lattice models in case of negative frequency dependence.

If aggregation is taken into account when choosing an initial arrangement in spatially explicit models, new insights could be gained about the time scale of competition. The length of competition, according to its magnitude, can either predestinate the weaker species to extinction with debt or give a surplus of time to have a chance to evolve and survive.

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