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Spatiotemporal Models in Biological and Artificial Systems

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Spatial Effects and Competitive Coexistence[†]

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Abstract. This paper presents simulation results of a spatially explicit, individual based, discrete state model of two species competing for growth sites. An organism's survival and reproduction usually depend on interactions with nearby individuals. Predicting how these local processes influence population levels and community-level patterns requires spatially explicit models. In environments disturbed by high birth and death rates, an inferior species could invade and coexist with a superior species. A larger interaction neighborhood decreased coexistence when species differed in dispersal rate, but increased coexistence when competitors differed in mortality rate. In an environment with low birth and death rates, the inferior species was generally excluded, but larger interaction neighborhoods increased the probability of coexistence.

1 Introduction

Many plants and animals have spatially localized interactions governing individual survival and reproduction [1, 2]. Thus, coexistence of ecological competitors may depend on the effects that local phenomena have on global population dynamics [3]. To explore a link between the individual interactions and population levels, we conducted a series of simulations of a spatially explicit, individual based, discrete-state competition model.

Unlike many traditional approaches, spatially explicit competition models allow for coexistence of a dominant and subordinate species. By definition, the dominant always has a local competitive advantage; coexistence may persist if the subordinate species disperses into enough sites opened by mortality [1]. In [4], we presented a spatial model where a dominant and a subordinate species compete probabilistically for growth sites. The model's analytic continuous approximation has a locally stable coexistence equilibrium where the subordinate species has a mortality disadvantage and no dispersal advantage. In this paper we study the corresponding discrete stochastic model via cellular-automata simulation.

Most previous two-dimensional cellular-automata studies of ecological interactions restrict spatial interaction to a site's four to eight nearest neighbors. We systematically vary the size of the neighborhood (the ecological stencil [4]) from which a site can be colonized, to see if (and how) demographic-parameter levels necessary for coexistence (and successful invasion of a common resident by a rare species) respond to stencil-size manipulation. In disturbed environments (high mortality and dispersal) larger stencils can make coexistence more or less likely, depending on whether the species differ in per capita dispersal,

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per capita mortality, or the ability to compete for space during development. However, in undisturbed environments (low mortality and dispersal) the resident species more strongly resists invasion, and stencil-size effects lessen.

2 The Model

The environment contains a large number of sites J ($J \gg 1$) arrayed as a rectangular lattice. At any time t , any given site is in one of three possible states. A site may be empty, or may contain one adult organism of either the superior or inferior species. Species are identified by the binary variable, $h \in \{0, 1\}$, with $h = 1$ indicating the superior competitor and $h = 0$ the inferior one. Any site k is surrounded by a set of neighboring sites δ such that a change of the state of site k depends only on the species residing at site k itself and at sites in δ . Hence, δ is called the ecological stencil for site k .

To develop the transition probabilities, consider dispersal of a species from a site within the stencil δ to an open site k . Only open sites are subject to dispersal which is characterized by a parameter ρ_h that represents the probability of the colonization of site k by species h from a site within δ in a time unit Δt . Let σ_h count sites in δ occupied by species h ; we assume that the σ_h sites affect dispersal independently. Then the probability of one or more type- h individuals successfully initiating development at an open site k , during a single time interval Δt , is*:

$$p_{hs} = 1 - (1 - \rho_h)^{\sigma_h}; \quad h \in \{0, 1\} \quad (1)$$

In most plant communities juveniles must compete for a site vacated through adult mortality. Let p_c represent the probability that a superior competitor ($h = 1$) reaches maturity when both species initiate development at the same site. Ordinarily, ecological superiority implies $p_c \geq \frac{1}{2}$. Combining assumptions, the probability that a type- h individual attains maturity after dispersing to an open site k is $p_{hw} = p_{hs}(1 - p_{\bar{h}s}) + p_{hs}p_{\bar{h}s}[\bar{h} - (\bar{h} - h)p_c]$, $h \in 0, 1$, where $\bar{h} = (1 - h)$ denotes the species competing with species h . Therefore, during a single time interval an open site is occupied by an individual of species h with probability p_{hw} ($h = 0, 1$), or remains open with probability $1 - p_{0w} - p_{1w}$.

If site k is occupied by a type- h adult at time t , that individual survives to time $(t + \Delta t)$ with probability $(1 - \mu_h)$. Mortality opens the site with probability μ_h .

The coexistence equilibrium assumes large stencils (equivalently, global dispersal). Larger stencil size diminishes "recruitment limitation", even for small ρ_h , since a given adult may colonize more open sites. Larger stencil size, then, can counter the inferior species' mortality disadvantage at the coexistence equilibrium. But when $|\delta|$ is reduced, each species becomes more spatially clumped. Sites open up faster in clumps of the inferior species, and the mortality difference can allow the superior species to exclude the inferior one locally and,

*In a continuous model, p_{hs} represents intensity of colonization which is the limit of the above probability with Δt tending to 0. Then, $p_{hs} = \rho_h * \sigma_h$

space during development. (Mortality and dispersal) the resiliency and stencil-size effects lessen.

is $J(J \gg 1)$ arrayed as a grid. Each site is in one of three possible states: occupied by the adult organism of either the resident or competitor and $h = 0$ the site is vacant. Neighboring sites δ such that $k \in \delta$ are the sites in the stencil for site k . Dispersal of a species from site k to open sites are subject to a probability p_{kw} that represents the probability of one or more individuals arriving at a site within δ in a time interval h ; we assume that the probability of one or more individuals arriving at an open site k , during

$$0, 1\} \quad (1)$$

for a site vacated through mortality or that a superior competitor develops at the same site. Combining assumptions, the probability after dispersing to site k is $(\bar{h} - h)p_c$, $h \in 0, 1$, where \bar{h} is the mean dispersal distance of species h . Therefore, during a time interval h , the probability of a site being occupied by a resident or competitor is $1 - p_{0w} - p_{1w}$. If a site is vacant, that individual survives with probability $1 - p_{0w} - p_{1w}$, and mortality opens the site with

probability $1 - p_{0w} - p_{1w}$ (equivalently, global dispersal limitation", even for small h). Larger stencil size, then, delays the time to reach the coexistence equilibrium, and the mortality difference between the superior and inferior one locally and globally. The limit of the

ultimately, globally. This result [5], that larger stencils should promote coexistence for a given mortality-rate difference, is interesting when compared to other models. Crawley and May [1] indicate that highly restricted dispersal may either increase or decrease the chance of coexistence when an annual competes for space with a dominant, vegetatively propagating perennial. The important point is that stencil size may interact with demographic differences to affect coexistence. Therefore, we varied $|\delta|$ over two orders of magnitude in simulations described below.

3 Experiments

Simulations were run on a MasPar MP-1 parallel computer in which the processing elements are arrayed as a two-dimensional grid. Thus, the model's sites map naturally onto the computer's architecture [5]. To avoid edge effects, We wrapped the 32×64 simulated sites so that opposite boundaries were adjacent. At each iteration, each site's transition probabilities were calculated for random selection of the next state. We ran simulations until either 2000 iterations [6] or an extinction occurred. The random number sequence was repeated for each parameter combination's initial run, as a simulation control. We ran some parameter combinations with 30 sequences to assess random variability.

Stencils were square with the affected site in the center. We varied stencil size by enlarging the square as follows: $|\delta| = (2r + 1)^2$ for $r = 1, 2, \dots, 15$.

To start a simulation we placed 16 individuals of the invading species on the grid clumped in three different ways: as a corner square, located randomly and independently, or dispersed uniformly. The resident species was randomly distributed over a fraction (0.67) of the remaining sites. The resident's initial density was constant across all simulations. Placement of the 16 initial invaders had little effect on the ensuing dynamics when $|\delta|$ was large, and promoted only unpatterned random variability among simulations with small stencils.

We investigated separately how dispersal probability ρ_h and mortality μ_h interact with stencil size to govern invasability and coexistence. For each demographic parameter we examined stencil-size effects in both a "disturbed" environment, and an "undisturbed" environment. Mortality and dispersal were larger in a disturbed environment, causing a relatively fast turnover of sites.

Each simulation assumes a resident species at demographic equilibrium and asks if a rare species can invade. Successful invasion requires the invader survive for 2000 iterations. Successful invasion leads to coexistence if the resident also remains extant for 2000 iterations. Otherwise, a successful invader excludes the resident. Table 1 outlines the sequence of our experiments.

3.1 Dispersal Difference in a Disturbed Environment

We first asked how stencil size affects coexistence when competitors differ in per capita dispersal probability ρ_h . Figure 1a shows ϵ_T values (invasability thresholds; see Table 1) for a disturbed environment. Note that all $\epsilon_T > 0$. Therefore, in a disturbed environment an inferior competitor can invade and

Section	3.1	3.2	3.3	3.4
ρ	$\rho(d_e, \mu, \delta) \pm \epsilon$	$\rho(d_e, \mu, \delta) \pm \epsilon$	$\rho(d_e, \mu, \delta)$	$\rho(d_e, \mu, \delta)$
μ	0.5	0.1	$0.5 \pm \epsilon$	$0.1 \pm \epsilon$

Each simulation began with the resident species at its single-species equilibrium density, d_e , for which $\mu_h = p_{hs}$. Hence, for each stencil size and μ -level, there is a unique ρ_h corresponding to equilibrium and defined by d_e , μ and δ . A constant $p_c = 0.5$ was used.

Table 1: Organization of Simulations

coexist with a superior species, provided $\rho_1 - \rho_0 < 2\epsilon_T$. Hence, competitive dominance might not preclude coexistence under these conditions.

Figure 1a also shows that ϵ_T decreases with stencil size (for $|\delta| > 9$), i.e., larger stencils allow a superior competitor to exclude an inferior species at a smaller demographic advantage. Stencil size and the superior competitor's dispersal probability interact in a complementary manner. That is, a decrease in one of these quantities need not diminish a superior species' capacity to exclude an inferior species, as long as the other quantity is increased. Surprisingly, this effect of increased stencil size does not depend on which species (superior or inferior competitor) invades the other (Figure 1a).

The superior species never went extinct in these disturbed-environment simulations. But the inferior species went extinct whenever $\epsilon > \epsilon_T$ (by definition of ϵ_T). For small stencils, time to extinction simply reflects the poorer species' initial density (hence resident vs. invader role; see Figure 2a). For larger stencils this difference disappears and times to extinction decline (Figure 2b).

For $\epsilon < \epsilon_T$, the species coexist in disturbed environments. When $(\epsilon_T - \epsilon)$ is large, the species are demographically similar and the inferior competitor is spatially dispersed in fewer relatively large clusters. As $(\epsilon_T - \epsilon)$ approaches zero, cluster count increases and then declines sharply near the invasibility threshold. The average cluster size decreases regularly as $(\epsilon_T - \epsilon)$ decreases.

The first main result is that larger stencils in disturbed environments permit the superior competitor to exclude the inferior one at a smaller difference in the species' per capita colonization probabilities. If the resident is superior to invader (due to, say, local adaptation) then coexistence for species differing in dispersal rate per individual is less likely as stencil size increases. However, if the difference between species is not excessive, the demographically inferior species can invade and coexist with the superior species.

3.2 Dispersal Difference in an Undisturbed Environment

We again analyzed stencil-size effects when species differ in ρ_h , but in an undisturbed environment (see Table 1). Figure 1b shows invasibility thresholds (ϵ_T). For small stencils ($|\delta| \leq 81$) $\epsilon_T > 0$ when superior species invades, and $\epsilon_T < 0$ otherwise. This implies that successful invasion requires the invader's dispersal probability exceed the resident species' ρ_h sufficiently. That is, a species

3.3	3.4
(d_e, μ, δ)	$\rho(d_e, \mu, \delta)$
$0.5 \pm \epsilon$	$0.1 \pm \epsilon$

ngle-species equilibrium density, d_e , and μ -level, there is a unique ρ_h constant $p_c = 0.5$ was used.

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$< 2\epsilon_T$. Hence, competitive these conditions. stencil size (for $|\delta| > 9$), i.e., include an inferior species at the superior competitor's manner. That is, a decrease superior species' capacity to quantity is increased. Sur- not depend on which species (Figure 1a).

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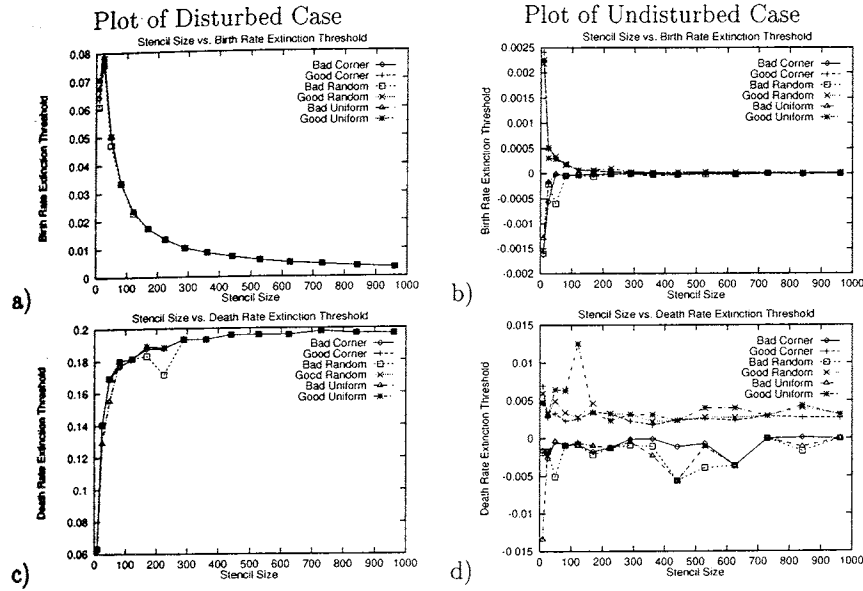


Figure 1: Extinction Threshold ϵ_T vs. Stencil Area $|\delta|$

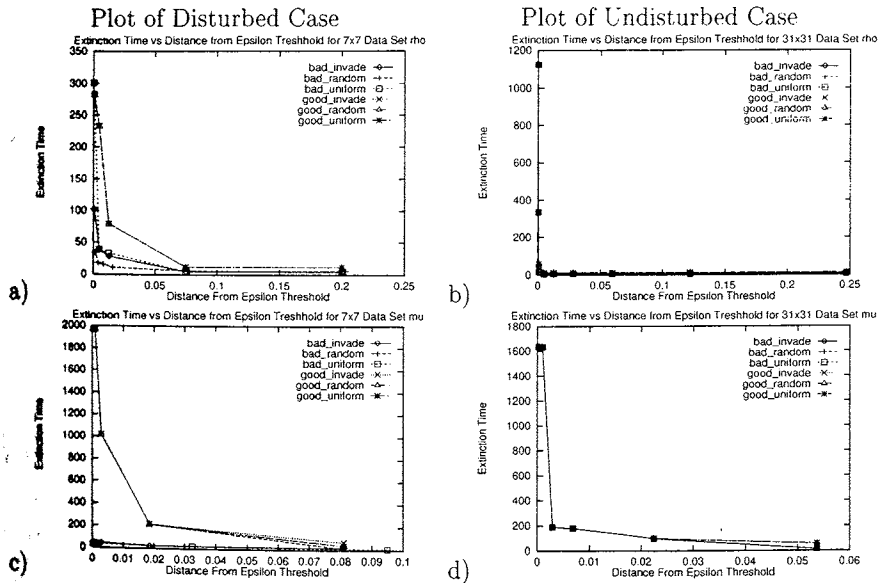


Figure 2: Time to Extinction vs. Stencil Size Plots

must be a sufficiently superior to invade successfully in an undisturbed environment. For this environment, the resident species' competitive dominance can preclude invasion and, hence, coexistence for smaller stencils.

As stencil size increases, ϵ_T converges toward 0, independently of which species invades (Figure 1b). Therefore, the demographic advantage needed to invade successfully declines as $|\delta|$ increases. The invading competitor must be superior at small stencils, but only demographically equivalent at larger stencil size, to invade successfully. Then, for a given difference in ρ_h values, the chance of successful invasion increases as δ grows in an undisturbed environment.

Successful invasion sometimes eradicated the resident species. In 10 of the initial 45 simulations at $\epsilon = \epsilon_T$, the invader drove the resident extinct; otherwise they coexisted. The resident's extinction was independent of stencil size, and was not simply an effect of the superiority needed to invade at small $|\delta|$.

Time to extinction did not depend on stencil size in these simulations. The average cluster size and the number of cluster in the undisturbed environment did not vary systematically with the species' difference in ρ values, but simply reflected the difference between coexistence and competitive exclusion.

Examining competitive coexistence when species differ in dispersal probability results in the following three ecologically important comparisons between disturbed and undisturbed environments.

(1) In a disturbed environment a demographically inferior species can sometimes invade and coexist with a superior resident. This need not be true in an undisturbed environment, where an inferior competitor has little chance of invading successfully.

(2) Larger stencils inhibit invasion by an inferior competitor in the disturbed environment. In the undisturbed environment successful invasion requires only a smaller demographic advantage as stencil size increases. Hence, increased stencil size promotes ecological invasion in an undisturbed environment, but successful invasion is generally less probable.

(3) At the invasibility threshold, coexistence always results in the disturbed environment (where $\epsilon_T > 0$), but for the undisturbed environment (where $\epsilon_T \leq 0$) coexistence or extinction of the resident may occur. The resident species is more entrenched at the undisturbed environment's lower mortality and dispersal probabilities; slower spatial and demographic turnover reduces the chance of competitive coexistence.

3.3 Mortality Difference in a Disturbed Environment

This analysis asks how stencil size influences coexistence in a disturbed environment when competitors differ in mortality. Figure 1c shows the invasibility thresholds, ϵ_T , with all $\epsilon_T > 0$. Therefore, a disturbed environment again allows a competitively inferior species (i.e. the species with the larger μ_h) to invade and coexist with an ecologically superior species.

Figure 1c also shows that ϵ_T increases with δ . Larger stencils require a greater mortality advantage for a superior competitor to exclude the inferior

ally in an undisturbed environment, the superior species' competitive dominance is maintained at smaller stencils.

0, independently of which demographic advantage needed to invade a competitor must be equivalent at larger stencils. Hence, in ρ_h values, the chance of invasion in a disturbed environment is the same as in an undisturbed environment.

resident species. In 10 of the simulations, the resident species went extinct; otherwise, the resident species was independent of stencil size. Hence, the chance of invasion needed to invade at small $|\delta|$ is the same as in these simulations. The chance of invasion in a disturbed environment is the same as in an undisturbed environment.

ence in ρ values, but simply competitive exclusion.

s differ in dispersal probabilities. The most important comparisons between the two environments are:

competitor in the disturbed environment. Successful invasion requires only a small ϵ . Hence, increased mortality in a disturbed environment, but

always results in the disturbed environment (where the superior species may occur. The resident species in an undisturbed environment's lower mortality and demographic turnover reduces

ment

istence in a disturbed environment. Figure 1c shows the invasibility of a disturbed environment again allows species with the larger μ_h to invade.

Larger stencils require a smaller ϵ for the superior competitor to exclude the inferior

one because they contain sufficient number of inferior individuals to maintain the rate at which that species occupies open sites [4].

As in the disturbed environment analyzed in Section 3.1, effects of $|\delta|$ on invasibility do not depend on whether the invader is the superior or inferior competitor and the superior competitor remained extant in nearly every simulation. Figures 2c and 2d show times to extinction for the inferior competitor (i.e., $\epsilon > \epsilon_T > 0$). When $|\delta|$ is small, the inferior competitor goes extinct faster as invader than as resident (as above). Small stencils produced the fastest extinction, since a particular mortality-probability difference more strongly favors the superior competitor when δ is small.

The increase of ϵ_T with stencil size directly contrasts with the dispersal-probability analysis for a disturbed environment. When mortality probabilities differ, an inferior competitor may coexist with an increasingly superior competitor as long as stencil size increases sufficiently [4]. If the superior competitor is the resident occupying a disturbed environment, the likelihood of invasion and coexistence for species differing in mortality probability increases as stencil size increases.

3.4 Mortality Difference in an Undisturbed Environment

We next analyzed stencil-size effects when μ_h differs between species, but in an undisturbed environment (see Table 1). Figure 1d shows the invasibility thresholds; absolute values of ϵ_T decline as δ increases. For most stencil sizes the invader needs a smaller mortality probability than the resident for successful invasion. That is, competitive superiority is usually required for successful invasion in an undisturbed environment (similarly to the case from Section 3.2). The variation in the magnitude of ϵ_T with $|\delta|$ implies that successful invasion is slightly more likely as stencil size increases, but dependence on $|\delta|$ is not strong.

Successful invasion in this experiment could result in coexistence, but the resident was excluded by the competitively superior invader in 41% of the simulations at $\epsilon = \epsilon_T$. Extinction of the resident was independent of stencil size. The undisturbed environment's lower demographic and spatial turnover gives a "priority effect" advantage to the resident. A successful invader must ordinarily be competitively superior; which often leads to the resident's extinction.

4 Conclusion

In disturbed environments larger stencils (hence greater dispersal distances) increased an inferior competitor's chance of invading and coexisting with a resident when the species differ in mortality rate or ability to compete for space. However, larger stencils made coexistence less likely when species differ in per capita colonization probability. Hence, the relationship between dispersal distance and coexistence depends on which ecological attributes differ between competitors, at least in disturbed environments.

Perhaps the most significant comparison is between disturbed and undis-

turbed environments. In the former case (high mortality and dispersal) a competitively inferior species can invade and coexist with a superior species, a result reported in previous spatially explicit analyses of competition [1]. However, in the undisturbed environment (low mortality and low dispersal) the resident species exploit the population dynamics' "spatial memory". Successful invasion usually requires the invader to be superior to the resident. Larger stencils may reduce the competitive advantage required for invasion: successful invasion in this environment may imply coexistence, but often results in the resident's extinction. Spatial heterogeneity in ρ_h , μ_h or p_c could be introduced, but is unnecessary to create complex spatial population patterns [2, 6, 7].

We have stressed the competitive consequences of ecological invasion and the difference between disturbed and undisturbed environments, but an application to evolutionary biology may also be reasonable. Suppose a rare mutant "invades" a spatially distributed population. In a disturbed environment, a superior genotype can always invade an inferior genotype. But the disturbed environment also may allow the inferior type to invade and coexist with the superior genotype. In undisturbed environments, an inferior type can rarely invade. Successful invasion requires the invader be superior to the resident: for small stencil sizes the invaded may need a substantial proportional demographic advantage to invade. Hence, undisturbed environments, in a sense, resist evolutionary change. The entrenched resident genotype can stay common until mutation, migration or recombination produces a much fitter type.

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