

Spatial Moment Equations for Plant Competition: Understanding Spatial Strategies and the Advantages of Short Dispersal

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ABSTRACT: A plant lineage can compete for resources in a spatially variable environment by colonizing new areas, exploiting resources in those areas quickly before other plants arrive to compete with it, or tolerating competition once other plants do arrive. These specializations are ubiquitous in plant communities, but all three have never been derived from a spatial model of community dynamics—instead, the possibility of rapid exploitation has been either overlooked or confounded with colonization. We use moment equations, equations for the mean densities and spatial covariance of competing plant populations, to characterize these strategies in a fully spatial stochastic model. The moment equations predict endogenous spatial pattern formation and the efficacy of spatial strategies under different conditions. The model shows that specializations for colonization, exploitation, and tolerance are all possible, and these are the only possible spatial strategies; among them, they partition all of the endogenous spatial structure in the environment. The model predicts two distinct short-dispersal specializations where parents disperse their offspring locally, either to exploit empty patches quickly or to fill patches to exclude competitors.

Keywords: stochasticity, space, competition colonization, spatial strategies, moment equations.

In order to persist in resource competition with other plants in a spatially variable environment, any plant must be able to perform at least one of three strategic tasks. It must colonize relatively unpopulated, resource-rich areas with its shoots or seeds; quickly exploit resources in those areas before other plants establish themselves and deplete resources; or tolerate local competition over the long term, specifically by reducing resource levels to pre-

vent other species from establishing. Some level of colonization and either exploitation or tolerance is necessary for long-term survival, but different plant types can specialize in particular tasks. This insight has appeared several times in the community ecology literature. MacArthur's *r*-selected species rely on a combination of colonization and exploitation, while his *K*-selected species rely on maintenance (MacArthur and Wilson 1967). The three specializations also map onto Grime's "triangle" of ruderal, competitive, and tolerant species, if we interpret the triangle narrowly as a set of ecological strategies for resource competition (Grime 1977, 1979). Finally, the classical competition-colonization trade-off (Levins and Culver 1971; Hastings 1980; Tilman 1994) emphasizes colonization and tolerance (competition), although, as has been pointed out (Pacala and Rees 1998), it ignores the potential for quick exploitation of a habitat before dominant competitors can take over. In an attempt to discuss these strategies without inventing too many new terms, we will call them "colonization," "exploitation" (Grace 1990), and "tolerance," although we emphasize that exploitation stands specifically for rapid (rather than thorough) exploitation. We assume that thorough exploitation of resources, which reduces resources to low levels, goes along with tolerance of low resource levels (Goldberg 1990).

Because they depend on colonization and exploitation of different locations in a variable environment, these competitive strategies implicitly depend on the spatial structure of the environment and the spatial capabilities of plants. There has been a long history of theoretical attempts to clarify the exact mechanisms underlying spatial strategies and spatial coexistence in ecological systems (Levins and Culver 1971; Horn and MacArthur 1972; Armstrong 1976; Hastings 1980; Shmida and Ellner 1984; Pacala 1986a; Crawley and May 1987; Nee and May 1992; Tilman 1994; Holmes and Wilson 1998; Pacala and Rees 1998). A whole spectrum of models, from pseudospatial patch models (models with competition within discrete patches and

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global dispersal between patches) to fully spatial cellular automaton models, has been developed to try to shed light on these problems.

This article presents yet another spatial competition model. We have three justifications for further trespassing in a much trampled field. First, having gone to the trouble of analyzing a fully spatial model, we shall end by concluding that there is not much new under the sun—all of the spatial phenomena alluded to in previous spatial studies can be subsumed under the three categories of colonization, exploitation, and tolerance, and our complete analysis of a spatial model suggests that no other strategies exist. Second, early spatial models all focus on long dispersal in the colonization and tolerance phases of spatial competition (colonization and competition *sensu* Tilman 1994 or ruderality and tolerance *sensu* Grime 1977, 1979), ignoring the possibility of specialization for short dispersal and rapid exploitation (Lehman and Tilman 1997; Durrett and Levin 1998; Holmes and Wilson 1998). Individual plants can exploit a patch by quickly growing larger or by recruiting clones or sexual offspring within the patch; in this article, we focus on the potential advantages of short dispersal and within-patch recruitment. Third, we present a new method for finding analytical approximations to a stochastic competitive process in continuous space, a problem that often requires the use of computational models (although see Durrett 1988). The great advantage of a fully spatial analytical approach is that it gives us some confidence that our results are complete, that we have neither eliminated a subset of possible strategies by reducing the system to a pseudospacial model nor overlooked a corner of parameter space as we might in a computational model.

The focus of spatial competition theory on colonization to the exclusion of exploitation comes partly from the obvious investment that plants make in dispersal specializations, such as winged seeds, and partly from modeling artifacts, which we will discuss in the next section. To avoid the potential for artifacts as much as possible, we explore a very general, fully stochastic and spatial model (see “Individual-Based Model”) that imposes few constraints on the demographic, competitive, or spatial parameters of individual species. However, this generality presents a technical challenge. Stochastic spatial models are notoriously difficult to analyze, with many results holding only in equal-longevity cases or in high-density, non-colonization-limited situations where any open space in the environment is immediately colonized (Bramson et al. 1989; Durrett 1992). We have no magic solution to the intractability of stochastic spatial processes. Instead, we work with approximate moment equations that describe changes in the mean densities and spatial patterns (covariances) of two competing species.

Classical ecological models such as the Lotka-Volterra

equations assume that all populations are large and well mixed, so they can ignore statistical and spatial fluctuations and track only the mean density of each interacting population. Such models are called first-order models because they track only the first moments of the spatial distributions of populations (the mean densities), assuming the variance and all higher moments are zero. First-order models can be extended by adding a parameter such as the negative binomial k , which relates the variance of the population to its mean (Hochberg et al. 1990; Hassell et al. 1991), but they still assume that this relationship is fixed rather than changing in time. Second-order models go farther, tracking the dynamics of the second moments (variances and covariances or spatial covariances) as well as the first moments (Grenfell et al. 1995), but they still assume that third and higher moments are zero or at least that they have some fixed relationship with the mean and variance (Satō et al. 1994). A few studies have even gone to third- and fourth-order models, which track the skew and kurtosis of population or genetic distributions (Nagylaki 1992; Turelli and Barton 1994; Dushoff 1997). Beyond this level, classical moment-generating function techniques can capture the complete dynamics of a stochastic process (Bailey 1964), but they typically work only for an extremely restricted class of problems (but see Comins et al. 1980).

In this article, we study second-order moment equations for a spatial point process where each individual is located at a point in a continuous two-dimensional arena. The first and second moments are the mean densities of each population and the spatial covariances, which are the covariances between plant densities at different spatial lags. Each species has an autocovariance that describes the clustering (positive covariance) or even spacing (negative covariance) within its population, and each pair of species has a cross-covariance that describes the spatial association or segregation between the two species. There is a clear connection between spatial processes and spatial covariances. Reproduction and local dispersal add new plants near an established adult and generate positive self-covariance or clustering, while competition preferentially thins overcrowded areas and generates negative covariance within and between species. The cross-covariance is only affected by competition and not by local dispersal, so spatial segregation (negative cross-covariance) always occurs and promotes exploitative strategies.

In order to derive a closed set of equations for the spatial covariances, we assume that the third spatial moments (which modify the conditional density of a plant's competitive neighborhood, given that it has at least one neighbor) are zero. In other words, we assume that the probabilities of finding pairs of plants at particular distances apart completely describes the spatial pattern. With this

approximation, which is accurate when each individual competes with a relatively large number of other plants (see “Moment Equations”), we derive a set of equations that predict the dynamics of density and spatial patterns for each species. Using these equations, we can evaluate which demographic and competitive parameters are required for different spatial strategies to work.

Thus, we can analyze a stochastic spatial model that incorporates individual-based rules of reproduction, local dispersal, mortality, and local competition. The results illuminate the differences between colonization and exploitation in a spatial context and show that colonization, exploitation, and tolerance represent all possible strategies in a simple but general spatial system. Colonization, exploitation, and a particular spatial mechanism for tolerance that we call a phalanx strategy each make use of a different part of the spatial structure that develops spontaneously from the balance of clustering and competitive thinning of plant populations. Together, these three strategies partition all of the spatial heterogeneity in the environment.

Figure 1 shows an example of a short-dispersing, exploitative strategy in action in a simple stochastic spatial model of competition (see “Individual-Based Model” for details). The resident species is the stronger nonspatial competitor: it has life-history and competitive parameters that would allow it to dominate if the invader dispersed globally, which would reduce the model to its nonspatial analogue. The two species coexist spatially even though both species compete and disperse on the same spatial scales. At equilibrium, individuals show interspecific spatial segregation; areas with high densities of the invader tend to have low densities of the resident and vice versa. As we will show, spatial segregation inevitably builds up in stochastic spatial multispecies populations, and spatial coexistence depends on the balance between intraspecific clustering or spacing and interspecific segregation. Rapid exploiters such as the invader in figure 1 survive because of interspecific segregation, using short dispersal to keep their offspring close to themselves, maximizing their opportunity to land in enemy-free space and to establish successfully. Our analysis will show how population dynamics generate spatial structure, and how spatial structure affects population dynamics and changes competitive outcomes.

The next section connects our model with existing theory and models of spatial competition and explains some of the differences between established results and our findings. “Stochastic Spatial Plant Competition” defines an individual-based model and describes the protocol for simulating it on the computer; it also defines some basic spatial statistics that describe the patterns shown in figure 1, which will form the foundation of our analytical ap-

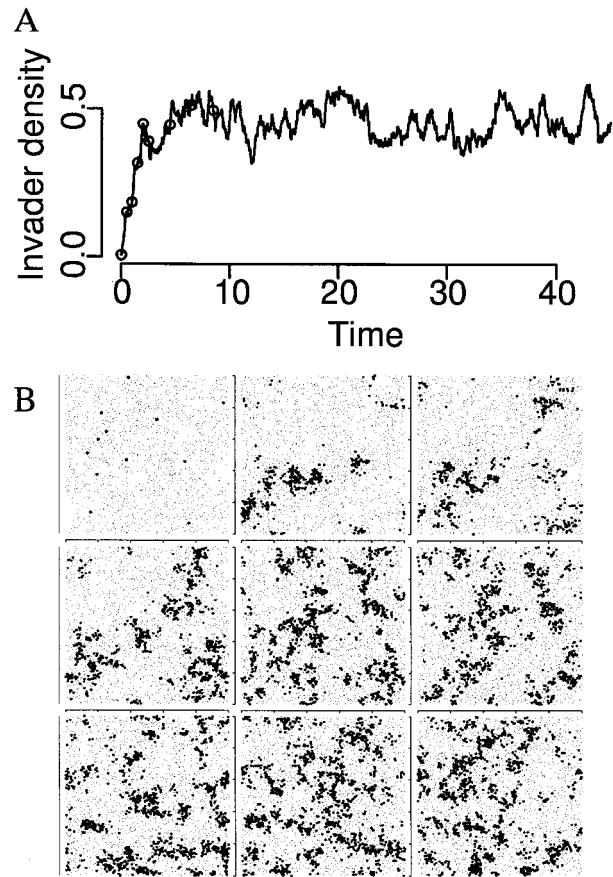


Figure 1: Invasion of a short-dispersal strategist (exploiter). An invader invades an equilibrium spatial distribution of the resident species that would repel it if both species had global dispersal. All competition and dispersal scales are equal. Parameters (see “Individual-Based Model” and table 1 for definitions): $f_i = 111.1$; $f_r = 2.0$; $\mu_i = 11.1$; $\mu_r = 1.0$; $\alpha_{ii} = 20$; $\alpha_{ir} = 110$; $\alpha_{ri} = 0.02$; $\alpha_{rr} = 1$; all scales (m_i, m_r) = 1; length = 50. A, Mean density of an invading species over time; points indicate the times of the snapshots shown in B. B, Spatial distributions: large dots are invaders, small dots are residents. Upper left-hand corner shows initial invasion; time flows left to right and top to bottom.

proach. “Moment Equations” discusses how to derive and use moment equations (technical details appear in the appendixes). “Results” shows how the invasion criteria derived from the moment equations describe different spatial strategies and how these spatial strategies partition the spatial variability of the environment, and “Discussion” explores the implications of these spatial strategies, connecting them with existing theories and empirical observations of spatial community dynamics.

Connections with Existing Theory

As discussed in the introduction, the problem of spatial plant competition has attracted a great deal of modeling effort. In predator-prey systems, in systems where individuals aggregate with conspecifics, and in competitive systems when interspecific competition is strong, endogenous spatial patterns form in spatial systems; a wide variety of models, including classical continuum models, have generated interesting results (Murray 1990; Solé et al. 1992; Hassell et al. 1994; Lewis 1994; Gandhi et al. 1998). Continuum models have not been widely used for competitive systems, however, because spatial patterns do not form spontaneously in continuum models of competitive systems except when interspecific competition is strong. Instead, modelers have traditionally made some compromise between pseudospatial models, which allow only global between-patch movement, and lattice models, which are analytically difficult (Pacala 1986a; Crawley and May 1987). All of the models along this trade-off curve between analytical tractability and generality are actually capable of generating results qualitatively similar to those presented here. However, because of apparently harmless decisions made to simplify analysis, they have largely missed the possibility of fast-growing or fast-reproducing, short-dispersing exploitative strategies—for example, competitive species in Grime (1977, 1979) or “successional niches” in Pacala and Rees (1998).

Two common and potentially troublesome assumptions of spatial competition models are a constant life span for all competing species and the use of pseudospatial patch models with a single adult per patch and fast within-patch dynamics. In models where all species have the same life span (e.g., in models of communities of annual plants), different aspects of fecundity are confounded and in turn cloud the distinction between colonizing and exploiting strategies. The intrinsic reproductive number R is the expected number of offspring produced by a plant in its lifetime in a noncompetitive environment, while the intrinsic reproductive rate r is the expected exponential growth rate of a plant population in a noncompetitive environment. The reproductive number is unitless, and the reproductive rate specifies per capita growth per unit time (see table 1). For communities where all species have the same life span, intrinsic rate and number are proportional to each other. Since (as we will show) colonization ability depends only on reproductive number while exploitation ability depends on reproductive number and rate, these two specializations become difficult to tease apart in models where plants cannot trade off short life spans for high reproductive rates.

Many spatial models use pseudospatial structure and allow only a single adult per site, with instantaneous dis-

placement of competitively inferior species by competitive dominants (Hastings 1980; Tilman 1994). While these simplifications are reasonable, their joint effect is to disallow both differences in growth rate and the possibility of within-patch recruitment, eliminating both possible modes of rapid exploitation. However, exploitation by local recruitment within empty neighborhoods is a possibility in spatial lattice models such as cellular automata, but it has been largely ignored in the impressive literature on the dynamics of lattice models because it does not occur between competitively symmetric species, requiring instead some difference in fecundity or growth rate (C. Neuhauser and S.W. Pacala, unpublished manuscript).

Another confusing aspect of pseudospatial models is the combination of fecundity, the tendency to disperse away from the home site, and dispersal distance into a single measure of colonization ability. Pseudospace combines these three properties in a single measure of colonization ability—the number of seeds landing outside of the home site. In contrast, Holmes and Wilson (1998) are careful to separate dispersal ability and fecundity in their spatial models. We will focus on dispersal ability, but most of our results, except those that parallel Holmes and Wilson's, will require some difference in either lifetime fecundity or rate of seed production to allow invasion of a weaker competitor.

More generally, we recognize that in most cases a mixture of life-history parameters and spatial parameters determines overall spatial competitive ability. For example, both long dispersal and high fecundity are generally required for a colonizing strategy. In this article we focus on competitive strategies that depend on endogenous spatial structure in a fully spatial habitat; we recognize that in some cases, analogous strategies exist in pseudospatial models.

Our models also make simplifying assumptions. Our main assumption is that dispersal and competition scales are relatively long and thus the effects of space are relatively weak; our models work well for competitive neighborhoods containing more than about a dozen neighbors. This is the opposite of the usual assumptions of spatial models (e.g., in pseudospatial models where only one individual can persist in a site or in lattice models where the competitive and dispersal neighborhoods often include only the four nearest neighbors). We assume weak spatial effects because our analysis requires it, but we have two reasons to be sanguine about this assumption. First, for many plant communities, the assumption of many neighbors appears to be a reasonable fit to the observed data (Pacala and Silander 1987). Second, having an assumption that is at the other end of a spectrum from most other models allows us to triangulate. Our model finds versions of all the strategies that occur in small-neighborhood models, but it also

Table 1: Symbols used

Parameter	Definition
Competition and life history:	
Individual level:	
f_i	Fecundity of species i
μ_i	Mortality of species i
α_{ij}	Competitive effect of species j on species i
Population level:	
$r_i (f_i - \mu_i)$	Intrinsic reproductive rate of species i
$R_i (f_i/\mu_i)$	Intrinsic reproductive number of species i
$K_i ([f_i - \mu_i]/\alpha_{ii})$	Nonspatial carrying capacity of species i
$\beta_{ij} ([\alpha_{ij}/\alpha_{ii}] \times [K_j/K_i])^a$	Relative competitive effect of species j on species i
Spatial parameters:	
D_i	Dispersal kernel of species i
U_{ij}	Competition kernel between species i and j
$\mathcal{K}(m)$	Generic kernel, scale parameter m
m, m_D, m_U	Scale parameters (of dispersal, competition)
φ_k	Relative scale of covariances (apps. B, C; $k = \{I, R, IR\}$)
Spatial quantities and population measures:	
Ω	Set of points in the spatial arena
h	Size of a discrete patch (app. A)
s	Distance (lag)
\bar{n}_i	Density of species i
c_{ij}	Spatial covariance of species i with j
\bar{c}_{ij}	Average spatial covariance of species i with j , weighted by $U_{ij} * D_i$
$c_{IR, k}$	Subdivisions of spatial segregation with different scales ($k = \{I, R, IR\}$)

Note: Subscripts (i, j) can equal I (invader) or R (resident).

^a We use this definition, rather than the more common $\beta_{ij} = \alpha_{ij}/\alpha_{ii}$, to simplify notation.

finds strategies that are disallowed in those models. Having looked at both ends of the neighborhood-size spectrum, we can hope that we have not missed any further categories of spatial community dynamics.

Despite these differences between our model and previous models, we can actually reconcile many of our results with those of previous studies. As found by Holmes and Wilson, when the competitively inferior species has long dispersal and the competitive dominant has short dispersal, the only requirement for invasion is that the competitive dominant be fecundity limited; the competitively inferior species need not have higher fecundity (“Colonization Strategies”). In contrast, when both species have equal dispersal scales, our model suggests that a competitively inferior species gains a colonization advantage as long as it has greater fecundity than the dominant species. This result agrees with patch models where, as in our model, the dominant species can only preempt sites, not displace the weaker species once it has established.

Our main conclusion is that previous models err only

by omission. For strategies that other models predict, our results agree qualitatively, up to the limits of different underlying assumptions. However, our model suggests an additional set of strategies that have until recently occurred only in verbal models of plant community dynamics (Grime 1977; Pacala and Rees 1998).

Stochastic Spatial Plant Competition

Individual-Based Model

Consider a community of perennial, clonal plants in a continuous, homogeneous environment. Each plant produces a constant number of offspring per unit time and has a constant probability of death. Different species may have different fecundity (f_i) and mortality (μ_i) rates.

When a plant reproduces, it disperses its offspring locally, not just between discrete sites, as in many ecological models of dispersal, but in a random direction and with a distance chosen from a probability distribution called the dispersal kernel (D_i). We get qualitatively similar answers using a variety of smooth, radially symmetric dispersal kernels, including exponential, Gaussian, and Bessel functions. Bessel functions (Abramowitz and Stegun 1965), although they are unfamiliar to most ecologists, have a respectable history in the study of dispersal (Skelam 1951; Broadbent and Kendall 1953; van den Bosch et al. 1990; Lande 1991). Modified Bessel functions of order 0 (K_0) also have a sensible mechanistic interpretation as the distribution of particles that move randomly out from the origin and stop with a constant probability per unit time. They are convenient to analyze, so we use them throughout this article whenever specific kernels are required. The scale parameter m gives the average dispersal distance of a seed dispersing according to a normalized Bessel function $1/(2\pi m^2)K_0(s/m)$.

Once the offspring arrives at its new location, it must survive competition from established plants. Establishment probability of species i decreases linearly with the local density of competitors of species j at rate α_{ij} , stopping at 0. The spatial structure of competition is more detailed than the usual within- and between-sites distinction of pseudospacial models or than counting nearest or next nearest neighbors as in most lattice-based models. Instead, each plant's local density is defined by a competition kernel (U_{ij}), a function of distance giving the competitive effect of an adult plant of a particular species a given distance away. In a mechanistic model, the local geometry of resource competition, for example, root overlap zones under competition for water or soil resources, or shading for light competition, would determine the competition kernel. As with dispersal kernels, we use Bessel functions whenever we need to specify a particular competition kernel (Gaussian distributions, which might be more realistic for some forms of resource competition, would give qualitatively similar answers).

We simulate the model on the computer using an $L \times L$ arena with periodic boundary conditions—the left and right edges and the top and bottom edges of the space are wrapped together to avoid edge effects. (We always use an arena with L much longer than the scales of dispersal and competition to avoid wraparound effects.) Starting with a random initial distribution of plants, the simulator takes small time steps to approximate a continuous-time process. In each time step, the simulator picks pseudorandom numbers to see whether each plant has died or reproduced. If it has reproduced, the simulator picks a random distance from the dispersal kernel and a random direction to see where its offspring disperses. It then cal-

culates the local density around that point to determine the offspring's establishment probability and picks another random number to see whether it establishes.

Density-dependent establishment occurs in plant communities from clonal swards to forests (Harper 1977; Goldberg 1982; Gross and Werner 1982; Peart 1989). Density-dependent mortality and fecundity (Harper 1977; Pacala and Silander 1985; Kobe 1996), which also occur widely, are equally straightforward to analyze and give qualitatively similar results.

In our model, establishment probability declines linearly with local density. We set the probability to 0 if it would otherwise be negative, which creates a nonlinear function of density. If the expected local density of residents competing with an invader is well below this cutoff point and the variance is small, then this nonlinearity does not matter; most or all of the individuals in the population will have realized fecundities falling on the linear part of the establishment function, and the expected fecundity will equal the fecundity at the expected local density. However, if the expected local density is near the cutoff or the variance is large, then we have to take the nonlinearity into account in calculating the expected fecundity. We discuss in "Accuracy of Moment Equations" how this correction limits accuracy for some parameter ranges and, more broadly in "Discussion," how nonlinear competition functions will affect spatial dynamics in general.

The competition kernel integrates to 1, so it determines just the scale and shape of the competitive neighborhood. For example, a typical field protocol for measuring local density would count the number of conspecific and heterospecific neighbors in a circular plot with radius ρ (Pacala and Silander 1987). This protocol assumes a uniform competitive neighborhood of the form

$$U_{ij}(s) = \begin{cases} 1/(\pi\rho^2) & s \leq \rho \\ 0 & s > \rho \end{cases} \quad (1)$$

A smoothly decreasing competitive neighborhood such as an exponential or Bessel function generalizes the uniform neighborhood by letting competition decrease gradually with distance. Normalizing the competition kernel means that we can adjust the scale and overall intensity of competition separately. In particular, as the spatial scale of competition becomes large, plants compete with a large number of neighbors but weakly with any particular neighbor, and the model converges to the (nonspatial) Lotka-Volterra competition equations, except for the cutoff of decreasing establishment probability at 0.

Although simple, this model connects to the classical Lotka-Volterra equations for large neighborhood sizes or large dispersal distances, it incorporates local competition and dispersal, and it allows us to consider some of the

mechanisms of interaction among plants. In principle, we can derive the competition kernels from mechanistic models of resource foraging. All of the processes included in the model can be calibrated at the individual level from greenhouse experiments or field data. The model omits a number of factors that clearly affect plant competition and coexistence: asymmetric competition for resources; environmental variability in space and time; and individual variability in size, foraging ability, and genetic makeup. We could incorporate many of these factors into the moment-equation framework but at the cost of increased complexity. This model is the simplest approach to stochastic, fully spatial plant competition.

Spatial Covariances

In order to understand where the spatial patterns in figure 1 come from and to lay the foundations for a dynamical model of such patterns, we need to define statistical measures of spatial pattern. We want statistics that will specify the degree of within-species clustering or thinning and the degree of between-species association or segregation.

The spatial covariance does the job. If we have a set of sample plots with mean density \bar{n} , and two particular plots at spatial locations x and y with population densities $n(x)$ and $n(y)$, then the spatial covariance for a spatial separation of $|x - y|$ is $c(|x - y|) \equiv \langle [n(x) - \bar{n}][n(y) - \bar{n}] \rangle$ where $|x - y|$ is the distance between x and y and angle brackets $\langle \cdot \rangle$ denote an expectation. (We assume a spatially homogeneous competitive arena, so that the covariance depends only on the distance between two points and not on their positions.) Random spatial patterns have zero spatial covariances at all distances, clustered patterns have positive covariances, and even patterns have negative covariances.

A two-species system has three covariances: two intra-specific covariances describe the clustering of each species with itself, and the cross-covariance describes the association or segregation between species (fig. 2B). As we will see, the cross-covariance is always negative in competitive systems; in the absence of positive interactions between species or environmental heterogeneity, interspecies competition always pushes clusters of different species apart. We refer to negative spatial covariances as negative association or positive spatial segregation: decreasing cross-covariance means increasing segregation.

The spatial covariances act on the community dynamics through the average covariance,

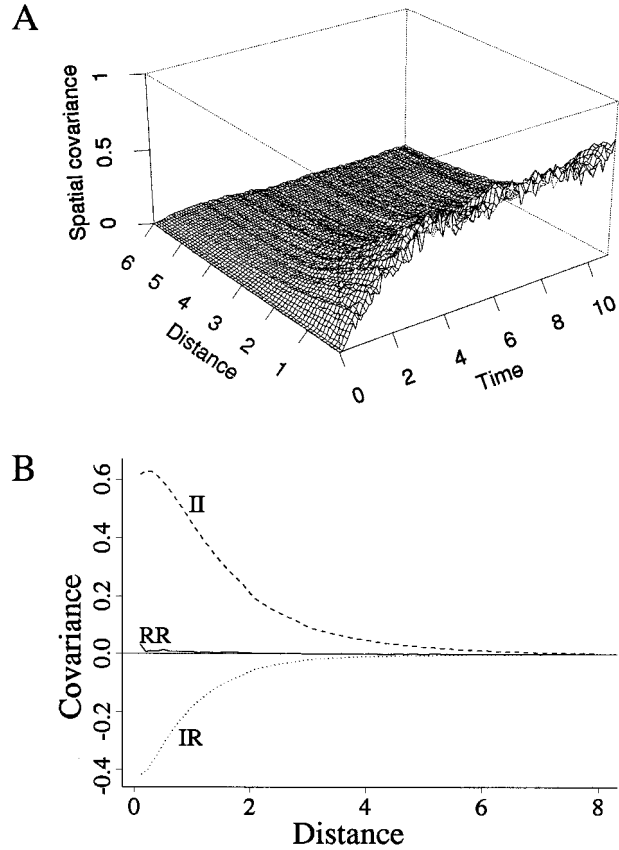


Figure 2: Summary spatial statistics for the spatial dynamics shown in figure 1. A, Spatial covariance of the invader (c_{ii}) as a function of distance and time. B, Spatial covariances as a function of distance, time-averaged between $t = 65$ and 90 : dashed line shows invader autocovariance (II), dotted line shows cross-covariance (IR), solid line shows resident autocovariance (RR).

$$\begin{aligned} \bar{c}_{ij} &\equiv \int_{\Omega} \int_{\Omega} D_i(|s - s'|) U_{ij}(|s'|) c_{ij}(|s|) ds' ds \\ &= \int_{\Omega} (D_i * U_{ij})(|s|) c_{ij}(|s|) ds, \end{aligned} \quad (2)$$

where $D_i * U_{ij}$ is the convolution of the dispersal and competition kernels. The covariance is weighted by this convolution because seedlings settle in a dispersal neighborhood D around their parents and must survive interference from adults within a competition neighborhood U around their landing site. The convolution of the dispersal and competition kernels ($D * U$) gives the result of combining the competition neighborhoods around every point in the

dispersal neighborhood: it defines the overall “establishment neighborhood.” This establishment-neighborhood weighting for the average covariance will also emerge naturally from our equations for the spatial dynamics (“Moment Equations”).

Moment Equations

Derivation

In order to see how spatial pattern itself builds up, to see what determines intra- and interspecific covariances, and to explain the origin of the crowding indices presented above, we derive equations for the dynamics of the mean densities and spatial covariances, the first two spatial moments. To derive an equation for the mean density, we break space up into small boxes, determine the expected change in occupancy of the boxes as a result of plant births and deaths, and take limits to get an equation in continuous space and time. Appendix A gives the technical details. As discussed in more detail there, the process of breaking space into discrete boxes is a temporary artifact of the derivation: the boxes are irrelevant to the population dynamics.

The resulting equations for the mean densities are just the Lotka-Volterra competition equations with corrections for spatial structure:

$$\frac{d\bar{n}_I}{dt} = r_I \bar{n}_I \left\{ 1 - \frac{\bar{n}_I + (\bar{c}_{II}/\bar{n}_I)}{K_I} - \frac{\beta_{IR}[\bar{n}_R + (\bar{c}_{IR}/\bar{n}_I)]}{K_R} \right\}, \quad (3)$$

$$\frac{d\bar{n}_R}{dt} = r_R \bar{n}_R \left\{ 1 - \frac{\bar{n}_R + (\bar{c}_{RR}/\bar{n}_R)}{K_R} - \frac{\beta_{RI}[\bar{n}_I + (\bar{c}_{IR}/\bar{n}_R)]}{K_I} \right\} \quad (4)$$

(see table 1 for parameter definitions). The subscripts *I* and *R* refer to the invader and resident species. In the rest of the article, we will be discussing invasions of competitively dominant resident species by competitively inferior invader species using spatial strategies.

The \bar{c} terms in equations (3) and (4) are the average spatial covariances weighted by the competition kernels, exactly as defined in “Spatial Covariances.” Thus, the numerators contain the neighborhood densities or the conditional densities of each species given the presence of a focal plant of a particular species; for example, $\bar{n}_I + \bar{c}_{IR}/\bar{n}_R$ is the average density of the invader in the vicinity of a resident individual. (Here we neglect the Poisson variance of each species, which would add one to the conspecific neighborhood density of each species; we can subtract a constant from the fecundity parameter to account for self-competition.)

To find the dynamics of the spatial structure itself, we need equations for the spatial covariances. We find these in essentially the same way that we found the equations for the means, by finding the expected change in the product of the occupancies of two locations separated by a distance *s* (the details are given in app. A).

As discussed, we drop third spatial moment terms in order to close the system. We arrive at the following general equation for the dynamics of the covariance between species *i* and *j* at a distance *s*:

$$\begin{aligned} \frac{\partial c_{ij}(s)}{\partial t} = & -(\mu_i + \mu_j) & \text{a} \\ & + f_i(D_i * c_{ij})(s) + f_j(D_j * c_{ij})(s) & \text{b} \\ & + 2\delta_{ij} f_i D_i(s) \bar{n}_i & \text{b} \\ & - \sum_{k \in \{I, R\}} \{ \alpha_{ik} [\bar{n}_k (D_i * c_{ij})(s) & \text{c} \\ & + \bar{n}_i (U_{ik} * c_{jk})(s)] \} & \text{c} \quad (5) \\ & - \sum_{k \in \{I, R\}} \{ \alpha_{jk} [\bar{n}_k (D_j * c_{ij})(s) & \text{c} \\ & + \bar{n}_j (U_{jk} * c_{ik})(s)] \} & \text{c} \\ & - \sum_{k \in \{I, R\}} [2\alpha_{ik} \delta_{ij} D_i(s) \bar{n}_i \bar{n}_k] & \text{c} \\ & - \bar{n}_i \bar{n}_j [\alpha_{ij} U_{ij}(s) + \alpha_{ji} U_{ji}(s)], & \text{c} \end{aligned}$$

where $A * B$ denotes a convolution of two quantities (as in eq. [2]) and δ_{ij} is a Kronecker δ ($\delta_{ij} = 1$ if $i = j$, 0 otherwise). Equation (5) looks complicated, but it divides easily into terms representing three simple processes. Reproduction and local dispersal (pt. b) generate clustering (positive covariance) as offspring settle near their parents; density-independent mortality (pt. a) pushes the spatial structure toward randomness (0 covariance), from either a clustered or an even distribution, as random individuals die; and density-dependent establishment (pt. c) generates even spacing (negative covariance) as individuals establish preferentially in less crowded areas.

We use the equations for the mean and spatial covariances to derive invasion criteria for the system, the conditions under which the spatial patterns that form during an invasion allow the invader’s population density to grow rather than shrink. The invasion criteria depend on the quasi-equilibrium covariances, the spatial patterns that occur when the resident species’ mean density and spatial covariance are fixed at its monoculture equilibrium and the invading species’ mean density is near 0. This procedure is equivalent to linearizing around the monoculture equilibrium of the resident species, where the invader is

absent, and finding the invasion eigenvalues for the full spatial system (app. B gives technical details).

The resulting invasion criteria have the following form:

$$\begin{aligned}
 \text{spatial invasion rate} &= r_I(1 - \beta_{IR}) & \text{a} \\
 &- \alpha_{II}(\bar{c}_{II}/\bar{n}_I) & \text{b} \\
 &+ \alpha_{IR}(\bar{c}_{RR}/\bar{n}_R) & \text{c} \\
 &+ \alpha_{IR}(-\bar{c}_{IR}/\bar{n}_I) & \text{d} \\
 &> 0. & \text{(6)}
 \end{aligned}$$

The first term, $r_I(1 - \beta_{IR})$, gives the nonspatial invasion rate (the invading species' growth rate at low densities in an equilibrium monoculture of the resident if both species had completely global dispersal). The spatial terms (lines b, c, and d) describe how the spatial structure of the population at quasi equilibrium changes the competitive ability of the invader. When the invader clusters with itself, its self-competition is increased, weakening its invasion (line b); when the resident clusters with itself, it reduces its own density and provides for more space for the resident to invade (line c). When spatial segregation (negative spatial association, which throughout this article we will consider $-\bar{c}_{IR}$) is strong, the invader competes less with the resident (line d).

Accuracy of Moment Equations

How accurate are the moment equations? Do they produce quantitatively or qualitatively accurate results in ecologically relevant parameter regimes? In a previous article (Bolker and Pacala 1997), we showed how well the moment approximation predicted the equilibrium mean and covariance for a single-species population with density-dependent mortality in a one-dimensional habitat. For large spatial scales, such that individuals interacted with >80 neighbors, the nonspatial, moment approximation and simulation results were indistinguishable; for intermediate spatial scales (eight to 80 neighbors), the moment approximations predicted the simulation results (which were different from the nonspatial results) within $\approx 10\%$; and for short spatial scales, fewer than eight neighbors, the moment approximations failed. Similarly, figure 3 shows how well the moment approximations predict the equilibrium mean densities (fig. 3A) and covariances (fig. 3B) for a two-species symmetric competition case: both species have the same fecundity and mortality parameters, but the within- and between-species competition coefficients differ (if they did not, we would have a spatial drift process). As discussed elsewhere (Pacala and Levin 1998),

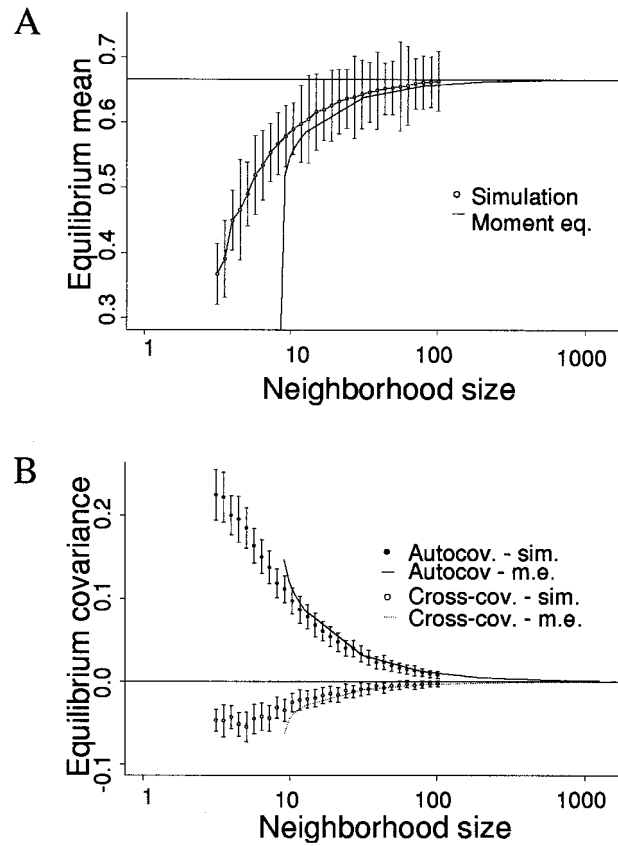


Figure 3: Accuracy of the moment equations as a function of neighborhood size for a symmetric two-species case. Parameters: $r = \{1, 1\}$; $R = \{1.2, 1.2\}$; $K = \{1, 1\}$; $\beta = \{0.5, 0.5\}$; $m_U = \{\{1, 1\}, \{1, 1\}\}$; $m_D = \{1, 1\}$; length = 50. Error bars give the standard deviations of these values, measured every 0.05 time units from $t = 10$ –50. Neighborhood size is defined as the area of a uniform neighborhood (eq. [1]) that gives the same average covariance as a given competition kernel: for a Bessel function kernel with scale parameter m , the neighborhood size equals $4\pi m^2$. A, Equilibrium mean as a function of neighborhood size. B, Equilibrium covariances (within and between species) as a function of neighborhood size.

a community of symmetric species develops within-species spatial clustering and between-species spatial segregation at equilibrium, changing the balance of intra- and inter-specific competition. Figure 3 shows that the results for the two-species, two-dimensional case are very similar to the single-species, one-dimensional case in our earlier article; here the moment equations work, producing sensible answers and predicting the full spatial system better than the nonspatial approximation, for neighborhood sizes of roughly 10–100 individuals.

How can we generalize from this example, which shows how the magnitude and effect of third moments varies with the number of neighbors in one particular system?

We do not have a complete answer because the general properties and spatial patterns associated with third moments are much less well known than those of spatial covariances. We do know from their definition that third moments describe the conditional density of a plant's neighborhood, given that it already has at least one neighbor. We can also show that third moments determine the variance of neighborhood densities, just as the second moments determine the means. On a more descriptive level, we know that landscapes with large-scale heterogeneity will have large variances in neighborhood density and hence large third moments. In particular, wave fronts and other patterns with sharp boundaries should have large third moments. Near sharp boundaries, plant densities change over a short distance while neighborhood densities, which are nearly the same for points on either side of the boundary, change more slowly. Second-order statistics like spatial covariances contain no more information than the neighborhood densities, so cannot describe these patterns accurately. Only statistics including the location of all the plants in the patch (higher moments) or statistics explicitly including spatial patch structure (spatial inhomogeneity) could capture this kind of spatial pattern (Hall and Gianakis 1995).

Results

Using the invasion criterion (eq. [6]), we can now analyze the ecological significance of endogenous spatial structure in the community. The invasion criterion connects the spatial structure of the community (invader and resident clustering and spatial segregation) with the colonization, exploitation, and phalanx growth spatial strategies. Each spatial strategy exploits a different aspect of the spatial community structure (spatial covariance), and each part of the spatial structure benefits exactly one strategy. The strategies completely partition the spatial variability of the environment caused by the clustering and segregation of the invader and resident species.

After a brief reminder of the important parameters governing spatial invasion and spatial strategies, this section will discuss each spatial strategy in turn, describing how each one operates and how it depends on life-history and dispersal parameters and giving an example of a simulated invasion depending on the particular strategy. The last part of this section discusses a general result emerging from the particular spatial strategies—that short dispersal, rather than long dispersal, is advantageous in communities of highly fecund species.

Life-History and Spatial Parameters and Spatial Invasion

In its most general form, with completely general life-history, competition, and spatial (dispersal and competition) parameters, the invasion criterion is still very complicated. We would like to simplify the criteria and to restrict the parameter space, if we can do it without sacrificing too much generality.

Our moment approximation restricts us to large competition and dispersal neighborhoods so that the neglected third moments do not grow too large. Analyzing the moment equations becomes more difficult the more different competition and dispersal scales there are, so for now we assume that competition neighborhoods are the same for all species ($m_{U_{ij}} = m_U$ for all i and j) and that, when a species has local dispersal, its competition and dispersal neighborhoods have the same scale ($m_D = m_U = m$). We will relax these assumptions later when we look at some numerical solutions of the invasion criteria ("General Cases: Numerical Calculation of Spatial Advantage").

This assumption gives us four possible spatial scenarios to examine, depending on whether the invader or the resident species have local or global dispersal. Any species that disperses globally avoids any direct effect of spatial structure since its offspring distribute themselves randomly, while local dispersers feel the full effect of spatial structure. As we will see, the global invader/local resident scenario corresponds to a pure colonization strategy (as in Crawley and May 1987 or Holmes and Wilson 1998), while the local invader/global resident scenario corresponds to either an exploitation or a phalanx strategy. These asymmetric scenarios contrast with the scenario where both species disperse locally, which allows a mixture of strategies, and the scenario where both species disperse globally, which reduces to the classical Lotka-Volterra competition model. By examining these four scenarios, we can explore four extreme sets of parameters, which allows us to interpolate (at least qualitatively) the behavior throughout parameter space. We will use numerical calculations to check our conclusions.

Finally, we modify the traditional assumption of complete competitive asymmetry slightly by assuming that, although the dominant species is secure against competitive displacement by the invader ($\beta_{RI} \ll 1$), the invader just barely loses to the dominant resident species (β_{IR} is just above 1). We will relax this assumption in "Phalanx Growth."

On a technical note, we will subdivide spatial segregation further into three parts. One has the same scale as the invader covariance, one has the same scale as the resident covariance, and one is a cross term that combines the invader and resident scales (pt. a is the spatial seg-

regation; pt. b is invader-scale segregation; pt. c is resident-scale segregation; and pt. d is cross-scale segregation):

$$\begin{array}{ll}
 \text{a} & (-\bar{c}_{IR}/\bar{n}_I) = (-\bar{c}_{IR,I}/\bar{n}_I) \\
 & + (-\bar{c}_{IR,R}/\bar{n}_I) \\
 & + (-\bar{c}_{IR,IR}/\bar{n}_I). \\
 \text{b} & \\
 \text{c} & (7) \\
 \text{d} &
 \end{array}$$

Separating the scales in this way will help us distinguish different spatial strategies below.

Colonization Strategies

The simplest example of a colonization strategy occurs when a globally dispersing species invades a short-dispersing, competitively dominant species (both species compete locally, with the same competitive neighborhood). This scenario illustrates the classical competition-colonization trade-off (Shmida and Ellner 1984; Tilman 1994; Holmes and Wilson 1998): when can a plant species overcome a competitive disadvantage by using space better?

Global Invader, Local Resident. A globally dispersing species can invade a locally dispersing resident when the resident clusters and forms a highly uneven monoculture, with gaps that the invader can exploit. Clusters form in monocultures when plants have low reproductive numbers, compensated for by tolerance of stress or poor resource conditions, and short dispersal scales. These properties describe a shade-tolerant or late-successional life-history strategy (Bolker and Pacala 1997). With equal competition and dispersal scales, the resident forms monospecific clusters, lowering its mean density below its nonspatial carrying capacity, if

$$R_R < 2. \quad (8)$$

The full invasion criterion for the global invader/local resident case, which determines when the effect of resident clustering (the only spatial effect in this case) is strong enough to overcome the nonspatial competitive disadvantage ($1 - \beta_{IR}$), is

$$1 - \beta_{IR} + \frac{\beta_{IR}}{4\pi m^2} \times \frac{R_R - \log(R_R - 1) - 2}{2 - R_R} > 0$$

(app. B). Invasion in this case depends only on the competition parameter β_{IR} , the spatial scale m , and the resident reproductive number R_R . If the invader is close enough to being able to invade in the nonspatial case ($\beta_{IR} \approx 1$), if competitive and resident dispersal scales are short (small

m) so that spatial effects are strong, and if the resident has a small reproductive number (low R) so that it clusters, then the invasion can succeed. This criterion matches the classical competition-colonization trade-off, where a species that is weakly excluded in a nonspatial arena can nevertheless invade, and coexist, in a spatial arena because the resident is such a poor colonizer (it has a small reproductive number and local dispersal) that it leaves empty habitat in the environment that the high- R , globally dispersing species can exploit.

Figure 4A shows the invasion of a globally dispersing species into such a monoculture. In the nonspatial case, the invader fails to establish, going extinct (in this particular realization) 35 time steps after introduction, while in the spatial simulation the invader succeeds. The moment equations correctly predict the qualitative result, but they underpredict the speed of invasion and the eventual equilibrium abundance of the invader. Closer examination shows that the nonlinearity induced by the cutoff of establishment probability at 0 causes the discrepancy. The cutoff makes establishment a nonlinear, concave-up function of density, and since there is variance in resident density, the invader's growth is faster than expected from the mean resident density because of Jensen's inequality (Gradshteyn and Ryzhik 1980; Smallwood 1996). We can estimate the variance in resident density perceived by the invader fairly accurately and use it to calculate a correction term, but the interaction of nonlinear competitive functions and spatial structure is potentially complex; we discuss the effects of nonlinear competition briefly in "Discussion."

Local Invader, Local Resident (Equal Scales). In the opposite spatial scenario, with a globally dispersing resident and a local invader, the resident clustering term disappears and there is no colonization advantage (see "Short-Dispersal Strategies"). In the equal-scales case, however, where both the invader and resident disperse locally, the colonization advantage incorporates an extra term, the resident-scale segregation term $\bar{c}_{IR,R}$, from (7). This term represents the part of the cross-covariance that has the same scale as the resident self-covariance. Clustering and segregation work in opposite directions. A large resident reproductive number promotes segregation, which benefits the invader, because it increases the resident's sensitivity to competition, but the same sensitivity also decreases clustering, harming the invader.

If $\beta_{IR} \approx 1$ (weak exclusion in the nonspatial case) and the resident has reasonably high fecundity ($R_R > 2$), then the criterion for a spatial advantage (the net effect of resident-scale segregation and resident clustering helps the invader) is $R_I > R_R$. As mentioned above, this result agrees with the results of patch models with an estab-

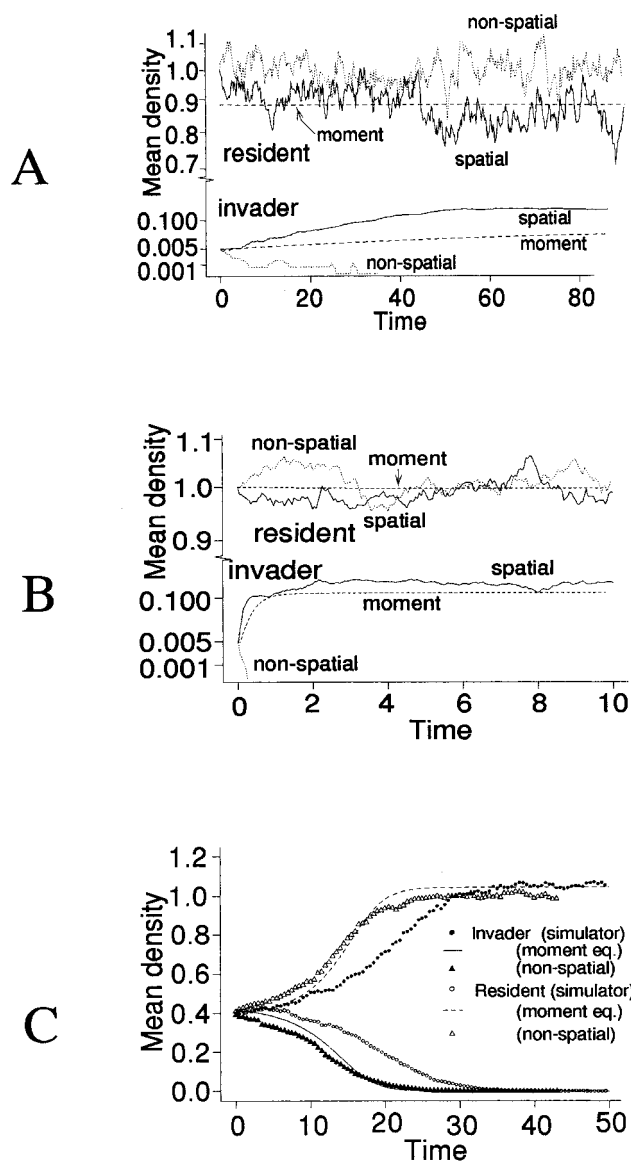


Figure 4: Spatial invasions: mean densities versus time. The panels show densities of invader (lower lines) and resident (upper lines) for one realization of a spatial simulation, the predictions of the moment equations, and, for comparison, one realization of a nonspatial simulation where both species disperse globally. *A*, Colonizer invading a competitively dominant resident. Parameters: $r = \{1, 1\}$; $R = \{10, 1\}$; $K = \{1, 1\}$; $\beta = \{1.1, 0.1\}$; $m_D = \{\infty, 0.909\}$; $m_U = \{0.909, 0.909\}$. *B*, Exploiter invading a competitively dominant resident. Parameters: $r = \{100, 1\}$; $R = \{10, 2\}$; $K = \{5, 1\}$; $\beta = \{1.1, 0.1\}$; $m_D = \{0.5, \infty\}$; $m_U = \{0.5, 0.5\}$. *C*, Phalanx invader. Parameters: initial density = $\{0.38, 0.42\}$; $r = \{1, 1\}$; $R = \{5, 5\}$; $K = \{1, 1\}$; $\beta = \{1.5, 1.5\}$; $m_D = \{1, \infty\}$; $m_U = \{1, 1\}$. Note that in 1/20 of the nonspatial runs, the invader was able to win by chance even though it started at a lower density (the spatial invasion succeeded in 10/10 spatial replicates).

lishment hierarchy, where stronger competitors can prevent colonization of weaker competitors but not displace them from existing sites. If the resident has very low fecundity ($R_R < 2$), the situation is more complicated (see app. D).

The main conclusion from this example—not a novel one—is that long-range dispersal or high fecundity can benefit an invading species (see also Durrett and Levin 1998). For the long-dispersal strategy to work, however, the local resident must form clusters in monoculture that reduce its mean density so that the global invader has space to colonize. Most realistic life-history parameters for plants lead to even spacing in monoculture or to extremely weak clustering (Bolker and Pacala 1997). Reproductive numbers (R) for plants are typically on the order of hundreds, if not thousands (Harper and White 1974), making a competition-colonization trade-off difficult unless we relax our assumptions and make the resident's dispersal scale much shorter than its competition scale, which is also biologically unrealistic. Thus, under symmetric, linear competition, a competition-colonization trade-off is unlikely to benefit a long-dispersing species unless there are additional sources of heterogeneity such as spatially patchy resource distributions or disturbance regimes that will lead to gaps in the resident's distribution. On the other hand, nonlinear competitive responses or size-structured competition (with adult plants such as forest canopy trees that are many times the size of seedlings) may increase the spatial heterogeneity caused by adult mortality and enhance colonization strategies.

Short-Dispersal Strategies

What about the converse case? Can a plant ever gain a competitive advantage by dispersing locally? The intuition derived from competition-colonization models (Tilman 1994) would say not, but we have seen that under the right conditions ($R_R > 2$) an invader can benefit from spatial segregation, which requires short dispersal. The two remaining spatial strategies, rapid exploitation and phalanx growth, both depend entirely on short dispersal.

If we let the resident disperse globally and give the invader local dispersal and competition scales equal to the resident's competition scale, the colonization (resident clustering and resident-scale segregation) terms discussed in the previous section disappear. Then we can understand the effect of spatial structure on the invasion, using only the balance between invader clustering and invader-scale and cross-scale segregation terms (7). These spatial structures define two different short-dispersal strategies. In a rapid exploitation strategy, when cross-competition is asymmetric ($\beta_{IR} \gg \beta_{RI}$), cross-scale segregation ($\bar{c}_{IR, IR}$) helps the invader. In a phalanx strategy, when interspecific

competition is strong ($\beta_{IR}\beta_{RI} \geq 1$), the net effect of invader clustering and invader-scale segregation helps the invader. These strategies are mutually exclusive; they cannot both work and still allow the invader to be only weakly excluded by the resident in the nonspatial case.

Rapid Exploitation. In the global resident/local invader scenario, an exploitation strategy applies (cross-scale segregation helps invasion) if

$$\frac{r_I}{r_R} > \frac{(R_I - 1)}{2 - \beta_{IR}(R_I - 1)} \quad (9)$$

and

$$\beta_{IR}K_I(R_I - 1) > \beta_{RI}K_R(R_R - 1). \quad (10)$$

The exploitation strategy depends on the invader's competitive inferiority in the nonspatial case ($\beta_{IR} > \beta_{RI}$), fast invader growth ($r_I > r_R$), and small size of invaders ($K_I > K_R$; holding β constant, a large K_I corresponds to more individuals per unit biomass or per unit resource, indicating smaller individuals). An exploiter is a weedy species that grows fast and reaches maturity quickly, exploiting ephemeral gaps in the distribution of the resident species. Because of its competitive inferiority, it cannot maintain control of the gap once a resident arrives, but by then it will already have produced and dispersed enough offspring to other sites to survive (remember that in our model, even "local" dispersal functions have some probability of long-distance dispersal because space is continuous and the dispersal kernels have long tails).

Figure 4B shows the invasion of an exploiter with short dispersal into a monoculture of a globally dispersing resident. In this case, the moment equations accurately predict the dynamics of the full system.

In the equal-scales scenario, criterion (9) is modified slightly to

$$\frac{r_I}{r_R} > \frac{(R_I - 1)}{2 - \beta_{IR}(R_I - 1)} \times \frac{R_R - 2}{R_R - 1}. \quad (11)$$

The extra term $(R_R - 2)/(R_R - 1)$ makes an exploitation strategy easier with a locally dispersing resident than with a globally dispersing resident.

Phalanx Growth. As suggested in the introduction, there is one case where endogenous spatial structure can help a tolerant strategy. This phenomenon, which we call phalanx growth, occurs when interspecific competition is stronger than intraspecific competition so that a plant can exclude heterospecific competitors by filling its neighborhood with its own offspring (Solé et al. 1992; Gandhi et

al. 1998). In the global resident/local invader scenario, a phalanx growth strategy applies (the net effect of invader clustering and invader-scale segregation helps invasion) if

$$\beta_{IR}\beta_{RI} > \frac{R_R + (1 - \beta_{IR})(R_I - 1)}{R_R - 1} \approx 1. \quad (12)$$

When does this criterion hold? In particular, what values of the right-hand side are possible in (12)? Since we assume that the invader cannot establish in a nonspatial setting, $\beta_{IR} > 1$ and so the second term in the numerator of the fraction is negative. Our model only applies when the invader's response to competition is approximately linear, so we can only allow parameters that give the invader a positive establishment probability, away from the 0 cutoff, when it is rare. This criterion, $f_I - \alpha_{IR}K_R > 0$, is equivalent to requiring $(1 - \beta_{IR})(R_I - 1) > -1$. Finally, resident reproductive number R_R must be >1 ; if it is >2 , the right-hand side of (12) is >1 . Thus, phalanx strategies typically apply when species gain an advantage by increasing their local density, which leads to founder control in the nonspatial model. Phalanx growth is a special case of a tolerant or space-holding strategy, where one species lowers local resource levels or otherwise makes a neighborhood uninvadable by increasing its local density. This strategy is available to any species that can tolerate its own environmental degradation, from shade-tolerant trees to allelopaths (Iwasa et al. 1998).

Because the phalanx strategy holds in a different part of parameter space from the previous strategies, we show a different kind of example from those shown in the colonization (fig. 4A) and exploitation (fig. 4B) examples. Rather than showing how spatial structure encourages invasion of a competitive subordinate, we show how it changes the balance between equivalent species in a founder-control situation. Figure 4C shows that the invader benefits from short dispersal; it can take over the habitat even when it starts from a lower density that would lead to its exclusion if all species had global dispersal (an effectively nonspatial model). As in the colonization example (fig. 4A), the moment equations correctly predict the qualitative outcome.

In the equal-scales scenario, the invasion criterion becomes

$$\beta_{IR}\beta_{RI} > \frac{R_R - 1 + (1 - \beta_{IR})(R_I - 1)}{R_R - 1}, \quad (13)$$

where the right-hand side is now slightly <1 ; as with exploitative strategies, phalanx strategies are slightly stronger against a locally dispersing resident than against a globally dispersing resident.

*General Cases: Numerical Calculation of
Spatial Advantage*

We have categorized spatial strategies and written down explicit expressions for the invasion criteria on the basis of special scenarios—either one of the two species has global dispersal or both have dispersal scales equal to their competition scales. For arbitrary competition and dispersal scales, we can still find the speed of invasion numerically for a particular set of competition life-history parameters.

To put the results from the previous section into context and to emphasize both the importance of reproductive number (R) in determining the outcome of spatial competition and the potential value of short dispersal strategies, we show one example of numerically computed spatial advantages (the difference between the speed of nonspatial and spatial invasions or the sum of the spatial terms in eq. [6]). Figure 5 shows the spatial advantage of the invader for a range of different invader and dispersal scales, with the competition scale fixed and equal for both species, for different reproductive numbers.

In figure 5A, both species have low fecundity. Long dispersal benefits the invader because low fecundity leads to strong clustering, which individuals can escape by long dispersal. The colonization advantage is strong, and long dispersal is advantageous, because $R_R < 2$. Interestingly, however, if the resident has very short dispersal, then the invader can increase its growth rate by dispersing a shorter distance (although still farther than the resident) because the advantage of increasing segregation outweighs the disadvantage of increasing self-clustering.

Conversely, if both species have high fecundity (fig. 5B), the invader can only overcome a competitive disadvantage by dispersing a shorter distance than the resident. With high fecundity, little clustering occurs. The only way to gain spatial advantage is to take advantage of segregation by short dispersal, keeping offspring within the relatively competitor-free neighborhood of their parents.

As claimed, these results show the importance of R and the potential advantages of short dispersal. In addition, they show that, even in intermediate cases when multiple spatial strategies (colonization and exploitation) operate simultaneously, we can understand the effects of space in terms of these strategies.

Discussion

The results of our analyses and numeric solutions have given us a great deal of food for thought. Endogenous spatial structure, as described by spatial covariances, separates naturally into three components each of which is exploited by a single spatial strategy. Colonization strategies use resident clustering and resident-scale segregation,

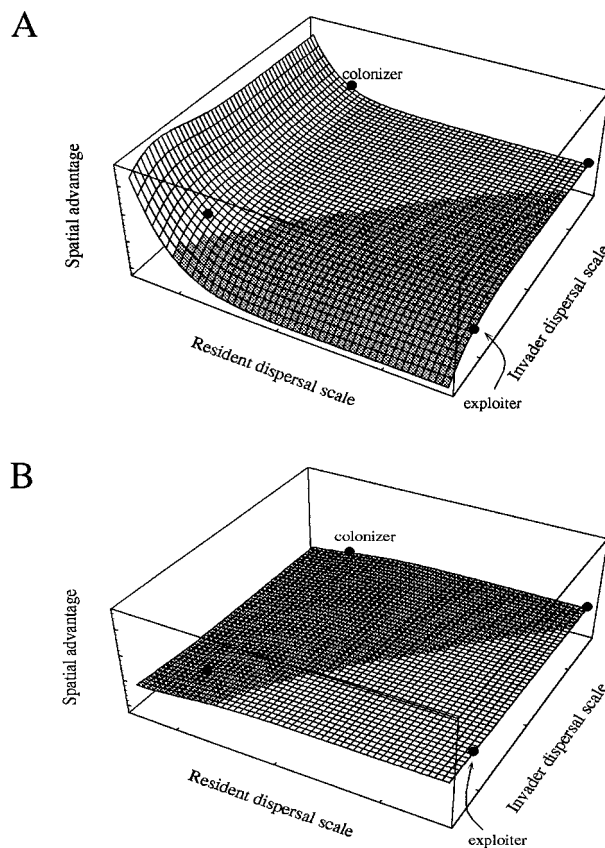


Figure 5: Spatial advantage (spatial part of the invasion eigenvalue) as a function of resident and invader dispersal scales, for small and large reproductive numbers. Other parameters: $r = \{1, 1\}$; $K = \{1, 1\}$; $\beta = \{1.1, 0.1\}$. Dark gray shows regions of spatial disadvantage; light gray shows regions of spatial advantage. Points show different special cases (both species globally dispersing; one species globally dispersing, the other dispersing locally with the same scale as the competition neighborhoods; both species locally dispersing with the same scale as the competition neighborhoods), as discussed in text. A, Small reproductive numbers: $R_I = R_R = 1.2$. B, Large reproductive numbers: $R_I = R_R = 10$.

phalanx growth uses invader clustering and invader-scale segregation, and exploitation strategies use cross-scale segregation. While each part of the spatial structure is used by exactly one strategy, more than one strategy can operate simultaneously. In particular, an invading species with intermediate dispersal can use both colonization and exploitation strategies, benefiting both from the resident's clustering and resulting in reduced density and from gaps in the resident's distribution. Colonization and exploitation have often been confounded in the past, partly because of modeling strategies but also because they are likely to occur together in natural communities. Since species can easily combine colonization and exploitation strategies and since both are effective strategies for weedy, early suc-

cessional species, we should not necessarily expect to find separate taxa of colonizers and exploiters in the wild.

These insights are not unique to our approach—all of the effects we have pointed out here can arise from pseudospatial models as well (Pacala and Rees 1998). The problem with patch models (and lattice models also) is not that they cannot capture the full spectrum of spatial strategies, but that they have been used with overly restrictive assumptions. Our model starts from a fairly general description of competition in continuous space and makes as few assumptions as possible about the temporal and spatial scales of competition and dispersal. In addition, it uses parameters that arise from the life-history strategies of individuals and can be measured in the field.

Several theoretical studies have suggested that spatial structure tends to slow ecological dynamics, reducing competition and bringing communities closer to random drift (Shmida and Ellner 1984; Hurtt and Pacala 1995; Lehman and Tilman 1997). Our model does not suggest such a general slowing-down. Although spatial structure always reduces interspecific competition in our models, it often intensifies intraspecific competition so much that competitive dynamics are actually faster than in the nonspatial case; the magnitude of the spatial invasion rate, determined by the balance of terms in (6), may be either larger or smaller than the magnitude of the nonspatial invasion rate. In fact, if competitive outcomes are finely balanced in the nonspatial case ($\beta_j \approx 1$), it is likely that spatial dynamics will increase the magnitude of the invasion eigenvalue, speeding up the final outcome of invasion whether it is coexistence or extinction. Higher-order moments may systematically slow down dynamics; in particular, we know from analogies to physical models such as the contact process that higher moments do retard dynamics when the reproductive numbers of individuals are just above 1 and the entire system approaches a critical point. However, no one knows whether ecological systems really display critical behavior, and the question of space and ecological timescales remains unresolved in general.

Finally, there is a connection between the short-dispersal strategy we call phalanx growth and the empirical observation that some species of clonal plants adopt different growth forms in different environments (Lovett-Doust 1981; Silvertown and Doust 1993). The “guerrilla” growth form, with widely dispersed ramets, generally occurs in nutrient-poor environments, while the “phalanx” growth form, with closely spaced ramets, occurs in nutrient-rich environments. These observations have little theoretical foundation, although Harada and Iwasa (1994) do discuss them briefly in the context of a lattice model.

Nutrient-poor environments should lead to low reproductive numbers (R) for all species, increasing clustering and favoring long-dispersal strategies (fig. 5A), and vice

versa (fig. 5B). While resource heterogeneity and other factors also affect the growth forms of clonal plants, and the connection between phalanx growth in our model and in the field is only suggestive at present, we hope to make a stronger case by investigating the measured demographic parameters of these species. In any case, we are encouraged that our analysis predicts a known phenomenon that we did not set out to model.

In the remainder of this discussion, we will suggest empirical tests of our conclusions, tie in our analyses with the insights gained from other (nonspatial and spatial) ecological research, and consider why the moment equations seem to overstate the advantages of short dispersal.

Empirical Tests

Our model is admittedly simple, but it makes testable predictions that could apply to competition in simple even-sized communities such as annual grasslands or dune communities or to competition between clonal perennials. The predictions that spatial pattern forms endogenously and that spatial pattern can affect competitive outcomes have both been tested by modeling and experiment (Pacala and Silander 1987; Pacala and Deutschman 1995; Pacala et al. 1996; Rees et al. 1996), but so far no one has empirically tested both of these predictions in the same system.

Several authors have suggested useful empirical tests based on the conclusions of patch models (Tilman 1994; Pacala and Rees 1998). Our suggestions do not supersede these tests, which manipulate nonspatial parameters such as fecundity and competitive exclusion. Instead, we focus on modifying the inherently spatial aspects of population dynamics by manipulating dispersal parameters.

To test for a classical competition-colonization trade-off (Tilman 1994), one needs to collect a large number of seeds from both species (which may be difficult because the competitively superior species typically has low fecundity) and introduce these seeds into experimental plots to overcome the colonization (fecundity) limitation of the dominant species; if the competitive inferior is excluded, we can infer that coexistence occurs through a competition-colonization trade-off. However, this manipulation confounds the effects of fecundity and dispersal; it boosts the individual fecundity f , which in turn affects all of the population-level life-history and competition parameters (r , R , K , β), as well as the dispersal scale. As we discuss further below, fecundity rather than dispersal governs the classical competition-colonization trade-off, and increasing fecundity without changing dispersal is difficult.

Our model, which is spatial rather than pseudospatial, suggests an easier manipulation that does not confound fecundity and dispersal; rather than providing extra seeds,

manipulate the spatial distribution of seeds by harvesting all seeds from the competitively dominant plants within an experimental plot and spreading them randomly throughout the plot. (This experiment should continue over several seasons to give spatial distributions and population dynamics of the community a chance to respond; how long depends on the life histories of the species in the community.) Since the competition-colonization trade-off depends on resident clustering and resident-scale segregation, which are maintained by local dispersal of the resident, this experiment should eliminate any competition-colonization advantage; if competitive exclusion results, it proves the existence of a competition-colonization trade-off.

Conversely, to test the hypothesized advantages of short dispersal and spatial segregation, one could collect the seeds of the competitively inferior species and disperse them randomly throughout the plot; this manipulation randomizes the competitive environments of seedlings, eliminating all spatial effects except resident clustering. If exclusion occurs, then a short-dispersal advantage—exploitation or phalanx growth—was maintaining diversity in the community. It is harder to separate exploiter and phalanx growth strategies by dispersal experiments, but the life-history and competitive parameters associated with these two strategies are quite different and should be easy to tell apart.

These mechanisms are not exclusive: one or both may operate in a given community. Measuring community changes following global dispersal seeds of both (or all) species in community will detect any community effects of spatial structure. Although it does not distinguish between competition-colonization and short-dispersal effects, it is a useful general test of spatial dynamics; in addition, it may detect the effects of a combination of short- and long-dispersal effects where either is too weak to detect alone.

Finally, instead of experimental manipulations, one could test our hypotheses observationally by calibrating an individual-based model of a community. Since all of the parameters in our model are defined at the level of individual performance, one can estimate all of the life-history (f, μ), competitive (α_{ij}), and spatial (U, D) parameters from lab or field observations. Running the calibrated model predicts the spatial structure and competitive outcomes expected from the community, which can be tested against field observations (and compared to the moment equations to see whether they are robust for a particular set of parameter values); propagating the estimated error in the measured parameters through the model and running multiple realizations of the stochastic model shows the range of uncertainty in the predictions (Pacala et al. 1996). The calibrated model can also be used to run sim-

ulated “experiments” and to quantify the sizes of the different clustering and segregation terms, which define the balance of spatial strategies maintaining diversity in the community. This approach extends the general idea of neighborhood models (Pacala 1986a, 1986b), in particular Rees et al.’s (1996) tests of the importance of spatial structure in reducing interspecific competition, by estimating the formation of spatial structure by local dispersal and competition as well as the effect of spatial structure on population dynamics and community structure.

Short Dispersal Advantages: Fact or Fiction?

Our model suggests strong advantages to short dispersal, and no possibility of a long-dispersal advantage, for most ecologically realistic situations (reproductive number R , or lifetime fecundity in the absence of competition, >2). Rather than deny the ubiquity of evolutionary adaptations for long dispersal, we use our system as a null model: what properties of natural plant communities beyond local competition and dispersal determine the ecological and evolutionary advantages of different spatial strategies? There are two fundamental, interacting pieces missing from our model: additional sources of variability (environmental heterogeneity, size structure, disturbance, etc.) and nonlinear competition functions.

Sources of Variability

Any process that makes the environment more spatially heterogeneous will enhance both the invader and resident clustering terms in our invasion criterion (eq. [6]), leading to long-dispersal advantages and competition-colonization trade-offs. Size-structured, asymmetric competition (as in perennial grassland or forest communities: Westoby 1982; Weiner and Thomas 1986; Kohyama 1993; Peterson and Squiers 1995; Schwinning and Fox 1995) and spatially correlated disturbance (by fire, wind, gophers, etc.: Pickett and White 1985; Moloney and Levin 1996) will both increase clustering by increasing the size and persistence of spatial gaps in a resident population, strengthening both the colonization and exploitation strategies.

Adding either size structure or correlated disturbance to the moment equation framework is straightforward. For a simple form of size structure, we could just make the competition neighborhoods of each species asymmetric, so that each dominant competitor interacted with many smaller invaders. This modification would work well for between-guild competition (between, e.g., grasses and trees) but less well for forest trees, which all attain the same maximum size. Understanding forest dynamics requires a size-structured model where individuals take time to grow and fill gaps. We are now exploring moment equa-

tions with vertical spatial structure, along the lines of Kohyama's work with the evolution of height distributions in stochastic populations (Kohyama 1992*a*, 1992*b*, 1993).

We can rederive the moment equations taking environmental heterogeneity, expressed as the spatial covariances of environmental variables, into account (D. Hiebler [unpublished manuscript] has applied this approach to lattice models). If resources are completely randomly distributed in space, then spatial variability will only change competitive outcomes if performance is a nonlinear function of environmental conditions because an individual's advantageous location is never passed on to its offspring. If resources are spatially correlated, and (e.g.) fecundity depends on local resource availability, a plant's offspring will inherit some of their parent's environment, increasing clustering because more offspring can establish locally. Without analyzing the model, however, it is hard to tell whether environmental heterogeneity will tip the balance toward short-dispersal advantage because areas near a parent plant are more favorable or toward long-dispersal advantage because these favorable areas encourage clustering.

Nonlinear Competition and Variance-Maximizing Strategies

When performance (survival, establishment, or fecundity) is a concave-up function of neighborhood density, a plant can increase the average performance of its offspring by increasing the variance of the environments they experience. As mentioned above, this advantage occurs because of Jensen's inequality (the mean performance across all environments is higher than the performance in the mean environment); it is the same advantage accruing to plants using dispersal in time or the storage effect (Chesson 1983, 1986) to persist in a temporally variable environment. Because the competition function is nonlinear, the benefit to offspring that land in good patches outweighs the loss to offspring that land in bad patches. With spatial segregation and environmental heterogeneity, there may be a trade-off between short dispersal, which allows the offspring to keep the benefits of their parent's environment, and long dispersal, which allows the offspring to find good patches elsewhere. Our guess is that a dual dispersal strategy combining mostly short-distance dispersal with a few long-dispersing propagules gives the largest increase in variance with the smallest decrease in performance in the mean environment.

Our neglect of third spatial moments is equivalent to assuming that neighborhood densities are Poisson distributed, with a mean and variance that we can calculate from

the mean densities and covariances. Given that the effects of both spatial covariance and nonlinear competition are small (we have assumed weak spatial effects through most of our analysis), nonlinearity directly affects only the change in the mean density. We compute the change in the mean by taking the expected value of the competition function over a Poisson distribution of neighborhood densities with the calculated mean and variance. We have actually calculated the changes in the mean allowing for nonlinearity for some of the examples shown above, and as expected it significantly improves the fit of the moment equations to the simulation results.

Even with random spatial patterns, nonlinear competition functions can lead to coexistence; with both spatial structure and nonlinearity, the range of possibilities increases enormously. We suspect the interaction of these two effects is extremely important in maintaining diversity in natural communities; one can imagine spatial gap specialists that exploit spatial covariance living side-by-side with nonspatial gap specialists that exploit neighborhood variance or, alternatively, that weedy species would combine both of these traits to coexist with resource monopolizing, competitively dominant species. We will explore this important interaction in a future article.

Conclusions

We have shown that colonization, rapid exploitation, and tolerance, three spatial strategies well known to plant community ecologists, emerge naturally from a simple model of spatial competition and local dispersal. Although more than one strategy can act simultaneously, each exploits a different part of the spatial covariance structure of the community; among them, the three strategies partition all of the spatial variability in the environment. Moment equations provide an analytic framework, based on measurable life-history and competitive properties of individuals, that synthesizes and clarifies the basic spatial dynamics of simple plant communities.

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APPENDIX A

Deriving Moment Equations

This appendix derives the moment equations for a two-species competitive system with density-dependent establishment. Another derivation is given in Bolker and Pacala (1997) for the single-species competition model with density-dependent mortality, and a similar derivation is given in Bolker et al. (in press).

We start by writing out the expected changes in occupancy of small areas of size h over small time steps Δt , taking expectations across different realizations, all starting from the same spatial configuration. We stress that the underlying locations and events are in continuous time and space and that starting the derivation with discrete space and time is for heuristic purposes only.

Our basic unit is $N_i(x)$, the number of individuals of species i in a region of size h around point x . The expected change in $N_i(x)$ in a small time step Δt , $\overline{\Delta N_i(x)}$, is the sum of the probabilities of different events multiplied by their effect on the number of individuals (Δt is short enough that only one event can happen). We need not be too specific at this point about whether we are in one- or two-dimensional space; as long as Ω is a (countably infinite) set of discrete regions that make up the entire space and can be indexed by their positions, the derivation below makes sense. We will denote the distance between two points x and y as $|x - y|$. (When we move to integrals of covariances below, we will integrate over all possible lags $s - s \in \{-\infty, \infty\}$ in one dimension or $s \in \{0, \infty\} \times \{0, 2\pi\}$ in two dimensions.)

Using the model defined in “Individual-Based Model,” we get

$$\begin{aligned} \overline{\Delta N_i(x)} = & \left\{ -\mu_i N_i(x) \right. & \text{a} \\ & + \left[\sum_{z \in \Omega} f_i N_i(z) \times h D_i(|x - z|) \right] & \text{b} \\ & \times \left[1 - \frac{1}{f_i} \sum_{j=1}^S \alpha_{ij} \sum_{y \in \Omega} N_j(y) \times U_{ij}(|x - y|) \right] & \text{c} \end{aligned} \quad (\text{A1})$$

$\Delta t,$

where part **a** is death, **b** is reproduction and dispersal, and **c** is establishment. Next we take a spatial average ($\langle \cdot \rangle$) on both sides, expanding summations and moving expectations inside sums:

$$\frac{\overline{\Delta N_i(x)}}{\Delta t} = -\mu_i \langle N_i(x) \rangle + \sum_{z \in \Omega} f_i h D_i(|x - z|) \langle N_i(z) \rangle - \sum_{j=1}^S \alpha_{ij} \sum_{y \in \Omega} U_{ij}(|x - y|) \langle N_i(z) N_j(y) \rangle. \quad (\text{A2})$$

Now we use our assumption that space is homogeneous. In particular we assume that the distribution of plants in space has second-order stationarity and isotropy (Diggle 1983; Cressie 1991), so that the distribution is entirely specified by mean densities that are independent of position and covariances that are a function only of distance between two points. Now $\langle N_i(x) \rangle$ is independent of x , so we drop the position (and angle brackets) and refer to it just as \bar{N}_i . The covariance $\hat{C}_{ij}(|x - z|)$, which, as noted above, is a function only of distance, equals $\langle N_i(x) N_j(z) \rangle - \bar{N}_i \bar{N}_j$.

Substituting these definitions into (A2), moving x to the origin because second-order stationarity implies that there is no preferred point in space (so that $|x - y| = |y|$) and using the fact that D and U both sum to $1/h$ (because they are the discrete analogues of kernels that integrate to 1), we get

$$\frac{\overline{\Delta \bar{N}_i}}{\Delta t} = f_i \bar{N}_i - \mu_i \bar{N}_i - h^{-1} \sum_{j=1}^S \alpha_{ij} \bar{N}_i \bar{N}_j - \sum_{j=1}^S \alpha_{ij} \sum_{z \in \Omega} \sum_{y \in \Omega} U_{ij}(|y|) D_i(|z|) h (\hat{C}_{ij}(|y - z|)/h). \quad (\text{A3})$$

Scaling to continuous space and time (dividing both sides of the equation by h), with $\bar{n}_i \equiv \lim_{h \rightarrow 0} \bar{N}_i/h$ and $\hat{c}_{ij} \equiv \lim_{h \rightarrow 0} \hat{C}_{ij}/h^2$, we get

$$\begin{aligned} \frac{d\bar{n}_i}{dt} &= f_i \bar{n}_i - \mu_i \bar{n}_i - \sum_{j=1}^S \alpha_{ij} \bar{n}_i \bar{n}_j - \sum_{j=1}^S \alpha_{ij} \int_{\Omega} \int_{\Omega} U_{ij}(|s|) D_i(|s' - s|) \hat{c}_{ij}(|s|) ds' ds \\ &= f_i \bar{n}_i - \mu_i \bar{n}_i - \sum_{j=1}^S \alpha_{ij} \bar{n}_i \bar{n}_j - \alpha_{ii} \bar{n}_i (U_{ii} * D_i)(0) - \sum_{j=1}^S \alpha_{ij} \int_{\Omega} (U_{ij} * D_i)(|s|) c_{ij}(|s|) ds \\ &= \left(f_i' - \mu_i - \sum_{j=1}^S \alpha_{ij} \bar{n}_j \right) \bar{n}_i - \sum_{j=1}^S \alpha_{ij} \bar{c}_{ij}, \end{aligned} \quad (\text{A4})$$

where we define the convolution of two kernels as

$$(A * B)(|s|) \equiv \int_{\Omega} A(|s|) B(|s' - s|) ds'.$$

In the second line in (A4), we have substituted

$$\hat{c}_{ii}(|s|) \equiv c_{ii}(|s|) + \bar{n}_i \delta(s). \quad (\text{A5})$$

In the last line, we define

$$\bar{c}_{ij} \equiv \int (U_{ij} * D_i)(|s|) c_{ij}(|s|) ds$$

and incorporate the $\bar{n}_i \delta$ term by modifying the effective fecundity $f_i' \equiv f_i - \alpha_{ii}(U_{ii} * D_i)(0)$.

The Dirac δ function in the covariance, an infinitely tall and thin spike at 0 that integrates to 1, so that

$$\int U_{ij}(|s|) \delta(s) ds = U_{ij}(0),$$

comes from our definition of covariance, and the scaling of h to 0. At some point as we go toward the continuous limit, h is small enough that there is never more than one individual per box. Then $\langle N_i^2 \rangle = \langle N_i \rangle$ and $\hat{c}_{ii}(0) = \lim_{h \rightarrow 0} (\bar{N}_i = N_i^2) h^{-2} = \bar{n}_i/h$, producing the δ function. (The expected value of $N_i N_j$, on the other hand, goes to 0 as $h \rightarrow 0$, so there is no δ function in the cross-covariance c_{ij} .) Heuristically, this term is a self-interaction term: no matter how small one scales the box immediately around a focal plant, the focal plant itself will always be there. In the mean equation, we can dispose of this term by incorporating it into the fecundity (any fecundity that we measure in the field will contain the self-competition term by default) or by defining it away, saying that $(U_{ii} * D_i)(0) \equiv 0$; in the covariance equation, however, it will have important consequences.

To derive the covariance equations, we follow essentially the same procedure, but we start from the expected change in the joint occupancy $N_i(x)N_j(w)$: in a small time Δt ,

$$\begin{aligned} \Delta \langle N_i(x) N_j(w) \rangle &= N_i(x) \Delta N_j(w) + N_j(w) \Delta N_i(x) + \Delta N_i(x) \Delta N_j(w) \\ &= N_i(x) \Delta N_j(w) + N_j(w) \Delta N_i(x) + O(\Delta t^2). \end{aligned} \quad (\text{A6})$$

The second line simplifies further to $2N_i(x)\Delta N_i(w)$ if $i = j$ and we assume that spatial sites are interchangeable. Following the definition of the covariance, we will eventually subtract off the expected change in the case of independence, $\langle \Delta N_i \rangle \langle \Delta N_j \rangle$, to get an expression for the covariance. Now we substitute in the same expressions for $\Delta N_i(x)$ and $\Delta N_j(w)$

as defined in “Individual-Based Model” and used in (A1), rearranging and moving expectations inside sums as we go:

$$\begin{aligned}
\Delta \langle N_i(x) N_j(w) \rangle &= [-(\mu_i + \mu_j) \langle N_i(x) N_j(w) \rangle \\
&\quad + f_i \sum_{z \in \Omega} h D_i(|z - x|) \langle N_i(z) N_j(w) \rangle \\
&\quad + f_j \sum_{z \in \Omega} h D_j(|z - w|) \langle N_i(x) N_j(z) \rangle \\
&\quad - \sum_{k=1}^S \alpha_{ik} \sum_{z \in \Omega} \sum_{y \in \Omega} h D_i(|z - x|) U_{ik}(|x - y|) \langle N_i(z) N_j(w) N_k(y) \rangle \\
&\quad - \sum_{k=1}^S \alpha_{jk} \sum_{z \in \Omega} \sum_{y \in \Omega} h D_j(|z - w|) U_{jk}(|w - y|) \langle N_i(x) N_j(z) N_k(y) \rangle] \Delta t.
\end{aligned} \tag{A7}$$

Next we expand terms of the form $\langle N_i(x) N_j(w) \rangle$ and $\langle N_i(x) N_j(y) N_k(z) \rangle$ in terms of moments, using the definition of the covariance and the triple expansion:

$$\begin{aligned}
\langle N_i(x) N_j(y) N_k(z) \rangle &= \bar{N}_i \bar{N}_j \bar{N}_k \\
&\quad + \bar{N}_i \hat{C}_{jk}(|z - y|) + \bar{N}_j \hat{C}_{ik}(|x - z|) + \bar{N}_k \hat{C}_{ij}(|y - x|) \\
&\quad + M_{ijk}(x, y, z),
\end{aligned} \tag{A8}$$

which we derive by expanding the central third moment $M_{ijk}(\underline{x}, y, \underline{z}) \equiv \langle [N_i(\underline{x}) - \bar{N}_i][N_j(y) - \bar{N}_j][N_k(\underline{z}) - \bar{N}_k] \rangle$.

Substituting this expansion, letting $M_3 = 0$, and subtracting $\bar{N}_i \langle \Delta N_j \rangle + \bar{N}_j \langle \Delta N_i \rangle$ to convert from the expected change in the joint product to the expected change in the covariance:

$$\begin{aligned}
\frac{\Delta \hat{C}_{ij}(|x - w|)}{\Delta t} &= -(\mu_i + \mu_j) \hat{C}_{ij}(|x - w|) \\
&\quad + f_i \sum_{z \in \Omega} h D_i(|z - x|) \hat{C}_{ij}(|z - w|) \\
&\quad + f_j \sum_{z \in \Omega} h D_j(|z - w|) \hat{C}_{ij}(|x - z|) \\
&\quad - \sum_{k=1}^S \alpha_{ik} \sum_{z \in \Omega} \sum_{y \in \Omega} h D_i(|z - x|) U_{ik}(|x - y|) [\bar{N}_k \hat{C}_{ij}(|z - w|) + \bar{N}_i \hat{C}_{jk}(|y - w|)] \\
&\quad - \sum_{k=1}^S \alpha_{jk} \sum_{z \in \Omega} \sum_{y \in \Omega} h D_j(|z - w|) U_{jk}(|w - y|) [\bar{N}_k \hat{C}_{ij}(|x - z|) + \bar{N}_j \hat{C}_{ik}(|x - y|)].
\end{aligned} \tag{A9}$$

Rearranging by pulling terms out of summations wherever possible, dividing both sides by h , and letting h and Δt go to 0, we get

$$\begin{aligned}
\frac{\partial \hat{c}_{ij}(|x-w|)}{\partial t} = & -(\mu_i + \mu_j) \hat{c}_{ij}(|x-w|) \\
& + f_i \int D_i(|z-x|) \hat{c}_{ij}(|z-w|) dz + f_j \int D_j(|z-w|) \hat{c}_{ij}(|x-z|) dz \\
& - \sum_{k=1}^S \alpha_{ik} [\bar{n}_k \int D_i(|z-x|) \hat{c}_{ij}(|z-w|) dz + \bar{n}_i \int U_{ik}(|x-y|) \hat{c}_{jk}(|y-w|) dy] \\
& - \sum_{k=1}^S \alpha_{jk} [\bar{n}_k \int D_j(|z-w|) \hat{c}_{ij}(|x-z|) dz + \bar{n}_j \int U_{jk}(|w-y|) \hat{c}_{ik}(|x-y|) dy].
\end{aligned} \tag{A10}$$

As in the derivation of the mean (eq. [A3]), we can move x to the origin (so that $|x-z| = |z|$, etc.) without loss of generality. Also as above, the last step is to use (A5) to pull self-interaction terms out of the covariances (\hat{c}); unlike in the mean equation, the terms including δ functions cannot be simply scaled or defined out of the equations. At this point, the equations for self-covariance (c_{ii}) and cross-covariance (c_{ij} , $i \neq j$) begin to differ because they have different self-interaction terms. We write out the general equation using a new piece of notation, the Kronecker δ ($\delta_{ij} \equiv 1$ if $i = j$, 0 otherwise). With this notation, we arrive at equation (5) in the main text.

None of the derivation so far has specified the form of the competition and dispersal kernels. Obvious choices for the kernels would be exponential or Gaussian distributions, some generalization of them, or (in two dimensions) Bessel kernels (Skellam 1951; van den Bosch et al. 1990; Lande 1991). Exponential ($\mathcal{K}(m, s) = 1/(2m) \exp(-|s|/m)$) and radially symmetric Bessel kernels ($\mathcal{K}(m, s) = 1/(2\pi m^2) K_0(|s|/m)$) are realistic, as well as being particularly convenient analytically; we will use one or the other, depending on whether we are working in one or two dimensions, henceforth. Since most of our expressions apply for all values of s , we will usually abbreviate $\mathcal{K}(m, s)$ as $\mathcal{K}(m)$.

APPENDIX B

Deriving Spatial Invasion Criteria

The spatial covariance equation (5) is a complicated-looking integral equation, but it has the important property that all of the covariance derivatives are either linear functions of kernels and covariances or linear functions of convolutions of kernels with covariances. Therefore, we can analyze the equations using Fourier transforms (James 1995): we denote the Fourier transform of a kernel $\mathcal{K}(m, x)$ by $\tilde{\mathcal{K}}(m, q)$ (alternatively, a covariance $c(x)$ transforms to $\tilde{c}(q)$). (We will abbreviate $\tilde{\mathcal{K}}(m, q)$ by $\tilde{\mathcal{K}}(m)$ where expressions do not depend explicitly on q .) Fourier transforms are linear, so we can interchange them with sums, integrals, or products with scalars. They also turn convolutions into products: $A * B$ transforms to $\tilde{A} \times \tilde{B}$ (this very useful property is actually the only reason we need Fourier transforms for the current problem). We can easily extend Fourier transforms to multidimensional cases: in particular, the two-dimensional, radially symmetric Fourier transform, known as the Hankel transform, has all the same properties as the standard one-dimensional transform (James 1995).

We start by taking the equilibrium covariance equations (setting the derivatives of [5] equal to 0), for fixed values of \bar{n}_I and \bar{n}_R . In particular, if we relabel the species as I (invader) and R (resident), and we take $\bar{n}_I \ll 1$ and $\bar{n}_R \approx \bar{n}_R^*$ (the monoculture equilibrium density of the resident), we have the quasi-equilibrium covariance equations. We can show that solving these equations and substituting the average covariances (\bar{c}) back into the equations for the mean densities ([3] and [4]) is equivalent to linearizing around the equilibrium $\{\bar{n}_I = 0, \bar{n}_2 = \bar{n}_2^*\}$ and solving for the invasion eigenvalues of the full spatial system. Heuristically, we look at the growth of the invader at a time after the spatial covariances have equilibrated but before the invader density has grown large. The spatial covariances involving the invader, \bar{c}_{II} and \bar{c}_{IR} , are small, of the same order as \bar{n}_I , so it is convenient to write expressions for the scaled covariances— \bar{c}_{II}/\bar{n}_I and \bar{c}_{IR}/\bar{n}_I .

In addition, we assume that the scale of dispersal and competition is relatively large, so that the effect of space on

the resident's density is small and can be separated cleanly from its nonspatial density. The equation for monoculture equilibrium density of species R is (from eq. [4])

$$\bar{n}_R^* + \frac{\bar{c}_{RR}}{\bar{n}_R^*} = K_R,$$

since \bar{c}_{RR} itself is $O(1/m)$, where m , the spatial scale of interactions, is large, we can say that $\bar{n}_R^* \approx K_R - \bar{c}_{RR}/K_R$.

Under these conditions, the relevant equations are

$$\frac{\bar{c}_{II}^*}{\bar{n}_I} = \frac{(f_I - \alpha_{IR}\bar{n}_R)\tilde{D}_I}{\mu_I - (f_I - \alpha_{IR}\bar{n}_R)\tilde{D}_I}, \quad (B1)$$

$$\frac{\bar{c}_{IR}^*}{\bar{n}_I} = \frac{-(\alpha_{IR}\tilde{U}_{IR} + \alpha_{RI}\tilde{U}_{RI})\bar{n}_R - \alpha_{RI}\bar{n}_R\tilde{U}_{RI}(\tilde{c}_{II}/\bar{n}_I) - \alpha_{IR}\tilde{U}_{IR}\tilde{c}_{RR}}{(\mu_I + \mu_R) - (f_I - \alpha_{IR}\bar{n}_R)\tilde{D}_I - (f_R - \alpha_{RR}\bar{n}_R)\tilde{D}_R + \alpha_{RR}\bar{n}_R\tilde{U}_{RR}}, \quad (B2)$$

$$\frac{\bar{c}_{RR}^*}{\bar{n}_R} = \frac{(f_R - \alpha_{RR}\bar{n}_R)\tilde{D}_R - \alpha_{RR}\bar{n}_R\tilde{U}_{RR}}{\mu_R - (f_R - \alpha_{RR}\bar{n}_R)\tilde{D}_R + \alpha_{RR}\bar{n}_R\tilde{U}_{RR}}. \quad (B3)$$

In order to simplify these expressions, we have to specify the form of the competition and dispersal kernels U_{ij} and D_i . Exponential and Bessel kernels have the convenient property (alluded to earlier) that their Fourier and Hankel transforms, respectively, are the same: $\tilde{K}(m, q) = 1/(1 + m^2 q^2)$, where q measures radial distance in the two-dimensional case. We can also use partial fractions to separate the expressions given above into sums of (Fourier transformed) exponential or Bessel kernels with different scale parameters: all of the necessary identities for the cases shown in this article are given in appendix C. Once we have solved the equations for the quasi-equilibrium covariances, we can express them all in terms of sums of exponential or Bessel kernels with different scale parameters and different coefficients.

The simplest cases to analyze are those when all dispersal and competition kernels have the same scale parameter, m ; are equal to 0, indicating global dispersal or competition; or are Dirac δ functions, indicating the limit of very short-range dispersal or competition, with $\tilde{K} = 1$. Otherwise, equations (B1)–(B3) can still be solved by symbolic algebra packages (if no more than three different kernels appear in the denominator, so that no polynomials higher than cubics come in) or numerically. In these cases the answers involve solutions of higher-order polynomials and linear systems and become too complicated for useful analytic insight, but we can still use them to explore the parameter space (fig. 5).

Globally Dispersing Invader, Locally Dispersing Resident

If the invader disperses globally ($\tilde{D}_I = 0$) and the resident disperses locally, the resident clustering, or \bar{c}_{RR} (B3), is the only nonzero term in the invasion criterion. Substituting equal-scale Bessel kernels ($\tilde{U}_{RR} = \tilde{D}_R = \tilde{K}(m)$) in (B3), converting to the $\{r, R, K, \beta\}$ set of parameters, and letting $\bar{n}_R = K_R$ gives

$$\frac{\bar{c}_{RR}^*}{\bar{n}_R^*} = \frac{(2 - R_R)\tilde{K}(m)}{1 - (2 - R_R)\tilde{K}(m)}. \quad (B4)$$

Applying (C2) and back-transforming gives

$$\frac{c_{RR}^*}{\bar{n}_R^*} = \frac{2 - R_R}{R_R - 1} \mathcal{K}(m\varphi_R), \quad (B5)$$

where the relative scale $\varphi_R = 1/\sqrt{R_R - 1}$. (We assume the effects of space are small [m is large], neglecting terms of order $1/m^2$.)

In general, we can express the solutions for the equilibrium covariances as sums of kernels with different scales

from the original scales of dispersal and competition (app. C). The new scales are of the form $m\varphi_k$, where m is the scale of the original kernels and φ_k is a scale factor (relative scale) that depends on life-history parameters; the subscript (I , R , or IR) denotes whether the scale factor depends on the parameters of the invader, the resident, or a combination. If φ is between 0 and 1, the scale of the covariance is shorter than the scale of the original kernel. If it is >1 , the scale of the covariance is longer than the scale of the original kernel. Using these scales directly instead of translating them into life-history parameters (such as $\varphi_R = 1/\sqrt{R-1}$) simplifies the notation; in particular, the covariances and invasion criteria for different special cases are often identical except for changes in the relative scales.

Integrating both sides of (B5), weighting with the convolution of the competition and dispersal kernels (using eq. [C4]), gives

$$\frac{\bar{c}_{RR}^*}{\bar{n}_R^*} = \frac{1}{4\pi m^2} \times \frac{(R_R - 1) - \log(R_R - 1) - 1}{2 - R_R}. \quad (\text{B6})$$

The numerator is always positive for $R_R > 1$, so the average covariance is positive if and only if $R_R < 2$. Substituting this value of \bar{c}_{RR} into the invasion criterion gives

$$1 - \beta_{IR} + \frac{1}{4\pi m^2} \frac{\beta_{IR}}{K_R} \times \frac{R_R - \log(R_R - 1) - 2}{2 - R_R} > 0. \quad (\text{B7})$$

Locally Dispersing Invader, Globally Dispersing Resident

In the converse case, the invader disperses and competes locally and the resident disperses globally but competes locally: $\bar{D}_R = 0$ and $\bar{U}_{RI} = \bar{U}_{RR} = \bar{U}_{IR} = \bar{U}_{II} = \bar{D}_I = \mathcal{K}(m)$. Substituting these kernels into (B1) and (B3), converting to the $\{r, R, K, \beta\}$ set of parameters (table 1), setting $\bar{n}_R = K_R$, applying (C2), and back-transforming gives the solutions for the autocovariances:

$$\frac{c_{II}^*}{\bar{n}_I} = (\varphi_I^2 - 1)\mathcal{K}(m\varphi_I), \quad (\text{B8})$$

$$\frac{c_{RR}^*}{\bar{n}_R} = (\varphi_R^2 - 1)\mathcal{K}(m\varphi_R), \quad (\text{B9})$$

with $\varphi_I = [(\beta_{IR} - 1)(R_I - 1)]^{-1/2}$ and $\varphi_R = R_R^{-1/2}$.

Substituting these solutions into (B2), again substituting alternate parameters, and using $\bar{n}_R = K_R$ gives a slightly uglier expression, but we can separate products of kernels using (C1) and then use (C3) to simplify the rest of the way.

The solution is

$$\begin{aligned} \frac{c_{IR}^*}{\bar{n}_I} &= \beta_{RI} \frac{K_R}{K_I} \times \frac{(1 - \varphi_I^2)(R_R - 1)}{\varphi_R^{-2} - \varphi_I^{-2}} \mathcal{K}(m\varphi_I) \\ &\quad - \beta_{IR} \frac{(1 - \varphi_R^2)(R_I - 1)}{\varphi_R^{-2} - \varphi_I^{-2}} \mathcal{K}(m\varphi_R) \\ &\quad + \frac{[\beta_{IR} K_I (R_I - 1) - \beta_{RI} K_R (R_R - 1)]}{K_I} \times \frac{(1 - \varphi_{IR}^2)}{\varphi_R^{-2} - \varphi_I^{-2}} \mathcal{K}(m\varphi_{IR}), \end{aligned} \quad (\text{B10})$$

with φ_I and φ_R as above, and

$$\varphi_{IR} = \left[\frac{r_I(R_R - 1) + r_R(R_I - 1)}{r_I\varphi_I^{-2}(R_R - 1) + r_R\varphi_R^{-2}(R_I - 1)} \right]^{1/2}.$$

These expressions give the covariances; to get the actual invasion eigenvalue, we need to determine the average covariances \bar{c}_{ij} from the covariances. We use (C4) to determine the weighted integrals of the kernels. The average resident covariance \bar{c}_{RR} is 0, despite the resident's nonzero covariance, because the resident has global dispersal ($D_R = 0$).

Dividing both sides by r_I , the invasion criterion (6) for the local invader/global disperser case becomes

$$\begin{aligned} (1 - \beta_{IR}) - \frac{1}{4\pi m^2 K_I} \times \frac{\varphi_I^2(1 - \log \varphi_I^2) - 1}{1 - \varphi_I^2} \\ + \frac{1}{4\pi m^2 K_R} \left\{ \beta_{RI} \frac{K_R(\varphi_I^2[1 - \log(\varphi_I^2)] - 1)(R_R - 1)}{K_I(1 - \varphi_I^2)(\varphi_R^{-2} - \varphi_I^{-2})} \right. \\ \left. - \beta_{IR} \frac{(\varphi_R^2[1 - \log(\varphi_R^2)] - 1)(R_I - 1)}{(1 - \varphi_R^2)(\varphi_R^{-2} - \varphi_I^{-2})} \right. \\ \left. + \frac{[\beta_{IR}K_I(R_I - 1) - \beta_{RI}K_R(R_R - 1)]}{K_I} \times \frac{\varphi_{IR}^2[1 - \log(\varphi_{IR}^2)] - 1}{(1 - \varphi_{IR}^2)(\varphi_R^{-2} - \varphi_I^{-2})} \right\} \\ > 0, \end{aligned} \quad (\text{B11})$$

using the values of $\varphi_{\{I, R, IR\}}$ given above. The criteria given in “Phalanx Growth” for when different clustering terms benefit the invader all follow from this expression. In fact, equation (B11) is nearly a general result.

Locally Dispersing Resident, Locally Dispersing Invader (Equal Scales)

To get the invasion criterion for the equal-scales case, we just substitute $1/\sqrt{R_R - 1}$ instead of $1/\sqrt{R_R}$ for the resident covariance scale φ_R in (B11) above and add the effect of resident covariance, which is given exactly as the second term on the left-hand side in (B7).

APPENDIX C

Kernel Identities

Assuming that $\tilde{K}(m) = \tilde{K}(m, q) = 1/(1 + m^2 q^2)$ (the one-dimensional Fourier transform of a bilateral exponential function or the Hankel transform of a Bessel function), some useful identities can be derived using partial fractions. The three basic identities needed are

$$\tilde{K}(m_1) \times \tilde{K}(m_2) = \frac{m_1^2}{m_1^2 - m_2^2} \tilde{K}(m_1) - \frac{m_2^2}{m_1^2 - m_2^2} \tilde{K}(m_2), \quad (\text{C1})$$

$$\frac{\tilde{K}(m_1)}{b + c\tilde{K}(m_1)} = \frac{1}{b + c} \times \tilde{K}(m_1\varphi), \quad \varphi = \sqrt{\frac{b}{b + c}}, \quad (\text{C2})$$

and

$$\frac{\tilde{\mathcal{K}}(m_1)}{b + c\tilde{\mathcal{K}}(m_2)} = \frac{1}{(b + c)m_1^2 - bm_2^2} \left[(m_1^2 - m_2^2) \times \tilde{\mathcal{K}}(m_1) + \frac{c}{b + c} m_2^2 \times \tilde{\mathcal{K}}(m_2\varphi) \right], \quad \varphi = \sqrt{\frac{b}{b + c}}, \quad (\text{C3})$$

where m_i , b , and c are constants ($b + c \neq 0$, $m_1 \neq m_2$, and $m_1 \neq \varphi$ in [C3]). All of the expressions used in this article can be derived using just these identities.

Other rational functions of transformed kernels have similar simplifications, although the expressions get uglier with increasing numbers of different scale parameters: a rational function with j distinct kernels in the denominator and k distinct kernels overall requires us to solve a j th order polynomial and a $k \times k$ linear system involving the roots of the polynomial.

The only other kernel-specific information needed is the weighted average of convolutions of kernels, which we use to calculate average covariances from covariances. We recall that

$$\bar{c}_{ij} \equiv \int_{\Omega} (D_i * U_{ij})(|s|) c_{ij}(|s|) ds.$$

It is actually easiest to perform this calculation in Fourier space. If we denote the inverse Fourier transform of \mathcal{K} by $\underline{\mathcal{K}}$, we can show that

$$\int ABdx = \int \tilde{A}\tilde{B}dq.$$

For two-dimensional radially symmetric functions, $\underline{\mathcal{K}} = 1/(4\pi^2)\tilde{\mathcal{K}}$, and so

$$\int_{\Omega} (D * U)(|s|) c(|s|) ds = \frac{1}{4\pi^2} \int_0^{2\pi} \int_0^{\infty} \tilde{D}(q) \tilde{U}(q) \tilde{c}(q) q dq d\theta.$$

Doing the integration for Bessel kernels ($\tilde{\mathcal{K}}(m) = 1/(1 + m^2q^2)$), we get

$$\int_0^{2\pi} \int_0^{\infty} [\mathcal{K}(m_1) * \mathcal{K}(m_1)](|s|) \mathcal{K}(m_2, s) ds d\theta = \frac{m_1^2 + m_2^2 [\log(m_2^2/m_1^2) - 1]}{4\pi(m_1^2 - m_2^2)^2}. \quad (\text{C4})$$

APPENDIX D

Equal-Scales Colonization Advantage

As discussed in the text, the colonization advantage (which we define as the resident clustering plus the resident-scale segregation, $\bar{c}_{RR} + (-\bar{c}_{IR,R})$) is positive for an invader with the same dispersal neighborhood as the resident species if $R_I > R_R > 2$. This criterion matches the result of a pseudospacial model with an establishment hierarchy. Pseudospacial models where competitive dominants can take over as well as preempt space lead to the more familiar requirement that $R_I^2 > R_R$ (Levins and Culver 1971; Hastings 1980; Tilman 1994). Although we classify it as a colonization advantage, this case does not work the same way as a classical competition-colonization trade-off. In the classical trade-off, a global-dispersing or fecund invader succeeds because clustering and local intraspecific competition lower the mean density of a colonization-limited resident. Here, in contrast, the resident density is higher than it would be in a nonspatial case, with global competition. A fecund invader uses spatial segregation to capitalize on inevitable open space within the resident population.

Oddly, when the resident has low fecundity, an invader must have even lower fecundity to benefit from colonization advantage in an equal-dispersal case: $R_I < R_R < 2$ is the colonization-advantage criterion. When the resident clusters, high resident fecundity does decrease one part of the spatial segregation, perhaps as a side effect of evening the invader's spatial distribution. However, the resident-scale segregation $\bar{c}_{IR,R}$ is only part of the spatial distribution. As we show in "Short-Dispersal Strategies," the spatial segregation associated with an exploitation strategy ($\bar{c}_{IR,IR}$) counterbalances $\bar{c}_{IR,R}$ whenever the resident clusters. In particular, increasing R_I always gives a net benefit to the invader if $\beta_{RI}\beta_{IR} < 1$.

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