

REPORT

Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity

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Abstract

In the presence of permanent spatial heterogeneity, local dispersal, especially short-range dispersal, can facilitate coexistence by concentrating low-density species in the areas where their rates of increase are higher. We present a framework for predicting the effects of local dispersal on coexistence for arbitrary forms of dispersal and arbitrary spatial patterns of environmental variation. Using the lottery model as an example, we find that local dispersal contributes to coexistence by enhancing the effects of environmental variation on scales longer than typical dispersal distances, which can be characterized solely by the variance of the dispersal kernel. Higher moments of the dispersal kernel are not important.

Keywords

Coexistence, dispersal, spatial ecology, spatial heterogeneity.

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INTRODUCTION

Local dispersal in a spatially heterogeneous environment can cause population levels to build up in favourable areas, which enhances coexistence mechanisms that are present when species differ in their responses to the environment. However, many models employ global dispersal for the sake of tractability and hence underestimate the possibilities for coexistence. Of the studies that consider how local dispersal affects species coexistence, most of them focus on the capacity of local interactions to generate aggregated population distributions in a uniform environment, so that competing species are segregated to some degree (Hassell *et al.* 1994; Comins & Hassell 1996; Durrett & Levin 1997; Kerr *et al.* 2002; Murrell & Law 2003). Spatial variation in relative abundance is an important factor in coexistence (Ives 1995); however, we are concerned with how local dispersal can concentrate a low-density species in those areas of a heterogeneous environment that most favour it. The few studies which treat local dispersal in a heterogeneous environment give conflicting results (Comins & Noble 1985; Bolker 2002). We explain these differences and present a framework capable of dealing with a broad variety of dispersal types and, explicitly spatial environmental variation, to derive some general insights into the effects of local dispersal on species coexistence.

Both long-lasting environmental heterogeneity and species-specific responses to the environment are necessary for

local dispersal to enhance the likelihood of coexistence. If the distribution of favourable habitat is different for each species – i.e. there are species-specific environmental responses – then a species which has become temporarily sparse will be able to exploit areas that favour it with relatively little interspecific competition (because the area is not so favourable to its competitors) or intraspecific competition (because it is sparse). In contrast, individuals from a more plentiful species face relatively strong intraspecific competition when in a favourable area. In other words, there is a strong, positive covariance between environmental conditions and competition for the plentiful species but only a weak covariance for the sparse species. Such differences in covariance between environment and competition drive the ‘spatial storage effect’ (Chesson 2000a) mechanism for coexistence, which can be present even with global dispersal. If the environmental differences are permanent (persistent over multiple generations), then local dispersal helps concentrate the sparse species in the areas that favour it and where it is least limited by interspecific competition. In this way, spatial variation and local dispersal boost the average per capita birth rates of sparse species and facilitate coexistence.

The spatial storage effect and the effects of local population buildup are quantified in Chesson (2000a) based on a generic, discrete-time model. If we define $n_{jx}^{(pr)}(t+1)$ as the expected density of species j offspring produced at location x at time $t+1$, then

$$n_{jx}^{(br)}(t+1) = \lambda_{jx}(t)n_{jx}(t), \quad (1)$$

where $n_{jx}(t)$ is the expected density of species j at location x at time t and $\lambda_{jx}(t)$ is the finite rate of increase of species j at location x at time t . The offspring then disperse, and $n_{jx}(t+1)$ represents the expected density of species j at location x and time $t+1$ after dispersal. Note that in formulating the dynamics in terms of expected density, we are ignoring demographic stochasticity. This should have little effect unless the number of individuals at a site is very low.

We can shift from the local scale to the global scale by taking a spatial average (indicated by an overbar):

$$\bar{n}_j(t+1) = \overline{\lambda_{jx}n_{jx}(t)} = \bar{\lambda}_j\bar{n}_j + \text{Cov}(\lambda_j, n_j) = \tilde{\lambda}_j\bar{n}_j(t), \quad (2)$$

where

$$\tilde{\lambda}_j = \bar{\lambda}_j + \text{Cov}(\lambda_j, v_j) \quad (3)$$

$$v_{jx} = \frac{n_{jx}}{\bar{n}_j}. \quad (4)$$

That is, the global dynamics are like the local production dynamics but with an effective finite rate of increase $\tilde{\lambda}_j$ equal to the spatial average of the local rate of increase λ_{jx} plus the covariance between local growth and the relative population density v_{jx} . The relative population density is simply the ratio of the local density to the average density over all locations. The growth–density covariance is taken over space and accounts for the fact that population levels may be higher in some locations than in others, and the rate of increase in these more populous spots will contribute more to the overall rate of increase of the population. We assume that species coexist if each species can invade when the other species are at the equilibrium spatial distributions that they would attain in the absence of the invader. This means that each species has a finite rate of increase greater than 1 when it is reduced to low density [the standard invasibility criterion (Gotelli 1995; Chesson 2000a)]. Thus, the condition for coexistence is that $\tilde{\lambda} > 1$ for each species as an invader. The contribution of the growth–density covariance to $\tilde{\lambda}$ demonstrates the importance of local dispersal and an explicitly spatial representation. Local dispersal can cause population levels to build up in favourable areas, which makes the growth–density covariance, $\text{Cov}(\lambda_j, v_j)$, positive. This covariance increases the global finite rate of increase, $\tilde{\lambda}_j$, and thereby promotes coexistence.

In analogy with ANOVA techniques, the finite rate of increase $\tilde{\lambda}_j$ can be further partitioned into the primary effects of the environment, competition, and the interaction between environment and competition (Chesson 2000a). Additional manipulations then allow one to re-express $\tilde{\lambda}_j$ as the sum of effects that do not depend on spatial variation

and the effects of three spatial mechanisms: ‘relative nonlinearity’ in local rates of increase, the spatial storage effect and the growth–density covariance [$\text{Cov}(\lambda_j, v_j)$], which enhances the spatial storage effect (Chesson 2000a). Spatially independent coexistence mechanisms, relative nonlinearity and the spatial storage effect contribute to $\tilde{\lambda}_j$, and can be present with global dispersal and local dispersal. The effects of local dispersal – the effects of an explicitly spatial representation – are contained entirely within $\text{Cov}(\lambda_j, v_j)$ for the model we use here, although in general, local dispersal can contribute to components of $\tilde{\lambda}$ as well.

In this paper, we use the framework of Chesson (2000a) to explore the effects of local dispersal on species coexistence. We present an expression for the growth–density covariance for arbitrary probability distributions of dispersal distance (dispersal kernels) and arbitrary patterns of environmental variation. Using the lottery model (defined below) as an example, we demonstrate how the parameter ranges where coexistence is possible increase when one considers local instead of global dispersal, and we highlight the effects of different forms of dispersal and different patterns of environmental variation. We find in particular that the contribution of local dispersal to coexistence depends only on environmental variation at scales longer than typical dispersal distances and that short-range dispersal facilitates coexistence most effectively. Furthermore, the variance of the dispersal kernel is sufficient to characterize dispersal distances – one need not measure higher moments.

The rest of this paper is organized as follows. In ‘The lottery model’, we define our example, the lottery model. We present a general expression for the growth–density covariance in ‘An expression for the growth–density covariance’, and discuss the implications of this expression in ‘Implications’. ‘Synthesis of spatial mechanisms’ is devoted to a review of the previous work on coexistence in a heterogeneous environment in the light of this work. We conclude in ‘Discussion’ with a discussion of our work and an outline of future directions.

THE LOTTERY MODEL

We demonstrate our results with the lottery model (Chesson & Warner 1981; Comins & Noble 1985; Chesson 2000a; Muko & Iwasa 2000), a model commonly used to understand the effects of environmental variation on competitive interactions. Here, we use a spatial version of the model with dispersing juveniles that compete for space to become sessile, semelparous adults. The lottery model is one of the simplest models with which one can demonstrate the effects of a varying environment and so has achieved the status of a standard example, much like the Lotka–Volterra

model or the contact process. The lottery model is most frequently used to represent marine organisms such as sessile invertebrates or coral reef fish. In this paper, we assume that adults die after reproducing, and so here, the model is perhaps best thought of in terms of annual plants. In the case of annual plants, ‘juveniles’ are seeds.

For the sake of simplicity, we assume that the environment is one-dimensional and can be represented as a series of patches, each of which can support a single individual. The ability of juveniles of a given species to capture space is a function of the environment type, which is assumed to vary in space but not time. The space-capturing ability of species j at location x is denoted by E_{jx} . For annual plants, E_{jx} could represent the product of germination probability and early seedling survival probability.

Let $n_{jx}(t)$ be the expected density of seeds of species j competing for space at location x at time t . We imagine that competition for a site is like a lottery, with the winner chosen randomly from the seeds competing at that site and the chances of a species seizing the site proportional to the number of seeds it has in the competition. This is not a fair lottery, however. For any given site, seeds from some species will be more likely to win than those of other species, with their advantage determined by E_{jx} . Mathematically, the expected number of species j individuals that establish themselves at x and become adults is

$$\frac{E_{jx}n_{jx}}{\sum_k E_{kx}n_{kx}}, \tag{5}$$

where the sum in the denominator runs over all species. The per adult fecundity of species j is F_j , so that the number of species j seeds produced at x that compete at time $t + 1$ is

$$n_{jx}^{(pr)}(t + 1) = \frac{F_j E_{jx} n_{jx}}{\sum_k E_{kx} n_{kx}}. \tag{6}$$

The mathematical framework introduced in Chesson (2000a) assumes that local reproduction takes the form $n_{jx}^{(pr)}(t + 1) = \lambda_{jx} n_{jx}(t)$, and so

$$\lambda_{jx} = \frac{F_j E_{jx}}{\sum_k E_{kx} n_{kx}}. \tag{7}$$

Equation 6 takes the initial number of seeds of each species, n_{jx} , as given and does not include seed dispersal. After reproduction, seeds disperse to the left and right, with the probability of dispersing from x to $x + z$ given by the dispersal kernel, $k(z)$. Thus, combining dispersal with reproduction, we find

$$n_{jx}(t + 1) = \sum_y k(x - y) \lambda_{jy} n_{jy}(t). \tag{8}$$

Equation 8 states that the number of individuals landing at location x at time $t + 1$ is equal to the number of individuals produced at location y at time t ($\lambda_{jy} n_{jy}(t)$) times

the probability of dispersing from y to x ($k(x - y)$), summed over all y . We want to find $\text{Cov}(\lambda_{jx}, v_{jx})$, so we need eqn 8 not in terms of population density, n_{jx} , but in terms of relative population density, $v_{jx}(t) = n_{jx}(t)/\bar{n}_j(t)$. A small amount of algebra yields

$$v_{jx}(t + 1) = \sum_y k(x - y) \frac{\lambda_{jy}}{\lambda_j} v_{jy}(t). \tag{9}$$

Note that eqn 9 is valid for all models of the form $n_{jx}^{(pr)}(t + 1) = \lambda_{jx} n_{jx}(t)$. Here we use the lottery model by taking eqn 7 as our definition of λ_{jy} .

In the next section, we restrict our attention to the case of two species, and it will be useful to derive a few two-species results here. First, consider the dynamics of the resident in the absence of the invader:

$$n_{rx}(t + 1) = \frac{F_r E_{rx} n_{rx}}{E_{rx} n_{rx}} = F_r. \tag{10}$$

We see that in a single step, the resident population achieves a spatially uniform equilibrium distribution, $n_{rx}^* = F_r$. Then, given a spatially uniform production of offspring, dispersal preserves the uniformity of their distribution in space, although individuals do move.

We can now find the invader’s local rate of increase:

$$\lambda_{ix} = \frac{F_i E_{ix}}{E_{rx} n_{rx}^* + E_{ix} n_{ix}}, \tag{11}$$

where subscripts i and r denote invader and resident quantities and n_{rx}^* is the equilibrium density of the resident in the absence of the invader. As the invader density is by definition very low, we can set $n_{ix} = 0$ in the denominator of eqn 11, and we know from eqn 10 that $n_{rx}^* = F_r$. Thus,

$$\lambda_{ix} = \frac{F_i E_{ix}}{F_r E_{rx}}. \tag{12}$$

AN EXPRESSION FOR THE GROWTH-DENSITY COVARIANCE

Environmental variation usually occurs on many spatial scales simultaneously. It would be useful if we could analyse the contribution of each spatial scale to the growth–density covariance separately and sum the contributions to obtain the net effect. Fortunately, Fourier transforms are ideally suited to this task. Fourier transforms decompose functions into a sum of sine waves at different frequencies, and one can loosely think of the Fourier transform of a function, evaluated at spatial frequency ω , as specifying how much of that function can be represented by a sine wave at frequency ω . (Recall that wave length equals $2\pi/\omega$.) Using Fourier transforms, we can separate the environmental variation into a series of sine waves and analyse the contributions to coexistence of each spatial scale separately. Thanks to the

additional properties of Fourier transforms, the effects of variation at these different spatial scales are additive.

We measure the environmental variation with the perturbation $\zeta_{ix} = (\lambda_{ix}/\bar{\lambda}_i) - 1$, which indicates how the local invader rate of increase differs from its spatial average. Specializing on the case of a lottery model with two species, we use eqn 12 to find $\zeta_{ix} = (\lambda_{ix}/\bar{\lambda}_i) - 1 = [(1/\bar{\lambda}_i)(F_i/F_r)(E_{ix}/E_{rx})] - 1$. Thus, ζ_{ix} is a measure of how much the ratio of the invader and resident environmental responses varies from spatial uniformity. Our expression for the growth–density covariance will use the spectral density of ζ_b , $S_\zeta(\omega)$, which is proportional to the square of the Fourier transform of ζ_b . (Fourier transforms and spectral densities are defined precisely in Appendix.)

We can now present our primary result:

$$\text{Cov}(\lambda_i, v_i) = \bar{\lambda}_i \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{\tilde{k}(\omega) S_\zeta(\omega)}{1 - \tilde{k}(\omega)} d\omega, \tag{13}$$

where $\tilde{k}(\omega)$ is the Fourier transform of the dispersal kernel and $\text{Cov}(\lambda_b, v_b)$ is the standard covariance over space of the two quantities λ_b and v_b , i.e. $(\lambda_i(x) - \bar{\lambda}_i)(v_i(x) - \bar{v}_i)$. Equation 13 states that the growth–density covariance is proportional to $[\tilde{k}(\omega)/(1 - \tilde{k}(\omega))]$, which contains information about how much dispersal occurs at frequency ω , summed over frequency, with $S_\zeta(\omega)$ weighting each term by how much environmental variation is present at that frequency.

It is the ratio of the invader and resident environments and not their separate values which are important for the lottery model. It therefore makes sense to measure the environmental responses on a logarithmic scale, so that the species are treated symmetrically [$\ln(E_1/E_2) = -\ln(E_2/E_1)$]. Let $\ln(F_j E_j) = \mu_j + \epsilon_{j\omega}$, $j = i, r$, where μ_j is constant, and $\epsilon_{j\omega}$ representing deviations away from μ_j , has spatial mean zero. Then $\tilde{\lambda}_i$, the invader’s global scale finite rate of increase, is

$$\tilde{\lambda}_i = (\mu_i - \mu_r) + \frac{1}{2} \text{Var}(\epsilon_i - \epsilon_r) + \text{Cov}(\lambda_i, v_i). \tag{14}$$

In the absence of spatial variation, $\tilde{\lambda}_i$ would equal the fitness difference, $\mu_i - \mu_r$. A spatially varying environment adds to $\tilde{\lambda}_i$ via $\frac{1}{2} \text{Var}(\epsilon_i - \epsilon_r)$ (the storage effect) and $\text{Cov}(\lambda_b, v_b)$ (the growth–density covariance). [Relative nonlinearity, another component of $\tilde{\lambda}$ defined in (Chesson 2000a), is zero for the lottery model.] The storage effect term and the growth–density covariance are stabilizing terms that, if strong enough, overcome fitness differences and permit coexistence as discussed in Chesson (2000b).

As an example, consider two species, 1 and 2, whose space-capturing abilities have the ratio $\ln(E_{1x}/E_{2x}) = b \sin(\omega, x)$. The choice of a sinusoidally varying environment is decidedly artificial. However, as noted previously, the contributions to coexistence from multiple spatial scales are additive, and so for simplicity, we consider environmental variation at a single

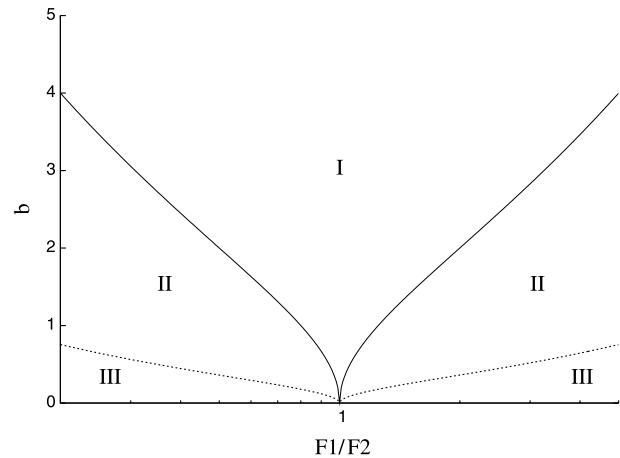


Figure 1 Coexistence region for environmental sensitivity (b) vs. the logarithm of the adult fecundity ratio (F_1/F_2). The environment varies according to $\ln(E_{1x}/E_{2x}) = b \sin(\omega, x)$. The frequency of environmental variation, ω_s is 0.1, and is measured in radians. In region I, coexistence is possible even if dispersal is global, while in region II, coexistence is only possible if there is limited dispersal. Coexistence is not possible in region III. The dispersal kernel for this figure had a variance of 13.2. (Only the variance of the dispersal kernel matters. See ‘Implication’ for a discussion of this.)

frequency. Figure 1 shows how strongly the environment must vary (b) for the species to coexist given a ratio of adult fecundities (F_1/F_2). Recall that for a species to coexist, $\tilde{\lambda}$ must be greater than 1 for both species, where $\tilde{\lambda} = \bar{\lambda} + \text{Cov}(\lambda_i, v_i)$. In region I, both species can coexist even if dispersal is global. Here, $\bar{\lambda}_i > 1$ for both species as invaders; the spatial storage effect is strong enough to overcome the fitness disadvantage of the inferior competitor. In region II, both species can coexist if there is limited dispersal. (This figure was generated using a particular choice of dispersal kernel, but, as discussed in ‘Implications’, any kernel with the same variance would result in the same boundary.) Here, $\bar{\lambda}_i < 1$, but $\text{Cov}(\lambda_b, v_b)$ lifts $\tilde{\lambda}$ above 1. This is the extra coexistence region provided by $\text{Cov}(\lambda_b, v_b)$. In region III, coexistence is not possible.

IMPLICATIONS

The way information about dispersal enters our expression for growth–density covariance has important consequences. Our knowledge of dispersal is contained in the Fourier transform of the dispersal kernel, $\tilde{k}(\omega)$. For all kernels, $\tilde{k}(0) = 1$, as the Fourier transform of a function evaluated at zero frequency is simply the integral of the function from $-\infty$ to ∞ , and, being probability distributions, all kernels integrate to 1. The transform $\tilde{k}(\omega)$ is close to 1 for ω close to zero [for ω small, $\tilde{k}(\omega) \approx 1 - \frac{1}{2} \text{Var}(k)\omega^2$], and so

$\tilde{k}(\omega)/(1 - \tilde{k}(\omega))$ is large when ω is small¹. These large values dominate the integral in eqn 13. This has two important implications.

First, as the integral in eqn 13 is dominated by low frequencies, we can replace $\tilde{k}(\omega)$ by the first two terms of its Taylor expansion about $\omega = 0$: $\tilde{k}(\omega) \approx 1 - \frac{1}{2}\text{Var}(k)\omega^2$. Thus, eqn 13 becomes

$$\text{Cov}(\lambda_i, v_i) = \bar{\lambda}_i \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{S_{\zeta}(\omega)(2 - \text{Var}(k)\omega^2)}{\text{Var}(k)\omega^2} d\omega. \quad (15)$$

Unless all the environmental variation is at frequencies that are high relative to $1/\sqrt{\text{Var}(k)}$, this approximation is highly accurate: none of the figures in this paper would change by more than a penwidth were we to use this approximation. This means that we can ignore higher order moments, which depend increasingly on the hard-to-measure tails of the dispersal kernel, and rely simply on the variance, which is much easier to estimate. This is in contrast to invasion studies, in which the invasion speed is determined largely by the tails of the invader's dispersal kernel (Mollison 1991; Kot *et al.* 1996). Figure 2 shows how the coexistence region depends on $\sqrt{\text{Var}(k)}$.

Second, only environmental variation at wavelengths longer than typical dispersal distances contributes much to $\text{Cov}(\lambda_i, v_i)$. Mathematically, this is easy. The factor $[(2 - \text{Var}(k)\omega^2)/(\text{Var}(k)\omega^2)]$ is large for $1/\omega \gg \sqrt{\text{Var}(k)}$,

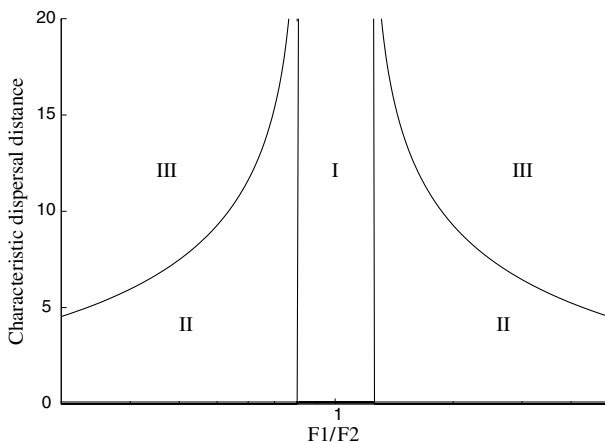


Figure 2 Coexistence region for characteristic dispersal distance $[\sqrt{\text{Var}(k)}]$ vs. the logarithm of the adult fecundity ratio (F_1/F_2). The environment varies according to $\ln(E_{1,x}/E_{2,x}) = b \sin(\omega_e x)$. The frequency of environmental variation, ω_e , is 0.1, and is measured in radians, while $b = 1$. In region I, coexistence is possible even if dispersal is global, while in region II, coexistence is only possible if there is limited dispersal. Coexistence is not possible in region III.

¹ $(\tilde{k}(\omega)/(1 - \tilde{k}(\omega)))$ is infinite when $\omega = 0$. However, for nonpathological examples, $S_{\zeta}(\omega) = 0$ when $\omega = 0$, and so the potential pole is suppressed.

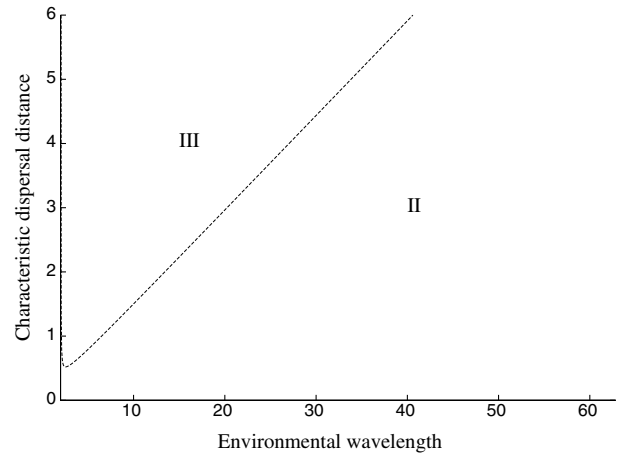


Figure 3 Coexistence region for characteristic dispersal distance $[\sqrt{\text{Var}(k)}]$ vs. the wavelength of the environmental variation. The environment varies according to $\ln(E_{1,x}/E_{2,x}) = b \sin(\omega_e x)$. The ratio of adult fecundities (F_1/F_2) is 2, while $b = 1$. Coexistence is not possible with global dispersal, but is possible with limited dispersal in region II. Coexistence is not possible in region III.

and the standard deviation of the dispersal kernel, $\sqrt{\text{Var}(k)}$, can be thought of as a characteristic dispersal distance. Wavelength equals $2\pi/\omega$, and so this inequality means that the factor $[(2 - \text{Var}(k)\omega^2)/(\text{Var}(k))]$ gives a lot of weight to wavelengths much larger than the characteristic dispersal distance. This finding stresses the importance of short-range dispersal, because it means that smaller values of $\text{Var}(k)$ give larger ranges of frequencies at which environmental variation contributes significantly to the growth–density covariance and give stronger contributions at those frequencies. This finding also makes sense biologically. If favourable areas are large relative to typical dispersal distances, then offspring of adults in favourable areas are likely to remain in those areas, which encourages population buildup there and enhances the spatial storage effect. Figure 3 shows coexistence regions as a function of the characteristic dispersal distance, $\sqrt{\text{Var}(k)}$, and the wavelength of the environmental variation.

SYNTHESIS OF SPATIAL MECHANISMS

Our work extends the findings of studies that consider species coexistence in a lottery model with permanent spatial heterogeneity but confine themselves to global dispersal for the sake of tractability (Chesson 1985; Muko & Iwasa 2000). Not only have we shown how to incorporate local dispersal and identified the importance of population buildup in favourable areas, but, by thinking in terms of the storage effect, we can also give intuitive explanations for results such as the Muko and Iwasa

finding that although spatial variation in mortality enables coexistence, variation in fecundity does not (Muko & Iwasa 2000). As dispersal is global, juveniles competing in a given patch come from all over the system. As there is no connection between fecundity in that patch and the competition experienced by juveniles that have landed there, plentiful species do not pay the price of high intraspecific competition in favourable areas. In the terminology of the storage effect, there is no covariance between the environment experienced and the competition experienced. Note, however, that if dispersal were local, so that competing juveniles were more likely to have come from the patch in question than from any other patch, then population levels would build up in high fecundity sites, and the resulting increase in competition would limit output from those sites. Thus, spatially varying fecundity could enable coexistence in the presence of local dispersal. Alternatively, variation in mortality can introduce covariance between environment and competition in the presence of either global or local dispersal. Where the environment favours adult persistence, there will be few vacancies for juveniles to occupy, and competition will be strong. The sedentary nature of the adults acts much like local retention of juveniles.

This work also extends studies which allow for some fraction of the offspring to be retained locally while the others disperse globally, such as in Chesson (2000a) and Comins & Noble (1985). Such stark representations of local retention offer a very clearcut, if unrealistic, demonstration of the importance of local buildup. It is shown in Chesson (2000a) that this kind of local retention leads to a positive $\text{Cov}(\lambda_i, v_i)$.

One way researchers have incorporated explicit space without adding too much complexity is by limiting their arena to two patches. Our findings parallel those of two-patch studies of coexistence, such as Pacala & Roughgarden (1982) and Amarasekare & Nisbet (2001). Amarasekare and Nisbet present a model with two patches of different quality, Lotka–Volterra competitive dynamics, and migration between patches at constant rates (Amarasekare & Nisbet 2001). They find that for two of their three situations, dispersal rates must be below critical thresholds for species to coexist. Likewise, Pacala and Roughgarden, working with diffusive movement in a two-patch competition model, found that dispersal of the resident increases competition in the habitat with the lower carrying capacity (Pacala & Roughgarden 1982). If an invader disperses into this area too frequently, then it is overwhelmed by the competition, and coexistence is not possible. We can restate the results of both of these studies by saying that the invader population must be partially retained in the areas which favour it, i.e. the growth–density covariance must be sufficiently positive.

The benefit of our approach over two-patch models is that we can accommodate arbitrary forms of environmental variation and arbitrary forms of dispersal. This helps to ensure the generality of our results as well as yielding insights that are only possible in this framework, such as the importance of kernel variance. One study that follows this more general approach is that of Bolker and Pacala, who investigate coexistence mechanisms in a homogeneous environment (Bolker & Pacala 1999). Although it is not identified explicitly, $\text{Cov}(\lambda_i, v_i)$ plays an important role in their coexistence criteria as well. If we return to the discrete time approximation used in their derivation, we can say that $\bar{n}_I(t + dt) \approx \tilde{\lambda}_I \bar{n}_I(t)$, where

$$\tilde{\lambda}_I = 1 + r_I \left\{ 1 - \frac{\bar{n}_I + (\bar{c}_{II}/\bar{n}_I)}{K_I} - \frac{\beta_{IR}[\bar{n}_R + (\bar{c}_{IR}/\bar{n}_I)]}{K_R} \right\} dt, \quad (16)$$

\bar{n}_I and \bar{n}_R are spatial averages of the invader and resident populations, and \bar{c}_{II} and \bar{c}_{IR} are spatial covariances averaged over a convolution of the dispersal and competition kernels. After some work, we can identify $\tilde{\lambda}_I$ as $1 + r_I \{1 - \bar{n}_I/K_I - \beta_{IR}\bar{n}_R/K_R\} dt$ and $\text{Cov}(\lambda_i, v_i)$ as $r_I [(-\bar{c}_{II}/K_I \bar{n}_I) - (\beta_{IR}\bar{c}_{IR}/K_R \bar{n}_I)] dt$. Note that without the $\text{Cov}(\lambda_i, v_i)$ term, this would reduce to a Lotka–Volterra competition model. For both Bolker and Pacala's model and ours, the effects of an explicitly spatial representation are contained in $\text{Cov}(\lambda_i, v_i)$, and for both studies, $\text{Cov}(\lambda_i, v_i)$ features prominently in the coexistence criteria.

Bolker has also discussed heterogeneous environments and has noted how population buildup in favourable areas fortifies species persistence, although he has not addressed species coexistence in this context (Bolker 2002). In particular, he notes that the greater the spatial variability in the environment, the more advantageous short-range dispersal is, as it tends to keep offspring in favourable areas.

As our environmental variation is fixed in time, 'fugitive' strategies, in which an inferior competitor can coexist with a superior competitor by being swifter to discover and colonize newly available habitat (Levins & Culver 1971; Hastings 1980; Tilman 1994), are not applicable. If there were temporal and spatial variation, we would expect the emphasis on local retention of offspring to change. Comins and Noble consider the lottery model with spatiotemporal variation in the environment (Comins & Noble 1985). They obtain analytic results for global dispersal and use simulations to investigate nearest-neighbour dispersal. In contrast with our results, they find that dispersal distances must be much larger than the scale of spatial variation in the environment if species are to coexist. The difference arises because they consider pure spatiotemporal variation, in which the environment at each

location changes over time independently of the environment at other locations. If favourable areas persist, then the best strategy of an organism is to settle offspring nearby, in the hope that they will land in a similarly favourable spot. However, if good patches are ephemeral, then the best strategy is to send offspring far and wide in the hope that a few of them will find a new good patch.

DISCUSSION

In this paper, we have derived an expression for the covariance between relative population density and local growth and demonstrated how this increases the parameter space over which coexistence is possible. The covariance expression is dominated by the low frequency terms. This has the consequence that local dispersal contributes to coexistence by enhancing the effects of environmental variation on scales longer than typical dispersal distances. Short-range dispersal facilitates coexistence most effectively. Restating this result somewhat differently, the scales of environmental variation that contribute significantly to the growth–density covariance depend on the scale of dispersal. Even if two species experience an identical pattern of environmental variation, the species with shorter-range dispersal will have a larger growth–density covariance because it is sensitive to environmental variation at a greater range of spatial scales and because the contributions within that range will be larger. The domination of the low frequency terms also means that dispersal distances can be characterized solely by the variance of the dispersal kernel – higher moments can be ignored. Biologically, this reflects the fact that rare, long-distance dispersal does not appreciably affect the degree of population buildup in favourable locations.

We have seen that short-range dispersal can provide a significant advantage when environmental variation is effectively permanent. If favourable areas are transient (e.g. carrion, puddles), then it is advantageous for at least some offspring to disperse long distances so that they can colonize newly favourable areas before the natal site becomes unfavourable. Such a situation might select for a leptokurtic dispersal kernel, with most offspring staying close to home and a few dispersing broadly. The more rapidly the environment changes, the more important long-distance dispersal will be, so that there may be an ideal balance between short and long-range dispersal for a given turnover rate (Levin *et al.* 1984).

The view of coexistence presented in this paper is a niche differentiation perspective. Within the context of the lottery model, the niche is Grubb's regeneration niche, and E_j represents environmental features favouring the establishment of species j (Grubb 1977). We assume that

the environment varies in space and that the different species have different resource needs and tolerances, so that each perceives a different spatial pattern of environmental quality. This variation is a semi-permanent feature of the environment, such as soil type, aspect or exposure, and so we find that the likelihood of coexistence is most enhanced when typical dispersal distances are short with respect to typical lengthscales of environmental variation, so that the offspring of individuals in favourable areas tend to remain in those areas, and populations of each species accumulate in the areas that favour them. Additional mechanisms for coexistence operate in spatially varying environments, such as relative nonlinearity or the spatial storage effect without the enhancement of local population buildup [see Chesson (2000a)], but these do not depend on dispersal distance and are beyond the scope of this paper.

Our expression for the growth–density covariance (eqns 34 and 13) holds not just for the lottery model but for any model that can be written in the form $n_{jx}(t+1) = \sum_y \kappa(x-y) \lambda_{jy} n_{jy}(t)$. However, the interpretation of the covariance expression is more complicated if the resident's equilibrium distribution in the absence of the invader (n_{rx}^*) is not spatially uniform. In that case, $S_\zeta(\omega)$ will be a function not only of the environmental variation, but also of n_{rx}^* . While it will still be true that it is the low frequency components of $S_\zeta(\omega)$ which matter, we will no longer be able to interpret this simply as long wavelength environmental variation. Similarly, λ_i will depend on n_{rx}^* , which will make it more difficult to compute. On the other hand, we should still be able to replace the Fourier transform of the dispersal kernel, $\hat{\kappa}(\omega)$, with $1 - \frac{1}{2}\text{Var}(\kappa)$. In the context of the lottery model, n_{rx}^* will not be spatially uniform if adult fecundity varies in space, if the number of the individuals able to occupy a site (here set to 1) varies in space, or if juveniles compete not only within a site but also to some degree with juveniles at neighboring sites. These issues are the subjects of future studies.

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APPENDIX. DERIVATION OF THE GROWTH-DENSITY COVARIANCE FORMULA

We begin with eqn 9 and assume that the invader has reached an equilibrium pattern of relative density. Thus,

$$v_{ix} = \sum_y k(x-y) \frac{\lambda_{iy}}{\bar{\lambda}_i} v_{iy}, \quad (17)$$

where the sum runs over all space.

We assume small perturbations from spatial uniformity in v_{ix} and λ_{ix} , defining

$$u_{ix} = v_{ix} - 1 \quad (18)$$

$$\zeta_{ix} = \frac{\lambda_{ix}}{\bar{\lambda}_i} - 1, \quad (19)$$

where u_{ix} and ζ_{ix} are $O(\sigma)$ and σ is a small parameter². (By $g(x) = O(\sigma^2)$, we mean that $\left| \frac{g(x)}{\sigma^2} \right|$ can be made less than or equal to any positive constant K for σ^2 small enough.) Substituting these definitions into the equation for the invader relative density at equilibrium, eqn 17, and simplifying, we find

$$u_{ix} = \frac{1}{1 + \psi} \sum_y k(x-y) (u_{iy} + \zeta_{iy} + u_{iy}\zeta_{iy} - \psi), \quad (20)$$

where

$$\psi = \frac{\bar{\lambda}_i - \bar{\lambda}_i}{\bar{\lambda}_i} = \frac{\text{Cov}(\lambda_i, v_i)}{\bar{\lambda}_i}. \quad (21)$$

The growth-density covariance equals $\bar{\lambda}_i$ times $\zeta_i u_{is}$ so, apart from the proportionality constant $\bar{\lambda}_i$, we could find $\text{Cov}(\lambda_i, v_i)$ at lag d by multiplying both sides of eqn 20 by $\zeta_{i,x-d}$ and taking the spatial average. (We will ultimately want only the covariance at lag 0, but it is helpful to solve for the covariance as a function of lag, as we want to take the Fourier transform.) However, if the system is spatially stationary, the spatial average will be equal to an expectation over an ensemble of replicates. We therefore set lag d equal to x , so that we are multiplying by ζ_{i0} , and take the expectation instead. Denoting the expected value by $\langle \cdot \rangle$, we define

$$\phi(x) = \langle \zeta_{i0} u_{ix} \rangle \quad (22)$$

$$R(x) = \langle \zeta_{i0} \zeta_{ix} \rangle \quad (23)$$

$$\eta(x) = \langle \zeta_{i0} u_{ix} \zeta_{ix} \rangle, \quad (24)$$

and noting that $\langle \zeta_{i0} (u_{iy} \zeta_{iy}) \rangle = \langle \zeta_{i0} (u_{iy} \zeta_{iy} - \psi) \rangle$, we find

$$\phi(x) = \frac{1}{1 + \psi} \sum_y k(x-y) [\phi(y) + R(y) + \eta(y)]. \quad (25)$$

This is a convolution and is most easily solved by taking the Fourier transform, which turns convolutions into

²The formalism presented in Chesson (2000a) assumes that E varies over a finite interval of length σ .

products. We use the following definition of the discrete Fourier transform:

$$\tilde{f}(\omega_s) = \sum_{j=-N/2+1}^{N/2} f(x_j) e^{-i\omega_s x_j}, \quad (26)$$

$$f(x_n) = \frac{1}{N} \sum_{s=-N/2+1}^{N/2} \tilde{f}(\omega_s) e^{i\omega_s x_n}, \quad (27)$$

where N is the number of lattice points, Δ is the distance between lattice points, $x_j = j\Delta$, and $\omega_s = s(2\pi)/(N\Delta)$. Taking the discrete Fourier transform of eqn 25, we obtain

$$\tilde{\phi}(\omega_s) = \frac{1}{1+\psi} \tilde{\kappa}(\omega_s) [\tilde{\phi}(\omega_s) + \tilde{R}(\omega_s) + \tilde{\eta}(\omega_s)] \quad (28)$$

and thus

$$\tilde{\phi}(\omega_s) = \frac{\tilde{\kappa}(\omega_s) [\tilde{R}(\omega_s) + \tilde{\eta}(\omega_s)]}{1 - \tilde{\kappa}(\omega_s) + \psi}. \quad (29)$$

$\text{Cov}(v_i, \lambda_i)$ at lag 0 is simply $\bar{\lambda}_i \phi(0)$, so all that remains is to take the inverse Fourier transform of eqn 29 and to evaluate it at $x = 0$:

$$\phi(0) = \frac{1}{N} \sum_{s=-N/2+1}^{N/2} \frac{\tilde{\kappa}(\omega_s) [\tilde{R}(\omega_s) + \tilde{\eta}(\omega_s)]}{1 - \tilde{\kappa}(\omega_s) + \psi}. \quad (30)$$

As we only seek an approximation to $O(\sigma^2)$, we can drop $\tilde{\eta}(\omega)$ from the numerator and ψ from the denominator in eqn 30. Thus,

$$\text{Cov}(\lambda_i, v_i) = \frac{\bar{\lambda}_i}{N} \sum_{s=-N/2+1}^{N/2} \frac{\tilde{\kappa}(\omega_s) \tilde{R}(\omega_s)}{1 - \tilde{\kappa}(\omega_s)}. \quad (31)$$

We can relate this expression more directly to our rate of increase perturbation, $\zeta_{i,x}$, by noting that $R(x)$ is the spatial autocorrelation of ζ_i at lag x . This allows us to use the Wiener-Khinchin theorem, which states that the autocorrelation of a function at lag x is equal to the inverse Fourier transform of the function's spectral density, evaluated at x . Thus,

$$R(x_n) = \frac{1}{N} \sum_{j=-N/2+1}^{N/2} S_\zeta(\omega_j) e^{i\omega_j x_n}, \quad (32)$$

where the spectral density of ζ_i , $S_\zeta(\omega)$, equals $\frac{1}{N} |\tilde{\zeta}_i(\omega_j)|^2$, and

$$\tilde{R}(\omega_s) = S_\zeta(\omega_s). \quad (33)$$

Thus,

$$\text{Cov}(\lambda_i, v_i) = \frac{\bar{\lambda}_i}{N} \sum_{s=-N/2+1}^{N/2} \frac{\tilde{\kappa}(\omega_s) S_\zeta(\omega_s)}{1 - \tilde{\kappa}(\omega_s)}. \quad (34)$$

If $S_\zeta(\omega_s)$ and $\tilde{\kappa}(\omega_s)$ do not contain any Kronecker delta functions ($\delta_{ij}=1$ if $i=j$, 0 if $i \neq j$), then it is safe to go to the limit of an infinite domain ($N \rightarrow \infty$):

$$\text{Cov}(\lambda_i, v_i) = \bar{\lambda}_i \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{\tilde{\kappa}(\omega) S_\zeta(\omega)}{1 - \tilde{\kappa}(\omega)} d\omega. \quad (35)$$

(We have here set Δ to 1.) This is our primary result.