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CHAPTER 12

Scale Transition Theory for Understanding Mechanisms in Metacommunities

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Introduction

Ecological findings on small spatial or temporal scales often do not extrapolate to larger scales (Wiens 1989; Kareiva 1990; Horne and Schneider 1995; Englund and Cooper 2003). This empirical pattern has a parallel in ecological theory. In many model systems, the rules devised for population dynamics on small spatial or temporal scales can be quite different from those that emerge on large scales (Levin 1992). For example, in models of host-parasitoid systems, the highly unstable Nicholson-Bailey model might describe local population dynamics, but combined with spatial environmental variation, these local-scale instabilities may give rise to dynamics on the larger spatial scale described by the potentially highly stable host-parasitoid models of Bailey et al. (1962) and May (1978). Indeed, theoretical examples abound where the rules assumed on a small scale lead to contrasting outcomes on a larger scale, including changes in stability properties of single species models, conversion of competitive exclusion into competitive coexistence, and more mundane cases simply involving changes in quantitative features of models, such as mean densities (Chesson 2001).

These results from theory are interesting for two reasons. First, they may explain at least some failures of small-scale experimental findings to translate to larger scales. Second, they may provide a means of extrapolating, or scaling-up, findings for small scales to larger scales. The metacommunity concept owes its importance primarily to these issues of changes in rules with changes in scale, as exemplified by early metacommunity models (Slatkin 1974; Hastings 1977, 1980; see review by Mouquet et al., chapter 10; Caswell 1978).

A complete ecological theory should explain community dynamics on all scales (Levin 1992). Critical interactions between individual organisms occur over a range of scales (Chesson 1998a; Murrell and Law 2003), but these scales are mostly small. Scaling up theoretical findings from small scales is therefore essential. In classical (Hanski 1999), or equivalently, strict metacommunity models (Chesson 2001), it is assumed that interactions between individuals take place within local communities, but also that local communities do not persist. It follows that the system as a whole cannot be understood without reference to the

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larger scale of many local communities, which we refer to here as the regional or metacommunity scale. This strict metacommunity scenario represents one extreme of spatial structure that pervades ecological systems. In spatially-structured systems generally, the implications of local-scale interactions are necessarily modified by dispersal between localities in different states.

Scale transition theory (Chesson 1998a) is an attempt to systematize the study of how local-scale dynamical rules become modified as larger scales are taken into account. It unites analytical, simulation, and empirical approaches to an ecological question through key explanatory quantities accessible in all three approaches. The broad outline of scale transition theory was formulated many years ago (Chesson 1978, 1981), but rising theoretical and empirical interest in scale-dependent phenomena implies broad potential for its use. In essence, scale transition theory explains changes in dynamical rules with changes in scale in terms of interactions between spatial or temporal variation and nonlinear dynamics on local spatial scales. Many ecological processes lead to nonlinear dynamics including intra- and interspecific competition, predation, and mutualism. At the same time, spatial heterogeneity is a pervasive feature of ecological systems. It should therefore not be surprising that their combined effects are important.

The scale transition approach describes local ecological interactions mathematically in order to characterize their nonlinear nature. It then scales-up by averaging the formulae describing local interactions over space. Regional dynamics are then described by the *mean field*, that is, regional dynamics in the absence of spatial variation, plus the *scale transition*, which quantifies how spatial variances and covariances of population densities and environmental factors interact with local nonlinearities to modify regional dynamics.

Traditional approaches to metapopulations emphasize colonization and extinction dynamics of local populations connected by dispersal, with limited attention to the details of local community dynamics (Nee et al. 1997, Mouquet et al., chapter 10). Scale transition theory provides an alternative framework to understanding metapopulations and metacommunities in which the details of local dynamics are central. Scale transition theory can be applied to systems in which colonization and extinction are important features of local communities, but it also applies broadly to spatially structured systems regardless of the importance of local extinction and recolonization. Thus, scale transition theory avoids the criticism of traditional metapopulation models that the basic model structure is too limited to apply to many systems in nature (Harrison and Taylor 1997).

To introduce the basic concepts of scale transition theory, we open with a discussion of how spatial variation in parasitism can stabilize host-parasitoid interactions. This example illustrates a fundamental formula for discrete-time models whereby average individual fitness over a spatial region is expressed in terms of a mean-field component, interactions between nonlinear fitness and spatial variance, and covariation between fitness and density. Next, we show how this for-

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mula applies to patch models, which we illustrate using a model with local logistic dynamics, and discuss the role of dispersal in generating the spatial variances and covariances critical to the scale transition. We then extend the discrete-time formulation to continuous time and use it to understand coexistence of competitors in spatial Lotka-Volterra and related models. Our final model development illustrates the full power of scale transition concepts in the study of coexistence of annual plant species in a spatially varying environment. In conclusion, we relate the scale-transition approach to other developments of spatial dynamics as applied to metacommunities. In chapter 13, Melbourne et al. apply the results presented here to three empirical systems.

General Discrete-Time Formulation of the Scale Transition for Variation in Space

An individual at some location x in space has a fitness λ_x, which measures the average contribution of an individual at x to the population after some defined interval of time. Space can be continuous or discrete. Thus, x might represent a patch, a point in continuous space, or a point on a discrete lattice. Time is assumed discrete. Continuous-time formulations are discussed later and replace λ_x with a per capita growth rate.

We use the example of host-parasitoid models, as presented in box 12.1, to introduce the fundamentals of scale transition theory. Host-parasitoid models have had a key role in the many decades of theoretical research that attempted to explain the persistence of exploiter-victim interactions (Hassell 2000; Murdoch et al. 2003). In host-parasitoid models, the primary factor affecting host fitness is the spatially-varying parasitoid density, P_x, and so $\lambda_x = f(P_x)$. Under Nicholson-Bailey assumptions for local dynamics, f is an exponentially declining nonlinear function, as illustrated by the solid line in figure 12.1. If the parasitoid were homogeneously distributed in space, this exponential decline in host fitness with parasitoid density would lead to violent fluctuations in regional-scale host and parasitoid densities, matching the local scale dynamics. In contrast, with enough spatial variation in parasitoid density, these violent fluctuations are replaced by convergence of the regional population densities on a stable equilibrium point, as discussed in box 12.1.

The Effects of Spatial Variation and Nonlinearity on Spatial Average Fitness

To understand how stability results from spatial variation in the host-parasitoid model, note that the spatial averages, $\overline{N}$ and $\overline{P}$, of host and parasitoid densities are the regional-scale densities. We then ask how the spatial average, $\overline{\lambda}$, of λ_x depends on these regional-scale densities. Particular formulae are given in box 12.1, but figure 12.1 gives a graphical illustration for the case where P_x varies between just two values equal to a fraction of $\overline{P}$ and a multiple of $\overline{P}$, which might occur if the

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Box 12.1. Spatial variation in host-parasitoid systems

The traditional discrete-time Nicholson-Bailey host-parasitoid model takes the form

$$\begin{aligned} N_{t+1} &= Re^{-aP_t}N_t \\ P_{t+1} &= N_t - R^{-1}N_{t+1} \end{aligned} \qquad (12.B1.1)$$

where N and P are respectively host and parasitoid density, R is fitness of unparasitized hosts, and a is the average rate at which individual parasitoids discover hosts (Hassell 2000). The negative exponential above, $\exp(-aP_t)$, is the fraction of hosts escaping parasitism. The second line of the equation simply says that the number of parasitoids in the next generation is equal to the number of hosts killed by them in the current generation. It is more commonly written $P_{t+1} = [1 - \exp(-aP_t)]N_t$, but our form is more general, and being linear in densities, does not change with spatial scale.

This model is notoriously unstable and much theoretical research has been directed toward modifications that predict stable coexistence of host and parasitoid. Of the many such modifications (Hassell 2000), we are concerned here only with those relating to spatial variation in the density of parasitoids. These modifications lead to changes in the first line of equation 12.B1.1, but not the more general second line.

The first line of equation 12.B1.1 implies that host fitness is $\lambda_t = R\exp(-aP_t)$. We can modify this equation by having the parasitoid density vary in space, denoting by P_x the density of parasitoids at location x. This density will change with time, but for simplicity of notation, a subscript indicating time is omitted. Host fitness as a function of local parasitoid density is then

$$\lambda_x = Re^{-aP_x}. \qquad (12.B1.2)$$

Here R is the host fitness in the absence of parasitism, P_x is the local parasitoid density, and a is the average rate at which individual parasitoids discover hosts.

Scale Transition for Independent Host and Parasitoid Distributions

May (1978) pointed out that when P_x is distributed in space according a gamma distribution, the average of λ_x over space takes the form

$$\bar{\lambda}_t = R(1 + a\bar{P}_t/k)^{-k} \qquad (12.B1.3)$$

where $\bar{P}_t$ is the average of P_x over space in year t, and $1/k$ is equal to the square of the coefficient of variation (CV) of the parasitoid distribution in

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space. When the hosts and parasitoids are distributed independently of one another, then, as explained in the text, the first line of equation 12.B1.1 can be validly replaced by

$$\overline{N}_{t+1} = \overline{\lambda}_t \overline{N}_t. \qquad (12.B1.4)$$

The model then predicts stable host and parasitoid coexistence provided the parasitoid CV is greater than 1.

For arbitrary spatial distributions of parasitoids, equation 12.B1.3 is replaced by

$$\overline{\lambda}_t = F\varphi(a\overline{P}_t), \qquad (12.B1.5)$$

(Chesson and Murdoch 1986) where φ is a function dependent on the relative distribution of parasitoids in space (the distribution of $P_x/\overline{P}$) and is called the Laplace transform in statistical theory. (Figure 12.1 provides a geometrical construction of φ for the simple case where parasitoid densities take on only two values.) The chief finding for the general case given by equation 12.B1.5 is that the CV criterion for stability applicable to gamma distributed hosts remains approximately applicable in this more general case (Hassell et al. 1991).

Scale Transition for Correlated Host and Parasitoid Distributions

Several implicit assumptions are involved in the above conclusions. First, as explained in the text, equation 12.B1.4 is only valid when the fraction of hosts parasitized is uncorrelated with host density. In other cases, the applicable equation for population dynamics is

$$\overline{N}_{t+1} = \tilde{\lambda}_t \overline{N}_t \qquad (12.B1.6)$$

where $\tilde{\lambda}_t$ is host individual average fitness, rather than host spatial average fitness ($\overline{\lambda}$). Second the distribution of $P_x/\overline{P}$ is assumed constant over time, which might not be true depending on the dispersal scenarios. The conclusions above about stability, however, continue to apply to the CV of the distribution of parasitoids per host, provided this CV does not vary importantly over time (Hassell et al. 1991). Equations 12.B1.3 and 12.B1.5 are valid for $\tilde{\lambda}$ replacing $\overline{\lambda}$ when the probability distribution of P_x is the per host distribution (Chesson and Murdoch 1986), but if the distribution of $P_x/\overline{P}$ over hosts varies with time, then k and φ must be given subscripts t to indicate that variation. How the distribution of $P_x/\overline{P}$ might vary over time depends on the nature of dispersal, which we have not addressed explicitly here.

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Scale Transition Approximations

We can use formulae 12.6–12.8 in the text to obtain approximations to $\tilde{\lambda}$. As $f(P_x) = Re^{-aP_x}$, $f'(\bar{P}) = -Rae^{-a\bar{P}}$ and $f''(\bar{P}) = Ra^2e^{-a\bar{P}}$. Hence, $\bar{\lambda}$ is approximated as

$$\bar{\lambda} \approx Re^{-a\bar{P}} + \frac{1}{2}Ra^2e^{-a\bar{P}}\,\mathrm{Var}(P), \qquad (12.B1.7)$$

and the fitness-density covariance is approximately,

$$\mathrm{Cov}(\lambda, \nu) \approx -Rae^{-a\bar{P}}\,\mathrm{Cov}(P, N)/\bar{N}. \qquad (12.B1.8)$$

These combine to give an overall value of $\tilde{\lambda}$ equal to

$$\tilde{\lambda} \approx Re^{-a\bar{P}}\left\{1 + \frac{1}{2}a^2\,\mathrm{Var}(P) - a\,\mathrm{Cov}(P, N)/\bar{N}\right\}. \qquad (12.B1.9)$$

These approximations serve to show the moderating effect of variation in parasitism on the relationship between $\tilde{\lambda}$ and $\bar{P}$, and how this relationship is affected by covariance between parasitoids and host density. Approximations like these, coupled with the corresponding approximations for $d\tilde{\lambda}/d\bar{P}$, allow the stability rule discussed here to be derived for cases where R is near 1, that is, when host fitness in the absence of parasitism is not too large (Hassell et al. 1991).

system consisted of just two patches. The dashed curve gives the relationship between $\bar{\lambda}$ and $\bar{P}$ that is traced out as $\bar{P}$ varies. The diamonds illustrate how this curve is calculated. The diamonds lie at the midpoints of line segments connecting (P_x, λ_x) points for pairs of low and high parasitoid localities. The midpoint of a line segment is necessarily the simple average of the endpoints of the same line segment. Because the function $f(P_x)$ curves up (is concave up; see box 12.2), the midpoints of the line segments are necessarily above the original curve. Thus, $\bar{\lambda} > f(\bar{P})$, that is, spatial average fitness ($\bar{\lambda}$, which equals $\overline{f(P)}$) exceeds that predicted by the local relationship between fitness and parasitoid density ($f(\bar{P})$). Of most importance for regional stability, the decline in $\bar{\lambda}$ as a function of $\bar{P}$ is much more moderate than the decline in λ_x as a function of P_x.

This effect of variation in parasitoid density on mean fitness is a particular illustration of the phenomenon of nonlinear averaging (box 12.2) where a nonlinear function of some variable quantity is averaged, and the result differs from the nonlinear function of the average of that variable quantity. Here $\lambda_x = f(P_x)$, but $\bar{\lambda} \neq f(\bar{P})$. When the nonlinear function f curves in a consistent direction (i.e., is concave up or concave down), the direction of the deviation between the average

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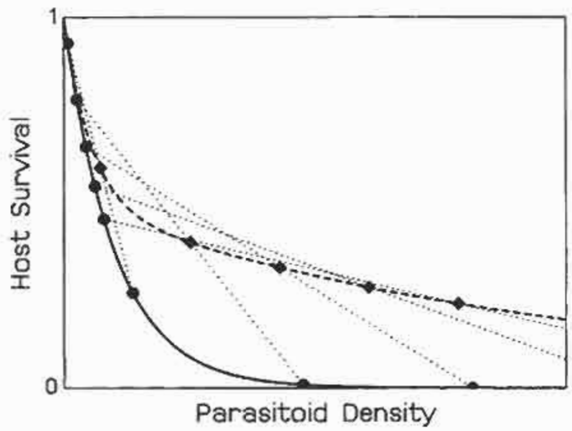

Figure 12.1 Decline in host density as a function of parasitoid density, locally in space (solid line: $\lambda_x = Fe^{-aP_x}$), and regionally (dashed line: $\bar{\lambda} = \overline{Fe^{-aP}} = F\varphi(a\bar{P})$) for the special case of variation in parasitoid density in space between just two values of P_x, one 5% of the mean and other 195% of the mean (i.e., $P_x = 0.05\,\bar{P}$ and $P_x = 1.95\,\bar{P}$). Note that the decline in host survival as parasitoid average density increases is much more moderate in the presence of spatial heterogeneity (dashed line) than in its absence (solid line). The ◆'s are at particular $(\bar{P}, \bar{\lambda})$ pairs illustrating the effect of Jensen's inequality on the relationship between $\bar{\lambda}$ and $\bar{P}$. The average of the two (P_x, λ_x) at the ●'s on each dotted line equals the particular $(\bar{P}, \bar{\lambda})$ pair at the ◆ in the center of the line. Because of the curvature of λ_x as a function of P_x, these averages necessarily lie above the values that would be given by the local λ-P relationship.

of the function $\overline{f(P)}$ and the function of the average $f(\bar{P})$ is predictable and is known as Jensen's inequality (box 12.2).

The Importance of the Fitness-Density Covariance and Individual Average Fitness

Given the more moderate behavior of the spatial average fitness as a function of average parasitoid density in the host-parasitoid model, it is not surprising that the regional-scale dynamics are more stable in the presence of spatial variation. To draw firm conclusions, however, we must determine the extent to which $\bar{\lambda}$ determines regional-scale population dynamics. If λ_x is fitness for the period t to $t + 1$, the $N_{x,t}$ individuals at location x and time t, give rise by reproduction and survival to $\lambda_x N_{x,t}$ individuals at time $t + 1$. If some of these disperse, then $N_{x,t+1} \neq \lambda_x N_{x,t}$, but assuming dispersers do not leave the region, the total density in the system at time $t + 1$ is nevertheless

$$\sum_x N_{x,t+1} = \sum_x \lambda_x N_{x,t}. \tag{12.1}$$

Dividing equation 12.1 by the number of local sites x in the system now shows

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Box 12.2 Properties of Nonlinear Averages

Basic to the scale transition is the idea of nonlinear averaging, that is, taking an average of some nonlinear function $f(W)$ of a varying quantity W (Chesson 1998a). Most introductions to statistics give some appreciation of nonlinear averages from the two different formulae for the variance (see, e.g. Ross 1997). We know that the variance $\mathrm{Var}(W)$ is defined as the average squared deviation from the mean:

$$\mathrm{Var}(W) = \overline{(W - \overline{W})^2}, \tag{12.B2.1}$$

but it also obeys the formula

$$\mathrm{Var}(W) = \overline{W^2} - (\overline{W})^2, \tag{12.B2.2}$$

that is, the variance of W is the difference between the mean of the square of W and the square of the mean of W. This formula rearranges to show that the mean of the square of W exceeds the square of the mean of W by an amount exactly equal to the variance:

$$\overline{W^2} = (\overline{W})^2 + \mathrm{Var}(W). \tag{12.B2.3}$$

This finding is a particular case of the result that the mean, $\overline{f(W)}$, of a nonlinear function, generally differs from the function of the mean, $f(\overline{W})$; here $f(W) = W^2$.

Jensen's Inequality

Unfortunately, only in special cases such as $f(W) = W^2$ do we know exactly how much the mean of the function and the function of the mean differ from each other. However, we can tell the direction of the difference if the function curves in a consistent direction, that is, it is concave, either up or down. If $f(W)$ is concave up, as indicated by $f''(W) > 0$, Jensen's inequality (Ross 1997) says that

$$\overline{f(W)} > f(\overline{W}), \tag{12.B2.4}$$

that is, the mean of the function is greater than the function of the mean. Naturally, for concave down functions ($f''(W) < 0$), the reverse inequality to inequality 12.B2.4 applies. For the particular case where $f(W) = W^2$, equation 12.B2.3 tells us that the amount by which $\overline{f(W)}$ exceeds $f(\overline{W})$ is simply the variance. Another example of an exact formula for $\overline{f(W)}$ is given in box 12.1 for the host-parasitoid. Figures 12.1 and 12.2 give graphical illustrations of Jensen's inequality, which are available for the simple case where W (respectively P and N in these figures) vary over just two values.

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Quadratic Approximations

Although the exact difference between $\overline{f(W)}$ and $f(\overline{W})$ is not often known, the following approximation

$$\overline{f(W)} \approx f(\overline{W}) + \frac{1}{2} f''(\overline{W})\mathrm{Var}(W), \tag{12.B2.5}$$

holds generally whenever $f(W)$ can be satisfactorily approximated by its second order Taylor expansion, and can be derived simply from the special case, equation 12.B2.3 (Chesson 1998a).

Multidimensional Nonlinearities

Ecological models often involve multiple quantities varying simultaneously. With two varying quantities, U and W, we need to understand averages, $\overline{f(U, W)}$, of functions nonlinear jointly in these varying quantities. The simplest two-variable nonlinear function with a joint nonlinearity is the product $f(U, W) = UW$. A simple extension of the variance formula (12.B2.3) leads to the relationship

$$\overline{UW} = \overline{U} \cdot \overline{W} + \mathrm{Cov}(U, W), \tag{12.B2.6}$$

that is, the mean of the product differs from the product of the means by an amount equal to the covariance of the two quantities (Ross 1997).

Special Nonlinear Forms in Spatial Models

In spatial models, we encounter nonlinear functions of two variables of the form $f(W)U$, where $f(W)$ is a nonlinear function of W separately. Application of formula 12.B2.6 shows that

$$\overline{f(W)U} = \overline{f(W)} \cdot \overline{U} + \mathrm{Cov}(f(W), U). \tag{12.B2.7}$$

This covariance in this formula can be approximated by the formula

$$\mathrm{Cov}(f(W), U) \approx f'(\overline{W})\mathrm{Cov}(W, U) \tag{12.B2.8}$$

to the same order of accuracy as the approximation 12.B2.5 by linearly approximating $f(W)$ as $f(\overline{W}) + f'(\overline{W})(W - \overline{W})$, using standard statistical arguments (Rao 1973). Substituting the approximation 12.B2.5 for $\overline{f(W)}$, we get the overall approximation

$$\overline{f(W)U} \approx \left\{ f(\overline{W}) + \frac{1}{2} f''(\overline{W})\mathrm{Var}(W) \right\} \overline{U} + f'(\overline{W})\mathrm{Cov}(W, U). \tag{12.B2.9}$$

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Nonlinearities in Patch Models

In the text, under the heading of patch models, we use expression 12.B2.9 in the special case where $N = W = U$, and so $\text{Cov}(W, U) = \text{Var}(N)$. Thus, expression 12.B2.9 implies

$$\overline{f(N)N} \approx \left\{ f(\overline{N}) + \frac{1}{2} f''(\overline{N})\text{Var}(N) \right\} \overline{N} + f'(\overline{N})\text{Var}(N)$$
$$= \left\{ f(\overline{N}) + \frac{1}{2} f''(\overline{N})\text{Var}(N) + f'(\overline{N})\text{Var}(N)/\overline{N} \right\} \overline{N}. \quad (12.\text{B}2.10)$$

But applying approximation 12.B2.5 to the function $F(N) = f(N)N$, we see also that

$$\overline{F(N)} \approx F(\overline{N}) + \frac{1}{2} F''(\overline{N})\text{Var}(N). \quad (12.\text{B}2.11)$$

However, as $F''(N) = f''(N)N = 2f'(N)$, we see that expressions 12.B2.10 and 12.B2.11 are in fact identical.

Checking Approximations

The approximations given here and used in the text work best when spatial variation is small in magnitude. Thus, they give the initial trends in the scale transition as spatial variation is introduced to a system. For any particular application with large spatial variation, it is necessary to check the accuracy of these approximations by some means. It is not difficult to calculate nonlinear averages numerically when the probability distributions for spatial variation are known, and thus check these formulae. When these distributions are not known, simulation or other numerical methods are needed to determine them.

that the dynamics of the regional-scale population density $\overline{N}$ are given by the equation

$$\overline{N}_{t+1} = \overline{\lambda N_t} = \tilde{\lambda}\overline{N}_t, \quad (12.2)$$

where $\tilde{\lambda}$ is the average of λ_x over all individuals in the population, and is given by the formula $\tilde{\lambda} = \overline{\lambda N_t}/\overline{N}_t = \sum_x \lambda_x N_{t,x}/\sum_x N_{t,x}$. Of most importance, average individual fitness determines regional-scale population dynamics, because equation 12.2 says $\overline{N}_{t+1} = \tilde{\lambda}\overline{N}_t$.

To relate average individual fitness, $\tilde{\lambda}$, to the spatial average fitness, $\overline{\lambda}$, we define the relative density at location x as $\nu_x = N_x/\overline{N}_t$, that is, the density at location x compared with the average density in the system. Then we see that $\tilde{\lambda}$ can be expressed as

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$$\tilde{\lambda} = \overline{\lambda \nu}, \tag{12.3}$$

the spatial average of $\lambda_x \nu_x$. Expression 12.3 is the average of a product, which is therefore equal to the product of the average, $\overline{\lambda} \cdot \overline{\nu}$, plus the covariance, Cov(λ, ν), between them (box 12.2). As $\overline{\nu}$ is necessarily 1, this means that

$$\tilde{\lambda} = \overline{\lambda \nu} = \overline{\lambda} + \mathrm{Cov}(\lambda, \nu), \tag{12.4}$$

(Chesson 2000a). Thus, we see that $\tilde{\lambda}$ differs from $\overline{\lambda}$ by the spatial covariance, Cov(λ, ν), between fitness of an individual at location x and the relative density there, which is called the fitness-density covariance (or growth-density covariance in Snyder and Chesson 2003).

For any system, equation 12.4 says that the spatial average fitness $\overline{\lambda}$ is equal to the average individual fitness $\tilde{\lambda}$ when the fitness-density covariance is zero. For the host-parasitoid model, the fitness-density covariance is zero whenever host density is uncorrelated with the incidence of parasitism, which is in fact not uncommon in nature (Pacala and Hassell 1991). In such cases, the conclusions above about $\overline{\lambda}$ are also conclusions about $\tilde{\lambda}$; that is, sufficient spatial variation in P_x stabilizes the host-parasitoid interaction (box 12.1). In cases where the fitness-density covariance is not zero, it is still possible for spatial variation to be stabilizing (box 12.1), but the relevant calculations have to include this covariance.

To generalize these ideas, fitness can be simply a nonlinear function of some factor W_x determined by the point x in space:

$$\lambda_x = f(W_x). \tag{12.5}$$

Ideally, W_x is some quantity whose spatial average is meaningful. In the host-parasitoid example, where $W_x = P_x$, the spatial average is simply parasitoid density on the larger spatial scale, which is both perfectly meaningful and useful. Such utility need not apply to other fitness factors; for example, choosing $W_x = \ln P_x$ would not help, because the spatial average of $\ln P_x$ is not meaningful.

General Scale Transition Formulae

For general fitness factors, a simple and standard approximation to Jensen's inequality allows us to see just how the scale transition works (Chesson 1998b; box 12.2). Here, equation 12.5 means that

$$\overline{\lambda} = \overline{f(W)} \approx f(\overline{W}) + \frac{1}{2} f''(\overline{W})\mathrm{Var}(W) \tag{12.6}$$

Thus, the relationship of average fitness to average W differs from the relationship that applies locally in space by an amount that is approximately proportional to the variance Var(W) of the fitness factor W. The proportionality constant $1/2\, f''(\overline{W})$ is a measure of the nonlinearity of the local-scale relationship between fitness and W_x at the mean of W_x.

To obtain the relationship between average individual fitness $\tilde{\lambda}$ and $\overline{W}$, we

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must add the fitness-density covariance to equation 12.6. As explained in box 12.2, this covariance can be approximated as

$$\mathrm{Cov}(f(W), \nu) \approx f'(\overline{W})\mathrm{Cov}(W, \nu). \tag{12.7}$$

Combining equations 12.6 and 12.7, we obtain a general purpose approximation to $\tilde{\lambda}$:

$$\tilde{\lambda} \approx f(\overline{W}) + \frac{1}{2} f''(\overline{W})\mathrm{Var}(W) + f'(\overline{W})\mathrm{Cov}(W, \nu). \tag{12.8}$$

The first term, $f(\overline{W})$, is simply the nonspatial formula for λ, and is commonly referred to in the literature as the "mean field." We define the "scale transition" to be the difference $\tilde{\lambda} - f(\overline{W})$, which is expressed here as the effects of variance on local nonlinear dynamics, $1/2\ f''(\overline{W})\mathrm{Var}(W)$, and fitness-density covariance, $f'(\overline{W})\mathrm{Cov}(W, \nu)$.

In box 12.1, this formula is applied to the host-parasitoid model to give a simple understanding of how $\tilde{\lambda}$ is changed by various spatial relationships. It applies generally, however, to spatial models represented in discrete time, whether they are spatially explicit, spatially implicit, patch models, lattice models, or continuous space models. Moreover, it does not matter whether population sizes, N_x, are represented as continuous variables, or are discrete. In continuous-space discrete-N_x models, for example, N_x is zero at most points in space, and takes the value one at places where an individual is present. In continuous space models, and in many lattice models, W_x is not simply a function of population densities and environmental factors at the point x, but instead depends on conditions around x expressed as a summary of the densities and environmental factors in a neighborhood centered at x (Neuhauser and Pacala 1999), or as averages of these factors weighted inversely with distance from x using functions called competition kernels (Pacala and Silander 1985). It should be noted, however, that approximations like those above work best when spatial variation in W_x is small, and so should be regarded primarily as giving the initial trends for the scale transition as spatial variation is increased from small values (box 12.2).

Patch Models

In patch-model approaches to spatial dynamics, the location of an individual has the resolution of a patch, and the dynamical equations are formulated in terms of the output of a patch, $\lambda_x N_x$. In the simplest models this output is just a function of N_x:

$$\lambda_x N_x = F(N_x). \tag{12.9}$$

Previous discussions of the scale transition have emphasized patch models pointing out that

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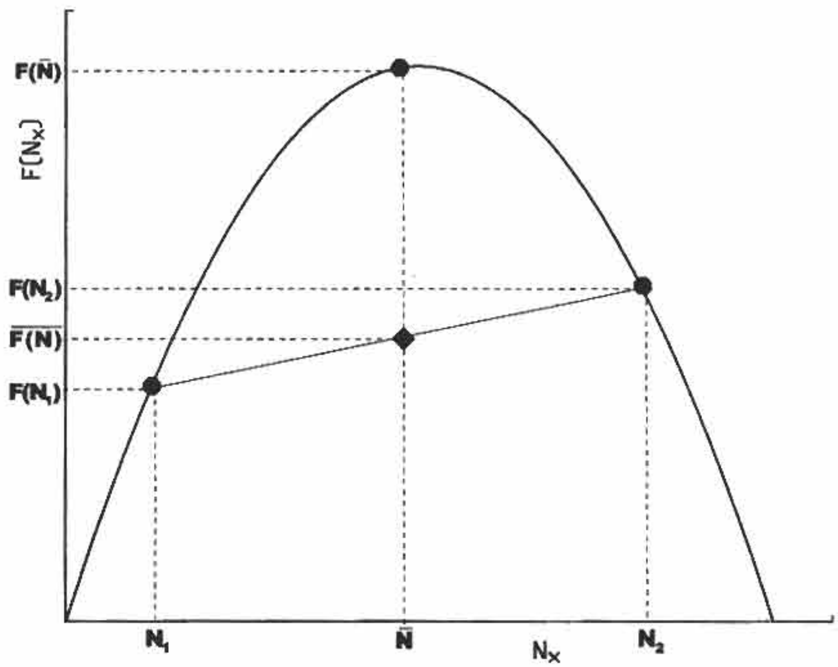

Figure 12.2 Scale transition for a patch model with $\lambda_x N_x = F(N_x)$, and density varying between two values with equal frequency, showing the construction of one point (◆) on the relationship between $\overline{F(N)}$ and $\bar{N}$. Note that the regional-scale output, $\bar{N}_{t+1} = \overline{F(N_t)} = \tilde{\lambda}\bar{N}_t$, lies below the output given by the local relationship, $F(\bar{N}_t)$. The particular curve represented here is the logistic.

$$\bar{N}_{t+1} = \overline{\lambda N} \approx F(\bar{N}_t) + \frac{1}{2} F''(\bar{N}_t)\mathrm{Var}(N). \tag{12.10}$$

Figure 12.2 shows how this works when N_x varies between just two values, for example if the regional scale consists of just two local-scale patches.

The curve in figure 12.2 is the logistic equation, that is, $F(N) = N[1 + r(1 - N/K)]$, for which $F''(\bar{N}) = -2r/K$. From equation 12.10, we obtain an equation for population dynamics in the form

$$\bar{N}_{t+1} = \bar{N}_t\left\{1 + r\left(1 - \frac{\bar{N}_t}{K}\right)\right\} - \frac{r}{K}\mathrm{Var}(N), \tag{12.11}$$

which is exact because the logistic equation is quadratic and so approximation (12.10) is exact. In box 12.2 it is shown that these patch-model approximations for the scale transition are special cases of the previous approximations focusing on $\tilde{\lambda}$. Note that here $F(N) = f(N)N$, $W = N$, $\mathrm{Var}(W) = \mathrm{Var}(N) = \mathrm{Cov}(W, N) = \bar{N}\mathrm{Cov}(W, \nu)$, and so equation 12.8 for $\tilde{\lambda}$ implies

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$$\overline{N}_{t+1} = \tilde{\lambda}\overline{N}_t \approx f(\overline{N}_t)\overline{N}_t + \frac{1}{2}f''(\overline{N}_t)\mathrm{Var}(N)\overline{N}_t + f'(\overline{N}_t)\mathrm{Var}(N), \quad (12.12)$$

where the first term of equation 12.12 is the mean field, and the second two terms are scale transition terms summing to 1/2 $F''(\overline{N})\mathrm{Var}(N)$ but dividing this quantity into the effect of variance in nonlinear fitness and the effect of fitness-density covariance.

For the logistic, the fitness function f is linear and so $f''(\overline{N}) = 0$. Thus, in the logistic all the effects of the scale transition come from the fitness-density covariance. Substituting the logistic formula $f'(\overline{N}) = -r/K$ into equation 12.12 reproduces the previous patch-model formula (equation 12.11) exactly. Alternatives to the logistic, such as the Ricker model (Chesson 1998a), and the Ayala-Gilpin θ-logistic model (Chesson 1991b) have nonlinear fitness functions, that is, $f''(\overline{N}) \neq 0$, and all terms of the regional equation 12.12 are nonzero with these models for local population dynamics.

Spatial Variance, Population Dynamics, and Dispersal

The development above omits explicit consideration of dispersal. By focusing on λ_x, or the output of a patch, $\lambda_x N_x$, the equations are correct for any mode of dispersal provided any mortality that occurs during dispersal is factored into λ_x (Chesson 1998a). The effects of dispersal are expressed by the relevant spatial variances and covariances, which we have left unspecified. To allow population dynamics to be fully understood, the way these variances and covariances change over time, and especially how they depend on mean population densities, needs to be known. Determining such relationships is the subject of moment closure approximation techniques (Bolker and Pacala 1997), and can be difficult and highly complex because these relationships depend not only on dispersal but also on local dynamics and environmental variation. However, in certain cases, these relationships are simply determined (Chesson 1998a). For example, if most individuals disperse, and dispersal is over long distances with the physical environment determining where individuals concentrate, then $N_{x,t}$ can be modeled as

$$N_{x,t} = U_x\overline{N}_t, \quad (12.13)$$

where U_x varies in space (and possibly in time also) encoding features of the physical environment that influence dispersal to location x. Here the relative density, ν_x, is simply U_x. With this model $\mathrm{Var}(N) = \mathrm{Var}(U)\overline{N}_t^2$, that is, the variance is proportional to the square of mean density, and so the coefficient of variation of density in space is constant over time, and determined by spatial variation in the physical environment. In contrast, when patchiness in space is determined by demographic stochasticity rather than environmental variation, long-distance dispersal implies that $\mathrm{Var}(N)$ is proportional to $\overline{N}_t$ (Chesson 1998a).

Substituting the model (equation 12.13) for the variance into the logistic for-

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mula (equation 12.11), leads to regional-scale dynamics that are logistic like the local-scale dynamics. Spatial variance has the effect of strengthening the density dependence at the regional scale, which is revealed as a lowered carrying capacity: The new value of K equals the old value divided by $(1 + \mathrm{Var}(U))$. The regional dynamics of the system are altered quantitatively by spatial variation, but the rules for regional dynamics do not differ qualitatively from the rules applicable to inputs and outputs of a patch at the local scale. However, when the linear fitness function, $f(N)$, of the logistic model is replaced by the more realistic nonlinear $f(N)$ of the Ricker model, regional-scale dynamics can be changed qualitatively by environmentally-dependent dispersal (Chesson 1998a). Although local scale dynamics may be chaotic in the Ricker model, environmentally-dependent dispersal can lead to highly stable regional dynamics. Similar, though much weaker effects, are possible from demographic stochasticity ($\mathrm{Var}(N)$ proportional to $\overline{N}_t$), in both the logistic model (Chesson 1998b) and the Ricker model (Chesson 1998a).

Continuous Time

From the perspective of the scale transition, the distinction between discrete time and continuous time is not large. In continuous-time models, λ_x is replaced by the local per capita growth rate $r_x = (dN_x/dt)/N_x$ as the fitness measure, with average individual fitness now denoted $\tilde{r}$. The growth of a population at the regional scale then takes the form

$$\frac{d\overline{N}}{dt} = \overline{rN} = \tilde{r} \cdot \overline{N} = \{\bar{r} + \mathrm{Cov}(r, \nu)\}\overline{N}. \qquad (12.14)$$

In cases where r_x has the representation $r_x = f(W_x)$, we have the general quadratic approximation

$$\frac{d\overline{N}}{dt} \approx f(\overline{W})\overline{N} + \left\{\frac{1}{2} f''(\overline{W})\mathrm{Var}(W) + f'(\overline{W})\mathrm{Cov}(W, \nu)\right\}\overline{N}, \qquad (12.15)$$

which specializes to forms analogous to equations 12.10 and 12.12 in the appropriate patch-model circumstances. Here $f(\overline{W})\overline{N}$ is the mean field, and the remaining terms give the scale transition in terms of local nonlinearity and fitness-density covariance.

Lotka-Volterra Competition Models

A particular illustration of the formula (12.15) has been given by Bolker and Pacala (1999) for a continuous space Lotka-Volterra competition model. In their model, W_x represents the total of intraspecific and interspecific competition experienced by an individual at x, which is assumed to be linearly related to the densities of competitors in neighborhoods centered on the point x. Their model can

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be simplified to a patch model without loss of information for our purposes. Then W_{ix} can be defined as $\alpha_{ii}N_{ix} + \alpha_{ij}N_{jx}$, where α denotes competition coefficients in the form advocated in Chesson (2000b), and $r_{ix} = f_i(W_{ix}) = r_i(1 - W_{ix})$, where r_i is the intrinsic rate of increase for species i. Thus, the local dynamical equation in the absence of dispersal is

$$\frac{dN_i}{dt} = r_i(1 - W_i)N_i = r_i\{1 - \alpha_{ii}N_i - \alpha_{ij}N_j\}\, N_i. \tag{12.16}$$

When expressed in this form, the criteria for species coexistence on the local scale are simply

$$\alpha_{jj}/\alpha_{ij} > 1, i \neq j, \tag{12.17}$$

that is, local-scale intraspecific competition must exceed local-scale interspecific competition Chesson (2000b).

As f_i is linear here, equation 12.15 is exact and reduces to

$$\begin{aligned}\frac{d\overline{N}_i}{dt} &= r_i\{1 - \overline{W}_i\}\overline{N}_i - r_i\{\mathrm{Cov}(W_i, \nu_i)\}\overline{N}_i \\ &= r_i\{1 - \alpha_{ii}\overline{N}_i - \alpha_{ij}\overline{N}_j\}\,\overline{N}_i - r_i\{\alpha_{ii}\,\mathrm{Var}(N_i) + \alpha_{ij}\mathrm{Cov}(N_i, N_j)\}.\end{aligned} \tag{12.18}$$

(Lloyd and White 1980 produced a similar expression using the concept of "mean crowding," which is an important precursor to scale transition concepts, but applies only to linear fitness functions.) In equation 12.18, the mean field is $r_i\{1 - \alpha_{ii}\overline{N}_i - \alpha_{ij}\overline{N}_j\}\,\overline{N}_i$, that is, the Lotka-Volterra equations (12.16) with regional variables substituted for local variables. The linearity of f_i means that the scale transition is simply the fitness-density covariance. Bolker and Pacala (1999) focus on spatial variation that arises from demographic stochasticity and spatially local dispersal, and uncover a variety of situations where the fitness-density covariance is responsible for species coexistence. For example, they note that a locally dispersing species with a high r_i can coexist with a superior competitor that lacks these traits even though the superior species excludes the other in the nonspatial case.

The most difficult feature of the Bolker and Pacala analysis is derivation of dynamical equations for the relevant spatial variances and covariances using moment closure approximation (see "Spatial Variance, Population Dynamics, and Dispersal" above). For a much simpler illustration of how coexistence may result from the fitness-density covariance terms in equation 12.18, assume that dispersal is rapid, and influenced by the physical environment so that N_{ix} is well approximated by $U_{ix}\overline{N}_i$, as in the previous section. Here the physical environmental effects encoded in U_{ix} may differ between species.

Defining $\sigma_{ii} = \mathrm{Var}(U_{ix})$ and $\sigma_{ij} = \mathrm{Cov}(U_{ix}, U_{jx})$ we have $\mathrm{Var}(N_i) = \sigma_{ii}\overline{N}_i^2$, and $\mathrm{Cov}(N_i, N_j) = \sigma_{ij}\overline{N}_i\overline{N}_j$. Substituting into equation 12.18, we obtain

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$$\frac{d\overline{N}_i}{dt} = r_i\{1 - \alpha_{ii}(1 + \sigma_{ii})\overline{N}_i - \alpha_{ij}(1 + \sigma_{ij})\overline{N}_j\}\overline{N}_i. \tag{12.19}$$

Here the dynamics at the regional scale are again given by Lotka-Volterra equations, but the competition coefficients differ from the local scale coefficients: α_{ii} is replaced by $\alpha_{ii}(1 + \sigma_{ii})$ and α_{ij} is replaced by $\alpha_{ij}(1 + \sigma_{ij})$. Applying standard Lotka-Volterra coexistence criteria from Chesson (2000b), it follows that the species coexist if

$$\frac{\alpha_{jj}(1 + \sigma_{jj})}{\alpha_{ij}(1 + \sigma_{ij})} > 1, \text{ or equivalently } \frac{\alpha_{jj}}{\alpha_{ij}} > \frac{1 + \sigma_{ij}}{1 + \sigma_{jj}},\ i \neq j. \tag{12.20}$$

The left hand inequality simply says that regional-scale intraspecific competition must exceed regional-scale interspecific competition. Variation in space modifies the regional-scale coefficients over the local coefficients, necessarily increasing regional-scale intraspecific competition, $\alpha_{jj}(1 + \sigma_{jj})$, because σ_{jj} is a variance and must be positive. However, regional-scale interspecific competition, $\alpha_{ij}(1 + \sigma_{ij})$, need not be increased because σ_{ij} can be negative or zero. Moreover, the covariance σ_{ij} equals $\rho\sqrt{\sigma_{ii}\sigma_{jj}}$, where ρ is the correlation in space between N_{ix} and N_{jx}.

A zero value of ρ means that the species use space independently, and the covariances are also zero. A ρ of 1, on the other hand, means identical use of space by the two species; and if the variances are equal, the covariances are the same as the variances. Then spatial variation terms cancel out of criterion 12.20 indicating for that case an absence of any effect of spatial variation on coexistence. However, identical use of space is unlikely, meaning that correlations in space are usually less than 1. Thus, whenever the variances σ_{jj} are similar for the two species (i.e., the species have similar coefficients of variation of density) the ratio $(1 + \sigma_{ij})/(1 + \sigma_{jj})$ is less than 1, and the criterion 12.20 is more easily satisfied. In particular, coexistence can occur at the region-scale even when local-scale interspecific competition exceeds local-scale intraspecific competition.

This example is just one illustration of how differences between species in the use of space can contribute to species coexistence. This possibility was first elucidated in spatial Lotka-Volterra models with rapid dispersal by Shigesada and Roughgarden (1982). Analogous to these spatial Lotka-Volterra competition models are discrete-time spatial models of insects competing for patchily distributed resources (Atkinson and Shorrocks 1981; Ives 1988). Coexistence is known to result in these models when intraspecific spatial aggregation is stronger than interspecific aggregation. Such spatial aggregation can be measured by variances and covariances analogous to σ_{ii} and σ_{ij} given here (Ives 1991). With few exceptions (Heard and Remer 1997; Remer and Heard 1998), the spatial coexistence mechanism in these models has been found to be equivalent to spatial niche differences (Green 1986; Chesson 1991; Hartley and Shorrocks 2002) or the spatial storage effect (Chesson 2000a).

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However, spatial variation need not always promote coexistence in these sorts of models. For example, the criteria (12.20) imply that coexistence might be converted into competitive exclusion when species covary positively in space and have very different spatial variances. Moreover, in other models for dispersal, such as slow short-distance dispersal, heavily influenced by demographic stochasticity (Bolker and Pacala 1999), the Lotka-Volterra equations are not recovered at the regional level, which means that regional dynamics are qualitatively different from local dynamics. In particular, the regional-level competition coefficients are density-dependent, and the regional-level coexistence criteria are far more complex than those above.

Coexistence Mechanisms in a Spatially Variable Environment

Scale transition ideas have been developed most extensively in the formulation and analysis of mechanisms of competitive coexistence in a variable environment (Chesson 2000a; Snyder and Chesson 2003). In variable-environment competition theory, particular biological processes generate particular types of nonlinearity and define distinct classes of coexistence mechanism. Aspects of this theory are illustrated here using the annual plant model defined in table 12.1.

As defined by equation 12.T1.1, the fitness of an individual seed involves two pathways in the life cycle. First, in any given year a seed may remain dormant, and either survive to the next year or perish. Second, it may germinate, then potentially survive as a seedling, grow, experience competition, and produce seed, some of which may perish before the next year. Each of these events occurs with a probability or magnitude determined by the life-history parameters defined in the table.

Each of the life-history parameters in the table could vary spatially with the environment in ways that differ between species, defining species-specific responses to environmental conditions. Competition is also spatially variable, and its magnitude at location x is expressed in the model by the quantity C_x (the competitive response), which combines the effects of intraspecific and interspecific competition for any species. However, we assume that C_x is the same for each species, precluding the possibility of coexistence in the absence of variation in fitness in space or time. Although not varying with species, C_x varies in space because population densities vary in space as a consequence of spatial variation in life-history parameters. In addition, and more importantly for species coexistence, C_x may be spatially variable because it is directly a function of two life-history parameters that may vary in space. These life-history parameters are the germination fraction G, which affects the initial number of competing seedlings, and V, which expresses seedling survival and growth, and hence demand for resources by an individual seedling as a function of the local physical environmental conditions. Thus, variation in G and V, due to spatial variation in the environment, of necessity leads to

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Table 12.1 Model of an annual plant community

$N_{jx}(t)$	The number of seeds in the seed bank of species j in patch x at the beginning of year t.
$\lambda_{jx}(t)N_{jx}(t)$	The amount of new seed produced by seeds that germinate, plus the survivors of the seeds that do not germinate by the end of year t for species j and patch x. $$\lambda_{jx}(t) = s_j(1 - G_j) + \frac{U_j Y_j V_j G_j}{C_x}, \qquad (12.T1.1)$$ with the following notation:
$\lambda_{jx}(t)$	The total output of a seed of species j at site x during year t (survival plus new production).
s_j	Survival of ungerminated seed.
$1 - G_j$	Fraction of seed not germinating.
U_j	Fraction of seed production of species j successfully incorporated into the seed bank by the beginning of the next year (seed not lost to predation, pathogens, or other means before being mixed into the soil surface).
Y_j	Seed production per surviving seedling of unit vigor in the absence of competition.
V_j	Seedling survival and vigor (size).
G_j	Fraction of seed of species j germinating.
a_j	Competitive effect of one seedling of species j.
$C_x = 1 + \sum_j a_j V_j G_j N_{jx}(t)$	Reduction in per capita seed output due to competition.
$f(E_{jx}, C_x) = s(1 - G) + UYE_{jx}G/C_x$	Example of f for the case where E_{jx} is V_j.
E^*, C^*	Reference values of E_{jx} and C_x chosen near their means (Chesson 2000a).
$\mathscr{E}_{jx} = f(E_{jx}, C^*) - 1$	Standard environmental response.
$\mathscr{C}_x = 1 - f(E^*, C_x)$	Standard competitive response.

the phenomenon of covariance between environment and competition (Chesson 2000a), which has a critical role in species coexistence, as we shall see.

To illustrate the behavior of the model under a variety of contrasting circumstances, we consider some simple extreme environmental scenarios (Chesson 1985). The first and simplest scenario is the case of pure spatiotemporal environmental variation where the environment fluctuates independently in space and time and, as a consequence, averages out to a constant in space and in time. Second is the case of pure spatial variation where the physical environment varies only spatially.

Several simplifying assumptions are introduced to facilitate analysis. First we consider spatial variation in just one parameter at a time, and we assume that the species have identical parameters except for those varying with the environment, which we term "environmental responses." Environmental responses are assumed here to differ between species in their means but not in their variances. Second, we assume that environmental responses vary independently between

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species over space or space and time. Third, we assume a patch model where plants interact with each other homogeneously within patches, but disperse between patches. Fourth, just two kinds of dispersal are considered: (a) widespread dispersal where all new seed is divided evenly between patches, and (b) widespread dispersal with local retention where a fixed fraction p of the new seed is retained in the natal patch. The number of patches will be assumed to be effectively infinite. Finally, we restrict attention to just two species. Much more general treatments of species coexistence in spatially variable environments are possible (Chesson 2000a), but require more detailed analysis than can be given here.

To analyze the model, we must first express the fitness of an individual in terms of spatially varying factors. Thus, using the equation 12.T1.1 in table 12.1, we write the fitness of an individual of any species j as a function, $f(E_{jx}, C_x)$, of the environmental response, which we denote generically as E_{jx}, and the competitive response, C_x. Then, to provide a unified treatment of models with different spatially varying life-history parameters, and indeed different basic models, these variables are transformed into the new variables, $\mathscr{E}_{jx}$ and $\mathscr{C}_x$, defined in table 12.1. These new variables are increasing functions respectively of E_{jx} and C_x, reflect the same underlying biological processes, and contain the same information. To define them (Chesson 2000a), one first chooses values E^* and C^* of E_{jx} and C_x near their means with the property that $\lambda_{jx} = 1$ when $(E_{jx}, C_x) = (E^*, C^*)$. Then $\mathscr{E}_{jx}$ is the change in λ_{jx} as E_{jx} moves away from E^* and $\mathscr{C}_x$ is the change in $-\lambda_{jx}$ as C_x moves away from C^*. These definitions mean that the effects of E_{jx} and C_x are translated into the separate effects of environment and competition on λ_{jx}. To obtain the joint effects of environment and competition on λ_{jx} all that is needed in addition to $\mathscr{E}_{jx}$ and $\mathscr{C}_x$ is the interaction between environment and competition. It follows that λ_{jx} is given in terms of $\mathscr{E}_{jx}$ and $\mathscr{C}_x$ by the generic equation,

$$\lambda_{jx} = 1 + \mathscr{E}_{jx} - \mathscr{C}_x + \gamma \mathscr{E}_{jx} \mathscr{C}_x, \tag{12.21}$$

where the single parameter γ is negative and defines how strongly E_{jx} and C_x (equivalently, $\mathscr{E}_{jx}$ and $\mathscr{C}_x$) interact in their determination of λ_{jx} (Chesson 2000a). This equation is true regardless of which life history parameter is represented by E_{jx} and regardless of the form of competition.

A product such as $\mathscr{E}_{jx}\mathscr{C}_x$ in equation 12.21 is the mathematically simplest form of an interaction between two variables in their determination of a third variable. An interaction between two variables is also a special form of multidimensional nonlinearity. The particular interaction in equation (12.21) stems directly from the product of E_{jx} and $1/C_x$ that occurs in λ_{jx} when E_{jx} is any of the life-history parameters U, Y, V, or G defined in table 12.1. This interaction occurs because the product $UYVG$ determines how much new seed an individual seed would return to the seed bank the following year in the absence of competition, and this amount is assumed to be reduced by a given proportion for a given magnitude of competition. Thus, if two locations differ in the value of $UYVG$, the same mag-

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nitude of competition would have a larger effect at the location with the higher value of *UYVG*.

To understand regional-scale dynamics of this model we need $\tilde{\lambda}$, which of course splits into the spatial average fitness and the fitness-density covariance: $\tilde{\lambda} = \bar{\lambda} + \mathrm{Cov}(\lambda, \nu)$ (equation 12.4). For $\bar{\lambda}$, equation 12.21 must be averaged over space. As discussed in box 12.2, the product nonlinearity $\mathscr{E}_{jx}\mathscr{C}_x$ introduces a covariance term into $\bar{\lambda}$, so that

$$\bar{\lambda} = 1 + \bar{\mathscr{E}}_j - \bar{\mathscr{C}} + \gamma\bar{\mathscr{E}}_j \cdot \bar{\mathscr{C}} + \gamma\mathrm{Cov}(\mathscr{E}_j, \mathscr{C}). \tag{12.22}$$

Equation 12.22 simplifies if we assume that environmental fluctuations are small in magnitude with small average differences between species, for then the term $\bar{\mathscr{E}}_j \cdot \bar{\mathscr{C}}$ is small in comparison with the other terms (Chesson 2000a), and can be neglected. Adding in the fitness-density covariance, we obtain

$$\tilde{\lambda}_j \approx 1 + \bar{\mathscr{E}}_j - \bar{\mathscr{C}} + \gamma\mathrm{Cov}(\mathscr{E}_j, \mathscr{C}) + \mathrm{Cov}(\lambda_j, \nu_j). \tag{12.23}$$

Expression 12.23 can now be used to study species coexistence by invasibility analysis (Chesson 2000a). In an invasibility analysis, one of the species, "the invader" labeled i, is set to zero density everywhere in space, and the other species, "the resident" labeled r, has dynamics that are independent of the invader. We wish to see if the invader can increase and enter the system, which means that it must have a value of $\tilde{\lambda}$ greater than 1. The species coexist according to the invasibility criterion if they can each increase as invaders.

Differences between resident and invader in the two covariance terms of expression 12.23 are critical to species coexistence. Table 12.2 gives the signs of these covariance terms for various scenarios where the sign can be determined, without further information, by the methods of Chesson (2000a). Full details will be published elsewhere, but in many cases, as shown here, the entries in the table can be determined quite simply and understood intuitively. Note that under the small variation assumption invoked here, the signs of covariances involving the competitive and environmental responses, $\mathscr{E}_{jx}$ and $\mathscr{C}_x$, are the same as those involving the original responses, E_{jx} and C_x. Thus, arguments relating to E_{jx} and C_x carry over to $\mathscr{E}_{jx}$ and $\mathscr{C}_x$.

Resident covariance between environment and competition, $\mathrm{Cov}(\mathscr{E}_r, \mathscr{C})$, is always positive when the competitive response C_x is directly a function of the environmental response E_{rx}. However, it can also be positive when $\mathrm{Cov}(\mathscr{E}_r, \nu_r)$ is positive, that is, when population density builds up in locations that are favorable based on the response of the organisms to the physical environment. The invader always has zero covariance between environment and competition because the invader's environmental response is never related to the cause of competition—when it has zero density, C_x is not a function of the invader's environmental response, and we have assumed that its environmental response is not correlated with that of the resident. However, covariance between fitness and density can be

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Table 12.2 Results of the annual plant competition model

Variable parameter	Type of environmental variation	Type of dispersal	Covariance between environment and competition: resident	Covariance between environment and competition: invader	Covariance between fitness and density: resident	Covariance between fitness and density: invader
V	spatiotemporal (st)	widespread (w)	+	0	0	0
	st	local retention (l)	+	0	−	+
	Pure spatial (ps)	w	+	0	0	0
	ps	l	+	0	+	+
G	st	w	+	0	−	0
		l	+	0	−	?
	ps	w	+	0	−	−
		l	+	0	?	?
YU	st	w	0	0	0	0
		l	0	0	−	+
	ps	w	0	0	0	0
		l	+	0	+	+

positive for the invader in cases with local retention and either sort of spatial variation. Local retention allows invader density to build up in environmentally or competitively favorable locations. (Although absolute invader density is zero for the invader, relative invader density is not: it is the limit of the ratio of two quantities each approaching zero.) For the resident, local retention mostly gives negative fitness-density covariance when environmental variation is spatio-temporal. This occurs because density builds up locally by chance runs of favorable local environments, increasing local competition. Since the current density is determined by previous environments, which are uncorrelated with the current environment, the component of the growth rate that is correlated with density is simply competition; therefore fitness-density covariance is necessarily negative.

To see if $\tilde{\lambda}_i$ is greater than 1 so that an invader can be successful, one notes that $\tilde{\lambda}$ for a resident ($\tilde{\lambda}_r$) must be equal to 1, assuming that the species comes to equilibrium in the region as a whole (but not necessarily locally in space). Note also that $\overline{\mathscr{C}}$ and γ are the same for the invader and resident under the assumptions above, and so subtracting the resident $\tilde{\lambda}$ from the invader $\tilde{\lambda}$ leads to the equation

$$\tilde{\lambda}_i - 1 = \Delta E + \Delta I + \Delta\kappa \tag{12.24}$$

Where

$$\Delta E = \overline{\mathscr{E}}_i - \overline{\mathscr{E}}_r, \tag{12.25}$$

is a comparison of mean responses to the environment,

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$$\Delta I = (-\gamma)\{\mathrm{Cov}(\mathscr{E}_r, \mathscr{C}) - \mathrm{Cov}(\mathscr{E}_i, \mathscr{C})\} \tag{12.26}$$

measures the spatial storage effect, and

$$\Delta\kappa = \mathrm{Cov}(\lambda_i, \nu_i) - \mathrm{Cov}(\lambda_r, \nu_r), \tag{12.27}$$

compares the fitness-density covariance for the invader and resident.

The three different terms in equation 12.24 have different effects on species coexistence, representing different classes of mechanism. The first term, ΔE, would yield competitive exclusion in the absence of spatial variation. It is an average fitness comparison between species (Chesson 2000b) and is the mean-field component. The second two terms, which are scale transition terms, have the potential to be positive. Indeed, from table 12.2 there are many instances where ΔI is clearly positive and several where $\Delta\kappa$ is clearly positive. These terms therefore have the capability of negating the average fitness differences, thereby counteracting the mean-field component and leading to situations where $\tilde{\lambda}_i - 1$ is positive for both species, permitting them to coexist as determined by the invasibility criterion.

The clearest situation applies to spatial variation in the vigor parameter V. Spatial environmental variation affecting the growing plant feeds into competition because bigger plants use more resources. Thus, for the resident species, there is always positive covariance between its environmental response and competitive response. The assumption that the two species have statistically independent responses to the environment means that the invader's environmental response is independent of its competitive response, which is determined by the density and environmental response of the resident. Thus, $\Delta I = (-\gamma)\mathrm{Cov}(\mathscr{E}_r, \mathscr{C})$, which is positive. With widespread dispersal of seeds, the local environment leaves no signature on population density, and so in that case $\mathrm{Cov}(\lambda_j, \nu_j)$ is simply zero. Thus, a positive spatial storage effect is found; if this is large enough, it would overcome average differences in the seedling survival rate, measured by ΔE, and permit the two species to coexist.

With local retention of seed, some effects on $\mathrm{Cov}(\lambda_j, \nu_j)$ are possible. For example, with spatiotemporal variation, the local resident density will reflect some past values of V, which will affect competition. However, density will not be correlated with the environmental component of λ_{rx} because of the independence of the environment over time. The net result is negative fitness-density covariance for the resident. The invader's relative density will be negatively related to that of the resident, reflecting previous competition. As a consequence, a weak positive $\mathrm{Cov}(\lambda_i, \nu_i)$ is expected. Thus, $\Delta\kappa$ will be positive, promoting coexistence.

Germination fraction variation is similar to variation in vigor in that it always leads to a positive storage effect through its effects on covariance between environment. However, its effects on fitness-density covariance are more complicated because higher local values of G cause local depletion of the seed bank. These

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cause changes in relative density regardless of local retention. Thus, only in the case of spatiotemporal variation with widespread dispersal is a clear conclusion possible. In that case the positive storage effect (ΔI) combines with positive $\Delta\kappa$ to give an overall fitness promoting effect of variation in the germination fraction.

The final particular case of note is variation in the final yield parameter Y (given vigor) or survival of seed predation, U. Variation in these parameters is assumed not to directly affect competition. This means that covariance between environment and competition does not occur in the case of spatiotemporal variation regardless of dispersal. However, it does occur in the case of pure spatial variation with local retention because local resident density increases with the fixed favorability of the environment, increasing local competition, and causing covariance between environment and competition. However, covariance between fitness and density also results. Although this is positive for both resident and invader, it is shown in Chesson (2000a) that in the absence of a persistent seed bank ($G = 1$, or $s = 0$), $\Delta\kappa$ is approximately $2[p/(1-p)]\{\mathrm{Cov}(\mathcal{E}_r, \mathcal{C}) - \mathrm{Cov}(\mathcal{E}_i, \mathcal{C})\}$, where p is the fraction of seed retained at the site. (Note that in Chesson (2000a) the factor 2 was inadvertently omitted.) Thus, $\Delta\kappa$ is positive, is proportional to the storage effect, and reinforces it, promoting coexistence.

Conclusions

Scale transition theory focuses on the mechanisms by which the rules for population dynamics on local scales become modified to produce different rules for dynamics on larger spatial scales. Many of the specific issues discussed here as part of scale-transition theory pervade analyses of spatial ecological models, including models formally identified as metacommunity models. The difference here is the focus on the interaction between nonlinearity in local population dynamics and spatial variation as the explanation of the important outcomes on larger spatial scales. In essence, the material presented here implies a research program in which the interaction between nonlinearities and spatial variation is explored for its mechanistic and biological content. Nonlinearities often arise from specific biological postulates such as the nature of interactions within and between species (Chesson 2001). The properties of these nonlinearities identify the kinds of patterns of spatial variation that are important to outcomes at the scale of the whole system.

In the metacommunity context, interactions between species, and between species and their environment, lead to particular kinds of nonlinearity. For example, in host-parasitoid systems, we have seen how the relationship between percent parasitism and parasitoid density is a critical nonlinearity arising from assumptions about parasitoid foraging (Hassell 2000) that implicates the coefficient of variation of parasitoid density as a critical aspect of spatial variation for predicting the dynamics of the metacommunity (box 12.1). In studies of competi-

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tion in a spatially variable environment, we have seen that a two-dimensional nonlinearity expressing the interaction between responses to the physical environment and responses to competition arises from life-history postulates. This nonlinearity implicates the covariance in space between the response to the environment and the response to competition as a critical aspect of spatial variation for coexistence at the regional scale. This covariance, together with the nonlinearity that makes it important, defines the species coexistence mechanism called the spatial storage effect.

We have seen here also an important distinction between average individual fitness, denoted by $\tilde{\lambda}$, and the spatial average of fitness $\bar{\lambda}$. This distinction was first discussed in the scientific literature by Lloyd (1967), who introduced the concept of mean crowding, applicable to the logistic model. Fitness-density covariance discussed here generalizes Lloyd's concept, and itself reflects a two-dimensional nonlinearity, the product of fitness and local density. This nonlinearity is present in all spatially structured systems, and we have seen how the fitness-density covariance arising from it modifies the stability conditions in host-parasitoid models, supplements the spatial storage effect in spatial competition models, and introduces a coexistence mechanism with properties very similar to the spatial storage effect in spatial Lotka-Volterra and similar models.

The role of the interaction between nonlinearities and spatial variation is less apparent in the approach to metacommunities that describes local densities simply in terms of presence and absence of a species (Nee et al. 1997). Nonlinearities in local population dynamics can only be represented in these models in limited and somewhat extreme ways because of the limitations on the state variables for local population densities. Nevertheless, nonlinearities in these presence-absence models have critical roles in the outcomes at the metacommunity scale (Chesson 2001).

The full scale transition program involves linkages between analytical methods, simulation and numerical methods, and experimental and observational approaches to understanding metacommunities. Analytical theory, as presented here, identifies the key nonlinearities and spatial variation associated with it. This stage is important especially in exploring the biological origin of nonlinearities and their mechanistic role. The nature of spatial variation has a critical mechanistic role, as most strikingly illustrated by the discussion of competition in a variable environment where the pattern of covariance between environment and competition arises from the way species relate to each other and to the physical environment. Techniques of moment closure (Bolker and Pacala 1999), pair approximation (Ellner et al. 1998), and Fourier analysis (Snyder and Chesson 2003) have the potential to expand understanding in this area by approximate analytical and numerical techniques.

In areas where approximations fail or need to be supplemented, simulation approaches can provide knowledge of the relevant variances and covariances or other measures of spatial variation applicable to the relevant nonlinearities. When simulation must be used for this purpose, it will generally be in association with analytical understanding of the nonlinearities and the mechanisms, as presented here. Thus, rather than simply use simulation to solve a problem, such as whether the species coexist, one can ask instead which mechanisms are involved. These mechanisms are quantified by calculating the measures of these mechanisms, such as the quantities ΔI and $\Delta\kappa$ in the assessment of species coexistence in a variable environment. Thus, the relative importance of different mechanisms is assessed quantitatively, and the comparison between different situations and different models is greatly facilitated.

Of most importance, this program extends to the empirical level, as illustrated by Melbourne et al. in chapter 13. Elements of models can be fitted to data to quantify the relevant nonlinearities. Spatial variances and covariances are found using variations on standard experimental and sampling designs. The same concepts and same quantities are used at all levels in the scale transition program, and so the ability to measure and test mechanisms quantitatively is greatly enhanced.

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Literature Cited

Atkinson, W. D., and B. Shorrocks. 1981. Competition on a divided and ephemeral resource. Journal of Animal Ecology 50:461–471.

Bailey, V. A., A. J. Nicholson, and E. J. Williams. 1962. Interaction between hosts and parasites when some host individuals are more difficult to find than others. Journal of Theoretical Biology 3:1–18.

Bolker, B., and S. Pacala. 1999. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. American Naturalist 153:575–602.

———. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theoretical Population Biology 52:179–197.

Caswell, H. 1978. Predator-mediated coexistence: A nonequilibrium model. American Naturalist 112: 127–154.

Chesson, P. 1978. Predator-prey theory and variability. Annual Review of Ecology and Systematics 9: 323–347.

———. 1991. A need for niches? Trends in Ecology and Evolution 6:26–28.

———. 1998a. Making sense of spatial models in ecology. Pages 151–166 *in* J. Bascompte, and R. V. Sole, eds. *Modeling spatiotemporal dynamics in ecology.* Springer, New York.

———. 1998b. Spatial scales in the study of reef fishes: A theoretical perspective. Australian Journal of Ecology 23:209–215.

———. 2000a. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58:211–237.

———. 2000b. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

———. 2001. Metapopulations. Pages 161–176 *in* S. A. Levin, ed. *Encyclopedia of biodiversity*. Academic Press, San Diego, CA.

Chesson, P. L. 1981. Models for spatially distributed populations: The effect of within-patch variability. Theoretical Population Biology 19:288–325.

———. 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263–287.

———. 1991b. Stochastic population models. Pages 123–143 *in* J. Kolasa, and S. T. A. Pickett, eds. *Ecological heterogeneity*. Springer-Verlag, New York.

Chesson, P. L., and W. W. Murdoch. 1986. Aggregation of risk: Relationships among host-parasitoid models. American Naturalist 127:696–715.

Ellner, S. P., A. Sasaki, Y. Haraguchi, and H. Matsuda. 1998. Speed of invasion in lattice population models pair-edge approximation. Journal of Mathematical Biology 36:469–484.

Englund, G., and S. D. Cooper. 2003. Scale effects and extrapolation in ecological experiments. Pages 161–213 *in* H. Caswell, ed. *Advances in Ecological Research*. Vol. 33. Academic Press, Amsterdam, The Netherlands.

Green, P. F. 1986. Does aggregation prevent competitive exclusion? A response to Atkinson and Shorrocks. American Naturalist 128:301–304.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, U.K.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 *in* I. Hanski, and M. E. Gilpin, eds. *Metapopulation biology: Ecology, genetics, evolution*. Academic Press, San Diego, CA.

Hartley, S., and B. Shorrocks. 2002. A general framework for the aggregation model of coexistence. Journal of Animal Ecology 71:651–662.

Hassell, M. P. 2000. *The spatial and temporal dynamics of host-parasitoid interactions: Oxford series in ecology and evolution*. Oxford, Oxford University Press.

Hassell, M. P., R. M. May, S. W. Pacala, and P. L. Chesson. 1991. The persistence of host-parasitoid associations in patchy environments. I. A general criterion. American Naturalist 138:568–583.

Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. Theoretical Population Biology 12:37–48.

———. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18:363–373.

Heard, S. B., and L. C. Remer. 1997. Clutch-size behavior and coexistence in ephemeral-patch competition models. American Naturalist 150:744–770.

Horne, J. K., and D. C. Schneider. 1995. Spatial variance in ecology. Oikos 74:18–26.

Ives, A. R. 1988. Covariance, coexistence and the population dynamics of two competitors using a patchy resource. Journal of Theoretical Biology 133:345–361.

———. 1991. Aggregation and coexistence in a carrion fly community. Ecological Monographs 61: 75–94.

Kareiva, P. 1990. Population dynamics in spatially complex environments: Theory and data. Philosophical Transactions of the Royal Society of London, series B, Biological Sciences 330:175–190.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lloyd, M. 1967. Mean crowding. Journal of Animal Ecology 36:1–30.

Lloyd, M., and J. White. 1980. On reconciling patchy microspatial distributions with competition models. American Naturalist 115:29–44.

May, R. M. 1978. Host-parasitoid systems in patchy environments: Phenomenological model. Journal of Animal Ecology 47:833–843.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. *Consumer-resource dynamics*. Princeton University Press, Princeton, NJ.

2005. Holyoak, M, Leibold, M.A., Holt, R.D., eds, Metacommunities: spatial dynamics and ecological communities, pp 279-306

Murrell, D. J., and R. Law. 2003. Heteromyopia and the spatial coexistence of similar competitors. Ecology Letters 6:48–59.

Nee, S., R. M. May, and M. P. Hassell. 1997. Two-species metapopulation models. Pages 123–147 *in* I. A. Hanski, and M. E. Gilpin, eds. *Metapopulation biology: Ecology, genetics, and evolution*. Academic Press, San Diego, CA.

Neuhauser, C., and S. W. Pacala. 1999. An explicitly spatial version of the Lotka-Volterra model with interspecific competition. Annals of Applied Probability 9:1226–1259.

Pacala, S. W., and M. P. Hassell. 1991. The persistence of host-parasitoid associations in patchy environments. II Evaluation of field data. American Naturalist 138:584–605.

Pacala, S. W., and J. A. Silander, Jr. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. American Naturalist 125:385–411.

Rao, C. R. 1973. *Linear statistical inference and its applications*. John Wiley, New York.

Remer, L. C., and S. B. Heard. 1998. Local movement and edge effects on competition and coexistence in ephemeral patch models. American Naturalist 152:896–904.

Ross, S. 1997. *A first course in probability*. Prentice Hall, Upper Saddle River, NJ.

Shigesada, N., and J. Roughgarden. 1982. The role of rapid dispersal in the population dynamics of competition. Theoretical Population Biology 21:253–373.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128–134.

Snyder, R. E., and P. Chesson. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecology Letters 6:301–309.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.