

CHAPTER 8

Making Sense of Spatial Models in Ecology

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Introduction

Spatial models in ecology are interesting and valuable primarily because they show that inclusion of spatial detail often quantitatively and qualitatively changes fundamental properties of population dynamics such as stability and species coexistence.¹⁻⁸ This phenomenon can also be expressed as a property of spatial scale, called the scale transition:⁹ the rules for population dynamics worked out for a local population (discounting migration) differ from the rules that are observed at the larger spatial scale of the whole population,¹⁰ which incorporates migration between local populations.

The scale transition can be understood as an interaction between spatial variation and nonlinear dynamics.^{4,9} In this context, nonlinearities mean that the contribution of an individual to future generations depends on intraspecific or interspecific densities, or in other words single- or multi-species density dependence. Such density dependence arises from direct and indirect interactions between individual organisms and has a spatial scale defined by the scale within which such interactions occur, for some given span of time. In spite of the fact that density dependence and spatial variation are often held in opposition in spatial models^{11,12} the effects of spatial variation are critically dependent on the nature and magnitude of density dependence.⁹

The spatial variation of relevance to the scale transition is spatial variation in the densities of organisms and spatial variation in the environment when such environmental variation affects the interactions between organisms.^{8,13-15} In general, there is no reason to expect the spatial scales of variation and the spatial scales of interactions between individuals to coincide, but as we shall see below, the relative scales of these phenomena are important to the scale transition. Also, spatial variation may be determined at least in part by population dynamics,¹⁶ and therefore, it should not be too surprising that spatial variation in population densities may depend on average population density. However, as we shall see below, the way spatial variation depends on the

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environment also affects the way spatial variation depends on average population density, with important consequences for the scale transition.

These considerations lead to a way of understanding spatial models in terms of three important components, which are the subject of this chapter: 1) nonlinearities in population dynamics; 2) the relative spatial scales of variation and density-dependent processes; and 3) the dependence of spatial variation on population densities. A common alternative approach to understanding the often perplexing results of spatial models is through approximation by other models that are deemed better understood. For example, metapopulation models often use presence or absence as state variables of local populations and couch understanding in terms of extinction and recolonization dynamics.¹⁶ Although approximation of other spatial models by such metapopulation models may indeed be an aid to understanding, the important role of nonlinearities may be obscured⁹ in the process and presence-absence descriptions of local populations permit expression of only the simplest kinds of nonlinear dynamics and spatial variation. Another approach¹⁷ approximates discrete spatial variation by continuous spatial variation, mainly as a computational aid. However, the method provides a good example of the interaction between nonlinear dynamics and variation on a small spatial scale.

I emphasize understanding over finding solutions to models. A realistic spatial model can be enormously complicated with far more information in its parameters and structure than one can hope to approach empirically. Without an understanding of how spatial models work we cannot know which of this information is important for a given purpose. Thus, I present here a theory of the scale transition, illustrated with simple single-species models. Being structured around three critical components of the scale transition, this work is intended to help systematize the study of spatial models. The three components are each amenable to empirical study separately or in combination. Thus, this way of understanding spatial models leads immediately to empirical approaches to assessing the importance of the spatial dimension.

The Role of Nonlinearities

For any given scale of temporal resolution, there is a spatial scale over which direct and indirect interactions between organisms can occur. This spatial scale of interaction may be specified in models by nonoverlapping areas of space ("patches") occupied by a local population within which interactions occur.^{4,18} Other models use overlapping areas ("neighborhoods") centered on the individuals in the population, and are especially useful for plant population studies.¹⁹ Whichever of these two means are used to specify the organization of interactions in space, the basic principles are the same and so I shall explain them using the conceptually simpler local population approach. So-called metapopulation models¹⁶ use the local population approach but refer to the local populations as populations, and refer to the total of all local populations as the "metapopulation." However, I follow the earlier terminology of ref. 11 which seems more natural.

The key to the scale transition begins with the simple observation⁹ that the density of a population is simply an average of the densities of its component local populations. Thus, if $N_i(t)$ is the density at time t of the i th local population, the quantity

$$\bar{N}(t) = \frac{\sum_{i=1}^k N_i(t)}{k} \quad 1)$$

is the density of the population as a whole. A change in scale from the local population to the whole population thus involves an averaging process, but such averaging interacts in a very important way with local population dynamics. How this occurs is most clearly seen when migration and local interaction and growth processes are separated in time. Thus, assume that within each unit of time, t to $t+1$ (for example, a year), migration takes place in the subinterval t to $t+h$, and local population growth involving interactions between individuals occurs in the subinterval $t+h$ to $t+1$. Local population density at the end of the growth and interaction period can then be written as:

$$N_i(t+1) = F(N_i(t+h)) \quad 2)$$

where F is some function. For example, if the interactions can be described as scramble competition, then the function F may take the Ricker form:

$$F(N_i(t+h)) = RN_i(t+h)e^{-\alpha N_i(t+h)} \quad 3)$$

where R represents the multiple by which the population would increase in the absence of density-dependent interactions and the fraction:

$$e^{-\alpha N_i(t+h)} \quad 4)$$

represents a reduction in this amount due to density-dependent interactions. These interactions mean that the function F specifies a nonlinear relationship. I shall use this particular nonlinear relationship as an illustration throughout, but the ideas presented are general.

The dynamics of the density of the whole population can now be found by combining Equations 1 and 2 to obtain:

$$\bar{N}(t+1) = \frac{\sum_{i=1}^k F(N_i(t+h))}{k} = \overline{F(N(t+h))} \quad 5)$$

an average of a nonlinear function of local population density. Now:

$$\overline{F(N(t+h))} \neq F(\bar{N}(t+h)) \quad 6)$$

when the function F is nonlinear. In other words, the average of the function is not equal to the function of the average, and this means that the dynamics of the whole population differ from the dynamics of the local populations over the period $t+h$ to $t+1$. Thus, a scale transition occurs as a result of averaging a nonlinear function or "nonlinear averaging" for short.

The easiest way to understand such nonlinear averaging is by a simple graphical technique⁹ applied to a simplified spatial distribution in which local populations are assumed to vary spatially over just two values of population

density. Consider Figure 8.1 with points *A* and *B* representing two different local populations with different local population densities at times $t+h$ and corresponding densities at time $t+1$. The thick curve on which these points lie is the graph of $F(N_i(t+h))$. If half the local populations in the system are at point *A* and the other half at point *B*, then the higher scale densities $\bar{N}(t+h)$ and $\bar{N}(t+1)$, being averages of the local densities, are specified by the point *D* on the midpoint of the line joining *A* and *B*. In the absence of spatial variation, the point *E* specifies the whole-population densities $\bar{N}(t+h)$ and $\bar{N}(t+1)$. Similarly, if the local populations were given by the points *B* and *C*, the large-scale or whole-population densities would correspond to the point *F*, with the point *G* giving the corresponding situation with no spatial variation.

Although restricted numerically to simple spatial distributions, this graphical technique nevertheless has several important lessons that are applicable to general spatial distributions. Nonlinearity, and hence density dependence, are essential for there to be any effect of spatial variation on large-scale dynamics. For if the graph of $F(N_i(t+h))$ were a straight line, the points *D* and *F* would coincide with the points *E* and *G* in Figure 8.1 giving no difference between higher scale dynamics with and without lower scale spatial variation. Second, the type of nonlinearity indicates the effect that spatial variation has. If the nonlinearity is concave, i.e., $F(N_i(t+h))$ curves over as it does over the range *AB*, then variation in local densities reduces $\bar{N}(t+1)$ over the value it would have without variation. Where the relationship curves up (is "convex," e.g., *BC*), $\bar{N}(t+1)$ is increased over that predicted without variation. Finally, it is apparent from the figure that the effect of variation on population dynamics at the larger spatial scale is very closely related to the magnitude of the variation. To gain a better appreciation of this relationship, an approximate quantitative approach is valuable.

For simplicity, we continue to make the assumption that there is no mortality during dispersal, and then it is possible to show that, approximately³⁴

$$\bar{N}(t+1) = F(\bar{N}(t)) + c\sigma^2 \quad 7)$$

where σ^2 is the variance in local population density and the quantity c may depend on population density, $\bar{N}(t)$, but not on σ^2 . Thus, we see that the effect of spatial variation on large-scale population dynamics is approximately proportional to the variance in local population densities. The quantity c measures the nonlinearity of F and is given by the formula:

$$c = \frac{1}{2} F''(\bar{N}(t)) \quad 8)$$

i.e., half the second derivative of F evaluated at $\bar{N}(t)$. This second derivative will be negative wherever F is concave, e.g., at point *E* of Figure 8.1, and positive whenever the curve is convex, e.g., the point *G* of Figure 8.1, thus explaining the effects of concave and convex nonlinearities observed in the figure.

The two approaches above are good for understanding the nature of the interaction between variation and nonlinearity. To see the full effects of this interaction on population dynamics, consider now a realistic spatial distribution, the negative binomial distribution²⁰ applied to the case where local dynamics follow the Ricker equation. If there is no mortality during dispersal, population dynamics on the whole population scale satisfy the equation:

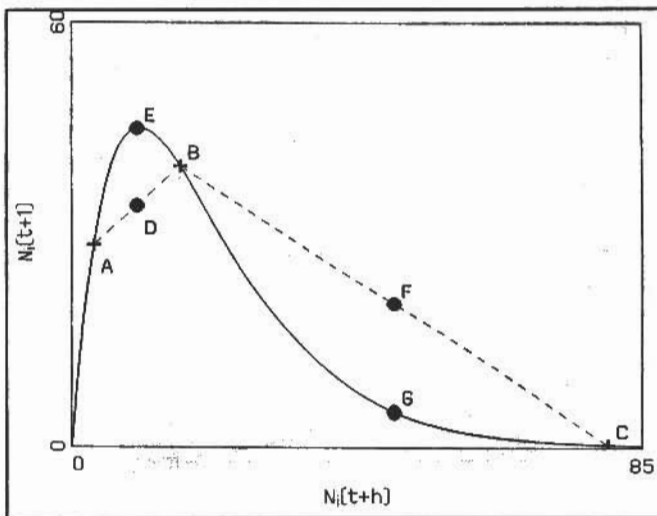


Fig. 8.1. Averaging the Ricker curve in space as explained in the text. Modified with permission from Chesson PL, In: Floyd, RB, Sheppard AW, DeBarro PJ. *Frontiers of Population Ecology*. CSIRO Publishing 1996:353-368.

$$\bar{N}(t+1) = F(\bar{N}(t+h)) = \frac{R' \bar{N}(t)}{(1 + \alpha' \bar{N}(t)/k)^{k+1}} \quad 9)$$

where $R' = Re^{-\alpha}$ and $\alpha' = 1 - e^{-\alpha}$. This relationship is shown as the dashed curves in Figure 8.2. The solid curve is the Ricker relationship:

$$\bar{N}(t+1) = R\bar{N}(t)e^{-\alpha\bar{N}(t)} \quad 10)$$

which would apply if there were no spatial variation. The Ricker curve gives population crashes from high densities, but the magnitude of population crashes at the level of the total population is markedly reduced by spatial variation. Indeed, as spatial variation increases (i.e., as k decreases) the crash disappears, and the dynamics of total population density appear instead like contest competition with no appreciable decline in $\bar{N}(t+1)$ for high values of $\bar{N}(t)$, belying the presence of scramble competition within local populations. The effect on population dynamics can be profound. The Ricker model gives fluctuating and even chaotic dynamics of large amplitude for $\ln R > 2$ (Fig. 8.3a). In contrast, all of the dashed curves depicted in Figure 8.2 yield stable population dynamics with rapid convergence on an equilibrium (Fig. 8.3b).

These results were derived assuming that there is no mortality during dispersal, but as shown in the Appendix to this chapter, such an assumption does not alter these conclusions, which simply result from an interaction between spatial variation and the nonlinearity of population dynamics. Nonlinearities can be understood in terms of the basic interactions between organisms. There are many facets to variation, but the most immediate issues for the study of the scale transition are the spatial scale on which variation occurs and the relationship between spatial variation and the density of the population.

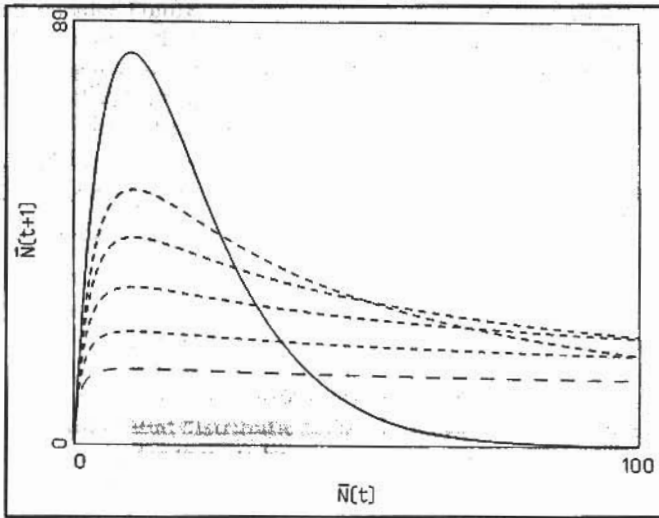


Fig. 8.2. The Ricker curve Eq. 10 and the model given by Eq. 9 plotted for $k = 0.1$ to 1 in an ascending order, with parameters $\ln R = 3$ and $\alpha = 0.1$. Modified with permission from Chesson PL. In: Floyd, RB, Sheppard AW, DeBarro PJ. *Frontiers of Population Ecology*. CSIRO Publishing 1996:353-368.

The Roles of Scales of Variation

In the development above, we have identified the local population as defining the scale of interactions between individuals, which is therefore the scale on which density dependence occurs. This scale may not be easy to determine and indeed, there may be multiple scales of density dependence related to specific sorts of interactions. For example, aggressive encounters leading to interference competition may operate on a much smaller spatial scale than the scale of depletion of resources, which is the scale of exploitative competition. Variation in abundance is relatively much easier to determine, and such variation is often seen to be multi-scaled in empirical studies.^{22,23} What are the effects of the relative scales of density dependence and spatial variation? To approach this question, I shall assume just one scale of density dependence, and continue to identify it with the "local population," and I shall adopt the model of nested scales of spatial variation in abundance that has been shown to be so useful in empirical studies.^{24,25}

First of all consider cases of variation on scales equal to and lower than the scale of a local population. The standard analysis of variance approach leads to the model:

$$N_i(t+h) = \bar{N}(t+h) + \epsilon_i^0 + \bar{\epsilon}_i^{-1} + \bar{\epsilon}_i^{-2} + \dots \quad (11)$$

where each ϵ represents a deviation from the mean density in the population that can be attributed to a particular scale. The superscripts are not powers but represent the scale, with scale 0 being the scale of density dependence, and scales -1, -2, and so on representing smaller scales such that a unit on any one scale consists of more than one unit the next lower scale. The deviations for scales lower than 0 (the local population scale) all have bars over them because they have the further structure:

$$\bar{\epsilon}_i^{-l} = \frac{1}{n_{-l}} \sum_{j=1}^{n_{-l}} \epsilon_{ij}^{-l} \quad (12)$$

where ϵ_{ij}^{-l} refers to density deviation specific to the j th unit on the scale $-l$ in the i th local population, and n_{-l} is the total number of such units in one unit on the scale of local populations. Thus, we see that variation on lower scales appears as averaged values on higher scales. The effect of this averaging is that lower scale variances contribute to higher scales essentially in inverse proportion to the number of lower-scale units in one unit of the higher scale. To see how this occurs we make the standard assumption that contributions to variance from different scales are uncorrelated. If we assume further that the different units on any given scale are also uncorrelated, then we find that:

$$\sigma^2 = \sigma_0^2 + \frac{\sigma_{-1}^2}{n_{-1}} + \frac{\sigma_{-2}^2}{n_{-2}} + \dots \quad (13)$$

where σ_0^2 is the variance of ϵ_i^0 and σ_{-l}^2 is the variance of ϵ_{ij}^{-l} .

Hierarchical analysis of variance commonly assumes a variance structure of this form, with one important difference. In analysis of variance, n_{-l} is the number of samples from scale $-l$ in a sampling unit on scale 0. For this formula to be accurate in the analysis of variance, samples need to be taken far enough apart to achieve statistical independence on the appropriate scale. Here, however, the n_{-l} are the actual number of units present, not simply the number sampled, and they may not be statistically independent. Therefore, some modifications to the formula (Eq. 13) will commonly be necessary.

One way of thinking about this is through a spatial correlation function:

$$\rho_{-l}(j, k) = \text{corr}(\epsilon_{ij}^{-l}, \epsilon_{ik}^{-l}) \quad (14)$$

where "corr" means the ordinary Pearson correlation. Statistical theory (e.g., ref. 26) shows that the contribution of scale $-l$ to variance observable on the the next scale up ($-l+1$) is:

$$\frac{\sigma_{-l}^2}{m_{-l}} \sum_{j=1}^{m_{-l}} \sum_{k=1}^{m_{-l}} \rho_{-l}(j, k) \quad (15)$$

where m_{-l} is the number of units on scale $-l$ in one unit on the scale $-l+1$. Now $\rho(j, k)$ may depend primarily on the distance apart and may converge to zero as this distance apart increases. Indeed, it is in this situation where the nested structure is most useful. Moreover, the quantity:

$$\frac{1}{m} \sum_{j=1}^m \sum_{k=1}^m \rho_{-l}(j, k) \quad (16)$$

is then likely to converge to some constant θ_{-l} as m increases. In this case, for large m_{-l} , Eq. 15 is then well approximated by:

$$\frac{\theta_{-l}}{m_{-l}} \sigma_{-l}^2 \quad (17)$$

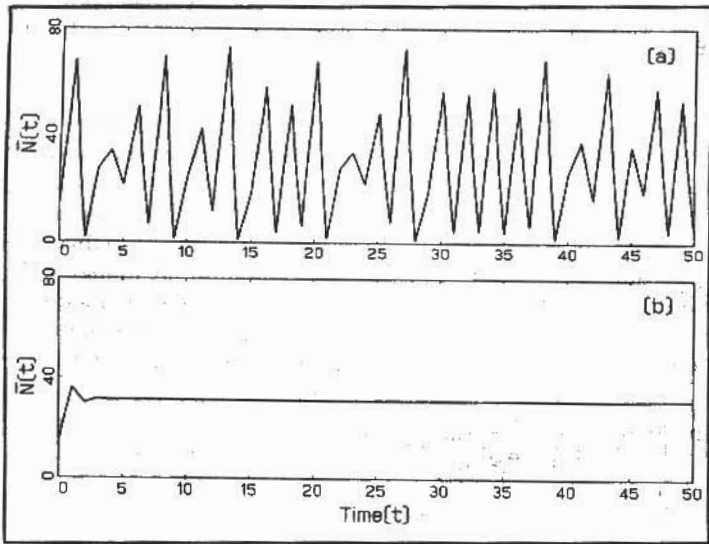


Fig. 8.3. Panel (a) Simulation of large-scale dynamics with no spatial variation, (Eq. 10) with parameters $\ln R = 3$ and $\alpha = 0.1$. Panel (b) Simulation of large-scale dynamics with negative binomial spatial variation, Eq. 9 with $k = 0.5$, and R and α as in (a). Modified with permission from Chesson PL. In: Floyd, RB, Sheppard AW, DeBarro PJ. *Frontiers of Population Ecology*. CSIRO Publishing 1996:353-368.

If variation arising on the $-l$ scale were statistically independent, then θ_l would simply equal 1. It follows that the ratio m_l/θ_l can be thought of as the equivalent number of independent units among the total of m_l on that scale. This number of independent units is in essence the "degrees of freedom" on that scale. To take account of spatial correlations on any given scale in equation 13 for σ^2 , n_l is replaced by $n_{l+1}m_l/\theta_l$ to give the equivalent number of uncorrelated units on the scale $-l$ in one unit on the scale of density dependence.

How does variation originating on higher scales than the scale of density dependence contribute to population dynamics on some yet larger scale? At issue is the total amount of variation between units on the scale of density dependence. If scales 1, 2, ... are defined as larger than the scale of density dependence (scale 0), then:

$$N_l(t+h) = \bar{N}(t+h) + \epsilon_l^0 + \epsilon_l^1 + \epsilon_l^2 + \dots + \bar{\epsilon}_l^{-1} + \bar{\epsilon}_l^{-2} + \dots \quad (18)$$

Note that in this case the scale of density dependence (scale 0) is contained in the other scales, and so variation from these other scales is not averaged over units in contributing to variation observable across units on the scale of density dependence, and so the variance on the scale of density dependence is:

$$\sigma^2 = \sigma_0^2 + \sigma_1^2 + \sigma_2^2 + \dots + \frac{\sigma_{-1}^2}{n_1} + \frac{\sigma_{-2}^2}{n_2} + \dots \quad (19)$$

Thus, variation on scales higher than the scale of density dependence contributes undiminished to the modification of the dynamics of the whole population,

while variation attributable to scales lower than the scale of density dependence contributes progressively less as the scale becomes smaller.

The Role of The Relationship Between Variance and Density

Empirically it is known that variance in local density can change with mean population size.^{20,27,28} Thus, the effect of variance on the scale transition (Eq. 7) depends on the density of the population, with potentially important effects on population dynamics.²⁹ I shall illustrate these possibilities by examining various ways that organisms may be distributed in space, and the resultant dynamics of the population.

Random distribution of organisms in space is described by the Poisson distribution, and the variance not only depends on the mean, but is actually equal to it. The effect of such variation on population dynamics is easy to assess in the Ricker model, for it implies the higher scale population dynamical equation:¹

$$\bar{N}(t+1) = R' \bar{N}(t) e^{-\alpha' \bar{N}(t)} \quad 20)$$

where $R' = Re^{-\alpha}$ and $\alpha' = 1 - e^{-\alpha}$ as defined above. Note first of all that Poisson variation has not altered the form of the population dynamical equation. The Ricker equation, reflecting scramble competition, still applies on the higher scale, but with modified parameters. The effect of these modified parameters is most clearly shown by examining the stability of the equilibrium in this system. The equilibrium is stable if $\ln R' < 2$,¹ i.e., $\ln R - \alpha < 2$, which compares with the criterion $\ln R < 2$ when there is no variation in local density. As the intraspecific competition coefficient α is positive, this means that Poisson variation does have some stabilizing effect on population dynamics in the Ricker, as one would expect from the graphical analysis of this model in the previous section, but this stabilising effect is not great unless the intraspecific competition coefficient is quite large. For example, if $\ln R = 3$, then α must exceed 1 for stability to result from spatial variation. In the Ricker equation, the local equilibrium population size is $\ln R / \alpha$ (de Jong¹), i.e., this local equilibrium must be less than 3 for Poisson variation to be sufficient to stabilize dynamics on the larger scale.

Very small local population sizes are not absurd when it is considered that the local population is defined in terms of the spatial scale of density dependence. Thus, in some populations, for instance plant populations, the spatial scale of density dependence may encompass just a few other individuals. Nevertheless, these results show that situations under which Poisson variation can have important effects on higher scale dynamics are restricted to small local populations. This fact is reflected by the coefficient of variation, which is generally regarded as a better indicator of the importance of variation than the variance alone. In the Poisson case, the coefficient of variation is $1/\sqrt{\bar{N}_i(t+h)}$, i.e., becomes very small as population densities increase, and for this reason, we should not be too surprised that Poisson variation only has large effects when average local population sizes are small.

In contrast, in the negative binomial, the variance increases as a quadratic function of the mean:

$$V(N_i(t+h)) = \bar{N} + \bar{N}^2 / k \quad 21)$$

where here \bar{N} is short for $\bar{N}(t+h)$. The formula for the coefficient of variation (Southwood²⁰) is $\sqrt{1/\bar{N} + 1/k}$, which can never be less than $1/\sqrt{k}$. Thus, if the clumping parameter, k , is small and constant, the effect of variation should not greatly depend on population density. We have already seen the strong effects that such negative binomial variation can have when local density dependence is given by the Ricker model (Eq. 3). Indeed, the conversion of population dynamics from scramble to contest form in Figure 8.2 is dependent on the low sensitivity of the coefficient of variation to population density. The stability criterion¹ is:

$$(k+1)[1-(1/R')^{k+1}] < 2 \tag{22}$$

which is always satisfied for $k < 1$ and $R' > 1$. Thus, stability occurs independently of the local equilibrium population size.

The above analysis treated k as a constant, as is commonly done in the literature on population dynamics. However, k need not be fixed. It could depend on the mean population density. For example, if k were proportional to population density, \bar{N} , say $k = a\bar{N}$, then the relationship (Eq. 21) for the variance would become:

$$V(N_i(t+h)) = \bar{N}(1+1/a) \tag{23}$$

with coefficient of variation $\sqrt{(1/\bar{N})(1+1/a)}$. Like the Poisson case, this coefficient of variation declines to zero as mean abundance increases. Substituting $k = a\bar{N}$ in Eq. 7 shows that:

$$\bar{N}(t+1) = R''\bar{N}(t)e^{-\alpha''\bar{N}(t)} \tag{24}$$

where:

$$R'' = R'/[1 + (1-e^{-\alpha})/a] \tag{25}$$

and:

$$\alpha'' = a\ln[1+(1-e^{-\alpha})/a] \tag{26}$$

Thus, we see that with this form of the negative binomial, large scale population dynamics remain in the Ricker form. The effect of spatial variation is not to alter fundamentally the nature of population dynamics on the larger scale, but to modify the parameters, as in the Poisson case.

The stability criterion for the Ricker model is here $\ln R'' < 2$, which can be expressed as:

$$\ln R - \alpha - \ln[1+(1-e^{-\alpha})/a] < 2 \tag{27}$$

The left-hand side is less than with Poisson variation, and so we see that this form of negative binomial variation does have a greater effect on stability than Poisson variation. However, its effect is not independent of local population size, because for small α the reduction in the left-hand side of Eq. 27 due to spatial variation is proportional to α and thus inversely proportional to equilibrium local population density. Moreover, the parameter a must be small in relation to α for the stability criterion to differ much from the case of Poisson variation.

These results raise a number of important issues, the first of which is the meaning of the parameter a in the second form of the negative binomial distribution above. Related to this question, however, is the question of how these different sorts of spatial variation arise, and whether there is some means of predicting the change in variation as a function of mean density. The Poisson distribution is the standard model of random spatial distributions, and may not seem to need explanation, but there are so many reasons for spatial distributions to be nonrandom that it is worthwhile identifying situations preserving the Poisson state. Poisson distributions can be maintained if individual organisms disperse independently of one another and environmental features, and if dispersal distances from places of birth are large compared with the mean spacing of parent organisms or other organisms.¹⁹

The negative binomial distribution with constant k arises from heterogeneous Poisson sampling,^{20,30} which can be considered a model of the case where organisms do migrate long distances as described above, independently of each other, but not independently of environmental features. Within the modelling framework considered here, this would mean that a given patch i can be assigned an attractiveness value, U_i such that the local population density $N_i(t+h)$ is Poisson with mean $U_i \bar{N}$, given U_i . Variation in U_i from patch to patch means that the actual spatial distribution is a Poisson mixture distribution.³¹ Application of the conditional variance formula²⁶ shows that the variance of local population size satisfies (Eq. 21) above with $1/k$ equal to the variance of U_i . The distribution of local population size, however, is not exactly negative binomial unless U_i has a gamma distribution.³¹ Nevertheless, the negative binomial with constant k is likely to be a good model whenever dispersing organisms tend to concentrate in particular places because of peculiar features of those places, not the other organisms there.

The negative binomial with k proportional to the mean population density arises from a different modification of the Poisson distribution. If organisms disperse randomly in space and so are distributed according to a Poisson distribution, but with each individual v giving rise independently to some variable number, M_v , of nondispersing offspring, then the total number of offspring in a patch has a so-called generalized Poisson distribution.³¹ Application of the conditional variance formula shows that the variance is given by Eq. 23, where a is the following function of the mean and variance of the distribution of offspring over individuals:

$$a = \{V(M_v)/E[M_v] + E[M_v] - 1\}^{-1} \quad (28)$$

Thus, for a to be small, the mean number in a clutch has to be large or the variance to mean ratio has to be large. Note, however, that for the distribution of offspring in a patch to be exactly negative binomial, M_v must have the highly skewed logarithmic distribution.³¹

These two different biological models for the negative binomial give different consequences for the scale transition. The negative binomial has large and qualitative effects when it arises from a spatially variable environment, but somewhat smaller and only quantitative effects when it arises from clumped distributions of offspring. These models, however, are highly idealized dispersal scenarios. Clumped distributions in nature are bound to involve environmental variation, limited dispersal, and the nature of local population

dynamics. They quite likely depend not just on the current population density in the system, but on previous population densities too. Thus, the dynamics of spatial distributions have the potential to introduce timelags into population dynamics, possibly of very long duration.³²

Discussion

I have tried to show how the scale transition can be understood in terms of an interaction between nonlinear dynamics and variation. Once the nonlinearities and variation are known, the scale transition is determined very simply by the nonlinear averaging process described above. However, as we have seen, it is important to understand the scales of variation relative to the scales of the interactions between individuals, as these are the scales on which the nonlinearities apply.

Variation can be dynamic, and because variation is essential to the scale transition, the dynamics of variation are important to population dynamics on the larger spatial scale. The critical issue is how the variance, or more generally, the spatial frequency distribution of local population density, changes over time. Given the dynamics of the variance (or the frequency distribution), other detail (e.g., the degree synchrony of the population fluctuations in different patches) is irrelevant. We have seen above how the spatial variance may be a function of the mean, which is the same as the large-scale or whole-population density. In that case, Equation 7 and its more exact but less general counterparts yield equations for large-scale population dynamics involving large-scale population density alone, and the problem of determining large-scale population dynamics is completely solved by these equations. In general, the variance is not likely to be so simply related to the mean, and past as well as present mean densities may be needed to predict the variance from the mean. In such cases, difference equations of an order higher than one would be needed to describe population dynamics on the larger spatial scale. In multispecies settings, the dynamics of the correlations between the distributions of different species are also an issue.^{18,33}

These ways of viewing the scale transition suggest programs of theoretical and empirical research into the nature of nonlinearities and the intricacies of spatial variation. As explained above, nonlinearities arise from density dependence considered broadly⁹ within and between species, and have long been objects of study in ecology. The nature of the nonlinearity has important effects on the scale transition. For example, convex and concave nonlinearities have opposite effects on the scale transition, as shown above and in ref. 34. The roles of various kinds of nonlinearities in the scale transition have been studied implicitly or explicitly in neighborhood models of plants,^{15,19} host parasitoid systems,^{35,7} and competitive systems.^{14,18,36} However, the most explicit treatment of nonlinearities in relation to the scale transition can be found in the study of temporal variation in competitive systems.^{37,38}

Environmental effects on density dependence can also be considered to be types of nonlinearities. In the treatment here, we have considered only the effects of the environment on the spatial distributions of organisms, but the parameter α expressing density dependence in the models above may vary in space, and such variation can easily be seen to create a scale transition very similar to that resulting from variation in local population densities. Such effects of spatially varying density dependence are well known in models of competitive interactions³⁹ where the density dependence is multispecies.

Little work has addressed the important question of the relative scales of variation and density dependence. The scale of density dependence seems in essence to be the spatial scale over which interactions between individual organisms occur during the relevant unit of time. This scale naturally arises in empirical studies of neighborhood competition,¹⁹ but to my knowledge there have been no explicit attempts at a theory of spatial scales of density dependence. However, consideration of the scale of resource utilization is an important beginning.⁴¹ Scales of spatial variation have received much more attention.^{22,25,42,43} Models cover a large spectrum. Hassell et al⁷ and Solé et al³³ have shown how local dynamics and migration can create or maintain variation essential to the scale transition. In other models^{8,39,44} environmental variation plays an important role contributing to variation in density or modifying density dependence on various scales.

Relationships between variance and average local population density are well-studied empirically, at least with insects.⁴⁵ Substantial modeling effort has been directed at understanding this relationship^{45,46} but none has been developed in concert with dynamical models addressing large-scale population dynamics. Modern computing power means that investigating these relationships and the scales of variation in spatial models are not difficult exercises. I have tried to show how such information is a route to understanding spatial models, especially the important issue of the scale transition.

This way of viewing spatial models permits a close link between theoretical and empirical studies. The many parameters of a spatial model will rarely be available empirically, yet the scales of variation and the relationships between means and variances can be known empirically with relative ease. Nonlinearities are a more difficult issue, but nevertheless, this approach represents an alternative to the common reductionist method, which requires the estimation of very many parameters and may lead to potentially unfathomable complexity from the effects and interactions of these parameters. The more holistic method advocated here promises a structured approach to understanding the role of space in the dynamics of populations in terms of meaningful components.

Appendix

Mortality during dispersal may be high, but the above developments ignore it completely. To see what this means, let s be the average individual survival rate of dispersing and nondispersing organisms from time t to $t+h$. The equations above relating $\bar{N}(t+1)$ to $\bar{N}(t)$ continue to apply but with $s\bar{N}(t)$ substituting for $\bar{N}(t)$. To see that this often leads to no essential change in our conclusions, let $m(t) = s\bar{N}(t)$ ("dispersal-mortality-corrected population density"), then the dynamics of $m(t)$ are given by the equations for \bar{N} above with m substituting for \bar{N} and sR substituting for R (or more generally sF substituting for F) throughout. If s is a constant (e.g. if migration rates and dispersal mortality rates are time- and density-independent), then m is just \bar{N} in different units, and the effect of mortality during dispersal is seen to be equivalent to having a smaller value of R , or more generally, a smaller F . Such smaller R s or F s do affect population dynamics, but do not affect the conclusions above about the interaction between spatial variability and nonlinearity. Mortality

during density-dependent dispersal is more complicated because then s is density dependent, but similar arguments show that its effects are equivalent to modifying the nonlinearity of F .

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