

Interim Report

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Population Growth in Space and Time: The Spatial Logistic Equation

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Abstract

How great an effect does self-generated spatial structure have on logistic population growth? Results are described from an individual based model (IBM) with spatially localised dispersal and competition, and from a deterministic approximation to the IBM describing the dynamics of the first and second spatial moments. The dynamical system incorporates a novel closure that gives a close approximation to the IBM in the presence of strong spatial structure. Population growth given by the spatial logistic equation can differ greatly from that of the non-spatial logistic model. Numerical simulations show that populations may grow more slowly or more rapidly than would be expected from the non-spatial model, and may reach their maximum rate of increase at densities other than half of the carrying capacity. Populations can achieve asymptotic densities substantially greater than or less than the carrying capacity of the non-spatial logistic model, and can even tend towards extinction. These properties of the spatial logistic equation are caused by local dispersal and competition which affect spatial structure, which in turn affects population growth. Accounting for these local spatial processes brings the theory of single-species population growth a step closer to the growth of real spatially-structured populations.

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Population Growth in Space and Time

The Spatial Logistic Equation

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Introduction

The logistic equation has a long and distinguished history in ecology. First formulated by Verhulst in 1838, and rediscovered by Pearl and Reed (1920), the equation was promoted to the status of a predictive law of population growth in writings by Pearl. As a law it proved somewhat controversial (Kingsland 1985:77 *et seq.*); widely cited data on population growth rarely give a close fit to the logistic equation (Hall 1988). Even the famous example by Gause (1934) of growth of populations of the protist *Paramecium aurelia*, reanalysed by Leslie (1957), contains some systematic departures from the logistic equation in the distribution of residuals (Leslie 1957, Williamson 1972:37).

There are at least three reasons why the logistic equation may fail to give an adequate description of population growth. First, the per-capita effect of density on population growth may not increase linearly with density. This is the cause of the discrepancy in Gause's experiment on *Paramecium*: the logistic equation underestimates the strength of density dependence at high density (Williamson 1972:37). Such problems can be corrected by introducing a third parameter into the logistic equation, the θ -logistic class of models, allowing the maximum rate of population growth to be achieved at densities other than half of the carrying capacity (Gilpin and Ayala 1973). Second, there may be a time delay in the operation of density dependence (Hutchinson 1948); time delays can occur in structured populations when density affects vital rates at particular ages or sizes. A time-delayed version of the logistic equation has been used with some success to describe the periodic time series found in certain species such as blowflies (May 1975:94 *et seq.*, Gurney *et al.* 1980).

Third, spatial structure may make it impossible for organisms to encounter each other in proportion to their average density. The random collision of individuals assumed in the logistic equation, often referred to as the 'mean-field' assumption (e.g. Law *et al.* 2000), may not represent interactions among organisms well. Harper (1977:4) was explicit in how unsatisfactory this assumption is in plant population biology, pointing

out that plants develop clumped spatial patterns and, in such clumps, individuals can experience strong effects of competition with their neighbours, even though there may be unexploited resources nearby. Empirical studies have shown that the 'plant's-eye' view of its population density can be far from the density averaged over space (Turkington and Harper 1979, Mahdi and Law 1987, Purves and Law 2002a).

Doubts about the validity of the mean-field assumption lead to the question: how great a departure from logistic population growth does spatial structure cause? To date there have been very few studies extending logistic population growth to a continuous spatial setting (Bolker and Pacala 1997, Bolker *et al.* 2000, see also Law and Dieckmann 2000a). Bolker and Pacala (1997) constructed an individual-based model (IBM) of birth, death and dispersal processes, derived a dynamical system of spatial moments (moment dynamics) from the IBM, and examined some asymptotic properties of the dynamical system. By doing this, they showed how the spatial structure at the asymptotic state was affected by the intrinsic rates of birth and death and the neighbourhoods over which interactions and dispersal take place. Parallel work in a discrete spatial setting is more tractable (Ellner 2001), although it has the drawback of being less readily linked to real ecological events that occur in continuous space.

This paper extends the study by Bolker and Pacala (1997) in several ways. First, we use IBMs to document some major departures from non-spatial logistic population growth that occur when dispersal and interactions are restricted to small neighbourhoods of individuals. Second, we change an assumption (a moment closure) that previously restricted the spatial logistic equation to relatively small departures from spatial randomness of individuals; this change is needed because of the large departures from randomness often observed in ecological communities (Condit *et al.* 2000, Purves and Law 2002a). Several moment closures are tested, including a new one that appears to provide a good approximation even in populations that develop strong spatial clustering. Third, we use the new closure to describe some effects of restricted dispersal and interaction neighbourhoods on transient and asymptotic dynamics of a spatially extended population with logistic-like properties. The study shows the spatial logistic equation has a richness in its dynamics, unanticipated from its non-spatial precursor, and this brings the theory of single-species population growth a step closer to the dynamics of real spatially-structured populations.

Individual-based model

At a microscopic scale, population growth is inherently stochastic: birth and death events occur at random creating and eliminating spatially discrete individuals (Durrett and Levin 1994); together with dispersal, these events lead to random variation from one individual to another in the neighbourhoods within which interactions occur. It is

therefore helpful to start with a stochastic process describing behaviour of individuals (often called an IBM in ecology), and to derive deterministic approximations from it. Both stochastic and deterministic methodologies have a part to play (Renshaw 1991), and recent research in spatial aspects of population dynamics has often followed this dual approach (Matsuda *et al.* 1992, Bolker and Pacala 1997, Law and Dieckmann 2000b, Ellner 2001).

Stochastic process

We consider a population of organisms of a single species living in a two-dimensional space; the space is continuous (as opposed to a discrete spatial lattice), homogeneous, and large enough for edge effects to be negligible (for simulations, we use periodic boundaries). An individual i , located at coordinates $x_i = (x_{i1}, x_{i2})$, is denoted by a Dirac delta function $\delta_{x_i}(x)$; the state of the population at time t is given by the function $p(x, t)$, which describes the locations of all individuals, this function being the sum of the delta functions of all individuals (Dieckmann *et al.* 1997, Dieckmann and Law 2000).

The IBM is a stochastic process in continuous time with events comprising birth, death and movement; these events take place in continuous time and may depend on the current state of the population (a Markov process). The probability per unit time $B(x, x', p)$ that an individual located at x produces an offspring at x' is given by

$$B(x, x', p) = b \cdot m(x' - x) \quad (1a)$$

where b is an intrinsic per capita birth rate, and $m(x' - x)$ is a dispersal kernel describing the probability density that a newborn individual comes to rest at a displacement $x' - x$ from its mother. The probability per unit time $D(x, p)$ that an individual located at x dies is given by

$$D(x, p) = d + d' \cdot \int w(x' - x) \cdot [p(x', t) - \delta_x(x')] dx' \quad (1b)$$

This death term comes in two parts, the first being an intrinsic per capita death rate d , and the second modifying the death rate in the presence of other individuals in a neighbourhood of x . The term $w(x' - x)$ is an interaction kernel (normalised so that its integral over x' is one), that weights the effect of a neighbour displaced by an amount $x' - x$ from x on the death rate at x . Multiplying by the density of individuals at x' , and integrating over x' , gives the overall effect of neighbours; the delta function $\delta_x(x')$ removes the individual at x , because it cannot compete with itself.

We construct the IBM in this way to keep a close connection to the familiar non-spatial logistic equation. The IBM corresponding to the non-spatial logistic equation would simply replace the integral in Equation (1b) with the density of individuals, ig-

noring their location in space (Renshaw 1991:59). This would give a density-independent component to per capita birth and death rates (parameters b and d), plus a component to the per capita death rate that increases linearly with population density (weighted by the parameter d'). The spatial extension assumes that dispersal of individuals is linked to births and that competition among individuals is linked to deaths; this is for the sake of clarity in developing the arguments, and alternative assumptions could readily be made (e.g. Bolker and Pacala 1997).

The dispersal and competition kernels determine the spatial component of the IBM. For simulating the IBM, functions for the kernels must be made explicit; we use bivariate Gaussian functions

$$m(x' - x) = \frac{1}{M} \exp\left(-\frac{|x' - x|^2}{2s_m^2}\right) \quad (2a)$$

$$w(x' - x) = \frac{1}{W} \exp\left(-\frac{|x' - x|^2}{2s_w^2}\right), \quad (2b)$$

each having one parameter s_m , s_w that measures the width of the kernel. A small value of s_m means that offspring are usually located close to their mothers, and a small value of s_w means that competition occurs predominantly with close neighbours. For practical purposes the tail of each kernel is truncated at three times the parameter value; the effect this has on the dynamics is very small. The kernels are normalised so that their integrals over $x' - x$ are unity, M and W being the normalisation constants.

Results from IBMs

Figure 1 shows results of illustrative realisations of the IBM obtained using a range of kernel parameters, each continuous line being the spatial mean density (the first spatial moment) itself averaged over 20 realisations of the IBM. To see the direct effect of the spatial extension, the parameters for birth and death rates (b , d , d') are kept constant throughout, and only s_m and s_w , affecting the width of the dispersal and competition kernels, are varied. In all cases the IBMs begin with 20 individuals placed at random locations in the unit arena. The constant birth and death parameters would give an equilibrium density of 200 individuals per unit area in the non-spatial logistic equation, shown as the dotted line in Figure 1.

It is striking how big a departure from the familiar non-spatial logistic growth the spatial extension can cause (Figure 1): compare the dotted line of the non-spatial logistic equation (Figure 1f) with results from the spatial IBM (Figure 1a-e).

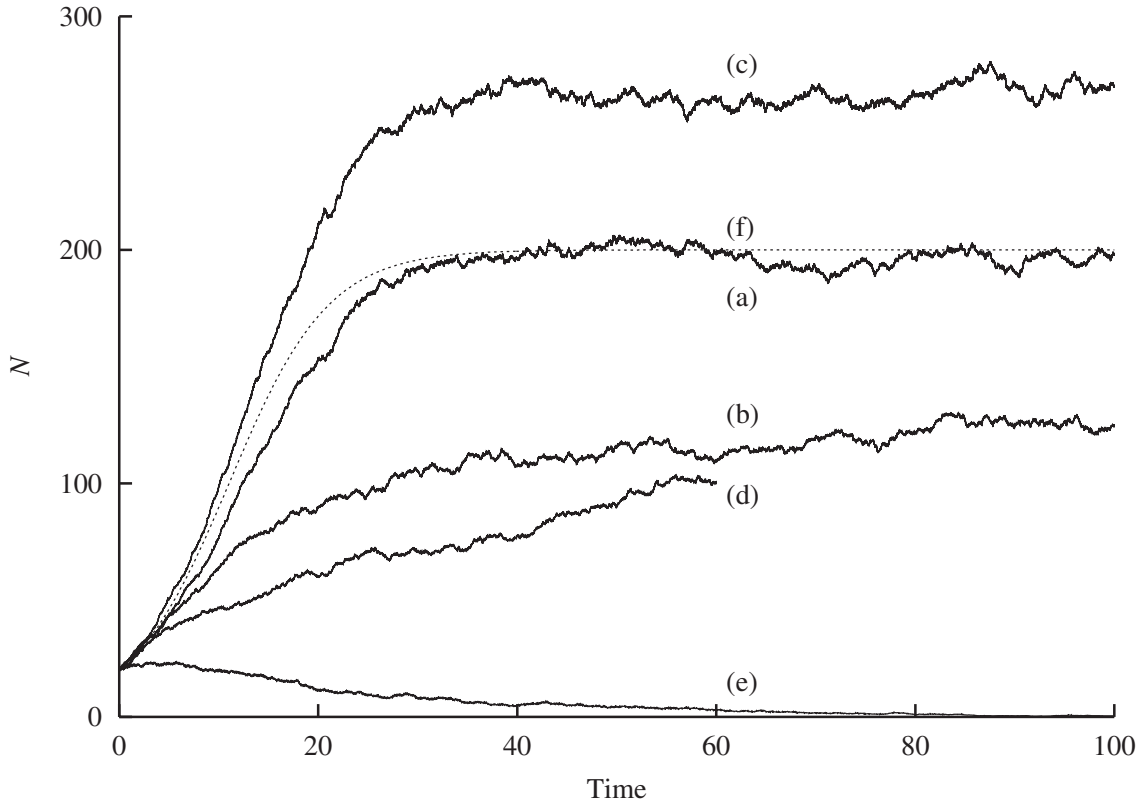


Figure 1. Spatial mean density (first spatial moment) over time from IBMs with contrasting kernel parameters for dispersal s_m and competition s_w . All simulations began with 20 individuals randomly dispersed across the unit arena; the time series shown are averages of 20 realisations of the IBMs. Kernel parameters: (a) $s_m = 0.12$, $s_w = 0.12$; (b) $s_m = 0.02$, $s_w = 0.12$; (c) $s_m = 0.12$, $s_w = 0.02$; (d) $s_m = 0.04$, $s_w = 0.04$; the simulation is stopped at $t = 60$, after which it overlaps with (b); (e) $s_m = 0.02$, $s_w = 0.02$; (f) growth of an equivalent non-spatial logistic population, shown as the dotted line. Parameters held constant throughout: $b = 0.4$, $d = 0.2$, $d' = 0.001$.

Although populations do not grow faster than in the non-spatial logistic equation at low density, they can increase much more slowly, and can even decrease. Both the asymptotic and transient dynamics are affected by the spatial extension. Asymptotic densities averaged over space can be much greater or smaller than those of the non-spatial logistic equation; it is even possible for a rapid, repeatable decline to extinction to occur. Transient effects on density include changes in the shape of the growth curve: populations growing according to the non-spatial logistic equation would reach their maximum rates of increase at one half of the equilibrium density, but this no longer holds under the spatial extension. In some circumstances, the familiar 'S'-shaped growth of the logistic equation is replaced by a growth transient that is approximately linear. Surprisingly, it is populations that stop growing at the lowest densities that take longest to reach the asymptotic state.

These deviations from the non-spatial logistic equation are generated simply by effects of the dispersal and interaction kernels on spatial structure. To understand the in-

terplay between vital processes and spatial structure, it helps to think of two forces that affect spatial structure in opposite ways. The first force is local dispersal of offspring: as the distance over which offspring disperse is made smaller (by reducing s_m), individuals are increasingly clustered in space. The second force is local competition: when the neighbourhood over which individuals compete is made smaller (by reducing s_w), mortality rates of close neighbours are increased, with the result that survivors are overdispersed. Thus, by altering the parameters s_m and s_w , the strength of forces for aggregation and overdispersion are changed. Below, we explain how this leads to the different kinds of population growth in Figure 1.

First, when s_m and s_w are both large (Figure 1a, 2a, 2b), offspring disperse over large distances and competition occurs with individuals even if they are quite remote. In these circumstances there is little tendency for spatial structure to build up (Figure 2c). The population dynamics come close to satisfying the mean-field assumption, and the asymptotic average density is close to the equilibrium of the non-spatial logistic equation.

Second, when s_m is small and s_w remains large (Figure 1b, 2e, 2f), the short distances dispersed generate a strong force towards aggregation. There is little to counter this because s_w is still large, and the outcome is therefore a strongly aggregated spatial pattern (Figure 2g). Aggregation is strong enough to increase population density in the region in which the competition operates above the value expected from the non-spatial logistic equation, notwithstanding the large value of s_w . These increased local densities stop population growth below the level expected from the non-spatial logistic equation. Notice also that the asymptotic state is approached rather slowly because the space available for the population can only be slowly filled from the foci of the initial colonists due to the short distances over which offspring disperse (Figure 1b).

Third, when s_w is small and s_m remains large (Figure 1c, 2i, 2j), the high rates of mortality of close neighbours generate a strong force towards overdispersion. But there is now little to counter overdispersion, because newborn offspring are widely dispersed over space; the outcome is therefore a spatial pattern with a strong tendency towards regularity (Figure 2k). A consequence of regularity is a deficiency of competitors in the immediate neighbourhood of an individual, and this permits population growth to continue to densities higher than expected from the non-spatial logistic equation; there is sense in which local competition leads to more efficient packing of individuals into the available space. The asymptotic state is approached quickly because individuals get rapidly to all parts of the arena due to the large distances over which offspring disperse (Figure 1c).

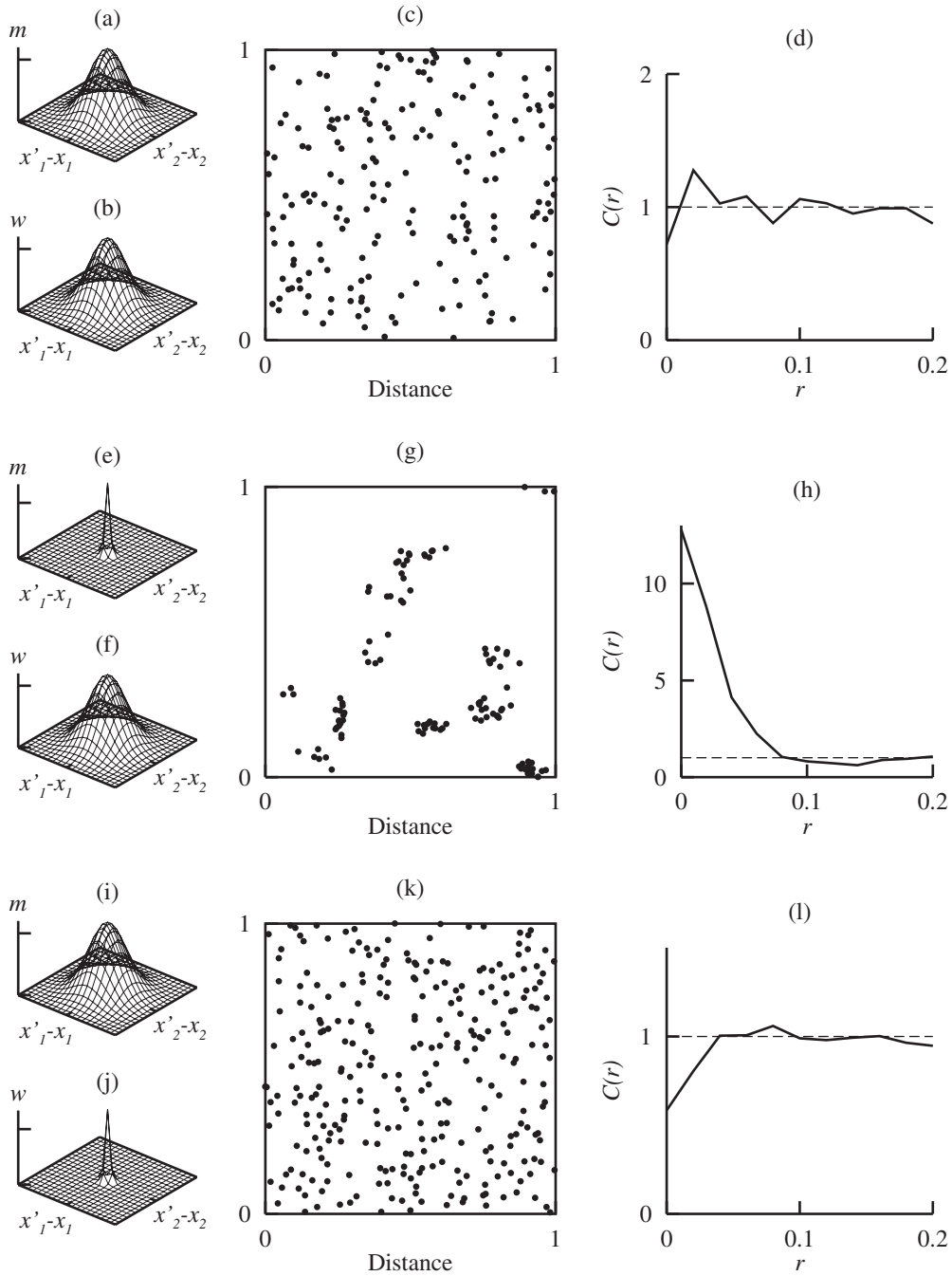


Figure 2. Effects of dispersal and competition kernels, on spatial structure in IBMs. Simulations started under the same conditions as those in Figure 1; results are shown at time 100. Row 1 has $s_m = 0.12$, $s_w = 0.12$: (a) dispersal kernel (b) competition kernel, (c) spatial pattern, (d) second radial moment of spatial pattern. Row 2 has $s_m = 0.02$, $s_w = 0.12$: (e) dispersal kernel (f) competition kernel, (g) spatial pattern, (h) second radial moment. Row 3 has $s_m = 0.12$, $s_w = 0.02$: (i) dispersal kernel (j) competition kernel, (k) spatial pattern, (l) second radial moment. Other parameters as in Figure 1. The second moments are given as functions of the radial distance of the pair and are normalised such that they would take value 1 in the absence of spatial structure, as shown by the dashed lines.

Fourth is a remarkable case of extinction when s_m and s_w are both small (Figure 1e). At the start it is rare for individuals to compete; this is because the initial colonists are low in density and positioned at random (they would have to be close together to interact). The population therefore starts to increase. However, offspring of the colonists are only dispersed over short distances, and clusters rapidly develop. Competition in these clusters is intense because of the small neighbourhoods over which individuals interact; mortality rates are consequently high, so high in fact that they exceed the rate of reproduction. The spatial mean density then starts to fall, a decline that continues down to the last few individuals. It is immaterial that density averaged over space is small because offspring of the remaining individuals still come to rest close to their mothers. Put another way, parents and offspring cannot escape from competition with one another, so the clusters implode and the population collapses. A mathematical analysis of the conditions for extinction of a population with local dispersal and competition is given by Etheridge (2001).

Spatial logistic equation

Although a lot can be learnt from running realisations of IBMs, it is time-consuming to track every microscopic birth and death event; moreover, the ecological signal can be hard to discern beneath the stochastic variation, and hard to analyse mathematically. A formalism that deals with the dynamics of macroscopic variables like population density would help.

In the case of the non-spatial logistic equation, this scaling up from microscopic events to macroscopic variables replaces a stochastic process of density-dependent birth and death events with the standard logistic differential equation, with the assumption that the area occupied by the population, and hence the population size, is large (Renshaw 1991:59). In the case of the spatial logistic equation matters are more intricate because of the coupling of spatial structure to birth and death events seen in the IBMs above; somehow the dynamical system has to hold in place some information on spatial structure and allow this structure to change over the course of time. Dynamical systems of spatial moments have recently been derived to do this (Bolker and Pacala 1997, Dieckmann *et al.* 1997, Dieckmann and Law 2000). Here we briefly describe such a system of equations, and give some numerical results on how the asymptotic state is affected by dispersal and competition.

Spatial moments

The state variables of the dynamical system are the first and second spatial moments. These moments are defined for a spatial pattern $p(x, t)$ as follows.

The first moment $N(p)$ is the density averaged over the space A in which the population lives

$$N(p) = \frac{1}{A} \int p(x,t) dx. \quad (3a)$$

The second moment $C(\xi, p)$ is the average density of pairs of individuals, the second individual in the pair being displaced by an amount $\xi = x' - x$ from the first

$$C(\xi, p) = \frac{1}{A} \int p(x,t) [p(x+\xi,t) - \delta_x(x+\xi)] dx; \quad (3b)$$

the delta function removes a degenerate pair in which the same individual would occur twice. In the figures below, we normalise the second moment by dividing by $N^2(p)$. The second moment holds second-order information about the spatial structure, as illustrated in Figure 2d, h, l, and can be thought of as a spatial covariance function (although note that it is not a central moment). The second moment has the advantage of being mathematically simple, which is important for the dynamical system described below, and also has been independently developed and used to summarise the spatial structure of populations in the field (Condit *et al.* 2000).

The third moment $T(\xi, \xi', p)$, although not a state variable, appears in the dynamical system below, and needs to be defined. This moment is the average density of triplets, where the second individual is displaced by ξ from the first, and the third individual is displaced by ξ' from the first:

$$T(\xi, \xi', p) = \frac{1}{A} \int p(x,t) [p(x+\xi,t) - \delta_x(x+\xi)] [p(x+\xi',t) - \delta_x(x+\xi') - \delta_x(x+\xi' - \xi)] dx. \quad (3c)$$

The integrand here is essentially the product of the three densities at the given displacements, the delta functions removing degenerate triplets in which the same individual would occur more than once.

Dynamical system

We use a dynamical system derived in Dieckmann and Law (2000); derivation of a similar system was given earlier by Bolker and Pacala (1997). The system describes how, on the average, the first two spatial moments change over the course of time (the average being over the ensemble of stochastic realisations), the state variables being $N(t)$ and $C(\xi, t)$. The differential equation for the rate of change of the first moment is given by

$$\dot{N}(t) = b N(t) - d N(t) - d' \int w(\xi') C(\xi', t) d\xi' \quad (4)$$

This differs from the non-spatial logistic equation only in that the term N^2 of the logistic equation is replaced the integral expression. The integral carries information about local spatial structure and couples the dynamics of the first moment to those of the second.

The differential equation for the rate of change of the second moment is somewhat more intricate, because birth and death events happen at both points in the pair

$$\begin{aligned}
\dot{C}(\xi, t) &= b \int m(\xi') C(-\xi + \xi', t) d\xi' & (a) \\
&+ b \int m(\xi') C(\xi + \xi', t) d\xi' & (b) \\
&+ 2 b m(\xi) N(t) & (c) \\
&- 2 d C(\xi, t) & (d) \\
&- d' \int w(\xi') T(\xi, \xi + \xi', t) d\xi' & (e) \\
&- d' \int w(\xi') T(\xi, \xi', t) d\xi' & (f) \\
&- 2 d' w(\xi) C(\xi, t). & (g) \quad (5)
\end{aligned}$$

Precise geometric interpretations for each expression in this equation are described in Law and Dieckmann (2000b). The second moment is a function of ξ , and one can think of Equation (5) as describing how, as time goes on, the function changes in shape as the spatial structure of the population changes.

A feature of the dynamical system in Equations (4), (5) is that the rate of change of the first moment depends on both the first and second moments, and the rate of change of the second moment depends on the first, second and third moments. This means that the dynamical system is not yet closed: it contains the third moment which, although a variable, is not included in the dynamical system. The third moment has to be replaced by some function of the first and second moments to close the dynamical system; such a function is called a moment closure. (Although not generally recognised, a similar issue applies in the standard non-spatial logistic equation; the mean-field assumption is in effect an assumption that the second spatial moment can be replaced by N^2 .) Several closures have been suggested in the literature (Bolker and Pacala 1997, Dieckmann and Law 2000, Law *et al.* 2001); these and a new closure are evaluated in the Appendix. We use a new closure:

$$T_4(\xi, \xi') = \frac{1}{5} \left[\frac{4 C(\xi)C(\xi')}{N} + \frac{C(\xi) C(\xi' - \xi)}{N} + \frac{C(\xi')C(\xi' - \xi)}{N} - N^3 \right], \quad (6)$$

because this gives a closer fit to the average of stochastic realisations than solutions using previous closures in populations that develop strong spatial aggregation (see Appendix), and also works quite well in a wide range of other spatial structures.

Population dynamics

Figure 3 shows that the deterministic model captures to a close approximation the average of the stochastic realisations in Figure 1, both in the transient behaviour and in the asymptotic state. To match the initial conditions of the stochastic realisations in Figure 1, these numerical integrations were initially set with the first moment at 20 individuals per unit area, and the second moment at 20^2 for all displacements ξ (equivalent to individuals being placed uniformly at random in the arena).

The cause of the different kinds of population growth becomes clearer on examining the time series of the second moment (Figure 4). Immediately after the start, the dispersal term (c) and interaction term (g) in Equation (5) start to distort the second moment from its initially flat shape: terms (c) and (g) ensure that uniform spatial randomness cannot in general be an attracting state (Bolker and Pacala 2000:396). One can think of (c) and (g) as the source of spatial structure and the other terms as distributing the structure across different displacements. Because the population density starts low in the simulations illustrated, the effect of dispersal is greater than that of interactions ($b \gg d'$), and the second moment starts by increasing (how far from the origin this extends depends on the parameter s_m of the dispersal kernel). But the interaction parameter s_w can affect spatial structure as soon as local aggregations start to develop, and the second moment develops a shape characteristic of the values of s_m and s_w .

A crucial feature of Equations (4) and (5) is that information on the shape of the second moment feeds back to the first moment through the integral term in Equation (4): in other words, population growth is now sensitive to spatial structure. When the second moment is large at small spatial displacements (spatial aggregation), the negative integral term in Equation (4) becomes greater, slowing down population growth, and giving eventually a low equilibrium density; this can be seen in the time series of the second moment in Figure 4b, and the corresponding first moment in Figure 3 (line b). When the second moment is close to N^2 , i.e. close to one after normalisation (spatial randomness), population growth rate and the equilibrium density are close to the non-spatial logistic equation (Figure 4a, Figure 3 line a). When the second moment is small for

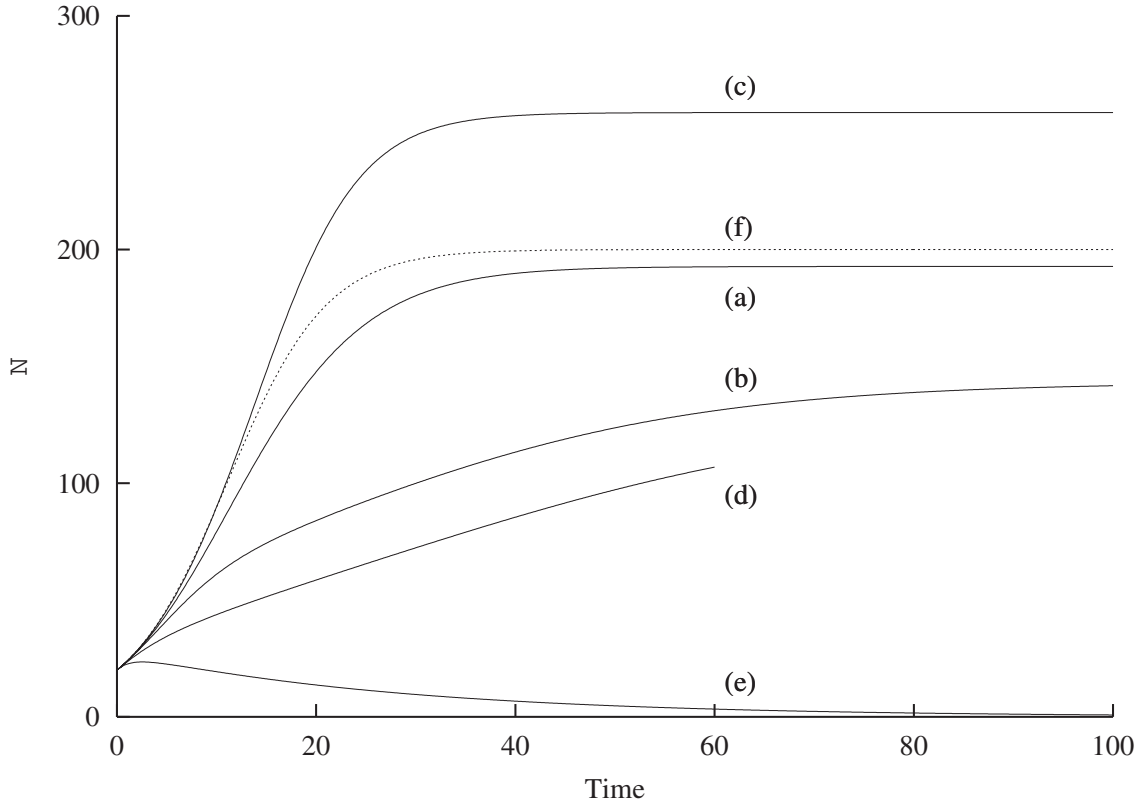


Figure 3. Time series of the first moment N , obtained by numerical integration of the spatial logistic equation. The growth of an equivalent non-spatial logistic population is shown as a dotted line. Parameter values are as in Figure 1; initial conditions are set to match those in Figure 1.

small spatial displacements (spatial overdispersion), population growth rate and the equilibrium density are high (Figure 4c, Figure 3 line c).

In the transient population dynamics, s_m plays a particularly important role, because wider dispersal permits more rapid filling of the space available. This is evident in Figure 5, which plots the rate of increase of the first moment (mean density) at half the equilibrium density ultimately achieved; even near the maximum value of s_m examined (0.12), the rate of increase shows little sign of having reached its greatest attainable value as a function of s_m . It can also be seen from the time series in Figure 3 that, in contrast to the non-spatial logistic equation, the populations do not in general reach their maximum growth rate at half the equilibrium density. This is because local density in the neighbourhood of individuals is somewhat uncoupled from the spatial mean density; under strong spatial aggregation the effects of high local density are felt early in population growth when mean density is still low; under strong overdispersion, mean density has to be much higher before the local density-dependent processes become important.

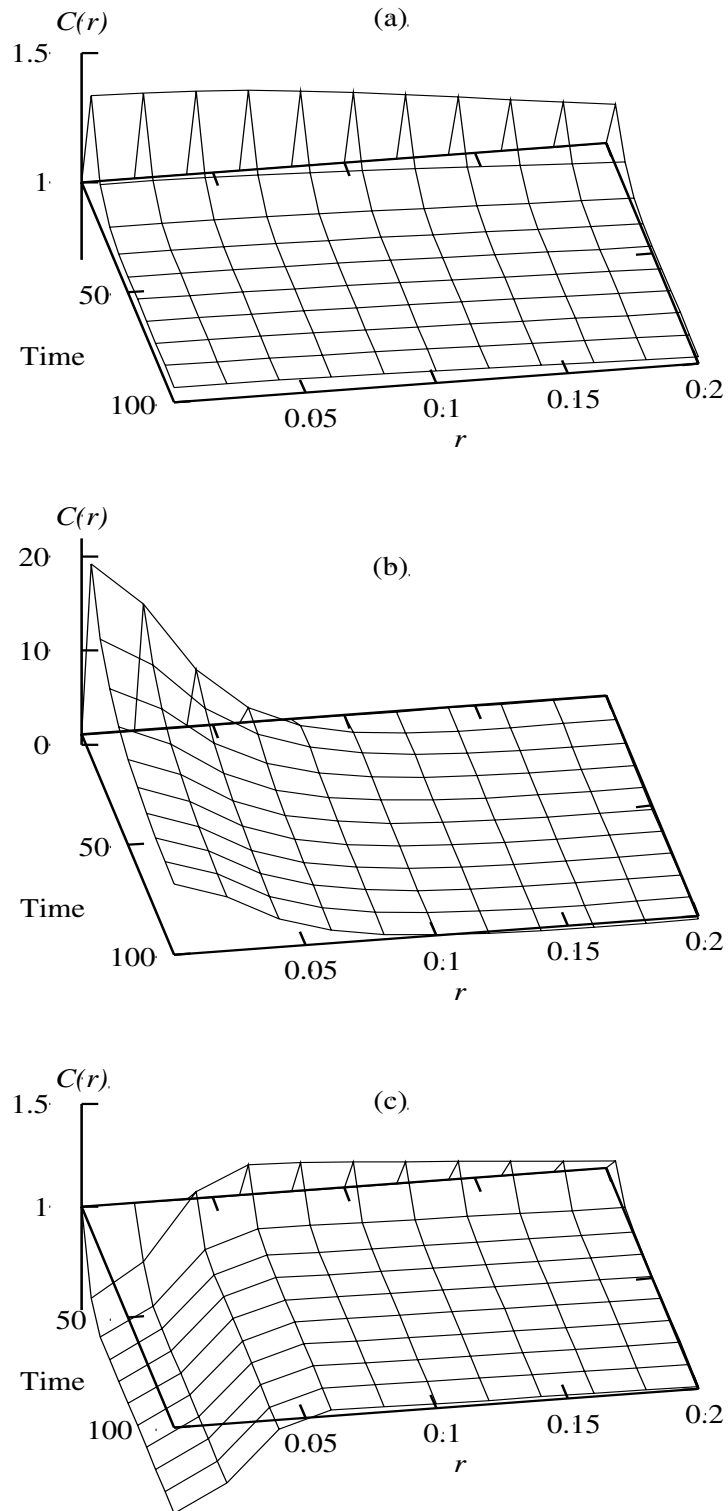


Figure 4. Time series of the second radial moment $C(r)$, obtained by numerical integration of the spatial logistic equation. Parameter values: (a) $s_m = 0.12$, $s_w = 0.12$; (b) $s_m = 0.02$, $s_w = 0.12$; (c) $s_m = 0.12$, $s_w = 0.02$. Parameters b , d , and d' held constant throughout with values as in Figure 1; initial conditions are set to match those in Figure 1.

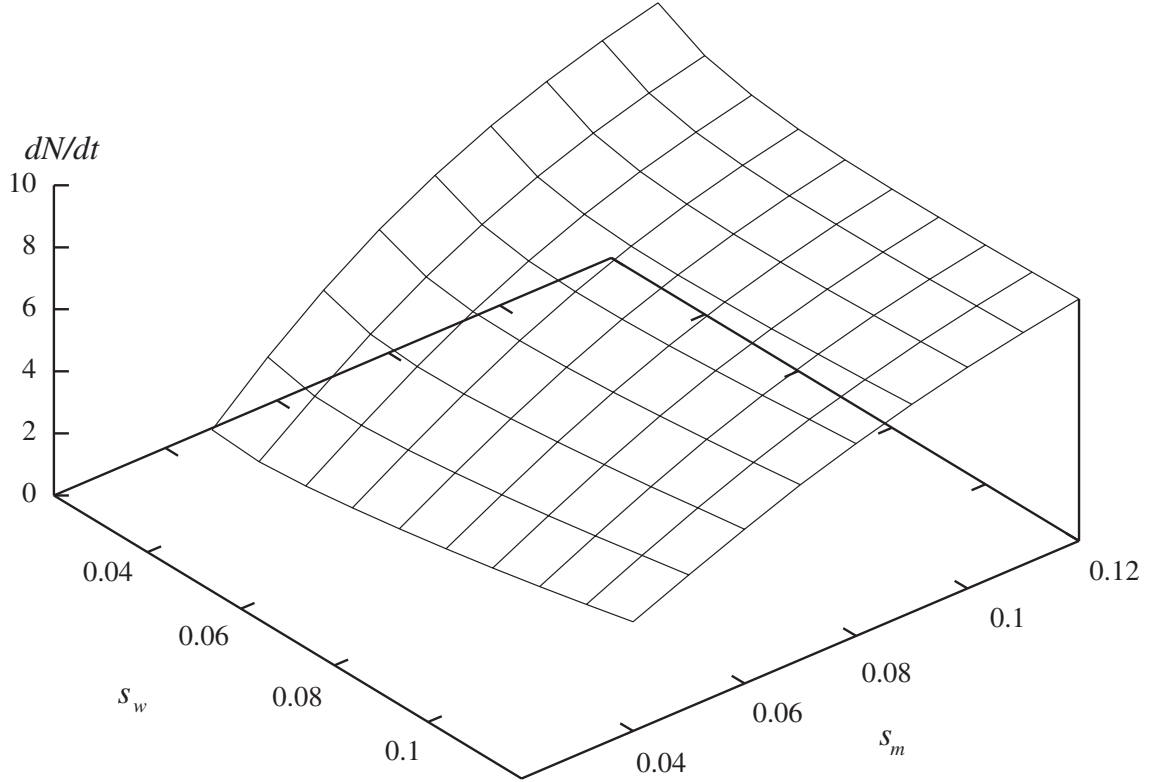


Figure 5. Rate of population increase at half the equilibrium density, as a function of s_m and s_w . Parameters b , d , and d' are held constant throughout with values as in Figure 1.

In the long term, equilibrium densities are strongly affected by both kernel parameters s_m and s_w (Figure 6a). These densities range from 0 to values much above the mean-field value of 200 and are closely related to the asymptotic spatial structure. The relationship can be seen from the asymptotic value of the second moment at the shortest displacement $C^*(0)$ in Figure 6b, which is roughly the mirror image of Figure 6a. The greater $\log C^*(0)$ is above 0, the more aggregated the asymptotic spatial pattern is; the lower $\log C^*(0)$ is below 0, the more overdispersed the pattern is (see Figure 2).

As would be expected, when s_m and s_w are both large, the equilibrium density is close to the mean-field value (Figure 6a). However, individually s_m and s_w have quite different effects on the equilibrium density. On the one hand, when s_m is kept small and s_w is increased, the equilibrium density tends towards that of the non-spatial logistic equation; this is because, even though spatial aggregation remains strong, individuals become blind to this structure as they interact over larger areas. On the other hand, when s_w is kept small and s_m is increased, the equilibrium density switches from values smaller than to values greater than those of the non-spatial logistic equation; this is because, for large enough s_m , the population is overdispersed in space, and individuals respond to the low density of neighbours in the immediate neighbourhood. The message is that wide dispersal at birth is not enough on its own to recover the mean-field dynamics closer to those of the mean field).

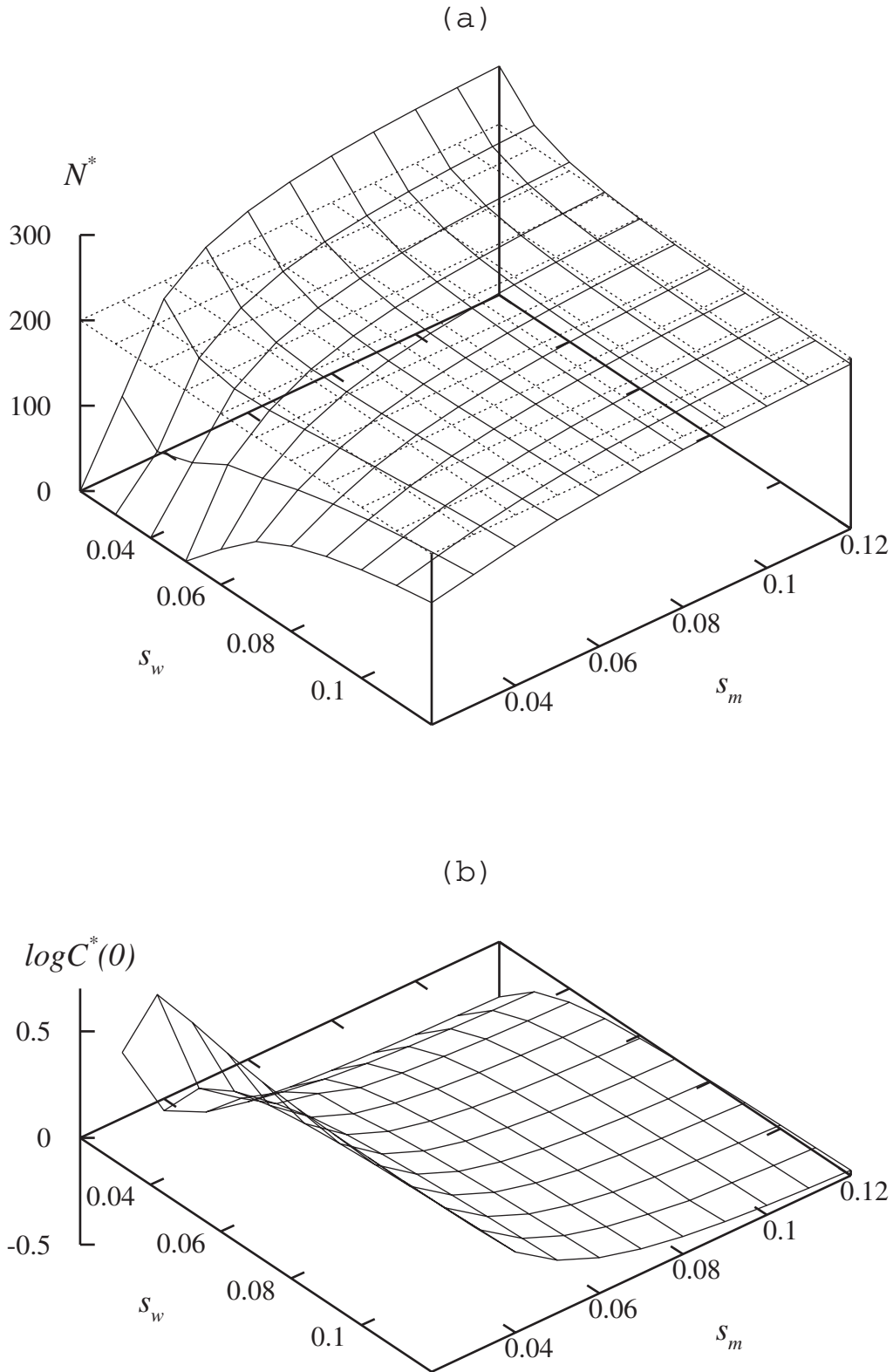


Figure 6. Asymptotic properties of the spatial logistic equation. (a) Equilibrium values N^* of the first moment for a range of values of s_m and s_w ; the dotted line shows the equilibrium value of the equivalent non-spatial logistic equation. (b) Asymptotic values $C^*(0)$ of the second radial moment at zero displacement; a value 1 (0 on log scale) indicates an absence of structure. Parameters b , d , and d' are held constant throughout with values as in Figure 1; integrations terminated when the change in N over an integration step 0.1 falls to 10^{-5} .

The shape of Figure 6a also matches predictions of the lattice pair approximation model of Ellner (2001: 443). Corresponding to Ellner's prediction 1a, the equilibrium density crosses from below to above the mean-field value, as s_m increases (for small enough s_w). Corresponding to his prediction 2, the equilibrium density crosses from above to below the mean-field value as s_w increases (for large enough s_m).

Discussion

The results demonstrate a wide range of dynamical behaviour in the spatial logistic equation and in the IBM from which it is derived, depending on the shape of the dispersal and interaction kernels. Populations differ in their transient dynamics, growing at different rates and having growth curves of different shapes. Populations also differ in their asymptotic states, with equilibrium densities ranging from zero to values much greater than the equilibrium density of the non-spatial logistic equation. Evidently, the effects of the spatial extension are fundamental. These results match and extend those of Bolker and Pacala (1997) on the spatial logistic equation, and are in keeping with many studies that point to the great importance of the spatial extension for ecological dynamics (e.g. Boerlijst and Hogeweg 1991, Hassell *et al.* 1991, 1994, Matsuda *et al.* 1992, Keeling *et al.* 1997, Levin *et al.* 1997, van Baalen and Rand 1997).

Evidently, a dynamical system of spatial moments, the spatial logistic equation, can provide a close approximation to average behaviour of the spatial moments of the IBM over a wide range of spatial structures. Although the new closure described above makes mathematical analysis difficult, there are several reasons why such analysis would be worth the effort, perhaps with the help of some simplifications. Quite apart from advantages for simulation, some basic questions are hard to answer from the IBM itself, and could be resolved by analysis of the equations of moment dynamics. For instance, is there a single asymptotic state, or are there alternative attractors that depend on the initial state? We have no evidence for the latter, but this cannot be ruled out from simulations alone. Can the asymptotic state(s) be characterised in terms of the parameters of the model, in particular the kernel parameters s_m and s_w ? In taking the mathematics forward, it needs to be remembered that the new closure for the third moment at present is only justified by the closeness of the fit of the spatial logistic equation to the IBM; a firmer foundation for choosing closures would be desirable. It should also be remembered that a dynamical system of first and second spatial moments can never be more than an approximation: if higher-order moments are important, the approximation will be poor.

Another reason why the mathematics of the spatial logistic equation is worth developing is that it brings the modelling of population growth a step closer to dispersal processes that matter and can be measured in real populations. Dispersal is obviously limited in many, if not most, plant and animal populations, and the results show how

important the shape of the dispersal kernel (of offspring) is for population growth. Dispersal kernels can be measured and indeed much effort has gone into their study in plant ecology (Harper 1977:33 *et seq.*) with the spatial spread of species in mind (e.g. Clark *et al.* 1998); yet we are not aware that the role of these kernels in transient and asymptotic densities of populations has been investigated. Our results suggest the dispersal kernel has a strong effect on the mean density at which population growth rate reaches its maximum (densities other than half the carrying capacity). Such an asymmetry is known from empirical studies, and has led to the θ -logistic class of models (Gilpin and Ayala 1973); the spatial extension here suggests a mechanistic foundation for these models.

The spatial logistic equation also points to the importance of interaction kernels in population growth. These are less well documented, although investigated by foresters interested in growth of wood volume (e.g. Biging and Dobbertin 1992, Soares and Tomé 1999); this study highlights the need for such information to tackle basic matters of population growth. A qualifier is that, in many plants at least, interactions depend on size as well as on distance; interaction kernels need eventually to be thought of as dynamic entities changing as competing individuals grow in size (Purves and Law 2002b). Size variation is not dealt with here, and there is some way to go to put dynamic kernels in place (but see Law *et al.* 2001).

As a practical matter, the importance of spatial structure has long been recognised in microbial population growth, to the extent that microbial cultures are routinely stirred. Pearsall and Bengry (1940) compared the growth of *Chlorella* cultures in darkness without shaking (where the cells settled at the bottom of the flasks), and with shaking twice a day. Population growth continued to higher densities in the presence of shaking, analogous to the difference between graphs (b) and (a) of Figure 1; they attributed this to local depletion of oxygen in the absence of shaking. Hansford and Humphrey (1966) noted that, in continuous culture of yeast at low dilution rates, cell yields can be increased by feeding the culture vessel from multiple points, and by mixing. Results of this kind point to the depressive effects of local aggregations on population growth.

A striking feature of the spatial logistic equation is the extinction of populations in which offspring and parents cannot escape from competition (Etheridge 2001) and, more generally, the slow growth of populations with strong aggregation. The width of the dispersal kernel relative to the interaction kernel is evidently critical for population growth. In the context of evolution, mutants with traits that cause greater dispersal escape more of the effects of competition and would be expected to replace residents with lower dispersal; this is consistent with evidence from observations and from simulation studies (Waser 1985, Ezoe 1998). Yet some formal analyses of diffusion rates show evolution of lower dispersal in a wide range of spatially heterogeneous environments (Dockery *et al.* 1998). These findings are less contradictory than might be supposed, be-

cause the model here deals with local spatial structure generated by the organisms themselves, whereas the diffusion models deal with spatial heterogeneity in the external environment (dispersing organisms then run the risk of ending up in places bad for survival or reproduction). In reality no doubt both aspects of spatial structure matter, and dispersal most likely evolves to an intermediate value dependent both on the innate tendency of organisms to develop spatial structure and also on the structure of the external environment. A formal framework incorporating both aspects of spatial structure would help understanding of how dispersal evolves and the levels of dispersal to be expected in nature.

Appendix

The dynamical system in Equations (4) and (5) has to be closed by replacing the third moment with some function of the first and second moments. Several functions have been suggested as possible closures (Bolker and Pacala 1997, Dieckmann and Law 2000). Here we evaluate these and another closure by comparing the numerical solutions they give in Equations (4) and (5) with the average of many realisations of the corresponding IBM. The spatial moments are all functions of time below but, for notational simplicity, we omit the time dependence.

The set of allowable closures is limited by two conditions that have to be satisfied (Dieckmann and Law 2000). First, in a population with individuals distributed at random, the closure should take the value N^3 , just as the second moment should be N^2 in these circumstances. Second, the rate of change over time of $C(\xi)$ should tend to $2N\dot{N}$ as ξ becomes large, which requires that $T(\xi, \xi') = N C(\xi')$ for large enough ξ (Dieckmann & Law 2000:439). These conditions are necessary, but not sufficient; a closure that satisfies the conditions above and used previously by Law and Dieckmann (2000a, b), is now known to generate an inconsistency in the spatial logistic equation (Hutson, personal communication). Condition 2 applies in the presence of births and deaths; when there are no births and deaths other kinds of closure are feasible (Murrell and Law 2000).

The closures below are called power-1, power-2 and power-3 according to whether they contain products of one, two or three second moments. The power-1 closure, which is equivalent to setting the third central moment to zero (Bolker and Pacala 1997), is

$$T_1(\xi, \xi') = N C(\xi) + N C(\xi') + N C(\xi' - \xi) - 2N^3. \quad (\text{A1})$$

The power-2 closure is

$$T_2(\xi, \xi') = \frac{1}{2} \left[\frac{C(\xi)C(\xi')}{N} + \frac{C(\xi)C(\xi' - \xi)}{N} + \frac{C(\xi')C(\xi' - \xi)}{N} - N^3 \right]. \quad (\text{A2})$$

The power-3 closure, which has been used in theoretical physics (Kirkwood 1935, Ziman 1979) and results from maximising the information content in the partition of the sample space (Grey 2001), is

$$T_3(\xi, \xi') = \frac{C(\xi)C(\xi')C(\xi' - \xi)}{N^3} \quad (\text{A3})$$

The closures can be thought of as giving increasing values of $T(\xi, \xi')$ close to the origin, in the sequence power-1, power-2, power-3.

In populations that grow with little spatial structure, all three closures give a pattern of population growth close to that of the non-spatial logistic equation. In populations

that develop regular spatial patterns, there are somewhat greater differences in population growth with these different closures. But the contrast between the closures is greatest when there is strong aggregation, as it is here that the third moment can deviate most from N^3 . For this reason, populations growing with strong spatial aggregation provide especially sensitive tests of closures; on this basis we use $s_m = s_w = 0.04$ to evaluate the closures below.

Figure 7 shows the spatial mean density over time obtained from the IBM (Figure 7a), together with the results of numerical integration of Equations (4) and (5) incorporating several closures for the third spatial moment. Growth of the first moment over time increases in the sequence of closures: power-1, power-2, power-3 (respectively Figure 7b, c, d). This sequence is to be expected because the value of the closure near the origin increases in the same order: the larger the value of the third moment near the origin, the larger are the negative terms (e) and (f) in Equation (5), the smaller the second moment is, the smaller the negative term is in Equation (4), and the larger the first moment is. It is clear that none of the closures provide a close approximation to the average of the stochastic realisations. The power-1 closure leads to a serious overestimate of the second moment at short displacements, and extinction of the population results (Figure 7b). Both the power-2 and the power-3 closures lead to an underestimate of the second moment at short distances, giving too great population growth, and too high an equilibrium density (Figure 7c, d).

Quite apart from dynamic considerations, we have found that the power-2 closure gives a good approximation to known third moments over quite a wide range of aggregated and overdispersed spatial patterns and, in particular, performs better than the other closures in the presence of spatial aggregation (Law *et al.* unpublished results). This motivates extending the power-2 closure above to a family of asymmetric power-2 closures that give different weights α, β, γ to the three corners that make up the triplet

$$T_4(\xi, \xi') = \frac{1}{\alpha + \gamma} \left[\frac{\alpha C(\xi)C(\xi')}{N} + \frac{\beta C(\xi) C(\xi' - \xi)}{N} + \frac{\gamma C(\xi')C(\xi' - \xi)}{N} - \beta N^3 \right]; \quad (\text{A4})$$

this family satisfies the necessary conditions for a valid closure given above. [The symmetric power-2 closure, Equation (A2), is obtained as $\alpha = \beta = \gamma = 1$.] Our numerical studies have shown that, by giving the first corner a weight about four times that of the others [see Equation (6)] dynamics close to those of the IBM are obtained (Figure 7e); this closure is therefore used for numerical integration in the text. In earlier studies

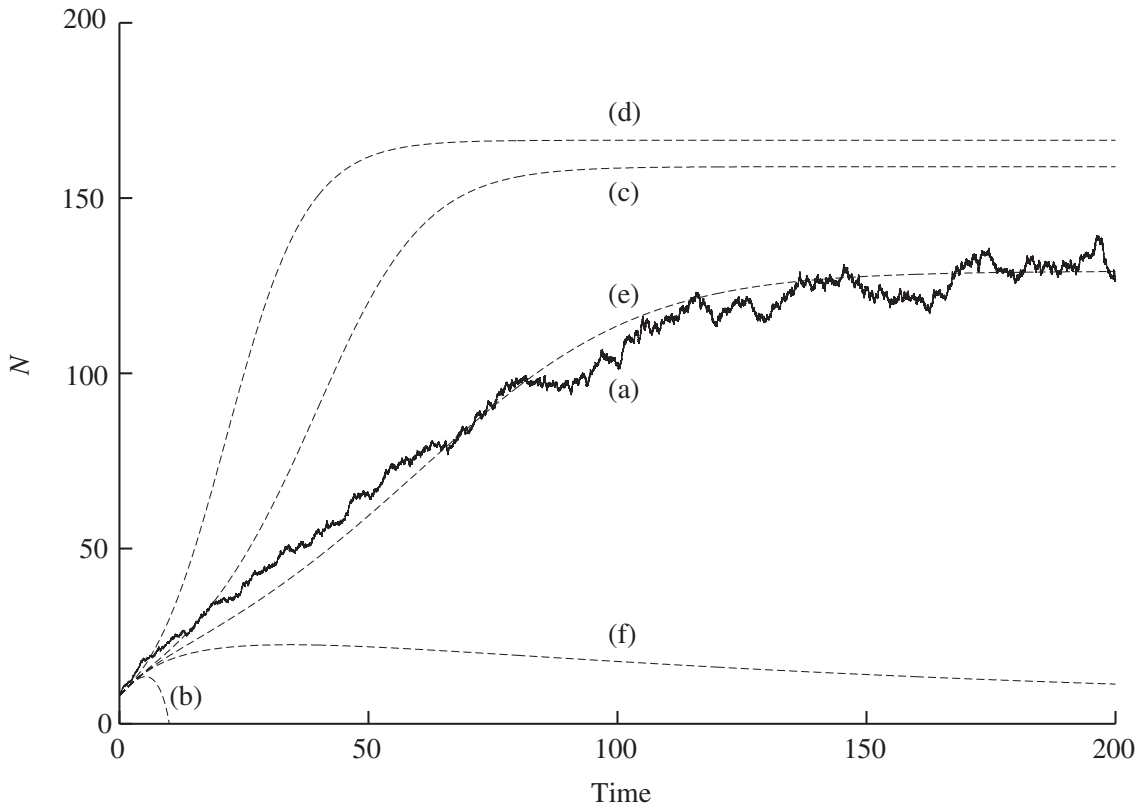


Figure 7. Numerical integrations of the spatial logistic equation with various closures. (a) Spatial mean density over time from the IBM (average of 20 realisations, against which the closures are evaluated); (b) symmetric power-1 closure; (c) symmetric power-2 closure; (d) symmetric power-3 closure; (e) asymmetric power-2 closure with $\alpha = 4$, $\beta = 1$, $\gamma = 1$; (f) asymmetric power-2 closure with $\alpha = 1$, $\beta = 0$, $\gamma = 0$. Parameter values: $b = 0.4$, $d = 0.2$, $d' = 0.001$, $s_m = 0.04$, $s_w = 0.04$.

(Law and Dieckmann 2000a, b), an extreme version was used ($\alpha = 1$, $\beta = \gamma = 0$); this is clearly not satisfactory for patterns with strong aggregation, such as the one used here (Figure 7f).

Although the asymmetric closure works well, two points should be borne in mind. First, in giving corners of the triplet different weights, a sixfold symmetry of the third moment is destroyed. The corners of the triplet are not interchangeable in the dynamical system, but the asymmetric power-2 closure should perhaps be seen as no more than a tool that permits computations, until this issue is resolved. Second the power-1 and power-2 closures contain a negative term that could lead to negative value under sufficiently strong overdispersion; this would be inconsistent with the fact that the third moment, being a product of densities, cannot take negative values.

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