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IIASA Interim Report
July 2002

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Interim Report **IR-02-040**

Causes and Effects of Small-Scale Spatial Structure in Plant Populations

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July 2002

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Abstract

Small-scale spatial structure is important in plant ecology. Plants interact primarily with their immediate neighbours and the view of the community as seen by an individual plant can be quite different from large-scale spatial average. We describe a spatial statistic that captures the plant's-eye view and use it to illustrate the strong spatial structure present in a grassland community. Many processes affect small-scale spatial stucture, including intraspecific competition, dispersal of propagules, interactions with other species and the spatial structure of the environment. Spatial structure in turn affects the the vital processes of growth, birth and death; the dynamics of plant communities thus involve a coupling of spatial structure and the vital processes. We describe recent work towards making this coupling explicit by means of individual-based models and the dynamics of spatial moments.

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Acknowledgments

We thank David Grey, Tomás Herben, Vivian Hutson, Hans Metz and Peter Lee for advice during the work towards this chapter, and English Nature and the Derbyshire Wildlife Trust for permission to use their nature reserves. The research was supported by a NERC studentship (DWP), a NERC/CASE studentship with the Central Science Laboratory MAFF (DJM), the International Institute for Applied Systems Analysis (Laxenburg, Austria), and the Wissenschaftskolleg zu Berlin.

Causes and Effects of Small-Scale Spatial Structure in Plant Populations

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1. Introduction

If plants in a community were located in space independently of one another, and if each small part of the space had the same probability of being occupied, the community would have no spatial structure. Such randomness is unusual. Plants in mesic environments are commonly clustered together in groups of conspecifics, and the spatial pattern of plants in arid environments can sometimes have the opposite property—a striking overdispersion of individuals (Cody 1986**)**. *Spatial structure* (a departure from a homogeneous Poisson process) is the norm.

The existence of spatial structure has profound implications for plant ecology because plants interact primarily with their close neighbours. The effects of neighbours of a plant are most evident above ground through shading, and are also felt below ground through the uptake of nutrients and water. Individuals outside the neighbourhood have relatively little effect on these processes—in particular, there is no reason to suppose that density averaged over some large spatial region, the so-called 'mean-field' assumption (Law *et al.* 2000), is of any significance (Mack & Harper 1977).

These points might seem too trivially obvious to mention were it not for the great difficulty plant ecologists have had in constructing a theory of population dynamics that holds them properly in place. Historically, plant population dynamics has taken its framework from animal ecology, together with the mean-field approximation widely used there. Yet this is not enough: somehow the information on local spatial structure, on which the growth of plants and ultimately their vital rates crucially depend, has to be accounted for. Without this, models at the theoretical core of plant ecology are dynamically insufficient (Lewontin 1974:8), and predictions about future states are liable to be seriously in error.

This chapter is concerned with small-scale spatial structure in plant communities, the readiness with which such structure is generated, how it can be built into plant-community dynamics, and the implications of such structure for plant population genetics. The thread that runs through all this is the need to replace the mean-field

assumption with what might be termed the 'plant's-eye view' (Turkington & Harper 1979; Mahdi & Law 1987) of the community. General interest in the spatial structure of plant communities goes back to the early days of plant ecology (Blackman 1935), but building the plant's-eye view into dynamical systems is a recent development.

2. Measuring the Plant's-Eye View of the Community

How can the plant's-eye view of the community be defined and measured? An appropriate measure must make use of the locations of individuals relative to one another, and a sensible starting point is a map showing the positions of individuals, or at least their presence and absence, at an appropriate spatial scale.

We suggest here a measure for a discrete spatial lattice, based on spatial covariance functions [see Condit *et al* (2000) and Law & Dieckmann (2000b) for an equivalent measure in continuous space]. To show how this is done, we use some maps of the presence and absence of species living in a flat alluvial meadow in the lower Derwent Valley National Nature Reserve near York, England (Purves unpublished data). The site is cut for hay in the early summer, then grazed regularly by sheep until flooding in the winter, and is species-poor, dominated by the grasses *Agrostis stolonifera*, *Holcus lanatus* and *Lolium perenne*. Maps of two of the species in a single quadrat are shown in Fig. 1a, b; the species are quite abundant, and it is not immediately obvious whether there is any spatial structure. Nonetheless, if the cells containing the plants are randomised (Fig. 1c, d), the resulting layouts appear less patchy, suggesting some spatial structure is present.

The plant's eye looks out at a neighbourhood surrounding the plant, rather than taking a global view of the mean density or cover ('global' here means the region covered by the whole map). One can think of concentric rings of increasing radius around a plant (Fig. 1b), a 'myopic' plant sensing only its very nearest neighbours, a less myopic one sensing the density further away. Near the plant, any local spatial structure causes departures from the global mean, giving a higher density of neighbours if there is aggregation, and a lower density if there is overdispersion. The neighbours may be conspecifics, but they can equally well be other species and ultimately every species can contribute to the neighbourhood.

Each plant has its own unique neighbourhood, and it is more helpful to have a summary statistic of the plant's-eye view averaged over the neighbourhoods of all individuals of a species in a given area. Stationarity of the spatial process needs to be assumed, as it does not make sense to think of an average of the neighbourhoods if the statistical properties of the map change from one location to another. Consider a grid of K cells, writing $p_i^{(x)}$ as the density of species i in cell with coordinates $x = (x_1, x_2)$ (density taking values 1 or 0 in Fig. 1). The mean density is given by

$$n_i = \frac{1}{K} \cdot \sum_x p_i^{(x)} \quad , \tag{1}$$

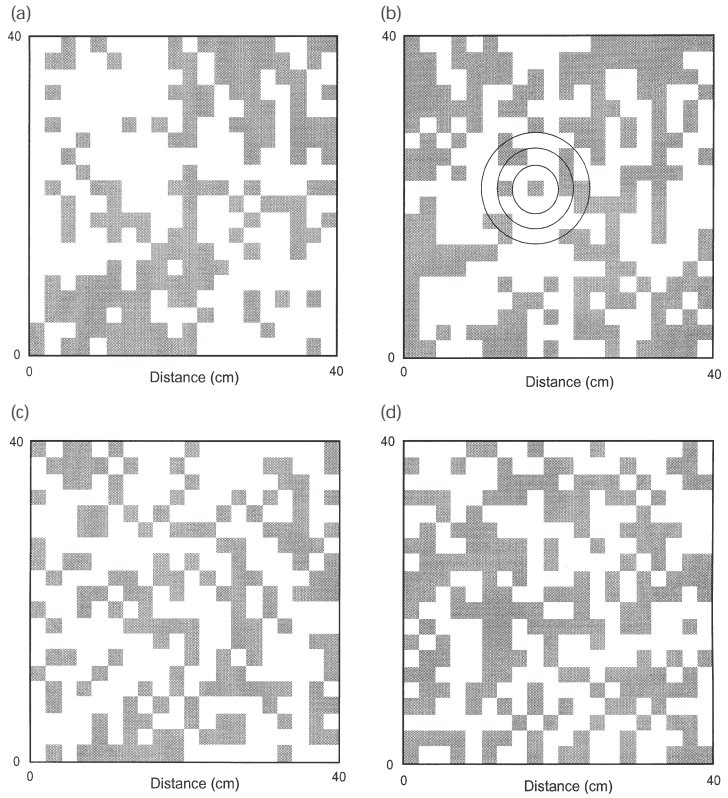


Figure 1. Maps showing presence (grey) and absence (white) of (a) *Agrostis stolonifera* and (b) *Lolium perenne* rooting in a grid of 2 x 2 cm cells measured in an alluvial meadow. Maps after randomisation of locations of (c) *A. stolonifera* and (d) *L. perenne.* The concentric rings around a plant in (b) are used to construct the plant's-eye view of the community.

and a statistic for the mean density of neighbours of species *j* displaced by a distance $\xi = (\xi_1, \xi_2)$ from individuals of *i* is

$$c_{ij\xi} = \frac{1}{|S_\xi|} \cdot \sum_{x \in S_\xi} p_i^{(x)} \cdot p_j^{(x+\xi)} , \qquad (2)$$

where $S_\xi = \{(x, x+\xi)\}$ is the set of pairs of cells with a displacement ξ, and $|S_\xi|$ is the number of such pairs and also allows for the finite size of the grid. The statistic can alternatively be measured in polar coordinates of radius *r* and angle ϕ (if there is no directionality, i.e. if the spatial process is isotropic, the radial dependence suffices). In statistical terms $c_{ij\xi}$ measures the spatial covariance with lag ξ, an auto-covariance for conspecific neighbours and a cross-covariance for neighbours of other species. Notice that $c_{ij\xi}$ is not a central moment because the cover is not expressed as a deviation from the means (n_i and n_j); the moment is chosen to be as simple as possible because we use it later as a state variable of a dynamical system. Various alternative statistics are to be found in the literature (Ripley 1981; Lotwick and Silverman 1982; Renshaw & Ford 1984; Burrough 1987).

Fig. 2 shows three covariance functions, each averaged over eight quadrats (like the one in Fig. 1), randomly located within a visually uniform region of the meadow. To display the functions, they are expressed in radial form (*L. perenne* is isotropic, but there is some anisotropy in *A. stolonifera*). The functions are normalised by dividing by

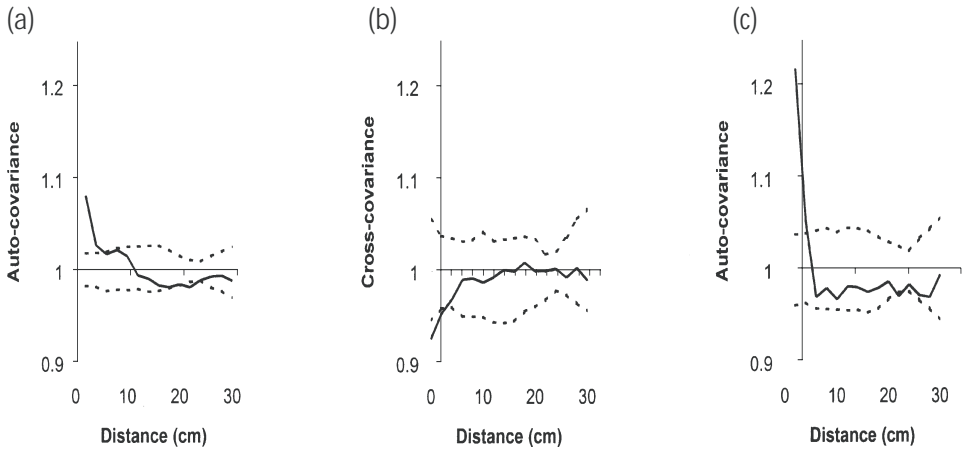


Figure 2. Spatial covariance functions computed for eight randomly positioned quadrates, including the one in Fig 1. (a) Auto-covariance function of *Agrostis stolonifera*, (b) cross-covariance function of *A. stolonifera* and *Lolium perenne*, (c) auto-covariance function of *L. perenne*. Continuous lines are values obtained from the data, and dashed lines are envelopes, showing the range within which 99% of the lines would lie under the assumption of randomness.

the value they would take in the absence of spatial structure, so that the functions are unity if spatial structure is absent; the normalising value is close to $n_i \cdot n_j$, but also allows for the finite size and boundaries of the quadrat. In both species, the auto-covariance functions are peaked at short distances, indicating some clumping of conspecifics, the clumps tending to be larger in *A. stolonifera* than in *L. perenne*, perhaps reflecting the stolon-forming habit of the former (regeneration from seed is relatively rare in mesic grasslands). The decline to around unity means that, as the neighbourhood becomes large, the auto-covariance function comes close to the mean-field value; thus, over the spatial scale investigated, structure is confined to a small neighbourhood. In contrast to the auto-covariance functions, the cross-covariance function between species is at a minimum at short distances, suggesting some spatial separation of the species.

Some variation in covariance functions would be expected simply as a matter of chance, and this needs to be distinguished from genuine spatial structure. This could be done in various ways (e.g. Lotwick & Silverman 1982; Coomes *et al* 1999); we use the following Monte-Carlo methods. For auto-covariances, the locations of cells containing the species are completely randomised, as illustrated in Fig 1c, d, and the auto-covariance recomputed. For cross-covariances, the spatial structure within species is held in place and the patterns of one species displaced by a random amount, wrapping the edges around on a torus (the displacement is constrained to be greater than the larger spatial structure within species, a distance of 10 cm here.). The randomisation is repeated a large number of times (we used 1000 replicates) to compute envelopes within which 99% of the functions would lie under the assumption of randomness, as shown in Fig. 2. The envelopes confirm the aggregation within species, the observed auto-covariance functions being outside or on the margin of the envelopes up to about 10 cm

in the case of *A. stolonifera* and 4 cm in the case of *L. perenne*. There is also some separation of the species at very short distances.

We suggest that spatial covariance functions of the kind described above provide a useful measure of the plant's-eye view of the neighbourhood. How far from the origin the plants sense their neighbourhoods depends on the context, as the distance is obviously affected by plant size. But it is clear in the meadow example that the composition of the immediate neighbourhood is far from the average: individuals find themselves in an environment in which conspecifics are over-represented and heterospecifics underrepresented when compared with the mean-field approximation.

3. Causes of Spatial Structure

There are many processes that contribute to small-scale spatial structure and result in a plant's-eye view that differs from the mean field.

3.1. Plant growth in even-aged monocultures

You need do no more than grow some plants together from uniform seed under uniform environmental conditions to break their initial symmetry and generate spatial structure. Those plants that emerge first are larger than later-emerging neighbours; those that have more space are larger before they come into contact with neighbours; larger plants have an advantage over their smaller neighbours in competition for limited resources. A well-documented size hierarchy develops (e.g. Obeid *et al* 1967; Ford 1975; Weiner 1985), often accompanied by an increased risk of death of small individuals (e.g. Mithen *et al* 1984).

Spatial structure in this kind of experiment becomes evident when the locations of large and small plants are measured. This was first demonstrated by Hozumi *et al* (1955) and Yoda *et al* (1957), growing corn in rows with 2 cm and 3 cm spacing between plants. After 16 days, they observed a negative auto-correlation of the fresh weight of a plant with its first, third and fifth neighbours, and a positive auto-correlation with the second, fourth and sixth; as one might expect, the auto-correlations changed with increasing age (and size) of the plants. Later, using a more elaborate design, Franco & Harper (1988) grew the annual *Kochia scoparia* in concentric arcs and found that plants in several odd-numbered arcs were shorter in height than those in even arcs; along a single arc, there was also a negative auto-correlation in weight of successive plants. It is thought that an arc of relatively large plants leads to suppression of the plants in the next arc, which releases the next arc from competition, and so on.

The close proximity of two plants may lead to the death of one or both, bringing about further change in spatial structure: aggregations break up, causing a shift towards overdispersion (Antonovics & Levin 1980). An experiment by Mithen *et al* (1984) on an even-aged stand of the annual plant *Lapsana communis* illustrates this; Fig. 3 shows the spatial arrangement of seedlings immediately after germination, distinguishing the plants destined to die from those still alive fifteen weeks later. The radial covariance functions (Fig. 3b-d) show strong aggregation among those that died (the function is peaked close to distance zero), although there are rather too few surviving individuals to draw conclusions about their spatial structure. The cross-covariance drops below unity

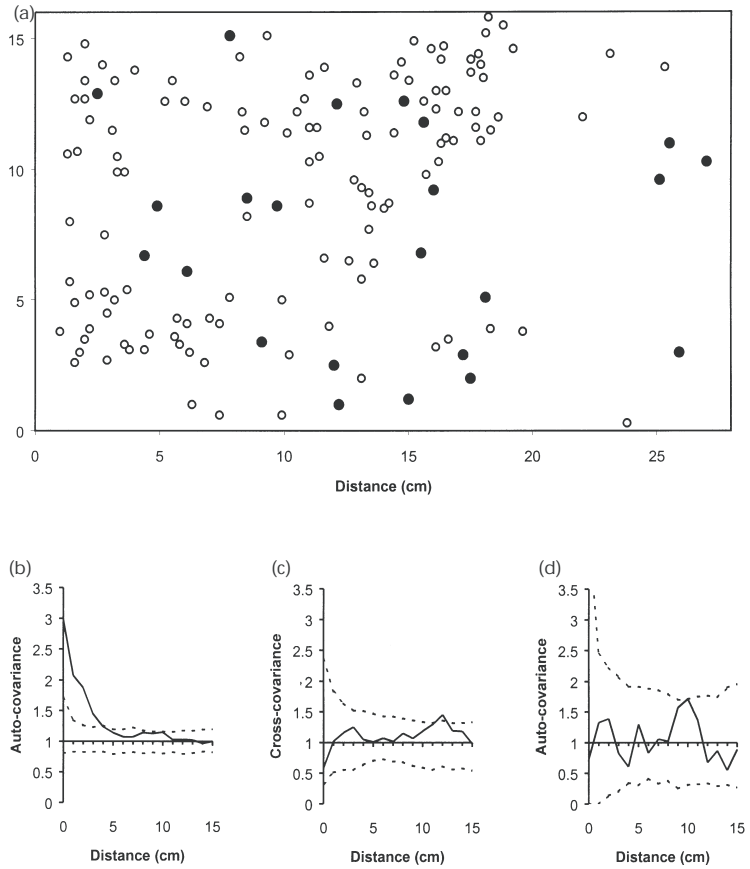


Figure 3. Map of seedlings of *Lapsana communis* at emergence, redrawn from Mithen *et al* (1984); those still alive 15 weeks later are filled circles, those that died are open circles. (b) Spatial auto-covariance function for plants that died; (c) cross-covariance function for surviving and dead plants; (d) auto-covariance function for plants that survived. Continuous lines are values obtained from the data, and dashed lines are envelopes showing the range within which 99% of the lines would lie under the assumption of randomness, calculated as in Fig. 2.

at short distances suggesting some separation of the survivors from those that died, but this is not statistically significant. A similar analysis was carried out by Kenkel (1988) on locations of dead and living individuals in a natural stand of jack pine *Pinus banksiana* following synchronous regeneration after a fire in the 1920s. This analysis also showed spatial aggregation of dead individuals and independence of the survivors from those that died, although in this case the survivors were themselves overdispersed.

3.2. Interaction kernels

At the heart of the structure that emerges in even-aged monocultures must lie some dependence of growth of an individual on its own state and the state of its neighbourhood. The function presumably depends on the size s and location x of the plant, and size s' and location x' of each neighbour, written here as the interaction kernel $w(s,s',x'-x)$. The overall effect of neighbours is the convolution product obtained from weighting the kernel by the density $p(x',s')$ of plants of size s' at x', and integrating over s' and x':

$$W(s,x,p) \quad = \int\int w(s,s',x'-x)\cdot\left[p(s',x') - \delta_s(s')\cdot\delta_x(x')\right] dx'\, ds'\,; \qquad (3)$$

The δs are Dirac delta functions introduced so that each plant is not counted as a neighbour of itself. Ultimately these neighbour-dependent effects on growth impact on reproductive output and risk of mortality: our understanding of plant population dynamics would be much improved if interaction kernels could be specified.

Attempts to characterise *w* have come primarily from theoretical reasoning (Benjamin & Hardwick 1986). The zone-of-influence model is particularly promising biologically (Wyszomirski 1983; Firbank & Watkinson 1985; Bonan 1988; Miller & Weiner 1989) although not altogether tractable mathematically. This model equates the size of a plant to a zone of influence around it: as plants grow, the zones of different plants meet, leading to competition in areas of overlap; competition can be symmetric, or asymmetric if the largest plant gets a disproportionate share of the resources (Weiner 1990).

Little is known about *w* from experimental studies. Silander & Pacala (1985) used an even-aged stand of *Arabidopsis thaliana* to search for a function of the neighbourhood of a plant that would minimise residual variation in its reproductive output. Simply counting the number of neighbours in a circle of 5 cm radius turned out to be as successful as a function incorporating distance to each neighbour. Nonetheless, a closer examination of the effect of distance, growing plants of *A. thaliana* with a single neighbour matched in size but increasingly distant, does show the expected quantitative dependence (Fig. 4).

3.3. Dispersal kernels

The neighbourhood interactions above apply once plants are rooted to the spot. Beyond the context of plant growth and mortality in even-aged monocultures, spatial structure is affected by the new locations that individuals come to occupy through reproduction and dispersal of propagules. Passive dispersal typically counteracts the breakdown of aggregations because most seeds fall close to the parent plant even if there are specific adaptations for dispersal (e.g. Harper 1977:33 et seq.); events such as occasional wind gusts that cause seeds to travel much farther (van Dorp *et al.*1996) would not normally change this. Seed dispersal by animals can, however, lead to movement over much longer distances (Isagi *et al* 2000; Ennos 2001).

Dispersal kernels have been studied more than interaction kernels because of the insight they give into two important phenomena. First is the size of the area over which individuals can be thought of coming from a panmictic unit, which depends both on pollen and seed dispersal (Crawford 1984; Meagher & Thompson 1987). Second are the paradoxically high rates of migration observed, for instance, in the northern movement of tree species after the last ice age (Clark *et al* 1998). Dispersal kernels can have fat tails with important consequences for rate of spread of populations (Nathan & Muller-Landau 2000). But, for small-scale spatial structure, the shape of the tail is less important than its shape at short distances, and the latter is easier to determine as it does not depend on rare events. Relatively simple functions may give enough information for this purpose; Greene and Johnson (1996), for instance, found that a negative

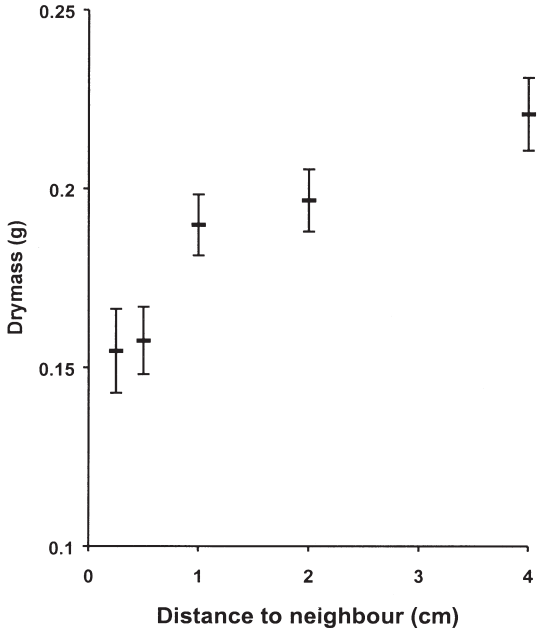


Figure 4. Mean (+/- standard error) plant dry mass after 32 days of *Arabidopsis thaliana,* grown from seed with a single neighbour placed at various distances. (Purves unpublished data)

exponential function gave a good approximation to the distance travelled by winged seeds from the edge of a forest into the surrounding landscape.

3.4. Environmental heterogeneity

Beneath the contributions to spatial structure caused by growth, birth and death, the abiotic environment leaves its own imprint. For example, Fig. 5a gives soil depth in a small area of species-rich calcareous grassland in the southern Pennines of England (Derbyshire Wildlife Trust Nature Reserve, Priestcliffe Lees). A spatial auto-covariance function for these data can be constructed, in the same way as for species-distribution data; Fig. 5b shows soil depths to be similar at the short spatial lags and somewhat different at intermediate lags; in addition, Fig 5c indicates some directionality (anisotropy). *Plantago lanceolata* (Fig. 5d) is associated with the deeper soils at lag zero, and *Thymus drucei* (Fig. 5f), with shallower ones; the spatial structure of these species thus reflects that of soil depth. One should however resist the temptation to think of coexistence of species in this diverse community as an outcome of niche separation on a soil-depth gradient, because there remain more than thirty other species, like *Sanguisorba minor* in Fig. 5e, distributed independently of depth; niche differentiation on this, and other axes thought to be important, is not sufficient to explain the high diversity (Mahdi *et al* 1989).

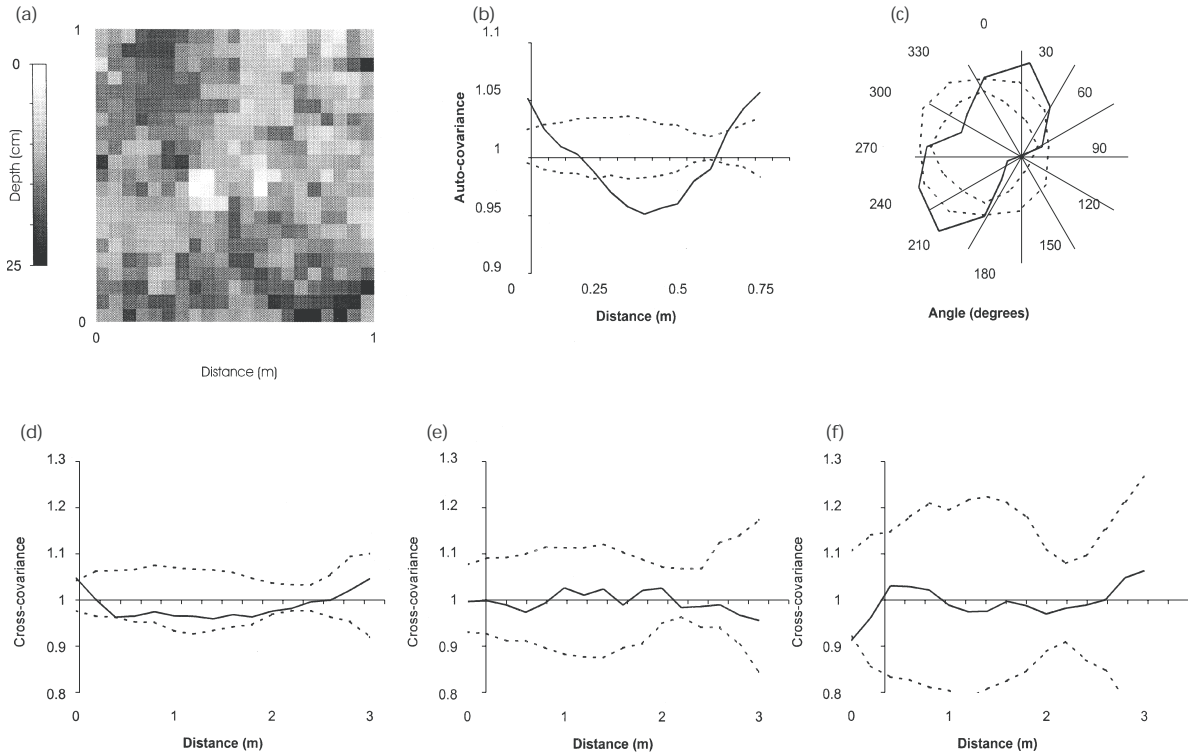


Figure 5. Spatial structure of soil depth and depth x species associations in a calcareous grassland. (a) Map of soil depth in an area 1 x 1 m, sampled at 5 cm intervals. (b) Radial auto-covariance function of soil depth. (c) Angular covariance function of soil depth; this is constructed in the same way as the radial auto-covariance, except that the lag is indexed by angle instead of by distance. Cross-covariance functions of soil depth with species from a larger grid of area 4 x 4 m sampled at 20 cm intervals, the species being: (d) *Plantago lanceolata,* (e) *Sanguisorba minor* and (f) *Thymus drucei* Continuous lines are values obtained from the data, and dashed lines are envelopes showing the range within which 99% of the lines would lie under the assumption of randomness, calculated as in Fig. 2. (Murrell unpublished data)

Obviously the biotic environment can also affect small-scale spatial structure, although, unlike the abiotic environment which tends to be fixed on the timescale of plant-community dynamics, the biotic environment has a spatial structure that itself changes over time. Well-known examples are the host-specific pathogens that cause mortality of tree seedlings close to the mother plant (e.g. Augspurger 1984; Packer & Clay 2000). Such pathogens counter the buildup of local aggregations in host populations, and have the potential to prevent single tree species from coming to dominate a community—the Janzen (1970), Connell (1971) hypothesis. However, other species in the vicinity are not inevitably negative in their effects (Stoll & Weiner 2000). Neighbouring plants can improve conditions for growth in various ways, including amelioration of extreme environmental conditions (Brooker & Callaghan 1998) such as high insolation in arid environments (Holzapfel & Mahall 1999) and cold in subarctic tundra (Carlsson & Callaghan 1991).

4. Dynamics of Spatial Structure

The plant's-eye view is evidently determined (1) by interactions among conspecifics that typically tend to break up aggregations of conspecifics, (2) by dispersal that tends to generate aggregations, (3) by spatial structure of the abiotic environment, and (4) by interactions with other species that generate or break up aggregations, depending on the kind of interaction. The examples above show repeatedly that the plant's-eye view can be far from the mean-field. Neither is the plant's-eye view fixed. As plants grow, give birth and die, there is continual flux in local spatial structure: the vital processes determine local spatial structure, and local spatial structure determines the vital processes. The challenge is to construct a theory of plant community dynamics that couples them together.

Here we describe some work towards this coupling. We develop the ideas in a continuous space because this is a good representation of the space that plants in reality occupy, and assume that edge effects are negligble by using periodic boundaries. [See Wissel (2000) for simulations in spatial lattices and Rand (1999) for pair approximation methods to describe the dynamics.]

4.1. Individual-based models (IBMs)

The approach favoured by ecologists when faced with complex spatial ecological processes is to simulate them as individual-based models (IBMs), in effect to compute realizations of the stochastic process (e.g. Cain *et al* 1995; Pacala *et al* 1996; Wissel 2000); this is the so-called Lagrangian approach (Turchin 1998:36). There is much to recommend this approach to the ecologist: it has appeal because it is algorithmic rather than mathematical; it allows much biological detail to be included, and gets closer than other approaches to the complexity of real ecological systems. We illustrate stochastic IBMs with two examples below.

The first example describes the growth of an even-aged monoculture of plants, in the absence of births and deaths. The IBM is specified by the state $p(s,x)$ at some point in time, comprising the size (mass) s and location x of each plant, together with the rate at which plants lose g^- and gain g^+ area

$$g^-(s) = \alpha \cdot s \tag{4a}$$

$$g^+(x,s,p) = \beta \cdot s^{2/3} \cdot \left[1 + W(s,x,p)\right]^{-1}. \tag{4b}$$

The terms $\alpha \cdot s$ and $\beta \cdot s^{2/3}$ describe size changes of an isolated plant: losses are assumed to be proportional to mass, and increments proportional to area; parameters α and β scale to rate of change of mass . The remaining term in Eq. (4b) reduces the rate of gain of area in the presence of neighbours, and thus depends on the spatial pattern; this uses the convolution product Eq. (3), with an interaction kernel

$$w(s,s',x'-x)\ \frac{\gamma\cdot s'^{2/3}}{(x'-x)^2}\cdot\begin{cases}1 & \text{if}\quad s'\geq s\\ 1-\varepsilon & \text{if}\quad s'<s\end{cases} \tag{4c}$$

(Thomas & Weiner 1989). The parameter γ denotes the overall strength of competition and ε determines competitive asymmetry (Weiner 1990), from symmetric (ε = 0) to completely asymmetric (ε = 1); the strength of competition attenuates with the square of the distance between the plants, and is proportional to the area of the neighbour.

Fig. 6a, b show the outcome of two realizations of the IBM, contrasting in the asymmetry of competion, the plants being positioned at the same locations at the start. Asymmetry has large effects on local spatial structure: neighboring plants show mutual inhibition under symmetric competition, whereas one plant gets an advantage over another under asymmetric competition. As a result, the spatial covariances of plant size develop differently over time (Fig. 6c, d). Under symmetric competition, adjacent individuals become similar in size, and deviations in the covariance from the mean field decrease nearly monotonically with increasing distance between plants. Under asymmetric competition, small plants tend to have large plants as neighbours at intermediate distances, in keeping with the results of experiments (Hozumi *et al* 1955; Yoda *et al* 1957; Franco & Harper 1988), and the covariance function develops a minimum.

The second example is a simple birth-death process of a single species in a spatial setting, taken from Law & Dieckmann (2000) [similar to IBMs used by Bolker & Pacala (1997) and Dieckmann *et al* [1997)]. The IBM is specified by the locations of plants $p(x)$, together with the death and birth rate for an individual at location *x*:

$$D(x,p) \quad = d \quad d' \cdot \int w(x'-x)\cdot\left[p(x')-\delta_x(x')\right]dx' \tag{5a}$$

$$B(x'-x)\ = b\cdot m(x'-x)\,. \tag{5b}$$

The death rate $D(x,p)$ contains an intrinsic death term *d*, and a neighbour-dependent term; the latter makes use of the interaction kernel $w(x'-x)$ (for simplicity now independent of size) to give each neighbour a weight according to its distance, and sums over all neighbours (the Dirac delta function δ excludes the target individual itself), finally scaling the overall effect of neighbours by d'. $B(x'-x)$ is the rate at which an individual at *x* gives rise to a new individual at x', assumed here to depend only on an intrinsic birth rate *b* and the dispersal kernel $m(x'-x)$.

Fig 7 shows the outcome of some realizations of the IBM. In Fig. 7a, the kernel parameters are set such that the neighbourhoods of interaction and dispersal are large, giving little spatial structure (Fig 7d); the population then settles slightly below the mean-field density of 200 in the unit area. Reducing the neighbourhoods of interaction and dispersal by the same amount emphasises the role of the dispersal kernel in generating aggregations (Fig. 7b, e). The plant's eye then perceives a crowded neighbourhood, and the population declines to a lower density (~140). A sufficiently big reduction in the interaction neighbourhood on its own has the consequence that two plants living close together are unlikely both to survive; the population thus becomes

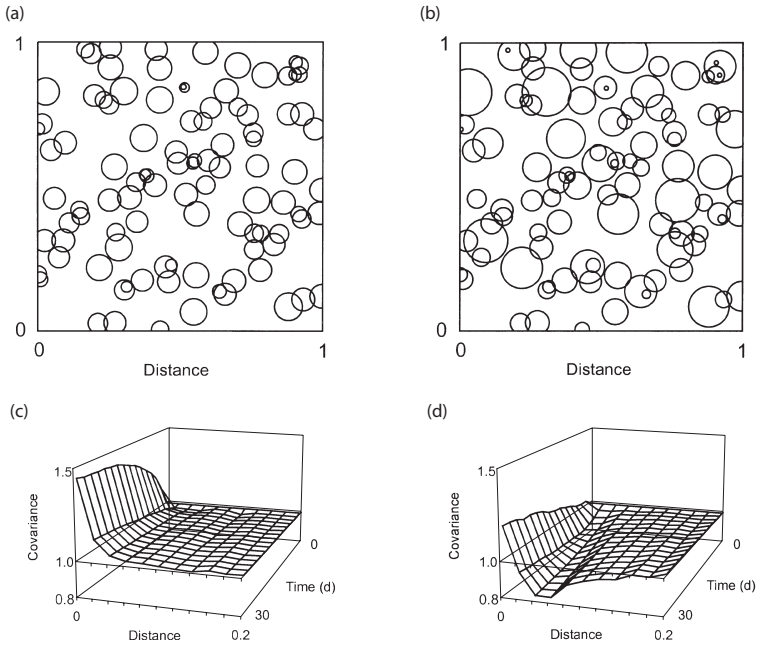


Figure 6 An IBM of growth of plants in an even-aged monoculture. At time 0, 100 individuals of mass 0.1 units are placed at random locations in an area of 70 × 70 units; individuals grow as shown in Eqs (4) depending on their current size and the size of neighbouring individuals with which they compete. (a) Size of individuals (area of circle proportional to mass $^{2}/_{3}$) after 32 days with symmetric competition (ε = 0); (b) size of individuals with asymmetric competition (ε = 0.9); locations of individuals are the same in the two realizations. Time series of the radial covariance of plant mass averaged over 50 realizations (c) with symmetric competition, and (d) with asymmetric competition. The radial moment is centralised by taking the deviation of plant mass from the mean plant mass at the current time. Other parameter values are α = 2.8, β = 14, γ = 4.1 x 10^{-4}, δ = 0.05.

over-dispersed at very short distances (Fig. 7c, f). To the plant's eye, the area is sparsely inhabited, and the population increases to a greater density (~270). Throughout these simulations *b*, *d* and *d′* are held constant; the changes in population density are caused entirely by the effects the kernels have on spatial structure. Evidently, even in this particularly simple ecological stochastic process (essentially a spatial, stochastic version of the logistic equation), the kernel parameters can lead to anything from a decline to low densities (some parameters can even cause rapid extinction), to densities much greater than the mean-field value. The spatial extension has fundamental effects on the dynamics.

4.2. Dynamics of spatial moments

Insightful though IBMs are, there are limits to what they can tell us about, for instance, the equilibrium states, attractors, and parameter dependencies of the dynamics. If you

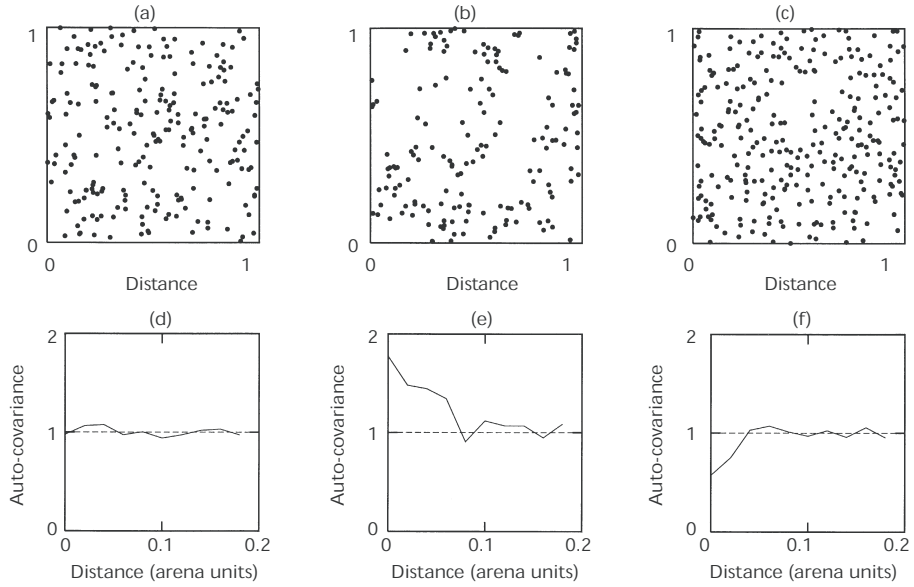


Figure 7. An IBM of growth of a single species population. At time 0, 200 individuals are randomly located in an arena of unit area; individuals die and give birth according to the rates shown in Eqs (5). Spatial patterns (a), (b), (c) depict the locations of individuals after 50 time units have elapsed; (d), (e), (f) give the corresponding auto-covariance functions. Gaussian kernels are used, truncated at a 3 x standard deviation (*sd*). The realizations differ in their kernel parameter values: (a) $sd_w = sd_m = 0.12$; (b) $sd_w = sd_m = 0.04$; (c) $sd_w = 0.02$, $sd_m = 0.12$; parameter values common to all realizations are: $b = 0.4$, $d = 0.2$, $d' = 0.001$.

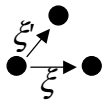
doubt this, consider how hard it would be to establish the main features of competition in the Lotka-Volterra model from simulations of IBMs. To gain deeper insights it helps to have dynamical systems that give good approximations to the IBMs. Recent research shows that dynamical systems of spatial moments can be derived from the stochastic processes, and in a sense these form a natural extension of the non-spatial dynamics used in ecology in the past. [The derivations are somewhat technical and are given elsewhere (Bolker & Pacala 1997; Pacala & Levin 1997; Bolker & Pacala 1999; Bolker *et al* 1999, 2000; Dieckmann & Law 2000; Murrell & Law 2000).] Here we concentrate on the general form of the equations and give an example to illustrate the ideas.

First some notation: We consider a multispecies community comprising a set of species $L = \{1,2,\mathrm{K}\ l\}$, living in a continuous, two-dimensional space of area A, large enough for edge effects to be negligible. The spatial moments are defined as:

$$N_i(p) = \frac{1}{A} \cdot \int p_i(x)\, dx \qquad \bullet \qquad (6a)$$

$$C_{ij}(\xi, p) = \frac{1}{A} \cdot \int p_i(x) \cdot \left[p_j(x+\xi) - \delta_{ij} \cdot \delta(\xi) \right] dx \qquad \bullet \xrightarrow{\xi} \bullet \qquad (6b)$$

$$T_{ijk}(\xi,\xi',p)=\frac{1}{A}\cdot\int p_i(x)\cdot\left[p_j(x+\xi)-\delta_{ij}\cdot\delta(\xi)\right]$$



$$\cdot\left[p_k(x+\xi')-\delta_{ik}\cdot\delta(\xi')\right]dx \qquad (6c)$$

where $p_i(x)$ is the density of plants of species *i* at *x*, and the δs are Dirac delta functions that remove self pairs. The diagram beside each equation tries to make clear the object being averaged across space; each circle represents a plant. Thus Eq. (6a) is the average density of single plants, the first spatial moment, and is a continuous version of Eq. (1). Eq. (6b) is the average density of pairs of plants displaced by ξ, the second spatial moment, a continuous version of Eq. (2); we take the second moment as measuring the plant's-eye view and normalise by dividing by $N_i(p)\cdot N_j(p)$ for graph plotting (which gives the second moment a value of unity if the plants are randomly dispersed). The hierarchy of moments can be continued: Eq. (6c) is the average density of triples of plants displaced by ξ and ξ', the third spatial moment, and so on.

Moment dynamics deal with the average change of the moments over time, the average being over the ensemble of stochastic realizations; we therefore remove the *p* argument, and introduce *t* to emphasise the dependence on time. For notational simplicity, we use the sets $N=\{N_i(t)\,|\,i\in L\}$, $C=\{C_{ij}(\xi,t)\,|\,i,j\in L\}$, $T=\{T_{ijk}(\xi,\xi',t)\,|\,i,j,k\in L\}$. In principle, a system of differential equations describing the rate of change of the spatial moments with respect to time can be constructed of the form:

$$\dot{N}_i(t)=F_i(N,C) \qquad \text{for all } i\in L \qquad (7a)$$

$$\dot{C}_{ij}(\xi,t)=F_{ij}(N,C,T) \qquad \text{for all } i,j\in L \qquad (7b)$$

$$\dot{T}_{ijk}(\xi,\xi',t)=F_{ijk}(N,C,T,\mathrm{K}) \qquad \text{for all } i,j,k\in L. \qquad (7c)$$

Eqs (7a) deal with the flux in average density of individuals, a familiar-enough concept in ecology. Less familiar are Eqs (7b): they describe the flux in density of pairs of individuals displaced by ξ, in effect accounting for changes in the second-order spatial structure caused by growth, birth and death of individuals. In other words, Eqs (7b) track the changing plant's-eye view (Sections 2 and 3). And Eqs (7a) and (7b) are just the start of a hierarchy of equations: (7c) describes the dynamics of density of triples, and so on.

Consider, for instance, the spatial version of the logistic equation (Law & Dieckmann 2000a); variations on this theme were given by Bolker & Pacala (1997), and Dieckmann *et al* (1997), with a detailed analysis of the model in the case of Bolker & Pacala (1997). The stochastic process in Eqs (5) gives dynamics of the first moment:

$$\dot{N}(t)=b\cdot N(t) \qquad \text{(a)} \qquad \bullet$$

$$-\,d\cdot N(t) \qquad \text{(b)} \qquad \circ$$

$$- d' \cdot \int w(\xi') \cdot C(\xi', t)\, d\xi' \qquad \text{(c)} \qquad \text{(8)}$$

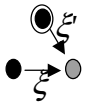
In case it is not intuitive what these contributions to flux of the first moment are, the diagrams on the right summarise the events, with the convention here and below that a grey circle represents birth of a new individual, an open circle a death, and a double circle a neighbour. Term (a) on the right-hand side is thus the contribution to the flux due to birth, (b) is the contribution due to intrinsic tendency to die, and (c) modifies the death rate due to interactions with other individuals in the vicinity. It is instructive to compare Eq. (8) with the familiar non-spatial (mean-field) logistic equation

$$\dot{N}(t) = b \cdot N(t) \;\; - d \cdot N(t) \;\; - d' \cdot N^2(t) \qquad ; \qquad \text{(9)}$$

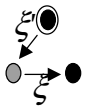
the only difference is that the density-dependent term N^2 is replaced by an integral weighting the plant's-eye view by the interaction kernel. In other words, the density-dependent effects in Eq. (8) are mediated by other plants in the neighbourhood, rather than by the average density; the dynamics of the first moment are now coupled to the second moment as in Eq. (7a).

Dynamics of the second moment are inevitably a good deal more more complicated than those of the first moment, because they deal with the flux in density of *pairs* of individuals displaced by ξ. From Eqs (5)

$$\dot{C}(\xi, t) \;\; = b \cdot \int m(\xi') \cdot C(-\xi + \xi', t) d\xi' \qquad \text{(a)}$$



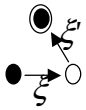
$$+ b \cdot \int m(\xi') \cdot C(\xi + \xi', t)\, d\xi' \qquad \text{(b)}$$



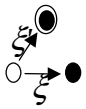
$$+ 2 \cdot b \cdot m(\xi) \cdot N(t) \qquad \text{(c) (d)}$$

$$- 2 \cdot d \cdot C(\xi, t) \qquad \text{(e) (f)}$$

$$- d' \cdot \int w(\xi') \cdot T(\xi, \xi + \xi', t) d\xi' \qquad \text{(g)}$$



$$- d' \cdot \int w(\xi') \cdot T(\xi, \xi', t)\, d\xi' \qquad \text{(h)}$$



$$- 2 \cdot d' \cdot w(\xi) \cdot C(\xi, t) \qquad \text{(i) (j)} \qquad \text{(10)}$$

This is less daunting than it might seem at first sight: each term still has a precise geometric interpretation, which we try to make intuitive in the corresponding diagram. Terms (a) and (b) describe the rate at which new pairs are formed due to births at a distance ξ' from the parent; the integration accounts for all locations of the parent, and makes use of the dispersal kernel of seeds $m(\xi')$. Terms (c) and (d) arise because one of the pair can itself be the parent. Terms (e) and (f) describe the intrinsic rate at which individuals die. Terms (g) and (h) modify the death rate due to neighbours located at a distance ξ', using the interaction kernel $w(\xi')$, the integration allowing for all individuals in the neighbourhood. Terms (i) and (j) allow for modifications to the death rate due to the other individual in the pair. Notice that all these terms come in groups of two because each kind of change applies to both individuals in the pair. Notice also that this equation has the general form of Eq (7b), depending on the first, second and third moments.

The extension from a single species to a two-species (or multispecies) community is straightforward. For two species, the dynamics of first and second moments, $N_1(t)$, $N_2(t)$, $C_{11}(\xi,t)$, $C_{12}(\xi,t)$, $C_{22}(\xi,t)$ keep track of local spatial structure both within and between species (Bolker & Pacala 1999; Law & Dieckmann 2000b). The extension to a spatially heterogeneous physical environment, such as that caused by the variation in soil depth in Fig. 5, also raises no further difficulties. Environmental heterogeneity can be treated as fixed on the timescale of population dynamics, but as having effects on local birth and death rates. Thus, for a single species (indexed 1) living in a heterogeneous environment (indexed 2), dynamics of $N_1(t)$, $C_{11}(\xi,t)$, $C_{12}(\xi,t)$ are used, the information about the environment entering through the cross-covariance. A version of this was given by Murrell & Law (2000) to describe the dynamics of movements of beetles in a complex ecological landscape, further simplified by the absence of births and deaths, with the result that the average density (first moment) could not change, leaving only the second moments $C_{11}(\xi,t)$, $C_{12}(\xi,t)$ as state variables.

4.3. Moment closures

It should be understood that Eqs (7) do not themselves form a closed dynamical system. The dynamics of the first moments depend on the second moments, the dynamics of the second moments depend on the third, and so on; the hierarchy of equations is coupled such that each depends on the next. To obtain a dynamical system, somehow the moment hierarchy has to be closed. Moment closures are unfamiliar in ecology, although the mean-field approximation, which has served ecology since the early part of the 20th century, can be thought of as a first-order closure with $C_{ij}(\xi,t)$ replaced by $N_i(t)\cdot N_j(t)$, leaving a dynamical system

$$\dot{N}_i(t) = F_i(N) \quad \text{for all } i \in L; \tag{11}$$

This can be seen, for instance, by comparing dynamics of the first moments in the spatial and non-spatial versions of the logistic equation, Eqs (8) and (9). The step plant ecology needs to make to hold the plant's-eye view in place is to replace the first-order closure with a second-order closure. This means replacing the third moment by some function of the first and second moments, to get a closed dynamical system of the form

$$\dot{N}_i(t) = F_i(N, C) \qquad \text{for all } i \in L \tag{12a}$$

$$\dot{C}_{ij}(\xi, t) = F_{ij}(N, C) \qquad \text{for all } i, j \in L\,. \tag{12b}$$

The choice of closure is an important research question that has yet to be fully resolved; Dieckmann & Law (2000) describe some closures and investigate their properties. To illustrate the use of a dynamical system to approximate the stochastic process, we use here a new power-2 closure (Murrell unpublished). Fig. 8 shows the fit between the first and second moments of the stochastic process and the moments obtained by integrating Eqs (8) and (10). The dynamical system captures some important features of the first and second moments, the density moving above or below the mean-field value of 200 given by the non-spatial logistic equation (Fig 8a, b). This comes about because the dynamical system keeps track of changes in the second moment, i.e. changes in the plant's-eye view. Corresponding to the aggregations that build up in the IBM in Fig 7b, the second moment of the dynamical system increases at short distances (Fig 8c), and this feeds back to the dynamics of the first moment (Eq. 8, term c). Where over-dispersion develops in the IBM (Fig 7c), the second moment of the dynamical system decreases at short distances (Fig. 8d), which again feeds back to the dynamics of the first moment.

We suggest that important effects of local spatial structure on populations can be dealt with by dynamical systems with second-order moment closures. These systems in effect introduce the dynamics of the plant's-eye view of the community, and eliminate the mean-field assumption that penetrates so deeply into ecological theory. But two notes of caution. First the success of the second-order closure depends on the absence of important higher-order spatial structure, and there are conditions under which it must fail as a satisfactory approximation. Second, there is still much to learn about appropriate moment closures, and it may be premature to go too deeply into analysis of the dynamical systems until issues about closures are resolved.

5. Local Spatial Structure in Population Genetics

The dynamical consequences of local spatial structure are potentially profound. This should not come as a surprise. Compare, for instance, the intricate feedbacks in the spatial version of the logistic equation Eqs (8) and (10) with the much simpler non-spatial version Eq. (9); it would be unrealistic to expect properties of a mean-field model in general to carry over to a spatially structured one. New phenomena are already emerging from spatial dynamics theory, such as the dependence of the equilibrium densities on the interaction and dispersal kernels shown above (see also Bolker & Pacala 1999; Rand 1999; Bolker *et al* 2000; Law & Dieckmann 2000b). It would be surprising if plant community dynamics in the field were not also contingent

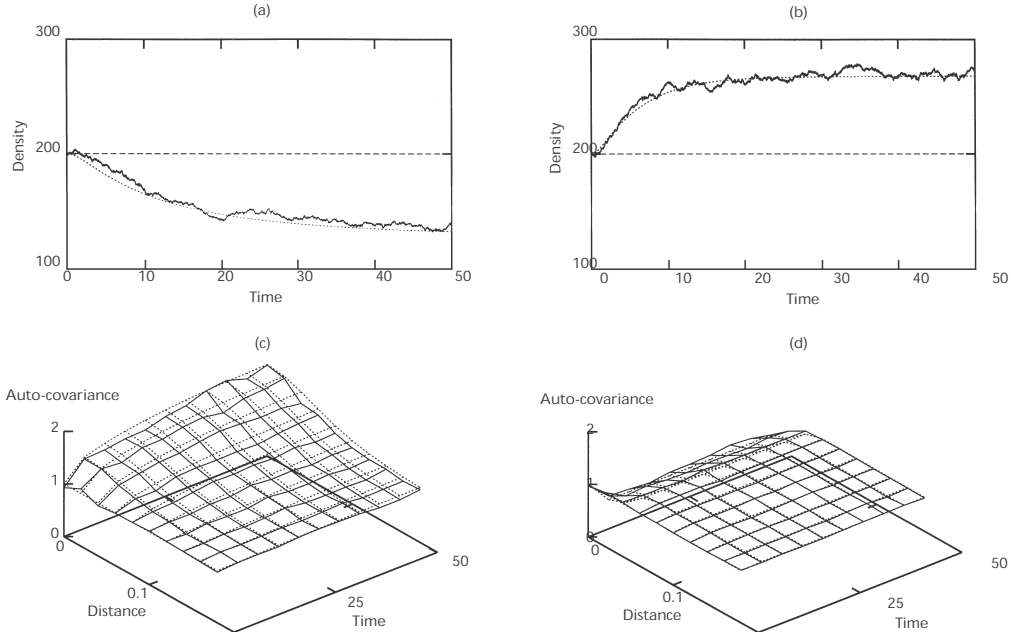


Figure 8 Comparison of first and second spatial moments of a single-species population over time, modelled as an IBM (continuous lines) and as a dynamical system (dotted lines). Simulations of the IBM start with 200 individuals randomly distributed over space, and periodic boundary conditions are used. Parameters are as in Fig. 7, with 'low density' values $sd_w = sd_m = 0.04$ in (a) and (c), and 'high density' values $sd_w = 0.02$, $sd_m = 0.12$ in (b) and (d). Moments of the IBM are computed from the spatial patterns and averaged over 20 realizations. Moments of the dynamical system are found from numerical integration of Eqs (8) and (10); distance units of the auto-covariances are as in Fig. 7. The dashed line in (a) and (b) gives the mean-field dynamics obtained from solving the logistic equation Eq. (9).

on local spatial structure. For example, in dune annual plants, aggregation of conspecifics and segregation of heterospecific individuals have major effects on competitive interactions (Rees *et al* 1996); in weeds, aggregation of conspecifics can promote persistence of species that are weaker competitors (Stoll & Prati 2001). Having said this, there are clearly circumstances under which mean-field models would be good approximations, for instance, if there is little spatial structure, or if individuals compete over large distances. Pacala and Silander (1990), for example, describe an experiment on two annual weed species with relatively weak spatial structure, where the mean-field approximation worked well.

What implications does local spatial structure have for plant population genetics? Broadly, this depends on the extent to which results from population genetics depend on the mean-field assumption.

Invasion of new mutants Consider, for instance, the fate of a rare mutant gene. When calculating the mutant's initial rate of increase in a well-mixed, mean-field system, one would assume a mutant frequency close to zero and a resident gene frequency close to one. However, in a spatially-structured system with limited seed dispersal, a local cluster of individuals carrying the mutant gene builds up, giving a frequency of mutant individuals in the neighbourhood far in excess of the mutant's mean frequency in the population. The initial growth of the mutant is then not settled by the dynamics of the first spatial moment alone: it also depends on the local spatial structure of the resident

and mutant, given above by the dynamics of both their first and second moments. Invasion criteria allowing for spatial structure have been suggested both for lattices (van Baalen & Rand 1998; Ferrière & Le Galliard 2000) and for continuous space (Bolker & Pacala 1999). It is evident from these studies that results from population genetics that depend on the rate of increase of mutants, such as protected polymorphisms and ESSs, can be altered by small-scale spatial structure.

Maintenance of polymorphism It is well known that spatial structure in the abiotic environment combined with limited movement can permit genetic polymorphism (Levene 1953). This was nicely demonstrated in cultures of *Pseudomonas fluorescens*, initially comprising a single genotype. Cultures without stirring (little movement) became polymorphic within three days and showed some spatial separation of the predominant phenotypes, whereas those with stirring (much movement) remained monomorphic (Rainey & Travasino 1998). Small-scale spatial structure generated by biotic processes increases the potential for genetic polymorphism still further. In a population with spatial aggregation, competition in small neighbourhoods can cause stronger inhibition of genes of common maternal ancestry at least (Kalisz *et al* 1999), promoting the coexistence of genes of different ancestries.

Evolution of dispersal Particularly interesting are mutants that affect local spatial structure itself (Olivieri 2001). Many phenotypic traits have effects on dispersal kernels, including plant growth form, inflorescence size, and mechanisms for pollen and seed dispersal, and genetic variation in such traits has been documented for many years (e.g. Clausen *et al* 1948; Aston & Bradshaw 1966). The capacity of such genes to increase when rare is very likely to be influenced by the small-scale spatial structures they generate (van Baalen & Rand 1998; Ferrière & Le Galliard 2000). Individuals carrying genes with low dispersal cluster more closely together than those with genes for greater dispersal, and are more adversely affected by their neighbours (also tending to carry the gene for low dispersal); Hamilton & May (1977) gave a schematic model to show the advantage of dispersal in these circumstances. On the other hand, in a spatially heterogeneous environment with small patches suitable for growth, poor dispersal could be a positive asset (Bolker & Pacala 1999). Models for evolution of dispersal that fail to keep track of local spatial structure could be misleading.

You have only to scratch the surface of plant population genetics to see the importance of local spatial structure of plants on the fate of genes; some of the most interesting predictions have in fact come from abandoning the mean-field assumption, for instance in the spread of populations (Antonovics *et al*). There already exists a large body of theory in population genetics for the dynamics in metapopulations on lattices with constant population size and no selection, stemming from the work of Wright and of Malécot (see review by Nagylaki 1989). A synthesis that brings together population-genetic and ecological theory, allowing for small-scale spatial structure, would be of much interest.

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