

A DYNAMICAL SYSTEM FOR NEIGHBORHOODS IN PLANT COMMUNITIES

RICHARD LAW^{1,3} AND ULF DIECKMANN²

¹*Department of Biology, University of York, York YO10 5YW, UK*

²*Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria*

Abstract. How should plant ecologists scale up from the fine-scale events affecting individual plants in small neighborhoods to the coarse-scale dynamics of plant communities? We give here a dynamical system, derived from an individual-based model, that captures the main effects of spatial structure. The individual-based model describes a multispecies plant community, living in a spatial domain, containing plants that (1) reproduce and die with rates that depend on other individuals in a specified neighborhood, and (2) move through seed dispersal and clonal growth. Over the course of time, substantial spatial structure can build up in such a community due to local interactions and dispersal. The dynamical system describes how the structure of local neighborhoods changes over time, using the first and second spatial moments of the individual-based model. We show, by means of an example of two competing species, that the dynamical system gives a close approximation to the behavior of the underlying individual-based model, and that the changes in local spatial structure as time progresses have fundamental effects on the dynamics.

Key words: *community dynamics; competition; competitive exclusion; dispersal; dynamical systems; individual-based models; moment dynamics; plant's-eye view; reproduction; seed dispersal; spatial ecology; stochastic processes.*

INTRODUCTION

Individual plants and animals are the natural starting point for much field-based ecology. The fate of an individual plant, for instance, is often contingent upon other plants in its immediate neighborhood (e.g., Pacala and Silander 1990, Tyler and D'Antonio 1995). Yet the questions that ecologists wish to address are often of an aggregate, macroscopic kind, such as what determines the abundance of species, and what determines the biodiversity of communities. Somehow ecologists need to scale up from these fine-scale (microscopic), neighborhood-dependent events to understand the coarse-scale (macroscopic) dynamics of coexistence and exclusion of species.

Plant ecologists use several methods for scaling up. In the past the favored method has been to assume that plants encounter one another in proportion to their average abundance over space, the so-called “mean-field” assumption. This leads to dynamical systems, relatively tractable from a mathematical point of view, from which much of theoretical ecology has been developed. But the small neighborhoods over which plants interact (Stoll and Weiner 2000), together with the nonrandom spatial structure typically found in plant communities (e.g., Mahdi and Law 1987), raise doubt as to whether the mean-field assumption is appropriate. An alternative, made popular by developments in computer technology, is to run computer simulations in an

explicit spatial setting following the fate of each individual (Crawley and May 1987, Cain et al. 1995, Pacala et al. 1996, Schwinning and Parsons 1996). Although this might seem to remove the need for scaling up altogether, there often remains a problem of how to obtain generic understanding of the macroscopic processes involved (Dieckmann et al. 2000).

How to scale up to the macroscopic dynamics from events acting on individuals in an explicit spatial setting remains a major challenge for ecologists (Levin et al. 1997, Tilman and Kareiva 1997, Dieckmann et al. 2000). This paper describes and tests a dynamical system for the macroscopic behavior of plant communities, derived from a spatially explicit model of individual plants. The paper builds on and extends a method involving the first two spatial moments of the individual-based model, sometimes referred to as the method of moments (Bolker and Pacala 1997, Dieckmann et al. 1997). The first spatial moments are simply the population densities of the species averaged over space, and the second moments measure the variability of densities over space. By incorporating the second spatial moments, the dynamical system tracks important aspects of the community's spatial structure and couples this structure to the dynamics of mean density, thereby allowing a feedback between the two. Such coupling is crucial in plant communities: the fate of individuals is affected by local spatial structure, and this in turn causes the spatial structure to change.

The paper extends earlier work on moment dynamics in several respects. (1) It introduces a simple function, the pair-density function, to describe the second-order

Manuscript received 26 May 1998; revised 20 April 1999; accepted 18 May 1999; final version received 19 July 1999.

³ E-mail: RL1@york.ac.uk

spatial structure. (2) It gives a closed dynamical system for the coupled dynamics of the first and second moments, for a plant community containing an arbitrary number of species, living explicitly in a continuous, two-dimensional space. (3) Putting the dynamical system side by side with an individual-based model of two competing plant species, it is shown that the outcome matches closely that of the individual-based model. The coupling of the first and second moments given by the dynamical system is fundamental to the outcome of competition. (4) The paper demonstrates that the terms involved in the dynamics of pair densities have precise geometric interpretations. (5) As a more technical footnote, the success of the dynamical system depends on a moment closure, which does not presuppose that the third central moment is negligible.

We begin by outlining a stochastic individual-based model of births, deaths, and movements in a continuous two-dimensional space, and we define first and second spatial moments as convenient measures for summarizing the emerging patterns. We then give and explain a dynamical system describing the behavior of the moments over the course of time. (The formal derivation of the dynamical system from the individual-based model is technical, and is given elsewhere [Dieckmann and Law 2000].) To keep the argument from becoming abstract, we illustrate each step in terms of a community comprising two competing plant species. Readers who wish to see what the dynamical system can do relative to the individual-based model, without going into the underlying formalism, should turn to the section labeled *Example*.

A STOCHASTIC BIRTH–DEATH–MOVEMENT PROCESS

Consider a plant community comprising n species in a large, continuous, two-dimensional space, with individuals located at points $x = (x_1, x_2)$ in this plane. (Individuals could be referenced by further properties such as age or size, but, for simplicity, we deal here only with species and location.) The spatial pattern of individuals of species i can be thought of as a function $p_i(x)$. Taking all n species together, the individuals form a multispecies spatial pattern at time t denoted by a vector of density functions $p(x) = (p_1(x), \dots, p_n(x))$; $p(x)$ thus describes the state of the system at time t . (We use Dirac-delta functions $\delta_x(x)$ to represent discrete individuals in these functions; for an individual at point x' , $\delta_x(x)$ is peaked at $x = x'$ and is 0 at all other points x [Dieckmann and Law 2000].) The process operates in continuous time in an environment with no spatial heterogeneity other than that generated by individuals themselves.

There are three primary stochastic events associated with an individual, namely, movement, death, and birth of offspring. Opportunities for movement of plants are obviously limited, but might arise through clonal growth; for the sake of completeness movement is

therefore included. For an individual of species i , located at point x in a pattern $p(x)$, we write the probability per unit time of movement to location x' as

$$M_i(x, x', p) = m_i(x' - x). \quad (1)$$

In other words, movement depends only on the intrinsic tendency for individuals of species i to move and on the distance moved $x' - x$. (More complicated dependencies could, in principle, be introduced.)

An individual of species i , located at point x in a pattern $p(x)$, has a probability per unit time of death:

$$D_i(x, p) = d_i + \sum_j \left[d_{ij} \int w_{ij}^{(d)}(x' - x) \times [p_j(x') - \delta_{ij} \times \delta_x(x')] dx' \right]. \quad (2)$$

The first term, given by the parameter d_i , is a neighbor-independent component of death, and is common to all individuals of species i . The term inside the summation describes how the death rate in species i depends on individuals of species j in the neighborhood of location x . The function $w_{ij}^{(d)}(x' - x)$ weights the effect of a neighbor of species j at x' according to its distance from x , the superscript d indicating that the weight applies to deaths; this function is multiplied by the density $p_j(x')$ of j at location x' . Essentially the integral adds up the contribution of each neighbor of species j , making allowance through the weighting function for the distance between individual j at location x' and individual i at x . The integrated expression is multiplied by a parameter d_{ij} , making the interaction species specific. It is easily forgotten that the individual of species i at location x cannot itself be a member of its neighborhood; the term $\delta_{ij} \times \delta_x(x')$ comprising the Kronecker delta δ_{ij} multiplied by the Dirac delta-function $\delta_x(x')$ subtracts this individual from the integrated expression (the Kronecker delta δ_{ij} takes value 1 when $i = j$, and 0 otherwise).

An individual of species i , located at point x in a pattern $p(x)$, has a probability per unit time of giving birth to an individual at location x' :

$$B_i(x, x', p) = \left(b_i + \sum_j \left[b_{ij} \int w_{ij}^{(b)}(x'' - x) \times [p_j(x'') - \delta_{ij} \times \delta_x(x'')] dx'' \right] \right) \times m_i^{(b)}(x' - x). \quad (3)$$

In most respects this birth term has the same structure as the death term (Eq. 2). The b_i and b_{ij} are parameters

TABLE 1. Nonzero parameters used in defining a community of two competing species.

State	Parameter	Value for species i	
		$i = 1$	$i = 2$
Death	d_i	0.2	0.2
	d_{i1}	0.001	0.002
	d_{i2}	0.0005	0.001
	$r_{i1}^{(d)}$	0.12	0.12
	$r_{i2}^{(d)}$	0.12	0.12
	$s_{i1}^{(d)}$	0.03	0.03
	$s_{i2}^{(d)}$	0.03	0.03
Birth	b_i	0.4	0.4
	$r_i^{(bm)}$	0.12	0.5
	$s_i^{(bm)}$	0.03	0.2

Note: Parameters are defined in *A stochastic birth-death-movement process*.

for neighbor-independent and neighbor-dependent births, respectively, and $w_{ij}^{(b)}(x'' - x)$ is a function for weighting the effect of neighbors, the superscript b indicating that the weight applies to birth. The main difference from Expression 2 is that there is dispersal at birth $m_i^{(b)}(x' - x)$, statistically independent of the production of offspring, which moves the offspring to a location x' with probability density $m_i^{(b)}(x' - x)$, the superscript b indicating that dispersal takes place at birth.

The probabilities per unit time above define a stochastic individual-based model that changes the spatial pattern of the community from one state $p(x)$ to another state $p'(x)$. While it may seem that Expressions 2 and 3 are rather intricate, it would not be easy to write general expressions for a species-specific neighborhood dependence with less information. The derivation of the equations for dynamics of the moments proceeds simply with the information above; the specific shapes taken by the functions m_i , $w_{ij}^{(d)}$, $w_{ij}^{(b)}$, $m_i^{(b)}$ are immaterial. The most important assumption in Expressions 2 and 3 is that births and deaths depend linearly on the local densities of neighbors; this assumption could, however, be removed for small departures from linearity by means of a Taylor approximation.

As an example, we consider a plant community comprising two species, with parameters as in Table 1. Movement is assumed to take place only through seed dispersal $m_i^{(b)}(x' - x)$; the location of each individual becomes fixed at the time of germination, as a result of which the function $m_i(x' - x) = 0$. We also assume for simplicity that neighborhood dependence operates only through deaths, so $b_{ij} = 0$. The species differ in two ways. (1) The first species is a stronger competitor, and interactions are set in such a way that species 1 would replace species 2 in the absence of any spatial effects. (2) Seeds of the second species can disperse farther (Fig. 1). In an explicitly spatial system, greater dispersal may help species 2 to avoid intraspecific competition, because offspring are more

likely to escape from the neighborhoods of their parents, and this in turn could affect the outcome of competition between the species. Communities with this kind of trade-off between competitive ability and dispersal have been much studied because of their potential to lead to coexistence of species (Skellam 1951, Hastings 1980, Crawley and May 1987, Tilman 1994, Dytham 1995).

Specifically, the dispersal properties of the species in the community are as follows. Seeds of species i move a random distance up to a maximum radius $r_i^{(bm)}$ relative to the parent. The direction is a random variable with a uniform probability density function, and the distance is a random variable with a normal probability density function, peaked at zero and having a standard deviation $s_i^{(bm)}$ determining its width; the normal distribution is truncated at $r_i^{(bm)}$, and normalized so that its integral is one. In other words, the distance r is drawn from a probability density function $1/z \times \exp[-r^2/(2 \times s_i^{(bm)2})]$, where $r \leq r_i^{(bm)}$, and z is the normalization constant.

Apart from the difference in competitive ability and seed dispersal, the species are ecologically equivalent; in particular they have the same functions and param-

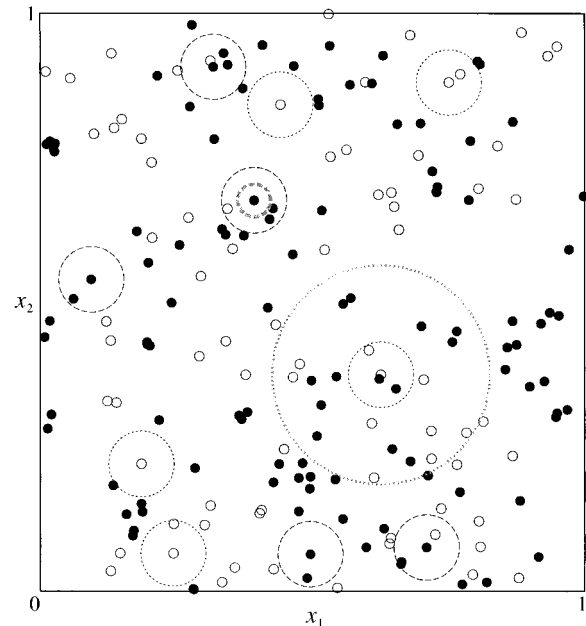


FIG. 1. A spatial pattern of two plant species showing neighborhoods of dispersal and interaction. The axes x_1 and x_2 are the spatial coordinates and are scaled to cover the range 0 to 1. Small circles mark points at which individuals are located; these are filled for species 1, and open for species 2. Larger dashed circles are neighborhoods for individuals of species 1; dotted circles are neighborhoods for species 2. Thick discontinuous boundaries are dispersal neighborhoods, with radii $s_i^{(bm)}$. Thin discontinuous boundaries are interaction neighborhoods of five individuals of each species, with radii $2 \times s_{ij}^{(d)}$. Parameter values are as in Table 1.

eters for neighborhood dependence of deaths. We assume that the effect of a neighbor on the chance of death of an individual is a normal function of the neighbor's distance, truncated at a radius $r_{ij}^{(d)}$, with a standard deviation $s_{ij}^{(d)}$ measuring how slowly the neighbor's effect diminishes with distance.

Fig. 1 shows a random sample of interaction neighborhoods of each species and illustrates why these neighborhoods are important. In the spatial pattern shown, species 1 is aggregated and segregated from species 2. Individuals of species 1 thus tend to live in a community locally dominated by conspecifics, at a density rather higher than the global average. Species 2, on the other hand, lives in a community in which the local density of conspecifics is close to the global average and in which the local density of species 1 is rather low. On the average, the species have a somewhat different "plant's-eye view" of the community (Turkington and Harper 1979, Mahdi and Law 1987). This affects the risks of mortality, which together with seed dispersal, affects the subsequent spatial structure; the new spatial structure affects the risks of mortality, and so on.

Evidently there is an intricate interplay between the spatial structure and the events affecting individuals over the course of time. The outcome of this is not immediately obvious, but some understanding can be gained from running a realization of the individual-based model (here with periodic boundaries), illustrated by two snapshots in Fig. 2. At time 0, 200 individuals of each species are distributed at random across the space. This density is markedly greater than the community can support, and substantial mortality occurs during the first five time units. By time 5, the spatial pattern (that used in Fig. 1) has developed a substantial amount of structure. Species 1, which has less dispersal, shows much more aggregation than does species 2; moreover, the species are not usually found together because, where they do so, species 1 tends to eliminate species 2.

FIRST AND SECOND SPATIAL MOMENTS OF THE INDIVIDUAL-BASED MODEL

The spatial patterns that develop during realizations of an individual-based model have their own intrinsic interest. But it is far from straightforward to characterize the major properties of the model simply by looking at the patterns. What is needed are statistics that capture its most important spatial features. The first and second spatial moments of $p(x)$ suggest themselves as obvious contenders. The first moment $N_i(p)$ of a pattern p ,

$$N_i(p) = \frac{1}{A} \int p_i(x) dx \quad (4)$$

is simply the average density of species i across a space of area A . As a second moment $C_{ij}(\xi, p)$, we use a

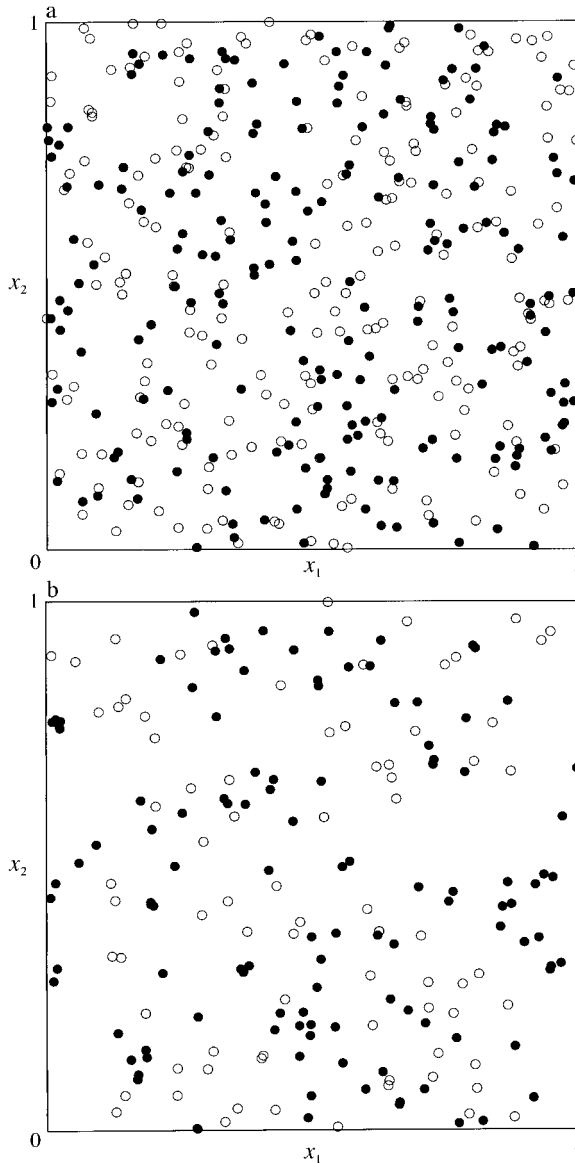


FIG. 2. Examples of spatial patterns of two competing plant species generated as a realization of the individual-based model described in the text using parameter values in Table 1. Axes are as defined in Fig. 1. (a) Time zero, which corresponds to a random initial distribution of 200 individuals of each species. (b) Pattern after five units of continuous time have elapsed, showing the spatial structure generated by interactions and dispersal. Filled circles are locations of individuals of species 1; open circles are locations of individuals of species 2.

product of pairs of densities for a spatial pattern $p(x)$:

$$C_{ij}(\xi, p) = \frac{1}{A} \int p_i(x) \times [p_j(x + \xi) - \delta_{ij} \times \delta(\xi)] dx. \quad (5)$$

This comprises a product of the density of individuals of species i and those of j at a distance $\xi = (\xi_1, \xi_2)$

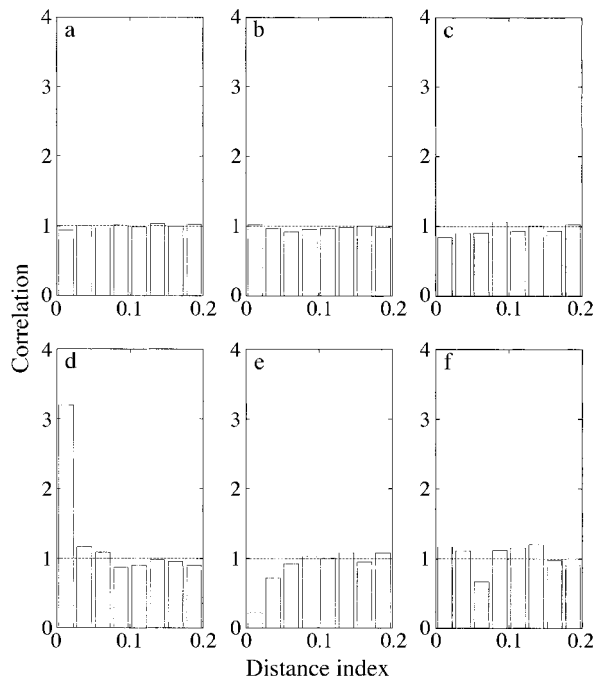


FIG. 3. Examples of spatial correlation functions computed for the spatial patterns in Fig. 2. The graphs in the first row are the correlations at time 0: (a) autocorrelation of species 1, (b) cross-correlation of species 1 and 2, (c) autocorrelation of species 2. Graphs (d), (e), and (f) in the second row are the corresponding correlations at time 5. The distance scale is the same as that in Fig. 1.

from i , averaged across a region of area A . The second moment is related to a spatial covariance, but is not a central moment, because the densities are not expressed as deviations from the means $N_i(p)$. (We use this non-central moment in preference to the central one, because this makes the equations for the moment dynamics simpler later on.) The term $\delta_{ij} \times \delta(\xi)$ is subtracted to remove a spurious term arising from a self pair at $i = j$ and $\xi = (0, 0)$, which Expression 5 would otherwise contain. Notice that the second moment is a function of the distance ξ of j from i , and needs to be thought of as a function describing a surface; we refer to it as an autocorrelation function when $i = j$, and as a cross-correlation function when $i \neq j$. When we show results about second moments below, we normalize the moment by dividing by the product $N_i(p) \times N_j(p)$ and refer to the moment as a spatial correlation function. Values of this function greater than one then indicate aggregation of individuals of species i and j , and values less than one indicate that these individuals are spatially segregated.

It is easiest to see the information carried in the second moment by examining its shape when calculated for some explicit spatial patterns. We have therefore computed the shape of the second moments for the spatial patterns in Fig. 2, and these are given in Fig. 3. The individual-based model is isotropic, and

this means that the pair densities depend only on the distances that separate the pairs, and not on the direction from i to j . In these circumstances, a spatial correlation has a similar shape in every direction from the origin, and we replace it by the radial correlation for the purpose of illustration. (The radial correlation is obtained by integrating the spatial correlation function over the angle around the circle.)

At time 0 (Fig. 3a, b, c), the correlation functions are close to unity at all distances, due to the random locations at which individuals were placed at the start (Fig. 2a). By time 5, however, substantial spatial structure has developed. Species 1, in keeping with its tendency to occur in small clumps, has a large autocorrelation close to the origin (Fig. 3d), but the correlation diminishes with distance, because spatial structure is localized. The autocorrelation function of species 2 is much flatter because dispersal at the time of reproduction is so much greater in this species (Fig. 3f). The spatial segregation of species 1 and 2 is evident in the small values of the crosscorrelation between the species close to the origin (Fig. 3e).

The spatial patterns in Fig. 2 come from a single realization of the underlying individual-based model. If we “reshake the dice” and run the process again, the spatial patterns that emerge are different. Repeated often enough, one can think of a probability density function $P(p)$ for the spatial pattern $p(x)$ at time t , arising from the individual-based model. To extract the generic features of the model, one needs the averages of the first and second moments across the ensemble of realizations, given by

$$N_i = \int P(p) \times N_i(p) dp \quad (6)$$

$$C_{ij}(\xi) = \int P(p) \times C_{ij}(\xi, p) dp \quad (7)$$

where dp means that the integration is over the space of functions p . The purpose of the next section is to give a dynamical system that describes the behavior of these moments Eqs. 6 and 7 over time.

Before giving the dynamical system, a third spatial moment needs to be introduced. Eventually this will not be present in the dynamical system, but it appears at an intermediate stage. We define the third moment, for a spatial pattern $p(x)$, as

$$\begin{aligned} T_{ijk}(\xi, \xi', p) &= \frac{1}{A} \int \{ p_i(x) \times [p_j(x + \xi) - \delta_{ij} \times \delta(\xi)] \\ &\quad \times [p_k(x + \xi') - \delta_{ik} \times \delta(\xi')] \\ &\quad - \delta_{jk} \times \delta(\xi - \xi')] \} dx. \end{aligned} \quad (8)$$

This is a natural extension of the second moment. It is essentially a triplet density, the product of the density of individuals of species i , times the density of indi-

viduals of j at distance ξ from i , times the density of individuals of k at distance ξ' from i , averaged across a region of area A . The delta terms are introduced as before to remove products arising from self pairs. The average of the third moment across the ensemble of realizations of an individual-based model is given by

$$T_{ijk}(\xi, \xi') = \int P(p) \times T_{ijk}(\xi, \xi', p) dp. \quad (9)$$

A DYNAMICAL SYSTEM FOR THE FIRST AND SECOND MOMENTS

The method of moments attempts to describe the dynamics of the moments in Eqs. 6 and 7 as a system of differential equations. The rates of change of the first moments are readily obtained by differentiating Eqs. 6 with respect to time, giving

$$\begin{aligned} \frac{d}{dt}N_i &= (b_i - d_i) \times N_i + \sum_j b_{ij} \times W_{ij}^{(b)} \\ &\quad - \sum_j d_{ij} \times W_{ij}^{(d)} \end{aligned} \quad (10)$$

where

$$\begin{aligned} W_{ij}^{(b)} &= \int w_{ij}^{(b)}(\xi') \times C_{ij}(\xi') d\xi' \quad \text{and} \\ W_{ij}^{(d)} &= \int w_{ij}^{(d)}(\xi') \times C_{ij}(\xi') d\xi'. \end{aligned}$$

The expressions $W_{ij}^{(b)}$, $W_{ij}^{(d)}$ make the metaphor of a "plant's-eye view" of the community (Turkington and Harper 1979) precise and formal. Each expression comprises the pair density at a distance ξ' weighted by the distance of j from i , and integrated over all distances; the weighting depends on the identity of the neighboring species and whether the event associated with the target individual is a birth or death. As the spatial structure of the community changes over time, so does the "plant's-eye view" as given by $W_{ij}^{(b)}$, $W_{ij}^{(d)}$. Thus $W_{ij}^{(b)}$ and $W_{ij}^{(d)}$ play a crucial role in coupling the dynamics of the first moment to the second-order spatial structure of the community. In this sense the method of moments can be said to provide a formal dynamical system for changes in neighborhoods of plant communities.

Although Eqs. 10 may seem unfamiliar at first sight, the well-known Lotka-Volterra equations are a limiting case as neighborhood size is made large. With $W_{ij}^{(b)}$ and $W_{ij}^{(d)}$ equal to $N_i \times N_j$, Eqs. 10 give

$$\frac{d}{dt}N_i = N_i \times \left(b_i - d_i + \sum_j (b_{ij} - d_{ij}) \times N_j \right). \quad (11)$$

Eqs. 11 assume that individuals encounter one another in proportion to their average abundance over space—the "mean-field" assumption, equivalent to assuming that spatial structure has no effect on the dynamics. The reason why the Lotka-Volterra equations emerge

is that the birth and death rates were made linearly dependent on neighborhood in defining the individual-based model above.

The dynamics of the second moments (Eqs. 7) can be thought of as keeping track of the flux in pairs of individuals of species i and j (pair densities), where j is a distance ξ from i . To account for all components of this flux is basically a matter of careful bookkeeping, but, because there are many terms, the right-hand sides of the differential equations 12 below are correspondingly somewhat complex. (In fact there are 10 types of event, for each type involving i , with an equivalent event involving j .)

The flux of the second moment is obtained by differentiating Eqs. 7 with respect to time. For clarity, we consider separately the contributions to the flux due to movements (at times other than birth), deaths and births, and some correction terms that keep track of self pairs:

$$\begin{aligned} \frac{d}{dt}C_{ij}(\xi) &= (\text{Movements}) + (\text{Deaths}) + (\text{Births}) \\ &\quad + (\text{Corrections}). \end{aligned} \quad (12)$$

Each term on the right-hand side of Eqs. 12 has a precise geometric meaning as a gain or loss of a pair ij , where j is a distance ξ from i . The geometry is shown in Fig. 4, and it will help understanding to keep this geometry in mind when looking at the components of Eqs. 12 below.

Movement of individuals at times other than birth can both create pairs at a distance ξ and cause them to disappear:

$$(\text{Movements}) = + \int m_i(\xi'') \times C_{ij}(\xi + \xi'') d\xi'' \quad (12.1)$$

$$+ \int m_j(\xi'') \times C_{ji}(-\xi + \xi'') d\xi'' \quad (12.2)$$

$$- |m_i| \times C_{ij}(\xi) \quad (12.3)$$

$$- |m_j| \times C_{ji}(-\xi). \quad (12.4)$$

Terms 12.1 and 12.2 are positive contributions to $C_{ij}(\xi)$. In term 12.1 an individual of i starts at a location such that j is a distance $\xi + \xi''$ from i and moves by an amount ξ'' , so that j is a distance ξ from i after this movement; the integration is needed to cover the full range of starting points ξ'' . Expression 12.2 is the corresponding term for species j . The term 12.3 is a negative contribution to $C_{ij}(\xi)$ that comes about from the loss of pairs at a distance ξ when movement of an individual of species i occurs and j is a distance ξ from i before i moves; the term $|m_i|$ is the total probability per unit time of movement ($|m_i| = \int m_i(\xi'') d\xi''$). Expression 12.4 is the corresponding term for species j .

The death terms always cause pairs to be lost, but this can happen both in a manner which is independent of the neighborhood, and in a manner dependent on the neighborhood:

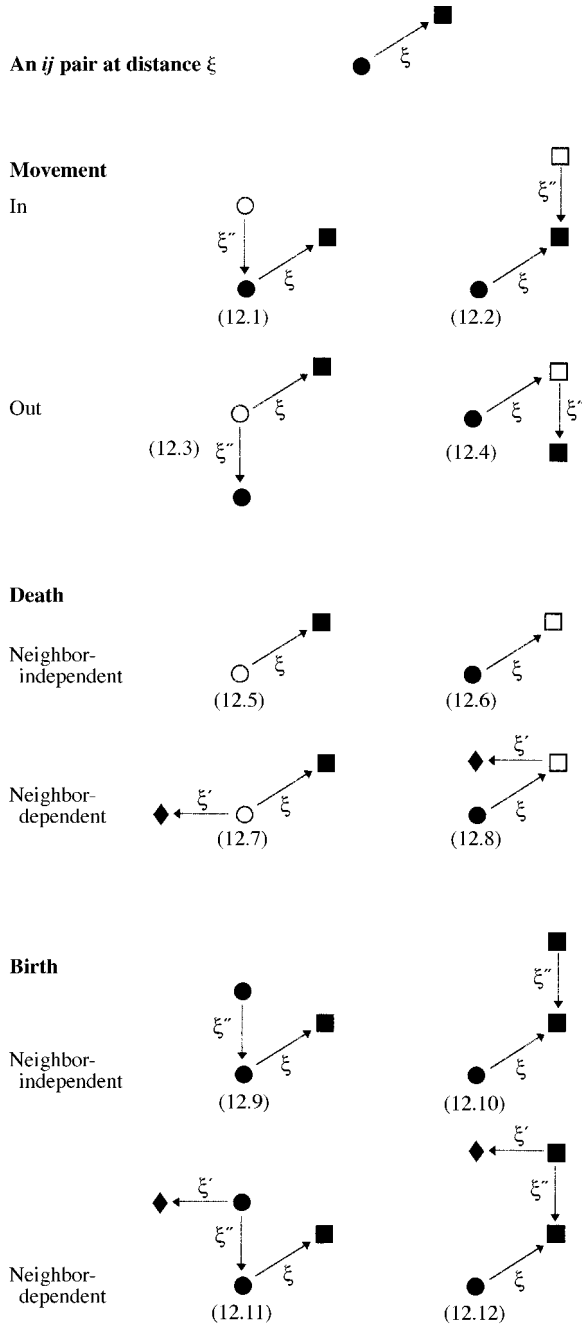


FIG. 4. Geometry of components of flux of the second spatial moment in Eq. 12. At the top is a pair of individuals ij of species i and j , with j at a distance ξ from i ; this pair can be created or destroyed by the events shown below in species i (first column) and j (second column). Circles represent individuals of species i , squares represent individuals of j , and diamonds represent those of k ; arrows are the vectors ξ , ξ' , and ξ'' used in the text; numbers denote terms on the right-hand side of Eq. 12. An open symbol indicates a location at which an individual is no longer present once the event has taken place.

$$(\text{Deaths}) = -d_i \times C_{ij}(\xi) \quad (12.5)$$

$$-d_j \times C_{ji}(-\xi) \quad (12.6)$$

$$- \sum_k d_{ik} \int w_{ik}^{(d)}(\xi') \times T_{ijk}(\xi, \xi') d\xi' \quad (12.7)$$

$$- \sum_k d_{jk} \int w_{jk}^{(d)}(\xi') \times T_{jik}(-\xi, \xi') d\xi'. \quad (12.8)$$

The neighborhood-independent terms 12.5 and 12.6 are straightforward, the ij pair being destroyed either by the death of i or by death of j . The neighborhood-dependent term 12.7 is more intricate because death is affected by a neighbor k of the ij pair. For this the third spatial moment $T_{ijk}(\xi, \xi')$ is needed, in other words the spatial density of triplets, comprising: (1) i , (2) j at a distance ξ from i , and (3) k at a distance ξ' from i . The integral is needed to sum over all individuals of k in the neighborhood of i . The term 12.8 is the corresponding neighborhood-dependent death term for species j .

The birth terms always bring new pairs into existence; like the death terms, births can occur in a manner independent of the neighborhood, or dependent on the neighborhood:

$$(\text{Births}) = +b_i \times \int m_i^{(b)}(\xi'') \times C_{ij}(\xi + \xi'') d\xi'' \quad (12.9)$$

$$+b_j \times \int m_j^{(b)}(\xi'') \times C_{ji}(-\xi + \xi'') d\xi'' \quad (12.10)$$

$$+ \sum_k b_{ik} \times \int w_{ik}^{(b)}(\xi') \times \int m_i^{(b)}(\xi'') \times T_{ijk}(\xi + \xi'', \xi') d\xi'' d\xi' \quad (12.11)$$

$$+ \sum_k b_{jk} \times \int w_{jk}^{(b)}(\xi') \times \int m_j^{(b)}(\xi'') \times T_{jik}(-\xi + \xi'', \xi') d\xi'' d\xi'. \quad (12.12)$$

The complication in this case is that newborn individuals disperse. In the case of neighborhood-independent births of i (Expression 12.9), we start with a parent of species i such that j is a distance $\xi + \xi''$ from the parent; the seed of i disperses a distance ξ'' relative to its parent, thereby forming a new pair such that j is a distance ξ from the seedling. The integration accounts for all the positions of the i parent from which this process could start. Expression 12.10 is the equivalent neighborhood-independent birth term for species j . The neighborhood-dependent term 12.11 has to allow for the effect of neighbors k on the births by the parent i and, like the death term, this requires the third spatial moment, here

$T_{ijk}(\xi + \xi'', \xi')$. The first integral sums over all individuals k in the neighborhood, and the second integral accounts for all the seed dispersal. Term 12.12 is the corresponding neighborhood-dependent term of species j .

The remaining eight terms correct for effects that were omitted from the third moment due to the elimination of self pairs:

(Corrections)

$$= -d_{ij} \times w_{ij}^{(d)}(\xi) \times C_{ij}(\xi) \quad (12.13)$$

$$-d_{ji} \times w_{ji}^{(d)}(-\xi) \times C_{ji}(-\xi) \quad (12.14)$$

$$+ \delta_{ij} \times m_i^{(b)}(-\xi) \times b_i \times N_i \quad (12.15)$$

$$+ \delta_{ji} \times m_j^{(b)}(\xi) \times b_j \times N_j \quad (12.16)$$

$$+ \delta_{ij} \times m_i^{(b)}(-\xi) \times \sum_k b_{ik} \times \int w_{ik}^{(b)}(\xi') \times C_{ik}(\xi') d\xi' \quad (12.17)$$

$$+ \delta_{ji} \times m_j^{(b)}(\xi) \times \sum_k b_{jk} \times \int w_{jk}^{(b)}(\xi') \times C_{jk}(\xi') d\xi' \quad (12.18)$$

$$+ b_{ij} \int w_{ij}^{(b)}(\xi + \xi'') \times m_i^{(b)}(\xi'') \times C_{ij}(\xi + \xi'') d\xi'' \quad (12.19)$$

$$+ b_{ji} \int w_{ji}^{(b)}(-\xi + \xi'') \times m_j^{(b)}(\xi'') \times C_{ji}(-\xi + \xi'') d\xi''. \quad (12.20)$$

Expression 12.13 is the contribution that j itself makes to the neighborhood-dependent death of i , and Expression 12.14 is the corresponding term for species j . The term 12.15 adds in pairs that are created between a parent of i and its offspring, when the newborn individual comes to be at a distance $-\xi$ from its parent, with Expression 12.16 being the corresponding term for species j . There is also an effect of k on this birth event given in Expression 12.17 and 12.18. Finally, Expression 12.19 (respectively 12.20) adds in the effect that j (respectively i) itself has on the neighborhood dependence of births in species i (respectively j). This completes the right-hand side for the dynamics of the second moment. We have in place a formal derivation for Eqs. 10 and 12; this is somewhat technical and will be published elsewhere (Dieckmann and Law 2000).

Notice that Eqs. 10 and 12 do not yet constitute a closed dynamical system because Eqs. 12 contain terms 12.7, 12.8, 12.11, and 12.12, depending on the third spatial moment. The set of equations has to be closed by replacing the third moment with an expression based on the first and second moments (Bolker and Pacala 1997, Dieckmann and Law 2000). The idea of a moment closure is not a familiar one in ecology, but it is implied by ecological models such as Eqs. 11 that ignore spatial

structure and replace the second moment in Eqs. 10 by the product of two first moments. Here we close the hierarchy of moments at order two instead of at order one, replacing the third moments in Eqs. 12 by

$$T_{ijk}(\xi, \xi') = \frac{C_{ij}(\xi) \times C_{ik}(\xi')}{N_i}. \quad (13)$$

We have chosen this closure for several reasons. It satisfies two checks on consistency, (1) recovering the dynamics of the first moment as the distance between pairs becomes large, and (2) recovering the dynamics of the first moment when the second moments are replaced by the products of first moments (mean densities) and interaction neighborhoods are made large. Other closures can be constructed that satisfy these checks, but the dynamics using closure 13 fit much better to stochastic processes we have investigated than do the dynamics using three other closures that we have also studied (Dieckmann and Law 2000). Closure 13 is different from the one that would be obtained by assuming that the third central moment is zero: the latter does not give a good fit when population density becomes low.

EXAMPLE

How good an approximation to the individual-based model is the macroscopic dynamical system in Eqs. 10 and 12? To answer this question, the population densities predicted by the dynamical system can be put alongside some realizations of the individual-based model. Here we examine the approximation for the community of two competing plant species with parameter values given in Table 1. Notice that Eqs. 12 are simplified by virtue of the assumptions made earlier: (1) that movement occurs only through seed dispersal, and (2) that neighbors affect only the probability of death. These assumptions leave half the number of terms on the right-hand side of Eqs. 12, namely, 12.5 to 12.10, and 12.13 to 12.16. We assume that, at time 0, individuals are randomly distributed in the plane.

First consider the dynamical behavior familiar from the Lotka-Volterra competition Eqs. 11; these are in effect the mean-field dynamics predicted by the first moments taken on their own. Here spatial structure is not taken into account, and the phase portrait suggests that species 1, the stronger competitor, should eliminate species 2 (Fig. 5a).

However, realizations of the stochastic process (Fig. 5b) show that the dynamics predicted from Eqs. 11 are incorrect: it is elimination of *species* 1 that actually takes place. (Each line in Fig. 5b corresponds to a mean path, here an average of 20 realizations starting from the same initial conditions.) The reason for the discrepancy between Fig. 5a and b is that offspring in species 1 are less well dispersed than those in species 2 and are less likely to escape from the neighborhoods of their parents. This places species 1 at a disadvantage

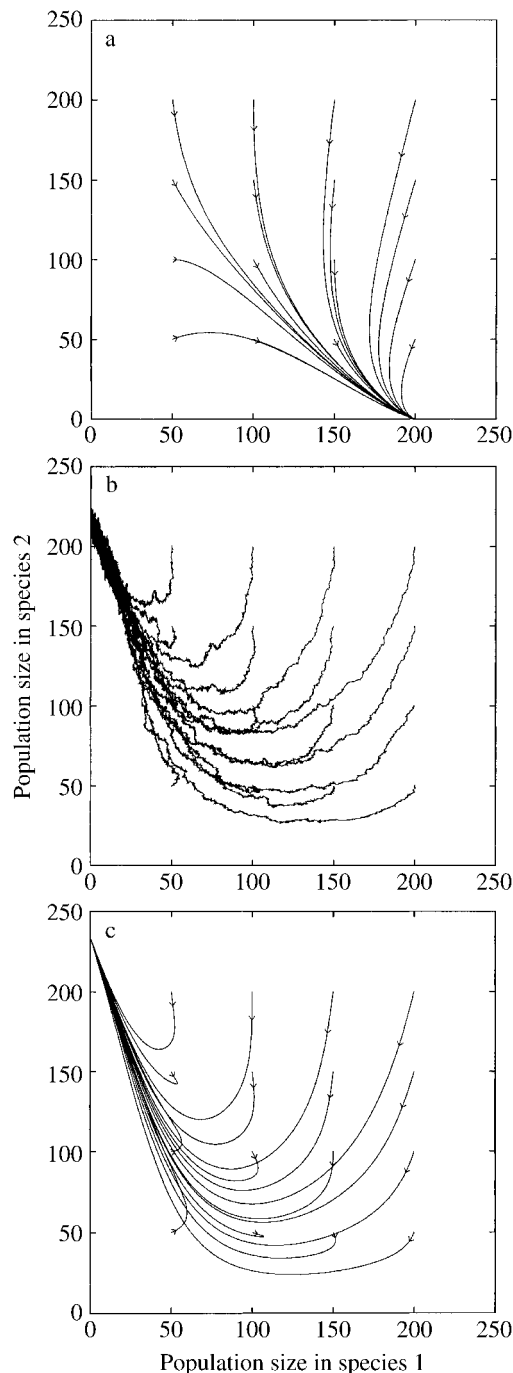


FIG. 5. Phase portraits showing the dynamics of two competing species. At time 0, individuals are placed at random locations in space; the trajectories are allowed to develop until time 100 from 16 starting points. Panel (a) assumes that there are no effects of space and uses Lotka-Volterra dynamics as in Eq. 11. Panel (b) shows the mean path of the stochastic process, here constructed from 20 realizations. Panel (c) gives the trajectories after coupling the first and second spatial moments using Eqs. 10 and 12.

relative to species 2, which is large enough for species 2 eventually to eliminate species 1. The mean-field dynamics do not carry information about the local neighborhoods, and are qualitatively in error.

The phase portrait using the coupled first and second moments (Fig. 5c) has flows quite different from those of the first moment on its own. There is now a close match between the trajectories and the mean paths of the stochastic process. Evidently, by coupling the dynamics of the first and second moments, we capture correctly important effects of spatial structure. (It should be borne in mind that the trajectories shown are projections into the plane of population densities of orbits from a higher dimensional system incorporating the second moment. This means that it is possible for trajectories to cross one another in the plane of population densities.)

The coupled dynamics of first and second moments hold in place much more information than just the spatial averages of population densities. The system keeps track of how the spatial structure of the community develops over time. Major changes in this structure take place, as the realization of the individual-based model in Fig. 2 has already demonstrated. Time series for the second moments show that the functions, which are initially flat, rapidly build up structure at short distances (Fig. 6). There is a pronounced increase in the autocorrelation of species 1 because of its limited dispersal, whereas the cross-correlation decreases because of the tendency of species 1 to eliminate species 2 where they occur in the same proximity. There is also some decline in the autocorrelation of species 2 at small distances.

The discrepancy between the moment dynamics and the nonspatial Lotka-Volterra dynamics in Fig. 5 is a direct consequence of the coupling of the first and second moments. At time 0, plants of both species are distributed at random across space and there is no spatial structure in the community. Plants therefore encounter one another in proportion to their average abundance over space, and the mean-field dynamics of the Lotka-Volterra model are a good approximation. This can be seen in Fig. 5c, because its orbits start by moving in the same direction as those of the nonspatial model in Fig. 5a, i.e., towards extinction of species 2, the weaker competitor.

Shortly after time 0, however, seed dispersal and neighborhood-dependent mortality begin to generate spatial structure in the community. Species 1, with neighborhoods increasingly dominated by conspecifics, experiences greater intraspecific competition; this depresses its mean density because large values of $C_{11}(\xi)$ at small distances inflate $W_{11}^{(d)}$ in Eqs. 10. Species 2, on the other hand, starts to escape some of the deleterious effects of species 1, as the species become segregated from one another; its mean density increases, because the small values of $C_{21}(\xi)$ at small distances diminish $W_{21}^{(d)}$ in Eqs. 10. Together, the increased competition in

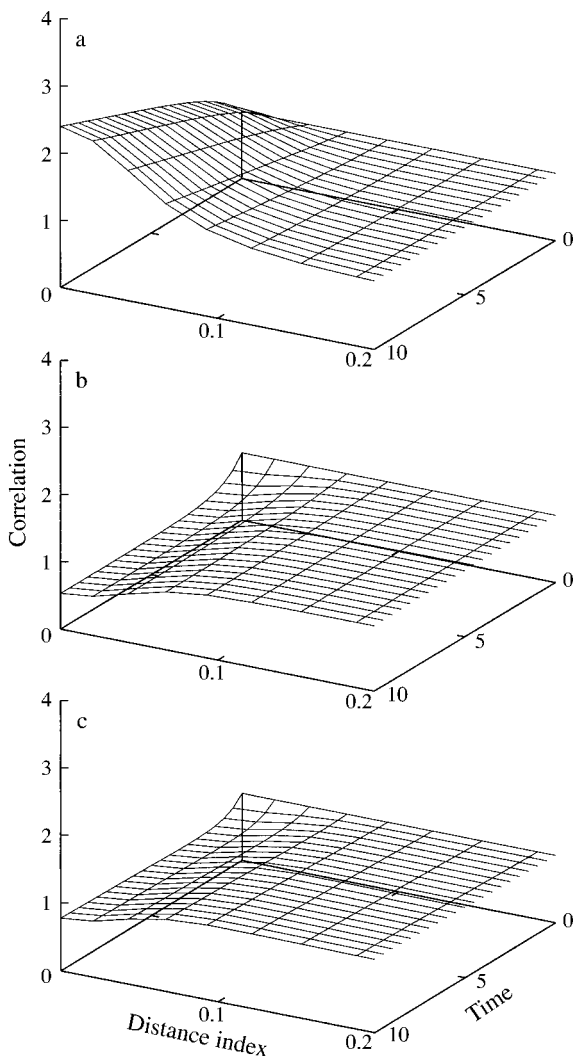


FIG. 6. Time series of radial correlation functions obtained from integrating Eqs. 10 and 12: (a) autocorrelation of species 1; (b) cross-correlation of species 1 and 2; (c) autocorrelation of species 2. The distance scale is the same as that in Fig. 1.

species 1 and reduced competition in species 2 are great enough to put species 2 at an advantage. This is the cause of the curl in the orbits in Fig. 5c, from pointing towards extinction of species 2 to pointing towards extinction of species 1. In other words, the difference between Fig. 5a and c is simply a consequence of spatial structure; the parameters of birth and death rates are the same; only the neighborhoods are different.

DISCUSSION

The main messages from this analysis are twofold. First, the method of moments is able to capture the dynamics of neighborhoods in a plant community closely enough to be a good approximation to an underlying individual-based model. In conjunction with work already in place (Bolker and Pacala 1997, Pacala

and Levin 1997, Bolker et al. 2000), moment dynamics establish a firm, formally derived link from spatially extended, individual-based, stochastic simulations, to macroscopic, deterministic, ecological models. Second, the effect of spatial structure on the dynamics is fundamental; in the example shown, spatial structure qualitatively reverses the outcome of competition, the weaker competitor surviving and the stronger competitor going to extinction.

Incorporating neighborhoods into community dynamics brings community theory a step closer to field ecology. This applies particularly in the context of plant ecology where the important processes often occur within small neighborhoods in spatially structured communities (Stoll and Weiner 2000), and there are a number of other ecological contexts, such as population dynamics in spatially structured landscapes (Murrell and Law 2000), in which this approach could also prove useful. There is still some way to go, however. Neighborhoods in plant communities change in size as focal individuals and their neighbors grow; in principle such an extension could be achieved by indexing individuals by size as well as by species, and by introducing a function for neighborhood-dependent growth.

Quite a lot can, of course, be learnt simply from running stochastic realizations of spatially extended, individual-based models, as Fig. 5b illustrates. Such realizations aid precise thinking about ecological processes (Pacala et al. 1996), can be useful tools for management (Turner et al. 1995), and are needed in any event to test deterministic approximations, as we have done above. Arguably, though, more will be learnt in the long run from deterministic approximations derived from the individual-based models, because it is likely to be easier to understand the generic properties of deterministic models (Dieckmann et al. 2000). For instance, it should be clearer what the asymptotic states are, whether these states are homogeneous in space and time, whether there are multiple attractors, what their basin boundaries are, how initial states (of both the first and second moments) determine which attractors are reached, and so on.

It will not come as a surprise that a dynamical system incorporating changes in neighborhoods can have much more complex behavior than systems ignoring spatial structure; the equations are, after all, more intricate and contain parameters for interactions and dispersal that are absent in simpler models. We think it likely that a large class of phenomena is waiting to be unearthed in these systems, even in the case of single-species systems, and that, as a result, some recasting of ecological theory may be needed. For instance, how plant species coexist has appeared to be a critical problem from Gause's competitive exclusion principle (Silvertown and Law 1987); this theory has its roots in the Lotka-Volterra competition equations and assumes that mean-field population dynamics apply. But spatial clumping of individuals within species is a common feature of

natural plant communities (e.g., Pielou 1974, Mahdi and Law 1987), and obviously reduces the importance of interspecific relative to intraspecific competition (Law and Watkinson 1989, Rees et al. 1996, see also Atkinson and Shorrocks 1981). With ecological models in place that properly incorporate such spatial structure, coexistence of species could turn out to be more readily achieved than previously thought (Pacala 1997, Pacala and Levin 1997).

Another phenomenon, unanticipated from nonspatial models, is that community dynamics, at least in the early stages, may be determined by the initial spatial structure. A random initial pattern at first gives dynamics close to mean-field; it is only as spatial structure builds up that substantial divergence from these dynamics can develop. Consider, for instance, the experiment by Pacala and Silander (1990) on a two-species mixture of annual weeds, initially distributed with a pattern close to random, and designed to test for departures from mean-field dynamics over the course of time; the mean-field model gave a good fit to the data, rather as one would expect in the early stages given the initial spatial structure. The initial spatial pattern has implications more generally in the design of plant competition experiments and community microcosms (Firbank and Watkinson 1990, Naeem et al. 1994); seeds of plant species are often scattered roughly at random across some spatial region, and this is likely to have its own effects on the outcome of competition in the short term. Reliable insights into competitive interactions may entail running such experiments for a number of generations, or setting the spatial structure close to its asymptotic state at the start. It is even possible, if there is more than one attractor, for different starting patterns to move the initial state from one basin to another, leading to different asymptotic states. Clearly, the role of initial spatial structure deserves more attention than it has received.

It is important to appreciate that the method of moments can never be more than an approximation to an underlying individual-based model, and there are circumstances in which it is likely to fail. If important properties of spatial structure lie in higher-order moments, then a second-order closure of the hierarchy is obviously not adequate. (It ought to be relatively straightforward to establish how serious a problem this is from analysis of multispecies spatial patterns of plant communities in the field.) In particular, the method rests on the idea that the average neighborhood of an individual adequately characterizes the spatial structure. If structure occurs at large spatial scales, so that individuals are either in one type of environment or another, the average may not help understanding of the dynamics. Interestingly, we noticed quite large single-species patches developing in our stochastic realizations; the success of the method of moments in these systems suggests that it could be quite robust, remaining reliable even if there are substantial departures from the

mean-field. Another constraint is that births and deaths are assumed to depend linearly on the density of neighbors; it is this that is responsible for the close link to Lotka-Volterra dynamics. But this assumption is not essential, and could be removed by a Taylor approximation for small departures from linearity.

In sum, the method of moments needs to be used cautiously with due regard to its limitations. But dynamics based on changes in neighborhoods have the potential to provide new insight into plant community dynamics. We believe that, as the basic core of theory is developed, the method of moments will lead to a much improved understanding about processes in ecology.

ACKNOWLEDGMENTS

We thank the organizer, O. Dieckmann, and the participants of a workshop on spatial interactions, held at the Lorentz Center, Leiden, the Netherlands, in October 1997, for stimulating discussions on the results presented here. In particular, we are grateful to J. A. J. Metz and M. H. Williamson for helpful comments on the work. The research was supported by the Wissenschaftskolleg zu Berlin, and by the International Institute for Applied Systems Analysis, Laxenburg, Austria.

LITERATURE CITED

- Atkinson, W. D., and B. Shorrocks. 1981. Competition on a divided and ephemeral resource: a simulation model. *Journal of Animal Ecology* **50**:461–471.
- Bolker, B. M., and S. W. Pacala. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology* **52**:179–197.
- Bolker, B. M., S. W. Pacala, and S. A. Levin. 2000. Moment methods for ecological processes in continuous space. In U. Dieckmann, R. Law, and J. A. J. Metz, editors. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge, UK, *in press*.
- Cain, M. L., S. W. Pacala, J. A. Silander, Jr., and M.-J. Fortin. 1995. Neighbourhood models of clonal growth in the white clover *Trifolium repens*. *American Naturalist* **145**:888–917.
- Crawley, M. J., and R. M. May. 1987. Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology* **125**:475–489.
- Dieckmann, U., T. Herben, and R. Law. 1997. Spatio-temporal processes in plant communities. Institute for Advanced Study, Berlin, *Jahrbuch* 1995/1996:296–326.
- Dieckmann, U., and R. Law. 2000. Relaxation projections and the method of moments. In U. Dieckmann, R. Law, and J. A. J. Metz, editors. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge, UK, *in press*.
- Dieckmann, U., R. Law, and J. A. J. Metz, editors. 2000. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge, UK, *in press*.
- Dytham, C. D. 1995. The effect of habitat destruction pattern on species persistence: a cellular model. *Oikos* **74**:340–344.
- Firbank, L. G., and A. R. Watkinson. 1990. On the effects of competition: from monocultures to mixtures. Pages 165–192 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, San Diego, California, USA.
- Hastings, A. 1980. Disturbance, coexistence, history, and

- competition for space. *Theoretical Population Biology* **18**: 363–373.
- Law, R., and A. R. Watkinson. 1989. Competition. Pages 243–284 in J. M. Cherrett, editor. *Ecological concepts*. Blackwell Scientific, Oxford, UK.
- Levin, S. A., B. Grenfell, A. Hastings, and A. S. Perelson. 1997. Mathematical and computational challenges in population biology and ecosystems science. *Science* **275**:334–343.
- Mahdi, A., and R. Law. 1987. On the spatial organization of plant species in a limestone grassland community. *Journal of Ecology* **75**:459–476.
- Murrell, D. J., and R. Law. 2000. Beetle movements in fragmented woodlands: a formal framework for landscape ecology. *Journal of Animal Ecology* **69**, *in press*.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- Pacala, S. W. 1997. Dynamics of plant communities. Pages 532–555 in M. J. Crawley, editor. *Plant ecology*. Second edition. Blackwell Science, Oxford, UK.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66**:1–44.
- Pacala, S. W., and S. A. Levin. 1997. Biologically generated spatial pattern and the coexistence of competing species. Pages 205–232 in D. Tilman and P. Kareiva, editors. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Pacala, S. W., and J. A. Silander Jr. 1990. Field tests of neighborhood population dynamic models of two weedy species. *Ecological Monographs* **60**:113–134.
- Pielou, E. C. 1974. *Population and community ecology*. Principles and methods. Gordon and Breach, New York, New York, USA.
- Rees, M., P. J. Grubb, and D. Kelly. 1996. Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist* **147**:1–32.
- Schwinning, S., and A. J. Parsons. 1996. A spatially explicit population model of stoloniferous N-fixing legumes in mixed pasture with grass. *Journal of Ecology* **84**:815–826.
- Silvertown, J., and R. Law. 1987. Do plants need niches? *Trends in Ecology and Evolution* **2**:24–26.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196–218.
- Stoll, P., and J. Weiner. 2000. A neighborhood view of interactions among individual plants. In U. Dieckmann, R. Law, and J. A. J. Metz, editors. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge, UK, *in press*.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- Tilman, D., and P. Kareiva, editors. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Turkington, R. A., and J. L. Harper. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *Journal of Ecology* **67**:201–208.
- Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Heijl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* **5**:12–16.
- Tyler, C. M., and C. M. D'Antonio. 1995. The effects of neighbors on the growth and survival of shrub seedlings following fire. *Oecologia* **102**:255–264.