IIASA
International Institute for
Applied Systems Analysis
www.iiasa.ac.at

On Scaling Up from Individual-Based Processes to Macroscopic Ecological Dynamics in Spatially-Extended Communities

Law, R. and Dieckmann, U.

IIASA Interim Report
May 1998

Law, R. and Dieckmann, U. (1998) On Scaling Up from Individual-Based Processes to Macroscopic Ecological Dynamics in Spatially-Extended Communities. IIASA Interim Report. IR-98-046 Copyright © 1998 by the author(s). http://pure.iiasa.ac.at/5602/

IIASA

International Institute for Applied Systems Analysis • A-2361 Laxenburg • Austria
Tel: +43 2236 807 • Fax: +43 2236 71313 • E-mail: info@iiasa.ac.at • Web: www.iiasa.ac.at

INTERIM REPORT IR-98-046/May

On Scaling Up from Individual-Based Processes to Macroscopic Ecological Dynamics in Spatially-Extended Communities

Richard Law (rl1@york.ac.uk)
Ulf Dieckmann (dieckman@iiasa.ac.at)

Approved by
Hans Metz (metz@iiasa.ac.at)
Project Leader, *Adaptive Dynamics Network*

Contents

Abstract

How should ecologists scale up from the microscopic events affecting individuals, to the macroscopic processes affecting populations and communities? This question is becoming important in theoretical ecology due to the increasing use of individual-based models of spatially-extended populations and communities. We give here a dynamical system, derived from an individual-based stochastic process, that describes the principal features of such a stochastic process. The stochastic process models a multispecies community of organisms living in a spatial domain, containing organisms that (1) give birth and die with probabilistic rates which depend on other individuals in a specified neighbourhood, and (2) move from one location to another. The dynamical system describes the change in the first and second spatial moments of the stochastic process, the first moments being the densities of species averaged over space, and the second moments being measures of the average spatial structure of the community in the vicinity of an individual. We show, by means of an example of two competing plant species, that the dynamics given by a simpler non-spatial model are qualitatively incorrect, whereas the dynamical system presented here gives a close approximation to the first and second moments of the underlying stochastic process.

Key words: Births, Community dynamics, Competition, Competitive exclusion, Deaths, Dispersal, Dynamical systems, Individual-based models, Moment dynamics, Plant neighbourhoods, Spatial ecology, Stochastic processes

Key phrases: A dynamical system for describing spatially-extended community dynamics; Moment dynamics approximate individual-based birth–death–movement processes; Scaling-up from individual-based models; Spatial structure causes qualitative changes in the outcome of competition between two species; A stochastic process for birth, death and movement of individuals in multispecies communities

About the Authors

Richard Law
Department of Biology
University of York
PO Box 373
York YO1 5Y, UK

Ulf Dieckmann
Adaptive Dynamics Network
International Institute for Applied Systems Analysis
A-2361 Laxenburg, Austria

Acknowledgements

We thank the organiser, O. Diekmann, 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.

On Scaling Up
from Individual-Based Processes
to Macroscopic Ecological Dynamics
in Spatially-Extended Communities

Richard Law
Ulf Dieckmann

Introduction

Individual plants and animals are the natural starting point for most field-based ecology. 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. How should ecologists scale up from the microscopic events affecting individuals to the macroscopic events affecting populations and communities? In developing a theoretical framework for describing the dynamics of ecological systems, scaling up is just as important an issue as it is in the field. Recent developments in computation have brought ecological modelling down to the level of the individual, often in explicit spatial settings (DeAngelis and Gross 1992, Judson 1994). But again, it is usually the macroscopic dynamics that emerge from individual-based models that are of interest.

Arguably, we need in ecology a framework to construct macroscopic dynamics of ecological populations and communities from the stochastic birth, death and movement events of individual plants and animals. This is a major challenge for theoretical ecology (Levin et al. 1997), which is being addressed by several methods, including the use of metapopulations, diffusion approximations and analysis of individual-based stochastic processes (Tilman and Karieva 1997, Dieckmann et al. 1998).

One promising approach is to construct a dynamical system comprising the first and second spatial moments of the underlying stochastic process (Bolker and Pacala 1997, Dieckmann et al. 1997). A first spatial moment is simply the spatial average of population density, and a second moment measures the variability of density over space. By introducing the second spatial moment, a dynamical system is put in place that tracks important aspects of the system's spatial structure and couples this structure to the dynamics of mean density, thereby allowing a feedback between the two. This is of general interest for terrestrial ecology, and becomes especially important in populations and communities of plants where individuals typically interact locally in small neighbourhoods and disperse over short distances (Stoll and Weiner 1998); here the local spatial structure can profoundly affect the dynamics.

Other approaches for describing spatially-extended stochastic processes, such as the pair-approximation method, have also been investigated (Matsuda et al. 1992, Harada and Iwasa 1994). Pair approximation is typically applied to systems on a discretized spatial lattice; the method describes the dynamics of the states of neighbouring cells in pairs, and in this way holds in place information on local spatial structure. But the discretization of space makes this approach less readily applicable to populations and communities in the field.

This paper builds on and extends the method of moments introduced by Bolker and Pacala (1997). The paper places in the literature equations for the dynamics of the first and second spatial moments of a community containing an arbitrary number of species, and having arbitrary functions for neighbourhood dependence and movement (while assuming a linear dependence of per capita birth and death rates on the density of neighbours). The model differs from previous work in the following ways: (1) it is explicitly constructed in a two-dimensional space, (2) it is given for a general *n*-species system, (3) it allows for movement both at birth (e.g. seed dispersal) and later on in life (e.g. clonal growth), and (4) the closure of the hierarchy of equations does not assume that the third central moment is negligible. We do not give the technical details of the derivation here. Instead we show, by means of an example of two competing species, that the dynamics predicted by the equations are a close approximation to those of the first and second moments of the underlying stochastic process.

We begin by outlining a stochastic process for births, deaths and movements in a continuous two-dimensional space, and define first and second spatial moments as convenient measures for summarizing the emerging patterns. We then give and explain a dynamical system describing the average behaviour of the moments over the course of time. To keep the argument from becoming abstract, we illustrate each step in terms of a community of two competing plant species, and show that the moment dynamics are able to capture fundamental effects of their spatial interaction. Readers who wish to see what the dynamical system can do without going into the formalism on which it is based should turn to the section labelled 'Example'.

A Stochastic Birth-Death-Movement Process

Consider a 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 $p(x)$ = $\big(p_1(x),\ldots,p_n(x)\big)$; $p(x)$ 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.) 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. 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

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

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

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

The first term, given by the parameter d_i, is a neighbour-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 neighbourhood of location *x*. The function $w_{ij}^{(d)}(x' - x)$ weights the effect of a neighbour of species *j* at x' according to its distance from *x*; this function is multiplied by the density $p_j(x')$ of *j* at location x'. Essentially what the integral does is to add up the contribution of each neighbour 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 neighbourhood; the term $\delta_{ij} \cdot \delta_x(x')$ 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'

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

In most respects this birth term has the same structure as the death term (2). The b_i and b_{ij} are parameters for neighbour-independent and neighbour-dependent births, respectively, and $w_{ij}^{(b)}(x''-x)$ is a function for weighting the effect of neighbours. 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 probabilities per unit time above define a stochastic process 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 neighbourhood 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 (2) and (3) is that births and deaths depend linearly on the local densities of neighbours; this assumption could however be removed for small departures from linearity by means of a Taylor approximation.

To motivate the argument below, we consider a plant community comprising two species, with parameters as in Table 1. In such a community, it is natural to assume that movements occur only at the time of seed production, so $m_i(x'-x)=0$; we also assume for simplicity that neighbourhood 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) The second species can disperse farther at the time of reproduction. In an explicitly spatial system, greater dispersal may help species 2 to avoid intra-specific competition, because offspring are more likely to escape from the neighbourhoods 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). Here we use the system simply to show the relationship between an individual-based model and the dynamics of its moments.

Specifically, the dispersal properties of the species in the community are as follows. Offspring 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 $\frac{1}{z}\cdot\exp\left(-\frac{r^2}{2\cdot s_i^{(bm)2}}\right)$, where $r \le r_i^{(bm)}$, and z is the normalization constant.

Table 1 Non-zero parameters used in defining a community of two competing species. Parameters defined in the text.

		Value for species *i*:	
	Parameter	$i = 1$	$i = 2$
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

Apart from the difference in competitive ability and movement, the species are ecologically equivalent; in particular they have the same functions and parameters for neighbourhood dependence of deaths. We assume that the effect of a neighbour on the chance of death of an individual is a normal function of the neighbour's distance, truncated at a radius $r_{ij}^{(d)}$, with a standard deviation $s_{ij}^{(d)}$ measuring how slowly the neighbour's effect diminishes with distance.

Fig. 1 shows two snapshots of the spatial patterns that develop in the course of a realization of this stochastic process (modelled with periodic boundaries). 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 departs strongly from randomness in two respects. First, species 1, which has less dispersal, shows much more aggregation than does species 2. Second, the species are not usually found together because, where they do so, species 1 tends to eliminate species 2; this leads to some spatial segregation of the species.

First and Second Spatial Moments of the Stochastic Process

The spatial patterns that develop during realizations of a stochastic process have their own intrinsic interest. But it is far from straightforward to characterize the major properties of a stochastic process simply by looking at the patterns. What is needed are statistics of the process 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

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

is simply the average density of species i across a space of area A, and needs no further explanation.

The second moment $C_{ij}(\xi, p)$ is a product of pairs of densities for a spatial pattern $p(x)$:

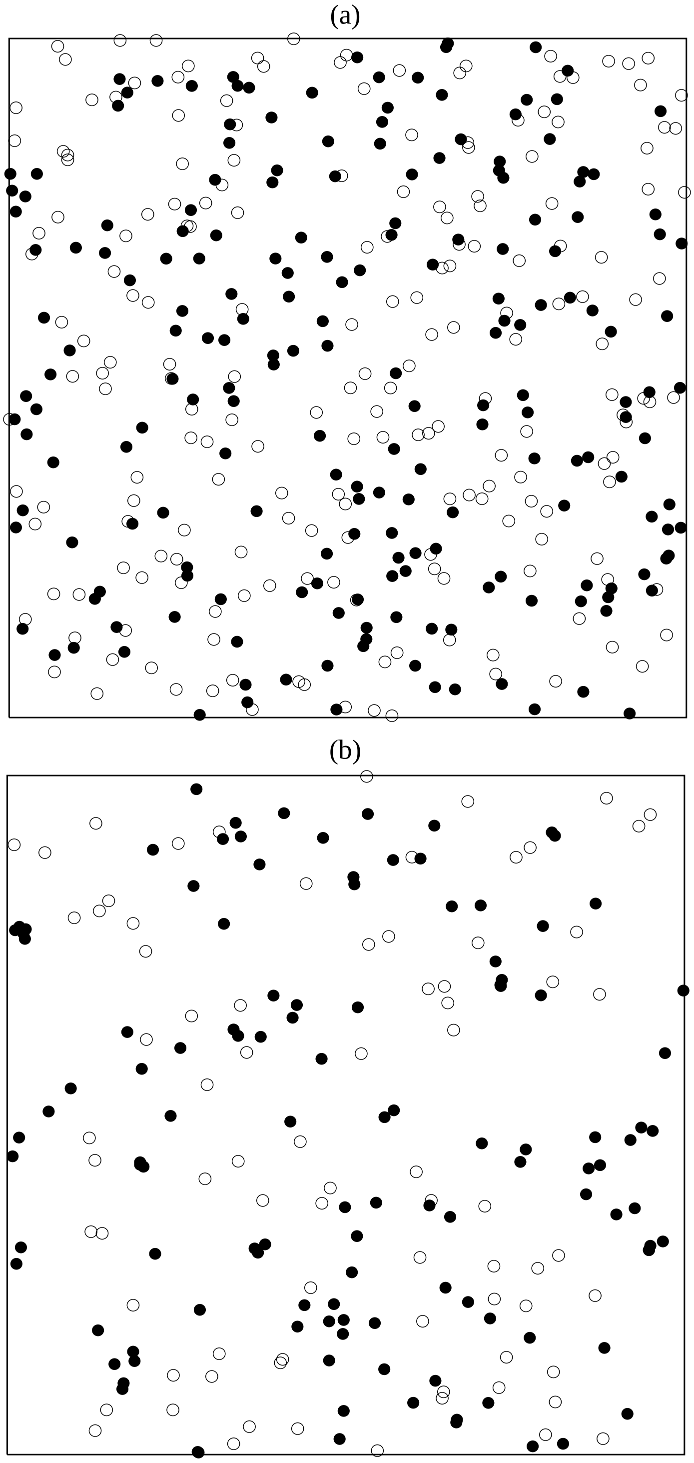

Figure 1 Examples of spatial patterns of two competing plant species generated as a realization of the stochastic process described in the text using parameter values in Table 1. (a) Time zero, corresponds to a random initial distribution of 200 individuals of each species. (b) Pattern after five units 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.

$$C_{ij}(\xi, p) \quad = \quad \frac{1}{A} \cdot \int p_i(x) \cdot \left(p_j(x+\xi) - \delta_{ij} \cdot \delta(\xi) \right) dx \quad . \tag{5}$$

It comprises a product of the density of individuals of species *i* and those of *j* at location ξ relative to *i*, averaged across a region of area *A*. The second moment we use 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 $\delta_{ij} \cdot \delta(\xi)$ is subtracted to remove a spurious term arising from a self pair at *i* = *j* and ξ = (0, 0) which expression (5) would otherwise contain. Notice that the second moment is a function of the location ξ of *j* relative to *i*, and needs to be thought of as describing a surface. When we show results about second moments below, we normalize the moment by dividing by the product $N_i(p) \cdot N_j(p)$ 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. 1, and these are given in Fig. 2. The stochastic process is isotropic, and this means that the pair densities depend only on the distance that separates the pairs, and not on the direction from *i* to *j*. In these circumstances, a spatial correlation has the same overall shape in every direction from the origin, and we replace it by the radial correlation for the purpose of illustration. (The radial correlation is a radial section through the spatial correlation function.)

At time zero (Fig. 2a, 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. 1a). By time five, however, substantial spatial structure has developed. Species 1, in keeping with its tendency to occur in small clumps, has a large auto-correlation close to the origin (Fig. 2d), but the correlation diminishes with distance, because spatial structure is localized. The auto-correlation function of species 2 is much flatter because dispersal at the time of reproduction is so much greater in this species (Fig. 2f). Notice also that the spatial segregation of species 1 and 2 is evident in the small values of the cross-correlation between the species close to the origin (Fig. 2e).

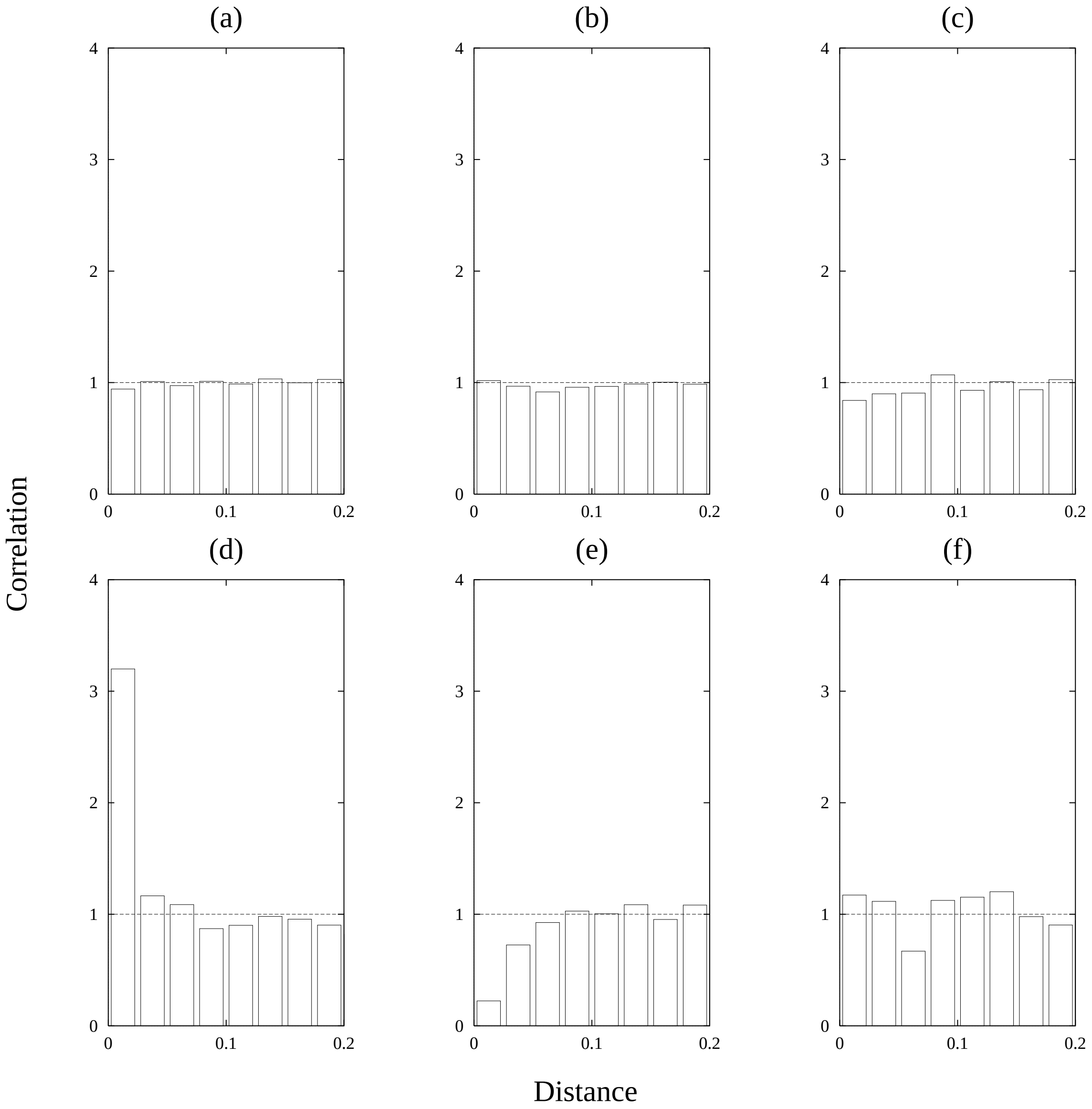

Figure 2 Examples of spatial correlation functions computed for the spatial patterns in Fig. 1. The graphs in the first row are the correlations at time 0: (a) autocorrelation of species 1, (b) cross-correlation of species 1 and 2, (c) autocorrelation of species 2. Graphs (d), (e) and (f) in the second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

The spatial patterns in Fig. 1 come from a single realization of the underlying stochastic process. 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 stochastic process. To extract the generic features of the stochastic process, one needs the averages of the first and second moments across the ensemble of realizations, given by

$$N_i \quad = \quad \int P(p) \cdot N_i(p)\, Dp \tag{6}$$

$$C_{ij}(\xi) \quad = \quad \int P(p) \cdot C_{ij}(\xi, p)\, Dp \tag{7}$$

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 behaviour of these moments (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

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

This is a natural extension of the second moment. It is esentially the product of the density of individuals of species i, times the density of individuals of j at location ξ relative to i, times the density of individuals of k at location ξ' relative to i, averaged across a region of area A. The delta terms are introduced as before to remove spurious products arising from self pairs. The average of the third moment across the ensemble of realizations of a stochastic process is given by

$$T_{ijk}(\xi, \xi') \quad = \quad \int P(p) \cdot T_{ijk}(\xi, \xi', p)\, Dp \quad . \tag{9}$$

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

$$\frac{d}{dt}N_i \quad = \quad (b_i - d_i)\cdot N_i \quad + \quad \sum_j b_{ij}\cdot W_{ij}^{(b)} \quad - \quad \sum_j d_{ij}\cdot W_{ij}^{(d)} \tag{10}$$

where $W_{ij}^{(b)} \quad = \quad \int w_{ij}^{(b)}(\xi')\cdot C_{ij}(\xi')\, d\xi'$

and $W_{ij}^{(d)} \quad = \quad \int w_{ij}^{(d)}(\xi')\cdot C_{ij}(\xi')\, d\xi'$.

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

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

Eqs (11) assume that each individual in the community experiences the same local neighbourhood; this is commonly refered to as the 'mean-field' assumption, and is equivalent to assuming the complete absence of spatial structure. So the only new feature about Eqs (10) is the neighbourhood dependence of birth and death rates introduced in the integrals, and the dependence on the second moments that arises from this. The reason why the Lotka-Volterra equations emerge is that the birth and death rates were made linearly dependent on neighbourhood in defining the stochastic process above.

The dynamics of the second moments (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 located at ξ relative to *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 ten types of event, for each type involving *i*, there being 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:

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

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 located at ξ relative to *i*. The geometry is shown in Fig. 3, 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 ξ and cause them to disappear:

$$\text{(Movements)} \ = \ + \int m_i(\xi'')\cdot C_{ij}(\xi+\xi'')\,d\xi'' \qquad (12.1)$$

$$+ \int m_j(\xi'')\cdot C_{ji}(-\xi+\xi'')\,d\xi'' \qquad (12.2)$$

$$- \ |m_i|\cdot C_{ij}(\xi) \qquad (12.3)$$

$$- \ |m_j|\cdot C_{ji}(-\xi) \ . \qquad (12.4)$$

Terms (12.1) and (12.2) are positive contributions to $C_{ij}(\xi)$. In (12.1) an individual of *i* starts at a location such that *j* is at location $\xi+\xi''$ relative to *i* and moves by an amount ξ'', so that *j* is located at ξ relative to *i* after this movement; the integration is needed to deal with 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 located at ξ relative to *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*.

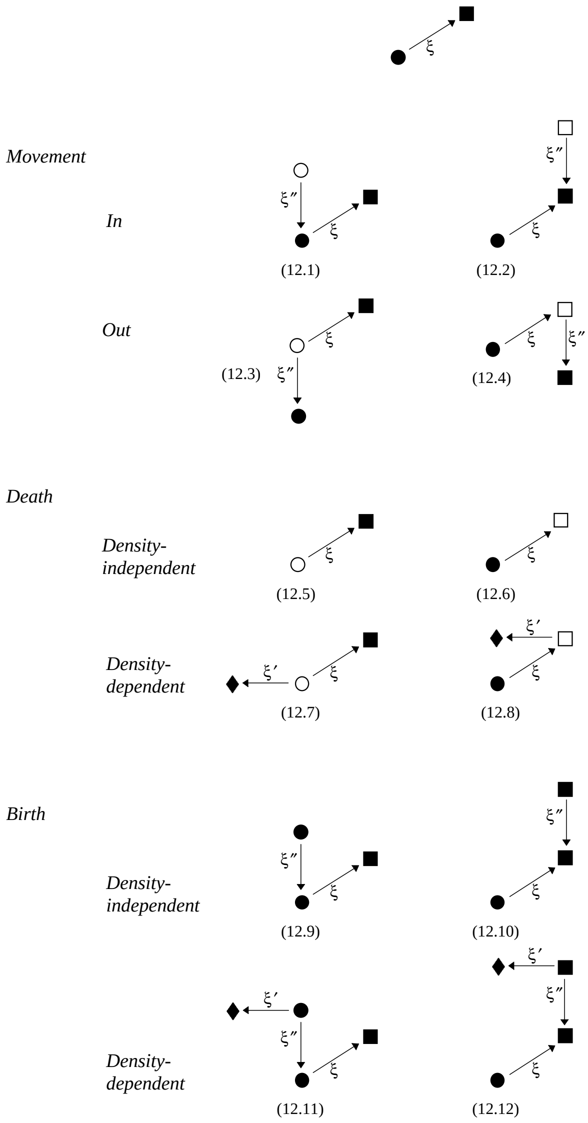

Figure 3 Geometry of components of flux of the second spatial moment in Eqs (12). At the top is a pair of individuals *ij* of species *i* and *j*, with *j* located at distance ξ relative to *i*; this pair can be created or destroyed by the events shown below in species *i* (first column) and *j* (second 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 Eqs (12). An open symbol indicates a location at which an individual is no longer present once the event has taken place.

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

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

$$- \; d_j \cdot C_{ji}(-\xi) \tag{12.6}$$

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

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

The neighbourhood-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 neighbourhood-dependent term (12.7) is more intricate because death is affected by a neighbour *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 location ξ relative to *i*, and (3) *k* at location ξ' relative to *i*. The integral is needed to sum over all individuals of *k* in the neighbourhood of *i*. The term (12.8) is the corresponding neighbourhood-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 neighbourhood, or dependent on the neighbourhood:

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

$$+ \; b_j \cdot \int m_j^{(b)}(\xi'') \cdot C_{ji}(-\xi+\xi'')\, d\xi'' \tag{12.10}$$

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

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

The complication in this case is that newborn individuals disperse. In the case of neighbourhood-independent births of *i* (12.9), we start with a parent of species *i* such that *j* is located at $\xi + \xi''$ relative to the parent; the newborn individual of *i* moves to location ξ'' relative to its parent, thereby forming a new pair such that *j* is located at ξ relative to the newborn individual. The integration accounts for all the positions of the *i* parent from which this process could start. Expression (12.10) is the equivalent neighbourhood-independent birth term for species *j*. The neighbourhood-dependent term (12.11) has to allow for the effect of neighbours *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 neighbourhood, and the second integral accounts for all the movements of newborn individuals. Term (12.12) is the corresponding neighbourhood-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:

$$\text{(Corrections)} \;=\; -\; d_{ij} \cdot w_{ij}^{(d)}(\xi) \cdot C_{ij}(\xi) \tag{12.13}$$

$$-\; d_{ji} \cdot w_{ji}^{(d)}(-\xi) \cdot C_{ji}(-\xi) \tag{12.14}$$

$$+\; \delta_{ij} \cdot m_i^{(b)}(-\xi) \cdot b_i \cdot N_i \tag{12.15}$$

$$+\; \delta_{ji} \cdot m_j^{(b)}(\xi) \cdot b_j \cdot N_j \tag{12.16}$$

$$+\; \delta_{ij} \cdot m_i^{(b)}(-\xi) \cdot \sum_k b_{ik} \cdot \int w_{ik}^{(b)}(\xi') \cdot C_{ik}(\xi')\, d\xi' \tag{12.17}$$

$$+\; \delta_{ji} \cdot m_j^{(b)}(\xi) \cdot \sum_k b_{jk} \cdot \int w_{jk}^{(b)}(\xi') \cdot C_{jk}(\xi')\, d\xi' \tag{12.18}$$

$$+\; b_{ij} \cdot \int w_{ij}^{(b)}(\xi + \xi'') \cdot m_i^{(b)}(\xi'') \cdot C_{ij}(\xi + \xi'')\, d\xi'' \tag{12.19}$$

$$+\; b_{ji} \cdot \int w_{ji}^{(b)}(-\xi + \xi'') \cdot m_j^{(b)}(\xi'') \cdot C_{ji}(-\xi + \xi'')\, d\xi'' \;. \tag{12.20}$$

Expression (12.13) is the contribution that *j* itself makes to the neighbourhood-dependent death of *i*, and (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 located at $-\xi$ relative to its parent, with (12.16) being the corresponding term for species *j*. There is also an effect of *k* on this birth event given in (12.17) and (12.18). Finally, expression (12.19) (respectively (12.20)) adds in the the effect that *j* (respectively *i*) itself has on the neigbourhood 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, unpublished).

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). 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

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

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 neighbourhoods 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. 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 stochastic process is the dynamical system Eqs (10) and (12)? To answer this question, the population densities predicted by the dynamical system can be put alongside some realizations of the stochastic process. Here we examine the fit in the case 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 movements occur only at birth, and (2) that neighbours affect only the probability of death. These assumptions leave us with 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 behaviour 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. 4a).

However, realizations of the stochastic process (Fig. 4b) show that the dynamics predicted from Eqs (11) are incorrect: it is elimination of *species 1* that actually takes place. (Each line in Fig. 4b corresponds to a mean path, here an average of 20 realizations starting from the same initial conditions.) The reason for the discrepancy between Fig. 4a and 4b is that offspring in species 1 are less well dispersed than those in species 2 and are less likely to escape from the neighbourhoods of their parents. This places species 1 at a disadvantage 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 neighbourhoods, and are qualitatively in error.

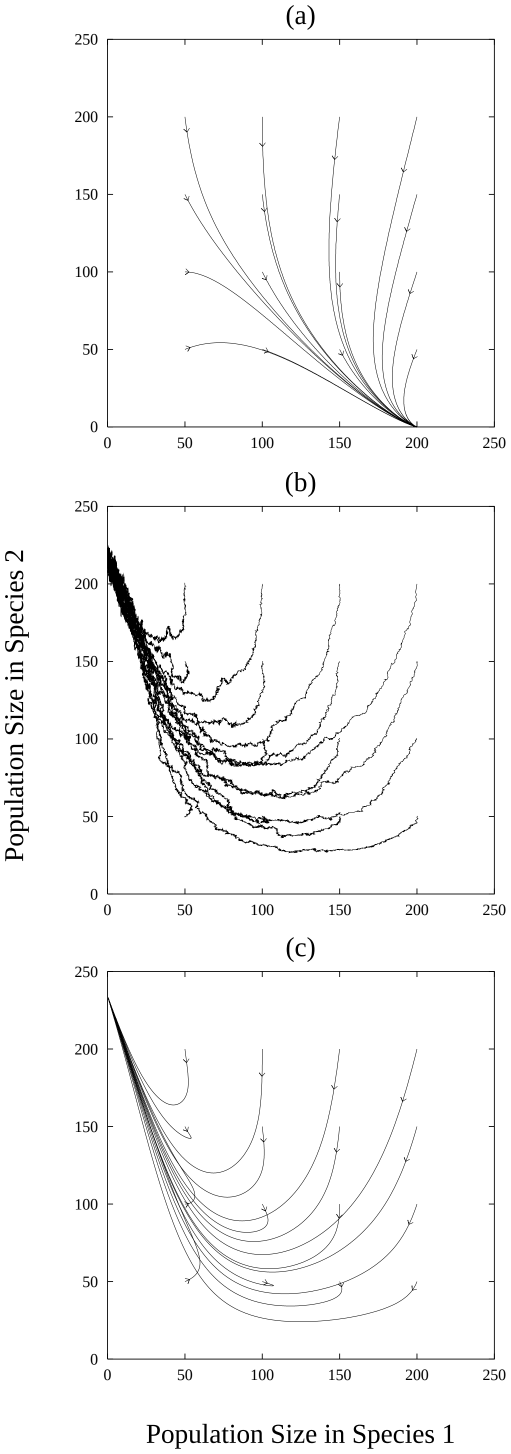

Figure 4 Phase portraits showing the dynamics of two competing species using parameters in Table 1. At time 0, individuals are placed at random locations in space; the orbits are allowed to develop until time 100 from 16 starting points. (a) Assumes that there are no effects of space and uses Lotka-Volterra dynamics, Eqs (11). (b) Shows the mean path of the stochastic process, here constructed from 20 realizations. (c) Gives the dynamics after coupling the first and second spatial moments using Eqs (10) and (12).

The phase portrait using the coupled first and second moments (Fig. 4c) has flows quite different from those of the first moment on its own. There is now a close match between the orbits 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 paths shown are projections into the plane of population densities of orbits from a higher-dimensional system incorporating the second moment, and this means it is quite possible for orbits 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 tracks the shape of the spatial correlation functions over time, describing the patterns that gradually emerge from local interactions and dispersal, in other words, how the spatial structure of the community develops over time. Major changes in spatial structure are taking place, as the realization of the stochastic process in Fig. 1 has already demonstrated. Fig. 5 shows the information carried in the spatial correlation functions corresponding to the snapshot at time five of the stochastic process in Fig. 1b. Species 1, with auto-correlations greater than one near the origin is clumped in space. Species 2, with auto-correlations less than one, is over-dispersed at short distances. The cross-correlations between the species are less than one at short distances, indicating segregation of the species in space. The shape of the functions in Fig. 5 can be compared with the observed shapes in Fig. 2, although it should be understood that the latter refer to a single realization whereas the former corresponds to a large ensemble of realizations.

Time series for the second moments are given in Fig. 6 to illustrate their dynamics; these series run over a period of ten time units, and correspond to the stochastic process on which Fig. 1 was based. To display the second moments, we have again made use of radial correlations. Observe that the functions, which are initially flat, rapidly build up structure at short distances. There is a pronounced increase in the auto-correlation 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 auto-correlation of species 2 at small distances. These changes in the spatial structure feed through to the dynamics of the first moment, and change the intensity of competition within and between species as time goes on.

The spatial correlation functions, being coupled to the first moments, have their own effects on orbits of population density. At the start, the absence of clumping of species 1 leaves species 2 at a disadvantage, and orbits in Fig. 4c initially have the same direction as the mean-field dynamics in Fig. 4a. As clumping builds up in species 1, species 2 gains an advantage over species 1, and starts to increase. This spatial effect gives rise to the curl near the start of some orbits in Fig. 4c, sometimes causing them almost to reverse their direction as they turn towards extinction of species 1.

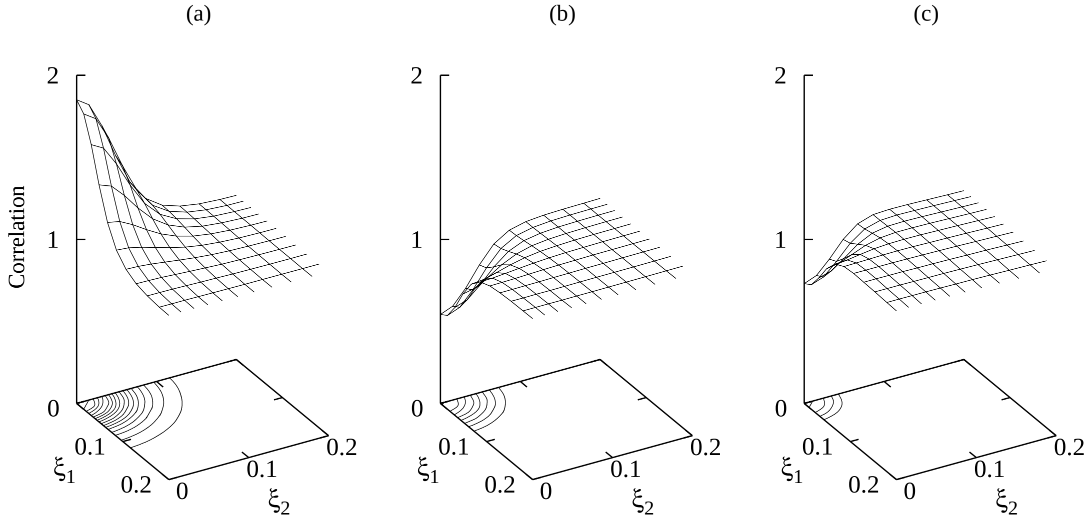

Figure 5 Spatial correlation functions given by the dynamics of the first and second spatial moments at time 5, for a system corresponding to Fig. 1. (a) Auto-correlation of species 1, (b) cross-correlation of species 1 and 2, (c) auto-correlation of species 2. Only the positive orthant of ξ is shown; the three other orthants have the same shape.

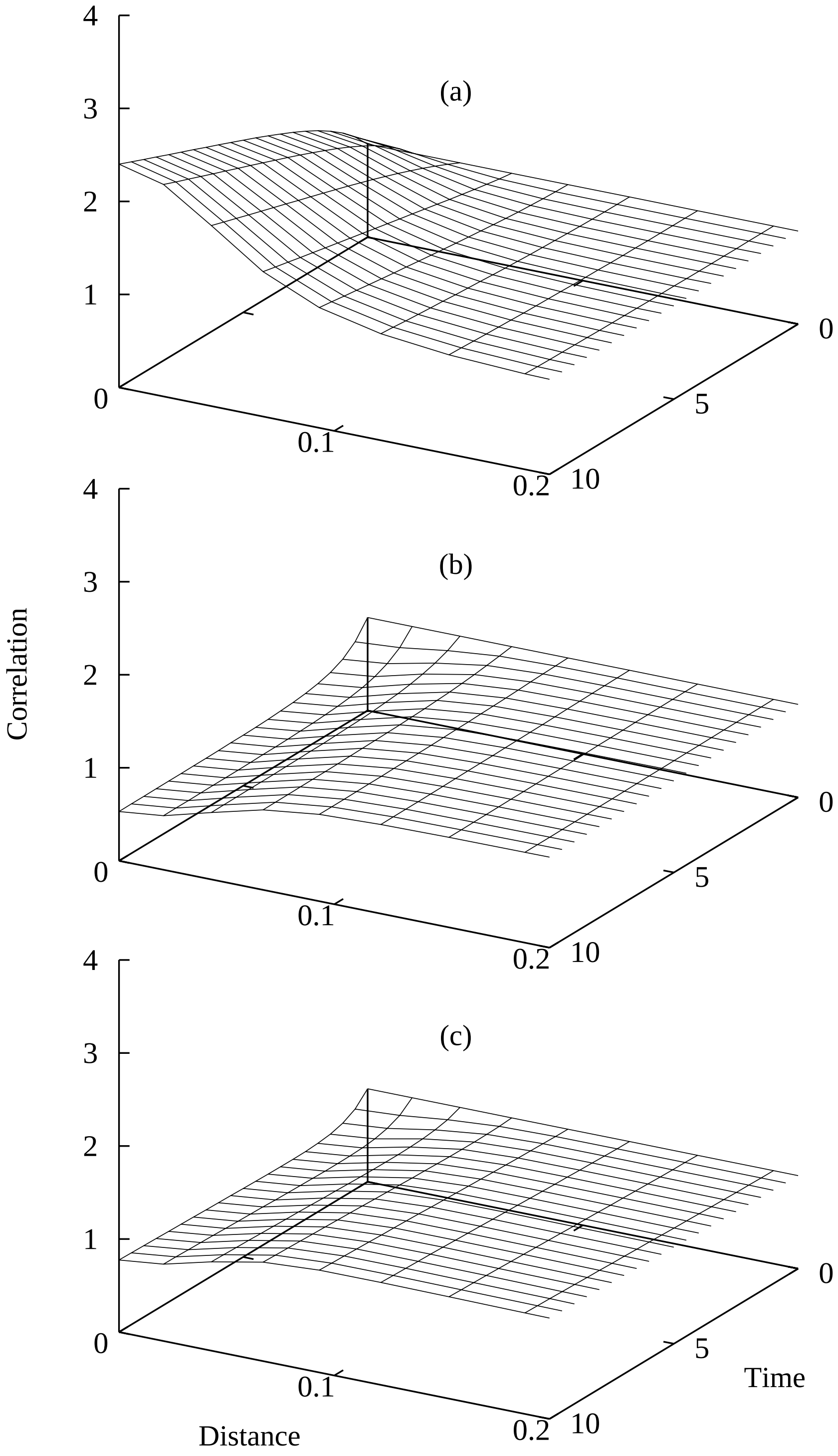

Figure 6 Time series of correlation functions for a system corresponding to Figure 1. Correlations are expressed as functions of radius. (a) Auto-correlation of species 1, (b) cross-correlation of species 1 and 2, (c) auto-correlation of species 2.

Discussion

The principal message from the results above is that a dynamical system is now available that captures the generic features of a community of interacting species, living in a continuous space, with stochastic births, deaths and movements. In conjunction with work already in place (Bolker and Pacala1997, Pacala and Levin 1997, Bolker et al. 1998), this establishes a firm, formally-derived link from spatially-extended, individual-based, stochastic simulations, to macroscopic, deterministic, ecological models. It is evident from the example above that, when the dynamics of the second moment are coupled to those of the first moment, basic effects of space on ecological processes can be exposed. Non-random spatial pattern in multispecies communities emerges from local interactions and limited dispersal of individuals, and in turn feeds back to affect these interactions.

Incorporating the dependence of the dynamical system on space brings community theory a step closer to ecology in the field. This applies particularly in the context of plant ecology where the important processes often occur within small neighbourhoods in spatially structured communities (Stoll and Weiner 1998), and there are a number of other ecological contexts, such as population dynamics in spatially structured landscapes (Dunning et al. 1995), in which this approach could also prove useful.

Quite a lot can, of course, be learnt simply from running stochastic realizations of spatially-extended, individual-based models, as Fig. 4b 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 how good deterministic approximations are, as we have done above. Arguably though, more will be learnt in the long run from deterministic approximations derived from the stochastic processes, because it is likely to be easier to understand the generic properties of the underlying stochastic processes from the deterministic models. 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 coupled dynamical system of first and second moments can have much more complex behaviour than systems just based on the first moment – 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 non-spatial 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 intial 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.

Choice of a moment closure may seem a purely technical matter, but our investigations suggest that it is critical. Closures which are second order with respect to the correlation functions (products of two correlation functions) appear to work best. The second-order closure we have used (Eq. 13) gave a close match between the cross-correlations observed in stochastic realizations and those predicted by the dynamical system, and this close fit plays an important part in bringing about the match between the phase portraits in Fig. 4b and 4c. But there is still room for improvement in the fit to the auto-correlations; it can be seen from Fig. 4c that the dynamical system gives an equilibrium density of species 2 after extinction of species 1 which is a little too high. A first-order closure we investigated, equivalent to assuming that the third central moment is zero (Bolker and Pacala 1997), became unstable at low population density. A third-order closure gave a phase portrait which was qualitatively incorrect. There are no systematic ways at present of establishing what kind of closure would be appropriate, and there is much that needs to be learnt about how best to close the hierarchy of equations in spatial ecology.

It is important to appreciate that the method of moments can never be more than an approximation to an underlying stochastic process, 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 collected in the field.) In particular, the method rests on the idea that the average neighourhood of an individual adequately characterises 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 neighbours; 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 the first and second spatial moments have the potential to provide new insight into spatially structured systems. 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 terrestrial populations and communities.

References

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., S. W. Pacala and S. A. Levin. 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. 1998. Moment methods for stochastic processes in continuous space and time. *In* U. Dieckmann, R. Law, and J. A. J. Metz, editors. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, England, *in press*.

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.

DeAngelis, D. L. and L. J. Gross. 1992. Individual-based models and approaches in ecology: populations, communities and ecosystems. Chapman and Hall, New York, USA.

Dieckmann, U., T. Herben, and R. Law. 1997. Spatio-temporal processes in plant communities. Institute for Advanced Study, Berlin, Jahrbuch 1995/96:296-326.

Dieckmann, U., R. Law, and J. A. J. Metz (editors). 1998. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, England, *in press*.

Dunning, J. B. Jr, D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications **5**:3-11.

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, USA.

Harada, Y. and Y. Iwasa. 1994. Lattice population dynamics for plants with dispersing seeds and vegetative propagation. Researches on Population Ecology **36**:237-249.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology **18**:363-373.

Judson, O. P. 1994. The rise of the individual-based model in ecology. Trends in Ecology and Evolution **9**:9-14.

Law, R. & Watkinson, A. R. 1989. Competition. Pages 243-284 *in* J. M. Cherrett, Editor. Ecological Concepts. Blackwell Scientific, Oxford, England.

Levin, S. A., B. Grenfell, A. Hastings, 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.

Matsuda, H. N., A. Ogita, A. Sasaki, and K. Sato. 1992. Statistical mechanics of population: the lattice Lotka-Volterra model. Progress in Theoretical Physics **88**:1035-1049.

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. 2nd Edition. Blackwell Science, Oxford, England.

Pacala, S. W., and J. A. Silander Jr. 1990. Field tests of neighbourhood population dynamic models of two weedy species. Ecological Monographs **60**:113-134.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements. II Estimation, error analysis and dynamics. Ecological Monographs **66**:1-44.

Pacala, S. W., and Levin, S. A. 1997. Biologically generated spatial pattern and the coexistence of competing species. Pages 205-232 *in* D. Tilman, and P. Karieva, editors. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, New Jersey, USA.

Pielou, E. C. 1974. Population and community ecology. Principles and methods. Gordon and Breach, 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.

Silvertown, J. & Law, R. 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 Weiner, J. 1998. A neighborhood view of interactions among plants. *In* U. Dieckmann, R. Law, and J. A. J. Metz, editors. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, England, *in press*.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology **75**:2-16.

Tilman, D., and P. Karieva (editors). 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, New Jersey, USA.

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.