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Spatio-Temporal Processes in Ecological Communities

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Ecological systems evolve in space and time. Until recently, however, research in ecology separately has focused either on the spatial domain (patterns) or on the temporal domain (processes). In this paper we describe novel approaches for progressing towards an integration of pattern and process, a goal long called for in ecology. First, we present a sequence of alternative stochastic models of spatially extended processes. Second, we advance two new methods for the estimation, or calibration, of model parameters from spatio-temporal processes observed in the field. Third, we provide tools for reducing the complexity of spatially extended ecological processes to manageable dynamical systems. Steps and techniques are illustrated in the context of data from a montane grassland community from the Czech Republic.

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1. INTRODUCTION

A spatio-temporal process is a spatial pattern of objects that develops over the course of time. Such processes arise in a number of contexts from distributions of particles in physics to distributions of organisms in the biosphere. They are of particular interest to plant ecologists because spatial structure is an obvious feature of terrestrial plant communities and is thought to play a central role in their dynamics. In fact, interest in spatio-temporal processes in plant ecology goes back at least to the 1930s, when A. S. Watt started to map the turnover of species in a grassland in the Breckland of England, keeping track of the spatial structure of the community. This and other work led him to suggest that the plant community might be understood as a system of patches cycling through several states (pioneer, building, mature and degenerate), the patches together forming a spatial mosaic (WATT 1947). These ideas became established as a cornerstone of plant ecology under the banner of 'pattern and process' (VAN DER MAAREL 1996).

Curiously, for a long time rather little was built on the foundations laid by Watt. Plant ecologists became engrossed in the spatial aspects of plant communities, rather than the link between spatial structure and temporal dynamics (e.g. GREIG SMITH 1957). Those plant ecologists who were interested in dynamical processes turned for inspiration more to animal ecology (e.g. HARPER 1977), and here the innate mobility of many animals means that spatial structure plays a role secondary to that of temporal processes. There are at least two reasons for the lack of interest of plant ecologists in spatio-temporal processes. The first is the labour required to obtain the data from natural communities, since regular censuses comprising detailed maps of the spatial pattern are needed. Second, there was no obvious formal mathematical structure within which such information could be analysed (STONE and EZRATI 1996); in other words, ecologists would have found it difficult to know what to do with the information once they had it.

But developments in mathematics, theoretical physics and computation are opening up new opportunities for achieving a synthesis of spatial and temporal aspects of plant ecology. These opportunities include modelling spatio-temporal processes on discretized lattice-like spaces (e.g. DURRETT and LEVIN 1994) and the investigation of their dynamics by techniques that go beyond simulation (MATSUDA et al. 1992, HARADA and IWASA 1994, RAND 1994, HENDRY and MCGLADE 1995, RAND and WILSON 1995).

This report comes in three parts: construction of stochastic models of spatially extended processes (Section 3), methods for estimation of model parameters from spatio-temporal processes observed in the field (Section 4), and reduction of the spatio-temporal process to a dynamical system in a relatively small number of dimensions (Section 5). To keep the research properly anchored in plant ecology, we used data from a grassland community from the Czech Republic, and we start with a description of this system (Section 2).

We ought to mention that, as well as the application to plant ecology, there are at least two other reasons why it is important to develop understanding of spatio-temporal processes. The first is that ecological theory has tended to proliferate into large numbers of rather ad hoc models. At the base of many of these special cases, we think there is a common formal framework, taking the form of individual-based spatio-temporal stochastic processes. It would help to clarify the subject if it could be shown how the major classes of models can be recovered as mathematical limits of the underlying stochastic processes. Second, spatially-extended data are becoming widely available from geographical information systems (GIS) technology and remote sensing by satellites; new mathematical and statistical techniques are going to be needed for the analysis of this information.

2. DATA

Grassland communities are a good source of data on spatio- temporal processes. These communities show fine-scale spatial patterns, and the patterns develop rapidly through time (DURING and VAN TOOREN 1988, VAN DER MAAREL and SYKES 1993). To a major extent, this is due to the frequent occurrence of clonal growth among grassland species, because daughters produced clonally tend to occur only in the close proximity of their mother plants. Further, as in all other terrestrial plant communities, interactions between plants are essentially short range; the growth and reproduction of a particular shoot responds not to an 'average' environment, but to that in its immediate neighbourhood. These two features make grassland communities particularly appropriate for treatment as spatio-temporal processes.

For our study, we used data from a mountain grassland in the Mts. Krkonoše (Riesengebirge), in the northern part of the Czech Republic. The grasslands in this area were created by clearing small patches in the original forests during the past few hundred years. Traditionally they have been maintained for hay, with mowing once or twice a year, grazing in late autumn and manuring once in several years. The rather stable management over several centuries has produced grasslands with a remarkably well differentiated species composition, ranging from rather species poor (ca. 10 species m^{-2}) to quite species rich (40 species m^{-2}) depending on altitude, water and nutrient regimes. Though artificial grasslands occur at all altitudes, true montane grasslands are restricted to altitudes from 800 m up to the timberline at about 1300–1400 m.

The particular data we used came from the Severka settlement (ca. 3 km NW of Pec pod Sněžkou, altitude 1100 m). The climate at the site is rather harsh, with cool summers and long winters with thick snow cover, usually lasting from November until the end of April; only one mowing per year can be sustained by the grassland. The plant community is rather species poor, and the four principal species which form the basis of our analysis were: *Anthoxanthum alpinum,* À. Löve et D. Löve, *Deschampsia flexuosa* (L.) Trin., *Festuca rubra* L., and *Nardus stricta* L. These are all clonal grasses (Figure 1), though their horizontal growth rates, branching frequencies and tussock morphologies differ. There are also other species in the grassland, but all of them occur at much lower abundance and may be safely assumed not to affect the dynamics of the four grasses substantially. Although the system is rather species poor at the large scale, the species coexist at the fine scale, the species density being 2–4 species / 10 cm^2.

In this grassland, four permanent plots of 50 × 50 cm were established in 1984–5, and subdivided into grids of 15 × 15 cells for recording the plants. The number of shoots of each species within each cell of each grid was counted each year in mid-July and, after recording, the plots and their surroundings were clipped at the height of 1 cm to simulate traditional management. This

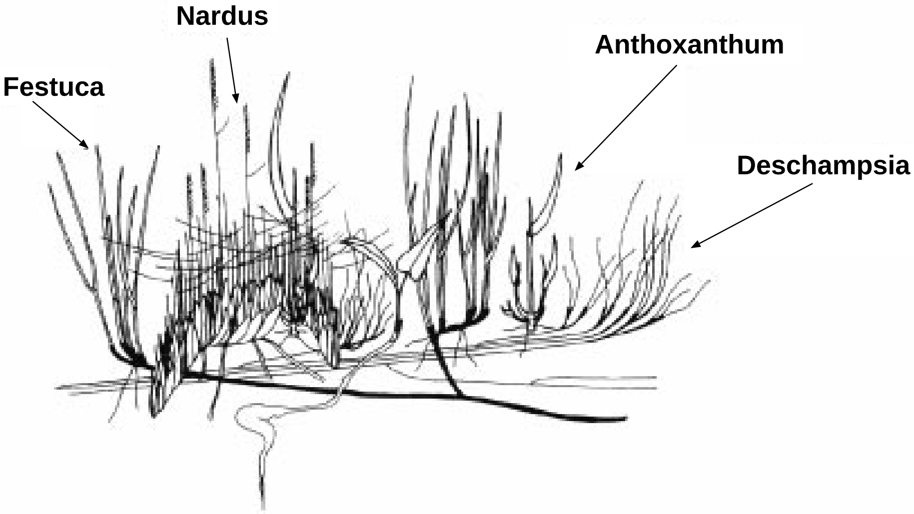

FIGURE 1. Four grass species used for analysis of spatio-temporal processes (drawn by Sylvie Pechacková).

procedure has continued up to the present time, and provides detailed information on the spatio-temporal process of the community. The information is illustrated for one of the permanent plots in Figure 2. The species clearly differ a lot in overall abundance, with Deschampsia being the most common; they also differ in spatial structure, and Nardus is especially clumped. In addition, the spatial structure of Anthoxanthum and Deschampsia is somewhat more labile through time.

Being discrete in space and time, the information from the permanent plots can be no more than an approximation to the full process. But, to record the community in continuous space, one would need the exact spatial location of each shoot, which would not be feasible. Owing to the short growing season, discretization of time to a single point each year is reasonable.

3. MODELS OF SPATIO-TEMPORAL DYNAMICS

3.1. Individual-based stochastic model in continuous space and time

The stochastic model starts with the notion of an individual represented as a point x in the plane. The locations of all individuals in each species i are collected into the set L_i; i.e. there is an individual of species i at the point x if and only if $x \in L_i$. The contribution of an individual of species i at point x' to the spatial density $p(x)$ of that species is given by the Dirac delta-function, a function which is peaked at $x = x'$ and is 0 at all other points x. The spatial density (pattern) in species i is obtained as the sum of all these individual

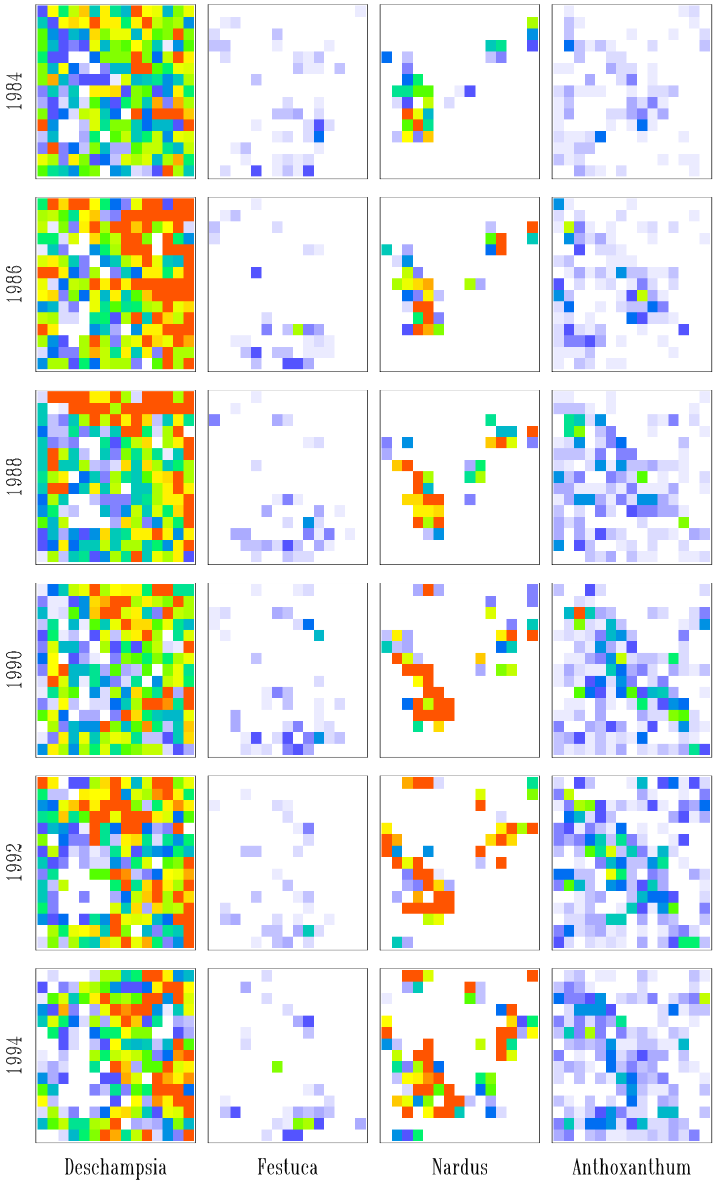

FIGURE 2. Observed spatial patterns of four grass species in a single plot, from 1984 to 1994; patterns are shown for alternate years. The color coding of cells within a large square indicates for one species and one census the number of shoots (red corresponds to high numbers, white indicates absence of the species). A column of large squares depicts the spatial pattern of one species through time; a row shows the spatial pattern of all species at a single time.

contributions

$$p_i(x) = \sum_{x' \in L_i} \delta_{x'}(x) \quad .$$

and the spatial pattern of individuals on all N species is then given by the vector of these density functions:

$$p(x) = (p_1(x), \ldots , p_N(x)) \quad .$$

Clearly $p(x)$ is but one of an infinite number of spatial patterns in which individuals could be laid out at an instant in time. Moreover the spatial pattern changes over the course of time, as random births, deaths and movements occur. It will help to think of the probability $P(p)$ that the community has the pattern $p(x)$. One can then envisage the changing pattern in space as a Markovian stochastic process, writing the rate of change of the probability with respect to time as

$$\frac{d}{dt} P(p) = \int Dp' \left[w(p|p') \cdot P(p') - w(p'|p) \cdot P(p) \right] \quad . \tag{1}$$

This is a function-valued stochastic process describing the flux of probability to and from the function $p(x)$, being the probability per unit time of the shift from function $p'(x)$ to $p(x)$; to cover all possible transitions in and out of $p(x)$, one has to integrate over all functions $p'(x)$.

The primary events acting at the microscopic individual level are births, deaths and movements. It is these that cause the shift from one spatial pattern to another, and can be disaggregated into these events:

$$\begin{aligned} w\,(p'|p) = & \sum_{i=1}^{N} \int dx'\, b_i(x', p) \cdot p_i(x') \cdot \Delta(p + \delta_{x'} \cdot u_i - p') && \text{(births)} \\ & + \sum_{i=1}^{N} \int dx'\, d_i(x', p) \cdot p_i(x') \cdot \Delta\,(p - \delta_{x'} \cdot u_i - p') && \text{(deaths)} \\ & + \sum_{i=1}^{N} \iint dx' dx''\, m_i\,(x', x'', p) \cdot p_i(x') \cdot \Delta\,(p - \delta_{x'} \cdot u_i + \delta_{x'} \cdot u_i - p') \quad . && \\ & && \text{(movements)} \end{aligned}$$

Here $b_i(x', p)$ (respectively $d_i\,(x', p)$) is the per capita probability per unit time for a birth (respectively a death) in species i at the point x' when the spatial pattern is given by $p(x)$. The term $m_i(x', x'', p)$ is the per capita probability per unit time for a movement from the point x' to x'' in species i when the spatial pattern is given by $p(x)$. The functions Δ are generalized delta functions that select the appropriate event taking pattern p to p', u_i being an N-vector having value 1 for element i and zero elsewhere. For example

$$\Delta\,(p + \delta_{x'} \cdot u_i - p') = 0 \text{ if } p' \neq p + \delta_{x'} \cdot u_i \quad ;$$

in other words, with a birth at point x' to species i, Δ allows an increment only to the probability $P(p+\delta_{x'} \cdot u_i)$ of spatial pattern $p+\delta_{x'}$; the probability of all other spatial patterns is unaltered. In formal terms, the generalized delta function is defined by the relation $\int Dp' F(p') \cdot \Delta(p-p') = F(p)$ for any functional F.

This completes the formalism needed to define the stochastic model. Once specific functions have been incorporated for the birth, death and movement events, realizations can be generated, and one can then see how spatial patterns develop through time. One can also investigate the dynamics of moments of the stochastic model; this becomes important for dealing with questions of dimension reduction.

3.2. Individual-based stochastic model in discrete space and continuous time

Although the dynamics should correctly be thought of in continuous space, information from the field is rarely available in this form. It is more likely to be discretized in some way, often as numbers of individuals within the cells of a 2-dimensional lattice, as in the case of our Krkonoše community. Some transformation of the formal stochastic framework is needed to deal with discrete space.

We write the number of individuals of species i in cell k of the lattice as $n_i^{(k)}$ with $i = 1, \dots, N$ and $k = 1, \dots, M$. The spatial pattern of species i at some instant in time is given by the matrix n_i of the numbers in each cell, and that of the whole community as the vector of matrices $n = (n_1, \dots, n_N)$. The changing pattern in space can be seen as a stochastic process analogous to Equation (1)

$$\frac{d}{dt}P(n) = \sum_{n'} \left[w(n|n') \cdot P(n') - w(n'|n) \cdot P(n) \right] \quad , \tag{2}$$

but now describing the flux of probability to and from the vector of matrices n. The abbreviation $\sum_{n'} = \sum_{n'^{(1\dots M)}_{1\dots N}}$ is used. As before, the probability per unit time of the transition from n to n' can be disaggregated into the births, deaths and movements:

$$\begin{aligned} & w(n'|n) = \\ & \sum_{i,k} b_i^{(k)} \cdot n_i^{(k)} \cdot \prod_{j,l} \delta\left(n'^{(l)}_j, n_j^{(l)} + \delta(i,j) \cdot \delta(k,l) \right) && \text{(births)} \\ & + \sum_{i,k} d_i^{(k)} \cdot n_i^{(k)} \cdot \prod_{j,l} \delta\left(n'^{(l)}_j, n_j^{(l)} - \delta(i,j) \cdot \delta(k,l) \right) && \text{(deaths)} \\ & + \sum_{i,k,k'} m_i^{(k,k')}(n) \cdot n_i^{(k)} \cdot \prod_{j,l} \delta\left(n'^{(l)}_j, n_j^{(l)} - \delta(i,j) \cdot \delta(k,l) + \delta(i,j) \cdot \delta(k',l) \right) . \\ & && \text{(movements)} \end{aligned}$$

Here $b_i^{(k)}(n)$ (respectively $d_i^{(k)}(n)$) is the per capita probability per unit time for a birth (respectively a death) in species i in cell k when the spatial pattern is given by n. The term $m_i^{(k,k')}(n)$ is the per capita probability per unit time for a movement from cell k to k' in species i when the spatial pattern is given by n. The term $\delta(i,j) \cdot \delta(k,l)$ is a product of Kronecker delta symbols, returning the value 1 when $j = i$ and $l = k$, and 0 otherwise. The product of the outer Kronecker delta symbols then selects the appropriate event taking pattern n to n'.

3.3. Individual-based stochastic model in discrete space and discrete time

Natural communities most often occur in seasonal environments, and it is important to have a formalism that allows for the fluctuations in ecological processes that result from this. To achieve this, the per capita transition probabilities per unit time are made time dependent: $b_i^{(k)}(n,t)$, $d_i^{(k)}(n,t)$ and $m_i^{(k,k')}(n,t)$. Thus, if time t is measured in years, the effects of seasonality can be reflected by assuming that these functions possess a period of 1. The per capita probabilities of birth for each time step are then obtained as

$$b_i^{(k)}(n) = \int_0^1 dt\, b_i^{(k)}(n,t)$$

and analogous equations hold for the processes of death and movement.

For ecological systems with this property, it is natural to transform the individual-based stochastic model (2) from continuous time to discrete time. Equation (2) is replaced by a recurrence relation describing the change in probability $P(n)$ from time t to $t+1$:

$$P_{t+1}(n) = \sum_{n'} \left[w(n|n') \cdot P_t(n') - w(n'|n) \cdot P_t(n) \right] \quad .$$

For a discrete-time formalism to be adequate, microscopic events (births, deaths, movements) that depend on n have to be sufficiently well separated in time. We make this explicit in the following equation:

$$w(n'|n) = \sum_{n'',n'''} w_m(n'|n'') \cdot w_d(n''|n''') \cdot w_b(n'''|n) \quad .$$

This is to be interpreted as a probability $w_b(n'''|n)$ that births take the spatial pattern to n''' given that it starts as n, times the probability $w_d(n''|n''')$ that deaths take the pattern to n'' given that it starts as n''', times the probability that movements take the pattern to n' given that it starts as n''. The summation allows for the different paths possible between n and n'. This separation of the microscopic events is needed because of their dependence on the current spatial pattern, and is not required for those events which are independent of pattern.

The birth term is:

$$w_b(n'|n) = \prod_{i,k} \sum_{\beta_1 \ldots n_i^{(k)}} \delta\left(n'^{(k)}_i, n_i^{(k)} + \textstyle\sum_j \beta_j\right) \cdot \prod_j \mathcal{P}\left(b_i^{(k)}(n), \beta_j\right) \quad .$$

Here $\mathcal{P}\left(b_i^{(k)}(n), \beta_j\right)$ is the probability that there are β_j births to parent j of species i in cell k, this being Poisson distributed with mean $b_i^{(k)}(n)$; the product over j then gives the joint probability of β_1 births to parent 1, β_2 to parent 2, and so on. The Kronecker delta symbol returns 1 when $n_i^{(k)} + \sum_j \beta_j = n'^{(k)}_i$, and 0 otherwise. The term $\sum_{\beta_{1\ldots n_i^{(k)}}}$ is to be understood as $n_i^{(k)}$ separate summations (one for each parent), over 0, 1, 2, ... offspring produced by the parent. The death term

$$w_d(n'|n) = \prod_{i,k} \mathcal{B}\left(d_i^{(k)}(n), n_i^{(k)}, n_i^{(k)} - n'^{(k)}_i\right)$$

is based on the binomial distribution $\mathcal{B}$, with $d_i^{(k)}(n)$ the per capita probability of death, $n_i^{(k)}$ the number of individuals, and $n_i^{(k)} - n'^{(k)}_i$ the number that die. The movement term is:

$$w_m(n'|n) = \prod_i \sum_{\mu^{(1\ldots M;1\ldots M)}} \prod_k \delta\left(n'^{(k)}_i, n_i^{(k)} + \textstyle\sum_{k'}(\mu^{(k',k)} - \mu^{(k,k')})\right) \cdot \prod_{k'} \mathcal{B}\left(m_i^{(k,k')}(n), n_i^{(k)}, \mu^{(k,k')}\right) \quad .$$

The element $\mu^{(k,k')}$ of the $M \times M$ matrix μ gives the number of individuals that move from cell k to k'. With per capita probability of movement from cell k to k' given by $m_i^{(k,k')}(n)$, and $n_i^{(k)}$ individuals in cell k, the probability that $\mu_i^{(k,k')}$ move to cell k' is obtained from the binomial distribution $\mathcal{B}$. The Kronecker delta symbol returns the value 1 when the net change in numbers of species i in cell k obtains $n_i^{(k)} + \sum_{k'}\left(\mu^{(k',k)} - \mu^{(k,k')}\right) = n_i'^{(k)}$, and 0 otherwise. The term $\sum_{\mu^{(1\ldots M;1\ldots M)}}$ is to be understood as a sequence of $M \times M$ separate summations, one for each pair (k, k'), over 0, 1, 2, ... individuals moving from cell k to k'.

This formalism defines a stochastic model in discrete space and discrete time which matches the kind of information most often available from plant communities. In particular, it provides an appropriate basis for a stochastic model of the Krkonoše community below.

4. Parameter estimation

Section 3 shows how to describe spatio-temporal processes in terms of individual-based stochastic models, but there is still a major bridge to be built before such models can be taken as a description of an observed spatio-temporal process. As in all modelling, we need (1) to specify appropriate functions to describe the process, in particular to determine rates for the occurrence of microscopic events, and (2) to obtain estimates for the values of parameters in these functions. The choice of functions rests on external knowledge about the system; in the case of births, deaths and movements of the clonal grasses in our Krkonoše community, such understanding is quite well developed, as described below (Section 4.1). But there is much less understanding as to how to obtain parameter values that best fit the data; here we suggest two techniques for doing this (Sections 4.2 and 4.3).

4.1. Functions to describe dynamics

We concentrate on a stochastic model in discrete space and time, as this matches the structure of the data described in Section 2. Consider a cell k on the lattice, and a set of neighbour cells $S(k)$. The state of cell k is given by the number of shoots of each of the four grass species it contains, written as $n(k) = \{n_i^{(k)} | i \in \{A, D, F, N\}\}$ (*A: Anthoxanthum; D: Deschampsia; F: Festuca; N: Nardus*). The state of the neighbourhood is written as $N^{(k)} = \left\{n^{(l)} | l \in S^{(k)}\right\}$.

The stochastic model should update the state of each cell on the basis of random births, deaths and movements of shoots. In keeping with the available evidence from grasslands (Jònsdòttir 1991, Duralia and Reader 1993), we assume that interactions occur through sensitivity of births to the presence of shoots in the immediate vicinity. The number of daughters born to a shoot of species i in cell k following census t is taken to be a Poisson-distributed random variable, with a mean given by

$$b_i^{(k)} = c_i \cdot \exp\left(\sum_{j \in \{A,D,F,N\}} a_{ij} \cdot n_j^{(k)}\right) \quad .$$

The interactions are species-specific, the parameter a_{ij} describing the effect of species j on i; it is this that leads to a coupling of the dynamics of species in the model. The other parameter c_i is the mean of the Poisson distribution in the absence of any other shoots. Deaths of individuals are assumed to be independent of the presence of other shoots, the probability that a shoot of species i survives from census t to $t + 1$ being s_i. To deal with movement of shoots, one needs to allow changes in position from one cell to another. Movements are small (Herben et al. unpublished results), and a four-cell neighbourhood (the 'north', 'east', 'south' and 'west' neighbours of cell k) is large enough to capture most that occurs. We write the probability that a shoot of species i in cell k at census t moves to either one of these neighbour cells by the next census as m_i. These movements induce a local coupling of the cells, and allow spatial structures to develop.

The stochastic model is now specified to the level of seven parameters (s_i, a_{iA}, a_{iD}, a_{iF}, a_{iN}, c_i, m_i) of species i. The s_i's have been estimated independently by field measurements, and can therefore be taken as known;

the values $s_A = 0.2$, $s_D = 0.7$, $s_F = 0.3$ and $s_N = 0.7$ are used below. The remaining six parameters of each species, denoted by the vector $v_i = (a_{iA}, a_{iD}, a_{iF}, a_{iN}, c_i, m_i)$ for species i, have to be estimated from the observed spatio-temporal process.

4.2. Model fitting from single-cell processes

One way to estimate the parameters v_i is to consider each cell as a separate item (LAW et al. 1997). The number of shoots of species i in cell k at census time $t+1$ can be thought of as a random variable which depends on the number of shoots of each species in cell k and the neighbouring cells at census time t $(n^{(k)}, N^{(k)})$, and the model parameters can be estimated by a regression of the values observed at $t+1$, $n_i'^{(k)}$, against the expected values $\tilde{n}_i'^{(k)}$ predicted by the model based on v_i. With the model described above, $\tilde{n}_i'^{(k)}$ is given by:

$$\tilde{n}_i'^{(k)} = s_i \cdot \left((1 - m_i) \cdot n_i^{(k)} \cdot \left(1 + b_i^{(k)}\right) + \frac{m_i}{4} \cdot \sum_{l \in S_k} n_i^{(l)} \cdot \left(1 + b_i^{(l)}\right) \right) \quad .$$

Notice that estimation can proceed separately for each species, because species other than i only enter into this equation through their numbers at census t.

Potentially there is a lot of information in the observed spatio- temporal process on which to base the estimation, there being $15 \times 15 \times 11$ values of $n'^{(k)}_i$ for each plot. But the number of cells that can be used needs to be restricted in several ways. First, boundary cells should be excluded because their neighbourhoods are incomplete. Second, there is little purpose served in including cell k if there are no shoots of species i in this cell or its neighbourhood or both at time t. Third, one may expect spatial and temporal correlations to be present that violate the statistical assumption of independence. Some subsampling of the cells is needed; we worked with one fifth of the cells, cycling through them in such a way that a five year period elapsed before returning to the same cell, as shown in Figure 3.

Estimation of the parameters v_i requires iterative adjustment of v_i by non-linear regression until the function

$$d_i = \sum_k \left(F\left(n_i'^{(k)}\right) - F\left(\tilde{n}_i'^{(k)}\right) \right)^2$$

reaches a local minimum. The function F is used to correct for a dependence of the standard deviation on the mean. Prior analysis indicated a power relationship $\sigma = a \cdot \mu^b$ between the mean m and standard deviation σ of the dependent variable, and the transformation $F(x) = x^{(1-b)}/(a \cdot (1-b))$ was used to remove this relationship. The parameters a and b were obtained from the relationship between the mean and standard deviation using a regression analysis on the untransformed data. As there might be concern as to the reliability of the technique, we tested the method on time series of data artificially generated with

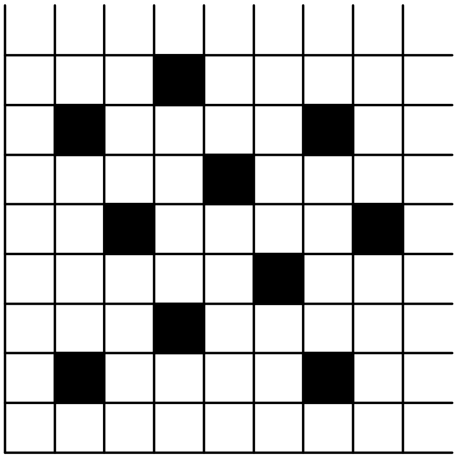

FIGURE 3. Tiling used for non-linear regression; cells chosen for analysis are shown as black. The starting position was displaced one cell to the right in successive years, so that each cell was revisited for sampling only after five years.

TABLE 1. Parameter estimates obtained from non-linear regression analysis. In cases where the 95% confidence limits of the estimate span zero, the estimate is shown in brackets.

Species (i)	a_{iA}	a_{iD}	a_{iF}	a_{iN}	c_i	m_i
Anthoxanthum	-0.031	-0.033	(-0.015)	-0.019	4.889	0.156
Deschampsia	-0.134	-0.037	-0.243	-0.178	0.983	0.358
Festuca	(-0.008)	(0.000)	-0.023	-0.135	2.481	0.066
Nardus	-0.151	(0.014)	0.068	-0.036	0.950	0.035

known parameter values, and found that the method recovers the parameter values with reasonable accuracy (HERBEN et al. 1997, LAW et al. 1997).

The results from parameter estimation confirm that the community is essentially competitive, as the interaction coefficients are predominantly negative (Table 1).

To the plant ecologist, the matrix of interaction terms has the interesting feature that it lacks diagonal dominance; in other words, intraspecific coefficients on the diagonal are not noticeably larger than the off-diagonal ones describing interspecific competition. The matrix also has the property of strong asymmetries in pairwise interactions; one can see this for instance in the comparison $a_{AD} = -0.033$ and $a_{DA} = -0.134$. Another distinctive feature is the lack of intransitivities that would allow cyclic replacement of one species by another; WATT'S (1947) notion of the mosaic cycle does not seem appropriate for this commmunity.

Interaction coefficients form the basic building blocks of community ecology, as they make community dynamics more than the sum of the independent dynamics of the species present. Yet they are particularly difficult to estimate, and ecologists have had to devise elaborate experimental schemes involving the manipulation of densities of plants to determine their values (GOLDBERG and BARTON 1992). Non-linear regression on spatio-temporal processes as described above opens up a new approach which holds some promise for achieving greater understanding of plant community dynamics. It has the important feature of being non-invasive; the interactions can be estimated without any external interference to the community.

4.3. Model fitting from spatio-temporal moments

The non-linear regression method (Section 4.2), by focusing on changes in single cells over single time steps, ignores the larger-scale spatial and temporal structure of the data. Such structure includes aggregations of shoots within species and the spatial distribution of one species relative to another (two aspects of spatial correlations); it also includes the location of clumps over the course of time (temporal correlations). As one can see from Figure 2, such patterns readily come about, and techniques of parameter estimation based on these larger-scale features would be using important information unavailable to the regression method above.

But to make use of such large-scale features, one needs to step outside the traditional statistical framework of regression analysis. There is no unique function which could be said to capture all the essential features of a spatio-temporal process; the mean number of shoots per cell, for instance, is not enough, as it lacks all information on the spatial structure. Consequently there is no unique measure of the goodness-of-fit between two spatio-temporal processes, such as one observed in the field and one given by a stochastic model. Novel approaches are needed, both to define measures of goodness-of-fit and to move down gradients in the parameter space until the difference between the patterns is minimized.

Here we describe a new method based on a gradient descent on a function of the first and second order moments of the spatio-temporal process. These moments capture a substantial amount of information about the larger-scale spatial and temporal structure of the data. The first moment of species i for year t is simply the mean number of shoots per cell, given by

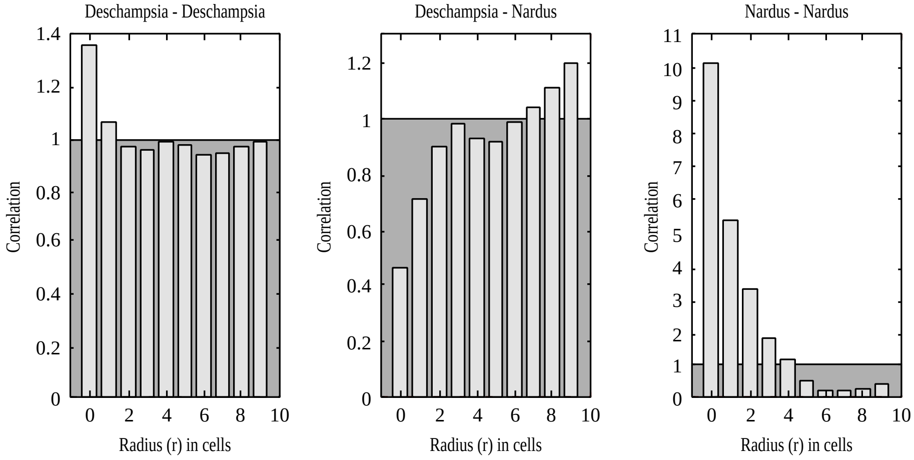

FIGURE 4. Spatial correlations $c_{ij}(t, \tau, r)$ of *Deschampsia* and *Nardus* for the grid data shown in Figure 2, with $t = 1984$, and time delay $\tau = 0$.

$$n_i(t) = \frac{1}{K} \cdot \sum_k n_i^{(k)}(t) \quad ,$$

where K is the number of cells. The second moment describes the spatio-temporal correlation at a distance r between species i at year t and species j at year $t + \tau$ and is given by:

$$c_{ij}(t, \tau, r) = \frac{1}{n_i(t) \cdot n_j(t+\tau)} \cdot \frac{1}{|S_r|} \cdot \sum_{(k_1,k_2) \in S_r} n_i^{(k_1)}(t) \cdot n_j^{(k_2)}(t+\tau) \quad ,$$

where $S_r = \{(k_1, k_2) | \text{dist}\,(k_1, k_2) = r\}$; the term $|S_r|$ is the number of elements in S_r, and corrects for the finite grid size. The term $n_i(t) \cdot n_j(t+\tau)$ normalizes the correlation such that $c_{ij}(t, \tau, r) > 1$ (respectively < 1) implies a positive (respectively negative) correlation at a distance r between species i at year t and species j at year $t + \tau$. Figure 4 shows that $c_{ij}(t, \tau, r)$ captures important features of the spatial structure of the data in Figure 2 in 1985. The strong tendency for *Nardus* to form aggregations appears as a large auto-correlation at small distances, whereas *Deschampsia*, which is much less clumped, has a weak auto-correlation. It can also be seen that the tendency for *Deschampsia* to be at low density in the vicinity of clumps of *Nardus* is reflected in a cross-correlation between the species which is less than 1.

The moments $n_i(t)$ and $c_{ij}(t, \tau, r)$ can be computed for an observed spatio-temporal process, and also for one generated using the functions in Section 4.1,

$\tilde{n}_i(t)$ and $\tilde{c}_{ij}(t,\tau,r)$, for some given parameters v_i. We use them to construct a function for each species i, the *pattern-deviation function* d_i, based on a weighted average of the difference between the moments of the observed process and those of the model. The smaller the value of this function, the better the parameters describe the observed spatio-temporal process. At the start of the simulated process, the stochastic model is set to the same spatial pattern as the data. As in Section 4.2, we do not attempt to estimate the parameters of all species simultaneously; the spatial patterns of species other than i are held at their field values when the stochastic model is run for species i.

The function d_i is defined as

$$d_i = w_n \cdot d_{ni} + (1 - w_n) \cdot d_{ci}$$

where

$$\begin{aligned} d_{ni} &= \sum_t w_t \left(N_i(t)\right)^2 \quad , \\ d_{ci} &= \sum_{j,t,\tau,r} w_{ij} \cdot w_{t\tau} \cdot w_r \cdot \left(C_{ij}(t,\tau,r)\right)^2 \quad , \\ N_i(t) &= \frac{n_i(t) - \tilde{n}_i(t)}{\left(n_i(t) + \tilde{n}_i(t)\right)/2} \quad , \\ C_{ij}(t,\tau,r) &= \frac{c_{ij}(t,\tau,r) - \tilde{c}_{ij}(t,\tau,r)}{\left(c_{ij}(t,\tau,r) + \tilde{c}_{ij}(t,\tau,r)\right)/2} \quad . \end{aligned}$$

The w's are weights given to the various moments and need to be chosen externally. We found it necessary to give the second-order moments a greater weight than the first-order one in order to get an improvement in the pattern; $w_n = 0.25$ was used. Moments later in the spatio-temporal process were given more weight corresponding to the greater opportunity for the stochastic model to diverge from the field spatial pattern the longer it runs. Auto-correlations ($i = j$) and cross-correlations ($i \neq j$) were given the same weight $w_{ij} = 0.25$. Correlations at large radii are likely to be affected by the finite size of the grid and were given a lower weight, using a negative exponential function of radius.

A particular value of the pattern-deviation function determines a manifold in a six-dimensional space of the parameters (i.e. $d_i = f(v_i)$). It is therefore possible to adjust the values of the model parameters iteratively in such a way that d_i goes to a local minimum. For this purpose, we developed a technique based on Powell's quadratically convergent method (Brent 1973). This algorithm takes sections across the surface in a window around the current parameter values, finds the minimum within the window on each section in turn, and updates the parameter values and the directions of the sections until no further reduction in d_i is possible. We could do no more than sample certain points along each section, because at each point the stochastic model has to be run and the moments computed. Some random variation is to be expected in the course of sampling the section, and we therefore used a least squares fit

Table 2. Parameter estimates obtained from gradient descent on the pattern-deviation function. The numbers are arithmetic means of the values obtained from iteration 41 to 50 of the gradient descent.

Species (i)	a_{iA}	a_{iD}	a_{iF}	a_{iN}	c_i	m_i
Anthoxanthum	-0.137	-0.026	-0.018	-0.016	9.900	0.520
Deschampsia	-0.085	-0.044	-0.292	-0.288	1.285	0.503
Festuca	-0.011	-0.000	-0.031	-0.109	3.627	0.101
Nardus	-0.090	0.010	0.039	-0.112	2.408	0.053

of the values of d_i to a cubic polynomial to find the local minimum along each section.

Checks on the pattern deviation function suggested that it could be rather rugged, and it is therefore important for the parameter values to be fairly close to the minimum when starting a gradient descent. For this reason, we set the parameters at the start to the values from non-linear regression (Table 1). Reductions in the pattern-deviation function were still obtained during the course of optimization for each species, and this indicates that some improvement in fit to the overall spatio-temporal process could still be achieved after non-linear regression.

Table 2 gives parameter values obtained from the gradient- descent method. The estimated values differ from those in Table 1 in that the c_i's tend to be larger, and intraspecific interactions appear stronger in *Anthoxanthum* and *Nardus*. Probabilities of movement between cells m_i's are also somewhat increased. Figure 5 gives a realization of the stochastic model using these parameter values. The realization was started in 1984 using the spatial pattern of shoots in the field as shown in Figure 2; this allows a direct comparison of the observed and simulated patterns in Figures 2 and 5. As one would expect from a stochastic realization, the exact patterns become different as time progresses; yet the major spatial features of the simulated and observed processes remain broadly comparable. There is still room for improving the match between the results of the model and patterns in the field, but this may require structural alterations to the model rather than improved methods of parameter estimation.

5. Dimension reduction

5.1. *A fundamental dilemma*

Sections 3 and 4 have dealt with the formal structure of models describing spatio-temporal processes in plant ecology, and how to estimate the parameters of these models. We now turn to questions of model analysis and interpretation, and here one is faced with a dilemma.

On the one hand, there are established analytical methods for investigating

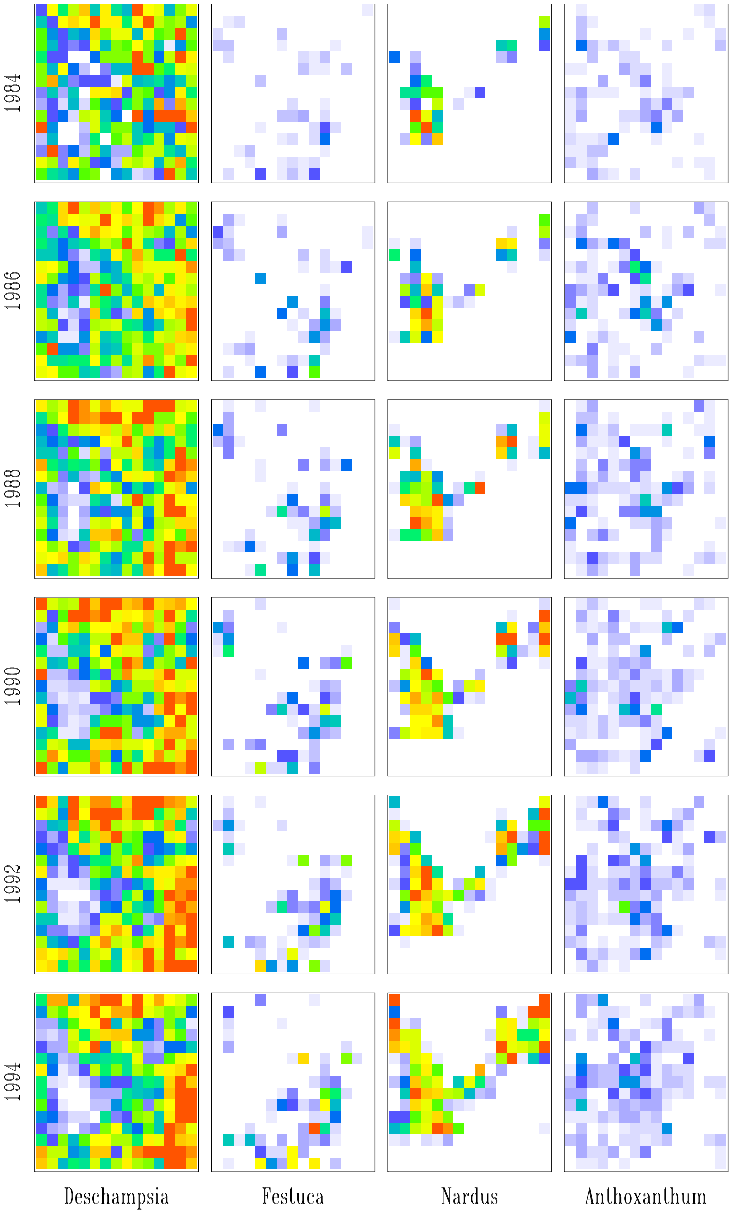

Figure 5. A realization of the stochastic model for community dynamics, based on the parameters in Table 2, estimated from gradient descent on the pattern-deviation function. Layout as described in Figure 2.

mean-field dynamics. But such mean-field models only reflect temporal change in the ecological system, and do not take into account any aspect of its spatial structure. This is why predictions from mean-field models can go widely astray as soon as the underlying ecological system is spatially heterogeneous. Nevertheless, mean-field models are convenient and tractable. The number of dynamical dimensions in such models equals the number of interacting populations within the ecological community, which may be as low as one; in the case of the Krkonoše community it would be four.

On the other hand, there are models for spatially heterogeneous communities such as those introduced in Section 3, as well as others like partial differential equations or cellular automata. These paradigms for modelling ecological systems in space all have one property in common: to describe the state of the system at any particular point in time a very large number of dynamical variables (in the order of hundreds, thousands or ten-thousands) has to be specified. Such numbers reflect the huge amount of information potentially present in a spatial pattern and are the reason why we refer to such models as high-dimensional. Dynamical models of this complexity entail poor efficiencies in numerical simulations and preclude utilizing the rich tool-box of analytical methods devised, for instance, in bifurcation theory. Even worse, the interpretation, prediction and understanding of complex spatial models can be close to impossible since it may be far from obvious on which quantities or abstract entities a mechanistic explanation of dynamical phenomena observed eventually should be based. Powerful predictions from ecological models are based either (i) on analytical methods – which for high- dimensional spatial models are always difficult and very often not feasible, or (ii) on heuristically establishing causal relations with qualitative conditionals and conclusions – a goal which is notoriously hard to achieve for the more complex spatially explicit models.

In summary, researchers investigating spatial dynamics in ecology are confronted with a decision either to use complex models that have a tendency to be incomprehensible, or to use models that are tractable but dangerously over-simplified.

5.2. The potential for dimension reduction

In this situation one might hope to find some middle ground comprising dynamical models of low dimensionality that capture essential features of spatial heterogeneity. Such models would combine the virtues of both extremes, simultaneously achieving sufficient accuracy and retaining tractability, whilst avoiding both over-simplification and excessive complexity. This is not an idle hope. Rand and Wilson (1995) have demonstrated that the spatio- temporal population dynamics of a particular three-species community can be reduced to a four-dimensional dynamical system. Evidently the introduction of a single extra dimension was sufficient to reflect the effects of spatial patterns within the community. Rand and Wilson employed a numerical (or top-down) approach and, as a consequence, an ecological interpretation of the fourth dynamical variable was not made. A constructive (or bottom-up) approach on the other hand would ensure that the dynamical variables introduced are readily interpretable, and also would give deeper insights into those aspects of spatio-temporal dynamics that are essential for shaping ecological change observed.

Why should techniques of dimension reduction conceivably work for spatio-temporal processes in ecology? Many ecological communities are characterized by two general features. First, the interactions between individuals in such systems operate at a local scale. In other words, the spatial distance over which one individual affects another is small relative to the spatial extension of the system as a whole. For example, in the Krkonoše community the interaction of tillers decays rapidly with spatial distance: interactions at 5 cm are already weak, and interactions over distances greater than 20 cm are negligible. Second, there are several sources of stochastic fluctuation in the population dynamics, including demographic stochasticity and environmental noise; these introduce perturbations that counteract the deterministic changes resulting from ecological interactions. Together these two features mean that deterministic effects predominate only at short spatial scales; deterministic influences over larger distances become drowned in the stochastic fluctuations. In consequence, spatial patterns which imply a high degree of spatial correlation between distant locations in space are very unlikely to be realized in such systems.

From this argument we can infer further that, of all the patterns possible, only those from a certain subset, characterized by the absence of long-range correlations, are at all likely to occur. The dynamics of such ecosystems thus effectively reduce to the set R of sufficiently likely patterns. The variables that distinguish patterns in the set R from patterns in the set R' (which are not in R) do not correspond to essential dynamical degrees of freedom and are dispensable. By removing them from the dynamical description of the full spatio-temporal model, the number of variables remaining and hence the dimensionality of the model is reduced.

5.3. Which statistics should be chosen?

When we refer to variables for describing spatio-temporal processes in a low-dimensional dynamical system, we are talking about various kinds of spatial statistics. At each time step of the spatial dynamics a particular pattern is realized. For example, in a discrete-space model, the pattern can be specified by simultaneously describing the state of each cell. Alternatively, a partial description of the pattern is given by counting the number of individuals in each species. Or one might specify the number of patches exceeding a certain size for each species. Or one could work from the frequency distribution of patch sizes, or employ specific indices, characterizing degrees of clumping or clump shapes, as is occasionally done in plant ecology. The set of spatial statistics we could consider for any given pattern appears to be inexhaustable. If aspects of spatial heterogeneity are to be included as dynamical variables, the choice of an appropriate set of spatial statistics has to be made. What should this be?

The simple answer is that no unique solution exists. But we can at least give some conditions that the statistics should meet. As a trivial first condition, these statistics are required to measure spatial heterogeneities. Second, they should possess a meaningful ecological interpretation. Third, they should be accessible to measurements in the field and, as far as possible, they should correspond to common practice in ecological field work. Eventually, and this is the strongest condition, a convenient set of spatial statistics can be subdivided into subsets S and S' such that:

C1. the statistics from S and S' together unambiguously characterize each of the spatial patterns possible,

C2. the statistics in S differentiate sufficiently well between spatial structures in R,

C3. statistics from S' assume constant values in R.

A slightly less demanding alternative to condition C3 is given by assuming that in R the values of statistics from S' can be inferred from the values of statistics from S. However, in this case redefining the statistics in S' by subtracting their predicted values obtained from S suffices to fulfill condition C3 again.

In addition to those sketched above, there is a further important condition for choosing statistics. The next section is concerned with this.

5.4. Relaxation projections

Initial configurations of a spatial ecological process can be taken from the set of all possible patterns, i.e. the union of the sets R and R' denoted by $R \cup R'$. In contrast, the set of patterns likely to be found after the process has run for a while is just R. So what happens in between?

In Section 5.2 we have seen that the mapping $R \cup R'$ results from the destruction of global correlations. For distances larger than the interaction range, the rate for this transition is proportional to the sum of demographic and environmental noise. In consequence, the decay of long-range order often is very fast relative to the dynamics of short-range correlations. This separation of time scales guarantees that, even when starting the spatio-temporal process from an arbitrary pattern in $R \cup R'$, after a short time τ a reduced dynamic, operating merely in R, obtains with good accuracy.

For ecological systems in the field that have been left sufficiently undisturbed in the past, the period τ will have already passed. Consequently, the entire dynamics $p(t)$ starting from a current pattern $p(0)$ will lie within R. Spatial statistics obeying C1 to C3 then provide the basis of a dimensionally reduced dynamical description. On the other hand, for ecological systems starting from an arbitrary initial pattern, the reduced dynamics have to apply to initial patterns in R' as well as R, and a further condition for the spatial statistics is helpful.

C4. At time t, the dynamics of any pattern starting from $p(0)$ in $R \cup R'$ with spatial statistics $S \cup S'$ and $S'(p(0))$ are well approximated by $S(p(\tau)) = S(p(0))$ and $S'(p(\tau)) = S'_\infty$, where S'_∞ is the set of constant values that the S' statistics take in R.

Mathematically the mappings $R \cup R' \to R$ and $S \cup S' \to S \cup S'_\infty$ are projections. They project the full space of possible patterns onto the subspace of those patterns likely to be realized after the fast degrees of freedom (i.e. the long-range correlations) have relaxed. Such mappings that mimic the relaxation process we therefore call *relaxation projections*. Any spatial statistics obeying conditions C1 to C4 define such relaxation projections. In general, projections are non-invertible mappings. Objects projected consequently carry a diminished amount of information. In particular, relaxation projections remove the dynamically non-essential information from a spatial pattern.

5.5. Correlation dynamics

Here we illustrate the general principles proposed in Sections 5.1 to 5.4, focusing on a single species, and using a model continuous in space and time as introduced in Section 3.1. To do this, we take a simple choice for the ecological rates,

$$\begin{aligned} d(x,p) &= D \quad , \\ m(x,x',p) &= M(x'-x) \quad , \\ b(x,p) &= B\left(n(x,p)\right) \quad . \end{aligned}$$

This means that the per capita death rate is a positive constant D, and that the per capita probability of movement from x to x' per unit time is a non-negative function of the distance between the points x and x'. The per capita birth rate is a non-negative function of the local abundance of individuals in the pattern p around location x, defined by

$$n(x,p) = \int dx'\, W(x'-x) \cdot p(x')$$

where $W(x'-x)$ is a weighting for locations x' at distance x' with x'. This illustrative ecological model thus incorporates birth rates which are locally density-dependent, while processes of death and movement occur independent of densities.

A particular set of spatial statistics fulfilling conditions C1 to C4 is given by correlation functions. For a pattern p of area A, spatial correlation functions of order n are defined by

$$C_n(\xi_1, ..., \xi_{n-1}, p) = \frac{1}{A} \cdot \int dx_1\, p(x_1) \cdot \prod_{k=1}^{n-1} p(x_1 + \xi_k) \quad .$$

Thus, the first-order correlation function

$$C_1(p) = \frac{1}{A} \cdot \int dx_1 \; p(x_1)$$

is just the global density of individuals within the spatial pattern p, whereas the second-order correlation function

$$C_2(\xi_1, p) = \frac{1}{A} \cdot \int dx_1 \; p(x_1) \cdot p(x_1 + \xi_1)$$

measures the density of pairs of individuals at distance ξ_1. Each higher-order correlation introduces a further distance ξ_2, ξ_3 , . . . , as individuals are taken in triples, quadruples, and so on.

In the space of all patterns, expected values C_1, $C_2(\xi_1)$, $C_3(\xi_1, \xi_2)$, . . . of the correlation functions are obtained as

$$C_n(\xi_1, ..., \xi_{n-1}) = \int Dp \; P(p) \cdot C_n(\xi_1, ..., \xi_{n-1}, p) \quad .$$

We use this to translate from a stochastic process $d/dt \; P(p)$ in the space of patterns p to a deterministic ynamic in the space of statistics C_n. As a first step, the dynamics of the first-order correlation-function C_1 are

$$\frac{d}{dt} C_1 = \frac{1}{A} \cdot \int Dp \; \frac{d}{dt} P(p) \cdot \int dx_1 \; p(x_1)$$

and, after some algebra, this yields

$$\frac{d}{dt} C_1 = \frac{1}{A} \cdot \int Dp \; P(p) \; \int dx_1 \left[B \left(\int dx_2 \; W(x_2 - x_1) \cdot p(x_2) \right) - D \right] \cdot p(x_1) \quad .$$

As we want to transform the right hand side of this equation to the form of correlation functions, we make the simplifying assumption that the function B is linear, $B(n) = B_0 + B_1 \cdot n$. The ecological implication of this assumption is that the per capita birth rate is linear in local abundance, i.e. it is of logistic or Lotka-Volterra type. From this we obtain

$$\frac{d}{dt} C_1 = (B_0 - D) \cdot C_1 \; + \; B_1 \cdot \int d\xi_1 \; W(\xi_1) \cdot C_2(\xi_1) \quad .$$

For spatially homogeneous systems the relation $C_2(\xi_1) = C_1 \cdot C_1$ holds and the dynamics of C_1 in this case simply reduce to the mean-field result

$$\frac{d}{dt} C_1 \quad = \quad (B_0 - D) \cdot C_1 \; + \; B_1 \cdot C_1^2 \quad .$$

For spatially heterogeneous systems, however, the mean-field result is incorrect and the dynamics of the first-order correlation function C_1 are contingent on those of the second-order correlation function $C_2(\xi_1)$. Therefore we need to work out the dynamics of C_2, and these are given by the equation

$$\begin{aligned}
\frac{1}{2}\cdot\frac{d}{dt}\,C_2(\xi_1) \quad &= \quad (B_0 - D - |M|)\cdot C_2(\xi_1) \\
&+ \quad B_1\cdot\int d\xi_2\; W(\xi_2)\cdot C_3(\xi_1,\xi_1+\xi_2) \\
&+ \quad \int d\xi_2\; M(\xi_2)\cdot C_2(\xi_1+\xi_2) \\
&+ \quad \delta(\xi_1)\cdot C_1\cdot\left(B_0 + B_1\cdot\int d\xi_2\; W(\xi_2)\cdot C_2(\xi_1)\cdot C_1^{-1}\right)
\end{aligned}$$

with $\int d\xi_1 M(\xi_1) = |M|$. We are omitting the delta peak at distance $\xi_1 = 0$, resulting from self-pairing. Notice on the right hand side of this equation that the dynamics of C_2 depend on that of C_3.

This observation can be generalized: independent of the order n we consider, the dynamics of C_n are contingent upon C_{n+1}. The sequence of equations that results is referred to as a *moment hierarchy*, and it prohibits the use of the dynamical equation for C_2, unless we simultaneously consider the dynamics of C_3 etc. We face a problem of *moment closure* which can only be resolved by truncating moment hierarchies using appropriate approximations. For instance, we already have seen that, with the relation $C_2(\xi_1) = C_1\cdot C_1$, we could remove the C_2 dependence from the C_1 dynamics, and obtain the mean-field equation.

We now can improve on the simple mean-field approximation by truncating the hierarchy of spatial correlation functions at order 2 instead of 1. This is achieved by the relation $C_3(\xi_1,\xi_2) = C_2(\xi_1)\cdot C_2(\xi_2)\cdot C_1^{-1}$, from which the following equation for the dynamics of C_2 is obtained:

$$\begin{aligned}
\frac{1}{2}\cdot\frac{d}{dt}\,C_2(\xi_1) \;=\; &\left(B_0 \;- D - |M| +\; B_1\cdot\int d\xi_2\; W(\xi_2)\cdot C_2(\xi_1+\xi_2)\cdot C_1^{-1}\right)\times \\
&\times C_2(\xi_1) \quad + \quad \int d\xi_2\; M(\xi_2)\cdot C_2(\xi_1+\xi_2) \\
&+ \quad \delta(\xi_1)\cdot C_1\cdot\left(B_0 + B_1\cdot\int d\xi_2\; W(\xi_2)\cdot C_2(\xi_1)\cdot C_1^{-1}\right).
\end{aligned}$$

As a result, the set of equations for the dynamics of C_1 and C_2 now is closed. The two equations provide a natural escape from the over-simplified mean-field models. By utilizing the second-order correlation function C_2, these dynamics are well suited to deal with the spatial heterogeneities that occur in many ecological systems.

These results are first steps towards more general techniques for reducing the complexity of spatial ecological models. A number of promising extensions can be considered.

First, the assumption of linearity made for the dependence of per capita rates (like e.g. B) on local abundances should be removed. This is important for two reasons. (i) The response of individuals to changes in their environment is often non-linear. (ii) Owing to stochastic fluctuations caused by the finite sizes of interaction ranges, local environments are bound to differ across individuals. Consequently the mean response of a population to a distribution of environments can differ from the response predicted for the distribution mean. To compensate for this effect *fluctuation corrections* are required; these act in addition to the *correlation corrections* derived above. This results in a two-fold moment hierarchy, that deals with departures from homogeneity originating either from spatial correlations or from stochastic fluctuations (DIECKMANN and LAW 1999).

Second, as long-range order is often absent in ecological systems, correlation functions carry essential information only for short distances. For this reason a short-range expansion of the equation for C_2 can provide a good approximation to its functional version. The dynamics of the correlation function might then be approximated by the dynamics of (i) its intensity at distance zero and (ii) its exponential range of increase or decay. This would achieve the goal of reducing the dynamical dimension of spatio-temporal models, making the dimension as low as three or even two in the case of single-species systems.

Third, some of the structural assumptions underlying the modeling approach presented could be relaxed. Individuals may be given internal degrees of freedom as well as spatial extension, environmental heterogeneities could be introduced, and the premise of pairwise interactions, presently pervading most research on spatial ecological systems, could be challenged.

Fourth, correlation functions are not the only choice of spatial statistics for dimension reduction (DIECKMANN and LAW 1999). There are several advantages of these functions: (i) truncating their moment hierarchy at correlation order 2 yields a natural extension of mean-field models, (ii) correlation functions are measurable and ecologically meaningful, and (iii) these functions are closely related to our understanding of correlation destruction and therefore are expected to define reliable relaxation projections. For particular systems, however, other projections might be more appropriate. Eventually a suite of successful projections and statistics should become available to help ecologists reduce complex spatio-temporal models to manageable low-dimensional representations.

6. CONCLUDING COMMENTS

We have defined three different classes of individual-based stochastic models to provide formal descriptions of spatio-temporal processes in ecology. With these models transitions between continuous and discrete representations both in the spatial and in the temporal domain are supported. This amounts to a first step in establishing a network of formal links between different classes of spatially explicit models in ecology. We also have devised two quite different techniques for estimating parameters of spatio-temporal models. These methods have the potential to uncover some of plant ecology's better guarded secrets, such as the strength of interactions between species. However, in particular the methods for fitting parameters based on spatio-temporal moments of observed and simulated processes are novel and require further exploration.

Systematic methods for the dimension reduction of spatio-temporal processes in ecology are just becoming available. Current results are promising, yet the strengths and shortcomings of these innovative techniques have to be delineated in more detail (LAW and DIECKMANN 1999, LAW and DIECKMANN in press). Many of the questions of interest to a plant ecologist depend on developments in this area. For instance, how appropriate are the mean-field approximations widely used in plant ecology? Can self-maintaining spatial patterns develop under reasonable assumptions about parameter values; in other words, is WATT'S (1947) paradigm of pattern and process supported by formal analysis? What conditions are needed for plant communities to generate their own spatial structure? Do alternative spatial or spatio-temporal structures (i.e. alternative attractors) develop when starting from different initial patterns? Low-dimensional dynamical systems that provide us with approximations to the full dynamics of spatio-temporal processes would be of great help in ecology in answering questions such as these.

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