

Spatial and space–time correlations in ecological models

Bryan K. Epperson *

Department of Forestry, Michigan State University, East Lansing, MI 48824, USA

Abstract

Space–time autoregressive moving average (STARMA) processes can be used to represent a wide range of theoretical models of ecological variation and statistical models for analyzing ecological data. Many discrete-time, discrete-space ecological processes can be analyzed using STARMA theorems. As an example, one focus is on population genetic models, and using STARMA we obtain not only the usual spatial variance and correlations, but also the space–time correlations. Examples show how this allows one to characterize general space–time population genetic processes in a new and more detailed way. STARMA processes include migration-drift models with general patterns of migration among populations. They also include processes with features that are more realistic for many natural population systems, including various forms of stochastic migration. The space–time correlations are particularly important because they allow us to connect data to theoretical processes, and they can be used for estimating migration rates, model-fitting, testing, and forecasting the future behavior of real systems. The space–time correlations also specify the relationship between spatial correlations at different spatial distances, thus bridging gaps between observations on spatial correlations and inferences about dispersal and selection, and other aspects of the underlying space–time process. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Space–time correlations; Ecological models; Migration; Spatial pattern; Spatial autocorrelation

1. Introduction

In the Congress address of the opening ceremony of the 1994 INTECOL Congress, Dr John Lawton emphasized the urgency and vitalness of modeling the propagation of small-scale ecological processes over time into large-scale spatial patterns. Most ecological variables fit the First Law of Geography: everything is related to everything else, but near things are more related than are distant things (for example, Tobler, 1972). This implies spatial autocorrelation: ecological

variables are rarely, if ever, randomly distributed in space. For several decades, statistical geographers have pointed out that space–time models (i.e. dynamic spatial models) are required to understand spatial patterns. This is particularly true for variables such as those in ecology, where ecological traits at nearby locations interact over time and not ‘instantaneously’ (as can occur in electrical fields, for example). In such cases, purely spatial models or analyses fail (for example, Haining, 1977, 1978, 1979). In this paper, we examine models that connect geographic or spatial patterns to space–time processes. The focus is on ecological genetics; however, some considerations

* Tel.: + 1-517-355-9597; fax: + 1-517-432-1143.

of general ecological variables are examined. As an example of the general methods, the high levels of spatial autocorrelations expected in geographic genetic distributions are used to estimate dispersal of individuals as a demographic component of ecological processes, using the information content in genetic variation. The models used are stochastic spatial time series (space–time autoregressive moving average (STARMA)), which are appropriate for studying many theoretical ecological processes (for example, Cliff and Ord, 1975, 1981; Ord, 1979). STARMA can be used to model and to estimate many types of interactions between locations via spatial proximity, and through time, in a way that properly accounts for spatial autocorrelations in real systems.

2. STARMA models of theoretical processes

In all of the processes, analyzed sites either are, or can be treated as, discrete areas, and their locations are in some sense regularly spaced (i.e. there is a well defined support; Hooper and Hewings, 1981). In general, there may be boundaries to the system of sites but, for notational convenience, we will here assume that the interactions among sites depend only on their relative locations, usually in terms of spatial order of proximity (i.e. the ‘spatial’ order on the support). Let $z_{\mathbf{x},t}$ denote the value of some ecological variable at a site whose location is defined by spatial coordinates in the vector \mathbf{x} , at generation t . Then, the general STARMA model has the stochastic equation:

$$z_{\mathbf{x},t} = \sum_{s=1}^m \sum_{\mathbf{b}} \phi_{\mathbf{b},s} z_{\mathbf{x}+\mathbf{b},t-s} - \sum_{s=1}^n \sum_{\mathbf{b}} \theta_{\mathbf{b},s} c_{\mathbf{x}+\mathbf{b},t-s} + a_{\mathbf{x},t} \quad (1)$$

The spatial summations in this equation are over all k coordinates contained in vectors \mathbf{b} , including $\mathbf{0}$. It is further assumed that there are finite numbers of sites that contribute interaction influences to any particular site. Thus, the summations are taken over a certain range of spatial lags for each spatial dimension k (i.e. b_k ranges from $-l_{1k}$ to l_{2k}). It is convenient to separate shared ($c_{\mathbf{x},t}$) from unshared ($a_{\mathbf{x},t}$) stochastic inputs

(Epperson, 1993a, 1994). The expected values, $Ez_{\mathbf{x},t}$, $Ec_{\mathbf{x},t}$, and $Ea_{\mathbf{x},t}$ are zero; all $c_{\mathbf{x},t}$ and $a_{\mathbf{x},t}$ have equal variances, σ_c^2 and σ_a^2 , respectively; and all $Ec_{\mathbf{x},t} \cdot c_{\mathbf{x}+\mathbf{b},t-s} = 0$ and $Ea_{\mathbf{x},t} \cdot a_{\mathbf{x}+\mathbf{b},t-s} = 0$ unless $\mathbf{b} = \mathbf{0}$ and $s = 0$, and $Ea_{\mathbf{x},t} \cdot c_{\mathbf{x}+\mathbf{b},t-s} = 0$ for all \mathbf{b} and s (Aroian, 1985). Note that this assumes the interactions are constant over the time of the process. However, the strength of interactions of past variables with different time lags may vary. The temporal order of the autoregressive component is m and that of the moving average component is n . Note that the temporal summations start from 1, and that instantaneous interactions are not possible. We have also assumed here that the variables have been mean adjusted and/or trend adjusted. Considerable results can be expressed for this general model, including identification of the partial space–time correlation function. However, in this paper, we will discuss in detail only systems that are Markovian in the sense that there are no time-lagged effects, and thus any time period depends only on the preceding time period. In this case, the stochastic equation simplifies to:

$$z_{\mathbf{x},t} = \sum_{\mathbf{b}} \phi_{\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t-1} - \sum_{\mathbf{b}} \theta_{\mathbf{b}} c_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t} \quad (2)$$

Here, we will consider, in detail, cases in which the relative strengths of shared stochastic inputs are the same as the autoregressive components, i.e. $-\phi_{\mathbf{b}} = \theta_{\mathbf{b}}$. Then, for such processes:

$$z_{\mathbf{x},t} = \sum_{\mathbf{b}} \phi_{\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t-1} + \sum_{\mathbf{b}} \phi_{\mathbf{b}} c_{\mathbf{x}+\mathbf{b},t-k} + a_{\mathbf{x},t} \quad (3)$$

It is important to note that the autoregressive component represented by the first term includes the expected or deterministic effects of values of the variable on communicating or interacting variables. The second term represents any of a wide variety of ‘moving average’ stochastic effects that are directly shared by multiple locations during a single time period, and due to their spatial proximity. The final term is an independent stochastic input that directly affects only one site during one time period, although it may constitute a summation of various direct stochastic inputs (Epperson, 1994).

In the case where there are no shared stochastic inputs, the equation simplifies further to:

$$s_{\mathbf{x},t+1} = \sum_{\mathbf{b}} \phi_{\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t} + a_{\mathbf{x},t+1} \quad (4)$$

This is a simplified STARMA process known as a space–time autoregressive (STAR) process (Epperson, 1993b), which in this case has temporal order one.

In general, unshared stochastic inputs increase the variance of the ecological variable, z , among sites, but do not change the pattern of spatial and space–time correlations; whereas shared stochastic inputs typically will induce different spatial and space–time correlations (Epperson, 1994).

In some situations, we may wish to consider only the short-term dynamics, which is straightforward. However, we may also want to characterize the stationary distributions in great detail. If temporal stationarity occurs, then the space–time covariances ($\gamma_{\mathbf{b},n}$) and correlations ($\rho_{\mathbf{b},n}$), as well as the purely spatial covariances ($\gamma_{\mathbf{b},0}$) and correlations ($\rho_{\mathbf{b},0}$), are defined in terms of the spatial (\mathbf{b}) and temporal (n) lags separating pairs of site variables in space and time (Hooper and Hewings, 1981). Thus, $\gamma_{\mathbf{b},n} = E(z_{\mathbf{x},t} z_{\mathbf{x}-\mathbf{b},t-n})$ for $n = 0, \infty$ and, for all spatial lag vectors \mathbf{b} , $\rho_{\mathbf{b},n} = \gamma_{\mathbf{b},n} / \sigma_z^2$, where $\sigma_z^2 = E(z_{\mathbf{x},t}^2)$ for all \mathbf{x} and t .

Introducing the backshift operator allows derivation of general conditions for stationarity, and results on correlations. B_t is the backshift operator in time, and B_i is the backshift operator in the negative (‘backward’) direction for each spatial dimension x_i . Thus:

$$z_{\mathbf{x}-\mathbf{b},t-n} = B_1^{b_1} B_2^{b_2} \dots B_t^n z_{\mathbf{x},t} \quad (5)$$

where $\mathbf{b} = (b_1, b_2, \dots, b_k)$. For the restricted case of temporal order one, Eq. (2) becomes:

$$z_{\mathbf{x},t} = \sum_{\mathbf{b}} \phi_{\mathbf{b}} B_1^{-b_1} \dots B_k^{-b_k} B_t z_{\mathbf{x},t} - \sum_{\mathbf{b}} \theta_{\mathbf{b}} B_1^{-b_1} \dots B_k^{-b_k} B_t c_{\mathbf{x},t} + a_{\mathbf{x},t} \quad (6)$$

If we let

$$\Theta(B_{\mathbf{x}}, B_t) = 1 - \sum_{\mathbf{b}} \phi_{\mathbf{b}} B_1^{-b_1} B_2^{-b_2} \dots B_k^{-b_k} B_t$$

$$\Theta(B_{\mathbf{x}}, B_t) = 1 - \sum_{\mathbf{b}} \theta_{\mathbf{b}} B_1^{-b_1} B_2^{-b_2} \dots B_k^{-b_k} B_t$$

then

$$\Phi(B_{\mathbf{x}}, B_t) z_{\mathbf{x},t} = \Theta(B_{\mathbf{x}}, B_t) c_{\mathbf{x},t} + a_{\mathbf{x},t} \quad (7)$$

In the case where the relative strengths of shared interactions are generally equal to those for deterministic (expected value) terms, Eq. (3) can be re-written:

$$\left(1 - \sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}} B_t\right) z_{\mathbf{x},t} = \left(\sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}} B_t\right) c_{\mathbf{x},t} + a_{\mathbf{x},t} \quad (8)$$

$$\Phi(B_{\mathbf{x}}, B_t) z_{\mathbf{x},t} = [-\Phi(B_{\mathbf{x}}, B_t) - \phi_{\mathbf{0}} B_{\mathbf{x}}^{\mathbf{0}} B_t + 1] c_{\mathbf{x},t} + a_{\mathbf{x},t}$$

The function $\Phi^{-1}(B_{\mathbf{x}}, B_t)$ (Epperson, 1993a) can be written

$$\Phi(B_{\mathbf{x}}, B_t)^{-1} = \sum_{d=0}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^d \quad (9)$$

Thus,

$$\begin{aligned} z_{\mathbf{x},t} &= [-1 - \Phi^{-1}(B_{\mathbf{x}}, B_t) \phi_{\mathbf{0}} B_t + \Phi^{-1}(B_{\mathbf{x}}, B_t)] c_{\mathbf{x},t} \\ &\quad + \Phi^{-1}(B_{\mathbf{x}}, B_t) a_{\mathbf{x},t} \\ &= \left[-1 - \phi_{\mathbf{0}} B_t \sum_{d=0}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^d\right. \\ &\quad \left.+ \sum_{d=0}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^d\right] c_{\mathbf{x},t} \\ &\quad \left.+ \sum_{d=0}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^d a_{\mathbf{x},t}\right. \\ &= \left[-\phi_{\mathbf{0}} \sum_{d=0}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^{d+1}\right. \\ &\quad \left.+ \sum_{d=1}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^d\right] c_{\mathbf{x},t} \\ &\quad \left.+ \sum_{d=0}^{\infty} \left(\sum_{\mathbf{b}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}}\right)^d B_t^d a_{\mathbf{x},t}\right. \end{aligned} \quad (10)$$

Another expression can be found using Eq. (8) directly, giving:

$$\begin{aligned} z_{\mathbf{x},t} &= \Phi^{-1}(B_{\mathbf{x}}, B_t) \left(\sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} B_{\mathbf{x}}^{-\mathbf{b}} B_t\right) c_{\mathbf{x},t} \\ &\quad + \Phi^{-1}(B_{\mathbf{x}}, B_t) a_{\mathbf{x},t} \end{aligned} \quad (11)$$

Stationarity for STARMA models depends only on the form of the autoregressive (AR)

terms, not the moving average (MA) terms. Stationarity for the restricted models requires that the inverse of $\Phi(B_x, B_t)$, $\Phi^{-1}(B_x, B_t)$, converges for $|B_t| \leq 1$ and all $|B_x| \leq 1$ (Taneja and Aroian, 1980). A sufficient but not necessary set of conditions for convergence of $\Phi^{-1}(B_x, B_t)$ is the situation where all of the ϕ_b are of the same sign, a finite number of them are nonzero, and $|\sum \phi_b| < 1$ (Epperson, 1993a). Thus, the models of shared stochastic effects are generally stationary if the corresponding models with only AR terms are stationary.

Stationarity conditions have a number of implications for applicability of STARMA to ecological processes in general. Models are much simpler if the interaction parameters (or some transformation of them, e.g. in time or in form) can be treated as approximately constant. However, if parameters change in a cyclic fashion, then modified STARMA models can be used (STARIMA). If parameters change in some systematic manner, then a multi-temporal lag STARMA model would be appropriate, and it could be stationary under some conditions (Pfeifer and Deutsch, 1980b).

Invertibility requires similar conditions for convergence of $\theta^{-1}(B_x, B_t)$, which in the present models is $\Phi^{-1}(B_x, B_t)(\sum \phi_b B_x^{-b} B_t)$, which has the same convergence properties as does $\Phi^{-1}(B_x, B_t)$. If a STARMA process is both invertible and stationary, then:

$$a_{x,t} = \Phi(B_x, B_t) \theta^{-1}(B_x, B_t) z_{x,t} \quad (12)$$

$$z_{x,t} = \theta(B_x, B_t) \Phi^{-1}(B_x, B_t) a_{x,t} \quad (13)$$

Thus, these processes can be expressed as infinite STAR processes, but we are more interested in expressing them as ‘infinite’ parameter space–time moving average (STMA) processes (Eq. (13)). In general, the generating function, $\Psi(B_x, B_t)$, can be used to obtain the coefficients for individual moving average inputs, $\psi_{b,n}$, for different spatial, \mathbf{b} , and temporal lags n of the infinite STMA representation of the process. The form of $\Psi(B_x, B_t)$ can be found through long division of $\theta(B_x, B_t)$ by $\Phi(B_x, B_t)$ (Taneja and Aroian, 1980; Hooper and Hewings, 1981). The $\psi_{b,n}$ can be used to find the variance and the spatial and space–time correlations, using Theorem 4.9 of Aroian (1985):

$$\sigma_z^2 = \sigma_a^2 \sum_{\mathbf{x}} \sum_{k=0}^{\infty} \psi_{\mathbf{x},k}^2 \quad (14)$$

$$P_{\mathbf{b},n} = \frac{\sum_{\mathbf{x}} \sum_{k=0}^{\infty} \psi_{\mathbf{x},k} \psi_{\mathbf{x}+\mathbf{b},k+n}}{\sum_{\mathbf{x}} \sum_{k=0}^{\infty} \psi_{\mathbf{x},k}^2} \quad (15)$$

Here, the summation limits are infinite in each spatial direction and in time. Finite spatial and temporal limits on the sums provide close approximations of σ_z^2 and $p_{\mathbf{b},n}$, because the $\psi_{b,n}$ rapidly approach zero as $k \rightarrow \infty$ or as the spatial lag in any dimension goes to infinity.

Other equations can be obtained that give relationships between different space–time correlations, from the autocovariance generating function (Aroian, 1985), or by multiplying Eq. (3) by $z_{\mathbf{x}+\mathbf{b},t-k}$ and taking expectations.

2.1. Demographic ecological genetic models

In population genetic models, the ecological variable is some genetic attribute and, for simplicity, we assume the variable $z_{x,t}$ denotes the frequency of a gene in each population defined by spatial coordinates in the vector \mathbf{x} , at generation t , in the adults, after genetic drift, but before migration. Each population contains N individuals. From each population, a group of emigrants may be chosen in various ways, depending on the model. The events that govern the genetic make-up of these groups determine the nature of the moving average terms (Epperson, 1994).

Each migrant group will move to different populations at vector locations $\mathbf{x} - \mathbf{b}$ each located at different spatial lags contained in the vector \mathbf{b} from \mathbf{x} , where they will form a proportion ϕ_b of the juveniles. (The ϕ_b are taken to be migration rates, and they are assumed to be constants.) These groups, and another proportion, m_∞ , controlled by an ‘outside systematic pressure’ (Malécot, 1973, 1975), and the remainder from the resident contributions, and finally genetic drift acting within each population, form the gene frequencies in the next adult generation, $z_{x,t+1}$. Here, we will consider only the cases in which the temporal order is one. Then the general equations for the processes considered in this paper have a

deterministic (AR) part (expected values) of the form:

$$E(z_{\mathbf{x},t+1}) = \left(1 - \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} - m_{\infty}\right) z_{\mathbf{x},t} + m_{\infty} z_{\infty} + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} z_{\mathbf{x} + \mathbf{b},t} \quad (16)$$

Letting

$$\phi_{\mathbf{0}} = 1 - \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} - m_{\infty}$$

we have the stochastic equation

$$z_{\mathbf{x},t+1} = m_{\infty} z_{\infty} + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} z_{\mathbf{x} + \mathbf{b},t} + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} c_{\mathbf{x} + \mathbf{b},t} + a_{\mathbf{x},t+1} \quad (17)$$

The first two terms (the deterministic components), together with the last term, constituted essentially all previous population genetic models, which had deterministic gene frequencies in migrant groups, until the models of Epperson (1994). It has been shown that the inverse, $\Phi^{-1}(B_{\mathbf{x}}, B_t)$, essentially always converges as a direct result of the population biological meaning of the migration parameters, i.e. all of the $\phi_{\mathbf{b}}$ are non-negative, and a finite number of them are nonzero, if $m_{\infty} > 0$ (Epperson, 1993b). Thus, the models of shared stochastic migration effects are generally stationary.

For the present processes of interest, we have

$$z_{\mathbf{x},t} = \Phi^{-1}(B_{\mathbf{x}}, B_t) \left(\sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} B_{\mathbf{x} - \mathbf{b}}^{-1} B_t \right) c_{\mathbf{x},t} + \Phi^{-1}(B_{\mathbf{x}}, B_t) a_{\mathbf{x},t} \quad (18)$$

Note that $z_{\mathbf{x},t}$ is the sum of two infinite moving average processes $\psi_{\mathbf{b},n}^{(c)}$ and $\psi_{\mathbf{b},n}^{(a)}$. For example, $\psi_{\mathbf{b},0}^{(c)} = 0$ for all \mathbf{b} (including $\mathbf{0}$), $\psi_{\mathbf{0},0}^{(a)} = 1$, and $\psi_{\mathbf{b},0}^{(a)} = 0$ for $\mathbf{b} \neq \mathbf{0}$. Examining for each temporal lag n in the first expression, for which in finding $\psi_{\mathbf{b},n}^{(c)}$, the first term is set to $d = n$, and for the second term, $d = n - 1$, we see that for $n > 0$, $\psi_{\mathbf{b},n}^{(c)} = \psi_{\mathbf{b},n}^{(a)} - \phi_{\mathbf{0}} \psi_{\mathbf{b},n-1}^{(a)}$. Thus, for example, $\psi_{\mathbf{b},1}^{(c)} = \phi_{\mathbf{b}}$ for $\mathbf{b} \neq \mathbf{0}$, and $\psi_{\mathbf{0},1}^{(c)} = 0$. The second expression gives

$$\psi_{\mathbf{n},k}^{(c)} = \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} \psi_{\mathbf{n} - \mathbf{b},k-1}^{(a)}$$

These relationships provide convenient ways to compute the $\psi_{\mathbf{b},n}^{(c)}$ from the $\psi_{\mathbf{b},n}^{(a)}$, which can be found from STAR analogues. Considering the variance, and spatial and space–time correlations, when calculating $E(z_{\mathbf{x},t} z_{\mathbf{x} - \mathbf{l},t - m})$, the expected values of the crossproducts between all $c_{\mathbf{x},t}$ and all $a_{\mathbf{x},t}$ are zero. Thus,

$$p_{\mathbf{b},n} = \left(\sigma_c^2 \sum \sum \psi_{\mathbf{n},k}^{(c)} \psi_{\mathbf{n} + \mathbf{b},k+n}^{(c)} + \sigma_a^2 \sum \sum \psi_{\mathbf{n},k}^{(a)} \psi_{\mathbf{n} + \mathbf{b},k+n}^{(a)} \right) + \left(\sigma_c^2 \sum \sum \psi_{\mathbf{n},k}^{2(c)} + \sigma_a^2 \sum \sum \psi_{\mathbf{n},k}^{2(a)} \right) \quad (19)$$

and,

$$\sigma_z^2 = \left(\sigma_c^2 \sum \sum \psi_{\mathbf{n},k}^{2(c)} + \sigma_a^2 \sum \sum \psi_{\mathbf{n},k}^{2(a)} \right) \quad (20)$$

Thus, there is always an increase in the variance of $z_{\mathbf{x},t}$ over the corresponding STAR process. It is convenient to partition Eq. (17) into two separate processes, one without $a_{\mathbf{x},t}$ and one without $c_{\mathbf{x},t}$. The infinite moving average coefficients for each process can be obtained from the Eq. (17), by omitting terms of $a_{\mathbf{x},t}$ and $c_{\mathbf{x},t}$, respectively. Where N is very large and $\sigma_c^2 \gg 1/8N \sum \phi_{\mathbf{b}}$, $a_{\mathbf{x},t}$ may be omitted. Where $a_{\mathbf{x},t}$ dominates, the process is a STAR process. The space–time covariances and variances of these separate processes are defined as $\sigma_z^{(c)2} = \sigma_c^2 \sum \sum \psi_{\mathbf{n},k}^{2(c)}$, $\gamma_{1,m}^{(c)} = \sigma_c^2 \sum \sum \psi_{\mathbf{n},k}^{(c)} \psi_{\mathbf{n} + \mathbf{l},k+m}^{(c)}$ and $\sigma_z^{(a)2} = \sigma_a^2 \sum \sum \psi_{\mathbf{n},k}^{2(a)}$, $\gamma_{1,m}^{(a)} = \sigma_a^2 \sum \sum \psi_{\mathbf{n},k}^{(a)} \psi_{\mathbf{n} + \mathbf{l},k+m}^{(a)}$. Defining similarly the separate correlations by simply dividing the covariances by the variances, Eq. (19) becomes:

$$p_{1,m} = \frac{\sigma_z^{(c)2} p_{1,m}^{(c)} + \sigma_z^{(a)2} p_{1,m}^{(a)}}{\sigma_z^{(c)2} + \sigma_z^{(a)2}} \quad (21)$$

It is also possible to obtain $\sigma_z^{(c)2}$ from $\sigma_z^{(a)2}$ and $\gamma_{1,m}^{(a)}$ or $p_{1,m}^{(a)}$ by substituting $\psi_{\mathbf{n},k}^{(a)} - \phi_{\mathbf{0}} \psi_{\mathbf{n},k-1}^{(a)}$ for $\psi_{\mathbf{n},k}^{(c)}$, giving $\sigma_z^{(c)2} = \sigma_z^{(a)2} \sum (\psi_{\mathbf{n},k}^{(a)} - \phi_{\mathbf{0}} \psi_{\mathbf{n},k+1}^{(a)})^2$. Expanding the binomial, considering the summation limits (which go from $k = 1$ to infinity), we have

$$\frac{\sigma_z^{2(c)}}{\sigma_z^2} = (1 + \phi_{\mathbf{0}}^2 - 2\phi_{\mathbf{0}} p_{0,1}^{(a)}) \frac{\sigma_z^{2(a)}}{\sigma_a^2} - 1.0 \quad (22)$$

In addition, substitutions can be used to relate $\gamma_{1,m}^{(c)}$ and $p_{1,m}^{(c)}$ to terms of $(\sigma_z^{(a)2}/\sigma_a^2)$, $\phi_{\mathbf{b}}$, and $p_{1,m}^{(a)}$.

2.2. An example

For models with lone spatial dimension, and with migration occurring only between strictly nearest-neighboring populations, the process equations can be written, in terms of backshift operators, as:

$$\left(1 - \sum_{b=-1}^{b=1} \phi_b B_x^{-b} B_t\right) z_{x,t} = (\phi_{-1} B_x^{-1} B_t + \phi_1 B_x^{-1} B_t) c_{x,t} + a_{x,t} \quad (23)$$

and,

$$z_{x,t} = \Phi^{-1}(B_x, B_t) (\phi_{-1} B_x^{-1} B_t + \phi_1 B_x^{-1} B_t) c_{x,t} + \Phi^{-1}(B_x, B_t) a_{x,t}$$

or,

$$z_{x,t} = \Phi^{-1}(B_x, B_t) [-\Phi(B_x, B_t) - \phi_0 B_x^0 B_t + 1] c_{x,t} + \Phi^{-1}(B_x, B_t) a_{x,t}$$

where

$$\Phi^{-1}(B_x, B_t) = \sum_{d=0}^{\infty} (\phi_0 + \phi_{-1} B_x^{-1} + \phi_1 B_x^{-1})^d B_t^d \quad (24)$$

Alternatively,

$$z_{x,t} = \left[\sum_{d=1}^{\infty} (\phi_0 + \phi_{-1} B_x^{-1} + \phi_1 B_x^{-1})^d B_t^d - \phi_0 \sum_{d=1}^{\infty} (\phi_0 + \phi_{-1} B_x^{-1} + \phi_1 B_x^{-1})^d B_t^d \right] c_{x,t} + \left[\sum_{d=1}^{\infty} (\phi_0 + \phi_{-1} B_x^{-1} + \phi_1 B_x^{-1})^d B_t^d \right] a_{x,t} \quad (25)$$

The moving average coefficients for the separate (partial) infinite STMA process for the $a_{x,t}$, i.e. $\psi_{n,k}^{(a)}$, are those of the corresponding STAR process with the same migration pattern, whose coefficients can be found using simple iterative computations (Epperson, 1993b). To find the MA coefficients, $\psi_{n,k}^{(c)}$, for $c_{x,t}$, first set k (for $k > 0$) and find the trinomial coefficients for which $n = s - u$, where s and u are the powers of B_x^{-1} and B_x^{-1} , respectively, in the expression $(\phi_b + \phi_{-1} B_x^{-1} + \phi_1 B_x^{-1})^k - \phi_0 (\phi_b + \phi_{-1} B_x^{-1} + \phi_1 B_x^{-1})^{k-1}$. Conveniently, the $\psi_{n,k}^{(c)}$ can also be found from the $\psi_{n,k}^{(a)}$.

Thus, $\psi_{n,k}^{(c)} = \psi_{n,k}^{(a)} + \phi_0 \psi_{n,k-1}^{(a)}$. In addition, $\psi_{n,k}^{(c)} = \phi_1 \psi_{n+1,k-1}^{(a)} + \phi_{-1} \psi_{n-1,k-1}^{(a)}$.

3. Some results for basic stationary processes

STARMA models give the entire space–time correlation structures for very general patterns of interactions via spatial proximity, and the power of the space–time correlations (in addition to the usual spatial correlations) in describing theoretical and real system is difficult to overstate. They tie spatial patterns to the underlying space–time processes. This is also completely new for population genetic theoretical models, and it is possible to exploit the STARMA theorems developed in the 1970s and 1980s (for example, Cliff and Ord, 1975; Ord, 1979; Taneja and Aroian, 1980; Aroian, 1985). These results constitute the first complete correlation description of dynamic (space–time) migration–genetic drift systems, and there are a number of important uses of this.

It is possible to obtain the spatial correlations for complex migration patterns in the realistic case where systems of populations are distributed essentially over two-dimensional space. Some examples of spatial correlations for models without shared stochastic inputs are shown in Figs. 1 and 2 for strictly nearest-neighbor migration cases in one dimensions, and where migration is isotropic (i.e. both nearest neighbors contribute equal numbers of migrants), and both nonzero ϕ values are equal. Typically, there are very high correlations (i.e. high genetic similarity) among near neighbors, and the correlations drop off as the distance between populations increases. Greater interaction (migration) rates result in higher correlations and lower variances. Only in the case where the ‘recall’ or control rate (the ‘outside systematic pressure’) is very large can the correlations be small.

The STAR or STARMA inversion methods also allow computations of spatial correlations specifically in terms of spatial lags rather than Euclidian distances. For example, in strict nearest-neighbor migration models in two dimensions, anisotropic migration rates can produce dimensional directionalities in the spatial correla-

tions (see, for example, Table 1). Although the correlations are the same for mirror images, there can be large differences for the same absolute size lag in different dimensions. Precisely this kind of directionality in genetic spatial correlations have been observed by Sokal (1988), Sokal et al. (1989) Sokal in European populations, and this is consistent with archaeological artifacts that indicate

several directional waves of migration from the southeast.

Tables 1 and 2 present some of the first space–time correlations calculated for geographical genetic models (for others, see Epperson, 1993a,b). Naturally, anisotropic migration results in directionalities within dimensions as well as between dimensions. Space–time correlations provide even more powerful distinctions created by anisotropic or directional interactions, with as little as a five-period time lag (Table 1).

As an example of the general models with shared stochastic inputs, consider the case of the strict stepping stone population genetic model with one spatial dimension:

$$z_{x,t} = \sum_{b=-1}^{b=1} \phi_b z_{x+b,t-1} + \phi_{-1} c_{x-1,t-1} + \phi_1 c_{x+1,t-1} + a_{x,t} \tag{26}$$

In general, σ_c^2 and σ_a^2 may depend, respectively, on the amount of shared and unshared stochastic migration effects, respectively, and σ_a^2 also depends on the drift variance. The moving average coefficients for the separate (partial) infinite STMA process for the $a_{x,t}$, i.e. $\psi_{n,k}^{(a)}$, are those of the corresponding STAR model with the same migration pattern, whose coefficients can be found using simple iterative computations (Epperson, 1993a). We have the equations $\psi_{n,k}^{(c)} = \psi_{n,k}^{(a)} - \phi_0 \psi_{n,k-1}^{(a)}$ and $\psi_{n,k}^{(c)} = \phi_1 \psi_{n+1,k-1}^{(a)} + \phi_{-1} \psi_{n-1,k-1}^{(a)}$. It is worth noting that the second expression also implies that all $\psi_{n,k}^{(c)}$, and hence all $p_{1,m}^{(c)}$, are non-negative, and that shared stochastic migration effects always increase the overall variance of z in mixed systems. All $\psi_{n,0}^{(c)} = 0$ and $\psi_{0,1}^{(c)} = 0$, $\psi_{1,1}^{(c)} = \phi_{-1}$, and $\psi_{-1,1}^{(c)} = \phi_1$, etc. In general, values of $\psi_{n,k}^{(c)} \ll \psi_{n,k}^{(a)}$. The variance ratios ($\sigma_z^{(c)2}/\sigma_c^2$) and correlations ($p_{1,m}^{(c)}$) for the separate process, $\{c_{x,t}\}$ can be calculated directly from the $\psi_{n,k}^{(c)}$ using Eqs. (19) and (20) (theorem 4.9 of Aroian, 1985), for several different sets of parameter values. Table 2 shows the spatial and space–time correlations for a typical case.

The spatial correlations ($p_{b,0}^{(c)}$) for a specific case for the separate process generated by $\{c_{x,t}\}$ only, for several sets of parameter values, are shown in Figs. 1 and 2 and spatial correlations for STAR

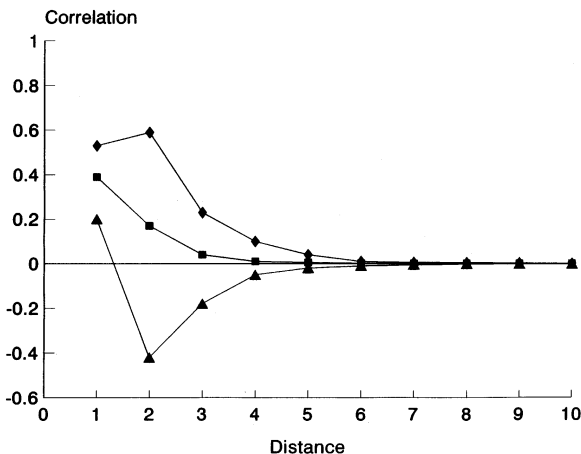


Fig. 1. Spatial correlations ($p_{b,0}$) between populations separated by b spatial lags for several one-dimensional stepping-stone models with outside systematic force $m_\infty = 0.01$ and with isotropic migration rates $\phi_{-1} = \phi_1 = 0.01$, from nearest neighbors. One model (■) has no shared stochastic migration effects (STAR). The other two have positive (◆) and negative shared stochastic migration effects (▲), respectively.

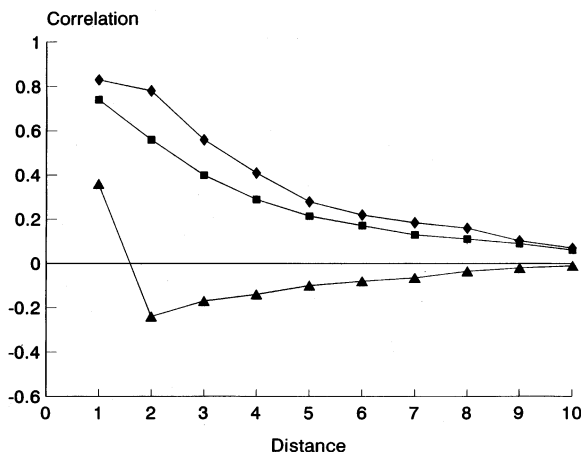


Fig. 2. Spatial correlations ($p_{b,0}$) for the models in Fig. 1, except that $\phi_{-1} = \phi_1 = 0.1$.

Table 1

Spatial correlations, $p_{b,a,0}$, and space–time correlations for temporal lag five, $p_{b,a,5}$, for a two-dimensional case with $m_\infty = 0.01$, $m_{-1,0} = 0.02$, $m_{1,0} = 0.01$, $m_{0,-1} = 0.01$, and $m_{0,1} = 0.06$.

	$P_{4,a,0}$	$P_{3,a,0}$	$P_{2,a,0}$	$P_{1,a,0}$	$P_{0,a,0}$	$P_{-1,a,0}$	$P_{-2,a,0}$	$P_{-3,a,0}$	$P_{-4,a,0}$
$p_{b,-3,0}$	0.00	0.01	0.02	0.05	0.08	0.05	0.02	0.01	0.00
$p_{b,-2,0}$	0.01	0.02	0.04	0.10	0.18	0.10	0.04	0.02	0.01
$p_{b,-1,0}$	0.01	0.02	0.07	0.18	0.41	0.18	0.07	0.02	0.01
$p_{b,0,0}$	0.01	0.03	0.08	0.26	1.00	0.26	0.08	0.03	0.01
$p_{b,1,0}$	0.01	0.02	0.07	0.18	0.41	0.18	0.07	0.02	0.01
$p_{b,2,0}$	0.01	0.02	0.04	0.10	0.18	0.10	0.04	0.02	0.01
$p_{b,3,0}$	0.00	0.01	0.02	0.05	0.08	0.05	0.02	0.01	0.00
	$P_{4,a,5}$	$P_{3,a,5}$	$P_{2,a,5}$	$P_{1,a,5}$	$P_{0,a,5}$	$P_{-1,a,5}$	$P_{-2,a,5}$	$P_{-3,a,5}$	$P_{-4,a,5}$
$p_{b,-3,5}$	0.00	0.01	0.03	0.06	0.10	0.06	0.03	0.01	0.00
$p_{b,-2,5}$	0.01	0.02	0.05	0.12	0.22	0.11	0.04	0.02	0.01
$p_{b,-1,5}$	0.01	0.03	0.07	0.20	0.46	0.19	0.07	0.02	0.01
$p_{b,0,5}$	0.01	0.03	0.09	0.26	0.70	0.23	0.08	0.03	0.01
$p_{b,1,5}$	0.01	0.02	0.07	0.17	0.32	0.15	0.06	0.02	0.01
$p_{b,2,5}$	0.01	0.02	0.04	0.09	0.14	0.08	0.04	0.01	0.01
$p_{b,3,5}$	0.00	0.01	0.02	0.04	0.06	0.04	0.02	0.01	0.00

Table 2

Spatial, $p_{a,0}$, and space–time, $p_{a,n}$, correlations for various generation lags, n , for the shared stochastic input components of a one-dimensional STARMA case with $m_\infty = 0.01$, $m_{-1} = 0.0405$ and $m_1 = 0.0814$.

Lag	$p_{5,n}$	$p_{4,n}$	$p_{3,n}$	$p_{2,n}$	$p_{1,n}$	$p_{0,n}$	$p_{-1,n}$	$p_{-2,n}$	$p_{-3,n}$	$p_{-4,n}$	$p_{-5,n}$
0	0.19	0.29	0.44	0.67	0.76	1.00	0.76	0.67	0.44	0.29	0.19
1	0.18	0.28	0.43	0.65	0.75	0.96	0.77	0.66	0.45	0.29	0.19
2	0.18	0.28	0.42	0.63	0.75	0.93	0.77	0.66	0.45	0.30	0.19
3	0.18	0.27	0.42	0.61	0.74	0.90	0.77	0.65	0.46	0.30	0.20
4	0.17	0.27	0.41	0.59	0.73	0.87	0.77	0.65	0.46	0.31	0.20
5	0.17	0.26	0.40	0.58	0.71	0.85	0.76	0.64	0.47	0.31	0.20
10	0.16	0.24	0.36	0.51	0.65	0.75	0.72	0.62	0.48	0.33	0.22
20	0.13	0.20	0.29	0.41	0.52	0.61	0.62	0.57	0.47	0.36	0.25

processes ($p_{b,0}^{(a)}$ in the present context) with the same parameter values are included for comparison. In every case examined, $p_{b,0}^{(c)} > p_{b,0}^{(a)}$, at least for the small values of b included in the comparisons. Thus, it appears that the addition of shared stochastic migration generally tends to *increase* spatial correlations in systems with one spatial dimension. Note that the relative ranking can vary over distance classes. Notice that when migration rates are very small, the spatial correla-

tions are not a strictly monotonically decreasing function of distance. Clearly, the autocorrelation curve is not exponentially decreasing as some geographers have claimed it should be the general rule, and the same is true for two-dimensional cases (Epperson, 1993b, 1994).

Another important feature is that $\sigma_z^{(a)2}$ increases as migration rates increase, opposite to the effects of migration rates in the STAR models. These results hold as long as the relative values of the

shared effects are the same as those for the migration rates, and we can use these results for partial processes to form mixed process simply by adjusting the values of σ_c^2 and σ_a^2 . In some cases, it is possible to estimate various effects from genetic data.

Similar results are observed for the strict stepping-stone migration model with two spatial dimensions. The developments follow those for the one-dimensional models. Figs. 1 and 2 show, for the one-dimensional case, the correlations for the STAR (or unshared effects only) models and for the completely shared partial processes. The latter are much greater than the former. For models with two spatial dimensions, the increases are even greater than those observed for the one-dimension models. This is due to the fact that $c_{x,t}$ is shared by the four nearest neighbors (which themselves are diagonal neighbors) of \mathbf{x} , but not by \mathbf{x} . For a thorough discussion of transitions among neighborhoods related to neighborhood configuration see Childress et al. (1996). Nonetheless, the results make it clear that stochastic migration can cause striking deviations from the paradigm of monotonic decrease for short distances (Epperson, 1994).

The case of the strict stepping-stone genetic model with one spatial dimension is unique in allowing a straightforward STARMA interpretation of negative correlations between migrant groups from the same source, which could result from various types of fission events. The process can be viewed as a partial process like the case for (positively) shared stochastic migration effects. To avoid confusion, we use $d_{x,t}$ instead of $c_{x,t}$:

$$z_{x,t} = \sum_{b=-1}^{b=1} \phi_b z_{x+b,t-1} - \phi_{-1} d_{x-1,t-1} + \phi_1 d_{x+1,t-1} + a_{x,t} \quad (27)$$

Eq. (26) is modified:

$$z_{x,t} = \Phi^{-1}(B_x B_t) (-\phi_{-1} B_x B_t + \phi_1 B_x^{-1} B_t) d_{x,t} + \Phi^{-1}(B_x B_t) a_{x,t}$$

Thus, there are two separate sets of the moving average coefficients, one for the separate (partial) infinite STMA process for the $a_{x,t}$, i.e. $\psi_{n,k}^{(a)}$, which are those of the corresponding STAR process

with the same migration pattern, and a second set for the $d_{x,t}$, i.e. $\psi_{n,k}^{(d)}$, for the fission stochastic inputs. Regarding the MA coefficients for $d_{x,t}$, note that all $\psi_{n,0}^{(d)} = 0$ and $\psi_{0,1}^{(d)} = 0$, $\psi_{1,1}^{(d)} = -\phi_{-1}$, and $\psi_{-1,1}^{(d)} = \phi_1$. It can also be shown that $\psi_{n,k}^{(d)} = \phi_1 \psi_{n+1,k-1}^{(a)} - \phi_{-1} \psi_{n-1,k-1}^{(a)}$. The $\psi_{n,k}^{(d)}$, and hence $p_{1,m}^{(d)}$, may be negative. One type of fission process is where $\phi_{-1} = \phi_1$, and here the negative effects are shared equally. We note that the change of sign for ϕ_{-1} rather than for ϕ_1 is arbitrary since stochastic inputs can be either negative or positive. The partial process $\psi_{n,k}^{(d)}$ can produce some very different types of MA coefficients. In the isotropic case, the shock at a location has no indirect or direct effect on future populations at the same location (i.e. all $\psi_{0,k}^{(d)}$ are zero).

The spatial and space–time correlations exhibit striking contrasts to other processes. Typical spatial correlograms are shown in Figs. 1 and 2. The correlations start positive, but are highly negative at distance class two, and slowly rise back up toward zero in an apparent asymptotic approach. It may be unrealistic for all of the stochastic events to be completely negatively shared, as in the partial process. However, this process, even as part of more complex mixed process, could still cause negative correlations at some spatial lags, depending on the relative sizes of $\sigma_z^{(d)2}$, $\sigma_z^{(c)2}$, and $\sigma_z^{(a)2}$.

In mixed processes, the relative weightings of the correlations of the partial processes can be derived from the degree of kinship in sample groups. For isotropic strict stepping-stone migration in one spatial dimension:

$$\sigma_c^2 = \frac{1 + (2\phi_1 N - 1)k}{16\phi_1 N} \quad (28)$$

where k is the correlation among members of an emigrant group (Rogers, 1987). When N is large, $\sigma_c^2 = k/8$. For sake of discussion, let us assume the kinship among survivors of genetic drift is moderate (thus, k in these groups must be very small for large N), and drift is effectively random, i.e. $\sigma_a^2 = 1/8$. If unshared effects are added to represent sampling of migrants from emigrants, then $\sigma_c^2 \gg \sigma_a^2$, because $\sigma_a^2 = (1 + 2\phi_1)/8N$.

The variances of gene frequencies can be computed as ratios, $\sigma_z^{(c)2}/\sigma_c^2$ or $\sigma_z^{(a)2}/\sigma_a^2$. Consider the

ratio of these two variances $(\sigma_z^{(c)2}/\sigma_c^2)/(\sigma_z^{(a)2}/\sigma_a^2) = V_r$. The ratio of the weights $\sigma_z^{(c)2}/\sigma_z^{(a)2}$ can be obtained by multiplying V_r by σ_c^2/σ_a^2 , which is roughly Nk if k is not too small and is $1/2\phi_1$ if $k=0$. Thus, modest kin-structure in emigrants causes shared stochastic migration to have greater effect than unshared inputs, when Nk is greater than the ratio V_r . In this case, the correlations will be more like those for the shared partial process. The value of k can approach 1.0 in cases where the emigrant group has small size, and in most cases, even when population sizes, N , are relatively small, the shared stochastic migration effects will dominate (Epperson, 1994). Generally, shared effects contribute little when $k=0$; however, they can make a substantial contribution when ϕ_1 is in the range of 0.1, even when $k=0$.

4. Statistical uses of STARMA models

STARMA models also form a sophisticated framework for well-defined statistical analyses, in addition to completely describing theoretical systems. STARMA models can also be used as statistical models for analyzing structures in real systems of populations. For example, we can take observed gene frequency or DNA data from different populations from two time periods, and estimate the spatial and space–time correlations. Then we substitute the estimated spatial and space–time correlations, into the Yule–Walker-type equations (Epperson, 1993a):

$$p_{\mathbf{b},n} = \sum_{\mathbf{m}} \phi_{\mathbf{m}} p_{\mathbf{b}+\mathbf{m},n-1} \quad (29)$$

(except for $n=0$, $\mathbf{b}=\mathbf{0}$). In general, the summation is taken over all spatial lags \mathbf{m} that exchange migrants, including $\mathbf{m}=\mathbf{0}$. In addition, the variance is given by:

$$\sigma_z^2 = \sigma_a^2 \left(1 - \sum_{\mathbf{b}} \phi_{\mathbf{b}} p_{\mathbf{b},1} \right)^{-1} \quad (30)$$

With such a set of linear equations for the estimated space–time correlations, we can estimate all of the parameters, i.e. the migration rates (in terms of proportions) and the strengths of systematic forces such as selection. From the equation

for the variance, we can also estimate the effective population size of populations, N . Alternatively, for allele frequency data per se, we can simply replace the stochastic variables $z_{x,t}$ in Eq. (1) with observed values, $Z_{x,t}$, and estimate all parameters using well-developed procedures such as least-squares estimator methods derived for STARMA models (Pfeifer and Deutsch, 1980a), or maximum likelihood (Larrimore, 1977).

More generally, we can use STARMA procedures to obtain many statistical objectives previously unavailable in population genetic analysis, for either DNA or allele frequency data, in a four-step process.

1. Identification of the limits to migration distances in the process underlying a real system of populations. From the estimates for the spatial and space–time correlations, we can estimate (Pfeifer and Deutsch, 1980a) the partial space–time correlation function, which can be defined as the correlation between two populations separated in time and space, conditioned on all spatially and temporally ‘intermediate’ populations. Most importantly, the spatial lag at which the partial space–time function cuts to zero identifies the maximum distance that migration occurs, or an estimate thereof if based on data. The temporal lag cut-off is at the maximum temporal lag in the system (e.g. it equals one in a Markovian system), which will indicate if overlapping generations is important. Similarly, the distance at which the original space–time correlation function truncates will indicate how important stochastic migration is.
2. Estimators of migration rates and other parameters. As already noted, now knowing the appropriate model and number of parameters to place in Eq. (1) or Eqs. (29) and (30), we can obtain estimates of the migration parameters, amount of shared stochastic migration effects, time-delay effects, and effective population size, using well-characterized procedures.
3. Model testing. We can test the goodness of fit of the data to our model, using standard least-squares (for example, Pfeifer and Deutsch, 1980a; Upton and Fingleton, 1985), based on

either Eqs. (29) and (30) (for molecular data), or Eq. (1) substituted with observed allele frequency data.

4. Forecasting. After the first three steps, and using the fitted model and the most recent generation(s) (one only present generation if Markovian) of data, we can project or forecast the expected values for future generations.

We are presently developing a computer software package to carry out all of these steps for a very broad set of STARMA models. The program is general and can be applied to many ecological variables, but it also allows specific analyses for population genetic models.

5. Discussion and conclusions

STARMA models fit a wide range of ecological conditions. They can be used both for statistical analysis of ecological data, and for modelling theoretical processes. These aims can be achieved whenever locations are or can be treated as discrete and where time is also discrete. It is important to distinguish the statistical aspects from the theoretical.

5.1. STARMA statistical models

Vast amounts of spatial data are being collected as spatially discrete data. For example, satellite images are collected, stored and analyzed as (discrete) pixels. Moreover, considerable space–time data are being accumulated as satellites and other image collecting mechanisms repeatedly scan areas, and this data is usually essentially discrete time data. While cartographic procedures are well developed in geographic information systems (GIS), spatial and space–time modelling and statistical analyses in GIS has lagged. STARMA models can be directly applied to such data.

STARMA models can be applied to data for two time periods, and the four-step procedure utilized (using the variance, spatial and space–time correlations and partial correlations) in order to: identify the spatial bounds of the ‘deterministic’ (expected or regressors), and unshared and shared stochastic interactions among locations

over one time period; to estimate the strengths of these various interactions; test for model fit; and forecast the system. It is paramount to utilize the space–time structure. In contrast, purely spatial models imply the usually unrealistic assumption that spatial interactions are instantaneous. Moreover, in the rare ecological situation where interactions are instantaneous, it is generally not straightforward to specify the possible forms of spatial interactions (Haining, 1977, 1978, 1979). Moreover, when process interactions are not instantaneous, purely spatial interaction models are purely descriptive, and do not lead to insights about the underlying process in space and time. In other words, purely spatial models allow little insight in the interpretation of how small-scale interactions develop larger scale spatial patterns. Finally, space–time models can be applied repeatedly to pairs of time periods, in order to test for changes in the interaction parameters. Moreover, STARMA type models can incorporate mean changes or systemic trends, as well as seasonal trends (STARIMA; for example, Bennett, 1979). Thus, STARMA is a very general statistical model, for discrete time–discrete space data, perhaps unique in that it both properly accounts for spatial autocorrelation in statistical characterizations of spatial patterns and ties spatial patterns to the underlying space–time process.

The interaction terms measured for different time periods may be, as a linear model, directly associated with many types of ecological process interactions. Ecological processes that can be modeled using STARMA include common processes where the variable is abundance and there are density interactions. In many cases, rates of spread are directly proportional to the incidences (an ecological variable) (Haggett et al., 1977; Cormack and Ord, 1979; Weidlich and Hagg, 1986). For example, disease spread is sometimes primarily density dependent (Antonovics, 1994). This condition meets the most limiting feature of STARMA models, namely that the ecological variables at different locations must have *linear* interactions. In processes where there are density interactions, the interactions may often be approximately linear. In many cases, the diffusion or rates of spread are directly proportional to the

incidences (which would be the ecological variable) (Haggett et al., 1977; Cormack and Ord, 1979): thus, STARMA would be a valid space–time model. Moreover, even in cases where the interactions are much more complex than a single parameter, comparisons of STARMA interaction terms measured for different time periods may provide considerable information on the more complex dynamics. In other words, these terms would provide an emergent property that is an outcome of perhaps several parameters. This is an open area for future research.

Nonetheless, it is important to point out that the necessity of linearity is a major limitation with STARMA approaches. There are likely to be many interactions among ecological variables that are not linear. One alternative for nonlinear models is wavelet analysis, which has been receiving a lot of interest (see, for example, Li and Loehle, 1995).

In the specific case of population genetics, STARMA models can utilize either DNA data or allele frequencies to completely describe a real system of populations in a four-step process: (1) identification of migration patterns; (2) estimation of migration rates; (3) tests of goodness of fit; and (4) forecasting. For example, it was shown that STAR models express spatial correlations in terms of the spatial lags in each spatial dimension. Thus, it is possible to characterize differences in correlations among dimensions ('dimensional directionality'; Epperson, 1993a), which can arise, for example, from directionalities or anisotropies in migration rates or patterns. Such directionalities were evident, for example, in spatial genetic data on European populations (Sokal et al., 1989), and they provided evidence, which is consistent with artifact evidence, of several directional waves of migrations from the southeast. Genetic data are particularly powerful because multiple genetic loci can be studied, which provides independent data on the same demographic processes. The power of STARMA models poses a number of advances in the analysis and interpretation of geographic distributions of DNA data, over and above the traditional methods.

5.2. STARMA theoretical models

For models of short-term dynamics, STARMA models are readily utilized. Thus, the theoretical space–time structures can be obtained. Naturally, such models can be very complex. However, relatively simple models in some cases capture the essential features and can then lead to insightful analytic expressions. For example, a model that has interactions (over one time period increment) only between nearest-neighbor sites may essentially fit many ecological processes. Then various methods of analyzing the Fourier transform can lead to relatively simple analytic results. Many features can be included in the spatial time series framework, including: complex interaction patterns; deterministic (expected or regression trend) influences; shared and unshared stochastic inputs; time-lagged interactions; and systemic and seasonal trends. Moreover, it is possible to extend STAR and STARMA to models with additional linearized coefficients, (STARR and STARMAR), which represent effects that depend on the location of a site. For example, we can include a number of spatial distributions of various aspects of the environmental values of populations. An important special case is unidirectional environmental clines in systems with two spatial dimensions. STARR and STARMAR models properly separate effects of migration patterns and genetic drift from environment by ecological variable cross-correlations, as well as the ecological variable correlations themselves.

Stationary distributions are of special interest and, in many cases, it is possible to obtain analytic results independent of initial conditions. In general, simple analytic results can be derived if the rates of interactions are fixed or changing regularly (e.g. cyclical). This may approximate many ecological processes, or some transformation of the process. We examined some restrictive (sufficient but not necessary) conditions for stationarity. Various other forms of conditions have been derived (for example, Pfeifer and Deutsch, 1980b). It is expected that many, but not all, ecological processes may obtain stationary distributions in theoretical models.

STARMA theoretical models have greatly expanded models of population genetics. Population genetic variation can serve as ‘markers’ or indicators of historical and demographic events. STAR processes model a completely general range of patterns and rates of migration; in fact, they include nearly all migration models, as well as many previously unstudied processes (Epperson, 1993a,b). For example, STAR can include migrational interactions that have delayed effects, which occur in humans and other populations with overlapping generations. Moreover, the space–time correlations (in addition to the spatial correlations and the variance) are analyzable using the STAR approach (Epperson, 1993a,b), and this is completely new to population genetics. Spatial correlations are defined as the correlations between populations in the same generation, but separated by a given spatial distance or set of lags in each spatial dimension. Space–time correlations are those between populations separated in time as well as space. It is difficult to overstate the importance of the space–time correlations. Space–time correlations connect observed spatial correlations to the parameters of the underlying space–time process. It is also possible to analyze trends in theoretical systems. For example, the number of spatial dimensions that a population exists in has marked effects on the correlation function (Epperson, 1993a). In two-dimensional systems, the correlation function on distance is not always monotonically, let alone exponentially, decreasing. Geographers have suggested that virtually all geographically distributed variables should be exponentially decreasing. Other examples include the first characterizations of the theoretical effects of anisotropy in migration rates, which can create directionalities in the spatial correlations (Epperson, 1993a), that have been observed in human populations (Epperson, 1993a; Epperson, 1993b). The effects of time-delayed migrational interactions can be investigated.

Modified STAR theoretical processes known as the space–time autoregressive moving average (STARMA) include a wide range of previously unstudied ‘stochastic migration’ effects (stochastic changes caused by sampling of individuals into migrant groups), which are important factors

needed to mimic what occurs in many real systems (e.g. where adults migrate), and which maintain the general range of migration patterns and statistical analogues (Epperson, 1994). There are two fundamental classes, distinguished by whether or not the stochastic migration effects are directly shared. Unshared effects do not affect the spatial or space–time correlations, but they do affect the variance (Epperson, 1993b, 1994), and thus can create serious and previously uncharacterized biases in popular measures of migrations rates based on the spatial variance. Under some conditions, shared stochastic migration effects can also cause changes in spatial and space–time correlations (Epperson, 1994). Although many theoretical aspects of population genetics STAR and STARMA in have been explored using STARMA (Epperson, 1993b), many others remain uncharacterized.

Acknowledgements

This work was supported in part by National Institutes of Health grant GM48453, and McIntire-Stennis project # 1774. Also acknowledged are the Institute for International Agriculture and Michigan Agricultural Experiment Station, and the Department of Forestry, Michigan State University, for funding travel to ISEM’95.

References

- Antonovics, J., 1994. The interplay of numerical and gene-frequency dynamics in host–pathogen systems. In: Real, L.A. (Ed.), *Ecological Genetics*. Princeton University Press, Princeton, NJ, pp. 129–145.
- Aroian, L.A., 1985. Time series in m dimensions: past, present and future. In: Anderson, O.D., Ord, J.K., Robertson, E.A. (Eds.), *Time Series Analysis: Theory and Practice* 6. Elsevier, Amsterdam, pp. 241–261.
- Bennett, R.J., 1979. *Spatial Time Series*. Pion, London.
- Childress, M.W., Rykiel, E.J., Forsythe, W., Li, B.-L., Wu, H., 1996. Transition rule complexity in grid-based automata models. *Landscape Ecol.* 11, 257–266.
- Cliff, A.D., Ord, J.K., 1975. Model building and the analysis of spatial pattern in human geography. *J. R. Stat. Soc. B* 37, 297–348.
- Cliff, A.D., Ord, J.K., 1981. *Spatial Processes*. Pion, London.

- Cormack, R.M., Ord, J.K., 1979. Spatial and Temporal Analysis in Ecology. International Coop, Fairland, MD.
- Epperson, B.K., 1993. Recent advances in correlation studies of spatial patterns of genetic variation. *Evolution. Biol.* 27, 95–155.
- Epperson, B.K., 1993. Spatial and space–time correlations in systems of subpopulations with genetic drift and migration. *Genetics* 133, 711–727.
- Epperson, B.K., 1994. Spatial and space–time correlations in systems of subpopulations with stochastic migration. *Theor. Pop. Biol.* 46, 160–197.
- Haggett, P., Cliff, A.D., Frey, A., 1977. *Locational Analysis in Human Geography*. Edward Arnold, London.
- Haining, R.P., 1977. Model specification in stationary random fields. *Geogr. Anal.* 9, 107–109.
- Haining, R.P., 1978. The moving average model for spatial interaction. *Trans. Inst. Br. Geogr.* 3, 202–225.
- Haining, R.P., 1979. Statistical test and process generators for random field models. *Geogr. Anal.* 11, 45–64.
- Hooper, P.M., Hewings, G.J.D., 1981. Some properties of space–time processes. *Geogr. Anal.* 13, 203–223.
- Larrimore, W.E., 1977. Statistical inference on stationary random fields. *Proc. Inst. Electr. Electron. Eng.* 65, 961–970.
- Li, B.-L., Loehle, C., 1995. Wavelet analysis of multiscale permeabilities in the subsurface. *Geophys. Res. Lett.* 22, 3123–3126.
- Malécot, G., 1973. Génétique des populations diploïdes naturelles dans le cas d'un seul locus. III. Parenté, mutations et migration. *Ann. Génét. Sel. Anim.* 5, 333–361.
- Malécot, G., 1975. Heterozygosity and relationship in regularly subdivided populations. *Theor. Pop. Biol.* 8, 212–241.
- Ord, J.K., 1979. Time-series and spatial patterns in ecology. In: Cormack, R.M., Ord, J.K. (Eds.), *Spatial and Temporal Analysis in Ecology*. International Coop, Fairland, MD, pp. 1–94.
- Pfeifer, P.E., Deutsch, S.J., 1980. A three-stage iterative procedure of space–time modelling. *Technometrics* 22, 35–47.
- Pfeifer, P.E., Deutsch, S.J., 1980. Stationarity and invertibility regions for low order STARMA models. *Commun. Stat. Simulat. Comput.* B9 (5), 551–562.
- Rogers, A.R., 1987. A model of kin-structured migration. *Evolution* 41, 417–426.
- Sokal, R.R., 1988. Genetic, geographic, and linguistic distances in Europe. *Proc. Natl. Acad. USA* 85, 1722–1726.
- Sokal, R.R., Harding, R.M., Oden, N.L., 1989. Spatial patterns of human gene frequencies in Europe. *Am. J. Phys. Anthropol.* 80, 267–294.
- Taneja, V.A., Aroian, L.A., 1980. Time series in m dimensions, autoregressive models. *Commun. Stat. Simulat. Comput.* B9 (5), 491–513.
- Tobler, W.R., 1972. Linear operators applied to areal data. In: Davis, J.C., McCullagh, M.J. (Eds.), *Display and Analysis of Spatial Data*. Wiley, London, pp. 14–37.
- Upton, G.J.G., Fingleton, B., 1985. *Spatial Data Analysis by Example*. In: *Point Pattern and Quantitative Data*, vol. 1. Wiley, New York.
- Weidlich, W., Hagg, G., 1986. Stochastic migration theory and migratory phase transitions. In: Griffith, D.A., Haining, R.P. (Eds.), *Transformations Through Space and Time*. Martinus Nijhoff, Dordecht, pp. 104–117.