Vegetatio 80: 107–138, 1989.

Spatial pattern and ecological analysis

Pierre Legendre[1] & Marie-Josée Fortin[2]
[1] *Département de sciences biologiques, Université de Montréal, C.P. 6128, Succursale A, Montréal, Québec, Canada H3C 3J7;* [2] *Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA*

Accepted 17.1.1989

Keywords: Ecological theory, Mantel test, Mapping, Model, Spatial analysis, Spatial autocorrelation, Vegetation map

Abstract

The spatial heterogeneity of populations and communities plays a central role in many ecological theories, for instance the theories of succession, adaptation, maintenance of species diversity, community stability, competition, predator-prey interactions, parasitism, epidemics and other natural catastrophes, ergoclines, and so on. This paper will review how the spatial structure of biological populations and communities can be studied. We first demonstrate that many of the basic statistical methods used in ecological studies are impaired by autocorrelated data. Most if not all environmental data fall in this category. We will look briefly at ways of performing valid statistical tests in the presence of spatial autocorrelation. Methods now available for analysing the spatial structure of biological populations are described, and illustrated by vegetation data. These include various methods to test for the presence of spatial autocorrelation in the data: univariate methods (all-directional and two-dimensional spatial correlograms, and two-dimensional spectral analysis), and the multivariate Mantel test and Mantel correlogram; other descriptive methods of spatial structure: the univariate variogram, and the multivariate methods of clustering with spatial contiguity constraint; the partial Mantel test, presented here as a way of studying causal models that include space as an explanatory variable; and finally, various methods for mapping ecological variables and producing either univariate maps (interpolation, trend surface analysis, kriging) or maps of truly multivariate data (produced by constrained clustering). A table shows the methods classified in terms of the ecological questions they allow to resolve. Reference is made to available computer programs.

Introduction

In nature, living beings are distributed neither uniformly nor at random. Rather, they are aggregated in patches, or they form gradients or other kinds of spatial structures.

The importance of spatial heterogeneity comes from its central role in ecological theories and its practical role in population sampling theory. Actually, several ecological theories and models assume that elements of an ecosystem that are close to one another in space or in time are more likely to be influenced by the same generating process. Such is the case, for instance, for models of epidemics or other catastrophes, for the theories of competition, succession, evolution and adaptations, maintenance of species diversity, parasitism, population genetics, population

growth, predator-prey interactions, and social behaviour. Other theories assume that discontinuities between homogeneous zones are important for the structure of ecosystems (succession, species-environment relationships: Allen *et al.* 1977; Allen & Starr 1982; Legendre *et al.* 1985) or for ecosystem dynamics (ergoclines: Legendre & Demers 1985). Moreover, the important contribution of spatial heterogeneity to ecological stability seems well established (Huffaker 1958; May 1974; Hassell & May 1974; Levin 1984). This shows clearly that the spatial or temporal structure of ecosystems is an important element of most ecological theories.

Not much has been learned up to now about the spatial variability of communities. Most 19th century quantitative ecological studies were assuming a uniform distribution of living organisms in their geographic distribution area (Darwin 1881; Hensen 1884), and several ecological models still assume, for simplicity, that biological organisms and their controlling variables are distributed in nature in a random or a uniform way (e.g., simple models of population dynamics, some models of forest or fisheries exploitation, or of ecosystem productivity). This assumption is actually quite remote from reality since the environment is spatially structured by various energy inputs, resulting in patchy structures or gradients. In fluid environments for instance (water, inhabited by aquatic macrophytes and phytoplankton, and air, inhabited by terrestrial plants), energy inputs of thermal, mechanical, gravitational, chemical and even radioactive origins are found, besides light energy which lies at the basis of most trophic chains; the spatio-temporal heterogeneity of energy inputs induces convection and advection movements in the fluid, leading to the formation of spatial or temporal discontinuities (interfaces) between relatively homogeneous zones. In soils, heterogeneity and discontinuities are the result of geomorphologic processes. From there, then, the spatio-temporal structuring of the physical environment induces a similar organization of living beings and of biological processes, spatially as well as temporally. Strong biological activity takes place particularly in interface zones (Legendre & Demers 1985). Within homogeneous zones, biotic processes often produce an aggregation of organisms, following various spatio-temporal scales, and these can be measured (Legendre *et al.* 1985). The spatial heterogeneity of the physical environment thus generates a diversity in communities of living beings, as well as in the biological and ecological processes that can be observed at various points in space.

This paper includes methodological aspects.

Table 1. Methods for spatial surface pattern analysis, classified by ecological questions and objectives.

1) Objective: Testing for the presence of spatial autocorrelation.
   1.1) Establish that there is no significant spatial autocorrelation in the data, in order to use parametric statistical tests.
   1.2) Establish that there is significant spatial autocorrelation and determine the kind of pattern, or shape.

   Method 1: Correlograms for a single variable, using Moran's I or Geary's c; two-dimensional spectral analysis.
   Method 2: Mantel test between a variable (or multidimensional matrix) and space (geographical distance matrix); Mantel test between a variable and a model.
   Method 3: Mantel correlogram, for multivariate data.

2) Objective: Description of the spatial structure.
   Method 1: Correlograms (see above), variograms.
   Method 2: Clustering and ordination with spatial or temporal constraint.

3) Objective: Test causal models that include space as a predictor.
   Method: Partial Mantel test, using three dissimilarity matrices, A, B et C.

4) Objectives: Estimation (interpolation) and mapping.
   Method 1: Interpolated map for a single variable: trend surface analysis, that provides also the regression residuals; other interpolation methods.
   Method 2: Interpolation taking into account a spatial autocorrelation structure function (variogram): kriging map, for a single variable; programs give also the standard deviations of the estimations, that may help decide where to add sampling locations.
   Method 3: Multidimensional mapping: clustering and ordination with spatial constraint (see above).

We shall define first what spatial autocorrelation is, and discuss its influence on classical statistical methods. Then we shall describe the univariate and multivariate methods that we have had experience with for the analysis of the spatial structure of ecological communities (list not necessarily exhaustive), and illustrate this description with actual plant community data. Finally, recent developments in spatial analysis will be presented, that make it possible to test simple interrelation models that include space as an explanatory variable. The methods described in this paper are also applicable to geology, pedology, geography, the earth sciences, or to the study of spatial aspects of the genetic heterogeneity of populations. These sciences have in common the study of observations positioned in geographic space; such observations are related to one another by their geographic distances, which are the basic relations in that space. This paper is organized around a series of questions, of increasing refinement, that ecologists can ask when they suspect their data to be structured by some underlying spatial phenomenon (Table 1).

Classical statistics and spatial structure

We will first try to show that the methods of classical statistics are not always adequate to study space-structured ecological phenomena. This will justify the use of other methods (below) when the very nature of the spatial structure (autocorrelation) is of interest.

In classical inferential statistical analysis, one of the most fundamental assumptions in hypothesis testing is the independence of the observations (objects, plots, cases, elements). The very existence of a spatial structure in the sample space implies that this fundamental assumption is not satisfied, because any ecological phenomenon located at a given sampling point may have an influence on other points located close by, or even some distance away. The spatial structures we find in nature are, most of the time, gradients or patches. In such cases, when one draws a first sample (A), and then another sample (B) located anywhere near the first, this cannot be seen as a random draw of elements; the reason is that the value of the variable observed in (A) is now known, so that if the existence and the shape of the spatial structure are also known, one can foresee approximately the value of the variable in (B), even before the observation is made. This shows that observations at neighbouring points are not independent from one another. Random or systematic sampling designs have been advocated as a way of preventing this possibility of dependence among observations (Cochran 1977; Green 1979; Scherrer 1982). This was then believed to be a necessary and sufficient safeguard against violations of the assumption of independence of errors. It is adequate, of course, when one is trying for instance to estimate the parameters of a local population. In such a case, a random or systematic sample of points is suitable to achieve unbiased estimation of the parameters, since each point a priori has the same probability of being included in the sample; we know of course that the variance, and consequently also the standard error of the mean, will be larger if the distribution is patchy, but their estimation remains unbiased. On the other hand, we know now that despite the random or systematic allocation of samples through space, observations may retain some degree of spatial dependence if the average distance between samples is smaller than the zone of spatial influence of the underlying ecological phenomenon; in the case of large-scale spatial gradients, no sampling point is far enough to lie outside this zone of spatial influence.

A variable is said to be *autocorrelated* (or *regionalized*) when it is possible to predict the values of this variable at some points of space [or time], from the known values at other sampling points, whose spatial [or temporal] positions are also known. Spatial [or temporal] autocorrelation can be described by a mathematical function, called *structure function*; a spatial autocorrelogram and a semi-variogram (below) are examples of such functions.

Autocorrelation is not the same for all distance classes between sampling points (Table 2). It can be positive or negative. Most often in ecology,

Table 2. Examples of spatial autocorrelation in ecology (non-exhaustive list). Modified from Sokal (1979).

Sign of spatial autocorrelation	Significant autocorrelation for	
	short distances	large distances
+	Very often: any phenomenon that is contagious at short distance (if the sampling step is small enough).	Aggregates or other structures (e.g., furrows) repeating themselves trough space.
-	Avoidance (e.g., regularly spaced plants); sampling step too wide.	Spatial gradient (if also significantly positive at short distance).

autocorrelation is positive (which means that the variable takes similar values) for short distances among points. In gradients, this positive autocorrelation at short distances is coupled with negative autocorrelation for long distances, as points located far apart take very different values. Similarly, an aggregated structure recurring at intervals will show positive autocorrelation for distances corresponding to the gap between patch centers. Negative autocorrelation for short distances can reflect either an avoidance phenomenon (such as found among regularly spaced plants and solitary animals), or the fact that the sampling step (interval) is too large compared to patch size, so that any given patch does not contain more than one sample, the next sample falling in the interval between patches. Notice finally that if no spatial autocorrelation is found at a given scale of perception (i.e., a given intensity of sampling), it does not mean that autocorrelation may not be found at some other scale.

In classical tests of hypotheses, statisticians count one degree of freedom for each independent observation, which allows them to choose the statistical distribution appropriate for testing. This is why it is important to take the lack of independence into account (that results from the presence of autocorrelation) when performing a test of statistical hypothesis. Since the value of the observed variable is at least partially known in advance, each new observation contributes but a fraction of a degree of freedom. The size of this fraction cannot be determined, however, so that statisticians do not know the proper reference distribution for the test. All we know for certain is that positive autocorrelation at short distance distorts statistical tests such as correlation, regression, or analysis of variance, and that this distortion is on the 'liberal' side (Bivand 1980; Cliff & Ord 1981); this means that when positive spatial autocorrelation is present in the small distance classes, classical statistical tests determine too often that correlations, regression coefficients, or differences among groups are significant, when in fact they are not. Solutions to these problems include randomization tests, the corrected *t*-test proposed by Cliff & Ord (1981), the analysis of variance in the presence of spatial autocorrelation developed by Legendre *et al.* (submitted), etc. See Edgington (1987) for a general presentation of randomization tests; see also Upton & Fingleton (1985) as well as the other references in the present paper, for applications to spatial analysis. Another way out, when the spatial structure is simple (e.g., a linear gradient), is to extract the spatial component first and conduct the analysis on the residuals (see: trend surface analysis, below), after verifying that no spatial autocorrelation remains in the data.

The situation described above also applies to classical multivariate data analysis, which has been used extensively by ecologists for more than two decades (Orlóci 1978; Gauch 1982; Legendre & Legendre 1983a, 1984a; Pielou 1984). The spatial and temporal coordinates of the data points are usually neglected during the search for ecological structures, which aims at bringing out processes and relations among observations. Given the importance of the space and/or time component in ecological theory, as argued in the Introduction, ecologists are now beginning to study these important relationships. Ordination and clustering methods in particular are often used to detect and analyse spatial structures in vegetation analysis (e.g., Andersson 1988), even though these techniques were not designed specifi-

cally for this purpose. Methods are also being developed that take spatial or temporal relationships into account during multivariate data analysis. These include the methods of constrained clustering presented below, as well as the methods of constrained ordination developed by Lee (1981), Wartenberg (1985a,b) and ter Braak (1986, 1987) where one may use the geographical coordinates of the data points as constraints.

Spatial analysis is divided by geographers into *point pattern analysis*, which concerns the distribution of physical points (discontinuous phenomena) in space – for instance, individual plants and animals; *line pattern analysis*, a topological approach to the study of networks of connections among points; and *surface pattern analysis* for the study of spatially continuous phenomena, where one or several variables are attached to the observation points, and each point is considered to represent its surrounding portion of space. Point pattern analysis is intended to establish whether the geographic distribution of data points is random or not, and to describe the type of pattern; this can then be used for inferring processes that might have led to the observed structure. Graphs of interconnections among points, that have been introduced by point pattern analysis, are now widely used also in surface pattern analysis (below), where they serve for instance as basic networks of relationships for constrained clustering, spatial autocorrelation analysis, etc. The methods of point pattern analysis, and in particular the quadrat-density and the nearest-neighbour methods, have been widely used in vegetation science (e.g., Galiano 1982; Carpenter & Chaney 1983) and need not be expounded any further here. These methods have been summarized by a number of authors, including Pielou (1977), Getis & Boots (1978), Cicéri *et al.* (1977) and Ripley (1981, 1987). The exposé that follows will then concentrate on the methods for surface pattern analysis, that ecologists are presently experimenting with.

Testing for the presence of a spatial structure

Let us first study one variable at a time. If the map of a variable (see Estimation and mapping, below) suggests that a spatial structure is present, ecologists will want to test statistically whether there is any significant spatial autocorrelation, and to establish its type unambiguously (gradient, patches, etc.). This can be done for two diametrically opposed purposes: either (1) one wishes to show that there is no spatial autocorrelation, because one wants to perform parametric statistical hypothesis tests; or (2) on the contrary one hopes to show that there is a spatial structure in order to study it more thoroughly. In either case, a spatial autocorrelation study is conducted. Besides *testing* for the presence of a spatial structure, the various types of correlograms, as well as periodograms, provide *a description* of the spatial structure, as will be seen.

Spatial autocorrelation coefficients

In the case of quantitative variables, spatial autocorrelation can be measured by either Moran's I (1950) or Geary's c (1954) spatial autocorrelation coefficients. Formulas are presented in App. 1. Moran's I formula behaves mainly like Pearson's correlation coefficient since its numerator consists of a sum of cross-products of centered values (which is a covariance term), comparing in turn the values found at all pairs of points in the given distance class. This coefficient is sensitive to extreme values, just like a covariance or a Pearson's correlation coefficient. On the contrary, Geary's c coefficient is a distance-type function, since the numerator sums the squared differences between values found at the various pairs of points being compared.

The statistical significance of these coefficients can be tested, and confidence intervals can be computed, that highlight the distance classes showing significant positive or negative autocorrelation, as we shall see in the following examples. More detailed descriptions of the ways of computing and testing these coefficients can be found

in Sokal & Oden (1978), Cliff & Ord (1981) or Legendre & Legendre (1984a). Autocorrelation coefficients also exist for qualitative (nominal) variables (Cliff & Ord 1981); they have been used to analyse for instance spatial patterns of sexes in plants (Sakai & Oden 1983; Sokal & Thomson 1987). Special types of spatial autocorrelation coefficients have been developed to answer specific problems (e.g., Galiano 1983; Estabrook & Gates 1984).

A *correlogram* is a graph where autocorrelation values are plotted in ordinate, against distances (d) among localities (in abscissa). When computing a spatial correlogram, one must be able to assume that a single 'dominant' spatial structure exists over the whole area under study, or in other words, that the main large-scale structure is the same everywhere. This assumption must actually be made for any structure function one wishes to compute; other well-known functions, also used to characterize spatial patterns, include the variogram (below), Goodall's (1974) paired-quadrat variance function, the two-dimensional correlogram and periodogram (below), the multivariate Mantel correlogram (below), and Ibanez' (1981) auto-D^2 function.

In correlograms, the result of a test of significance is associated with each autocorrelation coefficient; the null hypothesis of this test is that the coefficient is not significantly different from zero. Before examining each significant value in the correlogram, however, we must first perform a global test, taking into account the fact that several tests (v) are done at the same time, for a given overall significance level α. The global test is made by checking whether the correlogram contains at least one value which is significant at the $\alpha' = \alpha/v$ significance level, according to the Bonferroni method of correcting for multiple tests (Cooper 1968; Miller 1977; Oden 1984). The analogy in time series analysis is the Portmanteau Q-test (Box & Jenkins 1970). Simulations in Oden's 1984 paper show that the power of Oden's Q-test, which is an extension for spatial series of the Portmanteau test, is not appreciably greater than the power of the Bonferroni procedure, which is computationally a lot simpler.

Readers already familiar with the use of correlograms in time series analysis will be reassured to know that whenever the problem is reduced to one physical dimension only (time, or a physical transect) instead of a bi- or polydimensional space, calculating the coefficients for different distance classes turns out to be equivalent to computing the autocorrelation coefficients of time series analysis.

All-directional correlogram

When a single correlogram is computed over all directions of the area under investigation, one must make the further assumption that the phenomenon is isotropic, which means that the autocorrelation function is the same whatever the direction considered. In anisotropic situations, structure functions can be computed in one direction at a time; this is the case for instance with two-dimensional correlograms, two-dimensional spectral analysis, and variograms, all of which are presented below.

Example 1 – Correlograms are analysed mostly by looking at their shape, since characteristic shapes are associated with types of spatial structures; determining the spatial structure can provide information about the underlying generating process. Sokal (1979) has generated a number of spatial patterns, and published the pictures of the resulting correlograms. We have also done so here, for a variety of artificial-data structures similar to those commonly encountered in ecology (Fig. 1). Fig. 1a illustrates a surface made of 9 bi-normal bumps. 100 points were sampled following a regular grid of 10 × 10 points. The variable 'height' was noted at each point and a correlogram of these values was computed, taking into account the geographic position of the sampled points. The correlogram (Fig. 1b) is globally significant at the $\alpha = 5\%$ level since several individual values are significant at the Bonferroni-corrected level $\alpha' = 0.05/12 = 0.00417$. Examining the individual significant values, can we find the structure's main elements from the correlo-

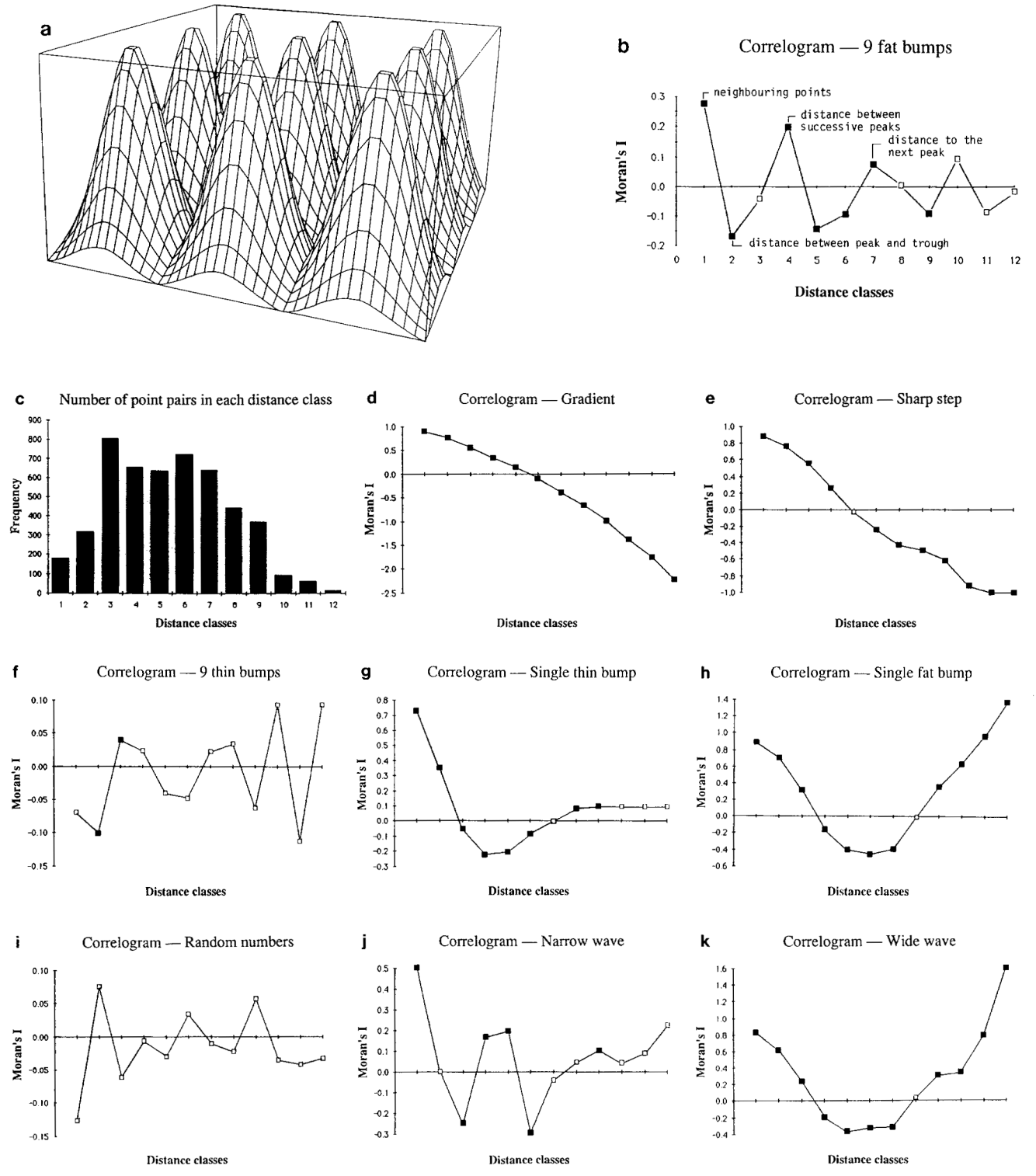


Fig. 1. All-directional spatial correlograms of artificial structures (see text). (a) depicts the structure analysed by the correlogram in (b). (c) displays the number of distances (between pairs of points) in each distance class, for all the correlograms in this figure. In the correlograms (b, d–k), black squares represent significant values at the $\alpha = 5\%$ level, before applying the Bonferroni correction to test the overall significance of the correlograms; white squares are non-significant values.

gram? Indeed, since the alternation of positive and negative values is precisely an indication of patchiness (Table 2). The first value of spatial autocorrelation (distance class 1), corresponding to pairs of neighbouring points on the sampling grid, is positive and significant; this means that the patch size is larger than the distance between 2 neighbouring points. The next significant positive value is found at distance class 4: this one gives the approximate distance between successive peaks. (Since the values are grouped into 12 distance classes, class 4 includes distances between 3.18 and 4.24, the unit being the distance between 2 neighbouring points of the grid; the actual distance between neighbours is 3.4 units). Negative significant values give the distance between peaks and troughs; the first of these values, found at distance class 2, corresponds here to the radius of the basis of the bumps. Notice that if the bumps were unevenly spaced, they could produce a correlogram with the same significant structure in the small distance classes, but with no other significant values afterwards. Since this correlogram was constructed with equal distance classes, the last autocorrelation coefficients cannot be interpreted, because they are based upon too few pairs of localities (see histogram, Fig. 1c).

The other artificial structures analysed in Fig. 1 were also sampled using a 10 × 10 regular grid of points. They are:

- Linear gradient (Fig. 1d). The correlogram has an overall 5% level significance (Bonferroni correction).
- Sharp step between 2 flat surfaces (Fig. 1e). The correlogram has an overall 5% level significance. Comparing with Fig. 1d shows that correlogram analysis cannot distinguish between real data presenting a sharp step and a gradient respectively.
- 9 thin bumps (Fig. 1f); each is narrower than in Fig. 1a. Even though 2 of the autocorrelation coefficients are significant at the $\alpha = 5\%$ level, the correlogram is not, since none of the coefficients is significant at the Bonferroni-corrected level $\alpha' = 0.00417$. In other words, 2 autocorrelation coefficients as extreme as those encountered here could have been found among 12 tests of a random structure, for an overall significance level $\alpha = 5\%$. 100 sampling points are probably not sufficient to bring out unambiguously a geometric structure of 9 thin bumps, since most of the data points do fall in the flat area in-between the bumps.
- Single thin bumps (Fig. 1g), about the same size as one of the bumps in Fig. 1a. The correlogram has an overall 5% level significance. Notice that the 'zone of influence' of this single bump spreads into more distance classes than in (b) because the phenomenon here is not limited by the rise of adjacent bumps.
- Single fat bump (Fig. 1h): a single bi-normal curve occupying the whole sampling surface. The correlogram has an overall 5% level significance. The 'zone of influence' of this very large bump is not much larger on the correlogram than for the single thin bump (g).
- 100 random numbers, drawn from a normal distribution, were generated and used as the variable to be analysed on the same regular geographic grid of 100 points (Fig. 1i). None of the individual values are significant at the 5% level of significance.
- Narrow wave (Fig. 1j): there are 4 steps between crests, so that there are 2.5 waves across the sampling surface. The correlogram has overall 5% level significance. The distance between successive crests of the wave show up in the significant value at $d = 4$, just as in (b).
- Wide wave (Fig. 1k): a single wave across the sampling surface. The correlogram has overall 5% level significance. The correlogram is the same as for the single fat bump (h). This shows that bumps, holes and waves cannot be distinguished using correlograms; maps are necessary. •

Ecologists are often capable of formulating hypotheses as to the underlying mechanisms or processes that may determine the spatial phenomenon under study; they can then deduct the shape the spatial structure will display if these hypotheses are true. It is a simple matter then to construct an artificial model-surface corresponding to these hypotheses, as we have done in Fig. 1,

and to analyse that surface with a correlogram. Although a test of significance of the difference between 2 correlograms is not easy to construct, because of the non-independence of the values in each correlogram, simply looking at the 2 correlograms – the one obtained from the real data, and that from the model data – suffices in many cases to find support for, or to reject the correspondence of the model-data to the real data.

Material: Vegetation data – These data were gathered during a multidisciplinary ecological study of the terrestrial ecosystem of the Municipalité Régionale de Comté du Haut-Saint-Laurent (Bouchard *et al.* 1985). An area of approximately 0.5 km^2 was sampled, in a sector a few km north of the Canada-USA border, in southwestern Québec. A systematic sampling design was used to survey 200 vegetation quadrats (Fig. 2) each 10 by 20 m in size. The quadrats were placed at 50-m intervals along staggered rows separated also by 50 m. Trees with more than 5 cm diameter at breast height were noted and identified at species level. The data to be analysed here consist of the abundance of the 28 tree species present in this territory, plus geomorphological data about the 200 sampling sites, and of course the geographical locations of the quadrats. This data set will be used as the basis for all the remaining examples presented in this paper.

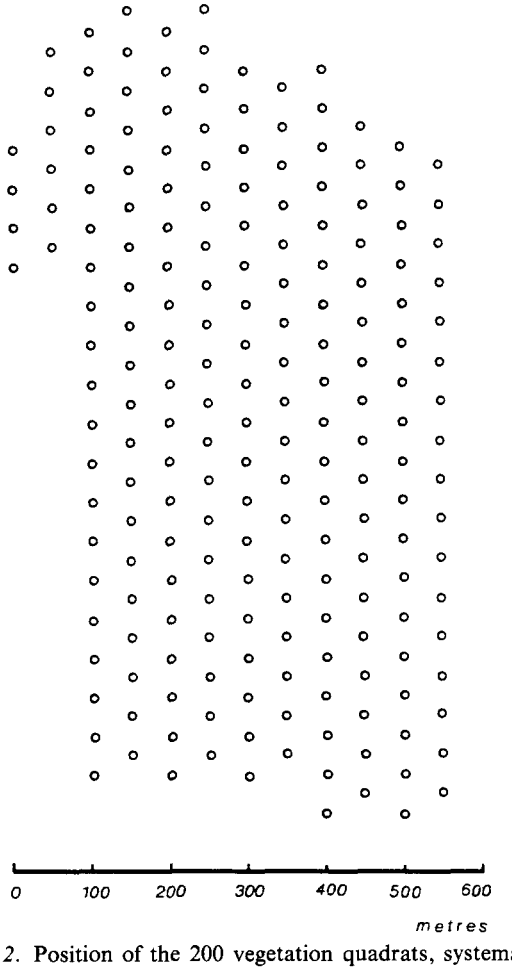


Fig. 2. Position of the 200 vegetation quadrats, systematically sampled in Herdman (Québec), during the summer of 1983. From Fortin (1985).

Example 2 – The correlogram in Fig. 3 describes the spatial autocorrelation (Moran's I) of the hemlock, *Tsuga canadensis*. It is globally significant (Bonferroni-corrected test, $\alpha = 5\%$). We can then proceed to examining significant individual values: can we find the structure's main elements from this correlogram? The first value of spatial autocorrelation (distance class 1, including distances from 0 to 57 m), corresponding to pairs of neighbouring points on the sampling grid, is positive and significant; this means that the patch size is larger than the distance between two neighbouring sampling points. The second peak of this correlogram (distance class 9, whose center is the 485 m distance) can be readily interpreted as the distance among peak centers, in the spatial distribution of the hemlock; see Fig. 10, where groups 3, 7 and 11 have high densities of hemlocks and have their centers located at about that

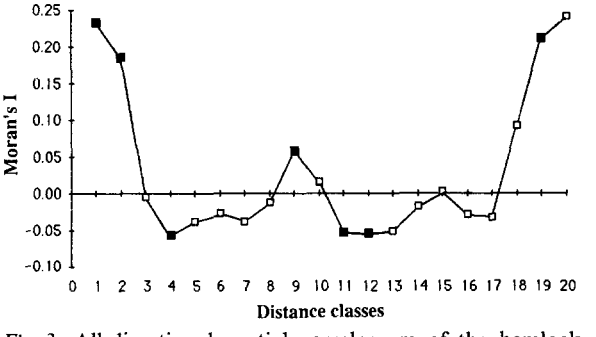


Fig. 3. All-directional spatial correlogram of the hemlock densities (*Tsuga canadensis*). Abscissa: distance classes; the width of each distance class is 57 m. Ordinate: Moran's I statistics. Symbols as in Fig. 1.

distance. The last few distance classes cannot be interpreted, because they each contain $<1\%$ of all pairs of localities. •

Two-dimensional correlogram

All-directional correlograms assume the phenomenon to be isotropic, as mentioned above. Spatial autocorrelation coefficients, computed as described in App. 1 for all pairs of data points, irrespective of the direction, produce a mean value of autocorrelation, smoothed over all directions. Indeed, a spatial autocorrelation coefficient gives a single value for each distance class, which is fine when studying a transect, but may not be appropriate for phenomena occupying several geographic dimensions (typically 2). Anisotropy is however often encountered in ecological field data, because spatial patterns are often generated by directional geophysical phenomena. Oden & Sokal (1986) have proposed to compute correlograms only for object pairs oriented in pre-specified directions, and to represent either a single, or several of these correlograms together, as seems fit for the problem at hand. Computing structure functions in pre-specified directions is not new, and has traditionally been done in variogram analysis (below). Fig. 4 displays a two-dimensional spatial correlogram, computed for the sugar-maple *Acer saccharum* from our test vegetation data. Calculations were made with the very program used by Oden & Sokal (1986); the same information could also have been represented by a set of standard correlograms, each one corresponding to one of the aiming directions. In any case, Fig. 4 clearly shows the presence of anisotropy in the structure, which could not possibly have been detected in an all-directional correlogram: the north-south range of *A. saccharum* is much larger (ca 500 m) than the east-west range (200 m).

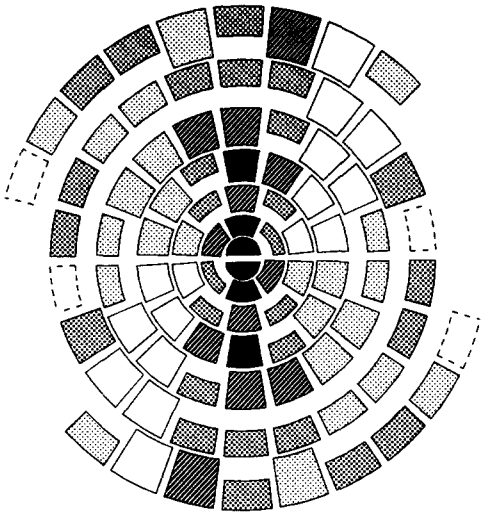


Fig. 4. Two-dimensional correlogram for the sugar-maple *Acer saccharum*. The directions are geographic and are the same as in Fig. 2. The lower half of the correlogram is symmetric to the upper half. Each ring represents a 100-m distance class. Symbols are as follows: full boxes are significant Moran's I coefficients, half-boxes are non-significant values; dashed boxes are based on too few pairs and are not considered. Shades of gray represent the values taken by Moran's I: from black ($+0.5$ to $+0.2$) through hachured ($+0.2$ to $+0.1$), heavy dots ($+0.1$ to -0.1), light dots (-0.1 to -0.2), to white (-0.2 to -0.5).

Two-dimensional spectral analysis

This method, described by Priestly (1964), Rayner (1971), Ford (1976), Ripley (1981) and Renshaw & Ford (1984), differs from spatial autocorrelation analysis in the structure function it uses. As in regular time-series spectral analysis, the method assumes the data to be stationary (no spatial gradient), and made of a combination of sine patterns. An autocorrelation function r_{gh}, as well as a periodogram with intensity $I(p, q)$, are computed.

Just as with Moran's I, the autocorrelation values are a sum of cross products of lagged data; in the present case, one computes the values of the function r_{gh} for all possible combinations of lags (g, h) along the 2 geographic sampling directions (App. 1); in Moran's I on the contrary, the lag d is the same in all geographic directions. Besides the autocorrelation function, one computes a Schuster two-dimensional periodogram, for all combinations of spatial frequencies (p, q) (App. 1), as well as graphs (first proposed by Renshaw & Ford, 1983) called the R-spectrum

and the Θ-spectrum that summarize respectively the frequencies and directions of the dominant waves that form the spatial pattern. See App. 1 for computational details.

Two-dimensional spectral analysis has recently been used to analyse spatial patterns in crop plants (McBratney & Webster 1981), in forest canopies (Ford 1976; Renshaw & Ford 1983; Newbery *et al.* 1986) and in other plants (Ford & Renshaw 1984). The advantage of this technique is that it allows analysis of anisotropic data, which are frequent in ecology. Its main disadvantage is that, like spectral analysis for time series, it requires a large data base; this has prevented the technique from being applied to a wider array of problems. Finally, one should notice that although the autocorrelogram can be interpreted essentially in the same way as a Moran's correlogram, the periodogram assumes on the contrary the spatial pattern to result from a combination of repeatable patterns; the periodogram and its R and Θ spectra are very sensitive to repeatabilities in the data, but they do not detect other types of spatial patterns which do not involve repeatabilities.

Example 3 – Fig. 5a shows the two-dimensional periodogram of our vegetation data for *Acer saccharum*. For the sake of this example, and since this method requires the data to form a regular, rectangular grid, we interpolated sugar-maple abundance data by kriging (see below) to obtain a rectangular data grid of 20 rows and 12 columns. The periodogram (Fig. 5a) has an overall 5% significance, since 4 values exceed the critical Bonferroni-corrected value of 6.78; these 4 values explain together 72% of the spatial variance of our variable, which is an appreciable amount.

The most prominent values are the tall blocks located at $(p, q) = (0, 1)$ and $(0, -1)$; together, they represent 62% of the spatial variance and they indicate that the dominant phenomenon is an east-west wave with a frequency of 1 (which means that the phenomenon occurs once in the east-west direction across the map). This structure has an angle of $\Theta = \tan^{-1}(0/[1 \text{ or } -1]) = 0°$ and is the dominant feature of the Θ-spectrum; with its frequency $R = \sqrt{(0^2 + 1^2)} = 1$, it also dominates the R-spectrum. This east-west wave, with its crest

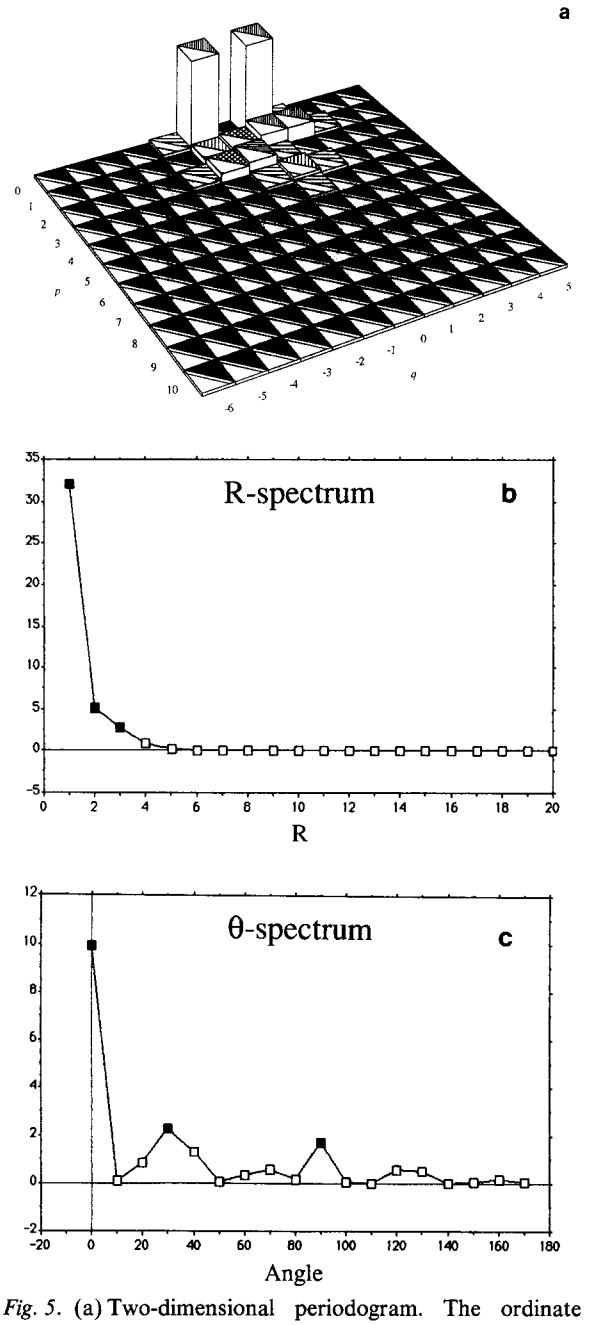


Fig. 5. (a) Two-dimensional periodogram. The ordinate represents the intensity of the periodogram. (b) R-spectrum. (c) Θ-spectrum. Bonferroni-corrected significant values in the spectra are represented by dark squares, for an overall significance level of 5%.

elongated in the north-south direction, is clearly visible on the map of Fig. 13a.

The next 2 values, that ought to be considered together, are the blocks (1, 2) and (1, 1) in the periodogram. The corresponding angles are $\Theta = 26.6°$ and 45° (they form the 4th and 5th values in the Θ-spectrum), for an average angle of about 35°; the R frequencies of the structure they represent are $\sqrt{(p^2 + q^2)} = 2.24$ and 1.41, for an average of 1.8. Notice that the values of p and q have been standardized as if the 2 geographic axes (the vertical and horizontal directions in Fig. 13) were of equal lengths, as explained in App. 1; these periodogram values indicate very likely the direction of the axis that crosses the centers of the 2 patches of sugar-maple in the middle and bottom of Fig. 13a.

Two other periodogram values are relatively high (5.91 and 5.54) but do not pass the Bonferroni-corrected test of significance, probably because the number of blocks of data in our regular grid is on the low side for this method. In any case, the angle they correspond to is 90°, which is a significant value in the Θ-spectrum. These periodogram values indicate obviously the north-south direction crossing the centers of the 2 large patches in the upper and middle parts of Fig. 13a ($R = 2$).

These results are consistent with the two-dimensional correlogram (Fig. 4) and with the variograms (Fig. 9), and confirm the presence of anisotropy in the *A. saccharum* data. They were computed using the program of Renshaw & Ford (1984). Ford (1976) presents examples of vegetation data with clearer periodic components. •

The Mantel test

Since one of the scopes of community ecology is the study of relationships between a number of biological variables – the species – on the one hand, and many abiotic variables describing the environment on the other, it is often necessary to deal with these problems in multivariate terms, to study for instance the simultaneous abundance fluctuations of several species. A method of carrying out such analyses is the Mantel test (1967). This method deals with 2 distance matrices, or 2 similarity matrices, obtained independently, and describing the relationships among the same sampling stations (or, more generally, among the same objects). This type of analysis has two chief domains of application in community ecology.

Let us consider a set of n sampling stations. In the first kind of application, we want to compare a matrix of ecological distances among stations (**X**) with a matrix of geographic distances (**Y**) among the same stations. The ecological distances in matrix **X** can be obtained for instance by comparing all pairs of stations, with respect to their faunistic or floristic composition, using one of the numerous association coefficients available in the literature; notice that qualitative (nominal) data can be handled as easily as quantitative data, since a number of coefficients of association exist for this type of data, and even for mixtures of quantitative, semi-quantitative and qualitative data. These coefficients have been reviewed for instance by Orlóci (1978), by Legendre & Legendre (1983a and 1984a), and by several others; see also Gower & Legendre (1986) for a comparison of coefficients. Matrix **Y** contains only geographic distances among pairs of stations, that is, their distances in m, km, or other units of measurement. The scope of the study is to determine whether the ecological distance increases as the samples get to be geographically farther apart, i.e., if there is a spatial gradient in the multivariate ecological data. In order to do this, the Mantel statistic is computed and tested as described in App. 2. Examples of Mantel tests in the context of spatial analysis are found in Ex. 8 in this paper, as well as in Upton & Fingleton's book (1985).

The Mantel test can be used not only in spatial analysis, but also to check the goodness-of-fit of data to a model. Of course, this test is valid only if the model in matrix **Y** is obtained independently from the similarity measures in matrix **X** – either by ecological hypothesis, or else if it derives from an analysis of a different data set than the one used in elaborating matrix **X**. The Mantel test cannot be used to check the conformity to a

matrix **X** of a model derived from the **X** data. Goodness-of-fit Mantel tests have been used recently in vegetation studies to investigate very precise hypotheses related to questions of importance, like the concept of climax (McCune & Allen 1985) and the environmental control model (Burgman 1987). Another application can be found in Hudon & Lamarche (in press) who studied competition between lobsters and crabs.

Example 4 – In the vegetation area under study, 2 tree species are dominant, the sugar-maple *Acer saccharum* and the red-maple *A. rubrum*. One of these species, or both, are present in almost all of the 200 vegetation quadrats. In such a case, the hypothesis of niche segregation comes to mind. It can be tested by stating the null hypothesis that the habitat of the 2 species is the same, and the alternative hypothesis that there is a difference. We are going to test this hypothesis by comparing the environmental data to a model corresponding to the alternative hypothesis (Fig. 6), using a Mantel test. The environmental data were chosen to represent factors likely to influence the growth of these species. The 6 descriptors are: quality of drainage (7 semi-quantitative classes), stoniness of the soil (7 semi-quantitative classes), topography (11 unordered qualitative classes), directional exposure (the 8 sectors of the compass card, plus class 9 = flat land), texture of horizon 1 of the soil (8 unordered qualitative classes), and geomorphology (6 unordered qualitative classes, described in Example 8 below). These data were used to compute an Estabrook-Rogers similarity coefficient among quadrats (Estabrook & Rogers 1966; Legendre & Legendre 1983a, 1984a). The Estabrook & Rogers similarity coefficient makes it possible to assemble mixtures of quantitative, semi-quantitative and qualitative data into an overall measure of similarity; for the descriptors of directional exposure and soil texture, the partial similarities contributing to the overall coefficient were drawn from a set of partial similarity values that we established, as ecologists, to represent how similar are the various pairs of semi-ordered or unordered classes, considered from the point of view of tree growth. The environmental similarity matrix is represented as **X** in Fig. 6.

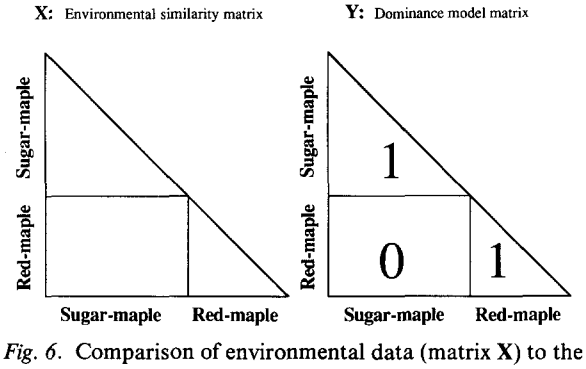


Fig. 6. Comparison of environmental data (matrix **X**) to the model (matrix **Y**), to test the hypothesis of niche segregation between the sugar-maple and the red-maple.

The ecological hypothesis of niche segregation between *A. saccharum* and *A. rubrum* can be translated into a model-matrix of the alternative hypothesis as follows: each of the 200 quadrats was coded as having either *A. saccharum* or *A. rubrum* dominant. Then, a model similarity matrix among quadrats was constructed, containing 1's for pairs of quadrats that were dominant for the same species (maximum similarity), and 0's for pairs of quadrats differing as to the dominant species (null similarity). This model matrix is represented as **Y** in Fig. 6, where it is shown as if all the *A. saccharum*-dominated quadrats came first, and all the *A. rubrum*-dominated quadrats came last; in practice, the order of the quadrats does not make any difference, insofar as it is the same in matrices **X** and **Y**.

One can obtain the sampling distribution of the Mantel statistic by repeatedly simulating realizations of the null hypothesis, through permutations of the quadrats (corresponding to the lines and columns) in the **Y** matrix, and recomputing the Mantel statistic between **X** and **Y** (App. 2). If indeed there is no relationship between matrices **X** and **Y**, we can expect the Mantel statistic to have a value located near the centre of this sampling distribution, while if such a relation does exist, we expect the Mantel statistic to be more extreme than most of the values obtained after random permutation of the model matrix. The Mantel statistic was computed and found to be significant at $p < 0.00001$, using in the present

case Mantel's t test, mentioned in the remarks of App. 2, instead of the permutation test. So, we must reject the null hypothesis and accept the idea that there is some measurable niche differentiation between *A. saccharum* and *A. rubrum*. Notice that the objective of this analysis is the same as in classical discriminant analysis. With a Mantel test, however, one does not have to comply with the restrictive assumptions of discriminant analysis, assumptions that are rarely met by ecological data; furthermore, one can model at will the relationships among plants (or animals) by computing matrix **X** with a similarity measure appropriate to the ecological data, as well as to the nature of the problem, instead of being imposed the use of an Euclidean, a Mahalanobis or a chi-square distance, as it is the case in most of the classical multivariate methods. In the present case, the Mantel test made it possible to use a mixture of semi-quantitative and qualitative variables, in a rather elegant analysis.

To what environmental variable(s) do these tree species react? This was tested by a series of a posteriori tests, where each of the 6 environmental variables was tested in turn against the model-matrix **Y**, after computing an Estabrook & Rogers similarity matrix for that environmental variable only. Notice that these a posteriori tests could have been conducted by contingency table analysis, since they involve a single semi-quantitative or qualitative variable at a time; they were done by Mantel testing here to illustrate the domain of application of the method. In any case, these a posteriori tests show that 3 of the environmental variables are significantly related to the model-matrix: stoniness ($p < 0.00001$), topography ($p = 0.00028$) and geomorphology ($p < 0.00001$); the other 3 variables were not significantly related to **Y**. So the three first variables are likely candidates, either for studies of the physiological or other adaptive differences between these 2 maple species, or for further spatial analyses. One such analysis is presented as Ex. 8 below, for the geomorphology descriptor. ●

The Mantel correlogram

Relying on a Mantel test between data and a model, Sokal (1986) and Oden & Sokal (1986) found an ingenious way of computing a correlogram for multivariate data; such data are often encountered in ecology and in population genetics. The principle is to express ecological relationships among sampling stations by means of an **X** matrix of multivariate distances, and then to compare **X** to a **Y** model matrix, different for each distance class; for distance class 1, for instance, neighbouring station pairs (that belong to the first class of geographic distances) are linked by 1's, while the remainder of the matrix contains zeros only. A first normalized Mantel statistic (r) is calculated for this distance class. The process is repeated for each distance class, building each time a new model-matrix **Y**, and recomputing the normalized Mantel statistic. The graph of the values of the normalized Mantel statistic against distance classes gives a multivariate correlogram; each value is tested for significance in the usual way, either by permutation, or using Mantel's normal approximation (remark in App. 2). [Notice that if the values in the **X** matrix are similarities instead of distances, or else if the 1's and the 0's are interchanged in matrix **Y**, then the sign of each Mantel statistic is changed.] Just as with a univariate correlogram (above), one is advised to carry out a global test of significance of the Mantel correlogram using the Bonferroni method, before trying to interpret the response of the Mantel statistic for specific distance classes.

Example 5 – A similarity matrix among sampling stations was computed from the 28 tree species abundance data, using the Steinhaus coefficient of similarity (also called the Odum, or the Bray and Curtis coefficient: Legendre & Legendre 1983a, 1984a), and the Mantel correlogram was computed (Fig. 7). There is overall significance in this correlogram, since many of the individual values exceed the Bonferroni-corrected level $\alpha' = 0.05/20 = 0.0025$. Since there is significant positive autocorrelation in the small distance classes and significant negative autocorrelation in

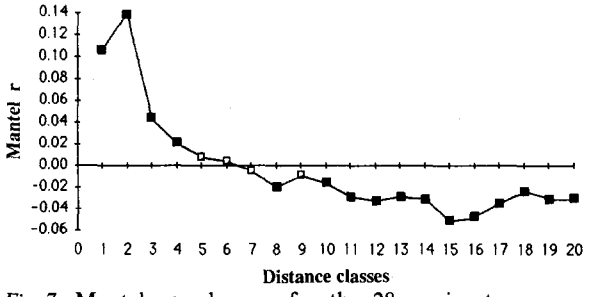


Fig. 7. Mantel correlogram for the 28-species tree community structure. See text. Abscissa: distance classes (one unit of distance is 57 m); ordinate: standardized Mantel statistic. Dark squares represent significant values of the Mantel statistic ($p \leq 0.05$).

the large distances, the overall shape of this correlogram could be attributed either to a vegetation gradient (Fig. 1d) or to a structure with steps (Fig. 1e). In any case, the zone of positive autocorrelation lasts up to distance class 4, so that the average size of the 'zone of influence' of multivariate autocorrelation (the mean size of associations) is about 4 distance classes, or (4 classes × 57 m) ≈ 230 m. This estimation is confirmed by the maps in Fig. 10, where many of the associations delimited by clustering have about that size. ●

Detection and description of spatial structures

As mentioned above, the different types of correlograms, outlined in the section entitled 'Testing for the presence of a spatial structure', do provide a description of spatial structures. Other methods, that are more exclusively descriptive, can also be used for this purpose. They are presented in this section.

The variogram

The semi-variogram (Matheron 1962), often called variogram for simplicity, is related to spatial correlograms. It is another structure function, allowing to study the autocorrelation phenomenon as a function of distance; however this method, on which the kriging contouring method is based (below), does not lend itself to any statistical test of hypothesis. The variogram is a univariate method, limited to quantitative variables, allowing to analyse phenomena that occur in one, 2 or 3 geographic dimensions. Burrough (1987) gives an introduction to variogram analysis for ecologists.

Before using the variogram, one must make sure that the data are stationary, which means that the statistical properties (mean and variance) of the data are the same in the various parts of the area under study, or at least that they follow the 'intrinsic hypothesis', which means that the increments between all pairs of points located a given distance d apart have a man zero and a finite variance that remains the same in the various parts of the area under study; this value of variance, for distance class d, is twice the value of the semi-variance function $\gamma(d)$. This relaxed form of the stationarity assumption makes it possible to use the variogram, or for that matter any other structure function (for instance spatial autocorrelograms), with ecological data. Of course, a large-scale spatial structure, if present, will necessarily be picked up by the structure function and may mask finer spatial structures; large-scale trends, in particular, should be removed by regression (trend surface analysis) or some other form of modelling before the presence of other, finer structures can be investigated.

There are two types of variograms: the experimental and the theoretical. The experimental variogram (semi-variogram) is computed from the data using the formula in App. 1. It is presented as a plot of $\gamma(d)$ (ordinate) as a function of distance classes (d), just like a correlogram. As noticed in App. 1, $\gamma(d)$ is a distance-type function, so that it is related to Geary's c coefficient. The experimental variogram can be used as a description of the structure function of the spatial phenomenon and in this way it is of help in understanding the spatial structure.

The variogram was originally designed by mining engineers, as a basis for the contouring method known as kriging (below). This is how it became known to ecologists, among whom its use is spreading (Burrough 1987). To be useful for

kriging, a theoretical variogram has to be fitted to the experimental one; the adjustment of a theoretical variogram to the experimental function provides the parameters used by the kriging method. The most important of these parameters are (1) the *range* of influence of the spatial structure, which is the distance where the variogram stops increasing; (2) the *sill*, which is the ordinate value of the flat portion of the variogram, where the semi-variance is no longer a function of direction and distance, and corresponds to the variance of the samples; and eventually (3) the *nugget effect* (see below). As in any type of nonlinear curve fitting, the user must decide what type of nonlinear function is wanted to adjust to his experimental variogram; this step requires both experience, and insight into the ecological process under study. Several types of theoretic functions are often used for this adjustment. 4 of them, the most common ones, are described in App. 1 and illustrated in Fig. 8. Differences between these theoretic functions lie mostly in the shape of the left-hand part of the curves, near the origin. A *linear variogram* indicates a linear spatial gradient; this model has no sill. *Gaussian, exponential* and *spherical variograms* give a measure of the size of the spatial influence of the process (patch size, if the phenomenon is patchy), as well as the shape of the drop of this influence as one gets farther away from the center of the phenomenon; the exponential model does not necessarily have a sill. A flat variogram, also called 'pure nugget effect', indicates the absence of a spatial structure in the data, at least at the scale the observations were made. The so-called *nugget effect* refers to variograms that do not go through the origin of the graph, but display some amount of variance even at distance zero; this effect may be caused by some intrinsic random variability in the data (sampling variance), or it may suggest that the sampling has not been performed at the right spatial scale. Variograms have recently been used to measure the fractal dimension of environmental gradients (Phillips 1985).

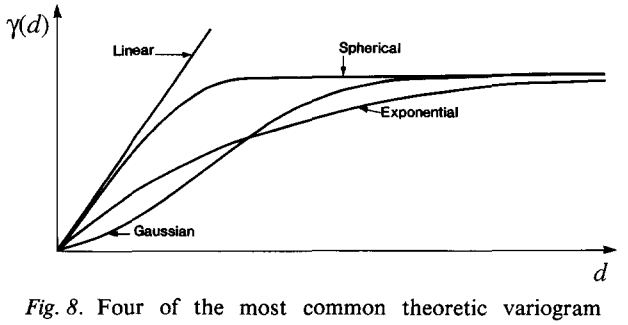


Fig. 8. Four of the most common theoretic variogram models.

Mining engineers compute separate variograms for different spatial directions, to determine if the spatial structure is isotropic or not. We have seen above that this procedure has now been extended to correlograms as well. The spatial structure is said to be *isotropic* when the variograms are the same regardless of the direction of measurement. 2 different kinds of anisotropy can be detected: geometric anisotropy and stratified anisotropy. Geometric anisotropy (same sill, different ranges) is measured by the *anisotropy ratio*, which is equal to the range of the variogram in the direction producing the longest range, divided by the range in the direction with the smallest range. Stratified (or zonal) anisotropy (different sills, same range) refers to the fact that the sills of the variograms may not be the same in different directions. In the presence of one or the other type of anisotropy, or both, there are three solutions to obtain acceptable interpolated maps by kriging: one can compute compromise variogram parameters, using the formulas in David (1977) or in Journel & Huijbregts (1978); secondly, one can use a kriging program that makes use of the parameters of variograms computed separately in different directions of the physical space (2 or 3, depending on the problem); or finally, one can use 'generalized intrinsic random functions of order k' (Matheron 1973) that allow for linear or quadratic trends in the data.

Example 6 – Experimental variograms were computed by Fortin (1985), for *A. saccharum*, in the 45° and 90° directions (window: 22°), and in all directions (Fig. 9). Comparing the 45° and 90° variograms shows the presence of anisotropy, as was observed in Fig. 4. The range in the 45° variogram (dashed line) is about 445 m, while the range in the 90° variogram is about 685 m, so that

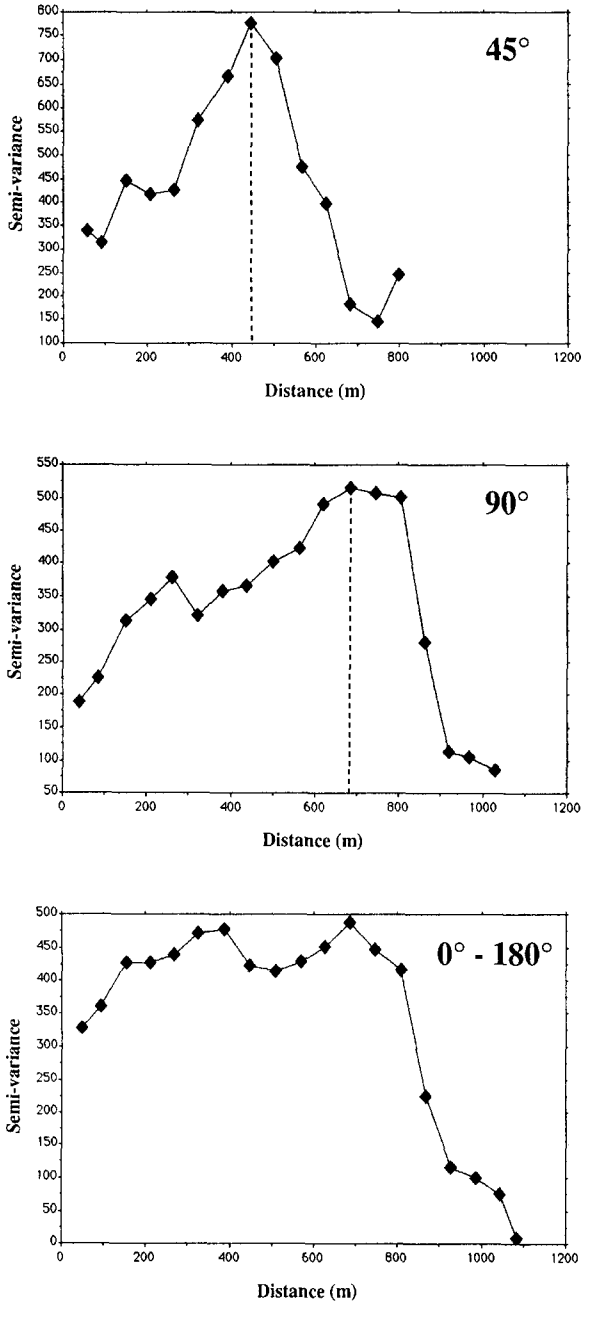


Fig. 9. Three experimental variograms computed for the *Acer saccharum* data. See text. Abscissa: distance classes. Ordinate: values of the semi-variance function $\gamma(d)$. Dashed lines: ranges. Modified from Fortin (1985).

the anisotropy ratio can be computed as 685/445 ≈ 1.5. The all-directions variogram does not clearly render this information. ●

Clustering methods with spatial contiguity constraint

Describing multivariate structures can be done by the methods of clustering, which are classical methods of multivariate data analysis, and in particular by clustering with spatial contiguity constraint. If the clustering results are represented on a map, the multivariate structure of the data – plant associations for instance – will be clearly described by the map.

Clustering with spatial contiguity constraint has been suggested by many authors since 1966 (e.g., Ray & Berry 1966; Webster & Burrough 1972; Lefkovitch 1978, 1980; and others), in such different fields as pedology, political science, economy, psychometry and ecology. Starting from multivariate data, the common need of these authors was to establish geographical regions made of adjacent sites (i.e., a choropleth map: see 'Estimation and mapping' below) which would be homogeneous with respect to certain variables. In order to do this, it is necessary (1) to compute a matrix of similarity among sites from the variables on which these homogeneous regions have to be based (of course, this step applies only to clustering methods that are similarity-based), then (2) proceed with any of the usual clustering methods, with the difference that one constrains the algorithm to cluster only these sites or site groups that are geographically contiguous. The constraint is provided to the program in the form of a list of connections, or spatial links, among neighbouring localities. Connections may be established in a variety of ways: see App. 1. Adding such constraints to existing programs raises algorithmic problems which we will not discuss here. Clustering with constraint has interesting properties. On the one hand, it reduces the set of mathematically possible solutions to those that are geographically meaningful; this avoids the well-known problem of clustering methods, where different solutions may be obtained after applying different clustering algorithms to the same data set; constraining all these algorithms to produce results that are geographically consistent forces them to converge towards very similar solutions. On the other hand, the partitions

obtained in this way reproduce a larger fraction of the structure's spatial information than equivalent partitions obtained without constraint (Legendre 1987). Finally, constrained agglomerative clustering is faster with large data sets than the unconstrained equivalent, because the search for 'the next pair to join' is limited to adjacent groups only (Openshaw 1974; Lebart 1978).

Example 7 – A vegetation map was constructed from our test data, as follows. (1) The same Steinhaus similarity matrix among stations was used as in Ex. 5; it is based upon the 28 tree species abundance data. (2) The spatial relationships among sampling quadrats were represented by a list of connections among close neighbours; the list was established in the present case by the Delaunay triangulation method (App. 1). The presence of a connection between 2 quadrats tells the clustering programs that these 2 localities are located close to one another and thus may eventually be included in the same cluster, if their ecological similarity allows. (3) Agglomerative clustering with spatial contiguity constraint was conducted on the similarity matrix. The spatial contiguity constraint was read by the program from the list of connections, or 'link edges', described above. We used a proportional-link linkage agglomerative algorithm (with 50% connectedness: Sneath 1966), that produced a series of maps, one for each clustering level (Legendre & Legendre 1984b). The map with 13 groups was retained as being ecologically the most meaningful (Fig. 10a); 5 quadrats remain unclustered at that level. Recognizing 13 groups implies that the mean area per association is 740000 $m^2/13$ = 56923 m^2/association, corresponding to an average area diameter of $(56923)^{1/2}$ = 238.6 m; this compares very well with the average size of the zone of influence of our species associations found in the Mantel correlogram, 230 m (Ex. 5).

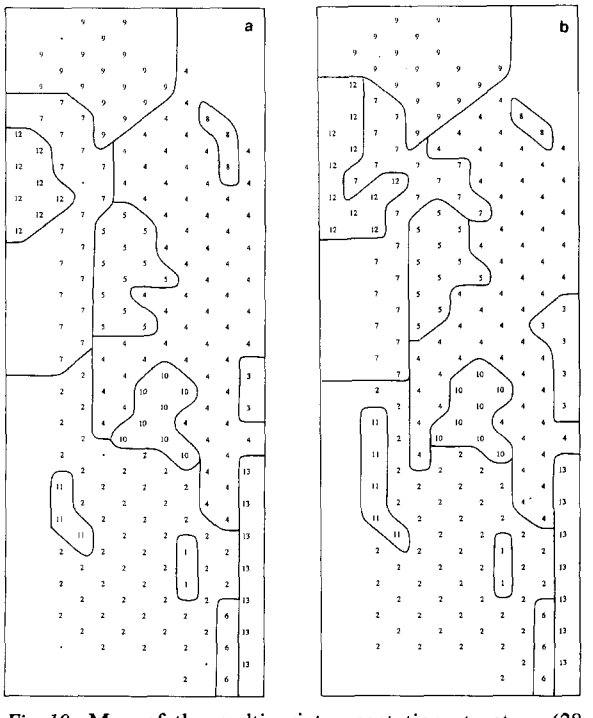


Fig. 10. Map of the multivariate vegetation structure (28 species), obtained by constrained clustering. (a) Space-constrained agglomerative proportional-link linkage, at the level where 13 groups were obtained; the five unclustered quadrats are materialized by dots. (b) Optimization of the previous map by space-constrained *k*-means clustering.

Agglomerative clustering may have produced small distortions of the resulting map, because of the hierarchical nature of the classification that results from such sequential algorithms. So, we tried to render our 13 groups as homogeneous as possible in terms of vegetation composition, using a *k*-means algorithm (MacQueen 1967) with spatial contiguity constraint. A *k*-means algorithm uses an iterative procedure of object reallocation to minimize the sum of within-group dispersions. This type of algorithm tends to produce compact clusters in the variable space (here, the vegetation data), which is exactly what we are looking for; there is no reason however to expect this phenomenon to affect the shape of the clusters in *geographic* space. We provided our program with the list of constraining connections computed in step 2 above, with the 13-group classification obtained in step 3 to be used as the starting configuration (temporarily allocating the 5 unclustered quadrats to the group that enclosed them geographically), and with a set of principal coordinates computed from the Steinhaus similarity matrix (since our *k*-means program computes within-group variances from raw variables, and not from a similarity or distance matrix). The

map of the optimized groups is shown in Fig. 10b. The number of groups remained the same, of course, but 19 objects out of 200 changed group (10%). 4 groups remained unmodified: groups number 1, 6, 10 and 13 in Fig. 10.

The 2 13-group classifications were compared to the raw species abundance data in a series of contingency tables. This work was facilitated by dividing first each species' abundance range into a few classes, following the method described by Legendre & Legendre (1983b). Comparing the interpretations of the 2 classifications, the groups produced by the *k*-means classification were slightly easier to characterize than those produced by the agglomerative classification. Their main biotic characteristics are the following:

- Open area, with rare *A. saccharum*: Group 1.
- *A. rubrum* stands, Group 2.
- Oldfield-birch stands, *Betula populifolia*, located between the *A. rubrum* and *A. saccharum* areas: Group 10.
- *A. saccharum* stands: Groups 4 and 12.
- Stands dominated by white pine *Pinus strobus* and aspen *Populus tremuloides*: Group 6.
- Hemlock stands, *Tsuga canadensis*: Groups 3, 7 and 11.
- Species diversity is highest in the three following groups of stands, dominated by black ash *Fraxinus nigra* and yellow birch *Betula alleghaniensis*:
  - In the bottom of a kettle, with aspen *Populus tremuloides*, white cedar *Thuja occidentalis* and American elm *Ulmus americana*: Group 5.
  - With red ash *Fraxinus pennsylvanica* and basswood *Tilia americana*: Groups 8 and 9.
- Fence-shaped region (formerly cleared land) characterized by white cedar *Thuja occidentalis* and American elm *Ulmus americana* but, contrary to group 5, with few *F. nigra* and *B. alleghaniensis*: Group 13. •

Univariate or multivariate data that form a transect in space, instead of covering a surface, often need to be summarized by identifying breaking points along the series. Several authors have proposed to use clustering methods with contiguity constraint in a single dimension (space or time). One such program was developed in P.L.'s lab to analyse ecological successions, with the explicit purpose of locating the abrupt changes that may occur along successional series of community structure; before each group fusion, a statistical permutation test is performed, that translates into statistical terms the ecological model of the development of communities by abrupt structure jumps (Legendre *et al.* 1985). Since then, this method has been used to segment spatial transects of ecological data (Galzin & Legendre 1988), as well as paleontological series (Bell & Legendre 1987). Other applications are in progress, including the reconstruction of climatic fluctuations by studying tree rings, and the segmenting of pollen stratigraphic data. Other methods for segmenting such series, taking into account the spatial or temporal contiguity of samples, have been proposed by Fisher (1958) for univariate economic data, by Webster (1973) for soil data, by Hawkins & Merriam for univariate (1973) and for multivariate (1974) geologic data, by Gordon & Birks (1972, 1974) and by Gordon (1973) for pollen stratigraphic data. This work has been summarized by Legendre (1987).

Causal modelling

Although empirical models are used by ecologists and have their usefulness, modelers often prefer to include only the specific (ecological) hypotheses they may have about the factors and mechanisms determining the process under study. The purpose of modelling is then to verify that experimental or field data do support these hypotheses ('causes'), and to confirm the relational way in which they are assembled into the model. Given the importance of space in our ecological theories, this review of spatial analysis methods would not be complete without mentioning how space can be included in the calculation of relationships among variables. 2 variables may appear related if both of them are linked to a common third one; space is a good candidate for creating such false correlations, since 2 variables may actually seem to be linked because they are driven by a

common spatial gradient. Even if correlation does not mean causality, the absence of correlation, monotonic or linear, is sufficient to abandon the hypothesis of a causal link between 2 variables. It is thus important for ecologists interested in causal relationships to check whether the spatial gradient of A could be explained, at least in part, by a spatially structured variable B, or if an apparent correlation between 2 variables is not to be ascribed to a common spatial structure (an unmeasured or untested space-structured variable causing A and B independently). There is still some way to go before space can be included as a variable in complex ecological models, but we will show how it can at least be included in simple models.

Partial Mantel test

How can a partial correlation between two variables be calculated, controlling for a space effect? Smouse *et al.* (1986) dealt with this problem and suggested expressing the variations of each of the two variables by matrices (**A** and **B**) that contain the differences in values between all sampling station pairs. On the other hand, as in the Mantel test, the 'space' variable is expressed by a matrix of geographic distances among stations (matrix **C**). Actually, matrices **A** and **B** could as well be multivariate distance matrices. A partial Mantel statistic is calculated between **A** and **B**, controlling for the effect of matrix **C**. The Smouse *et al.* partial Mantel statistic has the same formula as a partial product-moment correlation coefficient, computed from standardized Mantel statistics. Actually, the computations are done as follows in order to test the partial Mantel statistic between **A** and **B**, controlling for the effect of matrix **C**: (1) compute matrix **A'** that contains the residuals of the linear regression of the values of **A** over the values of **C**; (2) likewise, compute matrix **B'** of the residuals of the linear regression of the values of **B** over the values of **C**; (3) compute the Mantel statistic between **A'** and **B'** (which is just another way of obtaining the partial Mantel statistic between **A** and **B** controlling for **C**, as in Pearson partial correlations). (4) Test as usual, either by permuting **A'** or **B'**, or by Mantel's normal approximation. This is equivalent to what would be obtained by permuting all 3 matrices. Partial Mantel tests are not easy to interpret; Legendre & Troussellier (1988) have shown the consequences, in terms of significant Mantel and partial Mantel statistics, of all the possible three-matrices models implying space. As in the case of the Mantel test (App. 2), the restrictive influence of the linearity assumption has not been fully investigated yet for partial Mantel tests.

This type of analysis has numerous applications for studying variables distributed in space. Actually, 3 other forms of test of partial association involving 3 distance matrices have been proposed. 2 of these are based upon the Mantel test, one by anthropologists (Dow & Cheverud 1985), the second one in the field of psychometry (Hubert 1985); the third one involves multiple regressions on distance matrices (Manly 1986; Krackhardt 1988).

Example 8 – We will use our vegetation data to study the much debated question of the environmental control of vegetation structures. We will study in particular the relationship between vegetation structure and the geomorphology of the sampling sites. Of course, vegetation structures are most often autocorrelated, and this can be due either to the fact that biological reproduction is a contagious process, or to some linkage between vegetation and substrate conditions, since soil composition, geomorphology, and so on, are autocorrelated. So, if we find a relationship between vegetation and geomorphology, we will ask the following additional question: do the data support the hypothesis of a causal link between vegetation structure and geomorphology, or is the observed correlation spurious, resulting from the fact that both vegetation and geomorphology follow a common spatial structure, through some unstudied factor that could affect both?

Since our vegetation data are multivariate (28 tree species), they will be represented in the computations by a matrix of multivariate Steinhaus ecological similarities, as in Ex. 5. Space is repre-

Table 3. Above the diagonal: simple standardized Mantel statistics and associated probabilities. Below the diagonal: partial Mantel statistics and associated probabilities. Tests of significance are one-tailed.

Partial Mantel tests \ Mantel tests	Vegetation structure	Geomorphology	Space
Vegetation structure	–	0.15054 $p = 0.000$	0.17053 $p = 0.000$
Geomorphology	0.09397 $p = 0.000$	–	0.38073 $p = 0.000$
Space	0.12384 $p = 0.000$	0.36449 $p = 0.000$	–

sented by a matrix of geographic distances among quadrats. The geomorphology variable (6 unordered qualitative classes: moraine ridge, stratified till ridge, reworked till, kettle, relict channel, Champlain sea deposits) was used to compute a simple matching similarity coefficient. Similarities were transformed into distances ($D = 1 - S$) before computing the Mantel tests.

The results of the simple and partial Mantel tests are presented in Table 3. The 3 simple Mantel tests (above the diagonal) show that both the vegetation structure and the geomorphology are autocorrelated, as expected, and also that there exists a significant relation between vegetation and geomorphology. Notice that the Mantel statistic values do not behave like product-moment correlation coefficients, and do not have to be large in absolute value to be significant. All 3 partial Mantel tests (Smouse *et al.* 1986) are significant at the Bonferroni-corrected level $\alpha' = 0.05/3 = 0.01667$. Of special interest to us is the unique influence of geomorphology on the vegetation structure, compared to the influence of space. To decide among the various possible models of interrelations among these 3 groups of variables, we have to consider in turn all 3 possible competing models, and proceed by elimination, as follows. (1) The first model states that the vegetation spatial structure is caused by the spatial structure of geomorphology [Space → Geomorphology → Vegetation structure]. If this model were supported by the data, then we would expect the partial Mantel statistic (Space · Vegetation), controlling for the effect of Geomorphology, not to be significantly different from zero; this condition is not met in Table 3. (2) The second model states that there is a spatial component in the vegetation data, which is independent from the spatial structure in geomorphology [Geomorphology ← Space → Vegetation structure]. If this model were supported by the data, we would expect the partial Mantel statistic (Geomorphology · Vegetation), controlling for the effect of Space, not to differ significantly from zero, a condition that is not met in Table 3. (3) The third possible model (Fig. 11) claims that the spatial structure in the vegetation data is partly determined by the spatial gradient in the geomorphology, and partly by other factors not explicitly identified in the model. According to this model, all 3 simple and all 3 partial Mantel tests should be significantly different from zero. This is indeed what we find in Table 3.

Although this decomposition of the correlation would best be accomplished by computing standard partial regression-type coefficients (as in path analysis), we can draw some conclusions by looking at the partial Mantel statistics. They show that the Mantel statistic describing the influence of geomorphology on vegetation structure is reduced from 0.15 to 0.09 when controlling for the effect of space. The proper influence of geomorphology on vegetation is then 0.09, while the difference (0.06) is the part of the influence of geomorphology on vegetation that corresponds to the spatial component of geomorphology ($0.15 \times 0.38 = 0.06$). On the other hand, the partial Mantel statistic describing the spatial determi-

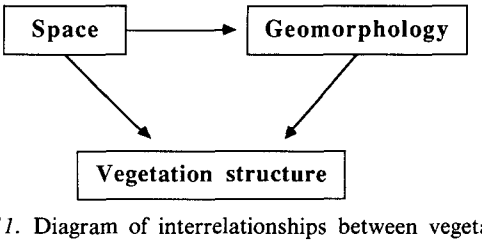


Fig. 11. Diagram of interrelationships between vegetation structure, geomorphology and space.

nation of the vegetation structure not accounted for by geomorphology is still large (0.12) and significant; this shows that other space-related factors do influence the vegetation structure, which is then not entirely spatially determined by geomorphology. Work is in progress on other hypotheses to fill the gap. •

Estimation and mapping

Any quantitative study of spatially structured phenomena usually starts with mapping the variables. Ecologists, like geographers, usually satisfy themselves with rather unsophisticated kinds of map representations. The 2 most common kinds are (1) divisions of the study area into non-overlapping regions, since 'many areal phenomena studied by geographers [and ecologists] can be represented in 2 dimensions as a set of contiguous, nonoverlapping, space-exhaustive polygons' (Boots 1977), and (2) isoline maps, or contoured maps, used for instance by geographers to represent altitudes on topographic maps, where the nested isolines represent different intensities of some continuous variable. Both types can be produced by computer software. Before attempting to produce a map, especially by computer, ecologists must make sure that they satisfy the following assumption: all parts of the 'active' study area must have a non-null probability of being found in one of the states of the variable to be mapped. For instance, in a study of terrestrial plants, the 'active' area of the map must be defined in such a way as to exclude water masses, roads, large rocky outcrops, and the like.

Since the map derives in most cases from samples obtained from a surface, intermediate values have to be *estimated* by interpolation; or, in the case of a regular sampling grid, one can map the surface as a juxtaposition of regular tiles whose values are given by the points in the center of the tiles. One should notice that interpolated maps can only represent one variable at a time; thus these methods are not multivariate, although it is possible in some cases to superpose two or three maps. When it does not seem desirable or practicable to map each variable or each species separately, it remains then possible to map, instead, synthetic environmental variables such as species diversity, or else the first few principal axes from a principal components or a correspondence analysis, for instance.

Several methods exist for interpolated mapping. These include trend surface analysis, local weighted averaging, Fourier series modelling, spline, moving average, kriging, kernel estimators, and interpolation by drawing boundaries (in which case the resulting maps may be called 'choropleth maps' or 'tessellations'). They have been reviewed by several authors, including Tapia & Thompson (1978), Ripley (1981, ch. 4), Lam (1983), Bennett *et al.* (1984), Burrough (1986, ch. 8), Davis (1986) and Silverman (1986). Computer programs can provide an estimate of the variable at all points of the surface considered; the density of reconstructed points is either selected by the user or set by the program. Contouring algorithms are used to draw maps from the fine grid of interpolated points.

Besides simple linear interpolation between closest neighbours, trend surface analysis is perhaps the oldest form of spatial interpolation used by ecologists (Gittins 1968; Curtis & Bignal 1985). It consists in fitting to the data, by regression, a polynomial equation of the x and y coordinates of the sampling localities. The order of the polynomial is determined by the user; increasing the order increases the number of parameters to be fitted and so it produces a better-fitting map, with the inconvenient that these parameters become more and more difficult to interpret ecologically. For instance, the commonly used equation of degree one is written:

$$\hat{z} = b_0 + b_1 x + b_2 y \qquad (1)$$

where $\hat{z}$ is the estimated value of the response variable z (the one that was measured and is to be mapped), while the b's are the three regression parameters. A second-degree polynomial model is:

$$\hat{z} = b_0 + b_1 x + b_2 y + b_3 x^2 + b_4 xy + b_5 y^2 \qquad (2)$$

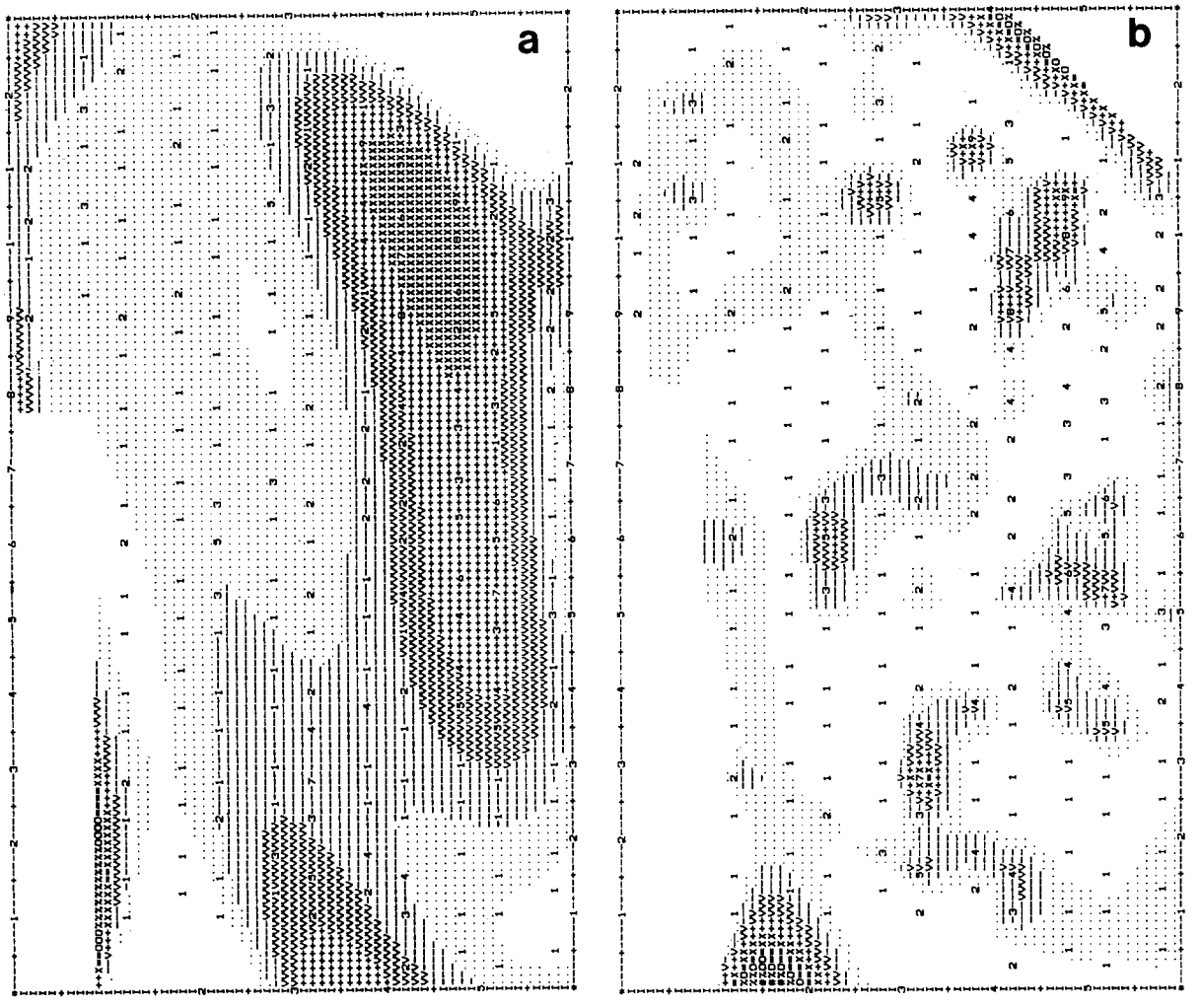


Fig. 12. (a) Trend surface map of *Acer saccharum*, sixth order polynomial. The observation points are identified by numbers. Shades of gray and numbers form a scale that represents the estimated frequencies of sugar-maples. (b) Map of the regression residuals. From Fortin (1985).

Besides the map of the fitted values ($\hat{z}$), trend surface analysis programs usually provide also a map of residuals ($z - \hat{z}$), representing the variation left undescribed by the interpolated map. Fig. 12a illustrates the map of the 6th order polynomial adjusted to the *A. saccharum* data. Compared to Fig. 13 (kriged map) the contouring obtained is still crude, although 28 parameters have been adjusted. Fig. 12b is the map of regression residuals, showing the variations in *A. saccharum* frequencies not expressed by the trend surface map. Burrough (1987) presents an example of trend surface analysis of soil data. Since trend surface analysis computes a single polynomial regression equation for the whole surface, the resulting map cannot have the precision that more local criteria can provide. For that reason, it is used in ecology mostly to compute and remove large-scale trends, using the first degree equation in most cases, prior to further spatial analyses that can be conducted on the residual values. Trends can also be detected and modelled by autoregressive methods (e.g., Edwards & Coull 1987). Another valid use of trend surface analysis is the predictive modelling of spatial distributions of organisms, using geographic coordinates alone as predictors; or, one can use other predictive variables to build such a model, alone

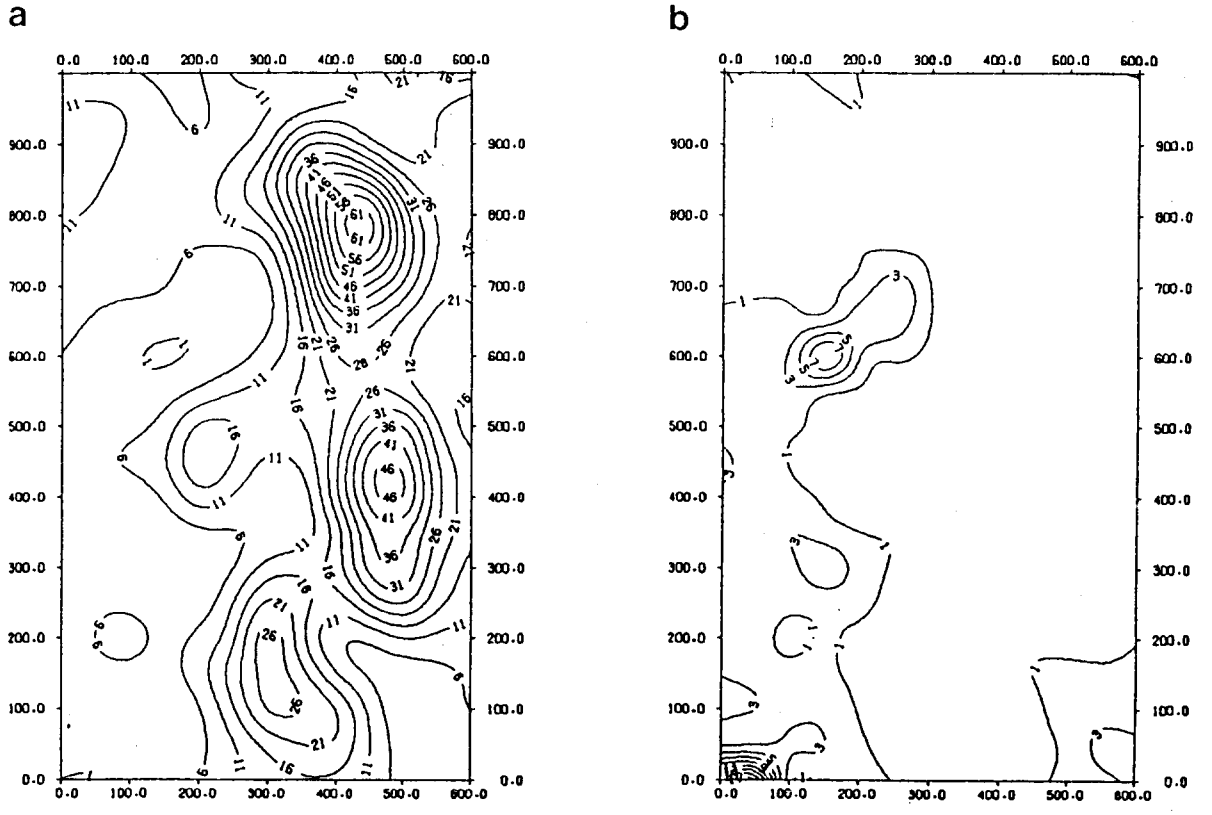


Fig. 13. (a) Map of *Acer saccharum* obtained by kriging, and (b) map of the standard deviations of the estimations. From Fortin (1985).

or in conjunction with geographic coordinates, using multiple regression or some other form of modelling.

Kriging, developed by mining engineers and named after Krige (1966) to estimate mineral resources, usually produces a more detailed map than ordinary interpolation. Contrary to trend surface analysis, kriging uses a local estimator that takes into account only data points located in the vicinity of the point to be estimated, as well as the autocorrelation structure of the phenomenon; this information can be provided either by the variogram (see above), or by generalized intrinsic random functions of order k (Matheron 1973) that allow to make valid interpolation in the case of non-stationary variables (Journel & Huijbregts 1978). The variogram is used as follows during kriging: the kriging interpolation method estimates a point by considering all the other data points located in the observation cone of the variogram (given by the direction and window aperture angles), and weighs them using the values read on the adjusted theoretic variogram at the appropriate distances; furthermore, kriging splits this weight among neighbouring points, so that the result does not depend upon the local density of points. Kriging programs produce not only a map of resource estimates but also one of the standard deviations of these estimations (David 1977; Journel & Huijbregts 1978); this map may help identify the regions where sampling should be intensified, the map being often obtained from a much smaller number of samples than in Fig. 13.

The problem of mapping multivariate phenomena is all the more acute because cartography seems essential to reach an understanding of the structures brought to light for instance by correlogram analysis. What could be done in the multivariate case? How could one combine the variability of a large number of variables into a single, simple and understandable map? Since

Table 4. The following programs are available to compute the various methods of spatial analysis described in this paper. This list of programs is not exhaustive.

Package	Methods of spatial analysis
BLUEPACK	Variogram, kriging.
CANOCO	Constained ordinations: canonical correspondence analysis, redundancy analysis.
CORR2D	Two-dimensional correlogram.
GEOSTAT	Variogram, kriging.
Kellogg's	Variogram, kriging.
NTSYS-PC	Simple Mantel test.
'R'	Spatial autocorrelation (quantitative and nominal data), simple Mantel test, partial Mantel tests, Mantel correlogram, clustering with spatial contiguity constraint, clustering with time constraint. A variety of connecting networks.
SAAP	Spatial autocorrelograms (Moran's *I* and Geary's *c*).
SASP	Two-dimensional spectal analysis.
SYMAP	Trend surface analysis; other interpolation methods.
UNIMAP	Variogram, kriging; other interpolation methods.

- The BLUEPACK package is available from: Centre de géostatistique et de morphologie mathématique, 35 rue Saint-Honoré, F-77305 Fontainebleau Cedex, France.
- The CANOCO program is available from Cajo J.F. ter Braak, Agricultural Mathematics Group, TNO Institute for Applied Computer Science, Box 100, NL-6700 AC Wageningen, The Netherlands.
- The CORR2D program written by Geoffrey M. Jacquez is available from Applied Biostatistics Inc., 100 North Country Road, Bldg. B, Setauket, New York 11733, USA.
- The GEOSTAT package is available from: Geostat Systems International Inc., 4385 rue Saint-Hubert, Suite 1, Montréal, Québec, Canada H2J 2X1.
- The Kellogg's programs are available from the Computer Laboratory, W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060, USA.
- The NTSYS package, developed by F. James Rohlf, is available in PC version from Applied Biostatistics Inc., 100 North Country Road, Bldg. B, Setauket, New York 11733, USA.
- 'The R package for multivariate data analysis', developed by Alain Vaudor (P. Legendre's lab.: see title page), is available for Macintosh microcomputers, VAX, and IBM mainframes. English and French speaking versions.
- The SAAP package is a set of FORTRAN programs available from Daniel Wartenberg, Department of Environmental and Community Medicine, Robert Wood Johnson Medical School, 675 Hoes Lane, Piscataway, New Jersey 08854, USA.
- The SASP program is available from E. Renshaw, Department of Statistics, University of Edinburgh, King's Buildings, Mayfield Road, Edinburgh EH9 3JZ, United Kingdom.
- SYMAP is not distributed any longer by Laboratory for Computer Graphics and Spatial Analysis, Harvard University, USA. It is however still available at many computing centers.
- UNIMAP is available from: European Software Contractors A/S, Nørregade, DK-2800 Lyngby, Denmark.

constrained clustering, explained in some detail above, produces groups that can be mapped – and indeed constrained clustering programs can be made to draw these maps directly (Fig. 10) – we have here a way of producing heuristic maps out of multivariate data. The methods of constrained ordination developed by Lee (1981), by Wartenberg (1985a, b) and by ter Braak (1986, 1987) are other ways of accomplishing this. They differ from the simple mapping of principal components or correspondence analysis scores, mentioned at the beginning of this section, in that they take into account the spatial relationships among samples; they resemble them in that it may be necessary to draw several maps in order to represent the variability extracted by all the important but orthogonal axes. MacDonald & Waters (1988) give examples of palynological maps obtained using Lee's *Most Predictable Surface Analysis* (MPS); other examples are found in Wartenberg (1985a,b). These methods should find ample use among community ecologists, who study essentially multivariate (multi-species) phenomena.

Conclusion

Where should ecologists stand? As we have seen, the physical environment is not homogeneous, and most ecological theories are based on precise

assumptions about the spatial structure of populations and communities. If we rely upon models that assume, as many still do for simplicity, that biological populations are distributed uniformly or at random in space, chances of obtaining valid predictions are small since the ecological reality is quite different. So, in the descriptive or hypothesis-generating phase of a research, ecologists who sample spatial distributions of organisms should consider *a priori* that their data are structured in space (i.e., are autocorrelated); they should then test for the presence of spatial autocorrelation, and describe the spatial structure using maps and spatial structure functions. In some cases, it may be adequate to remove large-scale spatial structures by regression or model-fitting in order to carry out classical statistical analyses on residuals, but in doing so, one must be careful not to remove one of the important determinants of the processes under study, since heterogeneity is *functional* in ecosystems. In the hypothesis-testing (model-testing) phase of a research, when two variables or groups of variables linked by a causal hypothesis are both autocorrelated, one should test whether their correlation, if significant, could be spurious and due to a similar spatial structure present in both. This in turn could give clues as to the identity of some other spatially autocorrelated causal variable that may have given them their common autocorrelated structure. In a world where spatial structuring is the rule rather than the exception, this precaution can prevent one from reaching unwarranted conclusions.

Statistical methods of spatial analysis (descriptive or inferential) are currently under development, and already they offer a way of answering many relevant questions about populations and communities (Table 1): demonstration of the existence of spatial or temporal structures, description of these structures, univariate or multivariate mapping, comparison with models, analysis of the influence of spatial structures on assumed causal links between variables, statistical analyses which do not assume the independence of the observations. Programs available for spatial analysis are becoming widely available. Some are listed in Table 4; this list is not exhaustive.

We can expect the spatial approach to ecological problems to bring about a quantic jump for ecologists and population geneticists who had learned a type of statistics where one had to hide space or time structures. It is now possible to use these structures and to integrate them into our analyses as fully-fledged controlled variables.

Acknowledgements

This is publication No. 339 from the Groupe d'Écologie des Eaux douces, Université de Montréal, and contribution No. 689 in Ecology and Evolution from the State University of New York at Stony Brook. We are indebted to Pierre Drapeau, Ph.D. student at Université de Montréal, who directed the sampling program that produced the data used for the various examples that illustrate this paper. Dr Michel David, École Polytechnique de Montréal, gave us instructions for and access to his GEOSTAT computer package, that we used for kriging. Geoffrey M. Jacquez, State University of New York at Stony Brook, revised the sections on two-dimensional spectral analysis. Alain Vaudor, computer analyst, developed some of the programs of 'The R Package for Multivariate Data Analysis' during and for the present study. We are grateful to Dr Robert R. Sokal, State University of New York at Stony Brook, who gave us access to Dr Neal L. Oden's two-dimensional correlogram program and provided computing funds to produce Fig. 4 of this paper. We are also indebted to Dr E. David Ford and Dr Cajo J.F. ter Braak for very helpful comments. This study was supported by NSERC grant No. A7738 to P. Legendre, and by a NSERC scholarship to M.-J. Fortin.

Appendix 1
Formulas and technical points

Spatial autocorrelation analysis

H_0: there is no spatial autocorrelation. The values of the variable are spatially independent. Each value of the I coefficient is equal to $E(I) = -(n-1)^{-1} \approx 0$, where $E(I)$ is

the expectation of I and n is the number of data points; each value of the c coefficient equals $E(c) = 1$.

H_1: there is significant spatial autocorrelation. The values of the variable are spatially dependent. The value of the I coefficient is significantly different from $E(I) = -(n-1)^{-1} \approx 0$; the value of c is significantly different from $E(c) = 1$.

$$I(d) = [n \sum \sum w_{ij}(y_i - \bar{y})(y_j - \bar{y})]/[W \sum (y_i - \bar{y})^2] \quad (1)$$

$$c(d) = [(n-1) \sum \sum w_{ij}(y_i - y_j)^2]/[2W \sum (y_i - \bar{y})^2] \quad (2)$$

These coefficients are computed for each distance class d. The values of the variable are the y's. All summations are for i and j varying from 1 to n, the number of data points, but exclude the cases where $i = j$. The w_{ij}'s take the value 1 when the pair (i, j) pertains to distance class d (the one for which the coefficient is computed), and 0 otherwise. W is the sum of the w_{ij}'s, or in other words the number of pairs (in the whole *square* matrix of distances among points) taken into account when computing the coefficients for the given distance class. Moran's coefficient varies generally from -1 to 1, but sometimes it can exceed -1 or $+1$ (Fig. 1d, h, k); positive values of Moran's I correspond to positive autocorrelation. Geary's coefficient varies from 0 to some indeterminate positive value which rarely exceeds 3 in real cases; values of c smaller than 1 correspond to positive autocorrelation. These coefficients can be tested for significance; formulas for computing the standard error of the estimated statistics can be found in Cliff & Ord (1981), Sokal & Oden (1978) and Legendre & Legendre (1984a). A special form of spatial autocorrelation coefficient for nominal (qualitative) data is described by Cliff & Ord (1981) and by Sokal & Oden (1978).

Technical points:

- Spatial autocorrelation analysis should not be performed with fewer than ca. 30 localities, because the number of pairs of localities in each distance class then becomes too small to produce significant results.
- There are two ways of dividing distances into classes: either by forming equal distance classes, or classes with equal frequencies. This last solution makes it possible to compute valid coefficients even in the right-hand part of the correlogram (Sokal 1983); with equal distance classes on the contrary, the number of pairs of points becomes too small for valid testing in the large distance classes (Fig. 1c).
- Spatial autocorrelation analysis cannot be performed with a data set that contains a lot of double zeros, because the degree of autocorrelation would then be overestimated and would reflect the fact that the localities share their absence for that variable, which is not what is intended in most applications.
- Euclidean distances between pairs of localities may not be the best way of expressing geographic relationships when analysing ecological data. Instead, one could use $1/d$ or $1/d^2$ (Mantel 1967; Jumars *et al.* 1977), or some other appropriate transformation (Estabrook & Gates 1984).
- In cases where the Euclidean distance is felt to be meaningless, one can use instead some topological network of connections between localities (see: Connecting networks, below) and compute distances in terms of number of edges along this network.

Two-dimensional spectral analysis

The spatial autocorrelation matrix contains all pairs of sample autocorrelation values r_{gh}, corresponding to all possible lags (g, h) where g is the lag along the x geographic axis of sampling and h is the lag along the y axis. Each value r_{gh} is the ratio of the sample autocovariance at lag (g, h) to the sample variance of the y_{ij}'s. The sample autocovariance s_{gh} is computed as

$$s_{gh} = (1/mn) \sum_{i=1}^{m-g} \sum_{j} (y_{(i,j)} - \bar{y})(y_{(i+g, j+h)} - \bar{y}) \quad (3)$$

where $0 \leq g < m$ and $-n < h < n$; m and n are respectively the number of rows and columns of the geographic sampling grid. The second summation is taken over $j = 1, \ldots, n-h$ if $h \geq 0$ and over $j = |h| + 1, \ldots, n$ if $h < 0$. There is no need to compute the whole autocorrelation surface ($-m < g < m$) since the surface is a reverse image of itself round either of the zero lag axes.

The Schuster periodogram can also be computed, again for all possible combinations of lags (g, h). The periodogram is a more compact description of the spatial pattern than the full two-dimensional correlogram. Periodograms and power spectra are often expressed as functions of frequencies instead of periods (frequency = 1/period). For convenience, frequencies are here multiplied by the size of the series (m or n) so that a wave that occupies the whole length (m or n) of a side of the sampling area has a frequency (p or q) of 1. The range of frequencies considered is then $p = 0, \ldots, (m/2)$ and $q = (-n/2), \ldots, ((n/2) - 1)$ where $(m/2)$ and $(n/2)$ are respectively the Nyquist frequencies (highest frequency in the observation window) in directions x and y of the sampling surface. The sign of q gives the direction of travel of the sine wave under study. As in time series analysis, the intensity of the periodogram $I(p, q)$, for each frequency combination, measures the amount of variance of variable y that is explained by the given combination of frequencies (p, q), after fitting to the data, by least squares, a Fourier series (sum of sines and cosines) with the given combination of frequencies. See formulas in Renshaw & Ford (1984), for instance. The periodogram is presented as a three-dimensional plot, with frequencies (p, q) along the axes of the controlling plane, and the intensity of the periodogram $I(p, q)$ as the response variable.

The polar spectrum of the data aims at measuring the *frequencies* and *angular directions* of the dominant wave pat-

terns present in the data. 2 graphs, first proposed by Renshaw & Ford (1983), are produced. The first one, called the *R*-spectrum, measures the frequencies of the waves forming the spatial pattern. The *R*-spectrum is a graph of the average response $I(p, q)$ of all the elements in the periodogram that have approximately the same frequency magnitude $R = \sqrt{(p^2 + q^2)}$. The second one, called the Θ-spectrum, measures the directions (angles) of the waves. It is presented as a graph of the average response $I(p, q)$ of all the elements in the periodogram that have approximately the same angle $\Theta = \tan^{-1}(p/q)$ $(0° \leq \Theta \leq 180°)$. In these graphs, the values along the abscissa (that is, the various R and Θ values) are first divided into a manageable number of classes before the graphs are drawn.

The $I(p, q)$ values have been scaled to have an average value of 1, so that a data set with no spatial structure should produce an *R*-spectrum and a Θ-spectrum with values close to 1. Since the individual values of $I(p, q)$ in the periodogram are approximately distributed as $(100/mn)\chi^2_{(2)}$, then they can be tested for significance against a critical value of $(100/mn)\chi^2_{(\alpha, 2)}$. In the same way, particular values in the graphs of the *R*- and Θ-spectra that correspond to intervals containing, say, k individual values of I, can be tested for significance against a critical value of $I = [1/(2k)]\,\chi^2_{(\alpha, 2k)}$. As in all cases of multiple testing, one should apply the usual Bonferroni correction and use the corrected significance level $\alpha' = \alpha/v$ where v is the number of tests performed simultaneously; this point had not been emphasized by the above-mentioned authors. Actual use of two-dimensional spectral analysis shows that the spectra are the most useful instruments for interpreting the spatial structure; the periodogram has more of a descriptive value.

Variogram

The experimental semi-variogram (often called the variogram) is a plot of the values of semi-variance as a function of distance. The estimator of the semi-variance function is

$$\gamma(d) = [1/(2n_d)] \sum [y_{(i+d)} - y_{(i)}]^2 \qquad (4)$$

where n_d is the number of pairs of points located at distance d from one another. The summation is for i varying from 1 to n_d. Just like Geary's c autocorrelation coefficient (above), this structure function is a distance-type function; the difference lies mainly in the denominator of the function.

Some of the most often used theoretic variogram models are the following (Fig. 8). Other models are proposed by Journel & Huijbregts (1978).

Linear model: $\gamma(d) = C_0 + bd$ where b is the slope and C_0 is the intercept (nugget effect).

Exponential model: $\gamma(d) = C_0 + C\,[1 - \exp(-|d|/a)]$ where C_0 is the nugget effect and C = sill $- C_0$; a is the range.

Spherical model: $\gamma(d) = C_0 + C\,[(3d/2a) - (d^3/2a^3)]$ if $d \leq a$, while $\gamma(d) = C_0 + C$ if $d > a$.

Gaussian model: $\gamma(d) = C_0 + C\,[1 - \exp(-d^2/a^2)]$.

Technical points:

- As in correlograms, variograms are computed for distance classes, which implies that the number of pairs of points used in the computation decreases as distance increases (Fig. 1c). Thus, only about the first two-thirds of a variogram should be taken into account when describing the spatial structure.
- With ecological data, the stationarity property is rare and the data often contain some overall trend, called 'drift' in the kriging jargon; drift can affect significantly the accuracy of kriging. Thus in the presence of non-stationarity and drift, the use of 'generalized intrinsic random functions of order k' is recommended, instead of a variogram, to estimate the autocorrelation structure.

Connecting networks

Graphs of interconnections among points are used to describe spatial interrelations for such data analysis methods as constrained clustering, spatial autocorrelation analysis, and other methods that require information about neighbouring localities. In the case of a regular square grid of sampling locations, the solution is simple, since one can connect each point to its neighbours in all 4 directions ('rook's move'), or else in all 8 directions ('queen's move') if he so chooses. If the regular sampling design has the form of staggered rows, as in Fig. 2 for instance, connections (also called 'link edges') may be established with neighbours in all 6 directions. If the sampling localities are irregular tiles that touch one another and cover the whole surface under study, a natural choice is to connect localities that have a border in common.

It often happens, however, that the sampling localities do not form a regular pattern. In such cases, one should wonder first if the ecological problem under study would not provide a natural way of deciding what the close neighbours are. If no such ecological criterion can be found, then one can rely on the more arbitrary geometric criteria. The most commonly used graph-theoretic criteria are the minimum spanning tree (Gower & Ross 1969), the Gabriel graph (Gabriel & Sokal 1969), or the Delaunay triangulation which is simply an algorithmic method of dividing a plane into triangles that obey some precise set of rules (Miles 1970; Ripley 1981; Watson 1981). It is interesting to note that the minimum spanning tree is a subset of the Gabriel graph, which in turn is a subset of the Delaunay triangulation.

Appendix 2
Theory of the Mantel test

Hypotheses

H_0: Distances among points in matrix **X** are not linearly related to the corresponding distances in matrix **Y**. When **Y** represents geographic distances, H_0 reads as follows: the variable (or the multivariate data) in **X** is not autocorrelated as a gradient.

H_1:Distances among points in matrix **X** are correlated to the corresponding distances in matrix **Y**.

Statistics

- Mantel (1967) statistic:

$$z = \sum_i \sum_j x_{ij} y_{ij} \qquad (5)$$

for $i \neq j$, where i and j are row and column indices.

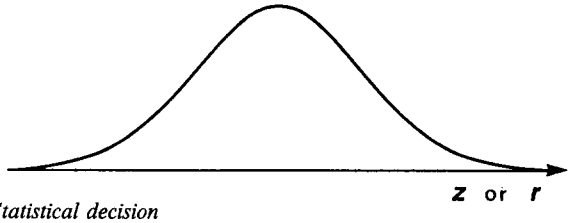
- Normalized Mantel statistic:

$$r = [1/(n-1)] \sum_i \sum_j [(x_{ij} - \bar{x})/s_x][(y_{ij} - \bar{y})/s_y] \qquad (6)$$

for $i \neq j$, where i and j are row and column indices, and n is the number of distances in one of the matrices (diagonal excluded).

Distribution of the auxiliary variable

- According to H_0, the values observed at any one point could have been obtained at any other point.
- H_0 is thus realized by permuting the points, holding with them their vectors of values for the observed variables.
- An equivalent result is obtained by permuting at random the rows of matrix **X** as well as the corresponding columns.
- Either **X** or **Y** can be permuted at random, with the same net effect.
- Repeating this operation, the different permutations produce a set of values of the Mantel statistic, z or r, obtained under H_0. These values represent the sampling distribution of z or r under H_0.



Statistical decision

As in any other statistical test, the decision is made by comparing the actual value of the auxiliary variable (z or r) to the reference distribution obtained under H_0. If the actual value of the Mantel statistic is one likely to have been obtained under the null hypothesis (no relation between **X** and **Y**), then H_0 is accepted; if it is too extreme to be considered a likely result under H_0, then H_0 is rejected.

Remarks

The z or the r statistics can be transformed into another statistic, called t by Mantel (1967), which can be tested by referring to a table of the standard normal distribution. This test gives a good approximation of the probability when the number of objects is large.

Like Pearson's correlation coefficient, the Mantel statistic formula is a linear model, that brings out the linear component of the relationship between the values in the two distance matrices. Strong non-linearity can probably prevent relationships from expressing themselves through the Mantel test; this led Dietz (1983) to suggest the use of a non-parametric correlation formula. The influence of lack of linearity, and of transformations in one or both of the distance matrices, has not yet been fully investigated.

References

Allen, T.F.H., Bartell, S.M. & Koonce, J.F. 1977. Multiple stable configurations in ordination of phytoplankton community change rates. Ecology 58: 1076–1084.

Allen, T.F.H. & Starr, T.B. 1982. Hierarchy – Perspectives for ecological complexity. Univ. of Chicago Press, Chicago.

Andersson, P.-A. 1988. Ordination and classification of operational geographic units in Southwest Sweden. Vegetatio 74: 95–106.

Bell, M.A. & Legendre, P. 1987. Multicharacter chronological clustering in a sequence of fossil sticklebacks. Syst. Zool. 36: 52–61.

Bennett, R.J., Haining, R.P. & Griffith, D.A. 1984. The problem of missing data on spatial surfaces. Ann. Assoc. Am. Geogr. 74: 138–156.

Bivand, R. 1980. A Monte Carlo study of correlation coefficient estimation with spatially autocorrelated observations. Quaest. Geogr. 6: 5–10.

Boots, B.N. 1977. Contact number properties in the study of cellular networks. Geogr. Anal. 9: 379–387.

Bouchard, A., Bergeron, Y., Camiré, C., Gangloff, P. & Gariépy, M. 1985. Proposition d'une méthodologie d'inventaire et de cartographie écologique: le cas de la MRC du Haut-Saint-Laurent. Cah. Géogr. Qué. 29: 79–95.

Box, G.E.P. & Jenkins, G.M. 1970. Time series analysis, forecasting and control. Holden-Day, San Francisco.

Burgman, M.A. 1987. An analysis of the distribution of plants on granite outcrops in southern Western Australia using Mantel tests. Vegetatio 71: 79–86.

Burrough, P.A. 1986. Principles of geographical information systems for land resources assessment. Clarendon Press, Oxford.

Burrough, P.A. 1987. Spatial aspects of ecological data. In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds), Data analysis in community and landscape ecology, pp 213–251. Pudoc, Wageningen.

Carpenter, S.R. & Chaney, J.E. 1983. Scale of spatial pattern: four methods compared. Vegetatio 53: 153–160.

Cicéri, M.-F., Marchand, B. & Rimbert, S. 1977. Introduction à l'analyse de l'espace. Collection de Géographie applicable. Masson, Paris.

Cliff, A.D. & Ord, J.K. 1981. Spatial processes: models and applications. Pion Limited, London.

Cochran, W.G. 1977. Sampling techniques, 3rd ed. John Wiley & Sons, New York.

Cooper, D.W. 1968. The significance level in multiple tests made simultaneously. Heredity 23: 614–617.

Curtis, D.J. & Bignal, E.M. 1985. Quantitative description of vegetation physiognomy using vertical quadrats. Vegetatio 63: 97–104.

Darwin, C. 1881. The formation of vegetable mould through the action of worms. John Murray, London.

David, M. 1977. Geostatistical ore reserve estimation. Developments in geomathematics, 2. Elsevier, Amsterdam.

Davis, J.C. 1986. Statistics and data analysis in geology, 2nd ed. John Wiley & Sons, New York.

Dietz, E.J. 1983. Permutation tests for association between two distance matrices. Syst. Zool. 32: 21–26.

Dow, M.M. & Cheverud, J.M. 1985. Comparison of distance matrices in studies of population structure and genetic microdifferentiation: quadratic assignment. Am. J. Phys. Anthropol. 68: 367–373.

Edgington, E.S. 1987. Randomization tests, 2nd ed. Marcel Dekker Inc., New York.

Edwards, D. & Coull, B.C. 1987. Autoregressive trend analysis: an example using long-term ecological data. Oikos 50: 95–102.

Estabrook, G.F. & Gates, B. 1984. Character analysis of the *Banisteriopsis campestris* complex (Malpighiaceae), using spatial autocorrelation. Taxon 33: 13–25.

Estabrook, G.F. & Rogers, D.J. 1966. A general method of taxonomic description for a computed similarity measure. BioScience 16: 789–793.

Fisher, W.D. 1958. On grouping for maximum homogeneity. J. Amer. Stat. Ass. 53: 789–798.

Ford, E.D. 1976. The canopy of a Scots pine forest: description of a surface of complex roughness. Agric. Meteorol. 17: 9–32.

Ford, E.D. & Renshaw, E. 1984. The interpretation of process from pattern using two-dimensional spectral analysis: modelling single species patterns in vegetation. Vegetatio 56: 113–123.

Fortin, M.-J. 1985. Analyse spatiale de la répartition des phénomènes écologiques: méthodes d'analyse spatiale, théorie de l'échantillonnage. Mémoire de Maîtrise, Université de Montréal.

Gabriel, K.R. & Sokal, R.R. 1969. A new statistical approach to geographic variation analysis. Syst. Zool. 18: 259–278.

Galiano, E.F. 1982. Pattern detection in plant populations through the analysis of plant-to-all-plants distances. Vegetatio 49: 39–43.

Galiano, E.F. 1983. Detection of multi-species patterns in plant populations. Vegetatio 53: 129–138.

Galzin, R. & Legendre, P. 1988. The fish communities of a coral reef transect. Pac. Sci. 41: 158–165.

Gauch Jr., H.G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.

Geary, R.C. 1954. The contiguity ratio and statistical mapping. Incorp. Statist. 5: 115–145.

Getis, A. & Boots, B. 1978. Models of spatial processes: an approach to the study of point, line and area patterns. Cambridge Univ. Press, Cambridge.

Gittins, R. 1968. Trend-surface analysis of ecological data. J. Ecol. 56: 845–869.

Goodall, D.W. 1974. A new method for the analysis of spatial pattern by random pairing of quadrats. Vegetatio 29: 135–146.

Gordon, A.D. 1973. Classification in the presence of constraints. Biometrics 29: 821–827.

Gordon, A.D. & Birks, H.J.B. 1972. Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. New Phytol. 71: 961–979.

Gordon, A.D. & Birks, H.J.B. 1974. Numerical methods in Quaternary palaeoecology. II. Comparison of pollen diagrams. New Phytol. 73: 221–249.

Gower, J.C. & Legendre, P. 1986. Metric and Euclidean properties of dissimilarity coefficients. J. Classif. 3: 5–48.

Gower, J.C. & Ross, G.J.S. 1969. Minimum spanning trees and single linkage cluster analysis. Appl. Statist. 18: 54–64.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, New York.

Hassell, M.P. & May, R.M. 1974. Aggregation in predators and insect parasites and its effect on stability. J. Anim. Ecol. 43: 567–594.

Hawkins, D.M. & Merriam, D.F. 1973. Optimal zonation of digitized sequential data. J. Int. Assoc. Math. Geology 5: 389–395.

Hawkins, D.M. & Merriam, D.F. 1974. Zonation of multivariate sequences of digitized geologic data. J. Int. Assoc. Math. Geology 6: 263–269.

Hensen, V. 1884. Ueber die Bestimmung der Planktons oder des im Meer triebenden Materials an Pflanzen und Tieren. Ber. Comm. Wiss. Unters. Deutsch. Meere 5.

Hubert, L.J. 1985. Combinatorial data analysis: association and partial association. Psychometrika 50: 449–467.

Hudon, C. & Lamarche, G. in press. Niche segregation between the American lobster (*Homarus americanus*) and the rock crab (*Cancer irroratus*). Mar. Ecol. Prog. Ser.

Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27: 343–383.

Ibanez, F. 1981. Immediate detection of heterogeneities in

continuous multivariate, oceanographic recordings. Application to time series analysis of changes in the bay of Villefranche sur Mer. Limnol. Oceanogr. 26: 336–349.

Journel, A.G. & Huijbregts, C. 1978. Mining geostatistics. Academic Press, London.

Jumars, P.A., Thistle, D. & Jones, M.L. 1977. Detecting two-dimensional spatial structure in biological data. Oecologia (Berl.) 28: 109–123.

Krackhardt, D. 1988. Predicting with networks: nonparametric multiple regression analysis of dyadic data. Social Networks 10: 359–381.

Krige, D.G. 1966. Two dimensional weighted moving average trend surfaces for ore evaluation. Jour. S. Afr. Inst. Min. Metall. 66: 13–38.

Lam, N.S. 1983. Spatial interpolation methods: a review. Am. Cartogr. 10: 129–149.

Lebart, L. 1978. Programme d'agrégation avec contraintes (C.A.H. contiguïté). Cah. Anal. Données 3: 275–287.

Lee, P.J. 1981. The most predictable surface (MPS) mapping method in petroleum exploration. Bull. Can. Petrol. Geol. 29: 224–240.

Lefkovitch, L.P. 1978. Cluster generation and grouping using mathematical programming. Math. Biosci. 41: 91–110.

Lefkovitch, L.P. 1980. Conditional clustering. Biometrics 36: 43–58.

Legendre, L. & Demers, S. 1985. Auxiliary energy, ergoclines and aquatic biological production. Naturaliste can. (Qué.) 112: 5–14.

Legendre, L. & Legendre, P. 1983a. Numerical ecology. Developments in environmental modelling, 3. Elsevier, Amsterdam.

Legendre, L. & Legendre, P. 1983b. Partitioning ordered variables into discrete states for discriminant analysis of ecological classifications. Can. J. Zool. 61: 1002–1010.

Legendre, L. & Legendre, P. 1984a. Écologie numérique, 2ième éd. Tome 2: La structure des données écologiques. Masson, Paris et les Presses de l'Université du Québec.

Legendre, P. 1987. Constrained clustering. In: Legendre, P. & Legendre, L. (eds), Developments in numerical ecology. NATO ASI Series, Vol. G 14, pp. 289–307. Springer, Berlin.

Legendre, P., Dallot, S. & Legendre, L. 1985. Succession of species within a community: chronological clustering, with applications to marine and freshwater zooplankton. Am. Nat. 125: 257–288.

Legendre, P. & Legendre, V. 1984b. Postglacial dispersal of freshwater fishes in the Québec peninsula. Can J. Fish. Aquat. Sci. 41: 1781–1802.

Legendre, P. & Troussellier, M. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnol. Oceanogr. 33: 1055–1067.

Levin, L.A. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. Ecology 65: 1185–1200.

MacDonald, G.M. & Waters, N.M. 1988. The use of most predictable surfaces for the classification and mapping of taxon assemblages. Vegetatio 74: 125–135.

MacQueen, J.B. 1967. Some methods for classification and analysis of multivariate observations. In: Le Cam, L.M. & Neyman, J. (eds), Proc. Fifth Berkeley Symp. Math. Stat. Probab., Vol. 1, pp. 281–297. University of California Press, Berkeley.

Manly, B.F.J. 1986. Randomization and regression methods for testing for associations with geographical, environmental and biological distances between populations. Res. Popul. Ecol. 28: 201–218.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27: 209–220.

Matheron, G. 1962. Traité de géostatistique appliquée. Tome 1. Éditions Technip, Paris.

Matheron, G. 1973. The intrinsic random functions and their applications. Adv. Appl. Prob. 5: 439–468.

May, R.M. 1974. Stability and complexity in model ecosystems, 2nd ed. Princeton Univ. Press, Princeton, New Jersey.

McBratney, A.B. & Webster, R. 1981. Detection of ridge and furrow pattern by spectral analysis of crop yield. Int. Stat. Rev. 49: 45–52.

McCune, B. & Allen, T.F.H. 1985. Will similar forest develop on similar sites? Can. J. Bot. 63: 367–376.

Miles, R.E. 1970. On the homogeneous planar Poisson point process. Math. Biosci. 6: 85–127.

Miller Jr, R.G. 1977. Developments in multiple comparisons. J. Amer. Stat. Ass. 72: 779–788.

Moran, P.A.P. 1950. Notes on continuous stochastic phenomena. Biometrika 37: 17–23.

Newbery, D.McC., Renshaw, E. & Brünig, E.F. 1986. Spatial pattern of trees in kerangas forest, Sarawak. Vegetatio 65: 77–89.

Oden, N.L. 1984. Assessing the significance of a spatial correlogram. Geogr. Anal. 16: 1–16.

Oden, N.L. & Sokal, R.R. 1986. Directional autocorrelation: an extension of spatial correlograms to two dimensions. Syst. Zool. 35: 608–617.

Openshaw, S. 1974. A regionalisation program for large data sets. Computer Appl. 3-4: 136–160.

Orlóci, L. 1978. Multivariate analysis in vegetation research, 2nd ed. Junk, The Hague.

Phillips, J.D. 1985. Measuring complexity of environmental gradients. Vegetatio 64: 95–102.

Pielou, E.C. 1977. Mathematical ecology, 2nd ed. J. Wiley & Sons, New York.

Pielou, E.C. 1984. The interpretation of ecological data. A primer on classification and ordination. John Wiley & Sons, New York.

Priestly, M.B. 1964. The analysis of two dimensional stationary processes with discontinuous spectra. Biometrika 51: 195–217.

Ray, D.M. & Berry, B.J.L. 1966. Multivariate socioeconomic regionalization: a pilot study in central Canada. In: Ostry, S. & Rymes, T. (eds), Papers on regional statistical studies, pp. 75–130. Univ. of Toronto Press, Toronto.

Rayner, J.N. 1971. An introduction to spectral analysis. Pion

Ltd., London.

Renshaw, E. & Ford, E.D. 1983. The interpretation of process from pattern using two-dimensional spectral analysis: methods and problems of interpretation. Appl. Statist. 32: 51–63.

Renshaw, E. & Ford, E.D. 1984. The description of spatial pattern using two-dimensional spectral analysis. Vegetatio 56: 75–85.

Ripley, B.D. 1981. Spatial statistics. John Wiley & Sons, New York.

Ripley, B.D. 1987. Spatial point pattern analysis in ecology. In: Legendre, P. & Legendre, L. (eds), Developments in numerical ecology. NATO ASI Series, Vol. G 14, pp. 407–429. Springer-Verlag, Berlin.

Sakai, A.K. & Oden, N.L. 1983. Spatial pattern of sex expression in silver maple (*Acer saccharinum* L.): Morisita's index and spatial autocorrelation. Am. Nat. 122: 489–508.

Scherrer, B. 1982. Techniques de sondage en écologie. In: Frontier, S. (ed.), Stratégies d'échantillonnage en écologie, pp. 63–162. Collection d'Écologie, 17. Masson, Paris et les Presses de l'Université Laval, Québec.

Silverman, B.W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London.

Smouse, P.E., Long, J.C. & Sokal, R.R. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst. Zool. 35: 627–632.

Sneath, P.H.A. 1966. A comparison of different clustering methods as applied to randomly-spaced points. Classification Soc. Bull. 1: 2–18.

Sokal, R.R. 1979. Ecological parameters inferred from spatial correlograms. In: Patil, G.P. & Rosenzweig, M.L. (eds), Contemporary quantitative ecology and related ecometrics. Statistical Ecology Series, Vol. 12, pp. 167–196. International Co-operative Publ. House, Fairland, Maryland.

Sokal, R.R. 1983. Analyzing character variation in geographic space. In: Felsenstein, J. (ed.), Numerical taxonomy. NATO ASI Series, Vol. G1, pp. 384–403. Springer-Verlag, Berlin.

Sokal, R.R. 1986. Spatial data analysis and historical processes. In: Diday, E. *et al.* (eds), Data analysis and informatics, IV. Proc. Fourth Int. Symp. Data Anal. Informatics, Versailles, France, 1985, pp. 29–43. North-Holland, Amsterdam.

Sokal, R.R. & Oden, N.L. 1978. Spatial autocorrelation in biology. 1. Methodology. Biol. J. Linnean Soc. 10: 199–228.

Sokal, R.R. & Thomson, J.D. 1987. Applications of spatial autocorrelation in ecology. In: Legendre, P. & Legendre, L. (eds), Developments in numerical ecology. NATO ASI Series, Vol. G 14, pp. 431–466. Springer-Verlag, Berlin.

Tapia, R.A. & Thompson, J.A. 1978. Nonparametric probability density estimation. Johns Hopkins Univ. Press, Baltimore.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69–77.

Upton, G.J.G. & Fingleton, B. 1985. Spatial data analysis by example. Vol. 1: Point pattern and quantitative data. John Wiley & Sons, Chichester.

Wartenberg, D. 1985a. Canonical trend surface analysis: a method for describing geographic patterns. Syst. Zool. 34: 259-279.

Wartenberg, D. 1985b. Multivariate spatial correlation: a method for exploratory geographical analysis. Geogr. Anal. 17: 263–283.

Watson, D.F. 1981. Computing the n-dimensional Delaunay tesselation with application to Voronoi polygones. Computer J. 24: 167–172.

Webster, R. 1973. Automatic soil-boundary location from transect data. J. Int. Assoc. Math. Geol. 5: 27–37.

Webster, R. & Burrough, P.A. 1972. Computer-based soil mapping of small areas from sample data. I. Multivariate classification and ordination. II. Classification smoothing. J. Soil Sci. 23: 210–221, 222–234.