SPATIAL AUTOCORRELATION: TROUBLE OR NEW PARADIGM?[1]

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Abstract. Autocorrelation is a very general statistical property of ecological variables observed across geographic space; its most common forms are patches and gradients. Spatial autocorrelation, which comes either from the physical forcing of environmental variables or from community processes, presents a problem for statistical testing because autocorrelated data violate the assumption of independence of most standard statistical procedures. The paper discusses first how autocorrelation in ecological variables can be described and measured, with emphasis on mapping techniques. Then, proper statistical testing in the presence of autocorrelation is briefly discussed. Finally, ways are presented of explicitly introducing spatial structures into ecological models. Two approaches are proposed; in the raw-data approach, the spatial structure takes the form of a polynomial of the x and y geographic coordinates of the sampling stations; in the matrix approach, the spatial structure is introduced in the form of a geographic distance matrix among locations. These two approaches are compared in the concluding section. A table provides a list of computer programs available for spatial analysis.

INTRODUCTION

Spatial autocorrelation may be loosely defined as the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations. Autocorrelation is a very general property of ecological variables and, indeed, of all variables observed along time series (temporal autocorrelation) or across geographic space (spatial autocorrelation).

Most natural ecological phenomena display geographical patchiness, and it is found at all spatial scales — from micrometres to continental and ocean-wide scales. Picturing the spatial variation of the variable(s) under study in the form of a map shows the structure to be smoothly continuous or marked by sharp discontinuities. Most real-case studies concern only a part of a spatial structure; the special case where the part under study essentially looks like a gradient is discussed at more length in the third section of this paper.

The statistical problem that accompanies the spatial structuring of ecological data can be illustrated using the following common case of spatially autocorrelated data. The observed values of the variable of interest — for instance, species composition — are most often influenced, at any given locality, by the species assem-

blage structure at surrounding localities, because of contagious biotic processes such as growth, reproduction, mortality, migration, and so on. In such a case, because the value at any one locality can be at least partly predicted by the values at neighboring points, these values are not stochastically independent from one another. This may come as a surprise to ecologists who have been trained in the belief that nature follows the assumptions of classical statistics, one of them being the independence of the observations. However, field ecologists know from experience that living beings in nature are distributed neither uniformly nor at random; the same applies to the physical variables that we use to describe environments. Following hierarchy theory (Allen and Starr 1982), we may look at the environment as primarily structured by large-scale physical processes — geomorphologic processes on land, currents and winds in fluid environments — that, through energy inputs, cause the appearance of gradients on the one hand, and of patchy structures separated by discontinuities (interfaces) on the other. These large-scale structures induce the formation of similar responses in biological systems, spatially and temporally. Within these relatively homogeneous zones, smaller scale contagious biotic processes take place that cause the appearance of more spatial structuring through reproduction and death, predator–prey interactions, food availability, parasitism, and so on. Spatial heterogeneity is then *functional* in ecosystems, and not the result of some random, noise-generating process, so it becomes important to study it for its own sake. One of
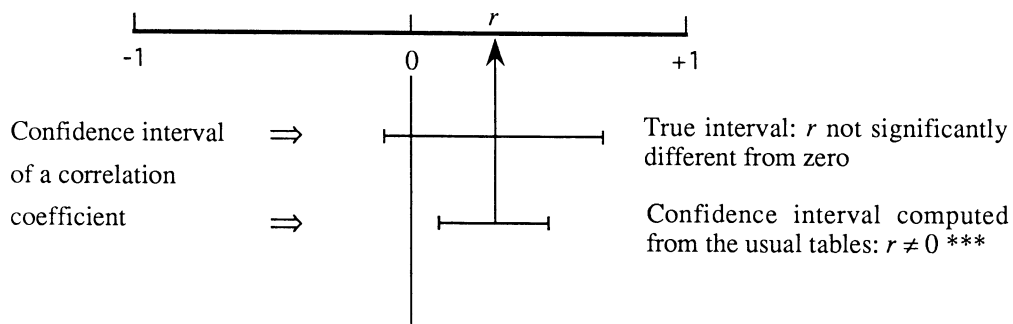
FIG. 1. Effect of spatial autocorrelation on tests of correlation coefficients for randomly generated, positively autocorrelated data.

the consequences is that ecosystems without spatial structuring would be unlikely to function. Imagine the consequences: large-scale homogeneity would cut down on diversity of habitats; feeders would not be found close to their food; mates would be located at random throughout the landscape; soil conditions in the immediate surrounding of a plant would not be more suitable for its seedlings than any other location on earth; newborn animals would be spread around instead of remaining in favorable environments; and so on. Irrealistic as this view may seem, it is still common in many of our theories and models describing population and community functioning. This shift in views translates into a new paradigm for ecologists: spatial structuring is an important component for ecosystems. The first message of this paper is then that we have to revise our theories and models, to make them include realistic assumptions about spatial and temporal structuring of communities. The second message is that statistical concepts and techniques are now becoming available to handle such data.

Autocorrelation in a variable brings with it a statistical problem: it impairs our ability to perform standard statistical tests of hypotheses. The reason can best be illustrated by the case of the correlation coefficient. The problem lies in the fact that, when both variables are positively autocorrelated, the confidence interval estimated by the classical procedure around a Pearson correlation coefficient is narrower than it is when calculated correctly, so one declares too often that the coefficient is significantly different from zero (Fig. 1; see Bivand 1980). With all other standard statistical tests, positive autocorrelation induces the same bias: computed test statistics are too often declared significant under the null hypothesis. Negative autocorrelation may produce the opposite effect, for instance in ANOVA. This problem is discussed in more detail by Cliff and Ord (1981), and by Dutilleul and Legendre (1992) in the context of the tests of normality (goodness-of-fit).

This question can be contemplated from the point of view of the degrees of freedom: in classical statistical testing, one counts one degree of freedom for each independent observation, and this procedure allows one to choose the statistical distribution appropriate for the given test. As we have seen above, the problem with autocorrelated data is their lack of independence or, in other words, the fact that new observations do not each bring with them one full degree of freedom. Indeed, knowledge of the variable's value at some locations gives the observer some prior knowledge of the value the variable will take at new locations. The consequence is that these new observations cannot be counted for one full degree of freedom. Corrections are available for the number of degrees of freedom and will be mentioned below.

The scope of this paper is threefold. First, I will show how spatial autocorrelation can be described and measured. Next, I will examine how valid tests can be performed. Finally, I will give substance to the new paradigm by presenting ways of introducing spatial structures into ecological modeling, in both univariate and multivariate situations. The paper by Dutilleul (1993a) addresses the companion problem of designing controlled experiments, especially in nature, in a spatially structured environment. The presence of spatial autocorrelation (two sites located near one another are unlikely to be independent from one another) is part of the larger problem of pseudoreplication (Hurlbert 1984) often encountered in mensurative and manipulative experiments.

ASSESSING SPATIAL STRUCTURES

The analysis of spatial ecological patterns comprises two families of methods. *Point pattern analysis* is concerned with the distribution of individual objects through space—for instance individual plants or animals. The chief purpose of this type of analysis is to determine whether the geographic distribution of data points is random or not and to describe the type of

pattern, in order to infer what kind of process may have created the observed structure. From this family of methods, the quadrat-density and the nearest neighbor methods have been widely used in vegetation science (Galiano 1982, Carpenter and Chaney 1983). Point pattern analysis will not be discussed further here, as it has been authoritatively reviewed by a number of authors listed in the last section of this paper.

Surface pattern analysis, on the other hand, is concerned with the study of spatially continuous phenomena. The spatial distribution of the variables is known, as usual, through sampling at discrete sampling stations. One or several variables are observed, each observation point representing its surrounding portion of space; the analysis of continuous transect data, such as echolocation data, is not specifically discussed here. Surface pattern analysis includes a family of methods designed to answer a variety of questions, which can be summarized under the following headings.

1) Description of spatial autocorrelation

Ecologists are first interested in quantifying the autocorrelation present in their data. The objective may be to demonstrate that no significant spatial autocorrelation is present (or remains, after it is extracted), in order to make valid use of the standard univariate or multivariate statistical tests of hypotheses. Or, the investigator may be interested in demonstrating that significant spatial autocorrelation is present, in order to use it in conceptual or statistical models. Spatial structures are first described through so-called structure functions, which allow us to quantify the spatial dependency and partition it along the various distance classes. The most commonly used structure functions are correlograms, variograms, and periodograms, which have been reviewed in more detail by Legendre and Fortin (1989). A correlogram is a graph in which autocorrelation values are plotted on the ordinate, against distance classes among sampling stations (localities) on the abscissa. Correlograms (Cliff and Ord 1981) can be obtained for single variables (Moran's I, 1950, or Geary's c, 1954, autocorrelation coefficients), or for multivariate data (Mantel correlogram: Sokal 1986). In all cases, a test of significance is available for each individual autocorrelation coefficient plotted in the correlogram; with proper correction for multiple testing, one can then determine whether a significant spatial structure is present in the data. (This test requires that the condition of second-order [or weak] stationarity be satisfied; that condition says that the expected value [mean] and variance of the variable over the study area must have constant and finite values, and the autocorrelation function must depend only on the length and orientation of the vector between any two points, not on their position in the study area.) The

shape of the correlogram also indicates the type of spatial structure. In a semi-variogram (often called a variogram for simplicity), the function of autocorrelation plotted on the ordinate is the semi-variance, a measure closely related to Geary's c autocorrelation coefficient. When computing a semi-variogram, one only assumes that the autocorrelation function is apt to describe the whole surface under study. (This relaxed form of stationarity is called the "intrinsic hypothesis," i.e., the increments $y_i - y_j$ must have zero mean and constant variance over the study area.) In the geostatistical tradition, semi-variances are not tested for significance, although they could be through the test developed for Geary's c, if the condition of second-order stationarity is satisfied. Statistical models can be fitted to variograms (linear, exponential, spherical, Gaussian, etc.) that allow the investigator to relate the observed structure to hypothesized generating processes. Because they measure the relationship between pairs of observation points located a certain distance apart, correlograms and variograms can be computed either for preferred geographic directions or, when the phenomenon is assumed to be isotropic in space, in an all-directional way. When the structure under study can be assumed to consist of a combination of sine waves propagated through space, a Schuster (1898) periodogram can be computed. The basic idea is to fit sines and cosines of various periods, one period at a time, and to determine the proportion of the series' variance (r^2) that can be explained by that period. In periodograms, the abscissa is either a period or its inverse, a frequency; the ordinate is the proportion of variance explained. Two-dimensional periodograms can be plotted for all combinations of directions and spatial frequencies (Priestley 1964, Ripley 1981, Renshaw and Ford 1984).

2) Estimation and mapping

Structure functions require an interpretation. Because their shape may not unambiguously correspond to a single type of spatial structure, they must be complemented by maps of various kinds representing the spatial variation of the variable(s) of interest, or sometimes the variations of the variables' variance. Recent reviews for ecologists are by Burrough (1987) and Legendre and Fortin (1989). Several programs are available for mapping (Table 3). The easiest way to obtain a contour map of a single variable is to use inverse-square distance, which is but one case of moving average interpolation (Ripley 1981), or other such interpolation methods. The older method of trend-surface analysis (Student 1914), in which the variation of the variable of interest is expressed as a function of the geographic coordinates of the sampling locations, does not produce very accurate maps except in the most

simple cases; it remains useful when ecologists want to remove a simple spatial structure, for instance a spatial trend or large-scale patches, from their data, either because they want to study finer scale spatial structures or because they hope that, after the spatial component is extracted, no significant spatial structure will be left in the data (see also the next section, *The special case of gradients*). The use of trend-surface functions in spatial modeling is also discussed below (Eq. 5). More sophisticated maps can be obtained by the geostatistical method of kriging, which makes use of variograms (above) to take the spatial autocorrelation into account during the interpolation process. (Among other applications, kriging is interesting for ecologists in that it allows an unbiased estimation of the amount of a resource available in a given area [stock assessment] even after nonrandom sampling, but this is by no means an easy task [Simard et al. 1992]. Notice, however, that if one of the classical types of random sampling [Cochran 1977] has been used in the survey sampling program, spatial means with associated standard errors can be estimated in the usual way, by means of using the design-based approach [de Gruijter and ter Braak 1990].) Rough maps can be obtained by attribution of the closest observed value to each locality (Thiessen or Dirichlet polygons method), or sloping Delaunay triangles connecting triplets of observed points can be drawn in three-dimensional plots; see Isaaks and Srivastava (1989). Finally, ecologists who are studying community structure, or other multivariate data sets, may not be interested in mapping individual species or variables. The geographic variability of the whole data set can be represented in any of three ways. The first is to compute a reduced-space ordination (correspondence analysis for species presence or abundance data; principal components or other scalings for other data for which linear relationships can be assumed) and to map the first few components separately; this method may fail to produce interesting maps, however, if the main components of the variability are not spatial. The second method, suggested by Legendre (1990), solves this problem; a canonical ordination (CCA or RDA: see *The raw data approach* below) of the multivariate data set is computed, constrained by a high-order trend surface equation; the resulting canonical variables are then mapped as above. The third method is to use clustering techniques, with or without constraint of spatial contiguity, to divide the map into more homogeneous subsets; see the review by Legendre (1987).

Spatial *and* temporal autocorrelation are present jointly in historical biogeographic studies. Recent reviews include Wiley (1988*a, b*), Humphries et al. (1988), Brooks (1990), and Legendre (1990). The concept of correlograms has recently been extended by Gittleman and Kot (1990) to phylogenetic cladograms, in which the abscissa corresponds to systematic categories; cladograms are also used by cladistic biogeographers.

THE SPECIAL CASE OF GRADIENTS

Ecologists are often studying small sections of larger scale autocorrelated spatial structures. These sections may look like gradients when, for instance, a mountain slope or a riverbank is the focus of the study. This type of study is so widespread that it has led to a considerable amount of ecological literature on *gradient analysis* (Whittaker 1967, ter Braak and Prentice 1988). Gradients can be seen as a spatial structure that can easily be expressed as a simple function of the x and y geographic coordinates of the sampling stations and extracted from the data before further analysis, thus satisfying the second-order stationarity condition described above. Legendre et al. (1990) have distinguished between "true" and "false" gradients; these can be formally defined as follows.

In a "true" gradient (trend), the value z_{ij} observed at any location (i, j) can be expressed as a function of its geographic coordinates x_{ij} and y_{ij}, plus an error term ϵ_{ij} that is independent from location to location. Thus, a linear gradient could be modeled by

$$z_{ij} = b_0 + b_1 x_{ij} + b_2 y_{ij} + \epsilon_{ij}. \tag{1}$$

In a true gradient, the error terms at neighboring points are not correlated with one another. A true gradient structure violates the stationarity assumption of most spatial-analysis methods because the expected value, given by $(b_0 + b_1 x_{ij} + b_2 y_{ij})$, varies from place to place as a function of the geographic coordinates. It should be removed from the data before proceeding, for instance by trend surface analysis.

In a "false" gradient, on the other hand, the gradient-like structure is caused by autocorrelation. There is no change in expected value (given by b_0) throughout the surface, although the value observed at each locality is partly determined by neighboring values:

$$z_{ij} = b_0 + \Sigma f(z_{i',j'}) + \epsilon_{ij}. \tag{2}$$

In this model, $\Sigma f(z_{i',j'})$ represents the sum of the effects of the points located within some distance d from the value z_{ij} that we are trying to describe. The summation is over the various distance classes, so that the value of interest is modeled as partly determined by some function f of all the other points on the surface. Assume for simplicity that the points sit on the nodes of a regular spatial grid. If a point is determined by its first neighbors only, then d concerns distance class 1 only, and the process is called "autoregressive of order 1." In the case of positive autocorrelation, the surface looks like a gently wobbling landscape. Isolation-by-distance models that have been extensively studied by population geneticists pertain to this class of low-order au-

toregressive models. If the influence of data points on others carries a long way through geographic space (through several distance classes d), and in a more or less linear fashion (function f being, for instance, the inverse of the geographic distance times the value at this neighboring point), then the surface will look more like a mountainous landscape. An ecologist who studies only one slope of such a landscape is well justified in retaining the gradient in the analysis, instead of removing it as in the case of a true gradient, because it is the structure to be analyzed and explained.

The problem, of course, is to tell true gradients from false ones. The ecological hypotheses of the investigator are of prime importance in making this decision; these in turn may depend upon the scale of the study. If the environmental variables are spatially structured and are assumed to be driving the species response (environmental control model, often used in large-scale studies: Whittaker 1956, Bray and Curtis 1957), then a gradient, if present in both the controlling and the dependent variables, is seen as a "true" gradient (trend) and should be removed from the community response data. If, however, the investigator considers that the spatial structure is the result of the dynamics of the population or community itself (biotic control model, often used in smaller scale studies: Southwood 1987), then the situation is often best considered as a "false" gradient (autocorrelation), which should not be removed before modeling. The difference is important when tests of statistical hypotheses are involved, or for modeling purposes, and not when simply interested in describing spatial structures.

TESTS OF STATISTICAL SIGNIFICANCE VALID IN THE PRESENCE OF AUTOCORRELATION

When spatial autocorrelation has been demonstrated to be present in data, several solutions are open to ecologists. First, one can attempt to remove the spatial dependency among observations so that the usual statistical tests can be used, either by removing samples until spatial independence has been attained (a solution that is *not* recommended because it entails a net loss of expensive information) or by filtering out the spatial structure using trend surface analysis or the method of spatial variate differencing (see Cliff and Ord 1981, section 7.4).

The alternative is to modify the statistical method in order to take spatial autocorrelation into account; this approach is to be preferred when such a method is available, especially in cases where spatial structuring is seen not as a nuisance but as a part of the ecological process under study (previous section). Cliff and Ord (1973) have proposed a method for correcting the standard error of the parameter estimates of the simple linear regression in the presence of autocorrelation. This method is extended to linear correlations, multiple regressions, and t tests by Cliff and Ord (1981: Chapter 7) and to the one-way analysis of variance by Griffith (1978, 1987). Bartlett (1978) has perfected a previously proposed method of correcting for the effect of spatial autocorrelation due to an autoregressive process in randomized field experiments, adjusting plot values by covariance on neighboring plots before the analysis of variance; see also the discussion by Wilkinson et al. (1983), as well as the papers of Cullis and Gleeson (1991) and Grondona and Cressie (1991). Cook and Pocock (1983) have suggested another method of correcting multiple regression parameter estimations by maximum likelihood, in the presence of spatial autocorrelation. Using a different line of approach, Legendre et al. (1990) have proposed a permutational method of analysis of variance for spatially autocorrelated data, in the common case where the classification criterion is a division of a territory into non-overlapping regions and one wants to test for differences among these regions.
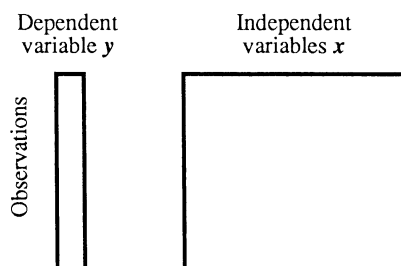
A step forward is proposed by Clifford et al. (1989), who test the significance of the correlation coefficient between two spatial processes by estimating a modified number of degrees of freedom, using an approximation of the variance of the sample correlation coefficient. Empirical results show that their method works fine for positive autocorrelation in large samples. Dutilleul (1993b) generalized the procedure and proposed an exact method to compute the variance of the sample covariance; the new method is valid for all sample sizes.

When methods specifically designed to handle spatial autocorrelation are not available, it is sometimes possible to rely on permutational tests, where the significance is determined by random reassignments of the observations; see also Potvin and Roff (1993). Special permutational schemes have been developed that leave autocorrelation invariant; examples are Besag and Clifford (1989), Legendre et al. (1990) and ter Braak (1990:Section 8). In complex problems, such as the preservation of spatial or temporal autocorrelation, the difficulty of the permutational method lies in the designing of an appropriate randomization procedure. The Mantel test, as well as the test of significance used in the canonical ordination CANOCO program (ter Braak 1988, 1990), both used in later sections of this paper to model the effect of the data's spatial structure, are permutational testing procedures.

INCORPORATION OF SPATIAL STRUCTURE INTO MODELING: THE RAW DATA APPROACH

If spatial heterogeneity is so important for the functioning of ecosystems, then models of ecosystem pro-

(a) Multiple regression

Dependent variable y Independent variables x

Observations

(b) Analysis of variance

Target variable y Classification criterion   Binary coding of the classification criterion

Observations

$=$

| 1 |
| 1 |
| 1 |
| 2 |
| 2 |
| 2 |
| • |
| • |
| • |
| $k-1$ |
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1 0 0  • • •  0 0
1 0 0  • • •  0 0
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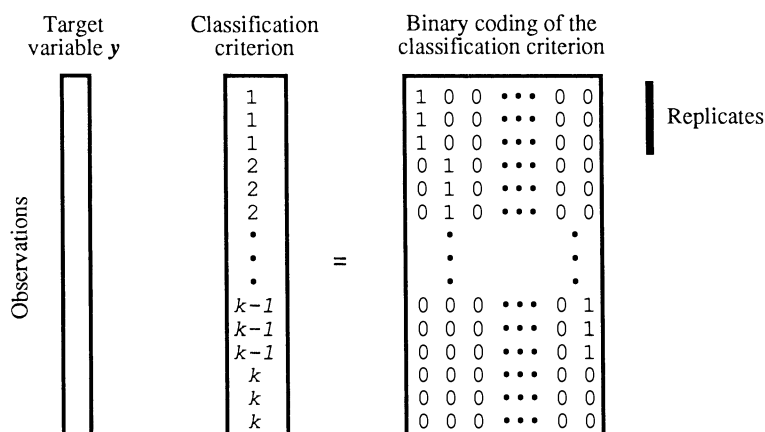
Replicates

FIG. 2. Classical approaches to data analysis. (a) Multiple regression. (b) Single-classification analysis of variance (one-way ANOVA); there are replicate observations within each group.

cesses may fall short of being optimal unless they include the spatial organization of the players, populations, and communities, among their predictor variables. Although this type of modeling is still in its infancy, two approaches have been proposed. The first one, described in this section, consists of expressing the spatial structure of the variables of interest as a linear combination of the geographic coordinates of the sampling stations. In the second approach (next section), the spatial structure is conveniently represented by a matrix of geographic distances among samples.

To understand how a spatial structure can be introduced into statistical models and combined with the environmental variables, we will look at various extensions of two classical approaches to data analysis: multiple regression and the analysis of variance. Let us first set the stage, however. In regression analysis (Fig. 2a), a set of independent, potentially predictive variables x are used to "explain" the variability of a dependent (or target) variable y. It is often postulated

that the relationships can be described by a linear model of the form

$$y = \beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n + \epsilon, \tag{3}$$

where the β_i are the regression coefficients and ϵ represents the error term, which leads to the usual estimates $\hat{y}$ of the values of y.

In single-classification analysis of variance (one-way ANOVA), on the other hand, we wonder how much of the target variable's variation can be explained by a classification criterion, through the decomposition model

$$SS_{\text{total of } y} = SS_{\text{among groups}} + SS_{\text{within groups}}, \tag{4}$$

where the SS are the sums of squares designated by the subscripts; let us assume that there are replicate measurements within each class (group) of the classification criterion. It is interesting to notice that the ANOVA variation partitioning can be computed using the multiple-regression technology, provided that the classi-
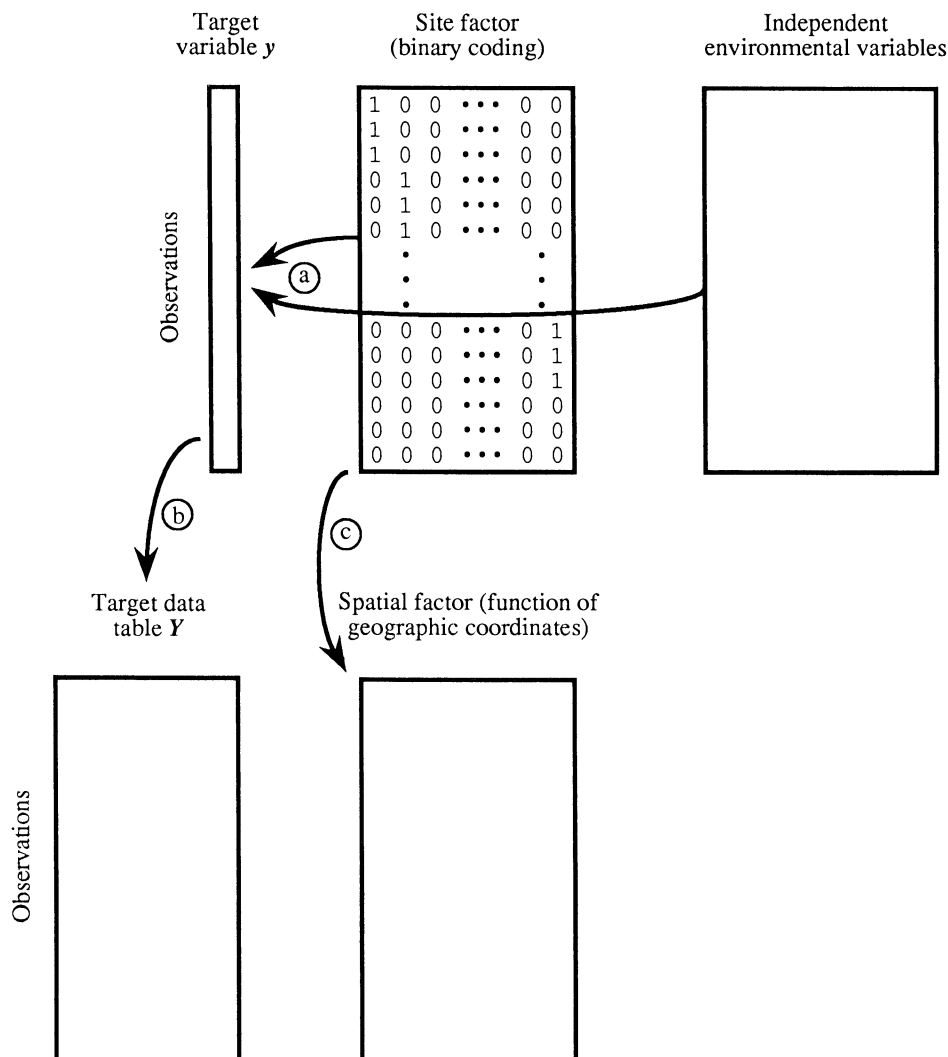
FIG. 3. Extensions of the linear modeling approach. (a) Partition of the variance of **y** between the site factor and the environmental variables. (b) Explanation of a target data table instead of a single target variable, using canonical analysis. (c) The "site factor" viewed as a "geographical-location" factor; geographic coordinates are used instead of binary "site" variables.

fication criterion (k classes) has first been coded into $(k - 1)$ binary variables, as in Fig. 2b; ter Braak (1987a) discusses this equivalence in more detail in an ecological framework. Ecologists can easily convince themselves of this equivalence by working out small examples on their favorite statistical package, using both methods; they will realize that the two ANOVA tables are identical.

The first extension that we will examine is called *partial regression analysis.* It applies to a single target variable *y.* In such an analysis (Fig. 3, arrows a), the explanatory potential specific to the matrix of environmental variables (r_1^2) can be studied after the site component is "partialled out." This preliminary op-

eration is easily done; the binary site variables are regressed onto each environmental variable in turn, and only the regression residuals are retained. The residuals are then used to model the target variable *y.* In the same way, the specific effect of the site factor on *y* can be studied after the environmental variables' effect (r_2^2) is partialled out. The combined effect of both the environmental and the site variables on *y* (r_3^2) can also be computed, by multiple regression of *y* on both sets of predictive variables combined. Following these regressions on the independent variables, the variation of *y* now contains four identifiable parts:

1) The environmental-variables fraction of the total variation of *y* is measured by the r_1^2 of the regression
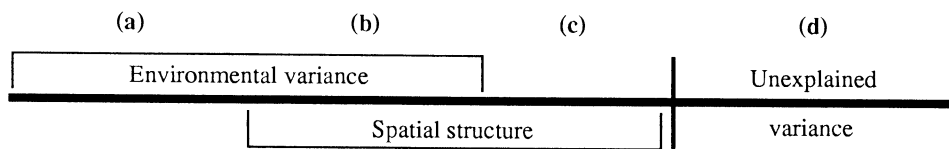
FIG. 4. Variance partitioning of the target data table; fraction (b) is the intersection of the environmental and spatial components.

on the environmental variables after the binary site variables are partialled out.

2) The among-sites fraction is measured by the r_2^2 of the regression on the binary site variables after the environmental variables are partialled out.

3) The interaction fraction is measured indirectly, by calculating $r_3^2 - (r_1^2 + r_2^2)$.

4) The unexplained variation $(1 - r_3^2)$.

The second extension consists of using a whole table of target variables instead of a single one (Fig. 3, arrow b). If Y is to be considered as a whole (when Y describes species assemblages, for example), the statistical methods to use in place of multiple regression form a family called *constrained ordination analyses* by ter Braak (1987b). Two forms are of interest here, depending on the nature of the data in the target data table: *redundancy analysis* and *canonical correspondence analysis*, both of which pertain to the canonical-correlation family of methods. Redundancy analysis (RDA: van den Wollenberg 1977) is to be used in the linear context, when the Euclidean distance appropriately represents the among-point relationships; it is equivalent to computing a multiple regression for each of the target variables (or, which is the same, a multivariate least-squares estimation using equation $\hat{B} = [X'X]^{-1}X'Y$: Finn 1974), followed by a principal components analysis of the fitted vectors. Canonical correspondence analysis (CCA: ter Braak 1986) is used in the unimodal context, when the chi-square distance appropriately describes the relationships among samples, as is the case for species presence/absence or abundance data. Partial forms of RDA and CCA are available, for instance in the CANOCO computer program (ter Braak 1988, 1990), which also allows us to perform a permutational test of significance of the sum of the canonical eigenvalues extracted during each run; this corresponds to the amount of variation of the dependent variables accounted for by the independent variables.

The third extension consists of replacing the table of binary site variables by a table of variables describing their spatial relationships (Fig. 3, arrow c), when the problems call for that. Following Legendre (1990), Borcard et al. (1992) have suggested use of some high-order polynomial function of the geographic coordinates of the sampling locations, built from their x and y coordinates on a map, as is customary in trend-sur-

face analysis. Regression analysis (partial or not) is then used to analyze single variables, and constrained ordination analysis (RDA or CCA, partial or not) in the case of multivariate dependent data sets. In the three-matrix case, four fractions of the variation can be identified, as above (Fig. 4); they can also be mapped and modeled separately if needed:

a) Nonspatial environmental variation.

b) Spatially structured environmental variation.

c) Spatial variation of the target variable(s) that is not shared by the environmental variables.

d) Unexplained, nonspatial variation.

Just as in partial regression analysis, the various fractions of variation (a), (c), (a + b), (b + c), and (a + b + c) can be tested for significance in partial constrained ordination. The third fraction, (c), is of special interest, because it points to a fraction of the variability that can be associated with a precise spatial structure—it is described by a function of the spatial coordinates x and y and may be mapped if necessary (Borcard and Legendre 1993)—but is not explained by the environmental variables at hand. In some cases, other environmental variables might be discovered that explain this fraction of variation. In other cases, this spatial fraction of variation may refer to biotic processes within the population or community that forms the target variable or data table, or to interactions of this population or community with other parts of the biotic community (disturbance dynamics, competition, predation, etc.).

When fraction (a) is very small, a false significant coefficient of determination can result if the common part (b) is not partialled out, as is the case in the many analyses where a target variable or data table is modeled by a set of environmental variables. Causality could falsely be attributed to the environmental variables, when in fact the correlation results from a common spatial structure present in both the dependent and independent data sets. This problem is discussed at some length by Legendre and Troussellier (1988).

Several examples of this partitioning procedure have been provided by Borcard et al. (1992). One of them concerns a community of oribatid mites in a peat blanket in Québec, in a rectangular area located between a bog lake and the surrounding forest. The variance of the 35 taxa submitted to analysis was partitioned among
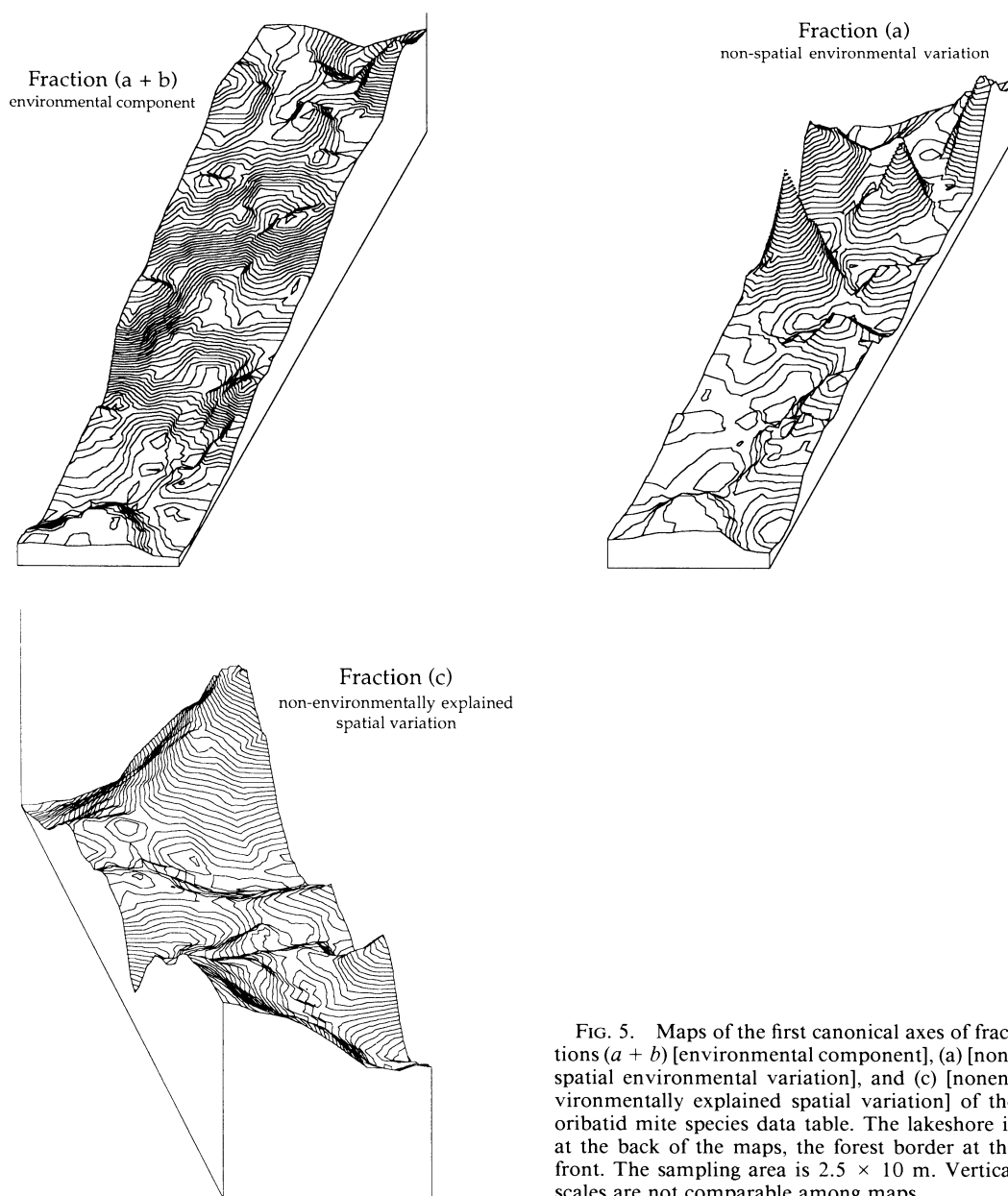
FIG. 5. Maps of the first canonical axes of fractions $(a + b)$ [environmental component], (a) [nonspatial environmental variation], and (c) [nonenvironmentally explained spatial variation] of the oribatid mite species data table. The lakeshore is at the back of the maps, the forest border at the front. The sampling area is 2.5 × 10 m. Vertical scales are not comparable among maps.

five environmental variables on the one hand and the following trend surface equation obtained by a forward selection procedure applied to the third-degree polynomial of spatial terms on the other (there is no intercept b_0 because all spatial terms had first been standardized):

$$f(x, y) = b_1 x + b_2 y + b_4 xy + b_5 y^2 + b_9 y^3. \quad (5)$$

Results of the partition obtained by partial canonical correspondence analysis are summarized in Table 1;

notice that the interaction, (b), between the two sets of independent variables is properly quantified. Fig. 5 presents three maps of the first canonical axes of various fractions of variation of the species data table. The first map, fraction $(a + b)$, contains two components: a smooth slope (fraction (b), not represented here), and a rough residual surface, fraction (a), containing a low-variance and a high-variance section, which is the real-case equivalent of the situation described in Fig. 2c of the Dutilleul paper (1993a). The third map, fraction

TABLE 1. Partition of the variation of the oribatid mite assemblage.

Source of variation	Fraction of variation of the species data table (%)
a) Nonspatial environmental	13.7
b) Spatially structured environmental	31.0
c) Nonenvironmental spatial	12.2
d) Unexplained	43.0

(c), that describes the nonenvironmentally explained spatial variation of the mite community, is quite different from the other two; its significance is discussed in more detail in Borcard and Legendre (1993).

Legendre (1990) presents another example that simply involves canonical correspondence analysis instead of the partial form. The method is used to obtain an ordination of a species-abundance data table that is constrained to be consistent with the geographic relations expressed by the trend-surface polynomial equation. The purpose is to obtain maps of the spatial-structure component of the data set, called (b + c) above, drawn from the canonical axes.

INCORPORATION OF SPATIAL STRUCTURE INTO MODELING: THE MATRIX APPROACH

Another approach will now be presented to include "space" as a predictor in statistical models, on an equal footing with the usual set of environmental variables. The spatial structure can naturally be represented by a geographic distance matrix among sampling stations—or some modification of such a matrix, for instance some sort of a connection matrix (see the last paragraph of this section). In the typical case, the geographic (Euclidean) distance is computed for all pairs of sampling stations, on the basis of their geographic coordinates, and assembled into a "spatial" distance matrix. If the biological and the environmental variables could also be represented in the form of distance matrices, then all three matrices could be compared by some form of correlation. Fortunately, a whole array of resemblance functions is available for computation of these matrices (Sneath and Sokal 1973, Orlóci 1978, Legendre and Legendre 1983, 1984, Gower 1985, Gower and Legendre 1986); they are adapted to the different mathematical types of data (binary, qualitative, quantitative, mixed types), to the inclusion or exclusion of double zeros, to the Q (comparison of objects) or R (comparison of variables) modes of analysis, and so on, so that one can model the correct concept of "resemblance" for the problem at hand.

Before going into the details of this modeling method, I must introduce the Mantel (1967) test, also called the Quadratic Assignment Procedure in psychometrics

(Hubert and Schultz 1976); this is the basic statistical instrument presently used for comparing distance matrices. In its basic form, the Mantel statistic is the sum of the cross-products of the corresponding distances in two matrices. The Mantel statistic can easily be normalized to take values between -1 and $+1$: each of the distance matrices must be standardized separately before the sum of cross-products is computed. The Mantel statistic then becomes equivalent to a Pearson product–moment correlation coefficient. Because of the dependencies among values in a distance matrix, this correlation coefficient cannot be tested in the usual way. It is tested instead against a distribution of values obtained by repeated random permutations of the rows and columns of one of the distance matrices and recomputation of the coefficient, each case corresponding to one of the possible realizations of the null hypothesis (Mantel 1967). It should be noticed that a correlation between two distance matrices is not equivalent to the correlation between the two variables behind these matrices or to the canonical correlation between two data tables; whereas canonical correlation analysis measures the correlation between two data tables, a matrix correlation r_{AB} measures the extent to which the variations in the *distances* of matrix **A** correspond to the variations in **B**. Statistics other than Mantel's have been suggested to measure the correspondence between distance matrices: Dietz (1983) and Hubert (1985) have suggested nonparametric correlation coefficients, whereas Jackson (D. A. Jackson, *unpublished manuscript*) has worked from Procrustes statistics. For future work, a power analysis of these statistics should be performed to help decide among them, under various conditions.

The next step needed for causal modeling was the development of the partial Mantel test procedure by Smouse et al. (1986). The partial Mantel statistic, noted $r_{AB\cdot C}$, allows testing for the correlation between matrices **A** and **B**, controlling for the effect of a matrix **C**. With the same caveat as above, a partial Mantel statistic is to be interpreted in much the same way as a partial correlation, since the algebra is the same. The first role of a partial test is to check for possible false correlations, before data are interpreted in a causal framework. Legendre and Troussellier (1988) have proposed to transfer to distance matrix modeling the bulk of knowledge acquired in causal analysis, and in particular the predictions made about the values of the simple correlations (De Neufville and Stafford 1971) and the partial correlations (Legendre and Legendre 1983, 1984) for different causal models. Fig. 6 provides the expectations for all possible causal models involving three matrices, in terms of the three simple and the three partial Mantel test values that can be computed.

Ecological applications of this technique to models

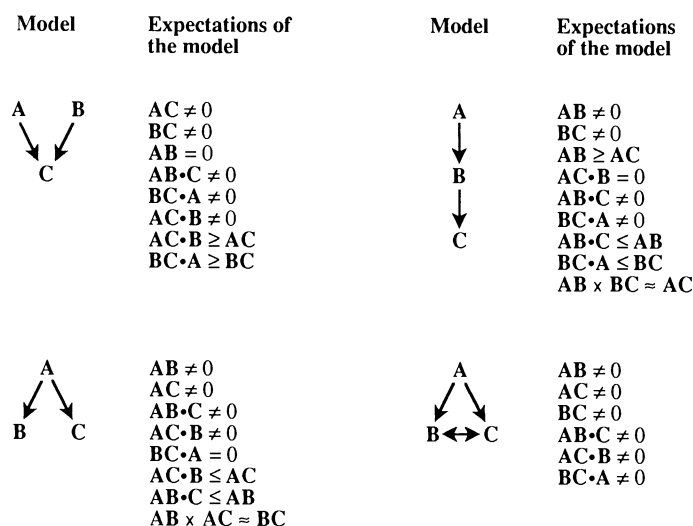| **Model**	**Expectations of the model**	**Model**	**Expectations of the model**
A B ↘ ↙ C	$AC \neq 0$ $BC \neq 0$ $AB = 0$ $AB \cdot C \neq 0$ $BC \cdot A \neq 0$ $AC \cdot B \neq 0$ $AC \cdot B \geq AC$ $BC \cdot A \geq BC$	A ↓ B ↓ C	$AB \neq 0$ $BC \neq 0$ $AB \geq AC$ $AC \cdot B = 0$ $AB \cdot C \neq 0$ $BC \cdot A \neq 0$ $AB \cdot C \leq AB$ $BC \cdot A \leq BC$ $AB \times BC \approx AC$
A ↙ ↘ B C	$AB \neq 0$ $AC \neq 0$ $AB \cdot C \neq 0$ $AC \cdot B \neq 0$ $BC \cdot A = 0$ $AC \cdot B \leq AC$ $AB \cdot C \leq AB$ $AB \times AC \approx BC$	A ↙ ↘ B ↔ C	$AB \neq 0$ $AC \neq 0$ $BC \neq 0$ $AB \cdot C \neq 0$ $AC \cdot B \neq 0$ $BC \cdot A \neq 0$

FIG. 6. Predictions of the four possible models of causal relationships involving three matrices, in terms of the expected results of the simple and partial Mantel tests. For simplicity, r_{AB} is noted **AB**, and so on. Stating that a relation is equal to zero means that the computed value should not be significantly different from zero, and conversely.

that include geographic distances are found in Burgman (1987), Legendre and Troussellier (1988), Legendre and Fortin (1989), and Leduc et al. (1992); this last paper uses partial Mantel tests in conjunction with path analysis computed from the Mantel statistics. Other interesting applications of the partial Mantel test to anthropology and population genetics are found in Sokal et al. (1986, 1987). Let us consider two of these applications. In the paper by Legendre and Troussellier (1988), the question is whether the well-established relationship between environmental heterotrophic bacteria and phytoplankton biomass (measured by chlorophyll *a*, CHL A) holds for two identifiable components of the bacterial heterotrophic community of a marine lagoon: the BNA bacteria, which are presumably of continental origin, and the MA, expected to be

mostly of marine origin (abbreviations as in the original publication). Both bacterial variables are well correlated to CHL A, but this pattern could be the result of a common spatial structure created by currents. The spatial structure is represented by a matrix, called SPACE, of Euclidean (or geographic) distances among the 63 sampling stations. The Mantel and partial Mantel statistics computed to make a choice between the two models are reported in Table 2. The nonsignificant partial Mantel relationship between BNA and CHL A, when the effect of SPACE is held constant, points to the model in Fig. 7a, which contradicts the hypothesis of control of the continental heterotrophs by phytoplankton; on the other hand, the nonsignificant partial Mantel relation between MA and SPACE, when CHL A is held constant, points to the model in Fig. 7b, which supports the hypothesis of phytoplankton control for the marine heterotrophs. Leduc et al. (1992) analyzed the relationship between the spatial distribution of adult trees, saplings, and environmental conditions (drainage, soil, and geomorphology), for 12 species in a 0.5-km² study area. They found that the spatial patterns

TABLE 2. Above the diagonal: simple Mantel statistics and associated probabilities. Below the diagonal: partial Mantel statistics, controlling for the effect of the third matrix, and associated probabilities. Tests of significance are one-tailed.

a) Analysis of the BNA–CHL A–SPACE relations

	BNA	CHL A	SPACE
BNA	···	0.258*	0.521*
CHL A	−0.006	···	0.505*
SPACE	0.468*	0.449*	···

b) Analysis of the MA–CHL A–SPACE relations

	MA	CHL A	SPACE
MA	···	0.325*	0.223*
CHL A	0.252*	···	0.505*
SPACE	0.073	0.469*	···

*Mantel test significant ($P < .001$).

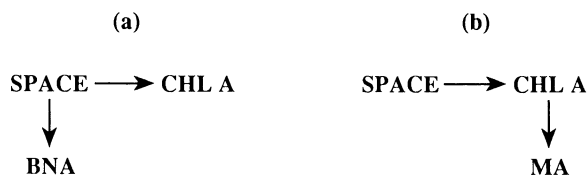**(a)**

SPACE ⟶ CHL A
↓
BNA

(b)

SPACE ⟶ CHL A
↓
MA

FIG. 7. Representation of the models supported by the data, (a) for the BNA and (b) for the MA heterotrophic bacteria.

TABLE 3. The following programs are available to compute the various methods of spatial analysis mentioned in the text. Only those methods are listed that are not available in general-purpose statistical packages.

CANOCO	Canonical (i.e., constrained) ordination methods: CCA, RDA. Available for MS-DOS and Macintosh microcomputers and for mainframes from Microcomputer Power, 111 Clover Lane, Department C9, Ithaca, New York 14850 USA.
CLADAREA	Area cladistic analysis. Wagner tree reconstruction (parsimony). Available from Willem N. Ellis, Instituut voor Taxonomische Zoologie, afd. Entomologie, Plantage Middenlaan 64, NL-1018 DH Amsterdam, The Netherlands.
COCOPAN	ANOVA for spatially autocorrelated regional data. Written by Alain Vaudor and Junhyong Kim. Available from P. Legendre's laboratory (see title page) for Macintosh microcomputers and IBM and VAX mainframes.
COMPONENT	Construction and comparison of area cladograms. Available from Roderic D. M. Page, Department of Zoology, University of Auckland, Private Bag, Auckland, New Zealand.
CORR2D	Two-dimensional correlogram. Written by Geoffrey M. Jacquez. Available from Applied Biostatistics Incorporated, 100 North Country Road, Building B, Setauket, New York 11733 USA.
GEO-EAS	Variogram, kriging. Contour mapping. Developed by EPA. Available for MS-DOS machines from ACOGS, P.O. Box 44247, Tucson, Arizona 85733-4247 USA.
GEOLIN	Variogram, kriging. Contour mapping. Also GEOSREC for nonlinear and BLUEPACK for nonstationary kriging. Available from Geovariances International, 1 rue Charles-Meunier, F-77210 Avon-Fontainebleau, France.
GEOSTAT	Variogram, kriging. Contour mapping. Available from Geostat Systems International Incorporated, 4385 rue Saint-Hubert, Suite 1, Montréal, Québec, Canada H2J 2X1.
GS+	Spatial autocorrelogram (Moran's I), variogram, kriging. Contour mapping. Available from Gamma Design Software, P.O. Box 201, Plainwell, Michigan 49080-0201 USA.
Kellogg's	Variogram, kriging. Contour mapping. Available from the Computer Laboratory, W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060 USA.
MacGRIDZO	Inverse distance and weighted least squares interpolation. Contour mapping. Available for Macintosh machines from RockWare Incorporated, 4251 Kipling St., Suite 595, Wheat Ridge, Colorado 80033 USA.
NTSYS-PC	Simple Mantel test; correspondence analysis. Developed by F. James Rohlf. Available in MS-DOS version from Exter Software Inc., 100 North Country Road, Building B, Setauket, New York 11733 USA.
The R package	Spatial autocorrelograms (Moran's I and Geary's c), simple and partial Mantel tests, Mantel correlogram, clustering with space and time contiguity constraint. ANOVA for regional data. Connection networks. Developed by Alain Vaudor (deceased; P. Legendre's laboratory). Available for Macintosh microcomputers, VAX, and IBM mainframes.
SAAP	Spatial autocorrelograms (Moran's I and Geary's c). Available from Daniel Wartenberg, Department of Environmental and Community Medicine, Robert Wood Johnson Medical School, 675 Hoes Lane, Piscataway, New Jersey 08854 USA.
SASP	Two-dimensional spectral analysis. Available from E. Renshaw, Department of Statistics, University of Edinburgh, King's Buildings, Mayfield Road, Edinburgh EH9 3JZ United Kingdom.
SURFER	Kriging from linear variogram only; other interpolation methods. Contour mapping. Available from Golden Software Incorporated, P.O. Box 281, Golden, Colorado 80402 USA.
SYMAP	Trend surface analysis; other interpolation methods. Contour mapping. No longer distributed by Laboratory for Computer Graphics and Spatial Analysis, Harvard University, USA, but still available at many computing centers.
UNIMAP	Variogram, kriging; other interpolation methods. Contour mapping. Available from European Software Contractors A/S, Nørregade, DK-2800 Lyngby, Denmark.

of tree species associated with hydric conditions are largely explained by the spatial distribution of the environmental conditions, while on the other hand, mesic-site species still displayed spatial structuring after controlling for the effect of the environmental conditions. Historical events (disturbances), as well as forest cover dynamics, are suggested as explanations for the latter.

Progress is still to be made in this elementary form of modeling. Spatial relationships can be construed in other ways than as a Euclidean distance matrix. Authors have used transformations such as the inverse, or the inverse of the square of the Euclidean distance, that give more importance to the small distance values (Jumars et al. 1977); other authors prefer to use connection schemes such as rook's or king's connections (Cliff and Ord 1981) for regular grids of samples, and Gabriel graphs of Delaunay triangulations (Upton and Fingleton 1985) for irregularly spaced points. An important step will be to learn how to analyze the n-independent-matrix case and to extend this type of analysis into path analysis; a proposal in this respect has already been made by Krackhardt (1988) for the special case of autocorrelated network data.

CONCLUSION

Studying spatial structures is both a requirement for ecologists who deal with spatially distributed data, and a challenge. It is the new paradigm for field ecologists interested in exploratory data analysis or in the modeling of ecological phenomena. Fortunately, statistical methodology is rapidly developing to assist us in doing so. As we have seen, most of the theories and models that we rely on to understand ecosystems assume, explicitly or not, some spatial structuring of the environment and of the biological communities. Until recently, we have been bound to ignore this structure by lack of appropriate methods for analyzing and modeling our data. We were led to stretch our statistics beyond their basic assumptions and, worse, to overlook one of the most important determinants of the functioning of ecosystems. This problem is easily realized when spatial structure is incorporated into models of ecological systems; the amount of explained variation often jumps to unexpected heights. One consequence is that it may be of no use to try to increase the fraction of explained variation by looking at more environmental variables, since the explanation of fraction (c) in Fig. 4, which may represent an important proportion of the previously unexplained variation, may perhaps be found in population or community-based spatial processes. Another is that much better predictions can be obtained when the spatial structure is included as such among the predictive variables. This inclusion will be even more efficient when non-

linear methods of modeling are introduced into spatial analysis.

The matrix approach is certainly to be preferred when the dependent variable naturally presents itself in the form of a resemblance or proximity matrix (genetic distances obtained by DNA or RNA pairing; preference or dominance data in behavior studies, in serology, etc.). However, all ecological applications reported above dealt with data that could have been handled through the raw-data approach just as well. In some of these papers, it was felt that resemblance coefficients gave greater flexibility in handling mixed-type data, as with the environmental data matrix of Leduc et al. (1992), that was computed from a mixture of ordered and nonordered variables. One could counter, however, that distance-based ordination methods (metric or nonmetric scaling) would always permit to transform a distance matrix back into an array of quantitative axes, thus allowing us to use the raw-data approach. The matrix approach, as presently developed, focuses on mere statistical testing and largely disregards estimation; future developments should focus on interpretative aspects. The raw-data approach, on the other hand, which also allows statistical testing, provides an estimation of the contribution of each independent and dependent variable with respect to the canonical axes, but is limited to the use of Euclidean or chi-square distances. The matrix approach allows both the small-scale (i.e., autocorrelation) and large-scale (i.e., trend) spatial dependencies to be modeled, while the raw-data approach, as developed so far, only allows us to model trends. While both methods seem to have been successful in enriching our understanding of spatial processes occurring in ecosystems, comparative studies are needed using cases where they both seem equally suitable.

FURTHER READING AND APPLICATIONS

Important references to the topics discussed above include, for point-pattern analysis, Pielou (1977), Cicéri et al. (1977), Getis and Boots (1978), Ripley (1981, 1987), and Upton and Fingleton (1985); for surface-pattern analysis, Cliff and Ord (1981), Ripley (1981), Upton and Fingleton (1985, 1989), Griffith (1987), and the review paper by Legendre and Fortin (1989); and for kriging and other mapping methods, the books of David (1977), Journel and Huijbregts (1978), and Isaaks and Srivastava (1989), as well as the review paper by Lam (1983). On canonical ordination, required reading is the chapter by ter Braak (1987b). Table 3 lists computer programs available from researchers that carry out the computations of the methods described in this paper; most of these methods are not available in major statistical packages. This list of programs is not exhaustive.

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