APPLICATIONS OF SPATIAL AUTOCORRELATION IN ECOLOGY

Robert R. Sokal and James D. Thomson
Department of Ecology and Evolution
State University of New York at Stony Brook
Stony Brook, New York 11794-5245 USA

Abstract - The methods of spatial autocorrelation analysis for both continuous and nominal variables are explained. Spatial correlograms depict autocorrelation as a function of geographic distance. They permit inferences from patterns to process. The Mantel test and its extensions are special ways of detecting autocorrelation in ecology. The methods are applied to the spatial distributions of ecological variables in two understory plants in the genus *Aralia*.

INTRODUCTION

Most problems in ecology have a spatial dimension because organisms are distributed over the surface of the earth. Ecologists have, for many years, studied problems involving the spatial distribution of individuals of a species and the joint distributions of several species. One way to examine such distributions is through the study of point distributions, a subject reviewed in another chapter, by B.D. Ripley, in this volume. Other spatial approaches in ecology are biogeographic and deal with the distribution of species over the face of the earth and with the congruence between spatial distribution patterns of different species (Lefkovitch 1984, 1985). The present chapter deals with yet another spatial aspect of ecological research, the statistical properties of surfaces formed by variables of ecological interest.

Typical data for such studies are sampling stations in geographic space, represented as points in the plane. These stations may be regularly spaced as in a linear transect or a lattice; in most applications they are irregularly distributed, as are plants in a field or islands in an archipelago. Defined regions or areas can be used as well. For purposes of analysis,

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each such unit would be considered a point. Irregular spatial distribution of the sample locations may reflect no more than the haphazardly chosen sites for specimen collection. However, the distribution of the sample stations may often impart important information about the populations. Because organisms are more common in one area than another, different densities of collection sites result. Such a pattern of distribution of sites may well be of interest and is dealt with by Ripley (1987) in this volume. However, for purposes of this chapter we shall consider the distribution patterns of points as given and focus attention on the variables mapped onto the points, one value per variable for each point. The variables may run the gamut of those studied in ecology, including biomass, population density, morphometrics, species diversity, gene frequency, and others. The data values observed at a set of sampling localities constitute a set of discrete observations assumed to have been taken from an underlying "surface". The observations may or may not have measurement error and the surface may or may not be continuous.

We shall focus on the spatial autocorrelation exhibited by the variables observed at the sampling stations. Spatial autocorrelation is the dependence of the values of a variable on values of the same variable at geographically adjoining locations. Early work in this field (Moran 1950; Geary 1954) was rapidly followed by applications to ecological work (Whittle 1954; Matern 1960). However, only with the important summary furnished by Cliff and Ord (1973) and its renewed application to biology (Jumars, Thistle and Jones 1977; Jumars 1978; Sokal and Oden 1978a,b) did the study of spatial autocorrelation begin to make an impact on ecological and population biological research.

Biological variables are spatially autocorrelated for two reasons: inherent forces such as limited dispersal, gene flow, or clonal growth, tend to make neighbors resemble each other; and organisms may be restricted by, or may actively respond to environmental factors such as temperature or habitat type, which themselves are spatially autocorrelated. Spatial autocorrelation methods may be used for description of surfaces as well as for making inferences from pattern to the process

that has produced the pattern We shall detail both aspects in the ensuing account, which is arranged as follows. The methodology is introduced first, followed by an account of its application. This will include aspects of inference about ecological processes from spatial patterns in the data. Finally, we shall present two ecological examples to illustrate the application of the methods.

THE METHOD

Spatial autocorrelation computations. Two coefficients are most frequently employed to describe spatial autocorrelation in continuous variables. Moran's coefficient (Moran 1950) is computed as

$$I = nS_{jk}w_{jk}z_jz_k/WS_jz_j^2,$$

and Geary's ratio (Geary 1954) as

$$c = (n - 1)S_{jk}w_{jk}(Y_j - Y_k)^2/2WS_jz_j^2.$$

In these formulas, n is the number of localities studied; S_{jk} indicates summation over all j localities from 1 to n and over all k localities from 1 to n, $j \neq k$; S_j indicates summation over all j localities from 1 to n; w_{jk} is the weight given to a connection between localities j and k (these weights are discussed below; w_{jk} need not equal w_{kj}); $z_j = Y_j - Y$, where Y_j is the value of variable Y for locality j and Y is the mean of Y for all localities; and $W = S_{jk}w_{jk}$, the sum of the matrix of weights, $j \neq k$. Details of the computation, as well as standard errors for testing the statistical significance of the spatial autocorrelation coefficient, are furnished by Cliff and Ord (1981) and, in simplified form, by Sokal and Oden (1978a).

Moran's I-coefficient resembles a product-moment correlation coefficient. It usually varies between -1 and +1; Cliff and Ord (1981) have shown that its upper bound ordinarily will be less than unity, but could exceed unity for an irregular

pattern of weights. The limits for Geary s *c* are 0 for perfect positive autocorrelation (similar neighbors) and a positive, variable upper bound for negative autocorrelation (dissimilar neighbors). In the absence of spatial autocorrelation, the expected value of *I* is $-1/(n - 1)$ and of Geary's *c* is 1. The results of employing *I*- and *c*-coefficients are generally similar, although, with unusually distributed weight matrices, results by the two methods may differ substantially (Sokal 1979). Following a Monte Carlo simulation study, Cliff and Ord (1981) conclude that "the *I*-test is generally better than the *c*-test although the margin of advantage may be slight".

The weights in the above formulas measure the connection or influence of locality *j* upon locality *k*. They can be functions of geographic distances between pairs of localities, such as inverse distances or inverse squared distances. These weights are assembled in an $n \times n$ matrix with a weight for each locality pair *jk*. An alternative approach uses a binary weight matrix, where 1 indicates connection or adjacency between two localities and 0 signifies the lack of such a connection. When the sampling stations represent regions, all regions sharing a common boundary may be connected, and those lacking such a boundary left unconnected. When the sample localities are points in a space, various geometric rules for establishing connectivity can be imposed (Tobler 1975). A common method for biological applications assumes that spatial influences take a direct path: In a Gabriel graph (Gabriel and Sokal 1969; Matula and Sokal 1980) two localities A and B are connected if, and only if, the square of the distance between A and B is less than the sum of the squares of the distances to any other locality C. Because a Gabriel graph connects nearest neighbors, it represents the paths of likely interaction (such as gene flow) among localities (Gabriel and Sokal 1969). An alternative design, the nearest neighbor or minimum spanning tree connection, is a subgraph of a Gabriel graph (Matula and Sokal 1980).

From a binary matrix connecting the localities, geographic distances between localities can be computed along the connections rather than directly (great circle or Euclidean

distances). The shortest distance between any pair of localities along a connecting graph is computed by a so-called cascade algorithm. Distances between adjacent localities will be the same for great circle distances or distances along Gabriel graphs. But distant localities will be farther apart when measured along a connectivity graph. In studies with a large number of localities, it probably does not matter which approach is chosen; direct distances require fewer computational steps.

Graphs of the relation between spatial autocorrelation coefficients and geographic distance are called *spatial correlograms*. They are computed by preparing a frequency distribution from the matrix of geographic distances between all pairs of localities and grouping these distances into a number of classes, each based on predetermined distance limits. For example, the first distance class might contain all locality pairs 0 to 20 m apart, the second distance class all those between 20 and 40 m, and so forth. The widths of the class intervals need not be the same. Some workers include approximately the same number of locality pairs in each distance class. It is furthermore not likely that the process under study is linear with distance, and greater refinement is generally required at close than at far distances. Both of these considerations lead to distance classes with unequal intervals. More than 10 to 15 distance classes are generally not useful. In our investigations, when the number of localities is small, we set up fewer distance classes so that no class contains fewer than 40 point pairs.

The weight matrix for each distance class is binary, a weight of 1 between a pair of localities indicating that the pair falls in this distance class and 0 that it does not. Using the binary weight matrix for each distance class, one computes the corresponding spatial autocorrelation coefficients and plots them against the geographic distance implied by the distance classes. The resulting correlogram summarizes the pattern of geographic variation exhibited by the surface of a given variable. Correlograms describe the underlying spatial relationships for a surface rather than its appearance, and are

probably closer guides to the processes that have generated the surfaces than are the surfaces themselves. Sokal and Oden (1978a) have illustrated the characteristic correlograms of various types of surface patterns. A unidirectional gradient shows a monotonically decreasing correlogram from positive to negative autocorrelation as distances increase from near to far. A bowl-like depression yields a similar correlogram that eventually reverts to positive autocorrelation at the farthest distance classes. Other surfaces show similarly characteristic correlograms. The distance at which the correlogram first reaches $-1/(n-1)$ is the distance at which positive spatial autocorrelation vanishes. In certain patchy environments this measure may be an indicator of the average size of homogeneous patches (Sokal 1979).

When the data are nominal, spatial autocorrelation is not estimated in the form of a coefficient, but as deviations of observed frequencies of like and unlike neighboring pairs from their expectations based on random spatial arrangement. Thus, when a distribution of individuals comprising three species, A, B. and C, is studied, one computes the frequencies of AA, BB, and CC pairs by a criterion of connectivity or adjacency as for continuous data. Then one computes the expected frequency of such pairs on the assumption of a random spatial arrangement. One also counts the frequency of adjacent unlike pairs, AB, AC, and BC, and compares them with their expectations, under a null hypothesis of spatially random placement of the three species. Thus, in this example, six deviations would be tested. Sometimes the frequencies of all unlike neighbors are summed for a single test irrespective of the particular pairs involved. The deviations have been shown to be asymptotically normally distributed and are tested against their standard deviation units (Cliff and Ord 1973, 1981). To construct a correlogram for each deviation type, one needs to plot the signed deviations from expectation as a function of spatial distance. As in the computation of distance classes for continuous measurement data, one can compute binary connectivity matrices showing neighbors at specified distances. For any one type of pair (species combination), great spatial distances will generally show no

departure from expectation. However, an area with two ecological regions in which the proportions of species differ, and for which interregional distances are greater than intraregional distances, would necessarily show a decrease in homotypic pairs over expectations at the higher distance and a corresponding increase in heterotypic pairs. An analogous phenomenon has been observed in two medieval cemeteries whose ABO blood groups have been determined by paleoserological methods and where graves in two regions of the cemetery were settled by different ethnic groups, apparently differing in their ABO gene frequencies (Sokal et al. 1986).

Ordinary spatial correlograms do not indicate the direction of clines. Oden and Sokal (1986) have developed a method of computing directed correlograms which permit the evaluation of spatial trends for different compass directions. The procedure is carried out by dividing the pairs of localities into direction/distance classes that indicate not only distance but also the compass bearing between the sampling stations.

Mantel approaches. An alternative procedure for estimating and testing spatial autocorrelation is the Mantel test. This test is carried out by an element-by-element multiplication of the weight matrix with a proximity matrix representing some similarity function between all pairs of localities, either with respect to a single variable or to numerous variables. Examples are genetic, morphologic, serologic, or geographic distances. Designating the elements of these two matrices as w_{jk} and d_{jk}, respectively, the Mantel test statistic Z is computed as

$$Z = S_{jk} w_{jk} d_{jk}$$

The null hypothesis tested is independence of the elements of the two matrices--the weight matrix (representing spatial distances) and the proximity (distance) matrix for the variable(s) studied. Expectations for moments of Z under this null hypothesis have been derived by Mantel (1967) who showed the distribution of Z to be asymptotically normal, leading to a straightforward significance test. Because of distributional uncertainties, the preferred way to test the significance of the

Mantel statistic is by a Monte Carlo test, in which rows and columns of one of the two matrices are randomly permuted, followed each time by recalculation of *Z*. Proposals for normalizing *Z* to a coefficient ranging from -1 to +1 have been made by Hubert and Golledge (1982), Hubert (1985), and Smouse et al. (1986). The Mantel test is a very general test with considerable appeal because of its simplicity. Hubert et al. (1981) have shown that by specifying the proximity matrix appropriately, spatial autocorrelation coefficients *I* and *c* can both be expressed as Mantel statistics. Among other useful applications, the Mantel test enables one to compute spatial correlograms for proximity matrices representing overall distances between pairs of localities based on numerous traits (such as biogeographic or genetic distances). In such cases conventional *I*- or *c*-coefficients cannot be evaluated. An example of an ecological application of Mantel tests is the work of Setzer (1985) on spatial and space-time clustering of mortality in gall-forming aphids of the genus *Pemphigus*.

Because distance data are so common in population biology and ecology, investigators have attempted to extend the Mantel test to analyzing three or more matrices simultaneously. Such multiple tests examine the interactions of several types of distances, for example, spatial, ecological, and genetic distances, or geographic, climatic, and faunistic distances. Three different approaches have been suggested within the last year for investigating the relations among three distance matrices. Let the three matrices to be compared be designated as **A**, **B**, and **C**. Dow and Cheverud (1985) propose to compare matrices **A** and (**B**-**C**), that is, they carry out a Mantel test between matrix **A** and the difference matrix, **B**-**C**. The matrices **B** and **C** must be comparably scaled before the subtraction. The Mantel test indicates whether $r_{AB} = r_{AC}$, and, by its sign suggests which of the two distance matrices **B** or **C** has the greater correlation with distance matrix **A**. The method assumes that associations of **A** with **B** and **A** with **C** exist, and that **A**, **B**, and **C** represent potentially spatially autocorrelated surfaces. Hubert (1985) computes **A.(BC)**, in which the matrix **BC** is the Hadamard (element-by-element) product of matrices **B** and **C**, and

tests the association between **A** and **BC** by means of the Mantel statistic. The question posed by Hubert is whether **A** has a significant matrix correlation with the **BC** product matrix which is supposed to embody the relations between **B** and **C**. It is assumed in this method that **B** and **C** have a significant association, and, as before, that **A**, **B**, and **C** are separately autocorrelated. Smouse et al. (1986) consider the correlation r_{BC} to be fixed and do not permit this correlation to be destroyed by permutation of either **B** or **C**. They compute the partial correlations $r_{AB.C}$ and $r_{AC.B}$ of the matrix elements. These authors test the significance of partial correlation $r_{AB.C}$ by computing residual matrices from the regressions of **A** on **C** and **B** on **C**, then obtaining the distribution of the partial correlation as a normalized Mantel product of the two residual matrices, permuting rows and columns of either matrix. This method assumes that r_{AB} and r_{AC} are significant and **A**, **B**, and **C** separately spatially autocorrelated. None of the methods has yet been corroborated by a Monte Carlo analysis of suitable autocorrelated surfaces to see whether independent but spatially autocorrelated surfaces fall into the acceptance region of the distribution of outcomes. An example of an ecological application of multiple Mantel tests is given in an analysis of causal factors of floristic composition of granite outcrops by Burgman (1986). Other examples are furnished below in this paper.

In some situations ordinary Mantel tests will not provide sufficient information on spatial relationships. Although the null hypothesis may be rejected in a given case, this does not automatically permit us to distinguish between two competing alternative hypotheses H_1 and H_2. Thus, if a set of populations for which densities or gene frequencies have been obtained can be grouped by two separate ecological criteria, how can one decide which criterion more nearly coincides with the spatial genetic pattern? When each of the alternative hypotheses specifies a set of mutually exclusive and jointly exhaustive groups (equivalence classes), as in the just postulated example, such alternative hypotheses can be tested by the appropriate use of restricted randomization techniques developed by N.L. Oden in

Sokal et al. (1986). An example will make this clear. Suppose we carry out a standard Mantel test of some variable against the grouping implied by the habitats of Figure 1a. Distances with

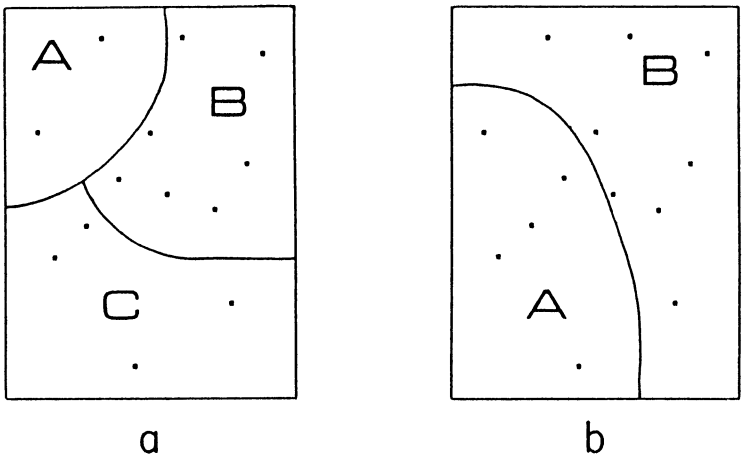

Figure 1. a. An area divided into 3 contiguous ecological regions A, B, and C. Sampling stations in each region are shown as tiny squares. b. The same area as in Figure 1a but divided up differently to represent a competing alternative hypothesis. There are only two ecological regions. A and B, by this scheme.

respect to the variable mapped onto the area studied are compared with distances implying occurrence of a pair of localities in the same or a different habitat by H_1. The complete permutation of the matrix for the standard Mantel test would test the null hypothesis that the grouping of the localities into three habitats creates no greater homogeneity within these habitats than any other arrangement of the localities. There may be, however, a competing alternative hypothesis H_2 as in Figure 1b. Suppose that two Mantel tests reject the null hypothesis of random arrangement against both alternative hypotheses. We may now carry out test (a) of H_1 as the null hypothesis against the alternative of H_2. This test involves the connection matrix of H_2 in the Mantel product, but allows permutations of points only within the groups of H_1. A test (b) of H_2 as the null against an H_1 alternative is similar.

Suppose H_1 is closer to the truth than H_2, but the null hypothesis of no spatial pattern is rejected against both alternative hypotheses because of the correlation between alternatives. In this case, we would expect test (b) to be significant but not test (a). The reverse results should occur when H_2 is closer to the truth than H_1. A pilot experiment along these lines has been carried out by Sokal et al. (1986). The approach of restricted randomization has a large, as yet unexplored, range of possibilities for hypothesis and significance testing in spatial analysis.

Significance tests. Individual spatial autocorrelation coefficients are tested using standard errors based on the expectations of their moments. Cliff and Ord (1981) have shown that both I and c are asymptotically normally distributed; significance is tested in the conventional manner. Adjustments are given by these authors for small sample sizes, and are usually built into the available computer programs. The overall significance of a correlogram cannot be evaluated on the basis of the individual autocorrelation coefficients, because these are not independent of each other. Oden (1984) developed a test for the significance of a correlogram against the null hypothesis of no autocorrelation whatsoever. He has also shown that the significance of an entire correlogram can be tested approximately using a Bonferroni or Sidak approach. After a spatial correlogram has been computed, it should routinely be tested for significance in this manner.

Two further tests are important in spatial autocorrelation analysis, but generally accepted procedures have not yet been worked out for them. These are tests of the following two null hypotheses, which concern different variables mapped onto the same set of localities and connections. 1. The spatial autocorrelation coefficients for the two variables are equal and at the same time significantly different from zero. 2. The spatial correlograms of the two variables represent the same spatial autocorrelation structure. An approach toward testing these hypotheses is currently being worked on by Neal L. Oden, based on results obtained by Wolfe (1976, 1977) and Dow and Cheverud (1985).

The issue of the reliability of correlograms obtained from surfaces is an important one in spatial autocorrelation work. Two kinds of errors should be considered. One is the subsampling error that would be observed if we were to take a single realization of n points from a surface, repeatedly subsample a number $n' < n$ points from it, and calculate correlograms based on these n′ points. If we did this, we would then have a distribution representing not only a generating function with the same parameter, but also the exact same realization. However, because the number of points would be less than the total number from which we sampled. there would be an error attached to the correlogram. This error should become greater as n′, the number of points sampled, decreases. Because one would only rarely encounter an example when this particular sampling model needs to be tested, this model of error is less useful biologically than the second type of error, realization error. Null hypotheses for most tests between correlograms in population biology involve different realizations of the same process. This is true whether the variable is different (the usual case, as in two population densities or gene frequencies), or the variable is identical (the rarer case, as when the same variable is studied at different time periods). Work estimating the relative magnitudes of these errors is currently under way in the laboratory of one of us (RRS).

APPLICATIONS OF SPATIAL AUTOCORRELATION ANALYSIS

Beyond the mere description of the spatial properties of the surfaces of variables, the methods outlined above are employed for reasoning from pattern to process. Such inferences are complicated by several difficulties. Different processes may give rise to the same pattern; two realizations of the same process may engender different patterns, and several processes may be working to produce a mixed or intermediate pattern that needs to be resolved into its components if the system is to be understood. We must be alert for these complications in the account and the examples that follow.

Inferences concerning population structure are based on the results of four procedures (Sokal 1983; Sokal and Wartenberg 1981). The first procedure is to calculate significance tests for heterogeneity of localities. These test the null hypothesis that the variable under consideration is identical in mean (or in frequency) for the set of localities being studied. For measurement data one employs analysis of variance, whereas for frequency data this is carried out by a G-test of homogeneity (see Sokal and Rohlf 1981, for a discussion of both methods). The second procedure is the computation of spatial correlograms by the techniques described above. The third procedure is the computation of similarity of spatial patterns. For those variables that show significant spatial structure, i.e., significant spatial correlograms following the methods of Oden (1984), one computes a measure of similarity of the pattern for all pairs of variables over the set of localities. To this end, product-moment correlation coefficients of all pairs of variables with each other are calculated over the localities and assembled in a matrix. The fourth procedure is the computation of similarity of significant correlograms. This can be done by computing the average Manhattan distance (Sneath and Sokal 1973) between these pairs of correlograms. Both matrices are subjected to UPGMA or k-means clustering (Sneath and Sokal 1973; Späth 1983) to detect interesting structure in the results.

Samples statistically homogeneous for one variable will usually lack spatial differentiation for that variable, permitting the rejection of some ecological hypotheses and the erection of others. Thus, homogeneity, when based on adequate sample sizes, is incompatible with adaptation to regional environmental differences or with genetic differentiation. But statistical homogeneity is compatible with an environmentally homogeneous area, or with random mating within the entire area under study. Spatial patterning in the variable may reflect the influence of a correspondingly patterned environmental variable. Alternatively, the spatial dynamics of the populations may be circumscribed in direction and/or distance, resulting in regional patterns. For example, if there are two populations that differ with respect to a given variable and one of these

populations migrates into the area of the second and interbreeds with it, the resulting spatial pattern for this variable will reflect the diffusion process. Setzer's (1985) work on aphid migration is an application of these principles.

Further inferences can be made by examining several variables for each population, studying similarities among their patterns, as well as among their spatial correlograms. Dissimilar patterns will reflect differences in the processes producing them. Examples would be differential responses by several variables to diverse environmental factors differing in spatial patterns, or migration at different rates and in different directions from several source populations. Different patterns usually result in different correlograms, but random processes, such as genetic drift, are an exception. Here, the same generating function yields independent patterns for frequencies of different genes, yet results in similar correlograms because the patterns have the same variance-autocovariance structure (Sokal and Wartenberg 1983). Variation patterns similar for two or more variables will also result in similar correlograms. Patterns may be similar because the variables concerned are functionally related. Thus dispersal patterns of seed-eating rodents and of the seedlings resulting from this dispersal should be similar. An alternative explanation for similar patterns would be responses to the identical environmental factor.

The types of inferences that can be made for ecological data have been enumerated by Sokal (1979). Homogeneity of variables of ecological interest in a study area is relatively rare, its coupling with spatially significant patterns even rarer. It could arise when observations drawn from the same population subsequently ordered themselves spatially. No such cases are known to us. Homogeneous variables that also lack spatial pattern indicate uniformity of the environment and of the source populations inhabiting it. Statistically heterogeneous variables of ecological interest will typically have spatial pattern. This may be due to differences in source populations inhabiting local areas, asynchrony of population growth among local population samples, or spatial patterning of

the resources or other environmental factors affecting the populations. The combination of statistical heterogeneity for the variables coupled with lack of spatial pattern should be the result of random settlement patterns from heterogeneous populations or random arrangement of environmental factors and resources. Similarities and differences between correlograms for different variables measured on the same population may be indicative of the differences in patterning of resources or in causation of the variables studied.

The potential range of application of the spatial autocorrelation techniques to ecology is considerable. The distance at which the correlogram first reaches $-1/(n-1)$ indicates the average distance at which the value of the variable cannot be predicted from its value at a given location. Sokal (1979) has shown that this value is related to patch size but because of the diverse shapes and distributions of patches and patch sizes in nature, the relation between this distance and patch parameters is a complex one. However, this is a subject well worth further investigation, since the underlying patch structure of much of the environment is cryptic and unknown. Inferences about patch structure must be made from biological response variables (population counts, biomass, gene frequencies). This aspect of inference is illustrated in one of the examples furnished below.

The mobility of organisms is another important ecological dimension. Whether the particular process investigated deals with dispersal and vagility or with migration of individuals or populations, the results of the process leave their record in terms of population counts and as frequencies of genetic or other markers. Spatial autocorrelation analysis also permits the testing of the observed patterns against different alternative hypotheses and the evaluation of the relative likelihoods of the separate alternative hypotheses. Although we furnish no example of such a test in this paper, relevant cases have been analyzed for large scale migration in humans (Sokal 1979; Sokal and Menozzi 1982) and for a small scale spatial data set testing alternative models in an archaeological example by Sokal *et al*. (1986).

When the variables studied are nominal or categorical, the questions addressed by spatial autocorrelation relate to the interdependence of observations. Cases in point are distributions of two or more species, the two sexes of one species (Sakai and Oden 1983), and of genotypes. Spatial patterns in such variables reveal something about the inherent populational and ecological processes of these organisms and about the spatial structure of the underlying environment that affects their distribution. We show an example in the distribution of the two sexes of *Aralia nudicaulis* below. Other examples are distributions of tree species (Sokal and Oden 1978b) and of fine structure in populations of mice (Sokal and Oden 1978b) and humans (Sokal et al. 1986).

Spatial autocorrelation takes on a special importance in ecology when one organism (say, a plant) constitutes a harvestable resource for a second organism (an animal), and the distribution of the former is nonrandom. In such a case, the autocorrelation pattern of the plant resource should influence the harvesting behavior of the animal. Such examples are likely to involve patterns in both time and space. For example, positive spatial and temporal autocorrelation of a food resource might favor site fidelity, either in the form of feeding territoriality or "trapline" behavior, in which an animal repeatedly visits a series of rewarding sites. Negative autocorrelation of resources should result in flexible behavior by the visitors: Pleasants and Zimmerman (1979) describe nectar standing crops in bee-pollinated plants as fitting a "hotspot-coldspot" pattern. Recently unvisited patches are "hot" because nectar has accumulated; recently visited patches are "cold" because their nectar has been drained. Bees forage systematically, making short flights after being rewarded at a flower, and flying longer distances after a disappointment. Thus they tend to stay in hot spots, turning them cold, and to pass over cold spots, allowing nectar resecretion to turn them hot again. Here, the foraging behavior generates and maintains the patchy resource pattern, and is at the same time well-suited for the exploitation of that pattern. The idea that foraging behavior should be responsive to the spatial distribution of the

food resource is an appealing one, but existing treatments tend to be highly informal, for want of an explicit language for describing such patterns. Spatial autocorrelation analysis can improve this situation; in this spirit, we offer two examples below, featuring two bee-pollinated species of *Aralia*. In these cases, the plants vary with respect to sexual expression, which might be expected to influence not only the foraging of the bees for pollen and nectar, but also the reproductive success of the plants.

EXAMPLES

Aralia nudicaulis. The first example is from a study of the spatial pattern of an understory plant, Wild Sarsparilla (*Aralia nudicaulis* L.) (Barrett and Thomson 1982). This is a rhizomatous perennial common to the boreal forest of North America. It forms large clones that grow by means of an extensive subterranean rhizome system. Clones are composed of aerial shoots (ramets), which can be vegetative or reproductive. Each ramet produces a single compound leaf and, if it is reproductive, a single umbellate inflorescence. *A. nudicaulis* is dioecious, each clone possessing flowers of one sex only. The study area in New Brunswick was visited during the first three weeks of June. In common with earlier observations (Barrett and Helenurm 1981), the study area in a forest site contained a larger number of males (1244) than of females (499). The pattern of distribution of the male and female ramets is shown in Figure 2. Vegetative ramets, which outnumber flowering ones by several times, are not shown in the figure.

The method of sampling the area has been described in detail by Barrett and Thomson (1982). For our purposes we need record only that the one- hectare sampling block was subdivided into one-hundred 10 x 10 m plots within each of which the position of each flowering ramet was mapped and its sex recorded. To determine fruit set without losses to frugivores, the female inflorescences were protected by nylon mesh bags after anthesis. This bagging was done only in the central 64

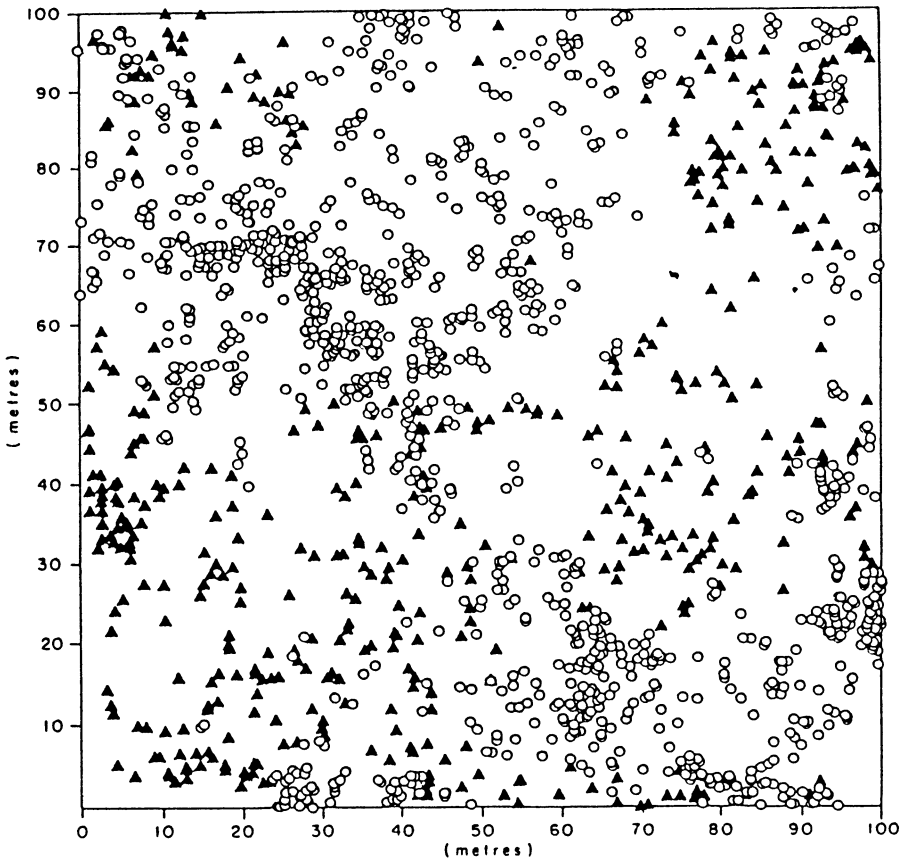

Figure 2. Distribution of male (circles; n = 1244) and female (triangles; n = 449) flowering ramets of *Aralia nudicaulis* within a 1-ha block of spruce-fir forest in central New Brunswick, June 1979. From Barrett and Thomson (1982).

quadrats of the block. When fruits were nearly ripe but not yet abscised, the infructescences were harvested. Fecundity was calculated as the number of fruits divided by the number of flowers. The unbagged infructescences were attacked heavily by animals, so that analyses involving fecundity consider only the inner 64 quadrats. Since 20 of these quadrats contained only males, fecundity could be defined for only 44 quadrats. The variables analyzed were *Aralia* density (numbers of male plus female ramets), percent female per quadrat, and three habitat variables, density of *Clintonia borealis* (Ait.) Raf. (Liliaceae), development of bracken (and shrubs), and canopy

cover (degree of tree canopy closure). *Clintonia* blooms synchronously with *A nudicaulis* in early June; both species are primarily pollinated by bumble bees. The three habitat variables were scored subjectively, using a 5-point scale.

The first analysis carried out was an examination of the randomness of the distribution pattern of the sexes. As can be seen from an examination of Figure 2, the sexes seem to be nonrandomly distributed, with clusters of each sex interspersed in the area. This question can easily be tested by means of nominal spatial autocorrelation analysis, considering males and females to be two nominal classes and calculating a correlogram of the deviations from expectation under the hypothesis of spatial randomness. Because the total number of 1743 ramets exceeded the capacity of our computer program, we drew 5 north-south transects traversing the sample area at equal intervals and recorded all plants within 0.5 m of the transect. The results for the three possible combinations and the 5 transects are shown in Table 1. In summary, male-male combinations show positive spatial autocorrelation (excess of observed over expected pairs) up to 20 m, whereas female-female combinations show significant positive autocorrelation up to 30 m (up to 60 m for transect 5). There is a large cluster of females in the eastern region of the study area (see Figure 2) so that it is easy to travel 60 m along transect 5 while still remaining within the female cluster. The male-female pairs show negative autocorrelation up to 20 m and positive values thereafter. On the basis of these findings we can show that the two sexes of this species are significantly spatially clumped. The clumps are somewhat larger for females with respect to area. In terms of ramet numbers, the clumps are larger for males, which are denser. The spatial nonrandomness of the data is corroborated.

Spatial correlograms for the six variables investigated are shown in Figure 3. We divided the distances into 10 distance classes of unequal intervals, to provide approximately equal frequencies of pairs in each distance class. We illustrate only the *I*-correlograms of these variables in Figure 3. All variables except fecundity show correlograms significantly different from the expectation of no autocorrelation by Bonferroni

Table 1. Nominal autocorrelations between sexes for 5 transects in *A. nudicaulis*.

Male-Male

	Meters									
Transect	*10*	*20*	*30*	*40*	*50*	*60*	*70*	*80*	*90*	*100*
1	+	+		-	-	-	-	-		
2	+		-	-	-			-		+
3	+	+			-					
4	+	-	-	-	-			+		-
5	+	+	-	-	-	-	-	-	-	-

Female-Female

	Meters									
Transect	*10*	*20*	*30*	*40*	*50*	*60*	*70*	*80*	*90*	*100*
1	+			-	-	-	-	-	-	
2		+	+		-	-	-	-	-	-
3	+		+	-		-	-	-	-	
4			+				-	-		-
5	+			+	+	+	-	-	-	-

Male-Female

	Meters									
Transect	*10*	*20*	*30*	*40*	*50*	*60*	*70*	*80*	*90*	*100*
1	-	-		+	+	+	+	+	+	
2	-	-	+	+	+	+		+		-
3	-	-								
4	-	+	+	+	+					+
5	-	-	+	+	+	+	+	+	+	+

Note: Entries in the table show the signs of deviations significant at $P < 0.05$.

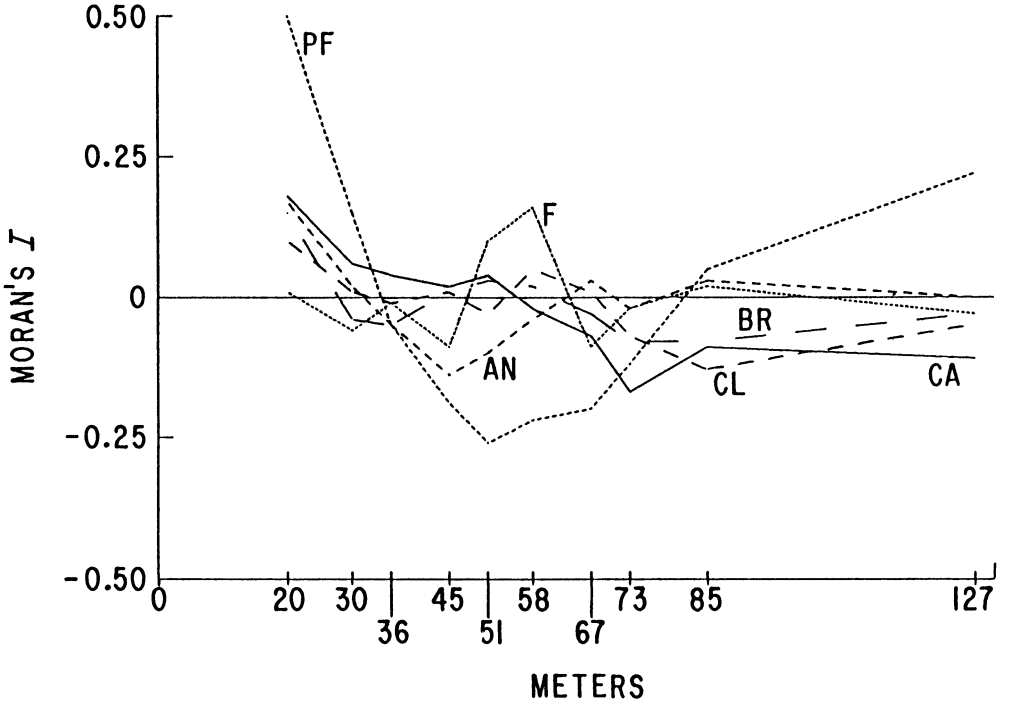

Figure 3. Spatial correlogram of 5 variables potentially related to reproduction in *Aralia nudicaulis*. Abscissa shows spatial distance in meters (upper limits of distance classes); ordinate gives Moran's *I*-coefficient. Abbreviations: AN--*Aralia* density, BR--Bracken development, CA--Canopy cover, CL--*Clintonia* density, F--fecundity, PF--percent female.

tests (Oden 1984). As is evident from the figure, the correlograms are quite dissimilar, furnishing evidence for different spatial structure in these variables. Canopy cover shows moderate significant positive autocorrelation (0.18) at 20 m and significant negative autocorrelation (-0.17) at 73 m and beyond. Bracken shows only moderate significant positive autocorrelation (0.15) at 20 m and no negative autocorrelation at substantial distances. *Clintonia* density has an even weaker local structure (0.10) at 20 m, with some negative autocorrelation at 85 m. *Aralia* density shows moderate but

significant positive autocorrelation (0.17) at 20 m, with negative autocorrelation (-0.14) commencing at 45 m but no significant patterns beyond 51 m. Percent female shows the strongest spatial pattern with highly significant substantial positive autocorrelation (0.50) at 20 m extending to distances of 30 m. Negative autocorrelation (-0.19) commences at 45 m as for *Aralia* density, but unlike that variable, continues significantly negative all the way to 73 m. Note that percent female has a significant positive autocorrelation of 0.22 at the greatest distance, 127 m, probably because females predominate in three corners of the plot and thus the majority of the largest distances possible are those with high female percentages. Finally, fecundity shows no spatial structure at all. Thus, it would appear that each of these variables, even though they may be functionally related to some degree, has its

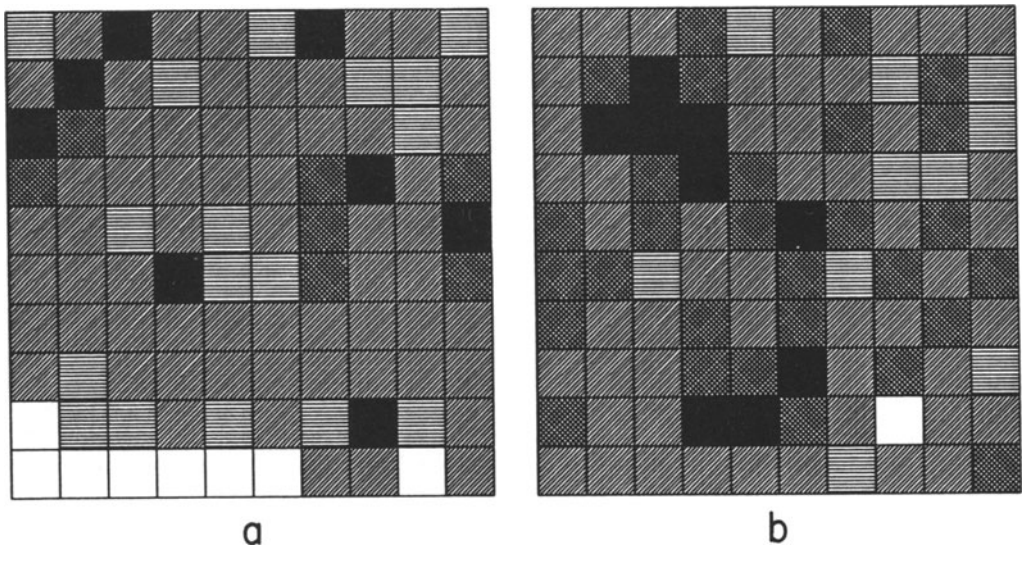

Figure 4. Values of ecological variables assessed for each quadrat in the one-hundred 10 X 10 meter plots. Shading indicates codes as follows: white--0, horizontal hatching--1, diagonal hatching--2, cross hatch--3, black--4.

own spatial pattern within the area.

In connection with our analysis of fecundity we had occasion to carry out a spatial autocorrelation analysis using only the inner 64 quadrats of the study area. To conserve space, the correlograms of this reduced data set are not shown. While the correlograms for the rest of the variables remained more or less the same, the correlogram for canopy cover changed appreciably. The reason for this change can be seen from the map for this variable (Figure 4a), where low values are found along the southern margin and there are patches of high canopy cover in the east center and in the northwest. Once the outer quadrats are removed there is little structure left in the variable, as reflected in the resulting nonsignificant correlogram. In contrast with canopy cover the amount of bracken shows relatively smooth contours from west to east, but with sufficient noise so as not to be a clearcut cline (Figure 4b). There is only the moderate significant positive autocorrelation at 20 m. This value was not changed by reducing the data matrix to the inner 64 quadrats.

The lack of similarity among correlograms is borne out by the lack of correlations among the variables over the area. The only even moderately sized correlation of real interest is between percentage female and *Aralia* density (-0.45). This occurs apparently because females are more sparsely distributed than the males, as can be seen in Figure 2. This in turn may be due to a higher flowering rate of the males; the overall ramet densities may be similar, if non-flowering ramets were taken into account. There is a weak correlation (-0.23) between *Clintonia* density and *Aralia* density. It is not surprising to find low correlations between these variables in view of the lack of similarity of the correlogram. However, it would have been possible for variables to be highly correlated yet show no spatial structure, as pointed out by Hubert et al. (1985). Multiple regression analysis of fecundity on the other ecological variables showed that only one variable seems to be affecting fecundity in any way--canopy cover with a negative effect on fecundity.

The data were also examined by pairwise Mantel tests of

various variables against spatial distances, and by multiple Mantel tests. We first examined pairwise relations between distances with respect to percent females, fecundity and *Aralia* density for the subarea reduced to 64 quadrats. *Aralia* density and percent female versus fecundity have nonsignificant and low correlations. The relationship between percentage females and *Aralia* density is marginally significant and yields a coefficient of 0.087. This confirms the earlier findings with respect to the negative correlation of *Aralia* density and percentage females. It must be remembered that in the Mantel analysis we are not dealing with correlations of variables but with correlations of distances between pairs of localities. Thus the new result informs us that localities that differ with respect to *Aralia* density also differ with respect to percentage females.

The multiple Mantel results are all based on residuals from multiple regression of spatial distances and distance matrices for *Aralia* density, fecundity, and percent females on distance matrices for canopy cover, bracken and *Clintonia* density. The residual matrices for spatial distances are paired with those for *Aralia* density, fecundity and percent females. Here the results are more clear cut. *Aralia* density is independent of space, as is fecundity, once the other three variables are kept constant. This is not surprising for fecundity, which showed no spatial structure at all. But apparently *Aralia* density also shows no further spatial pattern, once it is regressed on canopy cover, bracken and *Clintonia* density. Percent females, however, continues to show a clear spatial pattern, with a highly significant partial correlation of 0.150 for space versus percent females, the three habitat variables kept constant. This means that whatever factor determines female ramet production has a clear spatial pattern, not determined by either canopy cover, bracken or *Clintonia* density.

Barrett and Thomson (1982) measured fecundity because it seemed reasonable that the pollination process might be affected by the spatial patterning of the habitat variables or of the sexual morphs of *A. nudicaulis* for pollinators; dark shade from the tree or shrub layer might discourage pollinator flights;

pollinators might feed preferentially in areas of high *Aralia* density; they might prefer male plants for their pollen reward; or the pollination of females near the interior of large female clones might be limited by the lack of local pollen sources. In fact, however, none of these effects was strong enough to influence the spatial patterning of fecundity in a detectable way; the reproductive output of female ramets appeared to be independent of all the measured variables, which in turn suggests that fecundity may have been limited more by resources than by insufficient pollination.

The autocorrelation analysis does, however, economically describe the pattern of males and females in statistical terms. Table 1 is a summary of the main patterns evident in Figure 2: the large size of the (presumably clonal) patches, the larger size of the female patches than of the males, and the variation in patch sizes within a sexual type (as shown by the disparity among the transects). Similarly, the correlograms of Figure 3 abstract the spatial information content of the habitat variables. Although analysis of the interrelations of the variables gave mostly negative results, some inferences about process are still possible. For example, the persistence of clear spatial pattern in percent females, after the removal of all the habitat variables, is probably best attributed to the history of clone establishment. Indeed, there is reason to believe that the long-lived clones of A. *nudicaulis*--and possibly even some of the existing ramets (Bawa et al. 1982)--antedate the present forest, which has grown up since being clear-cut in 1940.

Aralia hispida. The second example comes from an investigation of bee foraging behavior on *Aralia hispida* (Thomson, Peterson, and Harder 1986). *A. hispida* plants are hermaphroditic, unlike those of *A. nudicaulis*, but their sexual functions are separated in time, rendering the plants "temporally dioecious". They bear numerous small flowers in inflorescences comprising several orders of umbels. Within each order of umbels, the flowers open synchronously; thus, flowering begins with a single primary umbel. After all of its flowers have opened and completed their function, the several secondary

umbels open in synchrony, then the tertiaries, etc. Larger plants commonly have three orders; four is very rare. All flowers open in a male or staminate condition, offering both nectar and pollen to insects. After all the flowers of an umbel have opened, shed their pollen, and stopped secreting nectar, a subset of them enter a female phase. In the female phase, the five previously connate styles separate, the stigmas become receptive, and nectar secretion usually resumes. Thus *A. hispida* is andromonoecious, i.e., it bears perfect flowers (with temporally separated male and female phases) and male-only flowers. The proportion of perfect flowers declines with increasing umbel orders, so the proportion of male-only flowers increases through time. As a consequence of the synchronized sexual changes within each order of umbels, a typical plant undergoes a series of temporal switches from male to female, one alternation per umbel order. The male phases last longer than the female phases--approximately 4-6 days and 2-3 days, respectively, depending on weather and on the clone. Thomson and Barrett (1981) give details on the temporal patterns of gender expression.

Furthermore, *A. hispida*, like *A. nudicaulis*, forms clonal patches through rhizomatous spreading, and the plants within a clone usually bloom in synchrony, such that all are male at the same time, then female at the same time, promoting outcrossing. This clonal synchrony should produce a pattern that, at any point in time, resembles that of *A. nudicaulis*--male and female patches--but is unlike that of *A. nudicaulis* in that the gender of the patches is continually changing. The sex ratio of a grid square would be expected to show temporal cycles if the area is dominated by a single clone or multiple clones that are in synchrony. If a square contains multiple clones that are out of synchrony, temporal patterns in sex ratio may be blurred. A stand of *A. hispida* was divided into 2 m squares and the boundaries marked by spray-painted lines. On three dates (10, 14, and 18 July 1984) during the *A. hispida* bloom, the numbers of open flowers in each square were counted. Flowers were either male or female, depending on their developmental stage. Numbers of male and female flowers and percent female flowers

were recorded for each square

In addition, a pollinator removal experiment was carried out as follows. Numerous bumble bee workers, of several species, were caught while feeding on *A. hispida* in the grid and given individual paint markings. These bees typically maintain small foraging areas that are stable for several days (Thomson, Maddison, and Plowright 1982; Thomson, Peterson, and Harder 1986). To determine whether bees would shift their foraging areas toward local areas of lowered competition, Thomson et al. (1986) performed the following experiment on 17 July 1984. During the morning, four *Bombus ternarius* workers were followed as continuously as possible, and the time spent by each bee in each grid square was recorded. Beginning at 1250 hours, all other bees that appeared in the northeast quarter of the grid were removed, while the four bees remained under observation for the rest of the day. Thomson et al. (1986) concluded that all four bees, as expected, shifted their foraging areas toward the removal area, and also rejected fewer umbels than control bees foraging elsewhere, an indication that the experimental bees were able to forage more efficiently following the reduction of competition (rejections indicate that an umbel has recently been drained of nectar).

The correlograms for *A. hispida* are shown in Table 2 for the three variables studied, separately for the three dates. For July 14, the correlogram has meaning only up to 24 m because only an 8 x 10 grid was censused. For number of male flowers on 10 July, there is moderate spatial structure with significant positive autocorrelation (0.19) at 4 m, and a weak, but significant negative trend at 16 m. On 14 July, there is significant positive autocorrelation (0.16) at 4 m, an appreciable negative value (-0.10) at 16 m and a significant positive autocorrelation (0.13) also for the last distance class (24 m). On 18 July the correlogram is not unlike that on 10 July. For number of female flowers on 10 July there is stronger autocorrelation (0.29) at 4 m, with weak but significant negative autocorrelation (-0.04) again at 16 m. One can conclude that there are relatively small patches with respect to numbers of female flowers with the change from positive to

Table 2. Spatial autocorrelation coefficients *I* for three flower census variables in *A. hispida* on three dates in 1984.

	Distance classes in m									
	4	**8**	**12**	**16**	**20**	**24**	**28**	**32**	**36**	**46**
Number of male flowers in bloom										
10 July	.19***	.01	.00	-.04*	-.02	.00	-.04	.01	.00	-.01
14 July	.16***	.01	-.06*	-.10**		.13**				
18 July	.17***	-.04*	-.02	.00	-.04**	.03	.01	.02	.00	-.02
Number of female flowers in bloom										
10 July	.29***	.02	.00	-.04**	-.02	-.02	-.03	-.05	.02	.02
14 July	.09	-.06	-.01	-.04		.08				
18 July	.17***	-.01	.01	-.01	-.02	-.02	-.03*	-.03	.01	.00
Percent female flowers in bloom										
10 July	.28***	.10***	-.01	-.06**	-.03	-.03	-.05	-.03	-.02	-.04
14 July	.03	.04	-.08*	-.06		.16*				
18 July	.14***	.00	.05***	.05**	-.06**	-.05*	-.06*	-.06*	-.05	-.04

Notes: Distance classes are identified by upper class limit only.

* $0.01 < P \leq 0.05$
** $0.001 < P \leq 0.01$
*** $P \leq 0.001$

negative autocorrelation taking place between 8 and 12 m. On 14 July no significant spatial structure is shown and on 18 July there is a pattern similar to that of 10 July for female flowers as well as to that of 18 July for male flowers. For percent female flowers in bloom, there is clear spatial structure on 10 July--significant autocorrelations (0.28 and 0.10) at 4 and 8 m,

respectively. Weak significant negative autocorrelation (-0.06) appears at 16 m. On 14 July there is weak negative autocorrelation (-0.08) at 12 m and an appreciable positive value (0.16) at 24 m. The data argue for a change to negative autocorrelation between 8 and 12 m. For the last census date (July 18) spatial autocorrelation at 4 m is 0.14. There are some significant weakly positive autocorrelations, at 12 and 16 m, and weakly negative values between 20 to 32 m. For this date it is not too clear at what distance positive autocorrelation ceases.

There is also a temporal structure to the gender patterns, as expected from our knowledge of the flowering biology of the plants. This emerges clearly when we compute appropriate multiple Mantel tests in the manner of Smouse et al. (1986) as partial correlations of the surfaces of percent females at the two dates with spatial distance kept constant. Between 10 July and 14 July, there is a negative partial correlation (r = -0.506, $P \leq 0.008$, but between 10 July and 18 July, the partial correlation of percent female is positive (r = 0.161, $P \leq$ 0.008. As would be expected, the correlation for 14 July and 18 July is also negative in sign (r = -0.217, $P \leq 0.008$). The alternation of negative and positive correlations through time is due, of course, to the synchronized gender shifts of the clones of *A. hispida*. There are various reasons why any particular 2 x 2 m square might not show gender cycling in this analysis. First, the square may contain two or more clones that are out of synchrony, such that some turn female as others turn male. In this case, little change in percent female would be apparent at the scale of the spatial sampling unit, although such changes are occurring within each plant contained in the sampling unit. Second, the four-day census interval may be shorter than the length of a given plant's gender phase. For instance, if a clone is male for five days, and if it has just turned male at the first census, it will still be male at the second census four days later. Because the male phases are several days longer than the female phases (Thomson and Barrett 1981), we would predict that squares with high values of percent female flowers on one census would be highly likely to yield low

values on the succeeding census, whereas squares with initially low values would often remain low, i.e., continue in the male phase for four days. This effect shows up very clearly in the scattergrams; there are virtually no squares that are predominantly female on consecutive censuses, but many that are predominantly male. Detection of the cyclic nature of gender in the *A. hispida* stand thus depends on a double correspondence of our sampling units with the scale of the variation. The spatial sampling units (2 x 2 m) had to be small enough to fall inside the patch size as revealed by spatial autocorrelation, and the temporal sampling units (4 day census intervals) had to correspond to the length of the gender phases. Had the censuses been eight days apart, our analysis would be blind to the existing variation.

The small-scale shifts of gender should have consequences for the bees that collect nectar and pollen from *A. hispida* flowers. The autocorrelational properties of pollen and nectar are conspicuously different. Both are patchily distributed in space, with similar, small patch sizes produced by the synchrony and spatial contiguity of clone members. The temporal distribution of nectar at any one patch will show positive temporal autocorrelation, because both sex phases produce nectar and because a patch with many flowers at one census is likely to have many flowers at the next census. Thus, bees might be expected to be conservative in their feeding locations, and to return repeatedly to flower-rich areas. They do this (Thomson et al. 1982).

The distribution of pollen, unlike that of nectar, will show strong negative temporal autocorrelation at short time intervals and strong positive temporal autocorrelation at longer intervals. A good spot for pollen collecting, therefore, will not remain a good spot for long. The spatio-temporal exigencies of pollen collection would then be expected to counter the conservative foraging-area tendencies favored by the nectar distribution; given that bees do maintain small foraging areas, we would expect that these areas should be larger than the spatial patch size so as to encompass numerous clones, or that the bees should move their foraging areas through time to track

the shifting locations of resource-rich patches. Both appear to be the case: the surfaces for 18 July (the census date closest to the removal experiment) indicate X-intercepts of 8 m for both male and female flower members. At that distance on the average, the numbers of each gender were independent to slightly negatively autocorrelated. It appears that the average diameter of the patches of high (and low) numbers of each gender is 4 m. Frequency distributions of the time spent in each grid square by individual bees (Figure 5) permit an estimate of the average side length of the visited area (described as a quadrilateral). For the four bees these estimates are 4.5, 6.5, 7.5, and 9.0 m, all greater than the patch diameter of the flowers. The moving of bees to less competitive areas has been demonstrated by

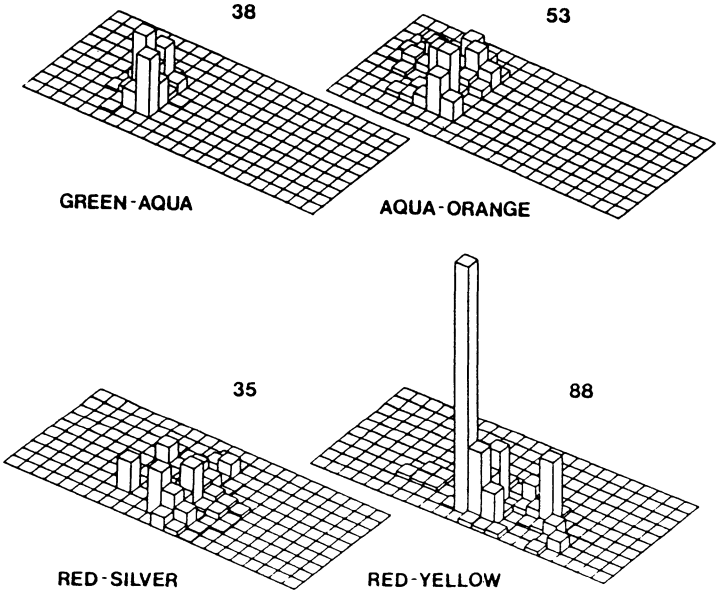

Figure 5. Representation of the use of space for foraging by four color-marked *Bombus ternarius* workers in a 20 X 44 m mapped stand of *Aralia hispida* on 17 July 1984. Heights of the vertical bars are proportional to the total amount of time spent by a bee in each 2 X 2 cell of the grid. The total observation time (min) is shown for each bee; in all cases, several different foraging trips contribute to the total. These observations were made after the bee removal experiment described in the text. From Thomson et al. (1986).

Thomson et al. (1986).

These autocorrelation analyses paint very different pictures of the two *Aralia* species. Both present a spatially patchy gender surface, but in *A. nudicaulis* the patches are large in size and stable in nature throughout the 2-3 week blooming period. In contrast to this rather calm surface, the gender surface of *A. hispida* is vividly dynamic, changing its character over the space of a few meters and the span of a few days. Clearly, these two congeneric plants of the North Woods present very different problems in resource tracking to their pollinators. We hope that our presentation of these examples will stimulate others to explore the usefulness of spatial autocorrelation techniques in describing patterns and inferring processes in ecology.

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