

## THE MEASUREMENT OF HORIZONTAL PATTERNS IN VEGETATION: A REVIEW AND PROPOSALS FOR MODELS

G. Bouxin, rue des Sorbiers 33, B-5101 Erpent, Belgium

**Keywords:** Horizontal pattern, Distance, Models, Monospecific, Non-parametrical tests, Plurispecific, Sampling, Vegetation

**Abstract.** General reviews of the concepts of pattern, of sampling methods, of the problems of scale and of the models for pattern analysis of grid and distance data are first presented. Models are then proposed. Tests for monospecific patterns, a sequential model associated with multivariate analyses for multispecific patterns, least-squares mapping associated with a distance technique, and complementary tests for distance patterns are presented. A discussion of future directions in pattern analysis concludes the text.

### Introduction

Phytosociological associations and other community-types are described by means of the species composition of vegetation - and concurrently or alternatively by environmental, physiognomic, structural or other characteristics - but with always the same objective of analytically superposing biotic and physical characteristics of similar dispersions. Pattern analysis is a fundamental tool of this, most obviously in vegetation studies concerned with the ground arrangement of plants.

There are many techniques to identify horizontal patterns. I attempt to organize these and describe them in a systematic manner. However, I do not plan to cover all techniques of pattern analysis, only a concise treatment of typical methods used for identification of pattern in the horizontal arrangement of plants. I will consider the concept of pattern, problems of scale, and sampling methods. A large part of the paper is on common mathematical models. The problems linked to pattern recognition are several: How to define pattern? What are the components? Which sampling frame is to be used? Which technique is suitable for a specific objective? Which null hypothesis is appropriate? What is the place of pattern analysis in vegetation study? I attempt to answer these questions in the sequel.

### Concepts of pattern

Pattern as used here is concerned with the horizontal dispersion of plants. Simply defined in Kershaw (1964) it is the spatial arrangement of individuals of a species. In Greig-Smith (1979) pattern is a state of the arrangement when it departs from randomness, with the latter regarded as the exception, irrespective of area size. In some circumstances, Greig-Smith (1979) speaks of 'distribution pattern', in others, 'spatial heterogeneity'. Pielou (1977) observes frequent confusion in this usage of 'distribution' and 'arrangement' which, she warns, must be avoided. According to her, 'distribution' should be used in its statistical sense, restricted to the

states of a variate which have a distribution, but not applied to describe the ground pattern of organisms which may form clusters, patches, clumps, aggregates, etc. Others give more general definitions. For example, Orłóci (1988) considers pattern as the manner of arrangement in space/time applicable to objects and relationships. Upton and Fingleton (1985) defines pattern as the zero-dimensional characteristic of a set of points which describes point locations in terms of the relative distances of one point to the next.

To Pielou (1977), two distinct features of pattern are important: intensity and grain. 'Intensity' is the extent to which density, or some other property, varies from place to place. In a pattern of high intensity the density differences are pronounced, that is, dense phases alternate with sparsely populated zones. When intensity is low, the density contrasts are slight. 'Grain' has to do with the size of the pattern units (clumps or patches) and is independent of 'intensity'. Some studies focus on 'grain' (Forgeard and Tallur 1986), leaving other features of pattern unexplored. It is to be noted that only simple patterns, such as aggregates, clumps, are completely defined by intensity and grain. Mostly, pattern is more complex and the notion of grain vanishes. For an efficient definition, a complex pattern requires description of its intensity as well as type, such as aggregate, clump, gaped, density variant, gradient type or a complex of these.

The pattern concept has been extended to environmental variables for which Kershaw (1958) and others (see Greig-Smith 1983, p. 88 et seq.) applied the methods of monospecific pattern analysis. The concept of pattern is, however, not limited to monospecific populations. It also applies to clearly defined community units such as associations, forest types, and other groupings. A multispecific pattern exists when two or more species have similar dispersions. In all cases, the pattern observed depends on the ground scale used, i.e., the sampling unit size and the area sampled. Multispecific pattern is especially sensitive to the scale effect. The

concept of multispecific pattern is important in phytosociology, since it provides a rigorous base for the definition of communities.

The study of causal factors and mechanisms are very important to understand pattern. However, this field will not be reviewed beyond reference to work presented in Bouxin and Gautier (1979, 1982), Duvigneaud (1983), Gimingham (1978), Greig-Smith (1979), Kershaw (1964), Pielou (1960 and 1961), Phillips and MacMahon (1981), Upton and Fingleton (1985), Watt (1947, 1981a, b), and Yeaton and Cody (1976) who treat the topic.

### Sampling for pattern

To characterize completely the sampling procedure, one must state the size and shape of the sampling unit, the type of recorded data, and the characteristics of the sampling frame. Different kinds of sampling units, data and frame have been used in pattern analysis. In the simplest case, the sampling units are equivalent to discrete habitable sites (Pielou 1977), such as the tree branches on which some caterpillar nests. Each branch constitutes a natural sampling unit. This case does not occur frequently in vegetation work, although the dispersions of the parasitic Loranthaceae represents an analogous example. Others include epiphytic plants (moss, lichen, fern, orchid, or other). The site is always a map locality where parameters are recorded.

Upton and Fingleton (1985) emphasize the difference between point pattern and quantitative data. For example, point patterns are usually analyzed based on counts within quadrats. Patterns of other types, such as spatial correlation pattern, usually use quantitative data in which the individual values (states a variable) are associated with fixed localities in logical progression, such as on a transect.

The quadrat is the most frequently used areal sampling unit; numerous examples for its use are mentioned by Chessel and Gautier (1984). Generally, it is square shaped. One plant organism can cover several neighbouring quadrats, which is not necessarily a drawback if the morphological properties are known. Using quadrat as the unit, many variables can be scored or measured: presence-absence, density (organisms, stems, shoots) cover, dry biomass, mean diameter, mean length of stems, fruit weight, number of leaves, leaf length, leaf width, soil depth, topography, water table level, salinity, ionic ratio, and many others such as, for instance, visual estimations of abundance-dominances (see also Chessel and Gautier 1984).

The sampling unit may also be a point, a pin or a line segment. Kershaw (1958) used point quadrats for taking contiguous cover readings along a transect. With a frame, the readings are taken at intervals, sometimes as small as 1 cm along a transect. Examples and simplified variants are described in Anderson (1961), Bouxin (1974), Corre and Rioux (1969), Forgeard and Tallur

(1986) and Poissonet (1969, in Chessel et Gautier (1984). Recordings based on points, crosshairs, or needles, may seem tedious, but are adaptable to rather large surveys as shown by Bouxin (1975). Line segments are also used by many (e.g. Lecompte 1973, Thiébaud 1976) to record different types of data. With points, presence data are obtainable. In addition, from a point distances can be measured to the first, second, third, or  $n^{\text{th}}$  nearest neighbour plant (Thompson 1956). The point may stand free or be defined as the center of stem (Galiano 1982b). With a pin, contacts with plant parts are counted but the number of contacts is influenced by the diameter and the inclination of the pin, and of course, by the wind (Goodall 1952, Gounot 1969, Kershaw 1958 and Warren Wilson 1959). The technique called "specific contact contributions" allows accurate description of the vertical vegetation structure, especially in heathland (Forgeard and Tallur 1986).

It is now clear that random siting of the sampling units is not well adapted to pattern analysis (Chessel 1978, p. 53). The intensity of pattern can be estimated, but nothing precise can be deduced about the type of pattern. Indeed, the variability of density is affected by quadrat siting. With random sampling, the portion of information due to relative position or distance vanishes. Random selection of quadrats is common (e.g., Heltshe and Ritchey 1984). A method of quadrat siting was developed by the Braun-Blanquet school for typification, but not recommendable for analysis of ground pattern.

The most classical sampling design for pattern analyses uses a grid of contiguous quadrats. In some methods (e.g. Greig-Smith 1952) the number of quadrats is a power of two. The rectangular grids and narrow transects of various sizes are also used. The repetition of the same sampling frame in neighbouring sites gives results less dependent on the site location or on the starting point. Many modifications are possible. For example, a linear application is found in Bouxin and Le Boulengé (1983) along a 22 km stream divided into 182 contiguous sections. Patterns are also definable with irregularly spaced quadrats or points, provided that the position of the sampling units is mapped. However, in the latter, pattern type and intensity are not so clearly defined as with regularly placed quadrats. Bouxin (1983) presented an example of savanna vegetation. The random placing of points for cover or distance measurements is no more recommended than the random placing of quadrats. In addition, the accurate placing of points in dense forest vegetation is very difficult. Pielou (1977) pointed out that one cannot obtain a random sample of the individuals in a population by selecting those that are nearest to random points. The latter procedure gives a biased sample in which relatively isolated individuals are over-represented. Regular placing of points along lines is preferred. In vegetation with re-

cognizable plant individuals (analogous to points), such as the annuals, most shrubs or trees, the organisms' locations are easily mapped (see least-squares methods in Rohlf and Archie 1978), possibly based on aerial photographs and a coordinate digitizer (Franklin et al. 1985). Forest mapping of tens of hectares or more is now possible. However, precaution must be taken as regards the growth patterns of some plants which result in the overlap and fusion of separate individuals to form a clump that cannot be distinguished from that produced by a single individual (Cox 1987). The inability to distinguish intimately fused individuals creates a bias toward perceiving uniformity, such as in the techniques of dispersion analysis based on theory relating to the dispersion of dimensionless points.

### Problems of scale

In analyses of pattern over small areas, it soon becomes evident to the observer that the conclusions could be dependent on the size and sometimes on the shape of the sampling area and unit. Greig-Smith (1964) gave an example with a map showing patches of higher density imposed on a general dispersion pattern at lower density. When this map is sampled with quadrats of varying sizes, the results show that the pattern appears to be random with small quadrats and with large quadrats, but non-randomness appears with quadrats of intermediate sizes.

Regular pattern cannot be detected with very small quadrats. In general, the larger the quadrat, the more distinct the departure from random expectation will appear, up to a point. Indeed, as quadrat size approaches the size of the patches, or the lacunae, the variance relative to the mean will rise sharply. The real problem is, of course, not the detection of non-randomness which is general, but the detection of the scale or scales at which non-randomness occurs. So it becomes possible to relate some environmental factors to the scales of the detected non-randomness (Kershaw 1964). The problem of scale logically led to the analysis of grids of quadrats, and to forms of geometrical sampling. Considering only the phanerogams, patterns have been revealed at much varying scales, starting from several centimeters (as for annuals) to large geographical areas. Examples are found in Bouxin (1975, 1976, 1977 and 1983), Bouxin and Gautier (1979, 1982), Bouxin and Le Boulengé (1983), Chessel and Donadieu (1977), Greig-Smith and Chadwick (1965), Lamont and Fox (1981), Mott and McComb (1974).

### Models for pattern analysis

Most approaches to the problem of pattern analysis refer to detection and measurement of the departure from randomness. A standard method consists of relating an observed number of individuals per quadrat to

the expected number derived from the Poisson series. A distribution is said to be Poisson when individuals are random dispersed in the available environment. Pattern may depart from random by being contagious when individuals are clumped together, or regular when individuals are scattered evenly on the ground. For these pattern types, the terms overdispersed and underdispersed were used, which lead to confusion (Greig-Smith 1964). The analytical scheme is classical: in a set of randomly placed quadrats, the number of individuals is recorded and the observed distribution is compared to the Poisson. Indices may be calculated and tested against the null hypothesis of random dispersion. Examples are found in Abernethy (1958), Ashby (1935), Blackman (1942), Clapham (1936), David and Moore (1957), Fracker and Brischle (1944), Lefkovich (1966), McGinnies (1934), Numata (1949 and 1954), Upton and Fingleton (1985) and Whitford (1949). Indices of aggregation, calculated from data obtained by sampling with quadrats of one size, are all measures of pattern intensity, such as Lloyd's (1967) index of patchiness, Morisita's (1959) index of dispersion  $I$ , or David and Moore's (1954) index of clumping. The deficiencies in the tests were clearly pointed out by Mead (1974): 'First, arising partly out of the difficulty of specifying realistic nonrandom patterns, the behaviour of these various test statistics under alternative hypotheses of nonrandom arrangements of plants is usually only intuitively understood. Secondly, and more seriously from the ecologist's point of view, the tests can only detect patterns of one scale'. It is ironic that pattern analysis had to be dominated by the triumvirate of concepts: random, regular, contagious. All knows that random and regular dispersions are uncommon.

Upton and Fingleton (1985) explored alternative patterns, but they encounter only a limited number. Among them, the generalized and compound distributions have been propounded. With generalized distributions, it is supposed that groups or clusters of individuals constitute the entities having a specified pattern and that the number of individuals per group is a random variate with its own probability distribution. Two distributions are well-known: Neyman type A or Poisson-Poisson, and the negative binomial or Poisson-logarithmic. With compound distributions, the expected number of individuals varies from unit to unit. An example is the Pearson type III distribution. Information about compound distributions can be found in Gérard (1970) and Pielou (1977). Once aggregation, or contagion, is detected at one scale, then it is likely to be present on numerous scales in any one site. Kershaw (1964) pointed out that the mathematical parameters employed to define the distribution and generate the series have no ecological meaning, or at least it is impossible to relate known ecological factors to these parameters. The preceding approaches are therefore of

little use for the ecologist.

Historically, the sampling technique is a key step in the methodology of pattern analysis. A grid of contiguous quadrats is used by Greig-Smith (1952). In this, each side of the grid is divided into a number of units, which is a power of 2, and the number of individuals per grid unit (block) is counted. An analysis of variance of the data is performed, the variance partition being nested between the different blocks. The pattern graph relates the variance to block size. The different scales of pattern appear as peaks. The block size at these corresponds to the mean area of the clumps. Many examples and references were given by Greig-Smith (1979) who applied the method to plants (with densities, frequencies, cover estimations, dry weight) and to environmental variables (exchangeable soil cations, % clay or silt, soil depth). The confidence limits for the variance/mean ratio were derived by Thompson (1958) and used by Greig-Smith (1961, 1964), but the presence of high aggregation or a large number of empty quadrats in a grid are conditions which prohibit the use of these limits. Finally, the division by the mean produces non-independent statistics of the different block sizes (see Mead 1974 and Chessell 1978). This however did not impede the use of variance/mean analysis in many applications by Erschbamer et al. (1983), Greig-Smith (1979) and Matlack and Good (1989). Greig-Smith (1979) explains the necessity of multiplying the grids to support the analysis. The form of the graph is the main feature of evaluation. In addition to the variance/mean ratio, I mention Morisita's (1959) index of dispersion, calculated for a series of different quadrat sizes. A transformation of the index to a standardized distance was based on a 95% confidence envelope. Peaks in the graph correspond to the scales of pattern in quadrat size units. Recent applications are found in Bowman (1986), Gill (1975), Lamont et al. (1981), Read and Hill (1985) and Williamson (1975). Orlóci (1971) developed another method in which he partitioned information. The data are counts of individuals in successive quadrats in a belt and the partitioning is nested with blocks of different size. Suzuki (1960, 1966) and Yarranton (1969) have described methods relating the quantity of a species in quadrats along a linear sequence to the distance traversed. Thiébaud (1976) studied the horizontal structure along lines, using the calculation of information in relation with the dispersion of species.

Beside the drawbacks of a hierarchical analysis of variance, several criticisms have been leveled against the nested arrangement of blocks, which may lead to ambiguous results in case of regular patterns. The limitation of block sizes to successive powers of two and the dependence of results on the starting point of the grid or transect are other criticized points. To free pattern analysis from some of these problems, Hill (1973) proposed a two-term local-quadrat method, which per-

mits the calculation of variance at block sizes no longer limited to powers of two. An improvement was suggested by Galiano (1982a) who used the 'new local variance'. This allows the accurate detection of the diameter of clumps. A Monte-Carlo simulation allows the testing of the null hypothesis and the estimation of confidence intervals (Galiano et al., 1987). Usher (1969, 1975, 1983) proposed a stepped blocked-quadrat variance method, in order to avoid the dependence of results on the starting point of blocking. Goodall (1961) introduced a minimum interspace between quadrats to avoid spurious correlations between adjacent quadrats through overlapping individuals, and later (Goodall 1974), a random pairing of quadrats at specified distances. He considered that the variance had to be referred to mean spacings between quadrat centers rather than to block sizes but the distribution of his statistics is in general incorrect (Zahl 1978).

Ludwig and Goodall (1978) proposed yet another method called paired-quadrat variance. I believe that the effect of the starting point on pattern description has little practical consequence, except with very regular patterns but such patterns are uncommon and often visually detectable. This problem will be considered in the following sections. The methods of paired quadrats also suffer of serious drawbacks: for the different spacings, the variances are calculated with only one quadrat size and so an important part of the variability remains unexplored! With the paired-quadrat or the stepped blocked quadrat methods, the variances at different quadrat spacings or block sizes are not independent, which is considered of lesser concern for strictly exploratory purposes by Ludwig and Goodall (1978). In addition, the paired- or blocked-quadrat methods are liable to give aberrant results with data including a high proportion of empty quadrats.

Alternative forms of test were proposed by Mead (1974) to overcome the lack of definition for different kinds of pattern. The possible kinds are certainly very numerous and associate with mechanisms all of which are difficult to characterize mathematically. Mead considers a grid of contiguous quadrats which can be grouped and arranged in a hierarchy. At each block size, he asks: 'Is the division of each block total into two half-totals random?' or 'Given the scores at any particular scale in the hierarchy are totals compatible with random pairing?'. The tests take a divisive or agglomerative hierarchy. The problem of the starting point with Mead's '2 within 4' randomization test was studied by Upton (1984) who used a normal assumption to obtain a chi-square approximation which combines the information from all possible starting points. The same procedure adapts naturally to cases where information is combined from separate transects.

An important step for the description of spatial patterns is the development of non-parametrical models

(see Chessel 1978, 1979, 1981, Chessel et al. 1973a, b, 1974, 1975, 1977a, b, 1978, 1984, Debouzie et al. 1975 and Gautier 1979). In these models, the observed dispersions are contrasted to sets of other possible dispersions which all are equiprobable a priori. The random assumption is the starting point in a process of data handling. The objective is not the rejection of an unrealistic hypothesis, but the determination of the alternative. A non-parametric model is thus a collection of dispersions with a uniform probability distribution and a group of random variables. The models are based on the equiprobability of

$$\binom{N}{M} = \frac{N!}{M!(N-M)!}$$

possible dispersions of  $M$  presences in a transect or a grid of  $N$  quadrats or points (presence-absence model);

- the  $N^P$  assignments of  $P$  objects to  $N$  quadrats (density model);
- the  $N!$  permutations of numerical data (permutation model).

Three variabilities are measured:

- the overall variability, characterizing differences between contents of blocks;
- the fixed-scale variability, linked to differences between two contiguous blocks of the same size, and
- the local variability, measuring heterogeneity between units in the same block.

With these, one is almost at a complete definition of spatial pattern. The overall variability identifies the pattern type; the fixed-scale variability permits the estimation of pattern intensity (the indices linked to both kinds of variability generally give similar results), and the fixed-scale variability depicts locally regular dispersions. Many statistics have been described and applications presented. Phytosociological applications with the presence-absence model are given in Bouxin and Le Boulengé (1983) and Bouxin and Gautier (1979, 1982). Other non-parametric tests exist. The number of runs (Gounot 1969) is an example, but applications are possible for one pattern scale only (Bouxin 1974).

Attention must be drawn to spatial autocorrelation: this is the property that a set of mapped data possesses whenever it exhibits an organized pattern (Upton and Fingleton, 1985), or, as Cliff and Ord (1981) describe it, whenever there is 'systematic spatial variation in values across a map'. This definition stresses 'values' and not positions. One is concerned with patterns in the values recorded at locations, as opposed to pattern in location per se. A number of separate statistics have been developed but an unifying statistic can be presented in terms of the general cross-product statistic (Upton and Fingleton, 1985, p. 154):

$$r = \sum_i \sum_j W_{ij} Y_{ij}$$

Here  $W_{ij}$  is a measure of the spatial proximity of locations  $i$  and  $j$ , while  $Y_{ij}$  is a measure of the proximity of  $i$  and  $j$  on some other dimension. The term  $W_{ij}$  is the element in the  $i^{\text{th}}$  row and  $j^{\text{th}}$  column of the matrix  $W$ .  $Y_{ij}$  occupies the same position matrix  $Y$ . Several definitions of  $Y_{ij}$  were propounded. Correlograms (or tables) are constructed to show how autocorrelations change with distance. First, distance has meant time distance, but correlograms were adapted to spatial distance. Applications of spatial autocorrelation in ecology can be found in Sokal and Thomson (1987). Legendre and Fortin (1989) show with examples how correlograms provide a description of the spatial structure. Spectral analysis (Ripley 1978) is a comparable technique which uses the periodogram. It has been widely used by statisticians, economists and engineers with data consisting of observations at constant time intervals. The idea is to express the observations as a linear combination of a set of waves. The analysis decomposes the pattern into sine and cosine waves. It is the only wave system for which the starting point is considered as being not crucial. It is easily related to block-size analysis which can be considered as decompositions of the pattern into square waves. The central tool is the periodogram  $I_p$  with  $p = 1, \dots, m/2 - 1$  ( $m$  is the number of observations along a line), the corresponding block sizes being  $m/2p$ . As usual, the null hypothesis is that the pattern is random. Tests are possible, which apply exactly only if the observations have a normal distribution. As expected, the results are rather independent from the starting point, but the interrelation of the peaks and troughs in the periodogram is complex and difficult to interpret. Two dimensional spectral analyses of spatial pattern were presented by Ford and Renshaw (1984) and Renshaw and Ford (1984). They consider that the technique is able to detect all the possible scales of pattern and sensitive to directional components. Of course, the periodogram and its  $R$  and  $\Theta$  spectra are very sensitive to repeatabilities in the data, but they do not detect other types of spatial patterns which do not involve repeatabilities (Legendre and Fortin 1989). Carpenter and Chaney (1983) compared the hierarchical analysis of variance, random pairing, two-term local variance methods and spectral analysis with simulated data. They concluded that the random pairing method estimated patch size more accurately than the other methods; spectral analysis was unable to partition components of grain. Applications of spectral analysis are found in Carpenter and Titus (1984), Franklin et al. (1985) and Kenkel (1988b). Newbery et al. (1986) consider that their experiment with spectral analysis must be regarded in an exploratory sense only, and should not be taken as constituting formal statistical tests of hypotheses.

Pattern detection was also attempted with distance measures. Distances are measured between randomly

selected points and plants or between randomly selected plants and neighbouring plants. Methods are described in Bary-Lenger (1967), Bray (1962), Catana (1963), Clark and Evans (1954, 1979), Cottam and Curtis (1956), Dice (1952), Eberhardt (1967), Holgate (1964, 1965a and b), Hopkins (1954), Moore (1954), Mountford (1961), Phillips and MacMahon (1981), Pielou (1959, 1962, 1977), Simberloff (1979), Skellam (1952), Thompson (1956) and Yeaton and Cody (1976). Clark and Evans's (1954) use an index to measure the intensity of pattern. Summaries are given by Diggle et al. (1976), Galiano (1982b), Goodall and West (1979) and Greig-Smith (1964). Extensive mathematical developments can be found in Upton and Fingleton (1985).

The purpose of making distance measurements between plants is the detection of competition between individuals of the same species or of different species. The main drawbacks and other characteristics of the methods are:

- the tests are used to detect non-randomness as in the quadrat methods, which is the most common case,
- several of the tests need density measurements in addition to distance,
- generally, the first nearest neighbours from random points or from random plants are taken into account,
- multidimensional applications are rare (Clark and Evans 1979), and
- field siting of random points or the choice of random plants is a long and arduous task.

Semisystematic sampling scheme was introduced by Byth and Ripley (1980) to overcome that objection. Starting with the mapping of trees, Kenkel (1988a) uses a modified Clark-Evans statistic, refined nearest neighbour analysis, combined count-distance analysis, and the bivariate combined count-distance analysis. Particular tests are given by Chessel et al. (1973a and 1975) who use a systematic sampling and define the statistical parameters needed to detect and quantify regular implantations. An interesting technique arose by the combination of two methods: the least-squares mapping based on interpoint distances, propounded by Rohlf and Archie (1978), and the method of plant-to-all-plants distances proposed by Galiano (1982b).

To map a forest, for instance with conventional methods of triangulation, a considerable effort is required. Rohlf and Archie (1978) presented a technique which makes it possible to map the exact location of sessile organisms with distance measures. Galiano's method comprises measurement of the distances between each point and all the rest. Once all distances are calculated they are arranged in classes and the number of distances per class is corrected with the area encompassed by each class. The final output is a histogram in which the number of distances per interval is plotted against growing separation from the point. These points will be developed in the next chapter.

For the detection of multispecific patterns, there is a general lack of specific statistics. Kershaw (1960, 1961, 1964) suggested that pattern could similarly be expressed as the level of association between species; once two species are positively or negatively related in a community, the population will be non-random and pattern analysis may proceed either based on analysis of variance or the correlation coefficient. Covariances between species are also calculated and analyzed in a similar way to the variance. Covariances and correlation coefficients may be derived from the two-term local quadrat variance method of analysis (Hill 1973 and Usher 1983). An approach based on information functions applied to co-occurrence matrices between species sampled by grids was developed by Feoli and Feoli Chiapella (1979) and Feoli et al. (1980). By this approach measures of heterogeneity are more important than measures from random expectation. Pielou (1977) has considered the problem of segregation between two species and attempted to define the pattern of each species in relation to the other without regard to the pattern of either in relation to the soil. The question asked, are two species randomly mingled or are they relatively clumped? If they are randomly mingled, they may be described as unsegregated; if not, they are to some extent segregated from each other. For studying relative patterns, Pielou (1977) recommended the use of nearest-neighbour methods. Peterson (1976) proposed a segregation index. For each species separately, segregation is measured by the ratio of the chance of finding it in the neighbourhood of another individual of its own kind to the unconditional chance of finding it in the whole community. Inter-type relations were also developed by Upton and Fingleton (1985) generally concerned with bivariate patterns. They consider the analysis using quadrats with a presence/absence cross-classification, or inter-quadrat correlation; transects with run tests; sophisticated distance methods with the nearest-neighbour table; and the point-plant and plant-plant distributions or the paired point-plant distances, inter alia. The drawbacks of these methods are obvious:

- pairs of species are taken into account when, in fact, patterns may be plurispecific,
- patterns are examined at one scale only, and
- some conditions of application are unrealistic.

The reader interested in the problem of two-way or multiway contingency tables from maps will find detailed mathematical developments and examples in Upton and Fingleton (1989).

But an important progress in the understanding of multispecific patterns was made with the use of correspondence analysis (or CA) as shown by Estève (1978) and used by Bachacou and Chessel (1979), Bouxin (1983), Bouxin and Gautier (1979, 1982), Galiano (1983), Gautier (1979) and Whittaker et al. (1979a and b). Estève (1978) explained that correspondence analysis was

a preferential tool for the study of a transect or a grid. The scores of the relevés belonging to a transect must be interpreted according to their spatial position; the graph of that function is the most informative in displaying homogeneous areas, transition zones and others with high floristical variation. Examples were given with north African steppe (Estève 1978), European alluvial forest (Bachacou and Chessel 1979), European limestone grassland (Bouxin and Gautier 1979, 1982), central African savanna (Bouxin 1983), Mediterranean grassland (Gautier 1979), and west European riparian vegetation (Bouxin and Le Boulengé 1983). Whittaker et al. (1979a and b) used reciprocal averaging (or RA, equivalent to correspondence analysis) to show pattern in a 100 sq. m strip sample in an Australian Mallee and in a 107 sq. m strip transect in a Texan mesquite grassland. In the same way, Olsvig-Whittaker et al. (1983) used detrended correspondence analysis (or DCA) to three strip transects from the Negev Desert. Gloaguen and Gautier (1981) further processed the CA scores of a grid by a non-parametrical index; Galiano (1983) processed the coordinates on the RA first axis, which could be analyzed by the traditional variance methods. Gibson and Greig-Smith (1986) also used ordination scores (from DCA) in a two or three-term local variance analysis; so they can quantify the scales of community pattern.

Two drawbacks in the use of RA are evident. In most cases, RA scores are calculated with only one quadrat size and the multispecific pattern analysis is carried out independently of the set of monospecific patterns. Regarding the general performance of RA, reference is made to Kenkel and Orlóci (1986).

Another approach is due to Glenn-Lewin and Ver Hoef (1988) who recorded species presence in a set of 300 contiguous small quadrats: the quadrats are grouped into increasingly larger block sizes and a local two-term covariance matrix of all species pairs is calculated for each block size. The covariance matrices are summed to form a total covariance matrix and the total covariance matrix is subjected to PCA. The eigenvalues of the total covariance matrix are partitioned into the amount that each block size contributed to each particular PCA axis; the partitioned eigenvalues are plotted against block size. The peaks of such a curve lies at the scale that contributed most to the PCA axis. The species that load most strongly on the PCA axis are those that contribute most to pattern. Thus, the technique indicates the intensity and scale of pattern and the species that are the most important contributors to pattern. Ver Hoef and Lewin (1989) also analyzed pattern diversity with multivariate analysis.

### Choice of models

The discussion of models concerns transects, grids and distance measures, but not spatial autocorrelation.

I prefer the non-parametrical tests which are not based on unrealistic hypotheses, such as a random dispersion. One of the best arguments in favour of the non-parametrical tests was given by Gautier (1979). According to this author, the non-parametrical models allow the choice of statistics with selective powers, i.e., statistics taking exceptional values for a precise alternative. A prevalent idea is to use several statistics each of which has its own field of sensitivity.

### Models for transects or grids, monospecific patterns

I considered the problem of selecting the starting point of the grid or transect and used the following scheme in a specific case: amongst a set of 182 contiguous relevés in a stream, a set of 160 contiguous relevés is moved along the stream with different starting points. Two statistics (non-parametrical dispersion index and the true contagion index, discussed later) are computed for each set position. For the same block size, the variation in the statistics is high while the block size is small and low for the large blocks ( $\geq 10$  relevés per block). Similar conclusions are in many other examples. Thus, the influence of the starting point is important with small pattern units only. With clumps, gradients, density variations, the main features of the pattern appear whatever starting point is used. I compute specific indices with several starting points. The values, jointly with Galiano's variances (Galiano et al. 1987), are sensitive in detecting clump size. The exact size of the clump, or patch, is not a prevalent objective. Gautier (1979) points out that a species may form clumps of varying sizes in the same transect.

Starting with a set of  $N$  quadrats, from a geometric sampling design, organized in  $B_K$  blocks of size  $K$ , each block size represents a spatial scale. Based on this, three cases are considered, differing in data: presence-absence, counts, and other qualities.

### The presence-absence model (Chessel and Gautier, 1984)

The variable  $p(i,j)$  has value 1 when the species is present in the  $j^{\text{th}}$  unit of the  $i^{\text{th}}$  block of size  $K$ ; when the species is absent,  $p(i,j)$  is 0.  $p_K(i,.)$  is the total number of presences in the  $i^{\text{th}}$  block,

$$p_K(i,.) = \sum_{j=1}^K p_K(i,j)$$

THE NON-PARAMETRICAL DISPERSION INDEX  $D_p$ . Let

$$P \leftarrow \sum_{i=1}^{B_K} p_K(i,.)$$

There are

$$\binom{N}{M} = \frac{N!}{M! (N-M)!}$$

possibilities of choosing  $P$  presences on a line or a grid which contains  $N$  quadrats. The null hypothesis is the equiprobability of all the possible dispersions of the  $P$  presences. The dispersion index at block size  $K$  is

$$D_p(K) = \frac{\sum_{i=1}^{B_K} [p_K(i, \cdot)]^2 - m_1}{\sqrt{v_1}}$$

where

$$m_1 = P \left[ \frac{(K-1)(P-1)}{(N-1)} \right] + 1$$

and

$$v_1 = \frac{2P(P-1)(K-1)(N-K)(N-P)(N-P-1)}{(N-1)^2(N-2)(N-3)}$$

$D_p$  is a measure of the overall variability in contents between the blocks.  $D_p$  follows a unit normal distribution. The utility of  $D_p$  is by providing a global test for dispersion at different block sizes. The maximum value of  $D_p$  for block sizes varying as a geometrical progression (ratio = 2) is less than 3 with  $\alpha = 0.05$  and less than 4.5 with  $\alpha = 0.01$ . Applications under less drastic conditions of block size also yielded satisfactory results.

THE TRUE CONTAGION INDEX  $E_p$  (Chessel and De Belair 1973, Chessel and Gautier 1984).  $E_p$  measures the differences between pairs of contiguous blocks of same size. In this model, of the  $\binom{N}{P}$  choices of the  $P$  points amongst the  $N$  are equiprobable. The null hypothesis states that the repartition of the presences in the two blocks of a pair is random. The heterogeneity between two blocks is measured by the variable

$$H = p_K(i_1, \cdot) - p_K(i_2, \cdot)$$

The mean and variance of  $H$  at different  $P$  is:

$$E(H; 1, N) = 1$$

$$E(H; 2k+1, N) = \frac{2k+1}{2k} \cdot E(H; 2k, N)$$

$$E(H; 2k, N) = \frac{N-2k}{N-2k+1} \cdot E(H; 2k-1, N)$$

$$V(H; P, N) = \frac{P(N-P)}{N-1} - [E(H; P, N)]^2$$

The true contagion index is

$$E_p(K) = \frac{1}{\sqrt{J}} \sum_{i=1}^J \left[ \frac{H_i - E(H_i)}{\sqrt{V(H_i)}} \right]$$

The summation is through  $J$  block pairs, each of which contains more than 1 presence and less than  $2K-1$  presences. If  $J \geq 10$ ,  $E_p$  can be compared to a unit normal distribution.  $D_p(K)$  and  $E_p(K)$  are complementary statistics; the curves of  $D_p(K)$  or  $E_p(K)$  with  $K$  are generally parallel and are adequate for the definition of pattern type:

- random if the tests are not significant at the different block sizes;
- one or several aggregates if  $D_p$  and  $E_p$  present their maximum at small block sizes
- one or several clumps if the maxima of  $D_p$  or  $E_p$  correspond to larger block sizes; clumps alternate with very sparsely populated zones;
- one or several gaps; under similar conditions as with aggregates or clumps; the gaps alternate with densely populated zones;
- a density variation under more or less continuous (regular or not) frequency variations; maxima with small- middle- or large-sized blocks;
- a gradient if  $D_p$  increases regularly with block size and if the maximum  $E_p$  score appears with the largest blocks; density variations are continuous and monotonic;
- complex, many kinds, revealed by two or more peaks of  $D_p$  or  $E_p$ . For instance, aggregates, gaps or clumps may have their own pattern.

The intensity of pattern is given by the maximal scores of the statistics, especially by  $E_p$ . Further information and examples are presented in Bouxin (1983), Bouxin and Gautier (1979, 1982), Bouxin and Le Boulengé (1983), Chessel and Donadieu (1977), Chessel and Croze (1978), Gautier (1979) and Hossaert-Palauqui and Gautier (1980).

#### The assignment model

Let  $n_K(i, j)$  denote the number of individuals belonging to the  $j^{\text{th}}$  unit of the  $i^{\text{th}}$  block of size  $K$ . If  $n_K(i, \cdot)$  is the total number of individuals in the  $i^{\text{th}}$  block of size  $K$ , the grand total is

$$n_K(i, \cdot) = \sum_{j=1}^K n_K(i, j)$$

THE CLASSICAL DISPERSION INDEX  $D_n$  (Chessel and Gautier 1984). The null hypothesis is the equiprobability of the  $N^M$  attributions of  $M (= n_K(i, \cdot))$  individuals to  $N$  blocks.  $D_n$  is a measure of the overall variability:

$$D_n(K) = \frac{\sum_{i=1}^{B_K} [n_K(i, \cdot) - \bar{n}_K]^2}{(B_K - 1) \bar{n}_K}$$

where

$$\bar{n}_K = \frac{\sum_{i=1}^{B_K} n_K(i, \cdot)}{B_K}$$

If  $M/N$  is large enough ( $\geq 5$ ),  $(N-1)$ .  $D_n$  is a chi-square with  $(N-1)$  degrees of freedom. If  $(N-1) > 30$ , then the quantity

$$\sqrt{2(N-1)D_n} - \sqrt{2N-3}$$

may be compared to a unit normal distribution. The statistics for different block sizes are not independent. It is often useful to use  $D_p$  after substitution of  $n_K(i, j)$  by 0 or 1 when the value is respectively lower or higher than a fixed value (for instance, the median or the average). A global test is then possible.

THE TRUE CONTAGION INDEX  $E_n$  (Chessel and Gautier 1984). In the general model of the equiprobability of the  $N^M$  assignments of  $M$  individuals to  $N$  blocks, the null hypothesis states that the repartition of individuals in the two blocks of a pair is random. The index is

$$E_n(K) = \frac{1}{\sqrt{L}} \sum_i \frac{[n_K(i_1, \cdot) - n_K(i_2, \cdot)] - m_3(i)}{\sqrt{\nu_3(i)}}$$

where

$$m_{(3)}(i) = \prod_{j=2}^P (2j-1)/(2j-2),$$

$$P = \text{INT} [(n_K(i_1, \cdot) + n_K(i_2, \cdot) + 1)/2]$$

and

$$\nu_3(i) = n_K(i_1, \cdot) + n_K(i_2, \cdot) - [m_3(i)]^2$$

The summation is over  $L$  block pairs, each containing more than two individuals.  $E_n(K)$  is useful when there are numerous block pairs ( $\geq 10$ ).  $E_n(K)$  does not require many individuals. To make a test, the normal probability law can be applied.

THE LOCAL VARIANCE  $E_{n^*}$  (Chessel and Gautier 1984).  $E_{n^*}$  is defined by local variance,

$$E_n(K) = \sum_i \frac{[n_K(i_1, \cdot) - n_K(i_2, \cdot)]^2}{n_K(i_1, \cdot) + n_K(i_2, \cdot)}$$

The summation concerns the  $L^*$  block pairs that contain at least 10 individuals.  $E_{n^*}$  is advantageous in cases of few block pairs. Its distribution law is a chi-square with  $L^*$  d.f (Mead 1974). Negative values of  $E_n(K)$  or  $E_{n^*}(K)$ , at small  $K$ , reveal regular dispersions.

The measure of the local heterogeneity  $L_{no}$  (Chessel and Gautier 1984). One considers here the repartition of individuals belonging to the same block between the units of the blocks. Two statistics can be used:

$$L_{no}(K) = \frac{1}{\sqrt{R}} \sum_i \frac{V_K(i) - m_5(i)}{\sqrt{\nu_5(i)}}$$

with

$$m_5(i) = K(1 - 1/K)^{n_K(i, \cdot)}$$

$$\nu_5(i) = K(K-1)(1 - 2/K)^{n_K(i, \cdot)} + m_5(i) - [m_5(i)]^2$$

and

$$L_{n^*} = \frac{1}{\sqrt{R}} \sum_i \frac{T_K(i) - m_6(i)}{\sqrt{\nu_6(i)}}$$

with

$$m_6(i) = \frac{n_K(i, \cdot)}{K} [n_K(i, \cdot) + K - 1]$$

$$\nu_6(i) = \frac{2[n_K(i, \cdot) - 1]n_K(i, \cdot)(K-1)}{K^2}$$

where  $V_K(i)$  is the number of empty units in the  $i^{\text{th}}$  block of size  $K$  and

$$T_K(i) = \sum_j [n_K(i, j)]^2$$

$L_{no}$  and  $L_{n^*}$  tested based on the unit normal distribution (0,1), permit the observation of locally regular dispersions without any interaction from other heterogeneity structures.  $L_{no}$  is powerful in the presence of empty units. Further information and examples of application for the assignment model are given by Chessel (1978 and 1979), Chessel and de Belair (1973) and Debouzie et al. (1975).

### The abundance model

In the model of the equiprobability of the  $N!$  permutations of the  $N$  numerical values, only the autocorrelation index exists (Cliff and Ord 1973). In its original form, in the test on this index, for any given variable and a random distribution of sampling points in space, the null hypothesis states the absence of correlation for values recorded at two neighbouring points. The model was adapted to the problem of pattern analysis un-

der geometrical sampling (Chessel 1981) with a particular neighbourhood structure, i.e., two sample units are linked if they are in the same block of size  $K$ . The model measures overall variability. For a complete grid,

$$\bar{x} = \frac{\sum_{i,j} x_K(i,j)}{N}$$

$$x_{i,j} = x_K(i,j) - \bar{x}$$

$$A = N(K-1), D = N(K-1)(K-2)$$

$$H_t = 2 \sum_{j=1}^N (x_{i,j})^2 / (N-1)$$

$$H_v = \left[ \sum_{i=1}^{B_K} \sum_{j_1 \neq j_2} (x_{i,j_1} - x_{i,j_2})^2 \right] / A$$

$$Z = H_v / H_t$$

$$E(Z) = 1$$

$$A^2 N(N-2)(N-3) \text{Var}(Z) = X_1 + X_2 + X_3$$

$$X_1 = [(N^2-3)-(N-1)^2 B_2] / A^2$$

$$X_2 = 2/A(N-1)[N^2-3N+3-(N-1)B_2]$$

$$X_3 = (N-1)(D+A)[(N^2-N+2)B_2-(N^2+3N-6)]$$

$$B_2 = N \sum_{i,j} (x_{i,j})^4 / \left[ \sum_{i,j} (x_{i,j})^2 \right]^2$$

Based on these, the autocorrelation index is

$$D_X = \frac{1-Z}{\text{vvar}(Z)}$$

When a spatial autocorrelation exists, i.e., a significant resemblance between two neighbouring point values, on average, the observed value of  $Z$  decreases and  $D_X$  becomes significant, positive. The distribution of  $D_X$  approximates the normal. If the  $x_K(i,j)$  are replaced by  $n_K(i,j)$ ,  $(B_K-1)D_n(K)$  is a chi-square with  $B_K-1$  d.f. With presence-absence data,  $D_X(K)$  is equivalent to  $D_P(K)$  and a global test is then possible. The statistics for different block sizes are not independent. The 0-1 conversion is useful as in  $D_n(K)$ . An application is described in Gloaguen and Gautier (1981). The combination of  $D_X(K)$  and, after transformation,  $D_P(K)$  and  $E_P(K)$  and the use of original data maps or histograms, generally allow a good description of pattern type and an estimation of pattern intensity.

Because it provides accurate information concerning the size and density of species clumps, Galiano's (1982a)

new local variance with its Monte-Carlo test based on the random permutation of data (Galiano et al. 1987) has great utility as a complement to the autocorrelation index. If the numerical values are represented by  $X_1, X_2, X_3, \dots, X_n$  in a set of  $n$  sampling units, the new two-terms local variance, is the average of:

$$1/2 (X_1 - X_2)^2 - 0, 1/2 [(X_2 - X_3)^2 - (X_1 - X_2)^2],$$

$$1/2 [(X_3 - X_4)^2 - (X_2 - X_3)^2], \dots,$$

$$1/2 [(X_{n-1} - X_n)^2 - (X_{n-2} - X_{n-1})^2]$$

for block size one and

$$1/4 (X_1 + X_2 - X_3 - X_4)^2 - 0,$$

$$1/4 [(X_2 + X_3 - X_4 - X_5)^2 - (X_1 + X_2 - X_3 - X_4)^2], \dots,$$

$$1/4 [(X_{n-3} + X_{n-2} - X_{n-1} - X_n)^2 - (X_{n-4} + X_{n-3} - X_{n-2} - X_{n-1})^2]$$

for block size two. The above expression expands to larger block sizes. New local variances detect clump size independently of interclump distances. The method allows very accurate detection of clump size and is particularly useful in the detection of small sized clumps. It can also be used with frequency data.

#### Models for grids, multispecific patterns

Many models are possible for multispecific pattern analysis. These include principal component analysis (PCA), correspondence analysis (CA), detrended correspondence analysis (DCA), nonmetric multidimensional scaling (NMDS) and one or several of the numerous other scaling and classificatory algorithms. The problem of scale remains. Ideally, when a relevé table is submitted to CA or DCA, several block sizes must be considered, within the consistent constraint of a geometrical sampling. Ver Hoef and Glenn-Lewin (1989) use multiscale ordination for detecting pattern at several scales. But in a relevé, species which are structured at very different scales, are collected together and the CA scores may be largely influenced by this superposition; but with no phytosociological significance. The co-occurrence of several rare species in a particular relevé gives a large score to the relevé, on the first or second axis, the variability of the other species being smoothed (see Bouxin 1983). The idea that a multispecific pattern analysis had to be preceded by a monospecific pattern analysis is appealing. In the processing of a relevé table, the following steps are appropriate:

- monospecific patterns are studied, using appropriate indices;
- for each block size, a structured species list is esta-

blished;

- for each block size, new simpler matrices are defined on the basis of the structured species; rare and unstructured species are deleted;
- these new matrices only are submitted to PCA, CA, DCA or NMDS and the problems of association or segregation between species is clarified;
- the PCA, CA, DCA or NMDS are used in the classificatory analyses.

This procedure has examples in Bouxin (1986, 1987a, b) and in Bouxin and Deflandre (1988). The presentation of the ordination scores is also important. Estève (1978) advises to take the relative position of the sampling units into account, i.e., on the map of the grid or the transect, bars whose heights correspond to the ordination scores are placed at the center of the block above or below the plane depending on whether the scores are positive or negative. A map is constructed for each significant axis and if the maps are lined up in the same figure, all the factors are presented simultaneously. Bachacou and Chessel (1979), Bouxin (1983), Bouxin and Gautier (1979, 1982), Bouxin and Le Boulengé (1983) and Gautier (1979), give examples. Nonmetric multidimensional scaling is now considered as one of the best strategies for recovering simulated coenoplane and real data (Bradfield and Kenkel 1987, Kenkel and Orlóci 1986).

As for monospecific patterns, many multispecific pattern types convolute to form higher complexity: multispecific aggregates, clumps, density variations, gradients, complex patterns. Many papers describe gradient research of general gradients (indirect gradient analysis). The results, however, may be of dubious value, since the existence of a general coenocline in a set of relevés is only an hypothesis amongst many possible others.

#### *Model for distance measure*

It was explained in the review that the combination of least-squares mapping propounded by Rohlf and Archie (1978) and the method of distance measures (Galiano 1982b) can bring a new dynamism in the processing of distance measures. The technique of mapping is described:

- select 3 points as a reference triangle (3 located plants or permanent reference markers);
- for each point (considered sequentially) within the study area, measure the distance between it and 3 previously recorded points;
- an initial estimate of the coordinates is established by using the law of cosines;
- an iterative procedure, applied to obtain the coordinates which yield the best least-squares fit of the original measured distances based on the coordinates, consists of two basic steps;
- the definition of a criterion which measures the de-

gree of fit between the observed and the computed distances (based upon a set of estimated coordinates);

- the construction of an optimization procedure which adjusts an initial set of coordinates in a way so as to increase the goodness of fit between the observed and computed distances.

Kenkel (1988a) introduced a variant of the method. He used the distance of an individual to the four corners of squares and coordinates were calculated with respect to each of the four pairs of adjacent corner points. A mean was calculated to obtain the final coordinate position. After the final coordinates have been obtained, computer programs can be used to compute various summary statistics to describe the spatial patterns. The distances to the 2<sup>nd</sup>, 3<sup>rd</sup>, ... n<sup>th</sup> neighbour are easily computed. With such a technique, the field work is rapid and no longer limited to very small areas. The maps can be drawn by a computer. Starting with the coordinates, Galiano's (1982b) pattern detection is as follows:

In order to avoid edge effects, two circles of different radii R1 and R2 are set. Plant-to-all-plants distances are measured for individuals inside the inner circle. From every point in the inner circle distances are measured to all other points in the inner circle and in the outer circle. The greatest size of aggregation that can possibly be detected is equal to R2-R1. Outside points are not considered in measuring plant-to-all-plants distances because the absence of data in their surroundings (as the sampling circle is limited) would distort the analysis by creating unwanted edge effects. The distances are calculated from the coordinates and they are arranged in classes. The number of distances per class is corrected according to the area encompassed by each class (a circle or a crown). The final output is an histogram in which the number of distances per interval is plotted against the growing separation distances from the plant. The histogram can be interpreted as a conditioned probability spectrum. In a random model, the probability spectrum does not show any obvious peak. With an aggregation phenomenon, the distribution of distances shows a fall in the number of distances per unit area with the steepness of the fall related to the size of the aggregate or the clump. While some peaks correspond to regularity, complex patterns can also be revealed. One of the method's advantages is the reliability in determining patterns, due to the high number of distances. In a population of 1000 individuals, traditional plant-to-plant distance tests would use a maximum number of 500 distances to evaluate pattern while here one would use  $500 \cdot 1000 / 2 = 250000$  distances on average (Galiano 1982b). The method can be adapted to plurispecific conditions.

Complementary tests may also be useful for the understanding of the spacing between individuals. A common question arises: Does competition between

individuals generate regular patterns? Some solutions to the recognition of regularity is described in Chessel et al. (1973a, 1975) in conjunction with systematic sampling along strip transects. Several portions of a map, in which the regularity has to be tested, is sampled along such a transect. In the transect of width  $h$ , for every plant whose center lies inside the strip, the abscissa  $t$  of that centre on the transect axis is noted. The transect is characterized by its length  $L$  and the number  $N$  of recorded plants.  $L$  is set to include  $N \geq 100$  plants.  $h$  is arbitrarily fixed from the density  $h = 1/D$ .

**THE DISTANCES TO THE  $J^{\text{TH}}$  NEXT NEIGHBOUR.** The values  $(t_2 - t_1), \dots, (t_{j+1} - t_j), \dots, (t_N - t_{N-1})$  are the  $N-1$  values of  $X_1$  which corresponds to the distance from a point to the first neighbour. The distance to the second neighbour is given by the  $\text{INT}[(n-1)/2]$  values  $(t_3 - t_1), (t_5 - t_3), \dots, (t_{2j+1} - t_{2j-1})$ , of  $X_2$ .  $X_j$  is the distance to the  $j$ th next neighbour. With the null hypothesis of a Poisson process, the variable

$$\frac{2j X_j}{\bar{X}_j}$$

has a chi-square distribution with  $2j$  d.f. Standard histograms give the relation between several length classes and their frequency. The null hypothesis which stipulates randomness is not a drawback, since the alternative is non trivial.

**THE TEST OF REGULARITY.** Let

$$X_{2j} = t_{2j+1} - t_{2j-1}$$

be the  $j^{\text{th}}$  value of the distance to the second next neighbour. The variable  $U$  whose  $j^{\text{th}}$  observed is defined by

$$u_j = \frac{t_{2j} - t_{2j-1}}{t_{2j+1} - t_{2j-1}}$$

has a  $(0,1)$  uniform distribution in a Poisson process. Thus the variable  $V = \text{Min}(U, 1-U)$  has a  $[0, 1/2]$  uniform distribution. If the pattern is regular, the low values of  $V$  are under-represented. In that case, the empirical distribution function of  $V$  is significantly lower than its theoretical distribution function which takes the value  $2x$  for  $0 \leq x \leq 1/2$ . For each of the  $n$  intervals defined by the distance to the second neighbour,

$$v_j = \text{MIN} \left[ \frac{t_{2j} - t_{2j-1}}{t_{2j+1} - t_{2j-1}}, \frac{t_{2j+1} - t_{2j}}{t_{2j+1} - t_{2j-1}} \right]$$

The  $n$  values are ranked in 10 classes  $[0, .05], [.05, .10], \dots, [.45, .50]$ . The observed frequencies being  $n_1, \dots, n_{10}$ ,

$$D_n = \text{MIN}_{1 \leq K \leq 10} \left( \frac{n_1 + n_2 + \dots + n_K}{n} - \frac{K}{10} \right).$$

The Kolmogorov-Smirnov test is applied with the limits for

$$\sqrt{n} D_n$$

given by  $-1.22$  (5%) and  $-1.52$  (1%).

**THE REGULARITY INDEX.** Given by

$$I_R = \frac{4 \sum_{j=1}^n v_{n-n}}{\sqrt{n}/3}$$

it has a unit normal distribution under the null hypothesis; a significant positive value indicates a local regularity. A unilateral test is used with limits  $1.64$  (5%),  $2.33$  (1%),  $3.09$  (0.1%).

## Computations

BASIC and IBM compatible programs are available from the author on  $5 \frac{1}{4}$ " or  $3 \frac{1}{2}$ " disks for the computation of the different  $D$ ,  $E$  and  $L$  indices with different starting points. Galiano's new local variance measure is also programmed. The programs are linked to a direct access file of the relevé tables; this allows numerous transformations (addition and suppression of lines, addition of a table to another, block formation, etc.). Programs for PCA, CA, NMDS and cluster analyses are also included.

## Conclusions and perspectives

The field botanist finds in this paper a set of well adapted indices reviewed and tests on these indices. With these tools he or she is no longer limited to recognize whether pattern is random, clumped, or regular, but can detect many types of non-random patterns in the vegetation. Although it is possible now to define many pattern types, the concept of pattern intensity remains rather intractable. Also, it is important to realize that similar numerical values of an index for different species do not have the same significance. Indeed, numerical values are only comparable between similar sampling conditions and between species of the kind for size, of the same life form, etc. As for the future, several aspects have to be mentioned:

1. Pattern analysis should be usable in computation with large surveys, whatever the constraints of the field work.

2. The development of Monte-Carlo test procedures (Galiano et al. 1987, Vaillant and Badenhausser 1989), based on simulation of the hypotheses of interest, will allow exact tests for indices whose sampling distribu-

tion is unknown.

3. The sampling design for the definition of pattern type and pattern intensity is not sufficiently studied. The sampling technique should be as flexible as possible and pattern analysis should not be limited to regular transects or grids (Bouxin 1987b). The standard approach to the study of vegetation in which sampling represents a first and data analysis a second step is criticized in Wildi and Orlóci (1987). They suggest an alternative where sampling and analysis run concurrently. The development of computerized sampling methods (see Podani 1987) will probably allow the optimization of sampling designs.

Some powerful techniques, such as spectral analysis has received insufficient attention in vegetation studies, yet they seem very promising. Frontier (1987) presented applications of fractal theory to ecology [a fractal is a descriptor of complexity of forms, such as the shape of vegetation patch (Orlóci 1988)]. Frontier believes that it is likely to become a fundamental tool for global analysis and modelling of ecosystems in the future. Some statistics, such as the circular statistics in Upton and Fingleton (1989) are also left unexplored. Clearly, new techniques and approaches are needed which can render monospecific and multispecific pattern analysis a rigorous basis for vegetation studies and a conceptual basis for phytosociology.

**Acknowledgements.** I am thankful to Professor L. Orlóci for technical suggestions and revisions of syntax.

## REFERENCES

- ABERDEEN, J.E.C. 1959. The effect of quadrat size, plant size and plant distribution on frequency estimates in plant ecology. *Aust. J. Bot.* 6: 47-58.
- ANDERSON, D.J. 1961. The structure of some upland communities. I. The pattern shown by *Pteridium aquilinum*. *J. Ecol.* 49: 369-376.
- ASHBY, E. 1935. The quantitative analysis of vegetation. *Ann. Bot., Lond.* 49: 779-802.
- BACHACOU, J. and D. CHESSEL. 1979. Etude des structures spatiales en forêt alluviale rhénane. III. Dispersion interspécifique et analyse des correspondances. *Oecol. Plant.* 14: 371-388.
- BARY-LENGER, A. 1967. Etude statistique de la dispersion spatiale des arbres en forêt. *Biom.-Praxim.* 8: 115-148.
- BLACKMAN, G.E. 1942. Statistical and ecological studies in the distribution of species in plant communities. I. Dispersion as a factor in the study of changes in plant populations. *Ann. Bot., Lond., N.S.* 6: 351-370.
- BOUXIN, G. 1974. Distribution des espèces dans la strate herbacée au sud du parc national de l'Akagera (Rwanda, Afrique centrale). *Oecol. Plant.* 9: 315-332.
- BOUXIN, G. 1975. Ordination and classification in the savanna vegetation of the Akagera Park (Rwanda, central Africa). *Vegetatio* 29: 155-167.
- BOUXIN, G. 1976. Ordination and classification in the Rugege forest (Rwanda, central Africa). *Vegetatio* 32: 97-115.
- BOUXIN, G. 1977. Structure de la strate arborescente dans un site de la forêt de montagne du Rwanda (Afrique centrale). *Vegetatio* 33: 65-78.
- BOUXIN, G. 1983. Multi-scaled pattern analysis: an example with savanna vegetation and a proposal for a sampling design. *Vegetatio* 52: 161-169.
- BOUXIN, G. 1986. Le traitement statistique des tableaux de relevés de végétation. 1. Les petits tableaux. *Biom.-Praxim.* 26: 49-72.
- BOUXIN, G. 1987a. Le traitement statistique des tableaux de relevés de végétation. 2. Les ensembles de tableaux et les grands tableaux. *Biom.-Praxim.* 27: 65-97.
- BOUXIN, G. 1987b. La végétation herbacée des ruisselets d'un massif boisé sur roches éodévonniennes, en Belgique. *Colloques phytosociologiques*. XV: 93-106.
- BOUXIN, G. and G. DEFLANDRE. 1988. Les groupements végétaux dans la pelouse calcaire de Belvaux. *Colloques phytosociologiques*. XVI: 619-628.
- BOUXIN, G. and N. GAUTIER. 1979. Structure de la strate herbacée dans deux pelouses calcaires du district mosan. *Oecol. Plant.* 14: 219-231.
- BOUXIN, G. and N. GAUTIER. 1982. Pattern analysis in Belgian limestone grasslands. *Vegetatio* 49: 65-83.
- BOUXIN, G. and E. LE BOULENGE. 1983. A phytosociological system based on multi-scaled pattern analysis: a first example. *Vegetatio* 54: 3-16.
- BOWMAN, D.M.J.S. 1986. Stand characteristics, understorey associates and environmental correlates of *Eucalyptus tetrodonta* F. Muell. forests on Gunn Point, northern Australia. *Vegetatio* 65: 105-113.
- BRADFIELD, G.E. and N.C. KENKEL. 1987. Nonlinear ordination using flexible shortest path adjustment of ecological distances. *Ecology* 68: 750-753.
- BRAY, J.P. 1962. Use of non-area analytic data to determine species dispersion. *Ecology* 43: 328-333.
- BYTH, K. and B.D. RIPLEY. 1980. On sampling spatial patterns by distance methods. *Biometrics* 36: 279-284.
- CARPENTER, S.R. and J.E. CHANEY. 1983. Scale of spatial pattern: four methods compared. *Vegetatio* 53: 153-160.
- CARPENTER, S.R. and J.E. TITUS. 1984. Composition and spatial heterogeneity of submersed vegetation in a softwater lake in Wisconsin. *Vegetatio* 57: 153-165.
- CASADO, M.A., G. ABBATE, C. BLASI and F.D. PINEDA. 1989. Pattern diversity analysis of a clearing in a *Quercus cerris* wood. *Vegetatio* 79: 143-149.
- CATANA, A.J. 1963. The wandering quarter method of estimating population density. *Ecology* 44: 349-360.
- CHESSEL, D. 1978. Description non paramétrique de la dispersion spatiale des individus d'une espèce. *Biométrie et Ecologie* 1: 45-135.
- CHESSEL, D. 1979. Etude des structures spatiales en forêt alluviale rhénane. II. Analyse de la dispersion horizontale monospécifique. *Oecol. Plant.* 14: 361-369.
- CHESSEL, D. 1981. The spatial autocorrelation matrix. *Vegetatio* 46: 177-180.
- CHESSEL, D. and F. HUBERT. 1973a. L'échantillonnage continu par distances en milieu steppique. *C.R. Acad. Sc. Paris, Série D* 277: 937-940.
- CHESSEL, D. and G. DE BELAIR. 1973b. Mesure de la contagion vraie en échantillonnage par carrés dans l'analyse des populations végétales. *C.R. Acad. Sc. Paris, Série D* 277: 1483-1486.

- CHESSEL, D. and D. DEBOUZIE. 1974. Mesure statistique de la dispersion spatiale des végétaux en échantillonnage systématique par présence-absence. C.R. Acad. Sc. Paris, Série D 278: 2027-2030.
- CHESSEL, D., D. DEBOUZIE, P. DONADIEU and D. KLEIN. 1975. Introduction à l'étude de la structure horizontale en milieu steppique. I. Echantillonnage systématique par distance et indice de régularité. Oecol. Plant. 10: 25-42.
- CHESSEL, D. and P. DONADIEU. 1977a. Introduction à l'étude de la structure horizontale en milieu steppique. III. Dispersion locale, densité et niveau d'implantation. Oecol. Plant. 12: 221-224.
- CHESSEL, D. and C. GAUTIER. 1977b. Des statistiques non paramétriques pour l'analyse des données binaires. Rev. Stat. Appl. 25: 57-73.
- CHESSEL, D. and C. GAUTIER. 1984. Statistical pattern analysis of a plant population measured by geometric sampling on a limited space. Handbook of Vegetation Science (Knapp, R. ed.), Dr. W. Junk Publishers, 4: 61-76.
- CHESSEL, D. and J.P. CROZE. 1978. Un indice de dispersion pour les mesures de présence-absence: application à la répartition des animaux et des plantes. Bull. Ecol. 9: 19-28.
- CLAPHAM, A.R. 1936. Over-dispersion in grassland communities and the use of statistical methods in plant ecology. J. Ecol. 24: 232-251.
- CLARK, P.J. and F.C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in population. Ecology 35: 445-453.
- CLARK, P.J. and F.C. EVANS. 1979. Generalization of a nearest neighbor measure of dispersion for use in K dimensions. Ecology 60: 316-317.
- CLIFF, A. and J.K. ORD. 1973. Spatial autocorrelation. Pion, London, 178 p.
- CORRE, J.J. and J.A. RIOUX. 1969. Recherches phytologiques sur les milieux psammiques du littoral méditerranéen français. Oecol. Plant. 4: 177-197.
- COTTAM, G. and J.T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451-460.
- COX, G.W. 1987. Nearest-neighbour relationships of overlapping circles and the dispersion pattern of desert shrubs. J. Ecol. 75: 193-199.
- DAVID, F.N. and P.G. MOORE. 1954. Notes on contagious distributions in plant populations. Ann. Bot., Lond., N.S. 18: 47-53.
- DAVID, F.N. and P.G. MOORE. 1957. A bivariate test for the clumping of supposedly random individuals. Ann. Bot., Lond., N.S. 21: 315-320.
- DEBOUZIE, D., D. CHESSEL, P. DONADIEU and D. KLEIN. 1975. Introduction à l'étude de la structure horizontale en milieu steppique. II. Le traitement statistique des lignes de placettes contiguës. Oecol. Plant. 10: 211-231.
- DICE, L.R. 1952. Measure of the spacing between individuals within a population. Contr. Lab. Vertebr. Biol. Univ. Mich., 55: 1-23.
- DIGGLE, P.J., J. BESAG and J.T. GLEAVES. 1976. Statistical analysis of spatial point patterns by means of distance methods. Biometrics 32: 659-667.
- DUVIGNEAUD, J. 1983. Quelques réflexions sur la protection et la gestion des pelouses calcaires. Natur. belges 64: 33-53.
- EBERHARDT, L.L. 1967. Some developments in distance sampling. Biometrics 23: 207-216.
- ERRINGTON, J.C. 1973. The effect of regular and random distributions on the analysis of pattern. J. Ecol. 61: 99-105.
- ESCHIBAMER, B., G. GRABHERR and H. REISIGL. 1983. Spatial pattern in dry grassland communities of the Central Alps and its ecophysiological significance. Vegetatio 54: 143-151.
- ESTEVE, J. 1978. Les méthodes d'ordination: éléments pour une discussion. Biométrie et Ecologie 1: 223-250.
- FEOLI, E. and L. FEOLI CHIAPELLA. 1979. Changements of vegetation pattern towards reforestation. Colloques phytologiques VIII: 73-81.
- FEOLI, E., L. FEOLI CHIAPELLA, P. GANIS and A. SORGE. 1980. Spatial pattern analysis of abandoned grasslands of the Karst region by Trieste and Gorizia. Studia Geobot. 1: 213-221.
- FORD, E.D. and E. RENSHAW. 1984. The interpretation of process from pattern using two-dimensional spectral analysis: modelling single species patterns in vegetation. Vegetatio 56: 113-123.
- FORGEARD, F. and B. TALLER. 1986. La recolonisation végétale dans une lande incendiée: étude de l'évolution de la structure de la végétation. Oecol. Plant. 21: 15-30.
- FRACKER, S.B. and H.A. BRISCHLE. 1944. Measuring the local distribution of Ribes. Ecology 25: 283-303.
- FRANKLIN, J.J., MICHAELSEN and A.H. SRAHLER. 1985. Spatial analysis of density dependent pattern in coniferous forest stands. Vegetatio 64: 29-36.
- FRONTIER, S. 1987. Applications of fractal theory to ecology. In Developments in Numerical Ecology. Edited by Pierre and Louis Legendre. NATO ASI Series. Series G: Ecological Sciences, vol. 14: 335-378.
- GALLIANO, E.F. 1982a. Détection et mesure de l'hétérogénéité spatiale des espèces dans les pâturages. Oecol. Plant. 17: 269-278.
- GALLIANO, E.F. 1982b. Pattern detection in plant populations through the analysis of plant-to-all-plants distances. Vegetatio 49: 39-43.
- GALLIANO, E.F. 1983. Detection of multi-species patterns in plant populations. Vegetatio 53: 129-138.
- GALLIANO, E.F., I. CATRO and A. STERLING. 1987. A test for spatial pattern in vegetation using a Monte-Carlo simulation. J. Ecol. 75: 915-924.
- GAUTIER, C. 1979. Analyse des grilles en présence-absence, cas mono- et multispécifique. Oecol. Plant. 14: 251-264.
- GERARD, G. 1970. Modèles de répartition spatiale en écologie animale. Biométrie-Praximétrie 11: 124-190.
- GIBSON, D.J. and P. GREIG-SMITH. 1986. Community pattern analysis: a method for quantifying community mosaic structure. Vegetatio 66: 41-47.
- GILL, D.E. 1975. Spatial patterning of pines and oaks in the New Jersey Pine Barrens. J. Ecol. 63: 291-298.
- GINGHAM, C.H. 1978. Calluna and its associated species: some aspects of co-existence in communities. Vegetatio 36: 179-186.
- GLENN-LEWIN, D.C. and J.M. VERHOEF. 1988. Scale, pattern analysis, and species diversity in grasslands. In Diversity and Pattern in Plant Communities, edited by H.J. During, M.J.A. Werger and H.J. Willems. SPB Academic Publishing bv, The Hague. 115-129.
- GLOAGEN, J.C. and N. GAUTIER. 1981. Pattern development of the vegetation during colonization of a burnt heathland in Brittany (France). Vegetatio 46: 167-176.

- GOODALL, D.W. 1952. Some considerations on the use of point quadrats for the analysis of vegetation. *Austral. J. Sci. Res. B* 5: 1-41.
- GOODALL, D.W. 1961. Objective methods for the classification of vegetation. IV. Pattern and minimal area. *Aust. J. Bot.* 9: 162-196.
- GOODALL, D.W. 1974. A new method for the analysis of spatial pattern by random pairing of quadrats. *Vegetatio* 29: 135-146.
- GOODALL, D.W. and N.E. WEST. 1979. A comparison of techniques for assessing dispersion patterns. *Vegetatio* 40: 15-27.
- GOENOT, M. 1969. Méthodes d'étude quantitative de la végétation. Masson, Paris, 314 p.
- GREIG-SMITH, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. *Annals of Botany, N.S.* 16: 293-316.
- GREIG-SMITH, P. 1961. Data on pattern within plant communities. I. The analysis of pattern. *J. Ecol.* 49: 695-702.
- GREIG-SMITH, P. 1964. Quantitative plant ecology. 2nd ed. Butterworth, London. 256 p.
- GREIG-SMITH, P. 1979. Pattern in vegetation. *J. Ecol.* 67: 755-779.
- GREIG-SMITH, P. 1979. Quantitative plant ecology. 3rd ed. Blackwell Scientific, London.
- GREIG-SMITH, P. and M.J. CHADWICK. 1965. Data on pattern within plant communities. III. *Acacia-Capparis* semi-desert scrub in the Sudan. *J. Ecol.* 53: 465-474.
- HELTSHIE, J.F. and T.A. RITCHIEY. 1984. Spatial pattern detection using quadrat samples. *Biometrics* 40: 877-886.
- HILL, M.O. 1973. The intensity of spatial pattern in plant communities. *J. Ecol.* 61: 225-236.
- HILL, M.O. and H.G. GAUCH, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- HOLGATE, P. 1964. The efficiency of nearest neighbour estimators. *Biometrics* 20: 647-649.
- HOLGATE, P. 1965a. Some new tests of randomness. *J. Ecol.* 53: 261-266.
- HOLGATE, P. 1965b. Tests of randomness based on distance methods. *Biometrika* 52: 345-353.
- HOPKINS, B. 1954. A new method for determining the type of distribution of plant individuals. *Ann. Bot. London* 18: 213-227.
- HOSSAERT-PALAUQUI, M. and N. GAUTIER. 1980. Régénération d'une lande après incendie. I. Evolution de la structure du peuplement végétal au cours de la première année. *Bull. Ecol.* 11: 373-386.
- KENKEL, N.C. 1988a. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.
- KENKEL, N.C. 1988b. Spectral analysis of hummock-hollow pattern in a weakly minerotrophic mire. *Vegetatio* 78: 45-52.
- KENKEL, N.C. and L. ORLÓCI. 1986. Applying metric and non-metric multidimensional scaling to ecological studies: some new results. *Ecology* 67: 919-928.
- KERSHAW, K.A. 1958. An investigation of the structure of a grassland community. I. The pattern of *Agrostis tenuis*. *J. Ecol.* 46: 571-592.
- KERSHAW, K.A. 1960. The detection of pattern and association. *J. Ecol.* 48: 233-242.
- KERSHAW, K.A. 1961. Association and co-variance analysis of plant communities. 49: 643-654.
- KERSHAW, K.A. 1964. Quantitative and dynamic ecology. Arnold, London, 183 p.
- LAMONT, B.B. and J.E.D. FOX. 1981. Spatial pattern of six sympatric leaf variants and two size classes of *Acacia aneura* in a semi-arid region of Western Australia. *Oikos* 37: 73-79.
- LECOMTE, M. 1973. Analyse des rapports climat-végétation par une méthode d'échantillonnage continu. *Bull. Soc. Sci. Nat. Phys. Maroc* 53: 37-61.
- LEFKOVITCH, L.P. 1966. An index of spatial distribution. *Res. Popul. Ecol.* 8: 49-59.
- LEGENDRE, P. and J.M. FORTIN. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.
- LLOYD, M. 1967. Mean crowding. *Journal of Animal Ecology*, 36: 1-30.
- LUDWIG, J.A. and D.W. GOODALL. 1978. A comparison of paired-with blocked-quadrat variance methods for the analysis of spatial pattern. *Vegetatio* 38: 49-59.
- MATLACK, G.R. and R.E. GOOD. 1989. Plant-scale pattern among herbs and shrubs of a fire-dominated coastal plain forest. *Vegetatio* 82: 95-103.
- MCGINNIES, W.G. 1934. The relation between frequency index and abundance as applied to plant populations in a semi-arid region. *Ecology* 15: 263-282.
- MEAD, R. 1974. A test for spatial pattern at several scales using data from a grid of contiguous quadrats. *Biometrics* 30: 295-307.
- MOORE, P.G. 1954. Spacing in plant populations. *Ecology* 35: 222-227.
- MORISITA, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. *Mem. Fac. Sci. Kyushu Univ. Ser. E.* 2: 215-235.
- MORI, J.J. and A.J. McCOMB. 1974. Patterns in annual vegetation and soil microrelief in an arid region of western Australia. *J. Ecol.* 62: 115-126.
- MOUNTFORD, M.D. 1961. On E.C. Pielou's index of non-randomness. *J. Ecol.* 49: 271-275.
- NEWBERY, D. McC, E. RENSHAW and E.F. BRUNIG. 1986. Spatial pattern of trees in kerangas forest, Sarawak. *Vegetatio* 65: 77-89.
- NUMATA, M. 1949. The basis of sampling in the statistics of plant communities. *Studies on the structure of plant communities. III. Bot. Mag., Tokyo* 62: 35-38.
- NUMATA, M. 1954. Some special aspects of the structural analysis of plant communities. *J. Coll. Arts Sci., Chiba Univ.* 1: 194-202.
- OLSVIG-WHITTAKER, L., M. SHACHAK and A. YAIR. 1983. Vegetation patterns related to environmental factors in a Negev Desert watershed. *Vegetatio* 54: 153-165.
- ORLÓCI, L. 1971. An information theory model for pattern analysis. *J. Ecol.* 59: 343-349.
- ORLÓCI, L. 1988. Detecting vegetation patterns. *ISI Atlas of Science. Animal and Plant Sciences.* 1: 173-177.
- PETERSON, Ch. H. 1976. Measurement of community pattern by indices of local segregation and species diversity. *J. Ecol.* 64: 157-170.
- PHILLIPS, D.L. and J.A. MACMAHON. 1981. Competition and spacing patterns in desert shrubs. *J. Ecol.* 69: 97-115.
- PIELOU, E.C. 1959. The use of point-to-point distances in the study of the pattern of plant populations. *J. Ecol.* 47: 607-613.

- PIELOU, E.C. 1960. A single mechanism to account for regular, random and aggregated populations. *J. Ecol.* 48: 575-584.
- PIELOU, E.C. 1961. Segregation and symmetry in two-species populations as studied by nearest neighbor relations. *J. Ecol.* 49: 255-269.
- PIELOU, E.C. 1962. The use of plant-to-neighbor distances for the detection of competition. *J. Ecol.* 50: 357-367.
- PIELOU, E.C. 1977. *Mathematical ecology*. Wiley and Sons, New York, 385 p.
- PODANI, J. 1987. Computerized sampling in vegetation studies. *Coenoses* 2: 9-18.
- READ, J. and R.S. HILL. 1985. Dynamics of *Nothofagus*-dominated rainforest on mainland Australia and lowland Tasmania. *Vegetatio* 63: 67-78.
- RENSHAW, E. and E.D. FORD. 1984. The description of spatial pattern using two-dimensional spectral analysis. *Vegetatio* 56: 75-85.
- RIPLEY, B.D. 1978. Spectral analysis and the analysis of pattern in plant communities. *J. Ecol.* 66: 965-981.
- ROHLF, F.J. and J.W. ARCHIE. 1978. Least-squares mapping using interpoint distances. *Ecology* 59: 126-132.
- SIMBERLOFF, D. 1979. Nearest neighbor assessments of spatial configurations of circles rather than points. *Ecology* 60: 679-685.
- SKELLAM, J.G. 1952. Studies in statistical ecology. I. Spatial pattern. *Biometrika* 39: 346-362.
- SOKAL, R.R. and J.D. THOMSON. 1987. Applications of spatial autocorrelation in ecology. In *Developments in Numerical Ecology*. Edited by Pierre and Louis Legendre. NATO ASI Series. Series G: Ecological Sciences, 14: 431-466.
- SUZUKI, K. 1960. The average variation rate as a method of statistical analysis for the mode of distribution of plants in plant communities. *Jap. J. Ecol.* 10: 168-171.
- SUZUKI, K. 1966. An analysis of the mode of spatial distribution of plants found in fallows and dune. *Jap. J. Ecol.* 16: 34-39.
- THIEBAUT, B. 1976. Etude des hêtraies de l'arc montagneux périméditerranéen, de la vallée du Rhône à celle de l'Ebre. II. Structure horizontale des hêtraies de la Montagne Noire (sud-est de la France). *Oecol. Plant.* 11: 53-69.
- THOMPSON, H.R. 1956. Distribution of distance in a population of randomly distributed individuals. *Ecology* 37: 391-394.
- THOMPSON, H.R. 1958. The statistical study of plant distribution patterns using a grid of quadrats. *Austral. J. Bot.* 6: 322-342.
- UPTON, G.J.G. 1984. On Mead's test for pattern. *Biometrics* 40: 759-766.
- UPTON, G.J.G. and B. FINGLETON. 1985. *Spatial data analysis by example. I. Point pattern and quantitative data*. Wiley and Sons. 410 p.
- UPTON, G.J.G. and B. FINGLETON. 1989. *Spatial data analysis by example. II. Categorical and directional data*. Wiley and Sons. 416 p.
- USHER, M.B. 1969. The relation between mean square and block size in the analysis of similar patterns. *J. Ecol.* 57: 505-514.
- USHER, M.B. 1975. Analysis of pattern in real and artificial plant populations. *J. Ecol.* 63: 569-586.
- USHER, M.B. 1983. Pattern in the simple moss-turf communities of the sub-antarctic and maritime antarctic. *J. Ecol.* 71: 945-958.
- VAILLANT, J. and I. BADENHAUSER. 1989. Etude de repartition d'individus sur transect ou grille régulière par tests de Monte-Carlo. *Biométrie-Praximétrie* 29: 153-172.
- VER HOFF, J.M. and D.C. GLENN-LEWIN. 1989. Multiscale ordination: a method for detecting pattern at several scales. *Vegetatio* 82: 59-67.
- WARREN WILSON, J. 1959. Analysis of the distribution of foliage area in grassland, in: *The measurement of grassland productivity*, ed. J.D. Ivins, London, 51-61.
- WATT, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- WATT, A.S. 1981a. A comparison of grazed and ungrazed grassland A in East Anglian Breckland. *J. Ecol.* 69: 499-508.
- WATT, A.S. 1981b. Further observations on the effects of excluding rabbits from grassland A in East Anglian Brecklands: the pattern of change and factors affecting it (1936-73). *J. Ecol.* 69: 509-536.
- WHITFORD, P.B. 1949. Distribution of woodland plants in relation to succession and clonal growth. *Ecology* 30: 199-208.
- WHITTAKER, R.H., L.E. GILBERT and J.H. CONNELL. 1979. Analysis of two-phase pattern in a Mesquite grassland, Texas. *J. Ecol.* 67: 935-952.
- WHITTAKER, R.H., W.A. NIERING and M.D. CRISP. 1979. Structure, pattern and diversity of a mallee community in New South Wales. *Vegetatio* 39: 65-76.
- WILDI, O. and L. ORLÓCI. 1987. Flexible gradient analysis: a note on ideas and application. *Coenoses* 2: 61-65.
- WILLIAMSON, G.B. 1975. Pattern and serial composition in an old-growth beech-maple forest. *Ecology* 56: 727-731.
- YARRANTON, G.A. 1969. Pattern analysis by regression. *Ecology* 50: 310-395.
- YEATON, R.I. and M.L. CODY. 1976. Competition and spacing in plant communities: the Northern Mohave Desert. *J. Ecol.* 64: 689-696.
- ZAHL, S. 1978. A comparison of three methods for the analysis of spatial pattern. *Biometrics* 33: 681-692.

*Manuscript received: December 1989*