Scale of Spatial Pattern: Four Methods Compared
Author(s): Stephen R. Carpenter and Jack E. Chaney
Source: *Vegetatio*, Vol. 53, No. 3 (Sep. 30, 1983), pp. 153-160
Published by: Springer
Stable URL: http://www.jstor.org/stable/20145976
Accessed: 23/02/2011 12:46

Scale of spatial pattern: four methods compared*

Stephen R. Carpenter & Jack E. Chaney
Department of Biology, University of Notre Dame, Notre Dame, IN 46556, U.S.A.

Keywords: Block size analysis, Contiguous quadrats, Grain, Methodology, Pattern, Spatial heterogeneity, Spectral analysis, Variance

Abstract

Four methods of pattern analysis were compared using simulated data. Simulated transects were of five types: 1) equal patch–equal gap, in which gap and patch length were equal, 2) unequal but fixed patch–fixed gap, in which patch length was approximately one sixth gap length, and transects in which 3) the length of the patch, or 4) gap, or 5) both varied randomly. The first peak of the variance-block size graph was used to identify patch size, instead of the more commonly used highest peak.

The random pairing method estimated patch size more accurately than hierarchical ANOVA, two-term local variance, or spectral analysis. The average position of the first peak (calculated from eight replicate random pairing analyses) detected correct average patch size, even when simulated patches were randomly placed or patch size followed a uniform distribution with a range twice the mean. Hierarchical ANOVA and two-term local variance confounded patch and gap lengths and therefore overestimated the patch size. The highest peak of spectral analysis detected the full cycle (patch + gap) of the pattern but was unable to partition the components of grain.

The expected variance of an independent, random pattern is suggested as a reference point for identifying meaningful peaks and troughs in random pairing analyses of field data. The method is illustrated by analysis of a transect through submersed aquatic vegetation.

Introduction

Spatial heterogeneity is a universal feature of communities and a long-standing problem for plant ecologists. Non-random patterns probably reflect environmental patterns as well as demographic processes of plants within the community. The ubiquity of spatial heterogeneity is often ignored by community theorists (Schaffer & Leigh, 1976). Schaffer & Leigh (1976) comment that insightful mathematical modeling of spatial pattern is hampered by lack of compact, interpretable descriptions of pattern. Pielou (1981) emphasizes that adequate analyses of spatial pattern require intense empirical investigation.

Pattern has two basic components: intensity and grain (Pielou, 1977). Intensity is the extent to which density changes from place to place in a community. Several indices of intensity are well established in the literature (Pielou, 1977), and were recently compared by Goodall & West (1979). Grain, the scale of patch size within a community, may reflect the underlying biological and environmental causes

* We thank R. P. McIntosh for comments on the manuscript, N. J. McCreary for sampling assistance, and Mr and Mrs O. J. Stewart for facilitating field work. Financial support was provided by the University of Notre Dame Faculty Research Fund, the U.S.E.P.A., and a Sigma Xi grant-in-aid. Computations were supported by the University of Notre Dame Computing Center.

Vegetatio 53, 153–160 (1983).

of spatial pattern. Unfortunately, it is laborious to collect data suitable for measuring patch size. Investigations are further complicated by the wide variety of analytical methods that have been proposed, which often yield conflicting results. Methods based on plant-to-plant distances attempt to describe the neighbor relations of the average plant, and are therefore useful for analyzing spatial relations of interacting populations (Pielou, 1962; Fowler & Antonovics, 1981; Schellner *et al.*, 1982; Galiano, 1982a). Where applicable, these methods are very informative, but in many field situations the neighbor methods are difficult to use because individual plants cannot be reliably distinguished and interplant distances cannot be measured without disturbing the vegetation. In such cases, methods based on quadrat or transect samples are preferable. This paper is concerned with methods for detecting grain size of single-species populations using quadrat or transect samples. These methods are broadly categorized as square wave or sine wave models (Ripley, 1978).

Square wave methods, including hierarchical analysis of variance and related techniques, have a long tradition of botanical usage. Hierarchical ANOVA has been applied to both grid and transect data (Greig-Smith, 1952; Kershaw, 1957). The general approach can be used with a variety of dispersion indices (Bouxin & Gautier, 1979, 1982). While the method has been used successfully, four problems are generally recognized: 1) block sizes are restricted to integral powers of two, 2) results are affected by the starting position on the grid or transect, 3) variances at different block sizes are not independent, and 4) patches and gaps are confounded. Confounding of patches and gaps can cause the variance peak to drift left or right of the true block size (Usher, 1969). In random patterns, the peak variance of hierarchical ANOVA usually occurs at half the sum of patch and gap sizes (Errington, 1973). Modifications of hierarchical ANOVA that do not depend on starting position were proposed by Hill (1973) and Usher (1975). Hill's two-term local variance method has the added advantage of estimating variance at any integral block size. All of these methods produce non-independent variance estimates for different block sizes, so conventional significance tests are not valid. Mead (1974) devised a test for pattern that can be applied simultaneously at several levels of a hierarchical ANOVA. Zahl (1974) adapted Scheffé's test for linear contrasts to contiguous quadrat data, producing a method that permits significance tests and, like the two-term local variance method, can use overlapping blocks. A major innovation in pattern analysis was Goodall's (1974) use of randomly paired quadrats. This technique uses any integral block size, is not affected by the starting position, and yields independent variance estimates at each block size.

Sine wave methods analyze spatial autocorrelation functions by Fourier transformation to variance spectra (Chatfield, 1980). Untransformed autocorrelation functions have also been used to study plant pattern (Gloaguin & Gautier, 1981). Bartlett (1964) introduced spectral analysis to plant ecology, but among ecologists oceanographers are the most extensive users of spectral analysis (Platt & Denman, 1975). Legendre *et al.* (1981) developed a version of spectral analysis appropriate for non-metric data. Spectral analysis estimates variance at any block size and allows use of several statistical tests for non-random pattern (Ripley, 1978; Chatfield, 1980).

Several previous papers have compared two or more of these methods (Hill, 1973; Usher, 1975; Zahl, 1977; Ripley, 1978; Ludwig & Goodall, 1978; Goodall & West, 1979). We are not satisfied with existing comparisons for two reasons. First, the random pairing method, which was praised by Pielou (1977) and has fared well in tests against other square wave methods (Ludwig & Goodall, 1978; Goodall & West, 1979), has not been compared with spectral analysis, which was strongly recommended by Ripley (1978) and is the most popular method in aquatic ecology (Platt & Denman, 1975). Second, not all comparative studies have considered the abilities of the methods to detect patch size over a range of simulated patterns from very simple to highly stochastic. Patterns in field data are obscured by various extraneous sources of variance, so it is important to know how the methods perform as extraneous variation increases. The major goal of this paper is to compare the abilities of random pairing and spectral analysis to detect patch size. Hierarchical ANOVA and two-term local variance methods are included because they have been widely used. Comparisons are based on simulated transects that range in complexity from deterministic cycles to cycles of random length.

Methods

Pattern analysis methods

Hierarchical ANOVA (Greig-Smith, 1952), two-term local variance (Hill, 1973), random pairing (Goodall, 1974) and spectral analysis (Platt & Denman, 1975) were used to compute variance at the various block sizes. The block sizes of both the first peak and the maximum peak were compared to the correct patch size. Variances were rounded to two significant figures to minimize effects of spurious peaks.

Hierarchical ANOVA, two-term local variance, and random pairing computations were performed in double-precision arithmetic using programs written by S.R.C. in SAS matrix language (SAS Institute, 1979). Spectral analysis was computed by the SPECTRA program (SAS Institute, 1979). The autovariance function was smoothed using Tukey's lag window (Chatfield, 1980).

Simulated transects

Each transect consisted of 512 units with a binary (presence/absence) data record for each unit, and contained 10 patches (clumps of units with 'presence' records) with a gap (series of 'absence' records) of at least one unit between each patch. Average patch size was 8 units, so that hierarchical ANOVA yielded a variance estimate of the exact patch size. The simulated transects followed one of five different combinations of fixed or stochastic patch and gap lengths. Names of transect types are of the form 'patch type–gap type' (e.g. Fixed–Random refers to a fixed patch lengths and a random gap length).

For Equal–Equal transects (EE), both the patch and gap length were set at 8 units. When patch and gap sizes are equal, many of the factors that bias positions of the peak are eliminated (Errington, 1973).

In Fixed–Fixed transects (FF), patch length was 8 units and the gap length was 43 units. In this situation pattern analysis methods may be influenced by both patch and gap length, and therefore overestimate patch size (Usher, 1969; Errington, 1973).

Fixed–Random (FR) transects introduced a stochastic element in the gap length. Gap length was 43 $\pm$ 2 units (uniform distribution) while the patch length remained 8 units. Analysis of such transects is complicated by the effects of the mean gap length being more than the patch length and the variability of the gap length.

Random–Fixed (RF) transects were complicated by variable patch length of 8 $\pm$ 2 units (uniform distribution). Analyses were also affected between the gap length and the mean patch length.

The Random–Random transects (RR) combined uniformly distributed random variation of $\pm$2 units in both the patch and gap length. The mean gap length (43 units) remained larger than the mean patch length (8 units).

The random pairing method was applied to three additional types of transects. 1) The effects of increasing variability of patch length were examined by analyzing simulated transects on which patches ranged in length from 0 to 16 units with mean patch length of 8. All possible patch lengths were equally probable. 2) The sensitivity of the random pairing method to random independent patterns was determined by analyzing simulated transects in which the score (0 or 1) of each unit was independent. The probability of presence was identical for each unit, and varied between 0.1 and 0.5 for different simulations. 3) The effects of irregular structure were studied by analyzing transects on which patches of various length (4, 8, 14, or 20 units) were randomly placed.

All transects were simulated by programs written by S.R.C. in SAS matrix language (SAS Institute, 1979). Simulated random variables were obtained as unformly distributed pseudo-random variates (SAS Institute, 1979).

Field data

Field data were collected from oligotrophic Roach Lake, at the University of Notre Dame Environmental Research Center (sec. 7 of T43N R8E, Vilas Co., Wisconsin, and sec. 10 of T44N R42W, Gogebic Co., Michigan, U.S.A.). During the summer of 1981 line transects approximately 28 m long were placed parallel to depth contours at depths between 1 and 3 m. Using SCUBA, presence or absence of each species was recorded for each 5 cm segment of the transects.

Results

Methods comparison

Patch size along the simulated transects was estimated using both the first peak and the highest peak calculated from the four different methods of pattern analysis (Table 1). To account for possible effects of starting position, average results using eight randomly chosen starting positions were computed. The first peak indicated patch size more accurately than the more commonly used highest peak.

In our preliminary studies, we found that results of any single random pairing analysis were highly variable and often did not correctly identify patch sizes. In subsequent applications we averaged results of eight separate analyses because the standard error of the mean first peak position from eight analyses was less than one unit. As the number of analyses was increased, the averaged result tended toward the correct patch size.

The random pairing method, as amended, correctly detected the patch size in all five of the simulated patterns (Table 1). Increasing the mean gap length and increasing the randomness of the simulation models did not cause a shift in the first peak position from the correct patch size of 8 units. The highest peak fell at approximately one half of the total patch and gap size in all models except EE.

Hierarchical ANOVA and two-term local variance detected the correct patch size in the simplest pattern, EE, but failed when the gap size was increased (FF pattern), or if randomness was added to either the patch or gap size or both (FR, RF and RR patterns). Both hierarchical ANOVA and two-term local variance peaked to the right of the correct patch size. Hierarchical ANOVA showed a peak at the next larger patch size. The two-term local variance method showed a peak at approximately one half of the total patch and gap size. For both of these methods, the first peak and the highest peak coincided.

Spectral analysis failed to detect the correct patch size in all simulated patterns. In the FF pattern it underestimated the actual patch size of 8. In the patterns with randomness, variance spectra peaked at patch sizes larger than the actual patch size. In the RR pattern, the first peak indicated a patch size one half the total patch and gap size. The highest peak obtained from spectral analysis fell very near the scale of a full cycle (patch + gap) in the FF, FR, RF and RR patterns.

Random pairing method: further analysis

The accurate detection of patch size by the random pairing method prompted us to explore its capabilities in more detail. Despite increasing variability in the size of simulated patches, the random

Table 1. Patch size estimated by four methods of pattern analysis for five types of simulated transects: Equal–Equal (EE), Fixed–Fixed (FF), Fixed–Random (FR), Random–Fixed (RF), and Random–Random (RR). Positions of the first and highest peak are tabulated for each method. The standard deviation of peak position in eight runs from randomly chosen starting points is listed in parentheses, unless equal to zero.

Method	First peak					Highest peak				
	EE	FF	FR	RF	RR	EE	FF	FR	RF	RR
Hierarchical ANOVA	8	16	16	14.3 (1.0)	16	8	16	16	14.3 (1.0)	16
Two-term local variance	8	22	22	22	22	8	22	22	22	22
Random pairing	7.9 (0.067)	7.9 (0.048)	7.6 (0.279)	7.7 (0.504)	8.3 (0.620)	24.1 (0.172)	29.9 (1.67)	24.4 (0.808)	25.4 (0.963)	23.3 (0.882)
Spectral analysis	3.2	12.5	16.6 (0.104)	14.5 (0.775)	25.6	5.3	51.2	51.2	51.2	51.2

pairing method closely approximated the true mean patch size (Fig. 1). Both the average position of the first peak and the position of the first peak of the pooled variance versus block size graph were near the true patch size.

For field applications it is desirable to compare the variance estimated by the random pairing method with the expected variance for binary data from a completely random, independent pattern. Suppose P is the proportion of sampling units that contain the species of interest, and Q is the proportion of sampling units that do not contain the species. Hence $P + Q = 1$. Consider the variance due to blocks of n sampling units. If all sampling units are independent, then the binomial distribution gives nPQ as the total variance at block size n. The total variance at smaller block sizes is $(n-1)PQ$. Therefore the variance due to block size n alone is $nPQ - (n-1)PQ = PQ$.

We tested this inference using Monte Carlo simulations. Transects of 100 independent sampling units were generated for selected values of P, and the random pairing method was used to estimate the variance at selected block sizes. Values of P between 0.1 and 0.5 produced values of PQ between 0.09 and 0.25, which were closely matched by the random pairing method (Fig. 2, left). Results shown are based on 20 transects at block size 10. Similar results were obtained at all block sizes studied (2, 4, 5, 8, 15, 16, and 20). The variance estimated by the random pairing method closely approaches PQ in samples as small as 10 transects (Fig. 2, center). Results shown were simulated with $P = 0.2$ and variance was estimated by the random pairing method at block size 10. Similar results were obtained at all other block sizes studied (2, 4, 5, 8, 15, 16, and 20). The averaged variance versus block size graph for 20 transects with average $PQ = 0.154$ illustrates the flat variance distributions typical of independent patterns (Fig. 2, right). In sum, the simulations support the use of PQ as the reference variance indicative of independent, random pattern.

Random pairing results were not confounded by irregular arrangements of patches (Fig. 3). When patches were relatively small (4 or 8 units), the true patch size fell within the 95% confidence limits of the mean first peak position calculated from eight random pairing analyses (Fig. 3, top panel). At small patch sizes, the first variance peak was usually larger than PQ. At the larger patch sizes (14 and 20 units), first peaks of individual random pairing analyses were usually less than PQ and underestimated true patch size. However, the mean position of the first peak larger than PQ accurately estimated patch size in all simulations (Fig. 3, center panel). When pooled variances from eight random pairing analyses were plotted against block size, the first peak was usually larger than PQ and provided a good estimate of true patch size (Fig. 3, lower panel).

The random pairing method was applied to field data for *Juncus pelocarpus* f. *submersus* (Fassett) growing at 1 m depth (Fig. 4). The first peak of eight pooled variance–block size curves lies at 40 cm. The peak is above PQ, indicating more variance than

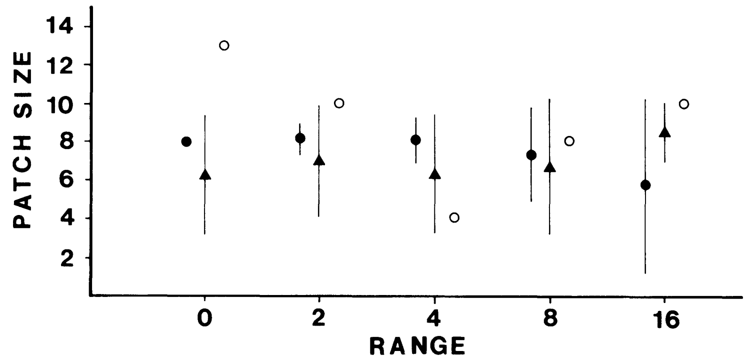

Fig. 1. Patch size estimated by the random pairing method versus range of patch length in simulated transects on which patch length was a uniformly distributed random variable with mean = 8. For each range, actual mean patch length (solid circle), average position of the first peak of eight random pairing analyses (triangle), and position of the first peak in the pooled variance–block size graph (open circle) are plotted. Vertical bars denote ± S.D.

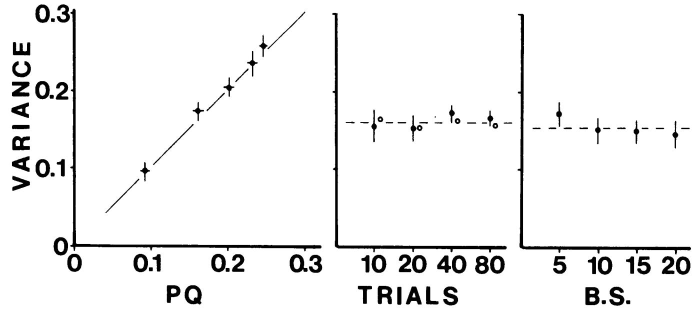

Fig. 2. Variance estimated by the random pairing method versus *PQ* (left), number of trial transects (center), and block size (right). Vertical bars show ± S.E. In the left panel, horizontal bars show ± the standard error of *PQ*, and the diagonal line denotes variance = *PQ*. In the center panel, the horizontal line is the theoretical *PQ* = 0.16, and open circles show actual mean *PQ* of the random transects. In the right panel, the horizontal line is the average *PQ* = 0.154 of 20 simulated transects.

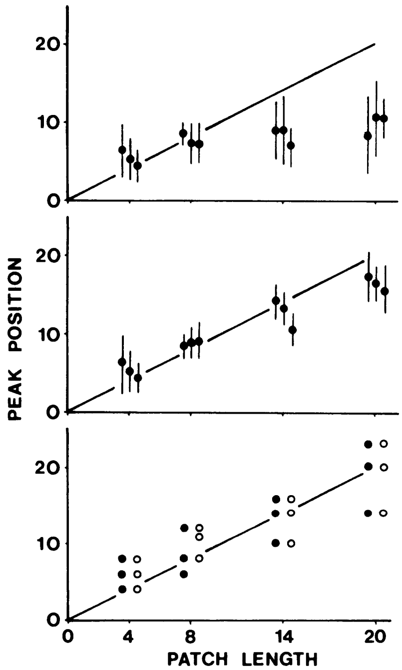

Fig. 3. Variance estimated by the random pairing method versus true patch size for transects with randomly placed patches of 4, 8, 14, and 20 units. Diagonal lines on each panel denote peak position equal to true patch size. Results are shown for three independent transects 500 units long containing ten patches each. Vertical bars are 95% confidence limits from eight random pairing analyses. Upper panel: first peak position versus true patch size. Center panel: position of the first peak larger than *PQ* versus true patch size. Lower panel: peaks of the pooled variance graph versus true patch size; solid circles denote first peaks, open circles denote first peaks larger than *PQ*.

would be produced by a random, independent pattern. The average position of the first peak in 8 analyses lies at 35 cm. The highest peak of the pooled variances lay at 240 cm. The average highest

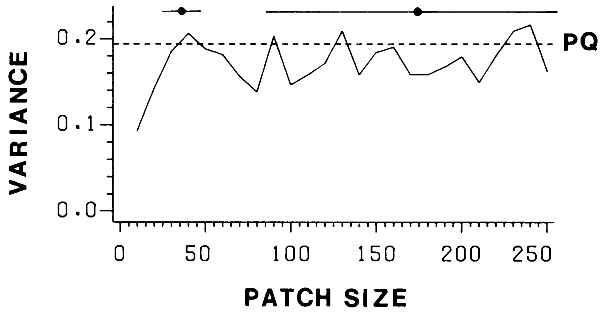

Fig. 4. Pooled variance of eight random pairing analyses versus patch size (cm) for *Juncus pelocarpus* f. *submersus*. The horizontal dashed line denotes *PQ*. Closed circles show the average positions of the first and highest peaks in the eight analyses, and horizontal bars show ± S.D.

peak position for the eight individual analyses was 180 cm, with a rather large standard deviation of 90.2 cm.

Discussion

Our results concur with those of previous studies showing that the random pairing method is superior to the hierarchical ANOVA and two-term local variance methods of pattern analysis. Hierarchical ANOVA and two-term local variance analyses do not distinguish patches from gaps (Pielou, 1977). Therefore, peak positions lie between patch and gap sizes. For all transects except EE, the variance peak of hierarchical ANOVA shifted to 16 units, consistent with results of Errington (1973). The variance peak of the two-term local variance method shifted to 22 units for all transects except EE.

The two-term local variance results were independent of starting position on the transect, as noted by Hill (1973). Peak positions of hierarchical ANOVA were only weakly affected by starting positon, even though variance at each block size depended on starting position.

Random pairing proved superior to spectral analysis in our comparisons. Present results do not demonstrate the sensitivity of spectral analysis to small-scale patterns suggested by Usher (1975). The highest peak in spectral analysis detected full cycles (patch plus gap), and the method is therefore useful when an estimate of full cycle length will suffice. However, spectral analysis, unlike random pairing, was unable to partion the components of grain.

Five advantages of the random pairing method emerge from our analyses. 1) The sum of patch and gap length is indicated by twice the block size of the highest peak of the variance–block size graph. 2) Patch size is accurately indicated by the position of the first peak of the variance–block size graph. 3) The expected variance of an independent, random pattern *(PQ)* provides a convenient reference point for identifying meaningful peaks and troughs. The first peak larger than *PQ* is a more reliable index of patch size than first peak, especially when patch size is large relative to quadrat size. 4) Mean patch length is accurately detected even when patch length is stochastic. 5) Patch size is accurately detected when patches are irregularly (randomly) placed. Other advantages of the random pairing method are discussed by Pielou (1977), Ludwig & Goodall (1978), and Goodall & West (1979).

The variability of individual random pairing analyses was noted by Ludwig & Goodall (1978), who solved this problem by calculating variances for all possible point pairs at each spacing. This exhaustive pairing analysis demands substantial computer time for large data sets. Our approach, using independent random samples of the set of all possible point pairs, is less costly to compute than exhaustive pairing analysis, yet yields reliable results. Confidence intervals for mean position of the first variance peak larger than *PQ* usually included the true patch size. Such confidence intervals are especially useful for interpretations of field data. No confidence interval is available when pooled variance from replicate analyses is plotted versus block size. However, first peaks of pooled variance curves were always near the true patch size.

Some statistical objections have been raised against the random pairing method. Zahl (1977) and Ripley (1978) criticize Goodall's (1974) test statistics. Zahl (1977) showed that random pairing was less likely to detect non-randomness, and more susceptible to incorrect decisions about the significance of departure from randomness, than both hierarchical ANOVA and Zahl's (1974) method. Goodall & West (1979) agree that hierarchical ANOVA has greater statistical power than random pairing. These statistical points do not negate the ecological usefulness of random pairing. The ubiquity of significantly non-random pattern is a firmly established property of plant communities. Departures from randomness, which hardly constitute novel observations, are readily tested for significance by a variety of methods (Pielou, 1977). However, mechanisms that generate and maintain pattern are poorly understood, and accurate descriptions of pattern are necessary before such mechanisms can be investigated (Schaffer & Leigh, 1976; Pielou, 1981). Random pairing is a superior method for describing pattern.

Once the grain size of pattern is identified, supplementary studies are needed to identify the underlying causes of pattern. For example, our field data showed a patch size of 30 to 50 cm (Fig. 4). Nests of pumpkinseed sunfish (*Lepomis gibbosus* L.) are abundant in Roach Lake and approximately the proper size to generate this pattern. The role of fish nests in vegetation patterns is now being investigated by direct observations of macrophytes colonizing marked nests and experimental manipulations of plants associated with artificial nests.

Results presented here are limited to single-species patterns. Multi-species patterns in contiguous quadrats have been studied by combining multivariate analyses with hierarchical and local variance approaches (e.g. Goodman, 1978; Whittaker *et al.*, 1979; Galiano, 1982b). Distance matrices for species or quadrats could readily be constructed by random pairing. Ordination of such distance matrices to investigate multi-species patterns is an interesting prospect for future research.

References

Bartlett, M. S., 1964. The spectral analysis of two-dimensional point processes. Biometrika 51: 299–311.

Bouxin, G. & Gautier, N., 1979. Structure de la strate herbacée dans deux pelouses calcaires du district mosau. Oecol. Plant. 14: 219–231.

Bouxin, G. & Gautier, N., 1982. Pattern analysis in Belgian limestone grasslands. Vegetatio 49: 65–83.

Chatfield, C., 1980. The analysis of time series. Halsted, N.Y. 268 pp.

Errington, J. C., 1973. The effect of regular and random distributions on the analysis of pattern. J. Ecol. 61: 99–105.

Fowler, N. & Antonovics, J., 1981. Competition and coexistence in a North Carolina grassland. I. Patterns in undisturbed vegetation. J. Ecol. 69: 825–842.

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

Galiano, E. F., 1982b. Detection et mesure de l'heterogénéité spaciale des espèces dans les pâturages. Acta Oecol. (Oecol. Plant.) 3: 269–278.

Gloaguin, J. C. & Gautier, N., 1981. Pattern development of the vegetation during colonization of a burnt heathland in Brittany (France). Vegetatio 46: 167–176.

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. & West, N. E., 1979. A comparison of techniques for assessing dispersion patterns. Vegetatio 40: 15–27.

Goodman, D., 1978. Applications of eigenvector analysis in the resolution of spectral pattern in spatial and temporal ecological sequences. INTECOL 2: 12–16.

Greig-Smith, P., 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Ann. Bot. 16: 293–316.

Hill, M. O., 1973. The intensity of spatial pattern in plant communities. J. Ecol. 61: 225–235.

Kershaw, K. A., 1957. The use of cover and frequency in the detection of pattern in plant communities. Ecology 38: 291–299.

Legendre, L., Fréchette, M. & Legendre, P., 1981. The contingency periodogram: a method of identifying rhythms in series of nonmetric ecological data. J. Ecol. 69: 965–980.

Ludwig, J. A. & Goodall, D. W., 1978. A comparison of paired- with blocked-quadrat variance methods for the analysis of spatial pattern. Vegetatio 38: 49–59.

Mead, R., 1974. A test for spatial pattern at several scales using data from a grid of contiguous quadrats. Biometrics 30: 295–307.

Pielou, E. C., 1962. Runs of one species with respect to another in transects through plant populations. Biometrics 18: 579–593.

Pielou, E. C., 1977. Mathematical Ecology. Wiley, N.Y. 385 pp.

Pielou, E. C., 1981. The usefulness of ecological models: a stocktaking. Quart. Rev. Biol. 56: 17–31.

Platt, T. & Denman, K. L., 1975. Spectral analysis in ecology. Ann. Rev. Ecol. Syst. 6: 189–210.

Ripley, B. D., 1978. Spectral analysis and the analysis of pattern in plant communities. J. Ecol. 66: 965–981.

SAS Institute, 1979. SAS User's Guide. Raleigh, N.C. 494 pp.

Schaffer, W. M. & Leigh, E. G., 1976. The prospective role of mathematical theory in plant ecology. Syst. Bot. 1: 209–232.

Schellner, R. A., Newell, S. J. & Solbrig, O. T., 1982. Studies on the population biology of the genus Viola. IV. Spatial pattern of ramets and seedlings in three stoloniferous species. J. Ecol. 70: 273–290.

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.

Whittaker, R. H., Niering, W. A. & Crisp, M., 1979. Structure, pattern, and diversity of a Mallee community in New South Wales. Vegetatio 39: 65–76.

Zahl, S., 1974. Application of the S-method to the analysis of spatial pattern. Biometrics 30: 513–524.

Zahl, S., 1977. A comparison of three methods for the analysis of spatial pattern. Biometrics 33: 681–692.

Accepted 18.3.1983.