

A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation

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Abstract. Spatial heterogeneity is a characteristic of most natural ecosystems which is difficult to handle analytically, particularly in the absence of knowledge about the exogenous factors responsible for this heterogeneity. While classical methods for analysis of spatial point patterns usually require the hypothesis of homogeneity, we present a practical approach for partitioning heterogeneous vegetation plots into homogeneous subplots in simple cases of heterogeneity without drastically reducing the data. It is based on the detection of endogenous variations of the pattern using local density and second-order local neighbour density functions that allow delineation of irregularly shaped subplots that could be considered as internally homogeneous. Spatial statistics, such as Ripley's *K*-function adapted to analyse plots of irregular shape, can then be computed for each of the homogeneous subplots. Two applications to forest ecological field data demonstrate that the method, addressed to ecologists, can avoid misinterpretations of the spatial structure of heterogeneous vegetation stands.

Keywords: Local density function; Point pattern; Ripley's *K*-function; Second-order local neighbour density function.

Abbreviation: CSR = Complete spatial randomness.

Introduction

Heterogeneity is a characteristic of natural ecosystems that can be observed both in space and time (Kolasa & Pickett 1991). In a spatial context, heterogeneity occurs when some quantitative or qualitative descriptors of an ecosystem vary significantly from one location to another. This variation can result either from exogenous factors, i.e. external to the biological community under study (soil, climate, etc.) or endogenous factors, i.e. inherent to the system's internal functioning (life-history variation, competition, etc.). For instance, soil properties, water availability and topography influence plant growth, population density or species abundance and consequently

affect vegetation dynamics and thus spatial structure (e.g. Newbery & Proctor 1984; Peterson & Pickett 1990; Tilman 1993; Huston & DeAngelis 1994; Couteron & Kokou 1997; Sabatier et al. 1997; Moreno-Casasola & Vázquez 1999). Moreover, natural processes such as birth, development, reproduction, competition, predation and senescence can induce a spatially heterogeneous pattern of populations (e.g. Sterner et al. 1986; Kenkel 1988; Forget 1994; Blate et al. 1998; Couteron 1998; Desouhant et al. 1998). Because the spatial organization of individuals in an ecosystem depends, to a great extent, on biological processes (Begon et al. 1986), heterogeneity of the spatial structure is often considered as the expression of a functional heterogeneity (Kolasa & Rollo 1991).

As far as sessile organisms are concerned, heterogeneity applies to the point pattern describing their physical location. Spatial point patterns that vary in a systematic way from place to place are thus called heterogeneous (Ripley 1981). However, interpretations of spatial variations of point locations in a specific study area may differ depending on observation scales: as compared with the size of the study area, fine-scale variations can generally be considered as elements of structure and broad-scale variations as heterogeneity (e.g. Wiens 1989; Kolasa & Rollo 1991; Holling 1992; He et al. 1994; Goreaud 2000). For instance, the patchy distribution of a tree species often determines repeated structures at a forest scale, whereas a single patch generates heterogeneity at a finer scale of a sampling plot.

Analysis of the spatial structure of heterogeneous point patterns is difficult, because the simple methods used to analyse spatial point patterns have been developed for homogeneous point patterns, i.e. for patterns resulting from stationary point processes whose properties are invariant under translation (e.g. Pielou 1969; Ripley 1981; Diggle 1983; Greig-Smith 1983; Upton & Fingleton 1985; Stoyan et al. 1987; Cressie 1993). Indeed, these methods often use indices or functions that are averaged over the whole study area and thus only

make sense for homogeneous processes. The classical exploratory approach with these methods is to compare a given point pattern to one generated by a Poisson process which corresponds to the null hypothesis of complete spatial randomness (CSR; Diggle 1983) and a stationary point process. For non-stationary processes the null hypothesis of CSR should be represented by inhomogeneous Poisson or Cox processes (see, for instance, Diggle 1983), but the corresponding mathematical tools are quite complicated (Dessard 1996; Batista & Maguire 1998). In practice, when one computes simple indices or functions of spatial statistics, one assumes, at least implicitly, that the underlying point process is stationary, i.e. that the pattern is homogeneous. This can sometimes lead to misinterpretation of spatial structure when the pattern is actually heterogeneous.

One solution is to define, within a heterogeneous study area, some smaller homogeneous subplots and to analyse the spatial structure within these separately. Two cases have to be distinguished, depending on the nature of the factor generating heterogeneity (Legendre & Legendre 1998). When an exogenous factor of heterogeneity is identified and mapped, one can partition the pattern into subplots corresponding respectively to different values of this factor. For instance, Collinet (1997; see also Forget et al. 1999 and Goreaud & Pélissier 1999) defined subplots of homogeneous edaphic properties from a soil map, in order to analyse the spatial structure of tree species in a rain forest of French Guiana. The problem is more difficult to solve when no exogenous factor responsible for heterogeneity of the point pattern is known.

This paper proposes a practical approach, intended for ecologists, based on the detection of endogenous variation of the pattern using local density and second-order local neighbour density functions that allow delineation of irregularly shaped and internally homogeneous patterns. The basic theory and functions are presented, followed by two applications of forest ecological data sets to demonstrate how the method can avoid, in simple cases of heterogeneity, misinterpretations of the spatial structure from Ripley's (1976, 1977) K -function which has been previously adapted to analyse plots of irregular shape (Goreaud & Pélissier 1999).

Theory

When no exogenous factor responsible for heterogeneity of a point pattern is identified, some homogeneous subplots can be defined from endogenous local properties of the pattern. Let us call $f(x,y)$ such a local property related to the point pattern of interest (e.g. density, mean height, species composition). The map of $f(x,y)$ can play

the same role as the map of an exogenous factor: homogeneous subplots can be defined as those that share the same or arbitrarily similar ranges of values of $f(x,y)$. In this paper, we propose the use of local density and second-order local neighbour density functions as endogenous factors to define homogeneous subplots.

Local density

Density, which corresponds to the number of points per unit area, is the simplest first-order characteristic of a point pattern. At any location, a value of this density is estimated on a small sampling region of area s by:

$$\hat{n}(x,y) = N(s) / s \quad (1)$$

where $N(s)$ corresponds to the number of points in s . For a homogeneous Poisson process of intensity λ , we have:

$$E [n(x,y)] = \lambda \quad (2)$$

In this case, $N(s)$ follows a Poisson distribution with parameter λs .

In this paper, the values of $\hat{n}(x,y)$ were estimated by computing $N(s)$ at each node of a systematic grid of elementary side a and covering the whole study area. The sampling region s is a circle of radius r , centred on the corresponding node. Thus, at the locations (x,y) near the boundary of the study area, the number of points in the sampling region is underestimated. In order to take this edge effect into account, we used the correction factor proposed by Ripley (1977) for his K -function: the contribution of point i to $N(s)$ corresponds to the inverse of the proportion of the perimeter of the circle centred at the node and passing through i , which is inside the study area (e.g. Goreaud & Pélissier 1999).

Note that, if $a < 2r$, the sampling regions overlap and the corresponding values of $N(s)$ are not independent, a situation quite usual in practice when the study region is small and the number of sampling points is high. Non-independence between samples prohibits formal statistical tests of the frequency distribution of $N(s)$ against its theoretical distribution. Therefore, we used a less rigorous but pragmatic approach, which consists of a combined analysis of the frequency distribution and the map of $N(s)$ to detect first-order heterogeneity and to partition the pattern into homogeneous subplots. Fig. 1 illustrates this approach on a virtual 1 ha plot where the two parts (south and north) correspond to independent realizations of Poisson processes with intensities 0.01 and 0.05, respectively (Fig. 1a). The frequency distribution of $N(s)$ has a clear bimodal shape corresponding to the mixture of the two Poisson distributions (Fig. 1b).

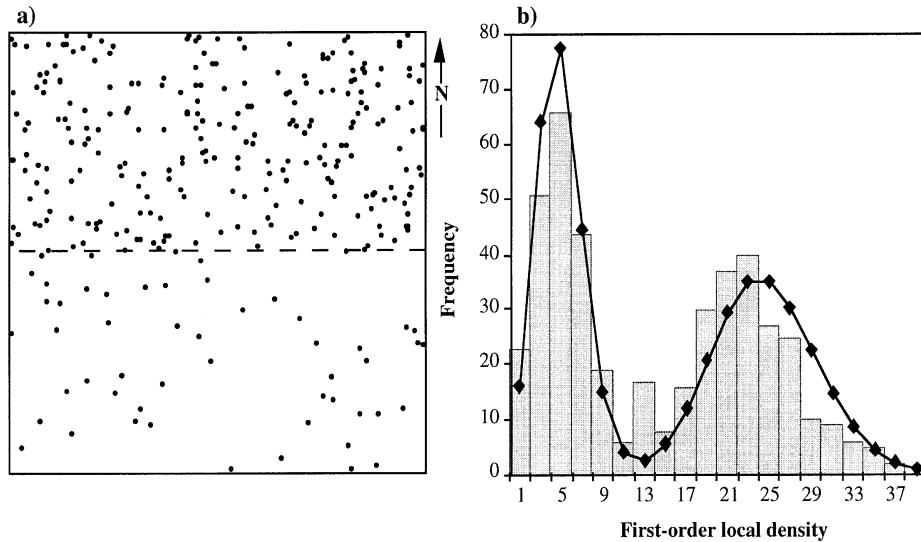


Fig. 1. Simulated heterogeneous point pattern in a 100 m × 100 m virtual plot. **a.** The two parts (south and north) correspond to independent realisations of Poisson processes with intensities 0.01 and 0.05, respectively. **b.** Frequency distribution of the local density function $N(s)$, computed in circles of radius 12.5 m regularly distributed on a systematic grid of 5 m × 5 m. The curve corresponds to the theoretical values expected for the mixture of the two Poisson distributions.

Second-order local neighbour density

The second-order property of a point pattern is related to the joint density of the occurrence of two points at a given distance (Ripley 1977; Diggle 1983). It characterises the number of points encountered in the neighbourhood of an arbitrary point of the pattern and allows interpreting the spatial structure in terms of interaction processes (aggregation, inhibition, etc.).

Sometimes, overall (first-order) local density is homogeneous while the fine-scale structure varies from one place to another within the study area. In this case the second-order characteristic of the pattern is termed heterogeneous. To allow close inspection of these characteristics of spatial patterns, we define an individual second-order local neighbour density function:

$$n_i(r) = N_i(r)/\pi r^2, \quad (3)$$

where $N_i(r)$ corresponds to the number of neighbours within a distance r of a given point i of the pattern. For points located near the boundary of the study area, the edge effect is corrected, as previously, using Ripley's (1977) local correcting factor. The function $n_i(r)$ is proportional to the individual function proposed by Getis & Franklin (1987) from Ripley's K -function and can be interpreted in terms of spatial structure around each point i . For a Poisson pattern of N points in an area A , the expected value of $n_i(r)$ at any distance r is $(N-1)/A$.

Compared to this constant value, a given estimation of $n_i(r)$ gives an idea of the local structure (aggregated or regular) around point i . Because $n_i(r)$ is linked to a specific point, it cannot be considered as a stochastic function of the process so no formal test is available. However, the frequency distribution and map of the values of $n_i(r)$ at a given distance r can be used, as above, to detect second-order heterogeneity.

Spatial analysis within homogeneous subplots

We chose to analyse spatial structure within homogeneous subplots by use of Ripley's K -function, which has the advantage of describing the spatial structure at different ranges simultaneously (Cressie 1993) and is a standardized measure that allows comparison of spatial patterns of various intensities. It has been used recently in many studies in plant ecology e.g. desert shrubs (Skarpe 1991; Haase et al. 1996), temperate (Duncan 1991; Moeur 1993; Szwagrzyk & Czerwczak 1993; Goreaud et al. 1998) and tropical forests (Pélissier 1998; Barot et al. 1999; Forget et al. 1999).

Under the assumptions of homogeneity (or stationarity) and isotropy (invariance by rotation) Ripley's K -function is defined for a process of intensity λ , so that $\lambda K(r)$ is the expected number of neighbours in a circle of radius r centred on an arbitrary point of the pattern (Ripley 1977 for more details). Instead of the K -function, the modified L -function, the classical estimator for which

$$\hat{L}(r) = \sqrt{\hat{K}(r) / \pi} - r \quad (4)$$

is generally preferred (Besag 1977). $\hat{L}(r)$ has a more stable variance than $\hat{K}(r)$ and is easier to interpret: $L(r) = 0$ under CSR; $L(r) < 0$ indicates that there are fewer neighbours within a distance r off an arbitrary point of the pattern than expected under CSR, so that the pattern tends to be regular; $L(r) > 0$ indicates that there are more neighbours within a distance r off an arbitrary point of the pattern than expected under CSR, so that the pattern tends to be clustered. For points closer to the boundary of the plot than to a neighbouring point of the pattern, $\hat{K}(r)$ requires an edge effect correction. In a previous paper, Goreaud & Pélissier (1999) introduced procedures that extend the use of Ripley's (1977) local correcting factor of edge effects to analysis of plots of irregular shape.

Worked examples: two applications in forest ecology

Data sets

We tested our approach on two examples taken from the field of forest ecology. The first data set represents a mixed *Quercus petraea*-*Fagus sylvatica* temperate forest stand in the managed Haye Forest, France. In this stand, tree growth and survival are highly dependent on the spatial interactions between trees (Goreaud et al. 1999). In order to understand the inter-specific relations between the species, Goreaud (2000) analysed a 1 ha plot in a 140 yr-old stand (Pardé 1981). He showed that this plot exhibited a structural heterogeneity of density, mean height of trees and mixture rate of trees with $\text{DBH} \geq 10$ cm, and hypothesised that this reflected heterogeneity of a soil factor. As no soil data were available, we used the local density (both species pooled) as an endogenous indicator of heterogeneity.

The second example data set is from an experimental plot in moist evergreen forest of Uppangala, Western Ghats, India (Pascal & Pélissier 1996), designed to monitor and study the long-term natural dynamics (Elouard et al. 1997a, b). In this forest, Pélissier (1997, 1998) showed a macro-heterogeneity of the spatial structure of trees with $\text{DBH} \geq 10$ cm, which was related to local variations of the dynamic processes ensuring forest renewal. In this paper a 0.8 ha plot with apparently homogeneous first-order characteristics, but heterogeneous second-order properties, was analysed.

Methods

In these examples we used local density and second-order local neighbour density functions as parameters to delineate contour lines of homogeneous subplots. The theory of regionalized variables gives a general framework to interpolate contour lines from values estimated at the nodes of a systematic grid (Matheron 1965; Cressie 1993). For the sake of simplicity, we used linear interpolations (Cleveland 1993) from values of local density and the second-order local neighbour density functions estimated at the nodes of a 10 m \times 10 m grid using the Lowess method (local weighted scatter-plot smoothing; Cleveland 1979). Local regression was computed over a number n of nearest neighbours, chosen to minimise the mean smoothing error (Cleveland & Devlin 1988). After drawing the contour lines, the homogeneous subplots were approximated by polygons in order to calculate Ripley's K -function with edge effect correction for plots of irregular shape.

In order to test the null hypothesis of spatial randomness, we computed a 95% confidence interval of $\hat{L}(r)$ using the Monte Carlo method (Besag & Diggle 1977) with 1000 simulated random patterns. At a given distance r , a value of $\hat{L}(r)$ outside the confidence interval is interpreted as a significant departure from CSR towards clustering or regularity. When the function stays outside the confidence interval at large distances, we can consider that the pattern is heterogeneous, because most of the points are concentrated in a dense part of the study area which could be interpreted as a cluster approaching the size of the study area. This cluster could not be considered as a repeated structure at the scale of the study region.

Computer programs used were implemented in C language and can be obtained on request to the authors. Modules of spatial data analysis and graphical display are at present available with documentation from the ADE-4 homepage (<http://pbil.univ-lyon1.fr/ADE-4/>; Thioulouse et al. 1997). The procedures to compute Lowess and to draw the contour lines were performed using ADE-4 package.

Results for example 1: first-order heterogeneity

We computed local density in circles of radius 12.5 m centred at the nodes of a 5 m \times 5 m systematic grid covering the 1 ha plot of the managed Haye Forest, France. This design allowed study of the spatial structure up to 25 m, but implied that the sampling regions were not independent. However, the non-Poisson and slightly bimodal shape of the frequency distribution of $N(s)$ (number of points per circle) indicated heterogene-

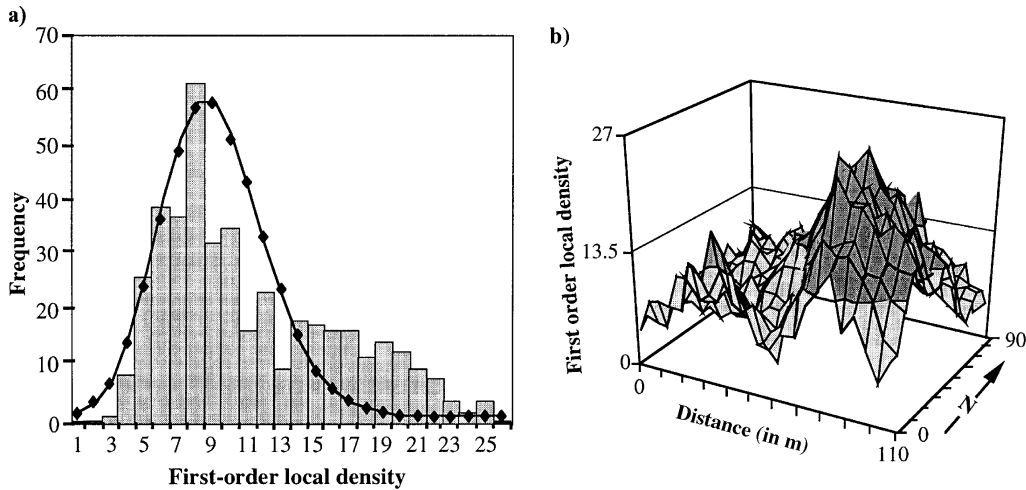


Fig. 2. Distribution of the local density function computed in circles of radius 12.5 m centred at the nodes of a 5m × 5m systematic grid in a 110m × 90 m plot of the managed mixed *Quercus-Fagus* stand of Haye Forest, France (example 1). **a.** Frequency distribution of $N(s)$ with the theoretical curve of the homogeneous Poisson distribution expected with an intensity parameter corresponding to the first mode. **b.** Spatial distribution of $N(s)$.

ity of the first-order characteristic of the pattern and allowed identification of two ranges of values [3;13] and [14;26] (Fig. 2).

In order to partition the plot into homogeneous subplots, we used the Lowess method to predict the values of the local density function at each node of a 10 m × 10 m systematic grid. The local regression was computed over the 12 nearest sampling points to minimise the mean smoothing error. We then delineated the contour lines of $N(s) = 13$ and $N(s) = 14$, by interpolation of the predicted values (Fig. 3). The use of a buffer zone between the two subplots improved their respective homogeneity by avoiding unclear transitions between the dense and sparse parts of the plot.

We then computed the L -function for the entire rectangular plot and within the two polygonal subplots. Trees in the buffer zone were not taken into account. In the entire plot (Fig. 4a) the curve exhibited a divergence towards clustering at large distances due to broad-scale heterogeneity related to the presence of a denser part. This prevents interpretation of fine-scale structure from the whole data set because $L(r)$ averages the characteristic structures of the two subplots. On the contrary, when computed within each subplot, the L -function remained within the confidence interval at large distances, which means that each subplot was homogeneous. Both within subplots analyses exhibited a significant regularity in the range 0-8 m, but with a higher intensity in the sparse one (Fig. 4b-c).

Results for example 2: second-order heterogeneity

In the 0.8 ha plot of the moist evergreen forest of Uppangala, India, the frequency distribution of the local density $N(s)$ (not shown) was unimodal, following a theoretical Poisson distribution. But, when computed over the entire plot the L -function, although lying within the confidence interval at large distances, showed a combination of an element of attraction at small distances (1 m) with an element of repulsion in the 2-7 m range (Fig. 5a).

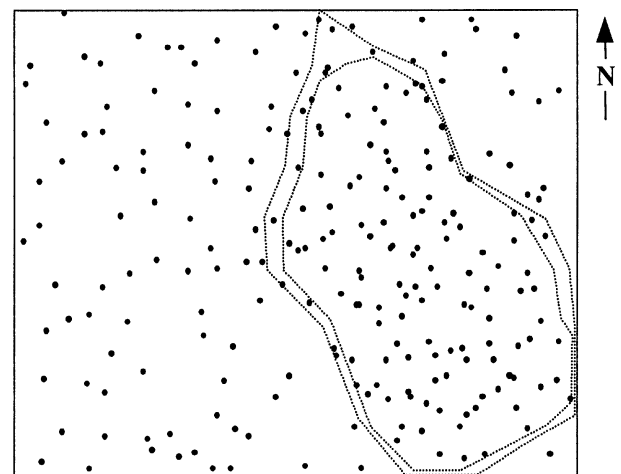


Fig. 3. Location map of 231 trees in a 110 m × 90 m plot in Haye Forest, France (example 1). The dotted lines were approximated from the contour lines of the local density, $N(s) = 13$ and $N(s) = 14$ (inner curve).

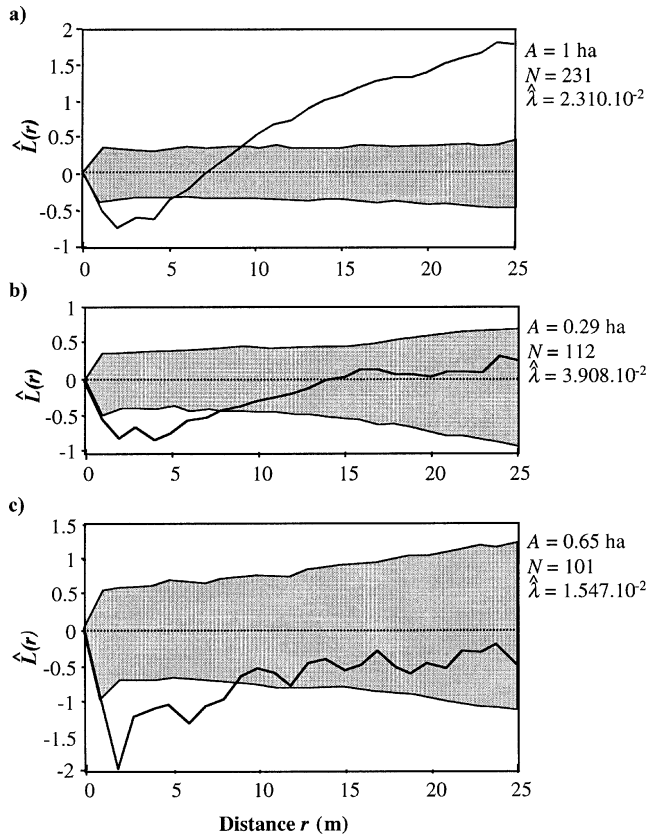


Fig. 4. Graphs of the L -function for the managed Haye Forest, France (example 1). Function computed: **a.** Over the entire $110 \text{ m} \times 90 \text{ m}$ rectangular plot; **b.** Within the polygonal dense part of the plot; **c.** Within the polygonal sparse part of the plot. Shaded envelopes correspond to the 95% confidence interval of the null hypothesis of complete spatial randomness.

We expected that the attraction effect would only concern one part of the plot so computed the second-order local neighbour density function, taking $r = 1 \text{ m}$. The frequency distribution of this statistic showed that a small proportion of trees had at least one neighbour within this distance. The spatial distribution showed, however, that these trees were more concentrated in the western part of the plot, thus representing second-order heterogeneity (Fig. 6).

In order to delineate homogeneous subplots, we used the Lowess method with the 20 nearest neighbours to predict the values of $n_i(r)$ at each node of a $10 \text{ m} \times 10 \text{ m}$ grid. We then drew by interpolation the contour line of the value $n_i(r) = (N-1)/A = 0.07262$. Twenty neighbours did not represent the minimum smoothing error, but corresponded to the range over which the smoothing error stabilised and the subplots delineated remained almost invariant. Fig. 6b shows the two polygonal

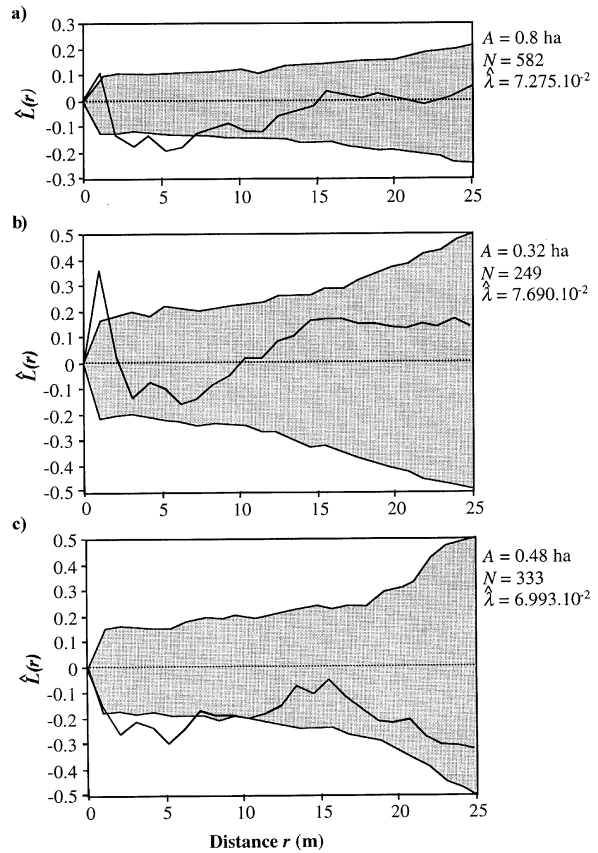


Fig. 5. Graphs of the L -function for the natural moist evergreen forest of Uppangala, Western Ghats, India (example 2). Function computed: **a.** Over the entire $100 \text{ m} \times 80 \text{ m}$ rectangular plot; **b.** Within the polygonal eastern part of the plot; **c.** Within the polygonal western part of the plot. Shaded envelopes correspond to the 95% confidence interval of the null hypothesis of complete spatial randomness.

subplots approximated from the contour line.

The L -functions computed within these subplots independently, showed that the two peaks observed in the entire plot were separate. Trees in the western part (Fig. 5b) exhibited a significant attraction effect at 1 m , while trees in the eastern part (Fig. 5c) exhibited a significant regularity in the range $2\text{--}7 \text{ m}$. This result emphasises that, even when the first-order properties of the point pattern are homogeneous, heterogeneous second-order characteristics can lead to different interpretations in terms of between-tree interactions.

Discussion and Conclusions

Because natural processes are highly dependent on the local environment (soil, topography, etc.) which is often heterogeneous, natural communities are seldom

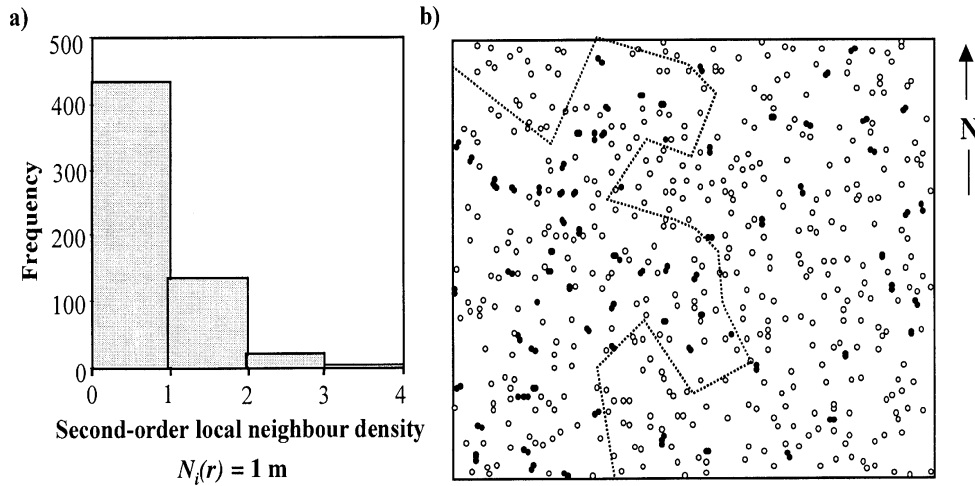


Fig. 6. Distribution of the second-order local neighbour density function computed in circles of radius 1 m centred on each point of the pattern in a 100 m \times 80 m experimental plot of the moist evergreen forest of Uppangala, Western Ghats, India (example 2). **a.** Frequency distribution of $N_i(r)$ for $r = 1$ m. **b.** Location map of 582 trees in the experimental plot with black points indicating $N_i(r) \geq 1$. The dotted line was approximated from the contour curve of the value of the second-order local neighbour density $n_i(r) = 0.07262$ at $r = 1$ m.

homogeneous. Therefore, spatial heterogeneity should be systematically investigated with the aim of being adequately taken into account in statistical analysis (Dutilleul 1993). Classical methods to analyse spatial point patterns usually involve the assumptions of homogeneity and isotropy. Our examples clearly illustrate how various kinds of heterogeneity can affect the methods of spatial data analysis, such as the frequently-used Ripley's function. Some methods dealing with anisotropy, such as orientation correlation functions (Stoyan & Benes 1991) and spectral analysis (Muggleston & Renshaw 1996) have been applied to biological data, but very few simple methods to deal with heterogeneous point patterns are available.

The heterogeneity of a point pattern can easily be detected when the available data exhibit a potential exogenous factor responsible for this heterogeneity. Even if this factor is not entirely mapped homogeneous subplots can be delineated through interpolations and contour lines. The problem is analogous when the structural heterogeneity concerns the first-order characteristics of the pattern, and the local density function can help in partitioning the pattern into homogeneous subplots. It will, however, often be more insidious when heterogeneity only affects the second-order properties of the pattern, in which case the superposition of various effects can occur. The method proposed in this paper can help in dealing with all these aspects of heterogeneity, following the principle that broad-scale environmental variations will tend to produce aggregated patterns and that these variations will be less pronounced at smaller scale. The major determinant of the pattern will then be

the nature of the interactions among individuals themselves (Diggle 1983).

The proposed approach is based on the delineation, within a heterogeneous study area, of subplots that could be considered as internally homogeneous, and characterization of the spatial pattern within these subplots. It is a general approach that could be used with most methods of spatial statistics subjected to preliminary hypotheses of homogeneity, in particular those based on distance measurements (see Diggle 1983; Upton & Fingleton 1985; Cressie 1993). However, using Ripley's (1976, 1977) second-order neighbourhood analysis adapted to analyse plots of irregular shape (Goreaud & Pélissier 1999) has the advantage of involving a set of similar functions to detect heterogeneity, to define the homogeneous subplots and then to characterise their internal spatial structure, thus reducing conceptual investment and computation time. Alternatively, this redundancy could lead to some bias such as the detection of non-significant random variations, although this risk is limited when the definition of the homogeneous subplots is carried out at a larger scale than that on which the structure of interest occurs. Such an approach is of course expected to be less precise than a statistical test of a specific spatial heterogeneous process (for instance, the spatial clustering processes in statistical epidemiology: Wartenberg & Day 1988; Diggle & Chetwynd 1991), but it is far easier to use for exploratory analysis in ecology when the underlying processes are unknown. In our examples, the method was successfully validated, as the final computation of the L -function in each homogeneous subplot stays within the confidence interval of

the null hypothesis of CSR at large distances.

The definition of homogeneous subplots will not be completely objective because the accuracy of the boundary depends on several parameters. Firstly, the local density, the number and the radius of the sampling regions limit the maximum size of the studied structures and samples may not be independent preventing the use of formal tests. Secondly, the contour delineation may vary according to the method used, linear interpolation from values predicted by the Lowess procedure allows variation of both the degree of smoothing of the local regression and the drawing resolution of the contour lines. Thirdly, the complexity of the polygons used to approximate the shape of the subplots determines the computation time and can limit the accuracy of the boundary definition. Finally, the definition of the subplots can sometimes be imprecise and a buffer zone between the different subplots can be of some use to avoid unclear transitions, as in example 1.

This paper deals with simple cases with a single factor of heterogeneity, but the method could be extended to more complex systems with several hierarchical levels of heterogeneity (Kolasa & Rollo 1991), for instance from a broad-scale exogenous macro-heterogeneity to first- and second-order fine-scale variations. The same general framework with the same adaptation of edge-corrections to irregular shapes could also be used with other functions of second-order neighbourhood analysis derived from Ripley's *K*-function and dealing with marked point patterns (Lotwick & Silverman 1982; Diggle 1983; Penttinen et al. 1992; Gouillard et al. 1995). In this case, homogeneity concerns the distribution of both the points and the marks which can be qualitative (e.g. tree species) or quantitative (e.g. tree diameter, height) characteristics of the points. This possible extension offers an interesting perspective for the study of heterogeneous multi-specific patterns or of forested landscapes with varying scales of patterns. The method may have some limits in certain cases where a density gradient exists leading to a flat local density frequency distribution. Therefore, the proposed method is no substitution for thorough measurements of heterogeneity factors, but should help ecologists to refine field investigations.

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