

# A comparison of methods for the statistical analysis of spatial point patterns in plant ecology

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**Abstract** We describe a range of methods for the description and analysis of spatial point patterns in plant ecology. The conceptual basis of the methods is presented, and specific tests are compared, with the goal of providing guidelines concerning their appropriate selection and use. Simulated and real data sets are used to explore the ability of these methods to identify different components of spatial pattern (e.g. departure from randomness, regularity vs. aggregation, scale and strength of pattern). First-order tests suffer from their inability to characterise pattern at distances beyond those at which local interactions (i.e. nearest neighbours) occur. Nevertheless, the tests explored (first-order nearest neighbour, Diggle's  $G$  and  $F$ ) are useful first steps in analysing spatial point patterns, and all seem capable of accurately describing patterns at these (shorter) distances. Among second-order tests, a density-corrected form of the neighbourhood density function (NDF), a non-

cumulative analogue of the commonly used Ripley's  $K$ -function, most informatively characterised spatial patterns at a range of distances for both univariate and bivariate analyses. Although Ripley's  $K$  is more commonly used, it can give very different results to the NDF because of its cumulative nature. A modified form of the  $K$ -function suitable for inhomogeneous point patterns is discussed. We also explore the use of local and spatially-explicit methods for point pattern analysis. Local methods are powerful in that they allow variations from global averages to be detected and potentially provide a link to recent spatial ecological theory by taking the 'plant's-eye view'. We conclude by discussing the problems of linking spatial pattern with ecological process using three case studies, and consider some ways that this issue might be addressed.

**Keywords** Point pattern · Spatial statistics · Ripley's  $K$ -function · Nearest neighbour · Neighbourhood density function · Poisson process

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## Introduction

The growing popularity of spatial ecology and increasing awareness of 'why space matters' has seen renewed interest in the application of spatial statistics in ecology (e.g. see Silvertown and Antonovics 2001). Interest in spatial patterns and processes by ecologists is not new (Watt 1947;

Skellam 1951). The analysis of spatial point patterns first became commonplace in ecology (and in disciplines such as geography and archaeology) in the 1950s and 1960s (Gatrell et al. 1996). At this time spatial point analyses could be divided into those based on distance (e.g. the nearest neighbour analysis of Clark and Evans 1954 and others) and those based on area (e.g. the quadrat-based methods described by Greig-Smith 1952 and others). Over the last two decades many methods have been developed for the analysis of spatial point data in a range of disparate disciplines. Often, these tests have been used by ecologists in a purely descriptive manner, with only a tenuous link to process (Barot et al. 1999). However, increasing computer power and the growth of spatially explicit simulation modelling in ecology has refocused attention on the interactions between pattern and process. The spatial arrangement of individuals within and among species, and associations between species and components of habitat, has been shown to have a significant influence on the dynamic behaviour of such models (e.g. Silvertown et al. 1992). It is also important to recognise how spatial dependence (e.g. spatial autocorrelation) may affect non-spatial inferential statistical techniques, which typically assume that model errors are independent (Carroll and Pearson 2000). Even if description and analysis of spatial pattern is not an important part of a formal statistical analysis, the effects of spatial pattern do warrant consideration (see Legendre 1994; Legendre et al. 2002).

Our purpose here is to compare and contrast the assumptions and performance of a range of methods of analysis for spatial point patterns and to make some suggestions as to which statistics to use, and when, and how their outcome may best be interpreted. It is not our intention to provide a rigorous mathematical treatment of the derivation of the tests we use here—for this, the reader should consult the primary literature (which often lacks the comparative evaluation we seek to provide). We believe that spatial statistics of the type described have most utility when used alongside a process-based or mechanistic investigation of the underlying processes driving the spatial patterns observed, whether experimental or model-based. Further, we are primarily interested in the application of these methods in a

heuristic manner or for exploratory data analysis (EDA).

## Basic concepts

### Point processes

While it is not the purpose of this review to provide technical definitions (for these see Cressie 1993; Stoyan et al. 1995; Diggle 2003), it is important to define the terms of relevance. A spatial point process is a “stochastic mechanism which generates a countable set of events  $\mathbf{x}_i$  in the plane” (Diggle 2003, p. 43). A point pattern is a realisation of a process (Gatrell et al. 1996), and is simply a collection of points ( $p_1, p_2, p_3, \dots, p_n$ ) distributed in some region  $R$ , which may be any shape or dimension but in ecological applications is usually regular and two-dimensional. Point processes and point patterns are fundamentally different in that a process is a theoretical stochastic model or random variable, whereas a pattern is a realisation of the process. Each point is defined by some set of coordinates and each such point is referred to as an ‘event’ (to distinguish them from arbitrary point locations on  $R$ : Diggle, 2003). In the simplest case, the event set will be made up solely of these locations. However, additional information is often attached to each event. Event sets labelled with such information are termed ‘marked’ patterns (Gatrell et al. 1996). Event sets, therefore, typically take the form  $\{[x_i, y_i; m_i]\}$ , giving the locations  $\mathbf{x}_i=(x_i, y_i)$  and the mark  $m_i$  (if included) in the region of observation (Stoyan and Penttinen 2000). In an ecological setting, the locations ( $\mathbf{x}_i$ ) might represent the position of stems, and the marks ( $m_i$ ) characteristics such as species, sex, age class, or health; although often categorical, marks can be continuous, especially where representing temporal phenomena (e.g. time of establishment).

A fundamental property of every point process is its intensity ( $\lambda(s)$ )—the expected number of events per unit area at the point  $s$ . The simplest spatial process is complete spatial randomness (CSR), termed the homogeneous Poisson process, with intensity  $\lambda$ . It has two important properties (Stoyan and Penttinen 2000, p. 72):

1. The number of events in any region  $A$  (with area  $|A|$ ) follows the Poisson distribution with a mean of  $\lambda|A|$ .
2. Given  $n$  events in  $A$  their positions follow an independent sample from the uniform distribution on  $A$ .

The first property states that under CSR the intensity of events will not vary across the region, and the second that events do not interact in the region (Diggle 2003). Commonly, observed events are then tested for departure from this CSR distribution. At a given scale, event sets may exhibit departure from CSR as either (i) clustering (aggregation in the bivariate case), or (ii) regularity (segregation), with CSR acting as the ‘dividing line’ between the two (Diggle 2003).

Spatial point patterns can be characterised in terms of their first-order and second-order properties, each the focus of different analyses. First-order properties are related to the mean number of events per unit area, while second-order properties are related to the (co)variance of the number of events per unit area. Thus, in the same way that the mean ( $\mu$ ) and variance ( $\sigma^2$ ) are the first and second moments of a regular probability distribution, the density ( $\lambda$ ) and covariance structure ( $\kappa$ ) are the first and second moments for a two-dimensional distribution (see Cressie 1993, p. 623 for formal definitions).

Finally, point processes can be described in terms of their stationarity and/or isotropy. A stationary process is one where all the statistical features of the process are the same at any location. Processes which are invariant under translation (moving every event the same distance in the same direction) are termed stationary or homogeneous; this means that the underlying characteristics of the pattern, such as the mean (first-order stationarity) and/or variance (second-order stationarity) of a variable are constant over the area under study. Those which are invariant to rotation are termed isotropic—that is, the characteristics of the pattern are the same in any direction (Guttorp 1991; Dale 1999; Diggle 2003).

#### Edge corrections

Most spatial statistics require some form of edge correction. Edge effects arise because the theoretical distributions for most spatial point statistics assume

an unbounded area, yet observed distributions are estimated from delineated regions (Dixon 2002b). Thus, corrections are required because events near the edge of region  $R$  will have fewer neighbours in some directions than others (i.e. large circles centred on events near the edge of  $R$  will contain fewer events than circles placed on events in the centre of  $R$  since part of their area will lie outside of the region). Three alternatives exist for dealing with edge effects: use of a weighted correction, use of an inner/outer guard area, and use of a toroidal ‘wrap’ (see Diggle 2003; Yamada and Rogerson 2003; Wiegand and Moloney 2004).

1. The weighted edge correction (Ripley 1977) weights pairs of points as a function of their relative locations. The weight,  $\omega_{ij}$ , for a pair of points  $i$  and  $j$  is given by the proportion of either the circumference or area of a circle, with its centre at point  $i$  and passing through point  $j$ , contained within the study region; if the circle is completely contained within the study area  $\omega_{ij} = 1$ , otherwise  $\omega_{ij} > 1$  (for further explanation see Haase 1995; Goreaud and Pélissier 1999).
2. The guard area correction uses a buffer area, with the events in the guard area used only as ‘destinations’ in measuring distance between events. The guard may be either internal or external to the region of interest. An obvious problem with guard methods is that they require collection of data not used in subsequent analyses (Yamada and Rogerson 2003).
3. Based on the assumption that the sampled area represents a small and representative part of a continuous pattern, the toroidal ‘wrap’ joins the top and the left of the study area to the bottom and the right, respectively (Yamada and Rogerson 2003). Diggle (2003) notes that the toroidal method can potentially be biased if, for example, a cluster falls near the edge of the study region, and so may be more suitable for simulation of realisations of some point processes, rather than for analysis of observed data. The same caveat holds if there is environmental heterogeneity in the study area being considered.

Yamada and Rogerson (2003) explored the power (Type-II error rate) of the various edge corrections (in the context of Ripley’s  $K$ -function), and conclude that

(i) edge-weighted and toroidal methods perform better than the guard methods, and (ii) if the purpose of an analysis is to detect/describe an observed pattern rather than to parameterise specific point process models, there is no drawback in not adopting any edge corrections, and, in fact, the non-correction method may outperform the outer guard method. They also analysed the width of the confidence envelopes produced by the three methods; width is important as it might be assumed that wider envelopes reduce a test's power (in general all edge corrections involve reducing bias at the expense of increased variance—Diggle, 2003). Yamada and Rogerson found that the toroidal correction produced the narrowest envelopes, followed by the weighted correction, no correction, and the guard methods; envelope width was found to increase with distance. It is worth noting that in some cases edges are 'real' (e.g. stream margins, etc.); Lancaster and Downes (2004) describe how point pattern analysis might proceed in such cases.

### Hypothesis testing

Since the distribution theory for even simple stochastic point processes may be mathematically unknown or intractable, and is further complicated by edge effects, tests of significance for spatial measures are usually constructed using Monte Carlo procedures (Besag and Diggle 1977; Diggle 2003). Monte Carlo simulation of the spatial process gives an estimate of the mean and the sampling distribution of the test statistic (Marriott 1979; Dixon 2002b). Rejection limits are estimated as simulation envelopes, typically, but not necessarily, based on a null hypothesis of CSR, using the same intensity as the observed pattern. For example, in the case of a one-tailed test of significance ( $\alpha$ ),  $n$  simulations (under the null hypothesis) are carried out, giving a distribution for the test statistic. The one-sided critical value is the  $\alpha(n+1)$ th largest value from the simulations and the simulated  $P$ -value is (the number of randomisations greater than the observed + 1)/( $n+1$ ) (Marriott 1979; Dixon 2002b). If the number of simulations is too small then the critical region for the statistic becomes 'blurred' and there is a variable probability of actually rejecting  $H_0$ , resulting in a loss of power (Marriott 1979). Diggle (2003) suggests that significance

envelopes based on 500 replicates seem appropriate (for  $\alpha = 0.01$ ). Similarly, as the number of events in the event set decreases, the test's power falls and the ability to discriminate between different patterns is lost (e.g. see Plotkin et al. 2000a).

The Monte Carlo approach can be used to test hypotheses other than that of CSR (Diggle 2003). In an ecological context, an early example of this type of model fitting is Stamp and Lucas' (1990) use of Poisson cluster processes to explore the aggregated spatial patterns produced by ballistically-dispersing plants; likewise Pélissier (1998) used Markov (Gibbs) point processes to explore patterns of species association in a moist forest in India. Using such models allows ecologically realistic hypotheses to be tested, and, if a model can be fitted, then estimated parameter values may allow its comparison with other sites (Diggle 2003). Batista and Maguier (1998) and Wiegand and Moloney (2004) provide further discussion of the process of fitting point process models to observed point patterns in an ecological setting.

There are two null hypotheses for bivariate spatial pattern: independence, and random labelling (Diggle 2003). These two tests are subtly different (Dixon 2002a; Goreaud and Pélissier 2003). As Goreaud and Pélissier (2003) discuss, spatial independence is an appropriate hypothesis where different processes determine the patterning of the two types of events a priori (e.g. different species) and random labelling is appropriate where the different types of events are the result of processes affecting the same population a posteriori (e.g. diseased vs. non-diseased individuals). The first hypothesis is tested by generating new event sets at the same intensity as the observed set but with a spatial distribution that conforms to the null hypothesis (usually CSR) and with labels randomly allocated among events in the same proportions as in the observed set. The second hypothesis is tested by maintaining the observed event positions and randomly re-labelling each event into one of the two sets. The two hypotheses can produce quite different significance envelopes, and Goreaud and Pélissier (2003) demonstrate that the use of an inappropriate null hypothesis can lead to the misinterpretation of spatial patterning.

Besides the options presented above, 'curve-wise' (goodness-of-fit) estimates of significance can be calculated in terms of deviation from some expected

model. These are tests that usually involve comparison of the entire estimated distribution function of some test statistic with that expected under the null hypothesis (Dixon 2002b). The advantage of this approach is that it provides a summary of the overall direction of pattern without placing too much importance on any single measurement. Such tests include Kolmogorov–Smirnov, Cramer–von Mises and Anderson–Darling type statistics—for example, if the observed cumulative distribution function (CDF) of nearest neighbour (NN) distances is termed  $\hat{G}(w)$  and the theoretical CDF as  $G(w)$ , then these tests are defined as (Dixon 2002b):<sup>1</sup>

$$\text{Kolmogorov–Smirnov}^1 : \sup_w |\hat{G}(w) - G(w)| \quad (1a)$$

$$\text{Cramer–von Mises} : \int_w (\hat{G}(w) - G(w))^2 \quad (1b)$$

$$\text{Anderson–Darling} : \int_w (\hat{G}(w) - G(w))^2 / G(w)(1 - G(w)) \quad (1c)$$

In some cases the curve-wise tests may provide only a weak test of deviation from the expected pattern, so it is important that they are considered alongside the empirically-derived distribution functions (Diggle 2003).

## Overview of point pattern analysis methods

To explore the usefulness of different methods of point pattern analysis we carried out a series of comparisons on various spatial point patterns. The specific tests that we use are described in Table 1, and the derivation and a full description of the tests can be found in the references therein. Global and local point pattern analyses and the SADIE method are used here to illustrate the strengths and weaknesses of different approaches to the analysis of point

patterns. Ripley (1981), Cressie (1993), Stoyan et al. (1995) and Diggle (2003), amongst others, provide comprehensive overviews of these methods. The performance of spatial point statistics is generally well known for simple spatial patterns (e.g. departure from CSR at only one scale). Here, we analyse five ‘real-world’ ecological event sets, and two artificial event sets (one univariate and one bivariate) showing pattern at multiple scales with known properties which act as references for the other analyses (Table 2).

The artificial point patterns were simulated using a Gibbs-type model (Diggle 2003). A Gibbs (also called a Markov) point process is defined by a function that represents the interaction ‘cost’ incurred between two points at some distance (Pélissier 1998; Diggle 2003). The pattern is simulated by means of sequentially selecting, deleting and moving events in order to minimise the sum of the interaction costs associated with every pair of events. Patterns were simulated following Eq. 2, with the bivariate process showing inter-specific interaction only, with the parent event set generated using a homogeneous Poisson process. This interaction function (Eq. 2) results in patterns that are aggregated at distances less than 10 units, but are regular thereafter.

$$h(u) = \begin{cases} -25 : u \leq 10 \\ 10 : 10 < u \leq 25 \\ -5 : 25 < u \leq 50 \end{cases} \quad (2)$$

where  $h(u)$  represents the interaction ‘cost’ at distance  $u$ .

## Univariate analyses

Six types of univariate analyses are compared here: first- and second-order tests, global and local tests, and homogeneous to inhomogeneous and combined tests. Five event sets were used to explore the way that the different statistical methods performed (Fig. 1). In the univariate case, interest is typically in the extent to which events show departure from CSR. Biologically, and in general terms, aggregation might arise from habitat heterogeneity or localised seed dispersal, for example, and regularity can result from intense competition for some limiting resource (e.g. water in arid environments).

<sup>1</sup> **sup** denotes the supremum—the least upper bound of a set of numbers

**Table 1** Brief description of the methods of point pattern analyses reviewed, with references to their derivation and use

Test statistic	Description	Reference
<i>First-order nearest neighbour</i>		
First-order nearest-neighbour <sup>u</sup>	Distance to closest event and deviation from theoretical expectation under CSR	Clark and Evans (1954)
Nearest-neighbour contingency table <sup>b</sup>	Contingency table test based on first-order nearest neighbour distances	Pielou (1961); Dixon (1994)
Diggle's $F(x)^u$ and $G(w)$ (refined nearest-neighbour)	Cumulative frequency of distances to closest event and deviation from theoretical expectation under CSR	Diggle (2003)
$n$ th-order nearest neighbour	Distance to 1 to $n$ closest events and deviations from expectation under CSR	Davis et al. (2000); Thompson (1956)
All events to all events	Distance from each event to every other event, binned into distance classes and analysed as absolute frequencies	Galiano (1982); Dale (1999)
<i>Second-order tests</i>		
Ripley's $K(t)$ (and $L(t)$ transformation)	Number of events within a circle of radius sequentially larger $t$ from each focal event, and deviation from expectation at each $t$ under CSR. Haase (2001) has modified this method so it can test for anisotropic associations	Ripley (1977); Lotwick and Silverman (1982); Haase (2001)
Neighbourhood density function (NDF( $t$ ))	Similar to Ripley's $K$ except non-cumulative, i.e. distance classes are annuli, not circles. The NDF is also known as the pair correlation function (Stoyan and Stoyan 1994) and the O-ring statistic (Wiegand and Moloney 2004).	Ward et al. (1996); Condit et al. (2000); Stoyan et al. (1995)
<i>Inhomogeneous tests</i>		
Inhomogeneous forms of Ripley's $K$ -function and the NDF	Forms of Ripley's $K$ and the NDF (or PCF) which do not assume first order homogeneity in the study region. Intensity is estimated at each event and this estimate is used to calculate the inhomogeneous form of the statistics	Baddeley et al. (2000)
<i>Local tests</i>		
Getis and Franklin's $L(d)$	Localised version of Ripley's $K$ in which $L(d)$ is calculated for each event individually, providing information concerning local trends in pattern (e.g. areas of aggregation vs. areas of regularity in the same plot)	Getis and Franklin (1987)
<i>Spatial analysis by distance indices (SADIE)</i>		
SADIEM <sup>u</sup>	Calculates the 'distance' from the event set to regularity by moving events until a regular Voronoi tessellation (approximating a hexagonal lattice) is achieved; allows calculation of index of aggregation ( $I_p$ ), test of departure from CSR, and diagnostic exploratory data analysis	Perry (1995)

u—Univariate event sets only, b—bivariate event sets only

Unless otherwise specified, tests can be carried out on both univariate and bivariate data

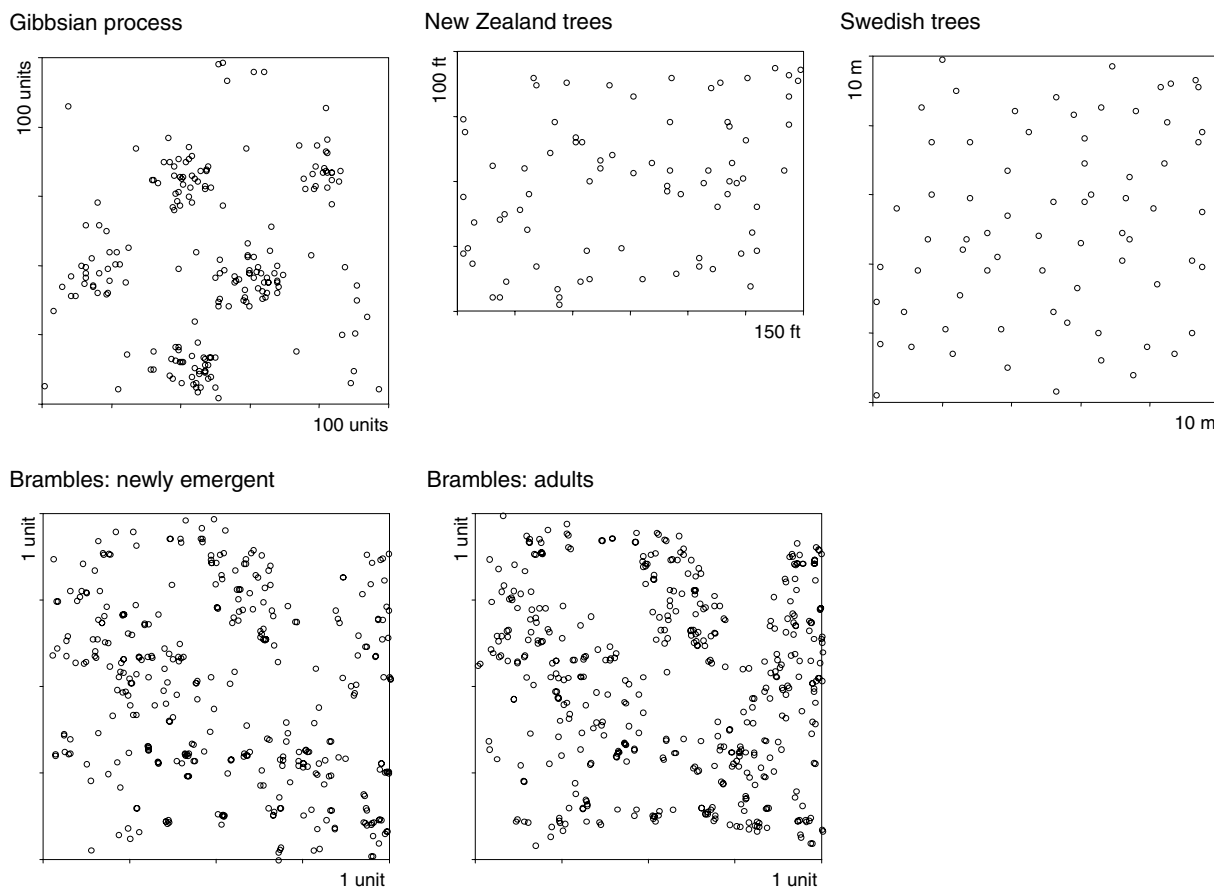
Note that different tests refer to distance using slightly different notation; the notation used here is consistent with that used in most of the relevant literature. For Diggle's  $F$  and  $G$ ,  $w$  denotes event–event NN distances (i.e. the distance between an event and its nearest neighbour) whereas  $x$  refers to point–event NN distances (i.e. the distance between a randomly selected point and its nearest event). For Ripley's  $K(t)$  and Getis and Franklin's  $L(d)$ , respectively,  $t$  and  $d$  refer to the radius of the circle being considered centred on each event, and for the NDF  $t$  refers to the distance from the event to the outer edge of the annuli being considered



**Table 2** Description of the simulated and ‘real world’ spatial point patterns used to describe the performance of the spatial tests; the Bramble canes, Lansing Woods and Longleaf Pines event sets are marked

Event set	Description	Reference and previous analyses
<i>Simulated patterns</i>		
Gibbsian sets	These patterns are simulated using Eq. 2. They are, in essence, segregated clusters; aggregation occurs at a distance of 10 units beyond which events are regular. The algorithm used to simulate the patterns is described in detail by Diggle (2003)	
<i>‘Real world’ patterns</i>		
Bramble Canes	Data giving location and age (newly emergent one- or two-years old) of canes of <i>Rubus fruticosus</i> in a field. Rescaled here to the unit plot. Hutchings (1979) considers the canes to be aggregated. Diggle (2003) models them with a Poisson cluster and a Cox process	Hutchings (1979); Diggle (2003)
New Zealand Trees	Locations of 86 <i>Nothofagus menziesii</i> (Silver Beech) trees in a 140 × 85 foot forest plot in Fiordland, New Zealand. They were collected by Mark and Esler (1970) and were also analysed by Ripley (1981, pp. 169–175). Ripley (1981) considers this pattern to follow an homogeneous Poisson model (i.e. CSR)	Mark and Esler (1970); Ripley (1981)
Swedish Pines	Locations of 71 pine saplings in a Swedish forest within a 10×10 m square. Ripley (1981) considers this pattern to follow a Strauss model (i.e. regularity), with an inhibition of ~0.7 m	Ripley (1981); Venables and Ripley (1997, p. 483); Baddeley and Turner (2000)
Lansing Woods	Locations and species of 2,251 trees within a 924 ft×924 ft (rescaled to the unit square) in Lansing Woods, Michigan USA (data originally collected by D.J. Gerrard). Individuals are classified by species into hickories, maples, red oaks, white oaks, black oaks and miscellaneous trees. Diggle (2003) found that patterns of hickories and maples strongly deviate from randomness and there is evidence of segregation between the two species. Conversely, the oaks are randomly scattered across the study region and are independent of the location of the other two species	Ripley (1981); Diggle (2003)
Longleaf Pines	The data contains the locations and diameters (DBH) of 584 longleaf pine ( <i>Pinus palustris</i> ) trees in a 200 × 200 metre plot in southern Georgia (USA); collected and analysed by Platt et al. (1988). This is a marked point pattern, which Platt et al. (1988, p. 507) describes as “... [a] mosaic of discrete clumps of juveniles and sub-adults superimposed upon a background matrix of widely spaced adults”; evidence for segregation between juveniles and adults was also found. A non-stationary pattern	Platt et al. (1988); Rathbun and Cressie (1994)

Datasets were extracted from the SpatStat library in the R software environment, and further descriptions of these data are available there (Baddeley and Turner 2004)



**Fig. 1** Maps of the univariate spatial event sets used: the simulated point pattern generated using a Gibbsian process (Eq. 1), the New Zealand Trees event set, the Swedish

Pines event set, and the bramble canes (newly emerged and adults) event set; see Table 1 for further descriptions

### *Nearest neighbour(NN) analyses: first and $n$ th-order<sup>2</sup>*

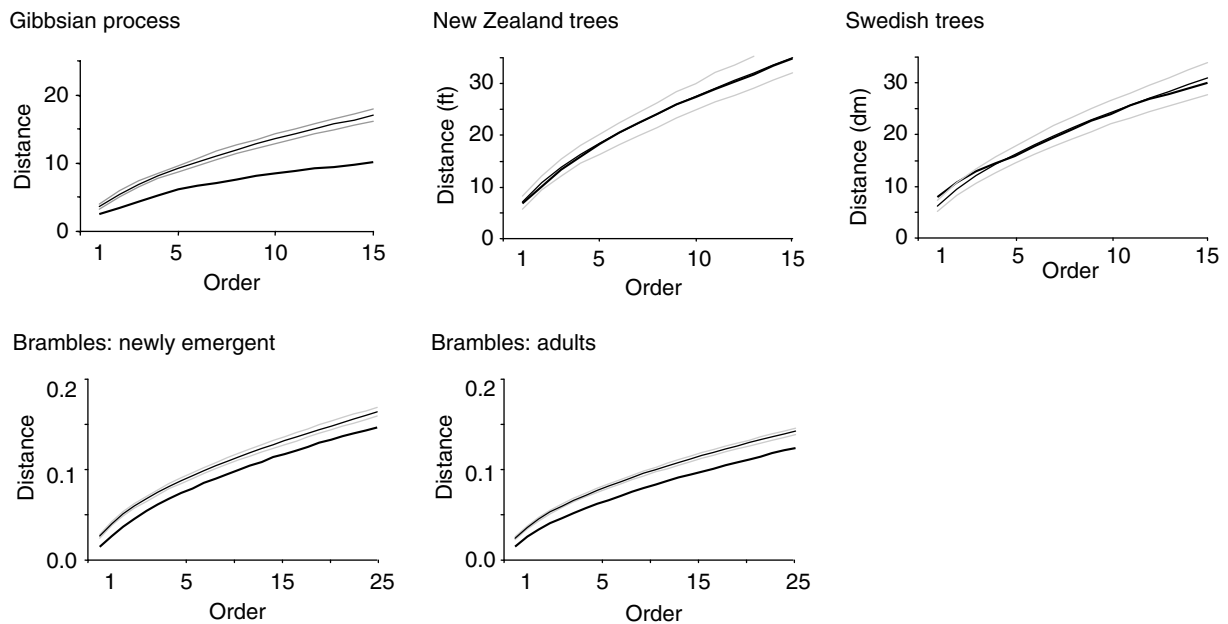
In all event sets analysed, except for the New Zealand (NZ) Trees set, there is significant evidence of departure from CSR based on the NN analyses (Table 3); this is supported by extending these analyses to higher-order neighbours (Fig. 2). The Swedish Pines set is significantly more regular than expected from a random distribution (i.e. larger average NN distance than under CSR) and the Gibbsian and Bramble Canes sets are significantly more clustered than expected from a random

distribution (i.e. shorter average NN distance than under CSR).

The  $n$ th-order nearest neighbour analysis considers points beyond the nearest neighbour (i.e. the second, third,...,  $n$ th closest points). It may be useful for identifying cluster size based on sharp breaks in the nearest neighbour distance, although because the calculated value is an average across all the  $n$ th-order distances such breaks may be obscured. The NZ Trees event set shows no departure from randomness at any of the orders analysed.  $n$ th-order analysis of the Swedish Pines pattern suggests regularity at orders up to four, after which the pattern is not significantly different from CSR. The Gibbsian and emergent and adult bramble canes events sets show significant clustering for all orders. None of the five analyses (Fig. 2) show sharp breaks suggestive of clusters of similar sizes. Furthermore, because the

<sup>2</sup> Note that this is a *different* use of ‘order’ to that discussed in the section on ‘Point Processes’, above. In the context of  $n$ th-order nearest neighbour tests, an event’s first-order nearest neighbour is its closest neighbour, the second-order nearest neighbour the next closest, and so on





**Fig. 2**  $n$ th-order nearest neighbour analyses for the four univariate event sets: NZ Trees, Swedish Pines, newly emergent bramble canes, bramble cane adults. In each chart, the thick black line shows the observed distance, while the thin black line the expected distance under CSR and the grey lines are 99%

simulation envelopes. Observed distances less than the expected value and outside of the envelope indicate a significant aggregation at that order of neighbour, distances greater than the expected value and outside of the envelope indicate significant regularity at that order

nearest neighbour order does not directly equate to distances it is difficult to interpret  $n$ th-order analyses.

#### *Refined nearest neighbour analysis: Diggle's $F$ and $G$ , all event-to-all events*

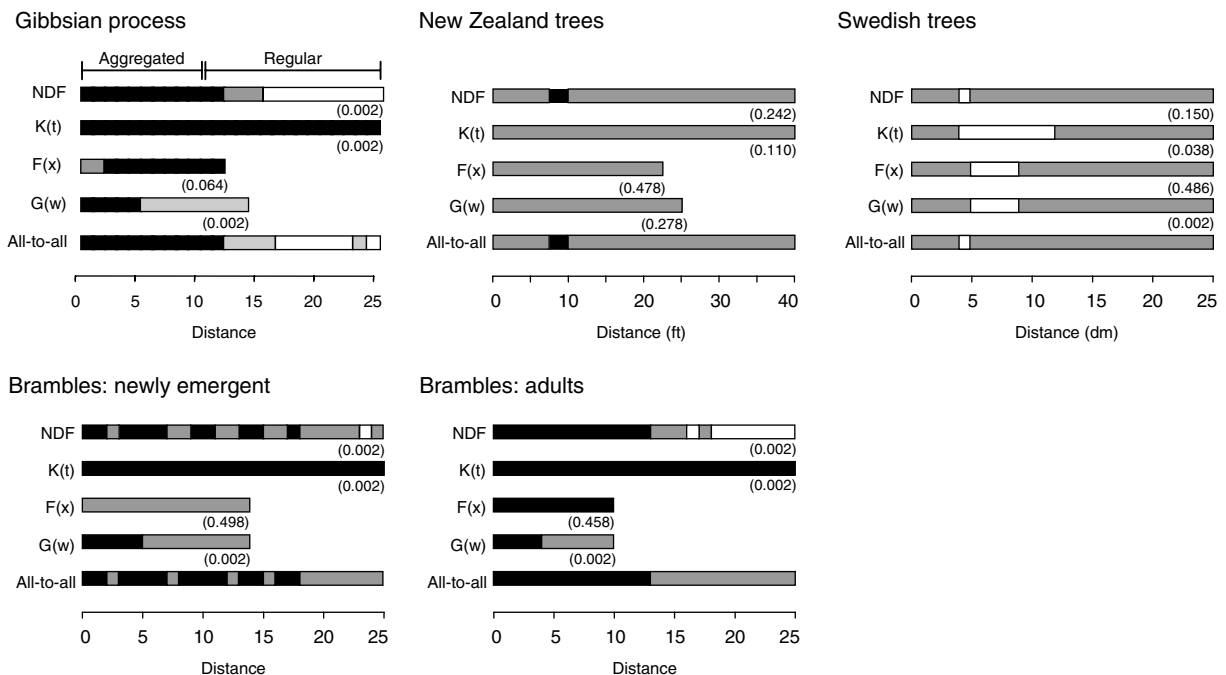
Refined NN analyses offer the advantage of being able to consider longer inter-event distances than the first-order NN measures and are more easily interpreted than  $n$ th-order NN tests. Applied to the test data, these three refined NN techniques did not always indicate the same patterns as the simpler NN tests. The Gibbsian event set is characterised as clustered at distances up to five units by Diggle's  $G$ ,

while Diggle's  $F$  suggests the pattern is random at distances less than three units but is otherwise aggregated (Fig. 3). The all-to-all test characterises the same pattern as being clustered up to a distance of 12, CSR from 12 to 16 and regular beyond that. Diggle's  $G$  characterises the pattern of both newly emergent and adult bramble canes as clustered at short distances and then random, while Diggle's  $F$  is random at all scales for the newly emerged canes and aggregated at all scales for the adults. The all-to-all test shows complex periodic clustering for the newly emerged canes, and clustering to a distance of 13 units for the adults. Diggle's  $G$  and  $F$  characterises the NZ Trees event set as being random at all

**Table 3** Nearest neighbour statistic values (Clark–Evans  $R$  and  $C$  statistics) for the univariate data sets examined; the edge corrections described by Sinclair (1985) were used

Pattern	$n$	NN Dist.	CSR Dist <sup>a</sup>	$z$ -score	CE $R$	$C$ -score	Reflexives
Gibbsian process	200	2.46	3.54±0.02	−8.23	0.69	−8.35	53
NZ Trees	78	6.84	6.76±0.16	0.20	1.01	−0.59	21
Swedish Pines	71	7.91	5.93±0.14	5.36	1.33	3.98	25
Brambles: emergent	359	0.015	0.026	−15.13	0.582	−14.94	116
Brambles: adult	464	0.014	0.024	−16.57	0.598	−16.38	152

<sup>a</sup>Average distance expected under CSR ± variance



**Fig. 3** Comparison of characterisation of pattern for the univariate inter-type event sets: simulated Gibbsian pattern, NZ Trees, Swedish Pines, newly emergent bramble canes, adult bramble canes. Grey areas indicate that the distribution does not differ from CSR for that distance interval, white, that it is segregated and, black that it is aggregated;

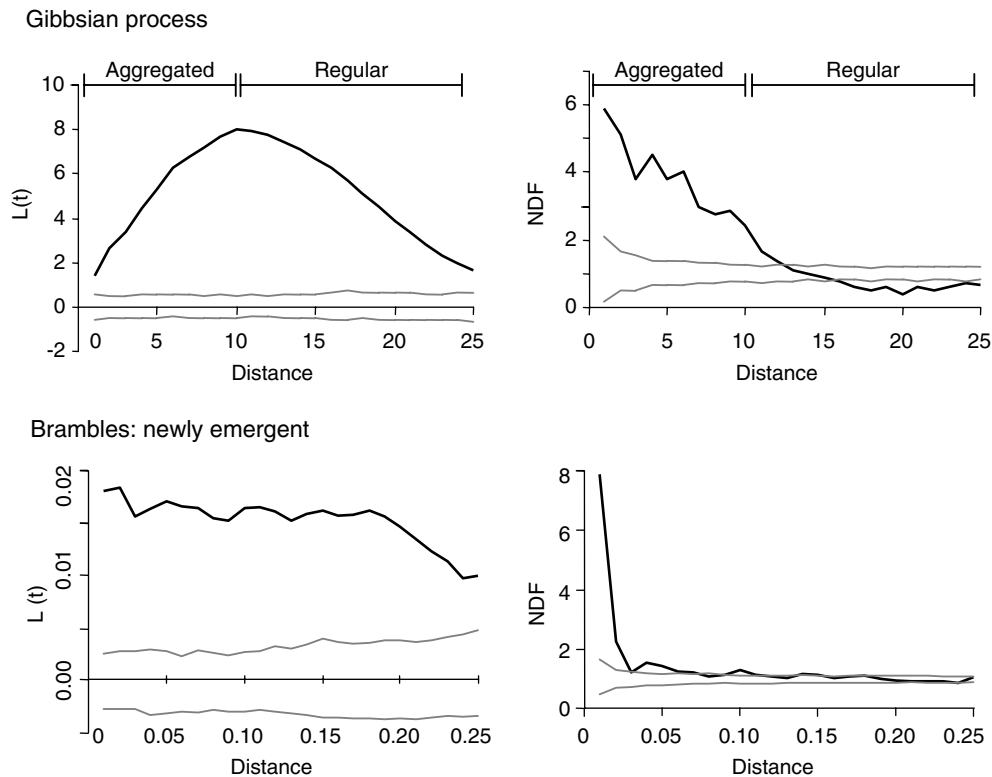
two-tailed test,  $P < 0.01$ . Numbers in parentheses below the bars indicate two-tailed  $P$ -value based on curvewise goodness-of-fit to the values expected under CSR, based on the Cramer-von Mises test (Eq. 1b); note that 0.002 is the least possible value for envelopes based on 499 replicates ( $0.002 = 1/500$ )

distances and the Swedish Pines pattern as random at short distances, regular at 6–9 decimetres and then random again. The all-to-all test describes the Swedish Pines as random, except for regularity at five units distance.

#### *Second-order analyses: Ripley's $K$ and the neighbourhood density function (NDF)*

The two second-order tests, Ripley's  $K$ , and the NDF, allow inferences to be made up to, or at, specific distances—as the former is a cumulative test, while the latter is not. These two tests characterise the Gibbsian event set as strongly clustered at shorter distances and regular at longer distances, but differ markedly in the distances over which clustering is detected (Fig. 3). The NDF correctly identifies the length scale of clustering in this event set but Ripley's  $K$  peaks at the maximum length scale of aggregation and continues to show clustering at all scales beyond this (including those at which the

process is regular; Fig. 4). Both the NZ Trees and Swedish Pines event sets are characterised in a similar manner to the nearest neighbour analyses described above (Fig. 3). The NZ Trees set is random at all distances for all tests, while the Swedish Pines set shows regularity at small scales (5–10 units); the scales over which the pattern is characterised as regular again varies with the test used. Both the newly emerged and adult bramble canes are also characterised as clustered at all scales by the  $K$ -function, but the NDF characterises the pattern as being random at some scales and aggregated at others. As with the all-to-all test, the NDF shows periodicity in the pattern—possibly reflecting the scale of clustering and distance between clusters. This variation between the tests is problematic—are the individuals clustered or not, and over what scales? The difference between Ripley's  $K$  and the NDF (and all-to-all) tests might stem, as discussed below, from one being cumulative and the other non-cumulative (see Fig. 4).



**Fig. 4** Comparison of Ripley's  $K$  and the NDF for the Gibbsian event set and the adult bramble canes; CIs are at the 99% level based on 499 randomizations

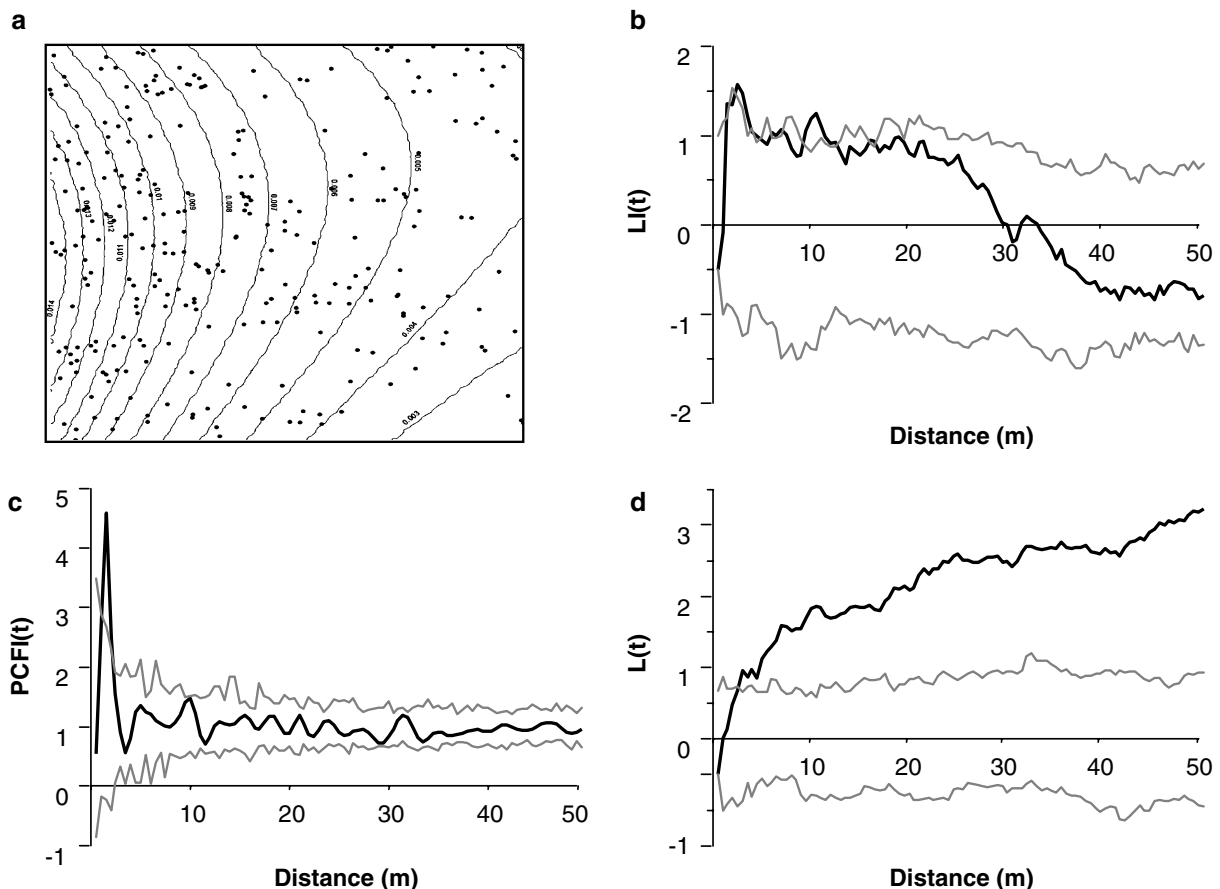
#### *Inhomogeneous point patterns: $K$ and NDF*

The second-order tests described above assume first-order homogeneity. In an ecological setting this is often not the case, and we might expect a pattern's intensity to vary in space with covariates such as the availability of soil nutrients or topographic position—that is, it is inhomogeneous. If the case for inhomogeneity is strong, then it becomes important to separate first-order and second-order effects in spatial analyses. One approach is to delineate internally homogeneous areas within the plot and analyse them individually (see Couteron et al. 2003; Wiegand and Moloney 2004). Alternatively, Baddeley et al. (2000) describe an inhomogeneous version of the  $K$ -function and the pair correlation function (PCF, analogous to the NDF). Their method involves generalising the homogeneous version of the  $K$ -function,  $K(t)$  to give an inhomogeneous  $K$ -function,  $KI(t)$ , by using estimates of intensity *at each event* instead of the globally averaged value. This approach allows analysis of inter-point interactions *after* allowing for first-order effects in the plot.

To illustrate the use of this method, we applied it to the longleaf pines event set (see Table 2, Fig. 5a). First, the first-order trend in log-intensity was modelled using a quadratic trend surface (see Diggle 2003, p. 105) as

$$\log \lambda(\mathbf{x}) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \gamma_1 x_1^2 + \gamma_2 x_2^2 + \delta x_1 x_2 \quad (3)$$

and intensities were then estimated at the events themselves. There is an apparent gradient in intensity running broadly left to right in the plot (Fig. 5a). We then estimated  $KI(t)$  and the PCF using this non-stationary model of intensity, revealing some clustering at distances up to 2–3 m (Fig. 5b, c). For comparative purposes we also estimated the  $K$ -function for the longleaf adults using the homogeneous form; both the qualitative trend (strong clustering at most distances for  $K(t)$  vs. weak aggregation at short distances for  $KI(t)$ ) and the actual values of the two functions differ (Fig. 5d); note that use of the inhomogeneous form



**Fig. 5** (a) Modelled first-order trend in intensity for the 271 longleaf pine adults (points); (b)  $L(t)$  transformation of  $KI(t)$  with envelopes on the basis of 499 simulations, (c) inhomogeneous PCF (analogous to the NDF) with envelopes on the basis of 499 simulations of an inhomogeneous Poisson process

of the  $K$ -function ( $KI(t)$ ) will give the same results as the homogeneous form ( $K(t)$ ) when the assumption of first-order homogeneity is met.

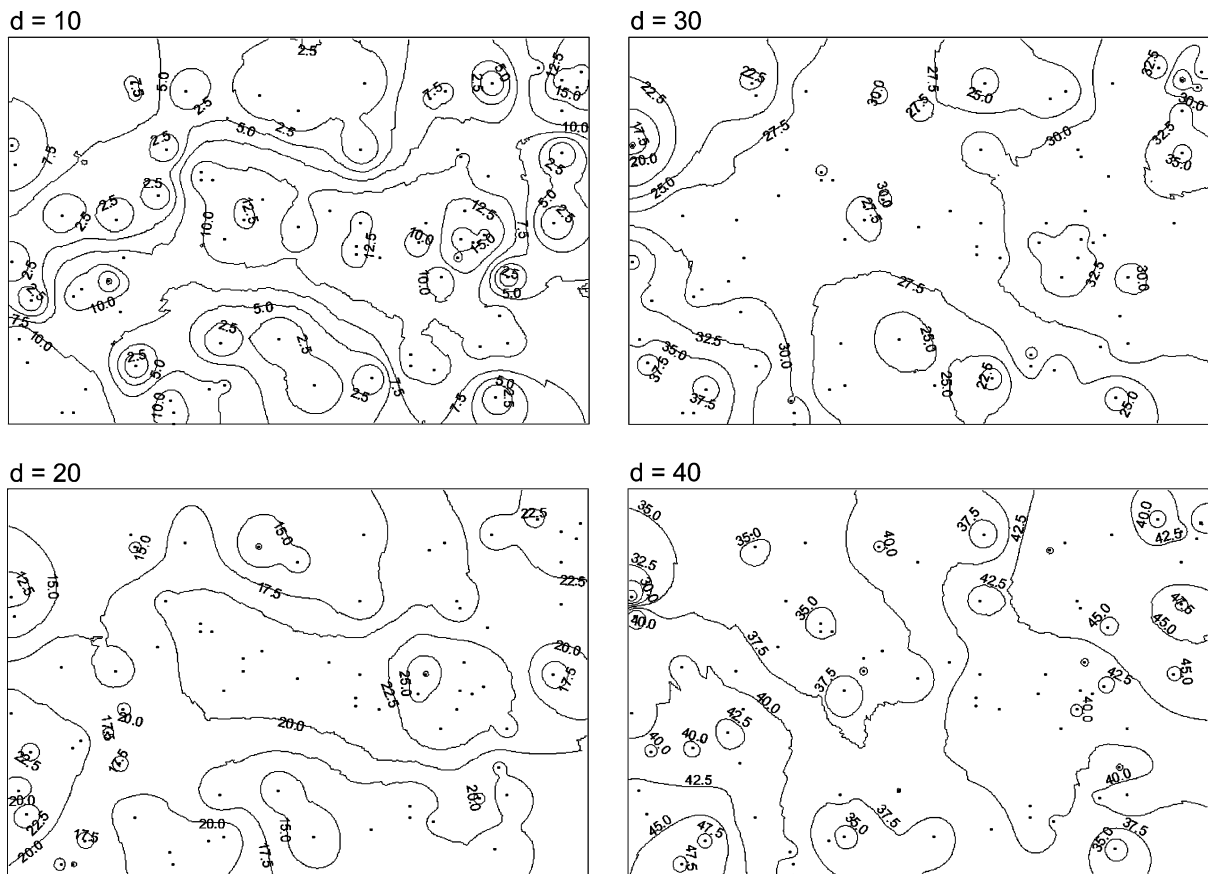
Pattern can arise from first and/or second-order effects, and it is important to try to tease the two apart (Gatrell et al. 1996). First-order structure can be described by an appropriate model before second-order structure is considered (e.g. the inhomogeneous  $K$ -function discussed above). However, partitioning spatial pattern into first-order (mean) and second-order (variance) effects needs careful and systematic attention, and as Baddeley et al. (2000, p. 336) note, “knowledge about the environment ... seems to be crucial in practice to make an informed choice between the homogeneous and the inhomogeneous setup”.

with intensity the same as that fitted to the observed data, (d)  $L(t)$  transformation of the homogeneous  $K$ -function for the longleaf pine adults (for comparative purposes). Analyses were conducted in R using the Spatstat library (Baddeley and Turner 2004)

#### Local statistics: Getis and Franklin's $L(d)$ <sup>3</sup>

All of the tests and statistics introduced thus far are ‘global’ in the sense that they provide an ‘average’ description of pattern across the entire study area. The problem with this approach is that it subsumes local variations in pattern in the averaging process (Fotheringham 1997). Local or mappable pattern statistics that highlight variations in pattern across the study region have been developed. For example, Getis and Franklin's (1987)  $L(d)$  statistic is similar to Ripley's  $K$ , except that a value is calculated and

<sup>3</sup> Note that in the literature  $L(d)$  is used both for Getis and Franklin's statistic and, in some cases, also for the variance stabilised Ripley's  $K$ -function



**Fig. 6** Contour map (2.5 unit interval) created by assigning to each individual in the NZ Tree pattern its  $L(d)$  value at  $d = 10, 20, 30$  and  $40$  ft (plot dimensions are  $100 \times 150$  ft)

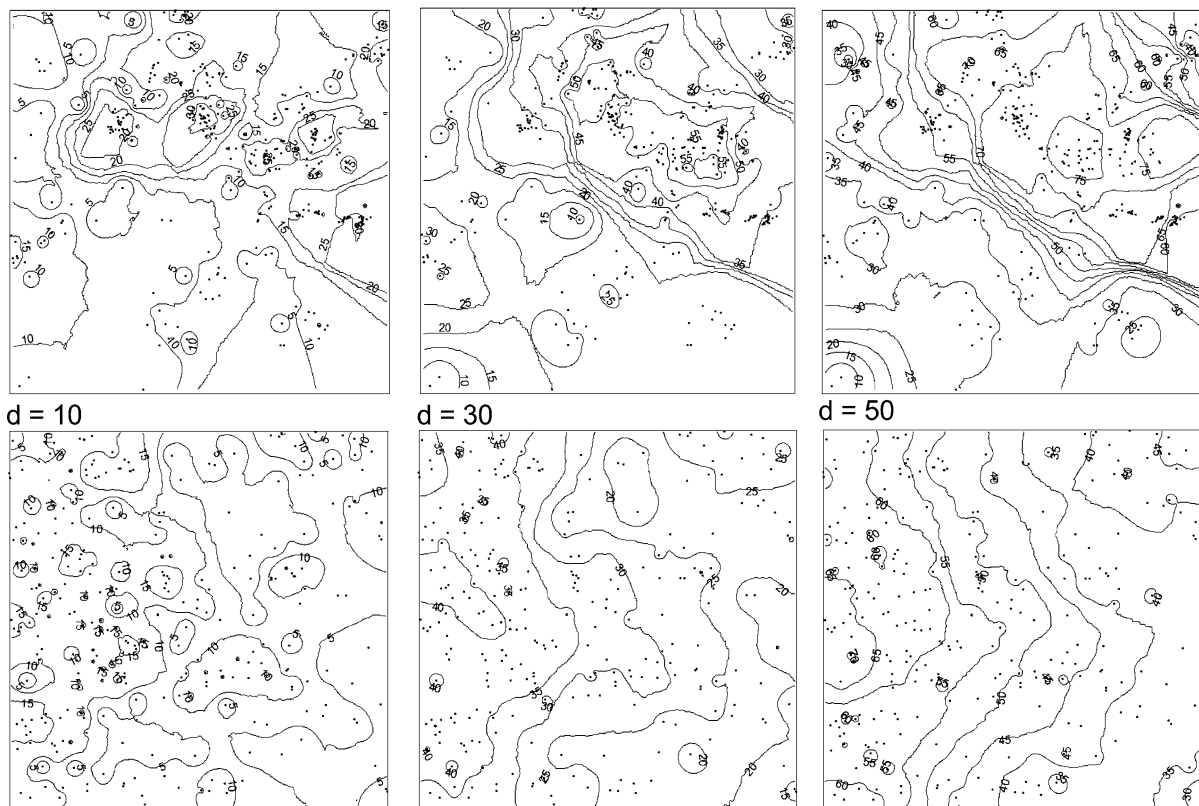
mapped for each individual event. This statistic is valid even if the point pattern is inhomogeneous, and the approach can be extended to other univariate (and bivariate) tests. Such local statistics can be displayed as contour maps (or shaded surfaces as in Getis and Franklin 1987) with the contours based on the values of  $L(d)$  for each individual at distance (length scale)  $d$ ; contours where  $d < L(d)$  denote areas of regularity and those where  $d > L(d)$  aggregation.

The univariate NZ Trees data set is characterised as showing CSR by the global tests (above), but the contour maps show that there are localised areas of clustering at all scales (Fig. 6). Likewise, although the global statistics characterise both the Longleaf Pines juvenile and adult patterns as highly aggregated, the local contour maps show that there are areas of much lower clustering and that the highly aggregated areas are themselves patchily distributed

across the study region (Fig. 7). Interestingly, the areas of localised strong clustering for the juveniles are in areas of low(er) clustering for the adults and vice versa. This is due to the pattern of recruitment in the system, which leads to the spatial separation of differently-aged cohorts. The visualisation advantages are clear—while the global tests above suggest there is spatial segregation and at what scale(s), the local tests can explicitly show *where* this is occurring. Thus the local form of the  $K$ -function ( $L(d)$ ) can be used (i) to indicate local areas of non-stationarity and (ii) to explore the influence of individual events on the magnitude of the global statistic.

#### *A combined global–local approach: spatial analysis by distance indices (SADIE)*

The SADIE method is based on an algorithm in which the observed events are iteratively moved until



**Fig. 7** Contour map (10 unit interval) created by assigning to each juvenile longleaf pine (top) and adult longleaf pine (bottom) its  $L(d)$  value at  $d = 10, 30$  and  $50$  m (plot dimensions are  $200 \times 200$  m)

they achieve a regular arrangement (Perry 1995). The ‘distance to regularity’ is assessed by summing the number of moves each event undergoes until regularity is achieved (on the basis of a comparison of the initial and final arrangements). The ratio of the mean distance moved under the observed relative to simulated CSR data is termed the index of aggregation  $I_p$  (Perry 1995). As well as this simple index of spatial pattern, SADIE provides spatially-explicit visual (or diagnostic) plots used for EDA. Respectively, these two analyses enable global and local descriptions of spatial pattern. Globally, the SADIE analyses support the conclusions of the NN analyses presented above (Table 4), suggesting that the NZ Trees set is random, the Swedish Pines set regular, and the bramble canes clustered (newly emerged and adults).

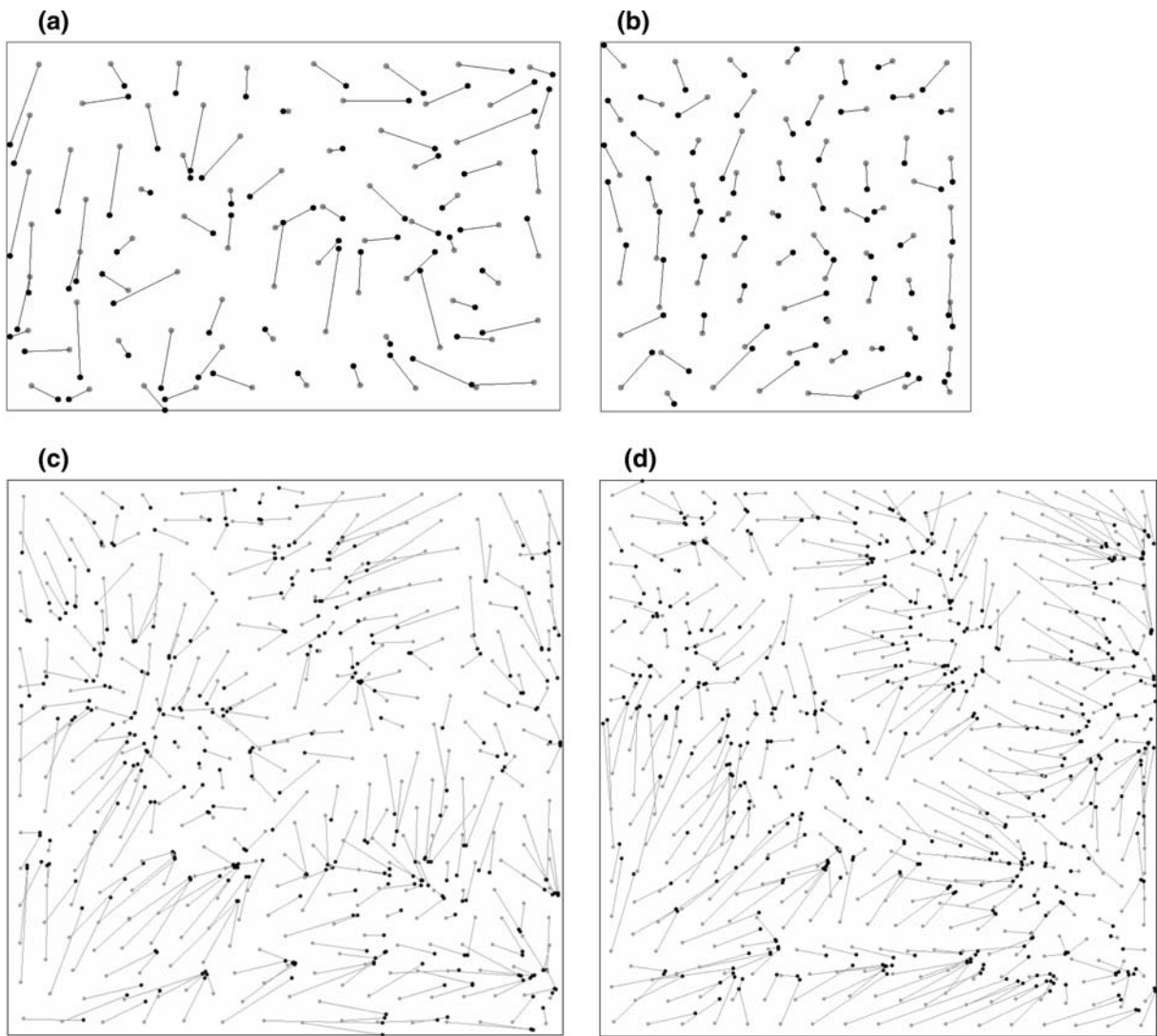
SADIE’s local analysis component derives from diagnostic visual plots, which consist of a map showing the original and the moved patterns with line segments connecting the pairs of points, termed the

‘initial and final’ (IAF) plot by Perry (1995). A distribution function of the length of the line segments ( $d_j$ ) can be plotted and compared with CIs generated under CSR (rank order vs.  $d_j$ ). Perry (1995) terms these EDFs (empirical distribution functions). The IAF plot of the NZ Trees pattern shows the random nature of the data (Fig. 8), with line segments showing a range of lengths ( $11.2 \pm 5.6$  vs.  $10.4 \pm 5.5$ ; observed vs. simulated under CSR—average  $\pm 1$ SD) but they do not, in general,

**Table 4** Summary statistics from the SADIE analyses;  $n$ =no. of events, OD=observed distance to regularity, RD = distance to regularity for CSR data,  $P_p$ =probability of as extreme aggregation under CSR,  $I_p$ =index of aggregation

Data set	$n$	OD	RD	$P_p$	$I_p$
NZ Trees	78	876.7	808.3	0.218	1.08
Swedish Pines	71	497.1	629.1	0.976	7.90
Brambles: emergent	359	27.1	14.4	0.002	4.03
Brambles: adult	464	33.6	15.8	0.002	1.89





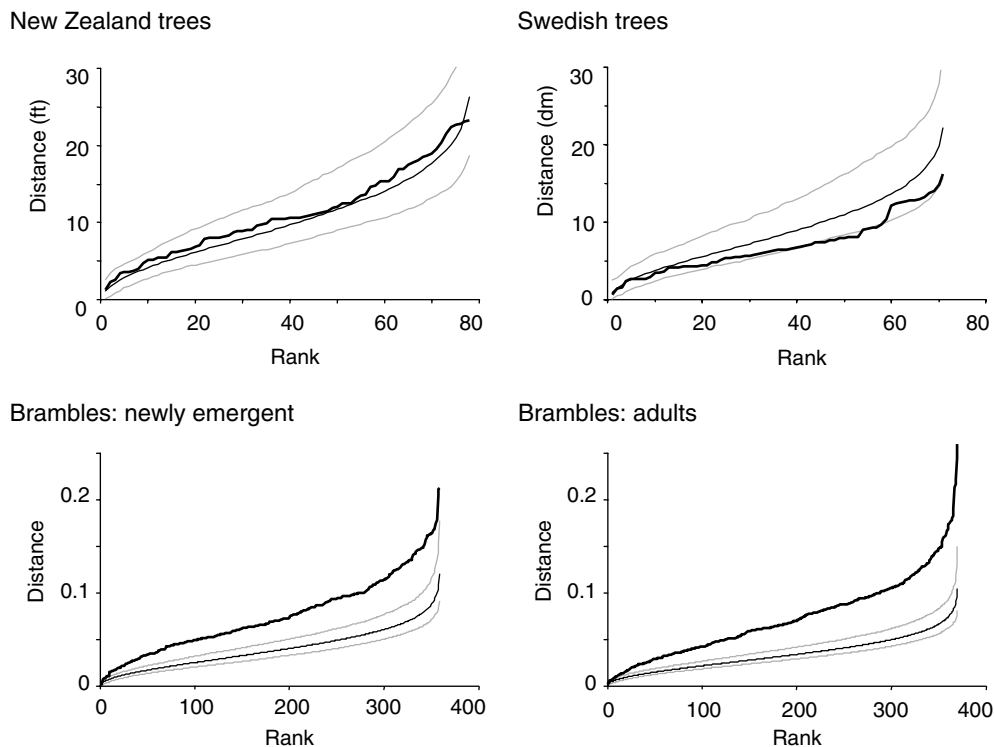
**Fig. 8** 'Initial-and-final' IAF plots for the univariate event sets: (a) NZ Trees, (b) Swedish Pines, (c) newly emergent bramble canes, (d) adult bramble canes. Black points represent the original location of the individuals and the grey points the regular pattern

overlap. The Swedish Pines IAF emphasises the degree of regularity in the data with many short line segments ( $7.0 \pm 3.5$  vs.  $8.8 \pm 4.7$ ), seemingly with no directionality and little overlap (supporting the high  $I_p$  and  $P_p$  values for this event set). The plots for the bramble canes, both newly emerged and adults, show more complex patterns, with variable length lines ( $0.08 \pm 0.04$  and  $0.03 \pm 0.02$  vs.  $0.07 \pm 0.04$  and  $0.04 \pm 0.02$ , respectively), many of which overlap; there also appears to be some directionality in the data with the line segments for the emergents radi-

ating out from distinct clusters. The EDF plots emphasise the conclusions drawn above, and highlight the skewed nature of the distribution of  $d_i$  for the clustered data (Fig. 9).

#### Bivariate analyses

Three event sets were used to explore the way that the different statistical methods performed in the bivariate case (association); that is, are events of type  $i$  aggregated or segregated with respect to events of



**Fig. 9** EDF plots for the univariate event sets: NZ Trees, Swedish Pines, newly emergent bramble canes, adult bramble canes

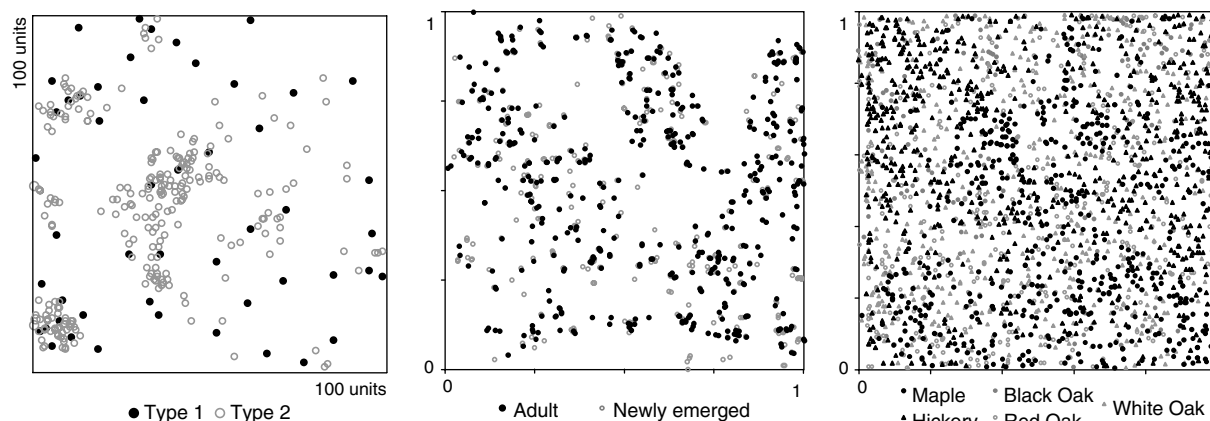
type  $j$  (Fig. 10). Biologically, such conditions could arise through competitive (regularity) or facilitative (aggregation/association) processes, for example. Following Goreaud and Pélissier (2003) confidence intervals were generated based on hypotheses of population independence (different cohorts and different species).

#### *Nearest neighbour contingency tables*

To analyse first-order interactions in bivariate (marked) event sets  $2 \times 2$  contingency tables can be used; both Pielou (1961) and Dixon (1994) describe methods for analysing association in this way. The Gibbsian process shows a strong degree of association (Table 5) for Dixon's  $S_{AA}$  and  $S_{BB}$  ( $P=0.036$  and  $P=0.02$ , respectively), but Pielou's  $S$  is not significantly different from random ( $P=0.325$ ). For both 'real world' event sets there is a high degree of segregation (Table 5) with Pielou's  $S$  and Dixon's  $S_{AA}$  and  $S_{BB}$  indices all significantly different from random ( $P<0.01$ ).

#### *Refined nearest neighbour analysis: Diggle's $G$ and all event-to-all events*

As expected, the bivariate refined NN tests characterise the Gibbsian process as showing aggregation (positive association) at short distances and segregation (negative association) at longer ones ( $t \geq 10$ ; Fig. 11). Diggle's  $G$  suggests some asymmetry in the spatial patterning of the two types. For the newly-emergent and adult bramble canes Diggle's  $G$  suggests aggregation at short distances. The all-to-all test characterises the two types as being aggregated at short distances (0–12 units). For the Lansing Woods hickories vs. maples, Diggle's  $G$  implies that (from distances greater than six to seven units), although the distribution of the hickories is independent of maples, maples are positively associated with hickories. Examination of the data (Fig. 10) clearly shows that while hickories are widely dispersed, the maples are not: while all maples are likely to be near a hickory, not all hickories are likely to be near a maple. However, Diggle's  $G$  is limited because the greatest



**Fig. 10** Maps of the three bivariate spatial event sets used: the Gibbsian point pattern, the Bramble canes event set (newly emerged vs. adults) and the Lansing Woods event set (hickory

vs. maple, with other species having smaller grey symbols); see Table 1 for further descriptions

testable maple-to-hickory NN distance is relatively low, so it is not possible to comment on the association at greater distances where the pattern might be stronger.

#### *Second-order analyses: Ripley's $K$ and the $NDF$*

As expected, the bivariate multi-distance/scale tests characterise the Gibbsian process as showing aggregation at short distances and segregation at longer distances ( $t \geq 10$ ). Again, there are differences between the cumulative and non-cumulative tests. For the Lansing Woods data set the bivariate tests are all very similar and, with only one small exception, describe the relationship between the hickory and maple trees as one of significant segregation at all distances examined. This supports the contingency table analyses presented above.

## Discussion

### Which test?

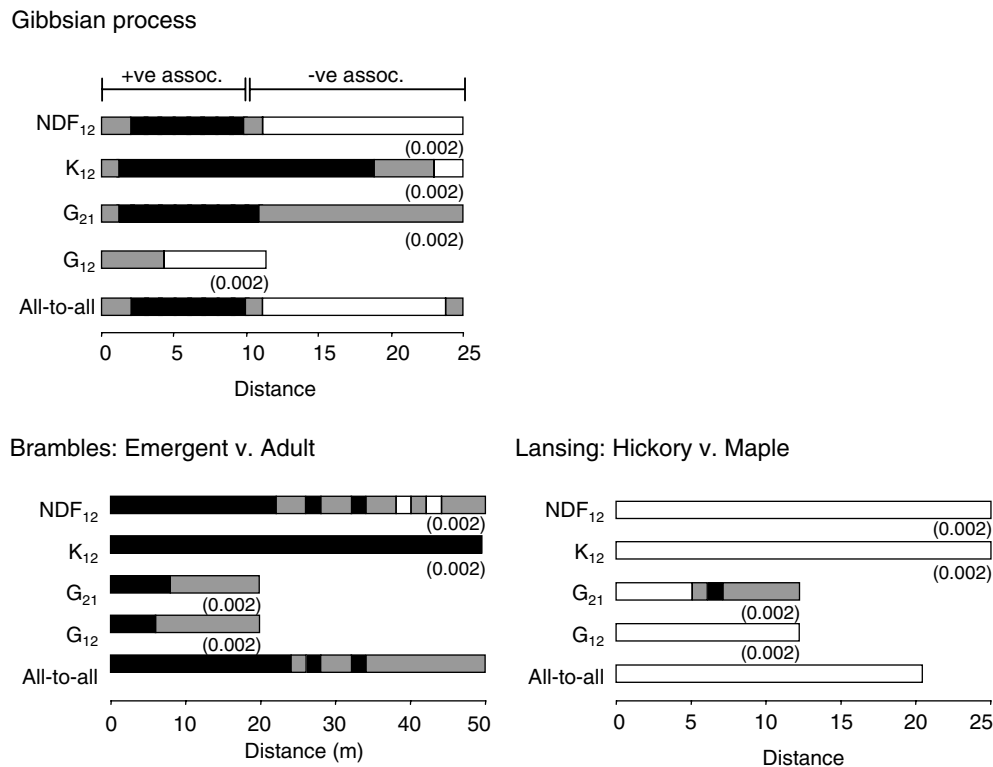
A large battery of statistics is available for analysing spatial point patterns. However, the question 'which

tests are more appropriate/powerful and when?' is not easy to answer. The judicious use of a combination of tests may well be the most informative approach; both Ripley (1981) and Diggle (2003) state that the various statistical tests should be used to complement each other.

The analyses considered above were divided into those derived from NN analyses (first-order and refined), and those based on second-order summary statistics. These two types of test have specific and clear advantages and disadvantages associated with them. NN analyses such as the Clark Evans statistic and refined nearest neighbour analysis (Diggle's  $F$  and  $G$ ), while conceptually simple, are limited to the scales over which first-order nearest neighbour interactions occur; they are 'short-sighted' (Stoyan and Penttinen 2000, p. 65). If events are strongly clustered or aggregated then they may consider pattern(s) only over very short distances and ignore the larger part of the data. They are also density-dependent, which may make their direct comparison across multiple event sets difficult (although summary curve-wise tests provide one potential solution). Indeed, Ripley (1979, p. 373) comments that, for analyses that solely use the nearest neighbour

**Table 5** Summary statistics derived from the NN contingency table (see Pielou 1961; Dixon 1994)

Pattern	Pielou's $S$	$S_{AA}$	$S_{BB}$	$P [S]$	$P [S_{AA}]$	$P [S_{BB}]$
Gibbsian process	−0.014	−0.81	0.68	0.325	0.036	0.002
Brambles: Emerg vs. Adult	0.0061	0.120	−0.09	0.584	0.246	0.856
Lansing: Hickory vs. Maple	0.53	1.16	1.28	0.002	0.002	0.002



**Fig. 11** Comparison of characterisation of pattern for the bivariate inter-type event sets: simulated bivariate Gibbsian pattern, bramble canes: newly emergent vs. adults and Lansing Woods—hickories vs. maples. Grey areas indicate that the distribution does not differ from CSR for that distance interval,

white, that it is segregated and, black that it is aggregated; two-tailed test,  $P < 0.01$ . Numbers in parentheses below the bars indicate two-tailed  $P$ -value based on curvewise goodness-of-fit to the values expected under CSR, based on the Cramer-von Mises test (Eq. 1b)

distance (e.g. the Clark Evans statistic) to test for ‘randomness’, ‘the value of an investigation that stops at that point seems limited’. Nevertheless, first-order NN analyses, bearing these limitations in mind, are useful tests for analysing spatial point patterns and may represent a logical first step in analysis. While  $n$ th-order NN analyses can circumvent these problems, they become difficult to interpret as the order increases (i.e. ‘what is the *ecological* significance of a deviation from CSR in the 13th-nearest neighbour?’). All event-to-all event analysis provides useful information, especially when coupled with underlying information about the average number of events per cluster. Dale (1999) comments that a potential problem with this test is that the method may fail to detect gaps in the spatial pattern; however, this was not observed in the analyses described here.

Second-order analyses provide information across a range of distances. A potential problem with some

of these statistics (e.g. Ripley’s  $K$ ) is that of ‘cumulative effects’. Because Ripley’s  $K$  is cumulative, values of the statistic at some distance  $t$  may be unduly influenced by its values at smaller distances (see Ward et al. 1996; Condit et al. 2000). Perry et al. (2002) found that at high densities there may be strong autocorrelation effects between successive values of  $K(t)$ . Nevertheless, an informal survey of the ecological literature over the last decade suggests that Ripley’s  $K$  appears to remain the ‘statistic of choice’. Because Ripley’s  $K$ -function is cumulative and the NDF is not, the tests allow for different inferences to be made (Wiegand and Moloney 2004). With Ripley’s  $K$ -function, we can ask if individuals of a species are aggregated or dispersed *up to* distance  $r$  with respect to individuals of another species, but *not* if they are aggregated or dispersed *at* distance  $r$ . However, the NDF allows us to ask if individuals are clustered/aggregated or

regular/segregated at specific distances. Thus, the two tests might be used to ask different ecological questions, and the difference between the two inferences, although subtle, is important. Because the NDF is a probability density function its interpretation is also (arguably) more intuitive than that of the cumulative  $K$ -function (Stoyan and Penttinen 2000). Nevertheless, because it is effectively a differenced version of the  $K$ -function, we might also expect the NDF to be more noisy, and sensitive to small sample sizes (Wiegand and Moloney 2004). Of course, these observations do not mean that the  $K$ -function is not useful, rather it means that we need to be aware of these issues when selecting and interpreting such tools.

The various tests also vary in their power (something that the analyses above implicitly explore). Diggle's  $F$  and  $G$ , and Ripley's  $K$  are known not to have the same power for all patterns (Barot et al. 1999).  $G$  is better at determining regularity and  $F$  better for aggregation; for aggregated patterns  $K$  has a little less power than  $F$ , but for regular patterns is higher than  $G$  (Diggle 1979). In some restricted cases Diggle's  $F$  and  $G$  may suggest deviation from CSR when the event set is actually CSR (see Thönnies and van Lieshout 1999). A surprising number of studies use just one method of analysis, and, by extension, thus consider only one aspect of pattern.

Recently, other types of spatial analysis have received considerable research attention. For example, spatially-sensitive regression methods (e.g. geographically weighted regression, GWR) and GLMs have been developed (Brunsdon et al. 1998). As with point pattern methods, these approaches are concerned with connecting spatial structure to process, but explicitly incorporate the effects of covariates on the observed patterns. For example, Shi and Zhang (2003) and Zhang and Shi (2004), explored links between spatial pattern and competition using localised forms of spatial autocorrelation measures (LISA) and GWR. The field of spatial analysis is wide, but many of what are often seen as disparate approaches share conceptual and methodological links (see Stoyan and Penttinen 2000; Dale et al. 2002). Using these different approaches alongside each other is likely to prove fruitful, and allow data to be explored from multiple perspectives.

## Local or global?

Local point pattern analysis methods have been relatively little used by ecologists, with most published research tending to present the results of a single global statistic. However, the use of local point pattern analyses seems to have much to commend it. It may be incorrect to assume that the results of a global description of spatial pattern apply equally to all parts of the study area, and useful insights can be gained by exploring spatial variations in the results. Local variations may be subsumed in global descriptions of spatial pattern; in some cases (e.g. epidemiological studies) the global characterisation of pattern would seem to be at odds with the aim of identifying localised clustering (Fotheringham 1997). As Fotheringham (1997 pp. 88–89) comments “simply reporting one ‘average’ set of results and ignoring any possible variations in those results is equivalent to reporting a mean value of a spatial distribution without seeing a map of the data”. As demonstrated above, patterns that approximate CSR on average may show segregation and aggregation in different locations at different scales (Figs. 6, 7). Recent competition theory emphasises spatial interactions and the ‘plant’s-eye view’ (Purves and Law 2002), and considerable theoretical research has highlighted that mean-field approaches are not always appropriate for describing ecological processes (e.g. see Amarasekare 2003; Bolker et al. 2003). The same seems likely to be true when describing ecological patterns.

Another advantage with both the localised form of Ripley's  $K$  and the SADIE analyses is that they provide spatially explicit visual information about the nature of the pattern of interest. Such visualisation is especially important in the EDA context in which many spatial analyses occur in ecology. Although there are criticisms of ‘pure’ visualisation in that (i) the way a map is presented can influence a viewer's conclusions (e.g. use of class intervals in choropleth maps) and (ii) the brain tends to see patterns even where they may not exist (e.g. CSR patterns are frequently described as clustered by viewers), when used objectively alongside quantitative measures, visualisation is a useful way of exploring trends in spatial data (see Unwin 1996; Fotheringham 1999).



Using local analyses, in conjunction with appropriate visualisation tools, variations within plots in aggregation can be seen and described in a way not possible using simple global statistical measures (Wilhelm and Steck 1998).

#### Extension beyond bivariate event sets

The tests described above can, at most, analyse bivariate data or be applied sequentially in a pairwise manner. However, full pairwise comparison is usually not practical in multivariate event sets with many different types of events (e.g. species, age-classes, etc.). For example, an event set containing 50 different species would require 2,450 ( $n \times [n-1]$ ) separate analyses; it would also be necessary to control for the family-wise Type I error rate. Such comparisons would also, of course, be unable to detect interactions involving more than two species. Furthermore, bivariate analyses do not necessarily explicitly consider the identity of the different types (e.g. species) involved, simply classing species as either (i) the species of interest, or (ii) some other species (e.g. Plotkin et al. 2000b). Thus, such tests, although applicable to multivariate event sets, may not consider the *identity* of each event. Dale (1999, p. 239) comments “...we have found no example of truly multi-species analysis in the sense of looking at combinations of species simultaneously ..”. Dixon (2002c) described multi-way contingency tables based on nearest neighbour distances for multiple species, and this offers one potential way to avoid performing a large number of pairwise tests (although it is limited to considering nearest neighbours only). van Lieshout and Baddeley (1996) describe an index (the *I*-function) based on a weighted average of the *J*-function (where  $J(w) = (1 - G(w)) / (1 - F(x))$ ) for multi-mark event sets. Nevertheless, in the area of multivariate point pattern, there is a need for further research and the development of analytical tools (see Podani and Czarán 1997; Podani et al. 1998; Shimatani 2001; Shimatani and Kubota 2004 for some attempts in this direction). For bivariate data it may be important to explore the degree of (a)symmetry in the interaction between events of different types. Diggle’s *G* and the NDF test are both asymmetric in their bivariate forms. For an isotropic process, the theoretical  $K_{12}(t)$  equals  $K_{21}(t)$ , as distances

are symmetric, with edge corrections resulting in different, but positively correlated, estimates for  $K_{12}(t)$  and  $K_{21}(t)$  but not information about asymmetry (Dixon 2002a). Eccles et al. (1999) present a bivariate index of asymmetry based on the coefficient of variation in the density distribution of events of different types.

#### Description vs. mechanism: what can we say?

Real and McElhany (1996, pp. 1011–1012) consider there to be two broad problems that spatial analyses in ecology seek to address:

1. The detection and assessment of spatial patterning.
2. Identification of the mechanisms that result in the formation of different types of spatial pattern in ecosystems.

Addressing the first problem is relatively easy, but attempting the second is much more difficult. First, we are trying to understand the dynamics of what is likely a hierarchically-organised stochastic system from a single temporal snapshot (often at a single scale). The expense and difficulty of collecting spatial data means that replicated sampling is uncommon. In general terms, because multiple process outcomes can result in or explain the same spatial pattern (equifinality), there are difficulties associated with inferring process from pattern, and so the two must be considered in tandem (Cale et al. 1989; Real and McElhany 1996). In reality not all of the possible processes that could generate a pattern will be as a posteriori plausible as each other, but it will often be the case that two or three equally plausible candidate explanations remain. Distinguishing between these equifinal alternatives will require the use of other (perhaps non-spatial) techniques, while using the knowledge derived from the spatial analysis, but is unlikely to be possible on the basis of any spatial point pattern analysis alone. As McArdle et al. (1997) discuss, the same problems may befall inference in the reverse direction (i.e. explaining pattern from knowledge of process). These problems also occur at a more technical level; for example, Baddeley and Silverman (1984) have shown that  $K(t)$  does not uniquely define point processes—two different processes can have the



same  $K(t)$  function (they show how a stationary non-Poisson process can generate a  $K$ -function identical to that of a homogeneous Poisson process). Likewise, depending on context, the same ecological process can generate different spatial patterns. Finally, it is important to realise that just because we characterise a spatial pattern as random (the typical null model) does not necessarily mean that the processes generating it are, of themselves, random (e.g. see Molofsky et al. 2002).

Moravie and Roberts (2003) provide a useful (and cautionary) example that serves to illustrate these issues. They used a stochastic spatially explicit individually-based model (IBM) of forest dynamics, to test whether stand structure (i.e. spatial arrangement of individuals) is a useful indicator of competitive interactions in the stand, as is often tacitly assumed. As their model is stochastic, it provides multiple outcomes for a single parameter set. Using the  $K$ -function to describe stand structure, they found high variability in spatial pattern produced under the same parameterisations (i.e. the same process results in multiple spatial outcomes), and suggest that only the ‘main trends’ were discernible; it was not possible to infer the type of competition (one- vs. two-sided) in the stand based on the simulated spatial patterns. Moravie and Roberts (2003) comment that in heterogeneous stands both biotic and abiotic effects will act to further confuse the links between pattern and process.

Despite these problems, two examples serve to illustrate how careful use of spatial pattern analysis can allow us to make cautious inferences about the underlying processes in the system(s) of interest. Barot et al. (1999) conducted a comprehensive analysis of spatial patterning of the palm *Borassus aethiopum* (Palmae) in relation to demographic and sex structure. They provide a series of hypotheses that might explain spatial patterning of the adult palms, and test these. The key trends were that (i) seedlings and juveniles are strongly aggregated while adults showed a pattern approaching CSR, or were very weakly aggregated, (ii) except for adult females, all stages are associated with patches of nutrient-rich soil, with association distances increasing with life-cycle stage, and, (iii) seedlings are associated with adult females. These patterns are closely linked to mortality trends over an individual’s life cycle, relating to the short-distance

dispersal of seeds from maternal plants, juveniles and young adults being limited to nutrient-rich patches, and the intense competition on nutrient patches favouring individuals that survive away from these patches. Most importantly, Barot et al. demonstrate how a careful use of spatial pattern analysis methods can be used to generate testable hypotheses about the underlying mechanisms driving the observed patterns. Barot et al. (1999) use several statistical tests to explore pattern—this is important as the tests are sensitive (as demonstrated here) to different aspects of pattern and vary in their power. Jolles et al. (2002) studied the spatial distribution of infection among Sea Fans (*Gorgonia ventalina*) by a fungus (*Aspergillus sydawii*), to assess the dynamics of secondary disease transmission. They state a series of spatial hypotheses about possible mechanisms of disease transmission on the Sea Fans. Jolles et al. found that where disease prevalence was low, diseased individuals had a random distribution; this suggests transmission via fungal material from terrestrial sources alone. Conversely, where disease prevalence was high, diseased individuals showed an aggregated distribution, indicative of secondary transmission. Their results suggest that disease transmission occurs both via direct physical contact and water-borne transmission (shedding of fomites). However, Jolles et al. (2002) could not separate the effects of small-scale local environmental variability (e.g. topography, flow conditions) from secondary transmission via contact as drivers of the aggregated pattern of diseased sea fans (the problem of apparent vs. true aggregation discussed by Real and McElhany 1996). Nevertheless, their analyses allow (i) the scale of the process to be estimated and (ii) explicit testing of hypotheses concerning the mechanisms operating in this system.

The common threads here are (i) the use of a priori hypotheses which are explicitly tested via the analysis, and (ii) the generation of testable hypotheses as an outcome of the spatial analyses. Using point pattern analysis to test explicitly stated a priori hypotheses has been advocated by Schurr et al. (2004) who argue that it is a useful means of avoiding data-dredging and is more likely to provide useful information on mechanism than an ad hoc approach; we agree. As Real and McElhany

(1996) and Jolles et al. (2002) emphasise, having detailed biological information about the system becomes crucial at this point. Using more realistic models for hypothesis testing (i.e. beyond the CSR) may also help (Wiegand and Moloney 2004). If each possible process model is treated as a general hypothesis, and then each parameterisation of each model as a tighter statement about that hypothesis, it may be possible to make some more concrete statements about the processes that are (or are not) capable of generating the observed patterns. Further, it seems more reasonable to use such analyses to reject, rather than explicitly identify, the processes at play.

## Conclusions

Analysis of spatial point pattern has a long history in plant ecology and there are a number of tests available to characterise and explore such data. However, these tests do not all perform equally and all have their weaknesses and strengths. As a result, it is suggested that a suite of statistics is used to characterise spatial point patterns, otherwise there is a risk that the description of the pattern will be partially determined by the test chosen. Certainly the most commonly used tests suffer from some serious limitations: nearest neighbour analysis and refined nearest neighbour analysis (Diggle's  $F$  and  $G$ ) are first-order only and are limited in the distances over which they can be applied, while Ripley's  $K$  shows strong effects at some scales as a result of its cumulative nature. In our comparative tests the less frequently used, neighbourhood density function (NDF) was the most consistent and robust descriptor. Local analyses provide a potentially useful means of taking the 'plant's-eye view', and thereby linking spatial pattern with ecological theory. Visualisation of the spatial pattern itself, especially in conjunction with other quantitative analyses, also provides a useful tool. The real goal and challenge of spatial analysis is linking pattern and process. We believe that (i) the use a priori hypotheses which are explicitly tested via the analysis, and (ii) the generation of testable hypotheses as an outcome of the spatial analyses will aid in this. The use of null models other than the CSR is likely to prove valuable in this process.

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