CHAPTER 3

Dimensions of spatial heterogeneity: a classification of non-, semi- and explicit spatial heterogeneity

INTRODUCTION

Understanding the causes of spatial heterogeneity in the abundance of organisms is central to ecology. The quantification of spatial pattern in biotic and abiotic variables, and how such pattern may influence species interactions and their responses to resources, is an ongoing research focus (Ives & Klopfer 1997; Stewart *et al*. 2000; Wiens 2000; Liebhold & Gurevitch 2002). Typically, species occurrences are aggregated and numbers of individuals are unevenly distributed across sites (Cole 1946; Perry *et. al*. 2002). Although aggregation is an inherent species property (a function of species dispersal and behavioural patterns), the occurrence of individuals at different densities across space may also reflect a response to biotic and abiotic environmental conditions (e.g. resource quality and availability) (Taylor 1984; Wiens 2000). The study of the aggregation of individuals is almost as old as ecology itself (Raunkiaer 1934; Cole 1946). That it remains a focus in ecology today (Perry *et al*. 2002) is testimony to its significance as an emergent property of responses of species to their environment, and its importance in interactions within and across trophic levels (Hassell & Pacala 1990; Sevenster 1996; Murrell *et al*. 2001; Plotkin *et al*. 2002; Porter & Hawkins 2003; Warren *et al*. 2003).

One of the consequences of the widespread significance of aggregation is the extensive array of methods that have and continue to be developed for its measurement (Dale *et al*. 2002; Perry *et al*. 2002). However, these methods differ in their information content, biological relevance, and conclusions regarding the form of spatial heterogeneity (e.g. clumped or random) that they identify (Perry 1998; Wiens 2000; Tenhumberg *et al*. 2001). Moreover, a distinction has recently been made between measures of spatial heterogeneity (*sensu* Wiens 2000) that do and do not incorporate spatial information, and the degree to which these methods provide solutions that are spatially explicit (Wiens 2000; Perry *et al*. 2002). In this

study we highlight the spatial reference-related (spatial co-ordinates, e.g. latitude and longitude) differences between methods in terms of both the data used and pattern identified (synthesizing the approaches of Wiens (2000) and Perry *et al*. (2002)).

We distinguish three major groups of methods, i.e. those that are spatially non-explicit, semi-explicit and explicit, and discuss their application to abundance and occurrence data. Distinguishing between these approaches has become particularly important with the continued proliferation of analytical methods (and associated terminology, see Dutilleul & Legendre (1993)) (e.g. Plotkin *et al*. 2002; Perry & Dixon 2002), and the absence of comprehensive empirical comparisons between them (see Dale *et al*. 2002 for theoretical relationships). We propose a classification scheme for various measures of spatial heterogeneity for both occurrence and abundance data, based on the degree to which the described pattern is spatially explicit. The framework provided allows measures and their strengths to be compared, highlights the most commonly used examples of these measures, and proposes a hierarchy of information content and biological relevance. We emphasize opportunities that exist for empirical comparisons of spatially explicit and non-explicit approaches to the measurement of spatial heterogeneity, and the potential value of spatially explicit approaches for the re-evaluation of theory developed using more traditional methods. The potential problems with quantifying different dimensions (i.e. the same entity with increasing amounts of available spatial information) of spatial heterogeneity but using them interchangeably, are illustrated using field-collected abundance data on an insect-herbivore, and the number of individuals parasitised and the imposed parasitism rate. Using these data we test whether the form of spatial heterogeneity found, for abundance data only, depends on the degree to which the method used to describe it is spatially explicit. We thus test if there is a difference between spatially non-explicit, semi-explicit and explicit methods in the form of spatial heterogeneity identified, and thus the conclusions drawn about aggregation.

Dimensions of spatial heterogeneity

Although the aggregation of individuals has been a recurring theme in ecology for many decades (Raunkiaer 1934; Cole 1946, Taylor 1984, Perry *et al*. 2002), until recently the lack of adequate spatial analytical methods has limited the examination of spatially explicit phenomena (Liebhold *et al*. 1993; Perry *et al*. 2002). The wide array of possible approaches to

the measurement and interpretation of aggregation that are now available were recently reassessed in light of current analytical developments (Coomes *et al*. 1999, Dale *et al*. 2002, Perry & Dixon 2002). However, these reviews do not consider the quantification of aggregation *per se* but rather any spatial pattern described in ecology. We use the term 'spatial heterogeneity', *sensu* Wiens (2000), to broadly encompass the array of spatial patterns (aggregation being only one of these) that can be described (Table 1, Fig. 1). Spatial heterogeneity can formally be defined as "discontinuities in space" (Wiens 2000), or pattern in spatial data (Liebhold & Gurevitch 2002), and may be quantified for either abundance (count), or occurrence (presence-absence) data. Although, spatially-referenced occurrence data can be transformed (with a loss of fine scale spatial information) to abundance per unit area (Perry & Dixon 2002; Perry *et al*. 2002), the use of untransformed occurrence data is common in ecology (Coomes *et al*. 1999; Plotkin *et al*. 2002 Wiegand & Moloney 2004). Therefore, defining terminology for spatial heterogeneity in both abundance and occurrence data will further contribute to unambiguous definitions in spatial ecology. Nonetheless, potential differences between the forms of spatial heterogeneity describe are likely to be greater for abundance than occurrence data, because spatial references are accompanied by recorded variable. Consequently, we focus on the differences between different degrees of spatial explicitness using abundance data (see Coomes *et al*. 1999; Plotkin *et al*. 2002; Wiegand & Moloney 2004 for detailed coverage of measures used to describe occurrence data).

The term ‘aggregation’ has commonly been used to denote the grouping of elements or a contagious condition of spatial heterogeneity. However, this term does not distinguish between the dimension (thus the level of spatial explicitness) used to quantify this form of spatial heterogeneity (i.e. the method used) (Wiens 2000). Because the form of spatial heterogeneity that is identified (e.g. overdispersed versus underdispersed, or regular versus aggregated, Table 1) may differ depending on the measure used to identify it (Perry 1998), the term 'aggregation' has become potentially misleading. Therefore, to allow unambiguous reporting of results, a need for formalised terminology to describe different forms of spatial heterogeneity has arisen. Here we use ‘aggregation’ as a loose, generic term for any grouping of elements (which is one form of spatial heterogeneity), and use the terminology outlined in Table 1 for reference to specific dimensions, measures and forms of spatial heterogeneity. The terms provided are

Table 1. Classification of spatial heterogeneity in abundance and occurrence data based on the degree of spatial explicitness (spatially non-explicit, semi-, and explicit). For each category an example of a measure used to determine the form of spatial heterogeneity is given. With each the measure terms and definitions used as well as synonyms (chronological order of use) and spatial applications or statistics used to quantify it are presented. Numbers in superscript denote source of terminology or example of recent use. For abundance data different measures to quantify correlation (A* vs. A^, with different symbols representing different data sets) are given. (Z), (D) and (X,Y) denote measured attribute, measured distance and spatial co-ordinates (e.g. latitude and longitude) respectively.

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
		1. Spatially non-explicit heterogeneity		
A) Statistical heterogeneity [1] (Z)	Skewness in the frequency distribution of counts; usually the relationship between the mean and variance [1]	Spatial distribution [2, 3]; Parametric intensity [4]; Density aggregation [5];	No spatial pattern applications [1, 4, 6, 7]; Spatially non-explicit modelling of species area relationships [3]	Poisson index of dispersion [8, 9]; Moore's index [10] Morista's index [10, 11]
Over dispersed [4, 10]	Variance greater than the mean – Negative binomial or geometric distribution [8, 12]	Aggregation [3, 9, 13]; Aggregated [14]		
Under dispersed [4, 10]	Variance smaller than the mean – Binomial distribution [12]	Uniform [12]; Regularity [9]; Regular [8]		
Dispersed [4]	Variance approaches the mean – Poisson distribution [8, 12]	Randomness [9]; Random [10]		
A* vs. A^) Correlation [15]	Magnitude of one variable measured at a sampling point changes as that of another changes [15]		Spatially non-explicit matching of variables	Spearman R [15]
B) Nearest neighbour distance [11] (D)	Distance between spatially referenced point and its nearest neighbour/s	Spatial distribution [16]	Test for spatial randomness with no spatial reference [11]	NN; kNN [10]

Table 1. continued

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
		2. Spatially semi-explicit heterogeneity		
A) Spatial structure [17] [(Z, X, Y), local pattern not incorporated [11]]	Values measured for points in space are similar, dissimilar or not related to neighbouring points	Surface pattern spatial heterogeneity [18]; Spatial abundance structure [19]	Allowance for spatial dependence in quantification of biological responses[7, 20]	Moran's *I* [17]; Trend surface analysis [17];
Spatial dependence [17]	Spatial structure in response variable due to spatial structuring in explanatory variables [20]		Sampling design [17]; Variance partitioning [17]	
Spatial autocorrelation [17]	Degree of dependence in error components of data due to neighbouring sites having an influence on the measured value [20]	Spatial clustering [21]	Identification of patch size [17]; Measuring correlation between neighbouring points [17]	
Positive autocorrelation [17]	Points close in space are more similar than expected by chance [17]			
Negative autocorrelation [17]	Points close in space are more dissimilar than expected by chance [17]			
No significant autocorrelation	Points close in space are spatially independent			
A* vs. A^) Cross-correlation [22]	Determine to which degree two data sets exhibit concordant periodic variations[17]		Describes relationship between co-occurring species [22]	Mantel statistic [17]

Table 1. continued

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
B) Spatial distribution [15, 23] (X, Y)	Physical position (distribution) of sample points in two-dimensional space [23]; Location of clusters of points in study arena [24]	Point pattern spatial heterogeneity [18]; Spatial aggregation [5]; Spatial clustering [24]	Presence-absence data [18]	Index of aggregation (SADIE-map) [6,23]
	3. Spatially explicit heterogeneity			
A) Spatial non-randomness [1] (Z, X, Y), local pattern incorporated[11]	Difference between physical arrangement of the counts and randomisations of these counts [1]	Spatial arrangement [4, 25]; Spatial distribution [6, 26]	Determination of overall pattern [1]	Index of aggregation (SADIE regular) [1, 10];
Regular [1, 4]	Sample counts are equally spread among sampling points			
Random [1, 4]	The spatial arrangement of counts is no different from that expected by chance			
Aggregated [1, 4]	Arrangement of counts are non-random [27]	Spatial aggregation [25]		
Spatial clustering [28]	Counts are clustered into patches (groups of high counts) and gaps (groups of low counts)	Spatial patchiness [6]	Identifying the location of patches and gaps [1]	Mean and local clustering values (SADIE red/blue) [6]
Local indices of spatial autocorrelation [29]	Describes spatial autocorrelation for each sampled data point [29]	Local spatial autocorrelation indices [30]	Determining local indicators of non-stationarity [29]; Detect outliers of the global spatial autocorrelation value[29]	LISA statistic[29]

Table 1. continued

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
A* vs. A^) Spatial Association [27, 31]	Degree of matching between two sets of spatially referenced counts [27, 31]		Method for detecting correlation between two sets of spatially referenced data [31, 32, 33]	Mean and local association values (SADIE Association test) [27]
Significant association [27, 31]	Spatial matching of clusters of two sets of data [27, 31]			
Significant dissociation [27, 31]	Spatial mismatching of clusters of two sets of data [27, 31]			
Non-significant association	Degree of spatial matching or mismatching is not significantly different from expected by chance			
B) Point-cluster analysis [24] (X, Y)	Number of sampling points connected to at least one neighbour within a minimum specified distance [24]	Spatial clumping [24]	To determine size and position of clusters of sampling points [24]	No statistic as yet, but rather descriptive, i.e. distance moved [24]

(1) Perry 1998; (2) He & Legendre 2002; (3) He & Gaston 2003; (4) Bohan *et al.* 2000a; (5) Tenhumberg *et al*. 2001; (6) Perry *et al*. 1999; (7) Jumars *et al*. 1977; (8) Bliss & Fisher 1953; (9) Perry & Hewitt 1991; (10) Dale *et al.* 2002; (11) Perry *et al*. 2002 (12) Iwasa *et al*. 1981; (13) Gross & Ives 1999; (14) Rosewell *et al*. 1990; (15) Zar 1984; (16) Williams *et al.* 2001; (17) Legendre & Legendre 1998; (18) Dutilleul & Legendre 1993; (19) Brewer & Gaston 2002; (20) Legendre *et al*. 2002; (21) Ni *et al*. 2003; (22) Rossi *et al*. 1992; (23) Perry 1995a; (24) Plotkin *et al*. 2002; (25) Perry 1995b; (26) Ferguson *et al*. 2000; (27) Perry & Dixon 2002; (28) Wiens 2000; (29) Anselin 1995, (30) Sawada 1999; (31) Winder *et al.* 2001; (32) Korie *et al*. 2000; (33) Thomas *et al*. 2001;.

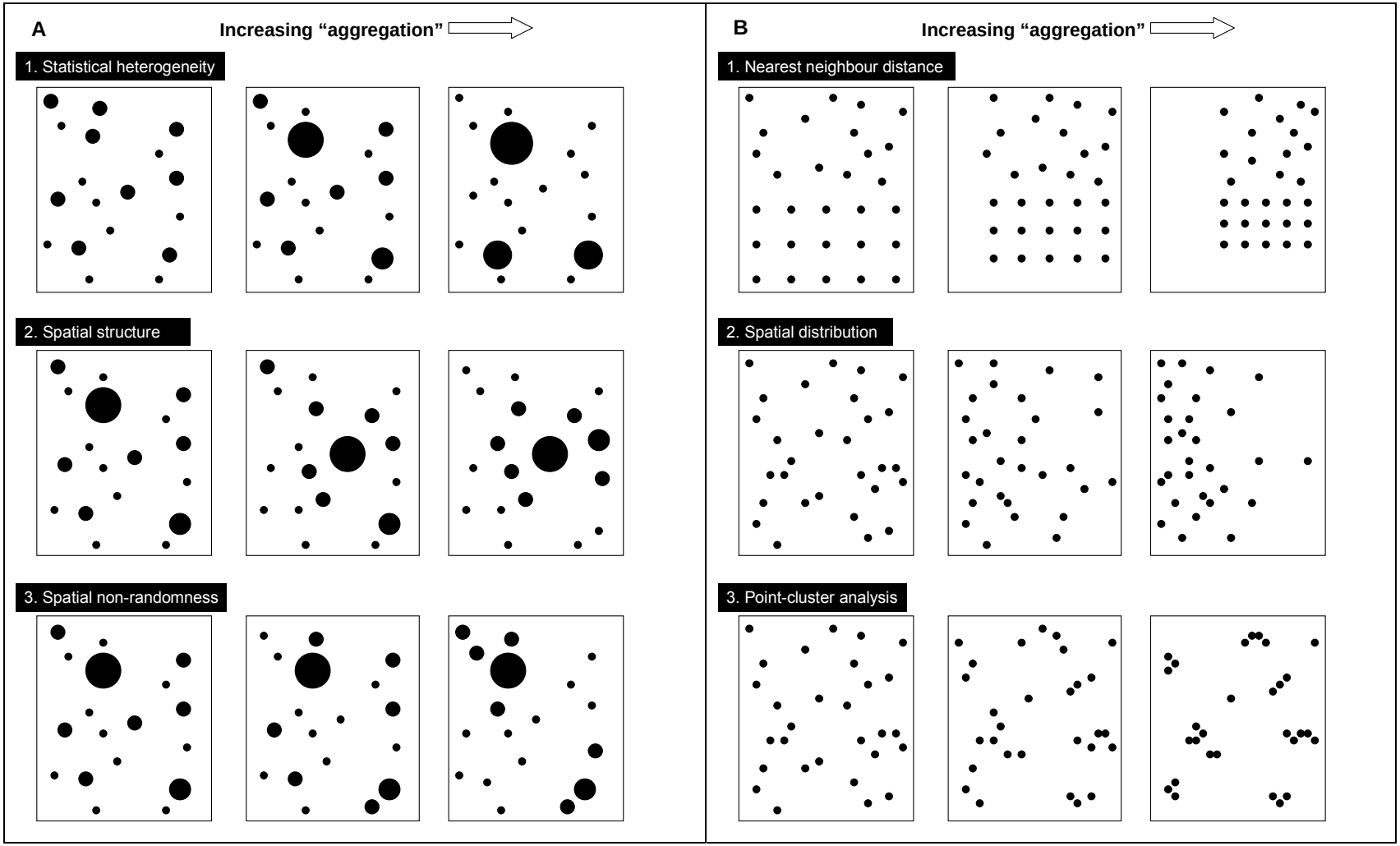

Figure 1. Different measures of spatial heterogeneity in abundance (A) and occurrence (B) data in ecology, with 'aggregation' increasing from left to right. Measures numbered 1, 2 and 3 represent spatially non-explicit, semi-explicit and explicit spatial heterogeneity respectively. In A. all sampling points within a study area/block have the same spatial references, with the size of a circle denoting the magnitude of a count at that sampling point. In B. each circle denotes the presence of an individual.

largely a synthesis of those in the literature, and their distinction here is intended to avoid confusion between the data type, category and form of spatial heterogeneity described by different measures of spatial heterogeneity (Table 1). In the following paragraphs I outline the three categories that vary in the degree to which they are spatially explicit, each generally represented by a single commonly used measure of spatial heterogeneity in abundance and occurrence data. The three dimensions are spatially non-explicit, spatially semi-explicit and spatially explicit heterogeneity (Table 1). In addition, for abundance data we list a method for each dimension of spatial heterogeneity used to correlate the spatial heterogeneity in two data sets.

Statistical heterogeneity and nearest neighbour distance (quantified for abundance and occurrence data respectively) can be considered measures of spatially non-explicit heterogeneity, because records are taken across a series of sampling points in a site, which are not spatially referenced (e.g. Williams *et al*. 2001) (Table 1, Fig. 1). In fact statistical heterogeneity can be said to be totally independent of spatial pattern. Nonetheless, not using spatial information (spatially non-explicit heterogeneity) can be seen as the preceding step of using spatial information (spatially semi- and explicit heterogeneity, Table 1) in a classification of spatial data use. Spatial structure (abundance data) (Legendre & Legendre 1998) and spatial distribution (occurrence data) (Perry 1995a), are measures of spatially semi-explicit heterogeneity, because although spatial dependencies or patterns can be accounted for (Perry *et al*. 2002), the heterogeneity described is not explicitly related to any particular location within the study site (i.e. the exact pattern of specific locations or areas within a site are unknown) (Wiens 2000). Spatial non-randomness and point-spatial clustering are measures of spatially explicit heterogeneity (Table 1, Fig. 1). These measures are spatially explicit because spatial heterogeneity may be related to particular sample points or areas within the study arena (Wiens 2000). For example, with spatial non-randomness the position of areas of comparatively high counts can be described, while point-spatial clustering describes the position and size (number of individuals) of groups of individuals (Plotkin *et al*. 2002).

The traditional, spatially non-explicit approach to the measurement of heterogeneity, statistical heterogeneity (Table 1), is merely the relationship between the variance and the mean of the frequency distribution of counts and can be quantified by the Poisson index of dispersion (Perry 1998) (Table 1, Fig. 1). Animal abundance, usually with many zero and few

large counts, is also considered overdispersed when fit by the negative binomial distribution (NBD) (Bliss & Fisher 1953; Williams *et al.* 2001). In such cases the index of aggregation of the NBD, *k*, is less than unity (Bliss & Fisher 1953). However, the ability of *k* to describe ecologically relevant spatial pattern has long been contested (Taylor *et al*. 1979). For example, the inverse of k behaves inconsistently over ranges of over dispersion even when the NBD fits the data, indicating the inadequacy of *k* to describe statistical heterogeneity (Taylor *et al*. 1979). Also, the NBD is not suitable for quantifying aggregation in patches of variable size (Sevenster 1996), or predicting abundance from occupancy in some cases (Warren *et al*. 2003). Furthermore, Perry & Hewitt (1991) and Perry (1995b) consider overdispersion to be of limited interest when investigating the spatial heterogeneity of individuals, because overdispersion in biological data is virtually universal (Taylor *et al*. 1978). The relationship between two variables described by statistical heterogeneity can only be determined by correlation (Table 1). Although the two data sets may share spatial references, spatial references are not included in the quantification of the relationship. Any correlation detected will therefore be spatially non-explicit.

The quantification of spatial structure, a semi-explicit approach, has also been used to measure spatial heterogeneity (Jumars *et al*. 1977; Dessaint *et al*. 1991; Loch & Zalucki 1998; Brewer & Gaston 2002) (Table 1, Fig. 1). If the values of any point-referenced, continuous variable are spatially dependent or spatially autocorrelated, then the data are spatially heterogeneous (Legendre & Legendre 1998; Wiens 2000; Perry *et al*. 2002) (Table 1). Positive autocorrelation, for example, indicates that adjacent values of a variable are more similar to each other than expected by chance (Sokal & Oden 1978; Koenig 1999). Determining this area of comparative homogeneity, or 'patch size' of biotic and abiotic variables is of particular interest in spatial ecology (Legendre & Fortin 1989; Koenig & Knops 1998; Koenig & Haydock 1999; Manson 2000). However, although spatial structure is quantified from spatially-referenced data, it does not incorporate information on patterns associated with physical positions (local pattern) (Perry *et al*. 2002), i.e. the value of an autocorrelation function is not influenced by the exact position of two sampling points in the study arena, only by their relative positions measured by the distance between them (Legendre & Legendre 1998). The spatial structure of two variables may be compared by cross–correlation methods (Table 1, see also Rossi *et al.* 1992). Although this allows the spatial references of each

variable to be considered, it is not possible to determine if the quantified spatial patterns match in a particular direction. Any relationship between the two variables will thus be spatially semi-explicit.

The more recent, spatially explicit approach to describing heterogeneity in spatially referenced count (abundance) data, involves the measure of spatial non-randomness (Perry 1998) (Table 1, Fig. 1). The quantification of this measure is based on the Spatial Analysis by Distance IndicEs (SADIE) method, which measures how much an observed arrangement of counts differs from a completely regular arrangement of the same counts (Perry 1995a). Using this method, spatial heterogeneity is quantified by an overall measure of non-randomness, as well as the degree to which individual sample counts contribute to overall clustering into patches (areas of high abundance counts) and gaps (areas of low abundance counts). The contribution of an individual sample to a local patch or gap is defined by a local clustering index (Perry *et al*. 1999; Perry & Dixon 2002). Consequently, local spatial pattern is dependent on the size of the count and its spatial position relative to neighbours (Perry *et al*. 2002). This is currently the most widely-used spatially explicit method that quantifies spatial heterogeneity from count data and simultaneously permits hypothesis testing (Bohan *et al*. 2000b; Ferguson *et al*. 2000; Korie *et al*. 2000; Thomas *et al*. 2001; Winder *et al*. 2001, Perry *et al*. 2002). Spatial association (Table 1) is a method that is able to determine overall and local (spatially explicit) matching in spatial heterogeneity based on spatial non-randomness (Perry & Dixon 2002). Because spatial association compares the spatial pattern of two variables instead of only counts, this method has greater power to detect significant relationships between them (Winder *et al*. 2001).

Developing largely as a separate field, geostatistics has also made attempts to describe spatially explicit heterogeneity (Anselin 1995; Sawada 1999). Local indices of spatial autocorrelation (LISAs) provide spatial information that is spatially explicit in much the same way that spatial non-randomness does (Table 1). With this measure the semi-explicit spatial autocorrelation index, which summarises largely all local autocorrelation indices, can be further scrutinised to detect areas of non-stationarity and to detect outliers of the global spatial autocorrelation value (Anselin 1995). Since this measure is very similar in conception to spatial non-randomness, LISA's were not calculated for this data set.

Although these three approaches have all been used, some extensively, to quantify spatial heterogeneity, few comprehensive comparisons have been made between them (although see Dale *et al*. 2002, Perry *et al*. 2002). However, the results of statistical heterogeneity analyses have been found to be unrelated to those of spatial structure (Dessaint *et al*. 1991) and spatial non-randomness (e.g. Perry 1995b; Perry 1998; Bohan *et al.* 2000a), although the latter relationship has not been fully explored. Furthermore, although *k* of the NBD is still regularly used to describe spatial heterogeneity (e.g. He & Gaston 2000; Tenhumberg *et al.* 2001; Williams *et al*. 2001), the conclusions reached using this measure have also not been quantitatively compared with the results of spatial structure and spatial non-randomness. Consequently, whether the degree of spatial explicitness of the measure used to describe spatial heterogeneity, i.e. statistical heterogeneity, spatial structure and spatial non-randomness, determines the form of spatial heterogeneity identified, has not been shown. Here, I thus test if these measures are interchangeable in the light of their current use, i.e. does the degree of spatial explicitness incorporated in a measure of spatial heterogeneity matter?

METHODS

Study Area

Gonometa postica populations were examined at five localities within the known (historic and recent records) outbreak range of this species, spanning a distance of 400km between the two furthest localities. The localities were Vryburg (26°59'S, 24°40'E) and Hotazel (27°15'S, 23°03'E) in North-central South Africa and Gabane (24°37'S, 25°46'E), Kumukwane (24°38'S, 25°40'E), and Kopong (24°31'S, 25°48'E) in South-Eastern Botswana. The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* Meyer and at the remainder, *Acacia tortillis* Hayne (both Mimosaceae) (Veldtman *et al*. 2002).

One site was selected at each locality, except at Vryburg where two sites (approximately 1.5 km apart) were selected. Sampling was standardized by delimiting an approximately rectangular area (plot) incorporating 100 trees at each site to compensate for possible tree-

density differences between host-plants and localities. An initial minimum of 40 first-generation cocoons per plot was a prerequisite for site selection.

Surveys of plots commenced in winter (June to July, 2000) and were repeated in mid summer (January, 2001). During the first survey, the number and fate of overwintering pupae were recorded. With the second survey, the resulting fate of those individuals that were alive in the first survey as well as the number of new first generation pupae were recorded. Similarly, the fate of these first generation pupae were followed (two subsequent surveys repeated at same periods as above) until mid-summer of the following year (January 2002).

Cocoon sampling

Within each plot every tree was carefully searched for cocoons. Cocoons were inspected to determine the fate of the pupa inside the cocoon, i.e. i) parasitised, ii) alive, iii) dead as a result of unknown causes, or iv) successfully emerged. This was indicated respectively by the i) presence or ii) absence of small emergence hole(s), iii) light weight of the cocoon or iv) a single large anterior emergence hole (pers. obs.). Parasitoid species responsible for parasitism may be identified from the shape and size of emergence holes left in the cocoon wall of a parasitised pupa (Veldtman *et. al* 2004). The number of pupae and parasitised pupae per tree were counted.

The position of each tree within a plot was measured at the main trunk of the tree with a hand held Global Positioning System (GPS). For trees in close proximity to each other the direction and distance between the two trees were noted and assigned to one of three categories (half, quarter and a tenth of the third (last) decimals of a minute) based on hand drawn maps which specifically documented this fine scale distribution of trees. These spatial co-ordinates were used in all spatial analyses.

For the investigation of the spatial pattern of parasitism, only sampling points (trees) with at least one pupa were included in analyses, as parasitism events can logically not be observed if there are no pupae. All counts of pupae or parasitised pupae were thus made per tree. At each site, pupae parasitised by different species of parasitoid were either analysed individually, or collectively ('all species') as a measure of total parasitoid mortality (see also Heads & Lawton 1983; Williams *et al*. 2001). Additionally we also considered the proportion of parasitised

pupae (parasitism rate from here on), which was transformed into integers by multiplying by ten and rounding off.

Quantification of spatial heterogeneity in abundance: what do the data say?

Spatial heterogeneity in three types of site recorded abundance data, namely number of pupae, number of parasitised pupae and parasitism rate (all per tree) were quantified using three measures, i.e. statistical heterogeneity (Table 1, A1), spatial structure (Table 1, A2) and spatial non-randomness (Table 1, A3), representing an increase in the degree of spatial explicitness with which the pattern was quantified (Table 1, Fig. 1A). This permitted direct comparison between the results of the three approaches in the conclusion reached regarding the form of spatial heterogeneity in the data.

Statistical heterogeneity

Statistical heterogeneity was quantified by determining the relationship between the mean and the variance of the frequency distribution for count data (Perry & Hewitt 1991) (Table 1). The Poisson index of dispersion (s^2/m) was calculated by dividing the sample variance by the sample mean (Perry & Hewitt 1991). If this index is close to unity the data have a Poisson distribution. When this index is smaller or greater than one it indicates that the distribution is under- and over dispersed and the data are best fit by a binomial or negative binomial distribution (or another over-dispersed distribution, e.g. gamma distribution) respectively (Table 1). Significant departures from randomness were determined by calculating $(n-1)*(s^2/m)$ and comparing it to the X^2_{n-1} distribution (Perry & Hewitt 1991).

Another measure of statistical heterogeneity, namely the index of aggregation, *k*, was also used to describe statistical heterogeneity. When the negative binomial distribution fits the data and the value of *k* is greater than unity (Bliss & Fisher 1953), count data are considered to be aggregated (Tenhumberg *et al.* 2001; Williams *et al*. 2001). The index *k* ranges from zero to infinity (∞) and the larger the value of *k* the greater the degree of aggregation (Bliss & Fisher 1953; Williams *et al*. 2001). The fit of the data to the negative binomial distribution (NBD) was tested using the method of Bliss and Fisher (1953), where *k* is first determined by a maximum likelihood solution and then used in the formula

$$U = s^2 - (\bar{x} + \bar{x}^2/\hat{k}_2) \quad (1)$$

to calculate the difference between observed and expected second moments. Adequate fit by the NBD is indicated if *U* falls within the range of its standard deviation (Bliss & Fisher 1953).

Spatial structure

Spatial structure was quantified using spatial autocorrelation (SAAP v 4.3 and Moran's *I*) (Wartenberg 1989), because there was no *a priori* evidence for spatial dependence in any of the biotic variables due to physical variables of the study sites (Legendre *et al*. 2002) (Table 1). The optimal number of equal-length distance classes was determined using Sturge's rule (Legendre & Legendre 1998). Overall correlogram significance (determined by comparing each distance class to a Bonferroni corrected α-level) was a prerequisite for the indication of spatial structure (Legendre & Legendre 1998). The size and significance of Moran's *I* values in distance classes with sufficient sample size were then examined. Often, when analysing biological data, the greatest Moran's *I* values are expected for the first distance class (Legendre & Legendre 1998).

Spatial non-randomness

SADIE methodology was used to quantify the degree of departure from spatial randomness for the spatially referenced (X,Y) count data in this study (Table 1). Spatial non-randomness is based on the distance to regularity (minimum cumulative distance to achieve a regular distribution of counts, thus when all sample counts are equal to the mean) that can be quantified for the data set as a whole (overall aggregation) or indicate the contribution of each sample point (degree of clustering) to local departures from randomness within the data set (Perry *et al*. 1999). The significance of overall aggregation was tested by dividing the actual distance to regularity by the average distances of randomisations of the sample counts, to give the index of aggregation (I_a) (Perry 1995a). This index summarises the spatial arrangement of the counts relative to one another (Perry *et al*. 1999; Perry & Dixon 2002). Although significance is actually tested, values of I_a of approximately 1.5 and greater indicate significant aggregation (Perry *et al*. 1999)

Whether or not there is evidence of overall aggregation, the degree of clustering in count data can be quantified (Perry & Dixon 2002). The index of clustering, *v*, provides information on the degree of clustering for each spatially referenced point based on the magnitude of the

count and its occurrence in relation to neighbouring counts. Clustering occurs in two forms, namely patches (counts greater than the sample mean, v_i) and gaps (counts smaller than the sample mean, v_j). For random arrangements of counts, v_i and v_j have expected values of 1 and -1. Values greater than these expected values indicate membership by the count of a patch ($v_i > 1.5$) or gap ($v_j < -1.5$) (Perry *et al*. 1999). Non-randomness is formally tested by comparing mean v_i and mean v_j values with their expected values of 1 and -1 for random arrangements (Perry *et al*. 1999). If mean v_i and mean v_j are not significant, the lack of overall, strong clustering into patches and gaps is indicated (Perry *et al*. 1999; Perry & Dixon 2002).

Within each plot, I_a, mean v_i and mean v_j was calculated for every parasitoid species that attacked pupae on more than 20% of the trees occupied by pupae. At densities lower than this (e.g. mean count per tree < 0.2), it is not possible to quantify overall aggregation and spatial clustering (Winder *et al*. 2001). The maximum ratio of non-zero values to total number of measured values that still allows the detection of significant spatial clustering (sufficient power) has been shown to be 4: 25 (Korie *et al*. 2000). In this study the lowest ratio was 9 to 38; within the specified limit. All non-randomness statistics were calculated with SADIEShell v. 1.21, red-blue analysis.

RESULTS

The number of pupae, number of parasitised pupae and parasitism rate varied greatly between sites (see Appendix). On average (± SE) there were 319 (± 66) pupae per plot occupying 52 (± 3) trees. Single parasitoid species parasitised an average of 50 (± 10) pupae on 22 (± 3) trees, while all parasitoids together parasitised 111 (± 25) pupae on 34 (± 4) trees per plot. There were thus marked differences in host abundance at the between sample (tree) scale in this study.

Quantification of spatial heterogeneity in abundance

In the following paragraphs the results of the three measures used to quantify spatial heterogeneity in *Gonometa postica*'s pupal and parasitised pupal abundance, as well as the parasitism rate of its parasitoids are reported.

Statistical heterogeneity

The number of pupae was over-dispersed in the majority of cases, but did not fit the NBD in any case (Table 2). Number of parasitised pupae was over-dispersed in two thirds of the cases and the NBD provided a significant fit in most cases. Parasitism rate was always over-dispersed but did not follow the NBD in a third of all cases. The discrepancy between presence of over-dispersion and adequate fit by the NBD was a result of more extreme over-dispersion than allowed for by this distribution (Bliss & Fisher 1953), evident from the large variance to mean ratios in these instances (Table 2, see also Warren *et al*. 2003). The index of aggregation of the NBD, *k*, was usually below 1.0 when the index of dispersion indicated significant over-dispersion, and greater than 1.0 or approached infinity when the data were not over-dispersed. Thus in terms of statistical heterogeneity the form of spatial heterogeneity identified was predominantly aggregated (Table 2, see Fig. 2a, c).

Table 2. Spatial heterogeneity (statistical heterogeneity, spatial structure and spatial non-randomness) for number of *Gonometa postica* pupae, parasitised pupae and parasitism rate (individual or all parasitoid species) per tree for each site. Statistical heterogeneity: s^2/m = the Poisson index of dispersion; fit by the negative binomial (NB) distribution: yes (Y) and no (N); k = the index of aggregation. Spatial structure: P(I) = overall Moran's I correlogram significance. Spatial non-randomness: I_a, overall index of aggregation. Form of spatial heterogeneity (FSH) quantified is indicated as being aggregated (A), random (R) or regular (E), or present (yes (Y)) and absent (no (N)). *, ** and *** denote significance at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ level respectively. - indicates value unavailable

Site	**Statistical heterogeneity**								**Spatial structure**				**Spatial non-randomness**			
Species or Category	Number of pupae				Parasitism rate				Number of pupae		Parasitism rate		Number of pupae		Parasitism rate	
	s^2/m	NB	k	FSH	s^2/m	NB	k	FSH	P(I)	FSH	P(I)	FSH	I_a	FSH	I_a	FSH
Vryburg1																
Pupae	4.39***	N	-	A					0.218	N			1.34*	A		
?*Palexorista* sp.	3.87***	N	-	A	2.79***	N	-	A	0.210	N	0.383	N	1.37*	A	0.85	R
All species	4.45***	N	-	A	1.73**	Y	∞	A	0.114	N	0.791	N	1.46*	A	1.13	R
Vryburg2																
Pupae	6.69***	N	-	A					0.281	N			0.92	R		
Brachymeria sp.	2.87***	Y	0.427	A	2.73***	Y	0.441	A	0.096	N	0.411	N	0.76	R	0.86	R
P. semitestacea	2.43***	Y	1.004	A	3.32***	Y	0.804	A	0.535	N	1.000	N	1.01	R	0.98	R
All species	3.95***	Y	0.972	A	2.37***	N	-	A	0.505	N	0.519	N	0.85	R	0.89	R
Gabane generation 1																
Pupae	11.12***	N	-	A					0.834	N			1.19	R		
Brachymeria sp.	3.80***	Y	0.279	A	3.84***	Y	0.225	A	0.891	N	0.001	Y	1.16	R	1.10	R
P. semitestacea	2.42***	Y	0.381	A	2.21***	Y	0.396	A	0.795	N	0.499	N	0.99	R	1.14	R
All species	5.85***	N	0.608	A	2.33***	N	-	A	0.637	N	0.043	Y	1.09	R	1.13	R

Table 2. continued.

Site	**Statistical heterogeneity**								**Spatial structure**				**Spatial non-randomness**			
Species or Category	Number of pupae				Parasitism rate				Number of pupae		Number of pupae		Parasitism rate		Number of pupae	
	s^2/m	NB	k	FSH	s^2/m	NB	k	FSH	P(I)	FSH	P(I)	FSH	I_a	FSH	I_a	FSH
Gabane generation 2																
Pupae	10.01***	N	-	A					1.000	N			0.90	R		
Brachymeria sp.	2.97***	Y	0.491	A	2.16***	Y	0.586	A	1.000	N	0.922	N	0.63**	E	0.75	R
P. semitestacea	2.29***	Y	0.317	A	4.07***	N	0.296	A	1.000	N	1.000	N	0.73*	E	0.90	R
All species	5.61***	Y	0.476	A	2.93***	N	-	A	0.659	N	0.621	N	0.74*	E	0.86	R
Kumukwane																
Pupae	3.82***	N	-	A					0.125	N			1.12	R		
?Tachinidae sp.	1.18	Y	2.391	R	5.19***	Y	0.219	A	0.654	N	0.825	N	0.86	R	0.75	R
P. semitestacea	1.31	Y	1.407	R	5.21***	Y	0.234	A	0.128	N	0.522	N	1.24	R	0.99	R
All species	1.56**	Y	2.319	A	3.79***	N	-	A	0.162	N	0.462	N	1.19	R	1.11	R
Kopong																
Pupae	1.26	N	-	R					0.508	N			0.94	R		
P. semitestacea	0.96	Y	∞	R	5.89***	Y	0.129	A	0.530	N	0.088	N	1.16	R	1.16	R
All species	0.90	Y	∞	R	4.19***	Y	0.428	A	0.324	N	0.898	N	0.96	R	1.09	R

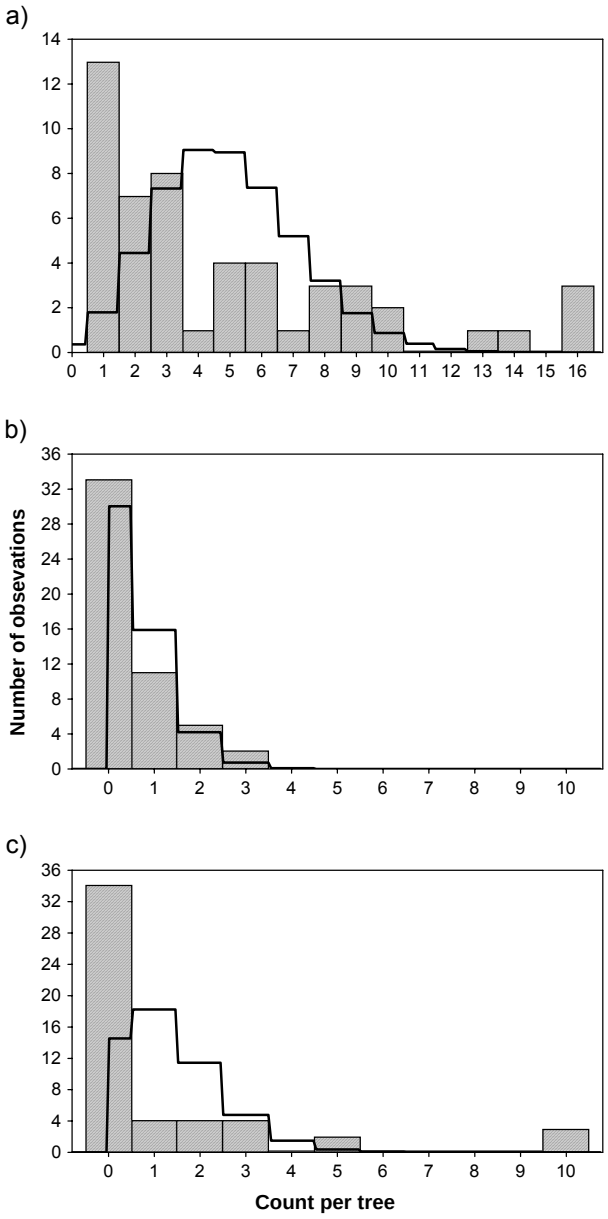

Figure 2. Statistical heterogeneity described by the frequency distribution of a) number of pupae, b) number of parasitised pupae and resulting c) parasitism rate of *P. semitestacea* at Kumukwane. Fitted line denotes an expected Poisson frequency distribution for the data. See Table 2 for specific statistics.

Spatial structure

No significant spatial structure (positive autocorrelation) was detected for number of pupae or number of parasitised pupae per tree (Table 2). No correlograms met the criteria of overall significance, and Moran's *I* was significant for the first distance class in only one case (number of pupae at Kopong) Other distance classes had significant Moran's *I* values but were characterised by small Moran's *I* values ($I < 0.2$), with only one or two isolated significant distance class per correlogram (e.g. Fig 3a-c). For parasitism rate there were two cases of overall correlogram significance (i.e. Gabane first generation pupae parasitised by *Brachymeria* sp. and all species, Table 2), but in both cases the first distance class was not significant, and only the second, and third and six distance class respectively was significant. For all three sets of abundance data, individual Moran's *I* values were small and significant for only one or two scattered distance classes, with no appreciable pattern overall (i.e. Moran's *I* values close to zero) (e.g. Fig. 3a, b, c).

Spatial non-randomness

Spatial heterogeneity in the counts of samples (Table 2), and their clustering into gaps and patches (Table 3), were generally not significant for either number of pupae or parasitised pupae and in no cases for parasitism rate. The pattern identified using this measure was thus mostly random (Fig. 4a, b, c). Exceptions that were significantly aggregated, were pupae and number of parasitised pupae at Vryburg1, (Table 2) with significant clustering into gaps and patches (Table 3). Another exception showing significant regularity was the number of parasitised pupae at Gabane (Table 2), with a significantly smaller degree of patchiness or gappiness than expected my chance (Table 3).

At Kumukwane, representative of other sites, although abundance data was mostly overdispersed (spatially non-explicit heterogeneity, Fig. 2), there was no significant spatial structure (semi-explicit heterogeneity, Fig 3.), or overall aggregation into gaps and patches, although certain sample points represented single sample point patches and gaps (spatially explicit heterogeneity, Fig 4).

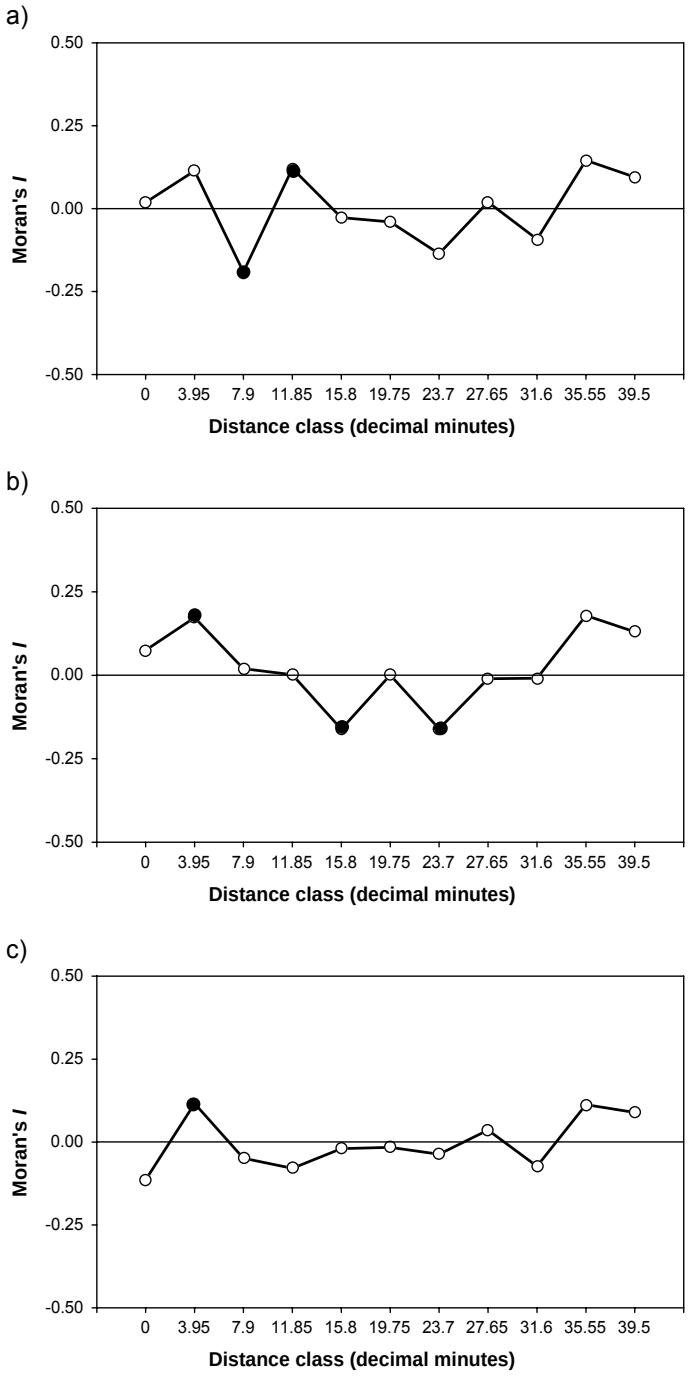

Figure 3. Spatial structure indicated by correlograms of Moran's *I* for a) number of pupae and b) number of parasitised pupae and resulting c) parasitism rate of *P. semitestacea* at Kumukwane. Significant distance classes are indicated with filled circles. See Table 2 for overall Moran's *I* correlogram significance. Number of point pairs per distance class: (1) 52; (2) 114; (3) 147; (4) 190; (5) 194; (6) 196; (7) 152; (8) 126; (9) 76; (10) 21; and (11) 10.

Table 3. Spatial non-randomness in terms of overall aggregation (also in Table 2) and local clustering of the number of *Gonometa postica* pupae and parasitised pupae, and resulting parasitism rate. n = number of non zero sampling points (maximum 100); I_a, overall index of aggregation; mean v_i and mean v_j, indices of clustering of patches and gaps respectively. * and ** denote significance at the $p < 0.05$ and $p < 0.01$.

Site	n	Number of pupae or parasitised pupae			Parasitism rate		
Species or Category		I_a	mean v_i	mean v_j	I_a	mean v_i	mean v_j
Vryburg1							
Pupae	53	1.34*	1.17	-1.48*			
?*Palexorista* sp.	40	1.37*	1.42*	-1.45*	0.85	0.97	-0.95
All species	46	1.46*	1.37	-1.55*	1.13	1.15	-1.24
Vryburg2							
Pupae	55	0.92	1.03	-0.96			
Brachymeria sp.	23	0.76	0.76	-0.76	0.86	0.89	-0.90
P. semitestacea	34	1.01	0.98	-0.93	0.98	1.00	-0.99
All species	42	0.85	1.03	-0.86	0.89	0.83	-0.83
Gabane (generation 1)							
Pupae	60	1.19	0.99	-1.22			
Brachymeria sp.	17	1.16	0.95	-1.20	1.10	1.06	-1.08
P. semitestacea	18	0.99	0.70	-1.01	1.14	1.34	-1.19
All species	35	1.09	0.86	-1.12	1.13	1.25	-1.16
Gabane (generation 2)							
Pupae	56	0.90	0.94	-0.84			
Brachymeria sp.	25	0.63**	0.71	-0.65**	0.75	0.74	-0.89
P. semitestacea	15	0.73*	0.75	-0.71*	0.90	0.55	-0.93
All species	32	0.74*	0.73	-0.74	0.86	0.81	-0.91
Kumukwane							
Pupae	51	1.12	0.76	-1.07			
?Tachinidae sp.	18	0.86	0.79	-0.86	0.75	1.02	-0.73*
P. semitestacea	17	1.24	1.07	-1.2	0.99	1.20	-0.94
All species	34	1.19	0.93	-1.00	1.11	1.30	-1.03
Kopong							
Pupae	38	0.94	0.87	-0.94			
P. semitestacea	9	1.16	1.10	-1.23	1.16	1.07	-1.18
All species	16	0.96	0.92	-1.03	1.09	1.13	-1.15

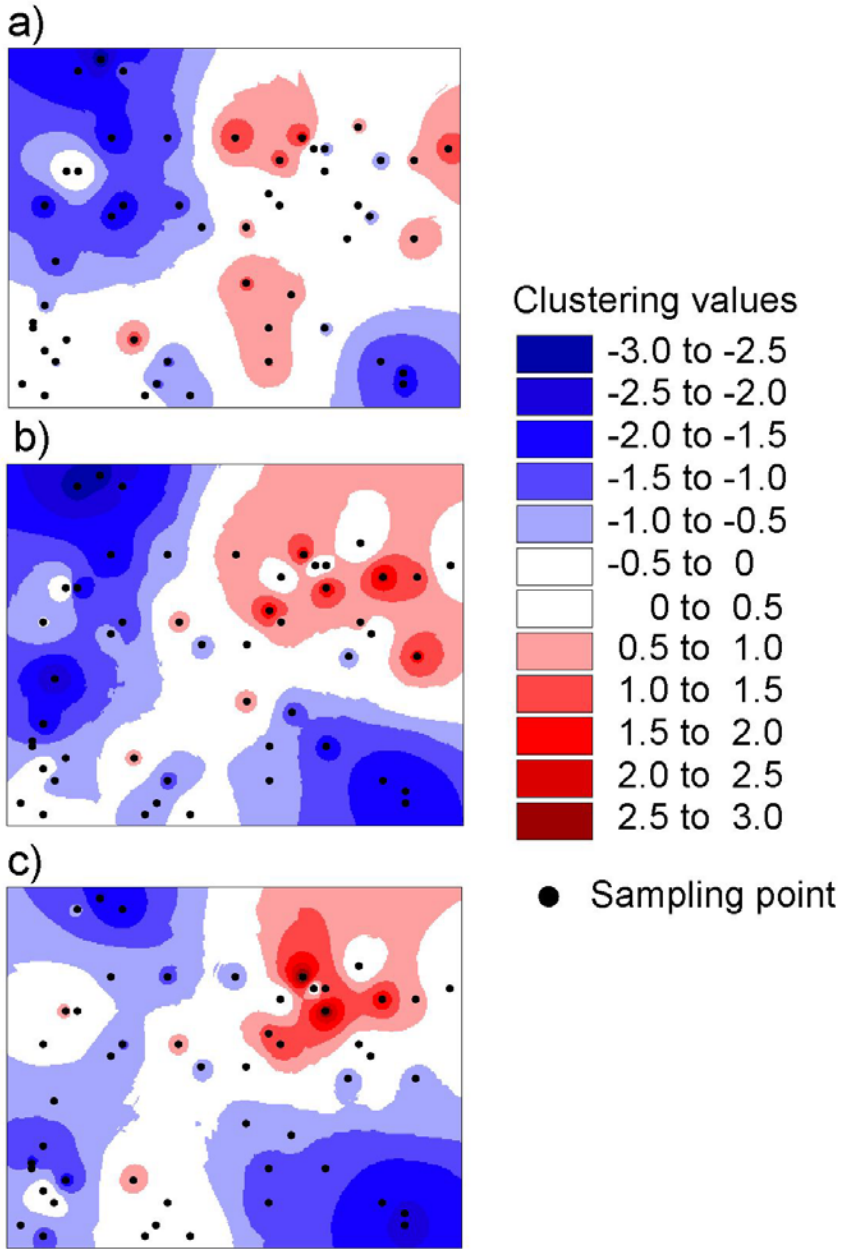

Figure 4. Spatial non-randomness indicated by least distance weighted interpolation of clustering indices of a) number of pupae, b) number of parasitised pupae and resulting c) parasitism rate of *P. semitestacea* at Kumukwane. Areas coded > 1.5 denote areas of significant positive (v_i), and < -1.5 areas of significant negative (v_j), clustering (Perry *et al*. 1999). See Table 2 for statistics.

DISCUSSION

The form of spatial heterogeneity detected for pupal abundance, parasitised pupae or parasitism rate at any particular site was inconsistent across the three methods used, and the methods were thus not interchangeable with respect to the form of spatial heterogeneity described. Data were in some cases over-dispersed (statistical heterogeneity), but spatially random (spatial structure and spatial non-randomness). Also, significant spatial non-randomness was present in the absence of spatial structure in some cases (e.g. Vryburg1, Gabane (second generation)). Thus, the spatially non-explicit approach demonstrated almost exclusively that the data were aggregated, while according to the semi-explicit approach the data were random in all cases. The spatially explicit approach also mostly indicated randomness, but did detect three cases of aggregation and regularity each. Therefore, using spatially referenced counts changed the conclusions reached regarding the form of spatial heterogeneity (from aggregated to random). Further, using a method that describes spatial heterogeneity at different locations within a site (thus spatially explicit), increased the ability to detect non-random spatial heterogeneity. This was also graphically visible from the three sets of data that these three measures were quantified for Kumukwane (Figs 2, 3, 4) (representative of the majority of localities).

Although spatial heterogeneity quantified in data is also a function of the scale of investigation (Wiens 2000), our study only compares different measures at the same scale, thereby controlling for scale. However, this study was limited in the sense that the data did not encompass the full range of possible patterns that are described by spatial non-randomness. For example in most cases there was no significant clustering into patches and gaps. Therefore it was unlikely that spatially semi-explicit heterogeneity would be identified with measures of spatial structure. It is suspected that if there were multi-sample point patches and gaps, that spatial structure would reveal stronger and significant patterns. Nonetheless, were this the case where these patches were, would not be known when quantifying spatial structure. In this study which compares the three dimensions of spatial heterogeneity, a measure of spatially explicit heterogeneity in abundance data provided the most detailed spatial information at the between-plant scale.

The problem with describing different forms of spatial heterogeneity correctly is partly a theoretical and partly a methodological problem. When the objective is to quantify spatially explicit heterogeneity, but a semi-explicit method is used, then the problem is methodological. On the other hand, when quantifying non-explicit spatial heterogeneity but interpreting it as equivalent to explicit spatial heterogeneity, then the problem is theoretical because the spatial heterogeneity described is not of a similar dimension. The diverse array of methods available to quantify spatial heterogeneity is partly due to the dimensionality of spatial heterogeneity (Wiens 2000). Methods cannot simply be selected based on data type or objective, but a relevant dimension also has to be considered. In some instances systems may be simple enough to be described by spatially non-explicit measures of spatial heterogeneity. If the objective is to simply know what the variation in count size between sample points are, then a frequency distribution will adequately describe the statistical properties of the data (Dutilleul & Legendre 1993). However, when values are autocorrelated, the form of spatial heterogeneity indicated by statistical heterogeneity will not differ from a scenario where no autocorrelation is present (Wiens 2000). As a consequence, potentially important information is lost. Repeating spatial patterns (i.e. multiple peaks of variability, see Legendre & Legendre 1998) may be more accurately described by semi-explicit measures, because differences between locations within data sets will be non-significant or weak. The presence of spatial autocorrelation indicates the size of an area that have sample points with counts more similar to each other, than samples further away (Legendre & Legendre 1998). However, although samples may have autocorrelated values, the position and number of areas with significantly higher or lower values compared to the entire data set is unknown. Also, when describing the average spatial heterogeneity of samples, local pattern is averaged out. In a similar manner that statistical heterogeneity cannot describe all the possible permutations identifiable with spatial structure, spatial structure cannot encompass all possible dataset pattern variations distinguished by spatial non-randomness. In this case aggregation, regularity and randomness (Table 1) refers to the spatial non-randomness of measured or recorded quantities for every spatially referenced sample point (Perry 1995; Perry 1998). Complex spatial mosaics may best be described by spatially explicit measures of spatial heterogeneity, which can allow for sample point differences in heterogeneity (see also Wiens 2000).

In population count data, there are two added complications with using spatial structure to describe spatial heterogeneity. First, spatial autocorrelation and other geostatistical methods assume stable covariance structure (Legendre & Legendre 1998; Perry 1998; Perry *et al*. 2002), which may not be the case for rapidly dispersing organisms with highly patchy occurrence in a study arena (Perry 1998). Second, Moran's *I* is sensitive to asymmetry as it increases the kurtosis and variance of the data that makes it harder for the correlogram to reach significance (Legendre & Legendre 1998). To counter this problem the data is usually normalized before computing correlograms to ensure that a single autocorrelation function can describe the area of study. However, counts comprising large numbers of zero values and high counts in close proximity may not fulfil the assumption of stable covariance structure or asymmetry (normality) (Perry 1998). This study shows that when sample points are spatially independent, but differ widely in abundance, local patterns are not detected by spatial structure. In some cases, although no significant spatial structure was detected, spatial non-randomness did indicate certain sampling points forming significant patches and gaps.

Therefore, a major difference between spatial structure and spatial non-randomness is the ability of spatial non-randomness to describe local (within-site) spatial heterogeneity. The value of an autocorrelation function is not influenced by position of two sampling points in a site, only by the distance between them (Legendre & Legendre 1998). When a measured variable is accompanied by a spatial reference at each sampling point, trend surface analysis and spatial autocorrelation can be used to describe spatial non-independence (Dutilleul & Legendre 1993; Legendre & Legendre 1998). However, these two methods cannot be used to make biological inferences regarding sample point specific local pattern (Perry *et al*. 2002), limiting the biological relevance of spatial structure for analysis of population count data (Perry 1998). Spatial non-randomness, based on both abundance and spatial position data, is currently the only option for describing spatial heterogeneity in abundance where local pattern is important (Perry & Dixon 2002; Perry *et al*. 2002).

The possible implications of not specifying the dimension of spatial heterogeneity when quantifying it, where aggregation in one dimension does not translate to aggregation in higher dimensions, may be severe. For example, in the host parasitoid literature heterogeneity in host parasitism risk (of which abundance is the most obvious, Hassell 2000) has been said to result in stable host-parasitoid populations cycles, if this risk is sufficiently aggregated (variance of

the hosts frequency distribution a certain times greater than the mean) (Hassell 2000). In the field of plant ecology, aggregation has been proposed to facilitate species coexistence (Murrell *et al*. 2001). In the following paragraphs the implications of the dimension of spatial heterogeneity affecting the form of spatial heterogeneity detected, are discussed. Both examples also illustrate the importance of using specific terminology to describe spatial heterogeneity in ecology.

Implications of quantifying spatially explicit heterogeneity

Studies concerning host-parasitoid interactions almost universally assume that the host species have heterogeneous abundance patterns (Godfray *et al*. 2000). However, current descriptions of aggregation in host abundance are still almost exclusively quantified by spatial heterogeneity (Hassell 2000). In fact the CV^2-rule, which specifies that the aggregation of hosts that lead to density dependent heterogeneity in attack rates, is described by a negative binomial frequency distribution of the data (Hassell 2000). The results presented here however suggest that semi-and spatially explicit dimensions of heterogeneity will not identify the same form of spatial heterogeneity as this spatially non-explicit dimension. In some laboratory or artificial field conditions the frequency distribution may adequately describe the effect of host abundance on parasitism, but more complex mosaics and patterns of spatial non-independencies may not. Therefore relevant (explicit) spatial pattern in host abundance may have been undescribed in previous studies, although being important in determining interactions between parasitoid and host.

The recent use of the experimental findings (Stoll and Prati 2001) to discuss the influence of aggregation on species coexistence (Murrell *et al*. 2001) highlights potential problems with using unspecific terminology for different measures of spatial heterogeneity (thus non-explicit, semi-explicit, and spatially explicit heterogeneity). In Stoll and Prati's (2001) study, the 'random' treatment consisted of point occurrences of plant seedling species mixes while the 'aggregated' treatment consisted of mono-specific area occurrences species mixes. This is consistent with the increase in aggregation specified for point-cluster analysis (Fig 1, B3). However, Murrell *et al*. (2001) illustrate an aggregated condition as the spatial distributions (Fig 1 B2) of two species not over lapping, and a random condition when species overlap occurrence and this overlap occurs at random. They thus imply that the spatially explicit result

of Stoll and Prati's (2001) experiment is similar to their theoretical, untested, illustration of the effect of semi-explicit occurrence of potentially competing species. Furthermore, the varied terminology used to describe spatial heterogeneity by Murrell *et al*. (2001) "…aggregation, segregation (overdispersion), and the spatial randomness..." is unspecific and confuses not only the category of spatial heterogeneity, but also the form described. By stating that 'aggregation' promotes species coexistence (e.g. Murrell *et al*. 2001; Stoll & Prati 2001) authors imply by default that spatial heterogeneity described by spatially non-explicit, semi- or explicit measures will have the same effect. In both examples, the advance of ecological theory is undoubtedly hampered by the use of vague terminology.

Consequently, the accepted theory behind parasitoids regulating host populations if they or their hosts are sufficiently aggregated, in terms of statistical heterogeneity, may not hold true for higher dimensions of spatial heterogeneity that are potentially more biological realistic descriptors of the host-parasitoid interaction. In the same manner, only one dimension of spatial heterogeneity of a species occurrence may promote species coexistence (i.e. as shown by Stoll & Prati 2001). Any pattern of statistical heterogeneity or spatial structure in a species occurrence will not necessarily have an influence on its coexistence with other species. The importance of the correct use and specifying of measures used in all biological fields where spatial heterogeneity is of theoretical importance is thus highlighted. This has implications for the traditional view of quantifying aggregation in ecology. Future studies will have the opportunity to test the consequences of how aggregation is quantified and interpreted.

This raises the important question of which measure gives the most correct description of spatial heterogeneity. Ultimately, the measure used to describe spatial heterogeneity should depend on the organism or interaction being studied (Wiens 2000), which in turn is dependent on the objective of the study. For example, the number of pupae per tree and the proportion of them parasitised describe an interaction between host and parasitoid. Considering parasitoid biology, theoretically the quantification of spatial heterogeneity, i.e. the spatial aggregation of hosts, is of vital importance in determining the existence of density dependent parasitism (Pacala & Hassell 1991; Gross & Ives 1999; Hassell 2000; Chapter 4). Because the type of spatial aggregation, regularity or randomness shown by pupae, number parasitised and parasitism rate was shown to be dependent on the measure of spatial heterogeneity used, it is vital that the correct form of spatial heterogeneity be recorded. In the case of *G. postica*, host

abundance represents a patchy resource for foraging parasitoids because pupae occur on trees that are irregularly spaced, and only a few single occurring trees have many pupae per tree (significant patch of high pupal abundance on a single tree), while the majority have few. Therefore, spatial heterogeneity in pupal abundance that is spatially explicit (locational) will include relevant spatial information not available from spatially non-explicit, or even semi-explicit categories.

In the future it is proposed that the quantification of aggregation in biology takes the data type, objectives, and the biology of the process under investigation in consideration. First, the type of data gathered should be classified as either abundance or occurrence data. Second the dimension of spatial heterogeneity relevant to the biological process being studied, as well as suitable for addressing the objectives needs to be chosen. Only hereafter is a specific associated measure chosen to quantify the form of spatial heterogeneity (i.e. Table 1). This procedure, as well as using specifically assigned terminology, will ensure that conclusions about the form of spatial heterogeneity can be compared between studies.

In summary this study illustrates that statistical heterogeneity and spatial structure are complimentary to spatial non-randomness. For example, statistical heterogeneity gives some information on aggregation at a scale smaller than at which the data was collected. Therefore, spatial non-randomness should be seen as another addition to the list of methods available to ecologists to describe spatial heterogeneity (see Dutilleul & Legendre 1993). However, the empirical comparison of spatially non-explicit, semi-, and explicit to approaches to the measurement of spatial heterogeneity in this study, highlights the need for specific definition of spatial heterogeneity and aggregation. Here the potential value of spatially explicit approaches for the re-evaluation of theory developed using more traditional methods has been highlighted. In the future the dimensionality of spatial heterogeneity should thus be considered when quantifying aggregation in ecological data.

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Appendix. Number of *Gonometa postica* pupae and the percentage parasitised at surveyed sites (Gen. = generation). The number of pupae, number of parasitised pupae as well as percentage parasitised (individual species or all combined) per plot is given. The number of trees (maximum 100) with at least one pupa or parasitised pupa, as well as the percentage of host occupied trees with at least one parasitised pupae is also shown.

Locality	Gen.	Number of		Parasitoid species or category	Number of parasitised		Percent parasitised	
		pupae	trees		pupae	trees	pupae	trees
Vryburg1	1	202	53	?*Palexorista* sp.	117	40	57.9	75.5
				All species	150	46	74.3	86.8
Vryburg2	1	426	55	*Brachymeria* sp.	69	23	16.2	41.8
				P. semitestacea	83	34	19.5	61.8
				All species	192	42	45.1	76.4
Gabane	1	505	60	*Brachymeria* sp.	36	17	7.1	28.3
				P. semitestacea	37	18	7.3	30.0
				All species	100	35	19.8	58.3
	2	439	56	*Brachymeria* sp.	64	25	14.6	44.6
				P. semitestacea	31	15	7.1	26.8
				All species	128	32	29.2	57.1
Kumukwane	1	252	51	?Tachinidae sp.	27	18	10.7	35.3
				P. semitestacea	23	17	9.1	33.3
				All species	75	34	29.8	66.7
Kopong	1	92	38	*P. semitestacea*	10	9	10.9	23.7
				All species	20	16	21.7	42.1