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## **Detecting spatial hot spots in landscape ecology**

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Hot spots are typically locations of abundant phenomena. In ecology, hot spots are often detected with a spatially global threshold, where a value for a given observation is compared with all values in a data set. When spatial relationships are important, spatially local definitions – those that compare the value for a given observation with locations in the vicinity, or the neighbourhood of the observation – provide a more explicit consideration of space. Here we outline spatial methods for hot spot detection: kernel estimation and local measures of spatial autocorrelation. To demonstrate these approaches, hot spots are detected in landscape level data on the magnitude of mountain pine beetle infestations. Using kernel estimators, we explore how selection of the neighbourhood size  $(\tau)$  and hot spot threshold impact hot spot detection. We found that as  $\tau$  increases, hot spots are larger and fewer; as the hot spot threshold increases, hot spots become larger and more plentiful and hot spots will reflect coarser scale spatial processes. The impact of spatial neighbourhood definitions on the delineation of hot spots identified with local measures of spatial autocorrelation was also investigated. In general, the larger the spatial neighbourhood used for analysis, the larger the area, or greater the number of areas, identified as hot spots.

While the term hot spot can have a specific meaning, it often relates to a location where something out of the ordinary has occurred (i.e. Ord and Getis 2001). This may be an overabundance of an event such as crime (Ratcliffe and McCullagh 1999), disease (Besag and Newell 1991), or species richness (Stohlgren et al. 2006). Another general definition considers hot spots as regions of high density that are separated by regions of lower density of some phenomenon (Hartigan 1975, p. 205, Azzalini and Torelli 2007). The reason for detecting hot spots is perhaps more singular than their definition. Detecting hot spots is a first step towards understanding processes that generate occurrences of atypical spatial patterns. By characterizing the nature of the processes, we can learn more about the complexity of systems (Getis and Boots 1978).

Although there are specific uses of the term hot spot in ecology, such as biodiversity hot spots (Myers et al. 2000), ecological hot spot definitions are typically related to locations abundance and require a threshold be applied to differentiate hot and non-hot locations (Gaston and David 1994, Flather et al. 1998, Stahl et al. 2001). As such they are often defined on a case-specific basis.

Hot spots are spatially explicit, in that they are detected at geographic locations and may be mapped. Definitions of hot spots may be based on thresholds that are spatially global or spatially local. Spatially global definitions compare the value for a given observation with those in the complete data set. As an example, a 5% threshold is applied to data

on the number of rare or endangered species (Gaston and David 1994). In contrast, spatially local definitions involve comparing the value for a given observation with locations in the vicinity of the observation. For instance, hot spots are located where the species diversity is much higher than in the surrounding neighbourhood (Prendergast et al. 1993), or may include locations that are spatially adjacent to the most diverse regions (Flather et al. 1998). A combination of local and global spatial methods may also be used, when a spatially global threshold is applied to a spatially local measure. We refer to these as partially local methods. As an example, a spatially local measure is the number of lynx attacks on livestock within a 5 km area and a global threshold may be use to delineate locations with the highest 5% of values (Stahl et al. 2001). In general, spatially local methods are more effective for detecting hot spots when study areas are large and processes tend to be nonstationarity. When non-stationarity exists the same high value may have different meaning depending on the location. For instance, the importance of high magnitude forest insect infestations may be different when detected amongst areas previously infested or previously uninfected. While local measures consider the context of the high magnitude events, global measures do not.

Given that all hot spots are spatially explicit, the definition and detection of ecological hot spots may benefit from approaches developed in geography, where the methods for detection of spatial clusters have received

considerable attention (Elliott et al. 2000). Two spatial analyses that are particularly transportable to hot spot detection in ecology are kernel estimators and local measures of spatial autocorrelation. These, and other geographical approaches, are already being used by ecologists to visualize spatial trends, and quantify spatial pattern and covariance in ecological data (Worton 1995, Fortin and Dale 2005, Shi et al. 2006). However, we have found few examples of the use of these methods in ecological hot spot definition or detection.

The first goal of this paper is to demonstrate spatial methods for defining and detecting hot spots in ecological data when information on population at risk is unavailable. The methods we emphasize are either spatially local, in that hot spots are defined based on values within a region, or partially local, in that hot spots are defined by applying a global threshold to data that has undergone a spatially local transformation. Given that hot spots tend to be defined with the use of an arbitrary threshold, the second goal of this paper is to explore how the selection of thresholds, and other methodological issues, impact the nature of the hot spots detected. Kernel estimation and local measures of spatial autocorrelation are demonstrated on a large area dataset on mountain pine beetle infestation magnitude.

There are many types of spatial ecological data (Fortin and Dale 2005, pp. 14-17). In this paper we assume that the phenomenon being studied is fully mapped, or that the spatial coverage of sampling is complete and representative of the population. Although some of the hot spot definitions explored in this paper could be applied to any type of spatial data, the emphasis is on areal and point data with quantitative attributes, collected over large spatial extents. In ecology, areal data are available from landscape level surveys on: fauna and flora (Prendergast et al. 1993), species richness (Gaston and David 1994, Stohlgren et al. 2006), species abundance (Brown 1984), and species endangerment (Flather et al. 1998). When data are collected for areas or plots that are small relative to the spatial extent of the study, spatial locations may be represented with point data with quantitative attributes that indicate the area center (Stahl et al. 2001).

# **Background: methods for defining and detecting hot spots**

#### **Kernel estimation**

Conceptually, kernel estimators are used to convert point data to continuous surfaces showing event density or intensity (Silverman 1986). The most common ecological use of kernel estimation is for home range detection (Worton 1995, Shi et al. 2006). An animal's home range reflects the primary area or habitat used normally by an animal (Burt 1943, p. 351) and kernels are a standard approach in its deliniation. Kernels are also used to enhance ecological edges or boundaries (Fortin and Dale 2005, pp. 206–209), and are employed in geographically weighted regression (GWR), a technique for spatial modelling of multivariate relationships (Shi et al. 2006).

Several properties of kernel estimators make them valuable for hot spot detection. Using kernel estimated

surfaces, it is easy to visualize locations of event abundance and scarcity, and the spatial variability in events or phenomena (Nelson et al. 2006). As well, hot spots detected with a kernel approach are easily investigated in terms of underlying continuous variables, such as elevation, temperature, or soil (Potvin and Boots 2004, Nelson et al. 2007). Since identifying hot spots with kernel estimation requires a spatially global threshold and incorporates the spatial distribution of area centroids or points, we categorize this method as partially spatially local.

The intensity  $\lambda(z)$  at a particular location z in a study area A can be estimated by the naïve kernel estimator

 $\hat{\lambda}(z) = \frac{\text{the number of events in a neighbourhood centered on } z}{\text{area of the neighbourhood}}$ 

(1)

However, since eq. (1) treats all events equally, lambda\_hat(z) is prone to discontinuous changes as z moves around the study area.

A more precise estimate,  $\hat{\lambda}_{\tau}(z)$ , which avoids the discontinuity problem, is defined by

$$\hat{\lambda}_{\tau}(z) = \frac{1}{p_{\tau}(z)} \left\{ \sum_{i=1}^{n} \frac{1}{\tau^{2}} k \left( \frac{(z-z_{i})}{\tau} \right) y_{i} \right\} \quad z \in A, \tag{2}$$

where z and A are defined as above;  $\tau$ , known as the neighbourhood size, is the radius of a circular neighbourhood centered on z; k() is the kernel, or a probability density function, which is symmetric around about the origin;  $z_i$  ( $i=1,\ldots,n$ ), are locations of n observed events; and  $y_i$  is the attribute value at  $z_i$ . The term  $p_{\tau}(z) = \int_A k[(z-u)/\hat{o}]$  du is an edge correction equivalent to the volume under the scaled kernel centered on z which lies inside of A (Diggle 1985).

The type of kernel k() determines how events within the neighbourhood will be weighted. Although theoretically important, kernel type has little impact on output (Silverman 1986, p. 43, Scott 1992, p. 133, Simonoff 1996, pp. 103–105). The standard kernel is the Gaussian. A good approximation of the Gaussian kernel that is computationally-less burdensome is the quartic kernel (Silverman 1986, pp. 76–77, Waller and Gotway 2004, pp. 132–133). Given that large data sets are the focus of this study we used the quartic form. Using the quartic kernel, eq. (2) becomes:

$$\hat{\lambda}_{\tau}(z) = \frac{1}{p_{\tau}(z)} \sum_{h_{i} < \tau} \frac{3}{\pi \tau^{2}} \left( 1 - \frac{h_{i}^{2}}{\tau^{2}} \right)^{2} y_{i}, \quad z \in A,$$
 (3)

where  $h_i = z - z_i$ , so that  $3/\pi\tau^2$  is the weight at location z ( $h_i = 0$ ) which drops smoothly to zero at  $h_i = \tau$ .

The amount of smoothing, controlled by the size of the neighbourhood ( $\tau$ ) over which point density is averaged, has a larger impact on kernel results (Kelsall and Diggle 1995). Small values of  $\tau$  will reveal small-scale features of the data, while larger values will reveal general features. There are several guides to follow when determining the optimal neighbourhood size (Bowman and Azzalini 1997, pp. 31–37); however, there is inevitably an element of subjectivity in choosing an appropriate value for  $\tau$ .

For marked data with quantitative attribute values, the neighbourhood size, or radius of  $\tau$ , may be determined using the optimal circular radius neighbourhood size for standard

multivariate normal distributions (Scott 1992, p. 152). The resulting  $\tau$  will be conservative since the normal is the smoothest possible distribution and will induce oversmoothing when applied to non-normal data (Bowman and Azzalini 1997, p. 31). Oversmoothing will lead to overestimation of the hot spot area, thus it may be helpful to incorporate an understanding of the phenomenon's ecology, or the structure of the data, to guide the selection of  $\tau$ . In fact, Atkinson and Unwin (2002, p. 1096) state "our experience leads us to believe subjective judgement based on a range of density surfaces is as good a method as any" for determining an appropriate neighbourhood size. We agree with this approach, and through this paper we attempt to demonstrate how a range of neighbourhood sizes may be determined, and the resulting impact of these different neighbourhood sizes on hot spot detection. When study areas are large, or the density of areas or points varies over space, there may be advantages to using variable or adaptive neighbourhoods (Brunsdon 1995), or anisotropic neighbourhoods that vary in size depending on direction (Bowman and Azzalini 1997,

Regardless of the size of neighbourhood used, once a kernel estimated surface is generated, a threshold must be defined in order to identify hot spots. A statistical method has been developed to determine whether the maximum kernel estimated value is statistically significant (Rogerson 2001). However, this approach is effective when only one hot spot exists, which is atypical in ecology. Kernel density estimation may be used to identify hot spots defined as locations where values are high relative to an expectation of randomness, or conditional randomness, using Monte Carlo simulations. For instance, in Nelson and Boots (2005) kernel density estimation was combed with randomization procedures to identify locations where the observed values of mountain pine beetle infestations were greater than expected based on a planar Poisson process conditioned on a model of forest risk. Most often, an arbitrary threshold will be applied to the kernel estimated surface. When hot spots are identified with kernel estimation, hot locations will be regions where high density estimates are separated from regions with lower density estimates (Azzalini and Torelli 2007). For details of software that may be used to implement kernel density estimation, see Supplementary material.

#### Local measures of spatial autocorrelation

Spatial autocorrelation is the notion that all things are related, and near things more than far (Tobler 1965). Positive spatial autocorrelation exists when nearby events are similar. Negative spatial autocorrelation exists when nearby events are dissimilar. Measures of spatial autocorrelation may be either global or local and are used quantitatively to evaluate the amount of spatial autocorrelation in a data set. Global measures characterize the nature of spatial autocorrelation for the entire study area using one value that summarizes average trends. For hot spot detection, local measures that quantify variations in spatial autocorrelation over a study area are preferable to global measures.

Although global measures of spatial autocorrelation are more commonly used by ecologists (Fortin et al. 1989, Liebhold and Gurevitch 2002), local measures of spatial autocorrelation are gaining popularity for quantifying spatial patterns (Fortin and Dale 2005, Franklin in press). For example, local measures of spatial autocorrelation have been used to quantify the spatial structure of aphid abundance (Cocu et al. 2005) and the spatial pattern of diversity in shrubs based on genetic or taxonomic units (Bickford et al. 2004). They are also used to identify spatial patches or clusters of homogenous events of phenomena characteristics. For instance, Whitmire and Tobin (2006) used local measures to identify unique colonies of gypsy moths based on trap data.

Local measures of spatial autocorrelation have two key advantages over other methods hot spot detection. First, as the name indicates, these approaches enable spatially local hot spot definitions. Second, as local measures of spatial autocorrelation are designed to assess the statistical hypothesis that observed patterns could have risen by chance, rejection of the null hypothesis can be used as the threshold for defining hot spots.

If the observed values  $x_i$ ,  $i \in \{1, \ldots, n\}$  of a random variable X are recorded at a set of n data sites, local measures of spatial autocorrelation take the general form of a cross-product statistic

$$\Gamma_{i} = \sum_{j} w_{ij} y_{ij}, \tag{4}$$

where  $w_{ij}$  is a measure of the spatial relationships of data sites i and j at a given time and  $y_{ij}$  is a measure of their relationship in attribute space (Getis and Ord 1992, Boots 2002).

There are several ways to define spatial relationships or spatial neighbourhoods (wii) when data are fully mapped, rather than representative of a sample (Fig. 1). A common definition is distance, where relationships are summarized for all locations (j) within some distance of location i (Fig. 1A, B) (Haining 2003, p. 80). A distance band is appropriate when data sites are regularly spaced and there is a conceptual reason to select a particular distance. When data sites are irregularly spaced, a distance band could result in some neighbourhoods having many sites and others with few. This can be dealt with by setting the neighbourhood size to some number (k) of nearest neighbours (Fig. 1C) (Haining 2003, p. 80). This controls the number of locations in each neighbourhood, although the area associated with each neighbourhood can then be variable. When adjacency is important, Voronoi or natural neighbours may also be used in the definition of neighbourhoods (Okabe et al. 2000, pp. 418–427). Voronoi polygons can be created for all data sites by assigning all locations in space to the nearest data site. Then, the natural neighbours of any given site are those sites whose Voronoi polygons share a boundary with the Voronoi polygon of the given site (Fig. 1D). By adding the natural neighbours of j to the neighbourhood of i it is possible to define multiple neighbourhood sizes (lags) (Fig. 1E). In the examples shown in Fig. 1, if i and j are neighbours, wij equals one and values of zero are assigned when i and j are not neighbours. Definitions can also be based on other measures of the interaction (Haining 2003, p. 84).

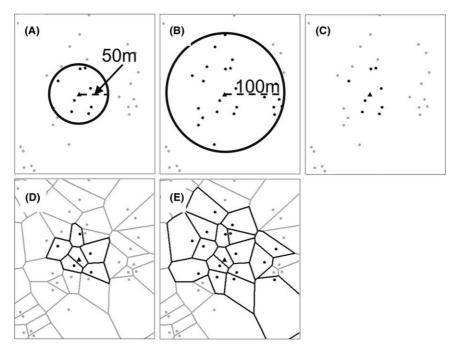


Figure 1. Spatial weights matrices or neighbourhoods can be defined in a number of ways. (A and B) Spatial relationships are defined by distance. (C) Spatial relationships are summarized for the k nearest locations. (D and E) Spatial relationships are defined by shared boundaries.

Local measures of spatial autocorrelation with attribute relationship definitions  $(y_{ij})$  that are well suited for hot spot detection include local Moran's  $I_i$  and local Getis  $(G_i^*)$ . Both of these measures characterize spatial autocorrelation in values that are extreme relative to the mean, thus aiding the detection of unusual events (Getis and Ord 1992, Anselin 1995).

For local Moran's  $I_i$  the attribute relationship in the cross product statistic is defined as  $y_{ij} = (x_i - \bar{x})(x_j - \bar{x})$  and

$$I_{i} = \left(\frac{z_{i}}{\left(\frac{\sum_{i} z_{i}^{2}}{n}\right)}\right) \sum_{j} w_{ij} z_{j}, \tag{5}$$

where  $z_i = (x_i - \bar{x})$ . Positive values of Moran's  $I_i$  indicate positive spatial autocorrelation in values that are extreme relative to the mean. Negative Moran's  $I_i$  indicate negative spatial autocorrelation in values that are extreme relative to the mean. When Moran's  $I_i$  approaches zero it could be that there is no spatial autocorrelation, or that spatial autocorrelation is present in values near the mean.

For hot spot detection, a Moran's scatterplot can be used to distinguish positive and negative spatial autocorrelation based on the attribute value of a location in relation to the attribute value of its neighbours. On a Moran's scatterplot, the x axis is the attribute value in deviation form and the y axis is a standardized average of the neighbour values also in deviation form (Anselin 1995). The upper right quadrant indicates high values surrounded by high values (high-high), the upper left quadrant indicates low values surrounded by high values (low-high), the lower right quadrant indicates high values surrounded by low values (high-low), and the

lower left quadrant indicates low values surrounded by low values (low-low) (Fig. 2). Depending on the application, hot spots could be defined by one or more of the Moran's scatterplot categories. For instance, high-high locations may be used to detect clusters of large values, while high-low locations may be used to locate local high outliers. Low-low and low-high locations are indicative of the absence of phenomena and will not be considered in the remainder of this paper.

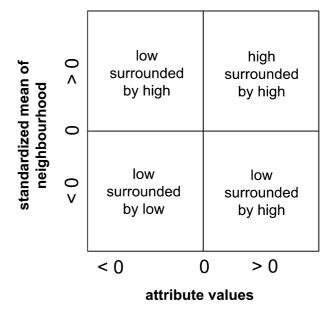


Figure 2. Moran scatter plot quadrants can be used to categorize locations base on the on the attribute value of a location in relation to the attribute values of neighbours.

Under some circumstances, the Moran's scatterplot can be combined with statistical testing to determine the significance of potential hot spots. Although the expected values of I<sub>i</sub> can be derived under the hypothesis of no local spatial autocorrelation (Sokal et al. 1998), the distribution does not follow a known distribution (Boots and Tiefelsdorf 2000), and so a randomization approach must be adopted for statistical testing.

The local Getis statistic only considers positive spatial autocorrelation and enables differentiation between clusters of similar values that are high or low relative to the mean (Getis and Ord 1992, Boots 2002). Using the Getis statistic, it is possible to identify spatial clusters of large and small attribute values. These are equivalent to the high-high and low-low clusters, respectively, as identified by I<sub>i</sub>, and the former may be considered hot spots. We employ the local Getis statistic with the following form:

$$G_i^* = \frac{\Sigma_j w_{ij} x_j}{\Sigma_i x_i}.$$

For  $G_i^*$  the value of i is included in the sum and the attribute relationship is defined as  $y_{ij} = x_i + x_j$ .

For  $G_i^*$  it has been shown that normality can be reasonably assumed when locations have at least eight neighbours (eight j for each i) (Ord and Getis 1995). Equations for calculating the expected mean and variance of  $G_i^*$  under the hypothesis of complete randomness are given by Boots (2002) and can be used to calculate z-scores for significance testing. For  $G_i^*$ , z-score values >2 are used to indicate hot spots of abundance, as locations identified will be spatial clusters of values that are extreme and high relative to the mean.  $G_i^*$  z-score values <-2 indicate spatial clusters of values that are extreme and low relative to the mean. These are often labelled cold spots and will not be considered here.

It should be noted that testing the statistical significance of all local measures of spatial autocorrelation is complicated by the presence of global spatial autocorrelation and issues of multiple and correlated tests (Boots 2002). Until these issues are overcome, it is best to use the statistical tests associated with local measures of spatial autocorrelation for data exploration, rather than as confirmatory statistical testing. Global measures of spatial autocorrelation should be presented when local measures are calculated, and when significant global spatial autocorrelation exists, the likelihood of falsely identifying significant local spatial autocorrelation increases (Ord and Getis 2001). For details of software that may be used to implement local measures of spatial autocorrelation, see Supplementary material.

### **Case study**

In this case study, we apply the methods outlined above, kernel estimators and local measures of spatial autocorrelation, to data on a forest insect pest. Through application of these methods we demonstrate how varying the parameters of spatial hot spot detection methods impacts the nature of the hot spots identified.

#### Study area and data

Forest insect pests cause tree mortality (Safranyik and Carroll 2006), defoliation (Whitmire and Tobin 2006), and forest disturbance (Fleming et al. 2002). In order to understand the characteristics of forests that are most prone to infestation by insect pests, it is helpful to locate hot spots of insect populations or forest damage (Nelson et al. 2007). The mountain pine beetle Dendroctonus ponderosae is a forest pest that is native to pine (Pinus spp.) forests throughout western North America. As a forest pest, the mountain pine beetle is of particular importance given that it is responsible for the largest forest epidemic on record, currently occurring in western Canada (Westfall 2006). Periodic population eruptions occur when an abundance of susceptible host trees coincides with climatic conditions amenable for beetle survival (Safranyik and Carroll 2006). Although epidemic populations are a natural component of forest disturbance, large infestations have substantial impacts and provide unique challenges to forest managers (Safranyik et al. 1974).

Understanding landscape-scale mountain pine beetle processes through experimental research is not feasible due to practical limitations, and so we rely on spatial patterns of infestation to gain insight on spatial processes. Determining the presence of infestation hot spots can be an important step in analyzing spatial and spatial-temporal patterns of infestation and in gaining insight on mountain pine beetle spatial processes. By identifying locations where the spatial pattern is unusual, and exploring the conditions in these areas, we can develop hypotheses on beetle processes and better understand conditions that lead to infestations.

Hot spot definitions and detection approaches are explored using mountain pine beetle infestation data from the Morice Timber Supply Area (TSA), which is located in west-central British Columbia Canada (54°24′N, 126°38′W) (Fig. 3–5). Covering an area of 1.5 million ha, Morice is dominated by lodgepole pine and spruce (*Picea* spp.) species.

The Morice TSA monitors the mountain pine beetle infestation using point-based, global positioning system (GPS) aerial surveys. Aerial surveys of mountain pine beetle infestations use indicators of pine mortality, mainly changes in crown foliage color, to monitor mountain pine beetle activity. During helicopter aerial surveys, clusters of visually infested trees are identified, typically those with yellow and red crowns, and a GPS is used to map cluster centers with a point. For each cluster, the number of infested trees is estimated and the infesting insect species recorded. Attributes have been shown to be accurate to  $\pm$ 10 trees for 92.6% of points (Nelson et al. 2006). The maximum area represented by a point is 0.031 km<sup>2</sup>, equivalent to a circle with a radius of 100 m (Nelson et al. 2006). For this study we used data from 2004, when a total of 16358 clusters and 130983 trees were detected to be infested. The frequency distribution of infestation cluster sizes (numbers of infested trees) demonstrates that attributes have a non-normal distribution, with small infestations being most common.

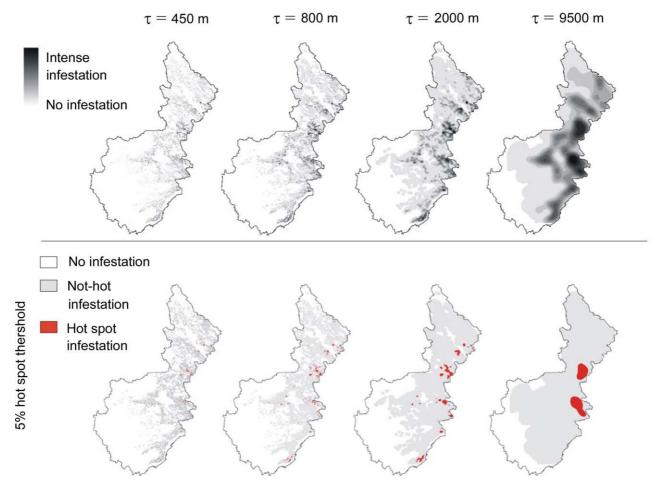


Figure 3. Kernel estimated surfaces generated with  $\tau$  equal to 450, 800, 2000, and 9500 m. A threshold of the highest 5% of values was used to identify hot spots for each definition of  $\tau$ . Hot spots are shown in red.

#### **Methods**

For large data sets, such as the mountain pine beetle data, computational speed is an important factor and the quartic kernel was used. The primary consideration in the application of a kernel estimator is the neighbourhood size  $(\tau)$  and using a combination of statistical and substantive considerations, described below, we defined a feasible range for  $\tau$  to be between 450 and 9500 m.

The lower limit, equivalent to a typical kernel containing at least one data point, was determined from the spatial distribution of the data points by identifying the area of influence associated with a typical data point. To do this we generated the Voronoi diagram (see above) of data points. Voronoi polygons had an average area of 0.63 km<sup>2</sup>. A circle of equivalent size has a radius 448 m, suggesting  $\tau$  ca 450 m.

The upper limit for  $\tau$  was determined using the optimal radius for standard multivariate normal distributions. For details we refer the reader to Scott (1992 p. 152). This value, meant for use with a normal kernel, can be converted for use with the quartic kernel using a scaling factor (Scott 1992, p. 142). The quartic kernel was calculated as 9546 m, suggesting an upper limit of ca 9500 m for  $\tau$ .

Further evidence of an appropriate  $\tau$  may be gathered by investigating the observed spatial dependence in the point data set for which kernel estimated values will be generated.

For the 2004 mountain pine beetle data, a variogram was generated from the locations and attribute values of the infestation clusters. The variogram range, or distance at which data variance is maximized, represents the spatial scale of dependence (Bailey and Gatrell 1995). The variogram range is 800 m.

Finally, biological theory on mountain pine beetle dispersal was exploited to suggest an appropriate measure of  $\tau$ . Mountain pine beetle disperse over both short and long distances. Long distance dispersal is typically wind driven and short distance dispersal occurs within stands (Furniss and Furniss 1972, Barclay et al. 1998). For selecting  $\tau$ , the maximum distance of short range dispersal, conservatively set at 2000 m (Barclay et al. 2005), is an indicator of the size of areas that are related due to nearby population movement and dependence.

On the basis of all of the above considerations, we set  $\tau$  equal to 450, 800, 2000, and 9500 m. An additional issue, which arises in software that represents kernel estimated values in a raster format, is the definition of surface cell size. We used a 200 by 200 m grid cell, as the data points represented circular areas with a maximum diameter of 200 m.

To define hot spots based on the kernel estimator, a spatially global threshold was applied. The typical threshold value applied in ecology is the 95th percentile (5%

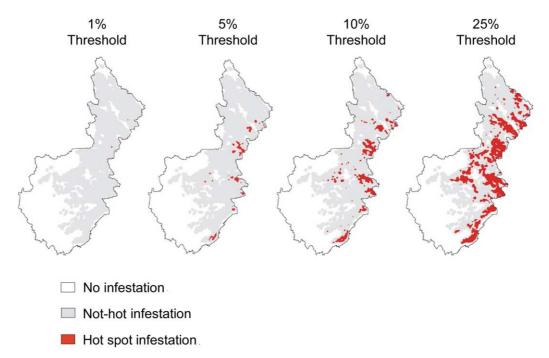


Figure 4. Hot spots detected from a kernel estimated surfaces having  $\tau = 2000$  m using different thresholds. Thresholds are used to define hot spots as the highest 1, 5, and 10% of kernel estimated values.

threshold) (Gaston and David 1994, Flather et al. 1998). We apply a 5% threshold to kernel estimated surfaces generated from  $\tau$  equal to 450, 800, 2000, and 9500 m. To consider the impact of thresholds, we also detect hot spots in the kernel surface generated from  $\tau$  equal to 2000 m using thresholds of 1, 5, and 10%. In order to quantify the impact of  $\tau$  and threshold values on hot spot detection, we compared the number and size of hot spots detected using

each definition. One of the benefits of using kernel estimation is that it enables comparison with continuous environmental variables. Therefore, we also calculated and compared the minimum and maximum elevation values associated with hot spots to quantify how relationships with landscape characteristics differ with hot spot definitions.

To aid interpretation of both Moran's  $I_i$  and  $G_i^*$  results, we quantified the number of neighbours that occur for each

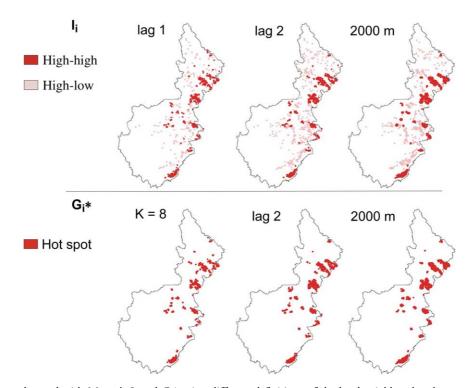


Figure 5. Hot spots detected with Moran's Ii and Gi\* using different definitions of the local neighbourhood.

spatial relationship definition used and calculated global Moran's I (Cliff and Ord 1981) using all spatial relationship definitions (i.e. distance, natural neighbours, and k nearest neighbours).

For Moran's I<sub>i</sub>, we detected hot spots using three spatial neighbourhoods. A distance based definition where neighbours include all locations within 2000 m of each centroid was used. We also used a natural neighbour definition, based on Voronoi polygons generated from the centroid of infestation clusters. Lag 1 and lag 2 natural neighbours were used. To detect hot spots, Moran's Ii results were categorized using a Moran scatterplot and significance determined using 99 randomizations and a critical value of 0.05. Hot spots are locations where the null hypothesis, that the spatial pattern is generated by a random process, is rejected. Moran's Ii enables two hot spot categories: clusters of high values and high values surrounded by low values. To assess the impact of spatial neighbourhoods on the detection of hot spots, the correspondence and confusion of hot spot categories detected with Moran's I<sub>i</sub> were compared.

To implement  $G_i^*$ , three spatial neighbourhoods were defined. For  $G_i^*$  normality can be assumed when there are at least eight neighbours in every local neighbourhood. A lag 1 contiguity neighbourhood definition typically has an average of six neighbours (Okabe et al. 2000), and as such is unsuitable for use with  $G_i^*$ . We set the minimum neighbourhood size to the nearest eight neighbours (i.e. k equals eight). We also used a lag 2 contiguity and 2000 m distance definition as in the analysis with Moran's  $I_i$ .  $G_i^*$  values were converted to z-scores, and hot spots, spatial clusters of infestation levels that were high and extreme, were identified when z-score values were >2. The correspondence of hot spots detected with  $G_i^*$  and different neighbourhood definitions were also compared.

#### **Results**

Hot spots detected by applying a 5% threshold to kernel intensity estimated surfaces generated with  $\tau$  equal to 450, 800, 2000, and 9500 m are shown in Fig. 3. With increasing  $\tau$ , the kernel estimator provides a more general visualization of spatial pattern. As a result of smoother surfaces, the infestation intensity appears more contiguous and hot spots become larger and fewer in number (Table 1). Variability in hot spot size increases as  $\tau$  increases from 450 to 2000 m. However, when  $\tau$  is 9500 m, there are only two

Table 1. Comparison of hot spot numbers and size identified as the top 5% of infestation density values in kernels generated with different sizes of  $\tau$ .

	$\tau\!=\!450\;m$	$\tau\!=\!800~m$	$\tau\!=\!2000~\text{m}$	$\tau\!=\!9500~\text{m}$
number of hot spots	152	126	27	2
minimum size (m <sup>2</sup> )	0.04	0.04	0.08	19.90
maximum size (m <sup>2</sup> )	1.68	6.00	56.16	249.72
average size (m <sup>2</sup> )	0.20	0.69	7.23	224.42
coeff. of variation in size	1.15	1.37	1.63	0.16

hot spots and the variance in size is low. The differences in kernel surfaces and associated hot spots requires consideration of which  $\tau$  is best. Given the issues of oversmoothing (Silverman 1986), we might suggest that  $\tau=9500$  m does not generate appropriate input for further analysis. The 450 m  $\tau$  is also problematic for visualization, as hot spots are very small relative to the overall study area. As such, we suggest  $\tau=800$  m or  $\tau=2000$  m are arguably more appropriate. When multiple neighbourhood sizes are valid, biological reasoning may become necessary to ensure appropriate neighbourhood size definition.

Over the entire study area, elevation values range from 549 to 2719 m (mean elevation = 1074 m). For hot spots identified using a 5% threshold and  $\tau$  = 450 m, elevations range from 581 to 1290 m (mean 888 m). When  $\tau$  = 800 m, elevations ranged from 568 to 1318 m (mean = 894 m); for  $\tau$  = 2000 m elevations range from 670 to 1354 m (mean = 905 m); and, when  $\tau$  = 9500 m elevations range from 653 to 1505 m (mean = 940 m).

Holding  $\tau$  constant at 2000 m, we varied the threshold used for hot spot detection. The results of thresholds of 1, 5, and 10%, that were applied when  $\tau$  equalled 2000 m, are visualized in Fig. 4. Larger thresholds lead to more, larger, and more variably-sized hot spots (Table 2). Larger thresholds also result in larger ranges of elevation being associated with hot spots. When a 1% threshold is applied, the associated elevations ranged from 806 to 1019 m (mean = 872 m). Using a 10% threshold, the range in elevation is 562-1437 m (mean = 917 m), while the use of a 25% threshold increases the range from 553 to 1572 m (mean = 912 m).

Global Moran's I indicates that the mountain pine beetle infestation data are significantly positively spatially autocorrelated regardless of neighbourhood definition (Table 3). The different definitions of spatial neighbourhoods changed both the configuration and number of neighbours associated with each centroid (i). k nearest neighbours is the only definition that controls the number of neighbours. When spatial relationships are defined using lag 1 and lag 2 neighbourhoods, there is less variation in the number of neighbours than when the 2000 m distance neighbourhood is used.

Visualizing local Moran's I<sub>i</sub>, it appears that the same general "zones" of significance occur regardless of how the neighbourhood is defined (Fig. 5). The tabulated results indicate that more significant locations are found when larger neighbourhoods are used (Table 4). Typically, when the result of Moran's I<sub>i</sub> changes with different neighbourhood definitions, the value will go from being a hot spot to a non-hot spot, or vice versa, and rarely changes hot spot category (i.e. from high-high to high-low). Correspondence

Table 2. Comparison of hot spot numbers and size identified using kernels where  $\tau$  = 2000 m and hot spots are defined using thresholds of the top 1, 5, and 10% of values.

	1%	5%	10%
number of hot spots	3.00	27.00	50.00
minimum size (m²)	0.64	0.08	0.04
maximum size (m²)	2.24	56.16	117.56
average size (m²)	1.29	7.23	10.65
coeff. of variation in size	0.65	1.63	2.21

Table 3. Global Moran's I and number of neighbours for mountain pine beetle infestation cluster data. The neighbourhoods are defined as k = 8, lag 1 natural neighbours, lag 2 natural neighbours, and a 2000 m distance.

weights	I (p-value)	median no. of neighbours	mean no. of neighbours	cv of neighbours	min no. of neighbours	max no. of neighbours
k=8	0.24 (0.01)	8	8	0	8	8
lag 1	0.19 (0.01)	6	5.99	0.27	3	16
lag 2	0.25 (0.01)	19	20.29	0.28	7	69
2000 m	0.17 (0.01)	42	46.3	0.58	1	162

between results is highest when the size of neighbourhoods is similar. Lag 1 and lag 2 comparisons of Moran's  $I_i$  results have 94.0% correspondence. For lag 1 and 2000 m comparisons there is 92.4% correspondence, and lag 2 and 2000 m results correspond in 89.9% of cases.

 $G_i^*$  results follow the same trend as Moran's  $I_i$  in that larger neighbourhood sizes result in more centroids having significant spatial patterns (Table 5). Correspondence in hot spots is higher when neighbourhood sizes are similar. Neighbourhoods of k=8 and lag 2 have 92.5% correspondence, k=8, and 2000 m has 87.0% correspondence, and of lag 2 and 2000 m has 90.9% correspondence. Visually, hot regions show consistency in location (Fig. 5).

#### Discussion

There are several approaches to assist with the detection of spatially explicit hot spots. In the mountain pine beetle example, we applied kernel estimated intensity surfaces and local measures of spatial autocorrelation. When using kernel estimation for hot spot detection, the analyst must set  $\tau$  and a hot spot threshold. As  $\tau$  increases, hot spots will become larger and fewer; as the hot spot threshold increases, hot spots will become larger and more plentiful. The kernel approach generates a smooth representation and enables comparison with other spatially continuous phenomena. When the threshold is held constant at 5%, and different sizes of  $\tau$  are used, the landscape conditions, in this case represented by elevation, vary. The smaller values of τ capture more localized trends and suggest hot spots are associated with lower elevations, indicative of valley bottoms. As  $\tau$  becomes larger, the elevations associated with hot spots tend to be higher, and represent hill slopes.

Table 4. Coincident Moran's  $I_i$  results for hot spot detected with different neighbourhood definitions.

	Not hot	High-high	High-low	Total
lag 1/lag 2				
Not hot	14639	128	71	14838
High-high	505	626	1	1132
High-low	271	0	117	388
Total	12 814	754	189	16358
lag 1/2000 m				
Not hot	13 953	124	75	14 152
High-high	991	629	5	1625
High-low	471	1	109	581
Total	12 814	754	189	16358
lag 2/2000 m				
Not hot	13 871	148	133	14 152
High-high	639	984	2	1625
High-low	328	0	253	581
Total	9894	1132	388	16358

Compared to hills, the area of a valley bottom is small and constrained, and trends associated with fine scale features are better investigated using small neighbourhoods.

When  $\tau$  is held constant and the hot spot threshold varied, the range of elevation values associated with hot spots increases with increasing  $\tau$ . In the case where  $\tau=2$  km and thresholds varied from 1 to 25%, the range of elevations associated with hot spots changes from 806–1019 m to 553–1572 m. This has implications when characterizing forest conditions associated with the most infested beetle locations, and indicates the benefit of considering the threshold carefully.

Moran's  $I_i$  enables two categories of hot spots to be detected, and statistical significance can be used in lieu of a hot spot threshold. All hot spots are detected in values that are extreme relative to the mean value. Hot spots may be defined as high values surrounded by high values, or outliers emphasized and detected as high values surrounded by low values. In contrast,  $G_i^*$  detects clusters of high values relative to the mean.

When Moran's I<sub>i</sub> and G<sub>i</sub>\* are implemented, the larger the spatial neighbourhood, the more locations identified as significant. This is not surprising as we would expect larger spatial neighbourhoods to identify spatial patterns associated with broader spatial processes. Therefore, when larger hot spots are of interest, or the spatial processes being studied are of coarse scale, it is best to use larger spatial neighbourhoods for detection.

It should also be mentioned that given Moran's  $I_i$  and  $G_i^*$  are computed relative to the global mean, spatial variability within a study area will be problematic for detecting hot spots, as the spatial extent of the study may impact the location of hot spots when non-stationarity is present. New methods for use with local measures of spatial autocorrelation are being developed to account for non-stationarity when computing local measures (Aldstadt and

Table 5. Coincident  $G_{\rm i}^{\ast}$  results for hot spot detected with different neighbourhood definitions.

	Not hot	Hot spot	Total
k = 8/lag 2			
Not hot	14 121	352	14 473
Hot spot	875	1010	1885
Total	14 532	1362	16358
k = 8/200  m	Not hot	Hot spot	Total
Not hot	13 191	319	13 510
Hot spot	1805	1043	2848
Total	14 532	1362	16358
2000 m/lag 2	Not hot	Hot spot	Total
Not hot	13 249	1224	14 473
Hot spot	261	1624	1885
Total	10 995	2848	16358

Getis 2006, Lin and Lu 2006), however these are beyond the scope of the current paper.

#### **Conclusion**

Hot spot definition and detection methods should be selected based on the specific goals of the application. When definitions are spatial, geographical methods may aid in hot spot detection. Kernel estimators are suitable when the aim is to identify general trends or areas with an abundance of a phenomenon. Kernel estimators also improve visualization and enable hot spots detected from point data with an attribute to be integrated with continuous data. In ecology, integration with spatially continuous data is valuable as environmental variables, such as elevation, temperature, precipitation, are often assessed in order to understand the processes that generate phenomena abundance. If the goal of an ecological study is to investigate fine scale features, one should be cautious in oversmoothing data using large neighbourhood sizes. While this paper focuses on point data with attributes, it is worth noting that kernel methods may also be used with point data that do not have attributes.

In contrast to kernel methods, measures of spatial autocorrelation require point, centroid, or area data with attributes. Hot spot detection with local measures of spatial autocorrelation, Moran's I<sub>i</sub> and G<sub>i</sub>\*, is useful when the aim is to identify clusters or outliers of values that are high and extreme relative to the global mean. Designed for testing the hypothesis that patterns have arisen by chance, local measures of spatial autocorrelation have an inherent approach for threshold selection, and are useful for determining if an individual location is, or is part of, a hot spot. Interestingly, kernel estimation and the high-low category of Moran's I<sub>i</sub> have conceptual similarities to wavelets (Fortin and Dale 2005, pp. 98–100), which have been used to detect high densities of phenomena such as plants (Csillag and Kabos 1996).

Hot spots detected in the mountain pine beetle case study highlight the importance of considering scale when conducting spatial analyses on ecological data. Regardless of the methods used, the larger the spatial neighbourhood, the greater the number or size of locations detected as hot. If the aim of hot spot detection is to identify broad areas for further investigation, the impact of spatial analysis scale may be minor. However, if the selection of individual locations is important, analysis must have a finer spatial resolution and analysis parameters will impact results. Given the importance of selecting the appropriate spatial scale for analysis, we have demonstrated a variety of approaches for defining spatial neighbourhoods. There will, however, always be an element of judgement in selecting the spatial scale for analysis and it is important to justify one's choice.

Spatially local methods that characterize spatial autocorrelation (Moran's I<sub>i</sub> and G<sub>i</sub>\*) appear more robust than kernel estimators, in that they are less affected by the choice of neighbourhood. Consequently, Moran's I<sub>i</sub> and G<sub>i</sub>\* may be more appropriate to use for hot spot detection when substantive knowledge about the phenomenon under consideration is sparse or poorly developed.

Quantitative geography and spatial science offer many ways to identify hot spots. In this manuscript we have focused on methods for detecting hot spots in areal and point data that have quantitative attributes, when the population at risk information is not available and data are collected over large areas. Spatial analysis techniques are available for detecting hot spots in other types of data. For instance, when data are points without attributes, as is commonly the case for radio telemetry data, the local kfunction (Franklin and Getis 1987) or Voronoi polygons (Okabe et al. 2000) may be used to identify locations where the spatial pattern is unexpected based on chance. When population at risk information is available, scan statistics may be used to identify unexpected spatial patterns (Coulston and Riitters 2003, Riitters and Coulston 2005). As well, when point or area data have binary attribute values, such as presence/absence, local join counts can be used to examine the likelihood that the spatial pattern results from a random process (Boots 2003, 2006).

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#### References

Aldstadt, J. and Getis, A. 2006. Using AMOEBA to create a spatial weights matrix and identify spatial clusters. – Geogr. Anal. 38: 327–343.

Anselin, L. 1995. Local indicators of spatial association – LISA. – Geogr. Anal. 27: 93–115.

Atkinson, P. J. and Unwin, D. J. 2002. Density and local attribute estimation of an infection disease using MapInfo. – Comput. Geosci. 28: 1095–1105.

Azzalini, A. and Torelli, N. 2007. Clustering via nonparametric density estimation. – Stat. Comput. 17: 71–80.

Bailey, T. C. and Gatrell, A. C. 1995. Interactive spatial data analysis. – Wiley.

Barclay, H. et al. 1998. Trapping mountain pine beetles Dendroctonus ponderosae (Coleoptera: Scolytidae) using pheromone-baited traps: effects of trapping distance. – J. Entomol. Soc. BC 95: 25–31.

Barclay, H. J. et al. 2005. Effects of fire return rates on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera: Scolytidae) and the use of patch metrics to estimate traversability. – Can. Entomol. 137: 566–583.

Besag, J. and Newell, J. 1991. The detection of clusters in rare diseases. – J. Roy. Stat. Soc. A 154: 143–155.

Bickford, S. A. et al. 2004. Spatial analysis of taxonomic and genetic patterns and their potental for understanding evolutionary histories. – J. Biogeogr. 31: 1715–1733.

Boots, B. 2002. Local measures of spatial association. – Ecoscience 9: 168–176.

Boots, B. 2003. Developing local measures of spatial association for categorical data. – J. Geogr. Syst. 5: 139–160.

Boots, B. 2006. Local configuration measures for categorical spatial data: binary regular lattices. – J. Geogr. Syst. 8: 1–24.

- Boots, B. and Tiefelsdorf, M. 2000. Global and local spatial autocorrelation in bounded regular tessellations. J. Geogr. Syst. 2: 319–348.
- Bowman, A. and Azzalini, A. 1997. Applied smoothing techniques for data analysis: the kernel approach with S-Plus illustrations.

  Claredon Press.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124: 255–279.
- Brunsdon, C. 1995. Estimating probability surfaces for geographical point data: an adaptive kernel algorithm. Comput. Geosci. 21: 877–894.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346–352.
- Cliff, A. D. and Ord, J. K. 1981. Spatial processes: models and applications. – Pion.
- Cocu, N. et al. 2005. Spatial autocorrelation as a tool for identifying the geographical patterns of aphid annual abundance. – Agricult. For. Entomol. 7: 31–43.
- Coulston, J. W. and Riitters, K. H. 2003. Geographic analysis of forest health indicators using spatial scan statistics. – Environ. Manage. 31: 764–773.
- Csillag, F. and Kabos, S. 1996. Hierarchical decomposition of variance with applications in environmental mapping based on satellite images. Math. Geol. 28: 385–405.
- Diggle, P. 1985. A kernel method for smoothing point process data. Appl. Stat. 34: 138–174.
- Elliott, P. et al. 2000. Spatial epidemiology: methods and applications. Oxford Univ. Press.
- Flather, C. et al. 1998. Threatened and endangered species geography. BioScience 48: 365–376.
- Fleming, R. et al. 2002. Landscape-scale analysis of interactions between insect defoliation and forest fire in central Canada. Clim. Change 55: 251–272.
- Fortin, M. J. and Dale, M. R. T. 2005. Spatial analysis: a guide for ecologists. Cambridge Univ. Press.
- Fortin, M. J. et al. 1989. Spatial autocorrelation and sampling design in plant ecology. Plant Ecol. 83: 209–222.
- Franklin, J. in press. Spatial point pattern analysis in plants. In: Reys, S. J. and Anslein, L. (eds), Perspective on spatial data analysis. Springer.
- Franklin, J. and Getis, A. 1987. Second-order neighborhood analysis of mapped point patterns. Ecology 68: 473–477.
- Furniss, M. M. and Furniss, R. L. 1972. Scolytids (Coleoptera) on snowfields above timberline in Oregon and Washington. Can. Entomol. 104: 1471–1478.
- Gaston, K. H. and David, R. 1994. Hotspots across Europe. Biodivers. Lett. 2: 108–116.
- Getis, A. and Boots, B. 1978. Models of spatial processes. Cambridge Univ. Press.
- Getis, A. and Ord, J. 1992. The analysis of spatial association by use of distance statistics. Geogr. Anal. 24: 189–206.
- Haining, R. P. 2003. Spatial data analysis: theory and practice.Cambridge Univ. Press.
- Hartigan, J. A. 1975. Clustering algorithms. Wiley.
- Kelsall, J. E. and Diggle, P. J. 1995. Non-parametric estimation of spatial variation in relative risk. Stat. Med. 14: 2335–2342.
- Liebhold, A. M. and Gurevitch, J. 2002. Integrating the statistical analysis of spatial data in ecology. Ecography 25: 553–557.
- Lin, S. and Lu, Y. 2006. Evaluating local non-stationarity when considering the spatial variation of large-scale autocorrelation. – Trans. GIS 10: 301–318.
- Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.
- Nelson, T. and Boots, B. 2005 Identifying insect infestation hot
- Download the Supplementary material as file E5548 from <www.oikos.ekol.lu.se/appendix>.

- spots: an approach using conditional spatial randomization. J. Geogr. Syst. 7: 291–311.
- Nelson, T. et al. 2006. Large-area mountain pine beetle infestations: spatial data representation and accuracy. For. Chron. 82: 243–252.
- Nelson, T. A. et al. 2007. Environmental characteristics of mountain pine beetle infestation hot spots. – B.C. J. Ecosyst. Manage. 8: 91–108.
- Okabe, A. et al. 2000. Spatial tessellations: concepts and applications of Voronoi diagrams, 2nd ed. Wiley.
- Ord, J. K. and Getis, A. 1995. Local spatial autocorrelation statistics: distributional issues and an application. – Geogr. Anal. 27: 286–306.
- Ord, J. K. and Getis, A. 2001. Testing for local spatial autocorrelation in the presence of global autocorrelation. J. Reg. Sci. 41: 411–432.
- Potvin, F. and Boots, B. 2004. Winter habitat selection by deer on Anticosti Island 2: relationship between deer density from an aerial survey and the proportion of balsam fir on forest vegetation maps. Can. J. Zool. 82: 671–676.
- Prendergast, J. R. et al. 1993. Correcting for variation in recording effort in analyses of diversity hotspots. Biodivers. Lett. 1: 39–53.
- Ratcliffe, J. H. and McCullagh, M. J. 1999. Hotbeds of crime and the search for spatial accuracy. J. Geogr. Syst. 1: 385–398.
- Ritters, K. H. and Coulston, J. W. 2005. Hot spots of perforated forest in the eastern United States. Environ. Manage. 35: 483–492.
- Rogerson, P. 2001. A statistical method for the detection of geographic clustering. Geogr. Anal. 33: 215–227.
- Safranyik, L. and Carroll, A. L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L. and Wilson, B. (eds), The mountain pine beetle: a synthesis of its biology and management in lodgepole pine. Natural Resources Canada.
- Safranyik, L. et al. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. – Forestry Technical Report No. 1, Natural Resources Canada.
- Scott, D. W. 1992. Multivariate density estimation: theory, practice, and visualization. Wiley.
- Shi, H. et al. 2006. Local spatial modeling of white-tailed deer distribution. – Ecol. Model. 190: 171–189.
- Silverman, B. W. 1986. Density estimation for statistics and data analysis. – Chapman and Hall.
- Simonoff, J. S. 1996. Smoothing methods in statistics. Springer. Sokal, R. R. et al. 1998. Local spatial autocorrelation in a biological model. – Geogr. Anal. 30: 331–354.
- Stahl, P. et al. 2001. Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. – J. Appl. Ecol. 38: 674–687.
- Stohlgren, T. J. et al. 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States.Biol. Invasions 8: 427–447.
- Tobler, W. 1965. Computation of the correspondence of geographical patterns. Pap. Reg. Sci. Assoc. 15: 131–139.
- Waller, L. A. and Gotway, C. A. 2004. Applied spatial statistics for public health data. Wiley-Interscience.
- Westfall, J. 2006. 2006 Summary of forest health conditions in British Columbia. British Columbia Ministry of Forests and Range.
- Whitmire, S. L. and Tobin, P. C. 2006. Persistence of invading gypsy moth populations in the United States. Oecologia 147: 230–237.
- Worton, B. J. 1995. A convex hull-based estimator of home-range size. Biometrics 51: 1205–1215.