

GEOSTATISTICS AND GEOGRAPHIC INFORMATION SYSTEMS IN APPLIED INSECT ECOLOGY

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INTRODUCTION

The cliché, "space is the final frontier", can be applied to insect population ecology in the same way we hear it so often from science fiction dramas. Historically, studies of insect population biology, have concentrated on changes through time, but patterns across spatial dimensions remain largely unexplored. The complexity and difficulty of handling multi-dimensional data has perennially hindered researchers in their quest to understand spatial phenomena. Some studies have attempted to quantify spatial variation in populations with the use of indices of dispersion (98) but these methods often fail to distinguish among different spatial patterns (50,34,81). The major impediments to research on spatial processes in insect ecology has thus been the lack of adequate analytical and data management tools. Recent development of two technologies has opened up new avenues for analyzing spatial patterns in insect populations: (a) geographical information systems (GIS) and (b) geostatistics.

A GIS is a set of computer programs that collect, store, retrieve, transform, display and analyze spatial data (9). Georeferenced data, such as insect densities, crop type, or soils, can be incorporated in a GIS to produce map layers or "coverages". A map layer, generally composed of only one type of data, is thus considered to have a "theme". Many of these themes that have a similar spatial extent can be combined to form a full GIS database. The GIS serves as a tool for analyzing interactions among and within the various spatially referenced data themes. Managing and analyzing large spatial databases would be impossible without this type of software.

While the advent of GIS has allowed entomologists to compile and manipulate spatially referenced data, characterization and modeling of spatial patterns is still difficult without an adequate set of statistical tools. Geostatistics are such tools; they are a family of statistics that describe correlations through space and/or time. Geostatistical procedures are used for: 1) quantifying and modeling spatial correlation at a spectrum of spatial scales through the use of semi-variograms, correlograms and covariance functions, and 2) interpolating between (and extrapolating beyond) sample points via kriging and related procedures. These methods have been widely used in applied petroleum and mineral geology; geostatistics have often provided improved predictions of the location of mineral and petroleum resources from limited data. While most past geostatistical applications have focused on geological problems, there is reason to believe that geostatistics will have broad applications to ecological problems (79).

Most of the published applications of GIS and geostatistics to insect problems are from the fields of forest and rangeland entomology; relatively few applications have been developed in agricultural systems. This phenomenon can be explained most easily by the geographic scale of management: forests and rangelands are usually managed as units covering 100 to 10,000 ha of spatially heterogeneous landscapes, but agricultural management typically operates on fields of only 10 to 100 ha of much more uniform composition (42, 9). We expect that GIS and geostatistics will become increasingly important in the management of agricultural and medical insect pests as area-wide pest management becomes more common in these systems.

GEOGRAPHIC INFORMATION SYSTEMS (GIS)

A GIS is a computer system capable of assembling, storing, manipulating, and displaying geographically referenced information. This broad definition includes a range of software functionality (13): at one end are mapping, image processing, digitizing, and computer aided design (CAD) software, which are designed for specific tasks such as the input, manipulation or display of spatially referenced data; at the other end of the spectrum is integrative GIS software. To be considered a true GIS, a system must be capable of *all* of the following: spatial data input, storage and retrieval of spatial data, spatial manipulations, and spatial data reporting (61,17). Below, we will clarify the role of these various sub-functions.

Storage And Retrieval

An essential feature of any GIS is the ability to digitally represent spatial/map data. Any 2-dimensional spatial object can be classified as either a point, line, or polygon. The approach taken to the problem of spatial representation varies among various GIS software packages (71). Many systems represent spatial data using raster images. These images are simply matrices of constant-sized cells, where each cell has a value. Groups of adjacent cells with identical values define a spatial object (Figure 1a). Another approach to spatial representation is the use of vectors. Under this approach, each object is represented by a series of vectors. A point is represented by a single vector of null length, a line or curve is represented by a series of connected vectors, and a polygon is represented by a series of connected vectors that enclose a geographic area (Figure 1b). An advantage of the vector approach is reduced data storage need; for example, the only data that must be stored to represent a polygon are the coordinates of the vertices. However, file compression methods often allow raster data representations to require no more file space than vector representations.

In all true GIS's, there are data attributes associated with each spatial object. Examples of attribute data are the name of a river, population density of a county, or soil type of a parcel. It is not uncommon for many attributes to be associated with a single spatial object. The mechanism used for storing attribute data varies among different software; some systems use "flat" ASCII files, while others use complex relational databases.

Data Input

An obvious prerequisite to any spatial analysis is the acquisition of spatially referenced data. This type of data may include paper maps, remotely sensed data, digital line graphs or field-acquired point data. Map data are typically input using a digitizer or scanner. A digitizer is an electromagnetic device that converts movements of a pointer into x and y coordinates that are used in the GIS to define the spatial position of points, lines, and polygons. A scanner is a device that performs a raster (grid) scan of the input medium and senses the light reflectance at each raster cell. This information is encoded in the computer as a raster image of the source medium. The spatial resolution of scanning devices typically ranges from 30 to 600 dots per inch. Often the source of spatial data may not be a paper map, but may already be in some sort of electronic medium. For example, remotely sensed data often exists as

multi-spectral representations using a raster system. Another example is electronically published government data sources, generally referred to as digital line graphs (DLG); these include map data of elevation, political boundaries, highways, land use, and soils (24,102,103). Most GIS's have utilities for importing data from a variety of data formats including product-specific GIS formats, multi-spectral formats, and various other raster and vector formats.

Spatial Manipulations

The functional utility of the GIS comes from its ability to manipulate spatially referenced data. Probably the most important manipulation, in terms of producing useful results, is the overlay process. Under this process, two or more map layers are combined, using a common georeferencing system, to produce a new map that is a combination of the attributes of these images. For example, one layer can be used to mask out portions of a second layer. In another example, one may calculate a new coverage that is the arithmetic sum of a specific attribute in a series of maps (e.g. total years of defoliation). When using overlays or other manipulations, care must always be taken to recognize that spatial and attribute error can be magnified as a result of the manipulation (10,73).

There are a variety of spatial measurement techniques that provide for analysis of map layers. These measurements include distances from a specific object, the area of a polygon, the length of a line, and the perimeter of a polygon. There are many permutations of these measurements. For example, several GIS's can be used to measure distances as a cost, where cost is computed as distance weighted by a function of an attribute in another coverage.

Another important set of functions is manipulation of the x , y coordinates for a given map layer. This includes "rubber-sheeting" in which the original coverage is distorted to coincide with geo-reference points of another coverage. This function is useful when overlaying two or more map layers which may originate from different map projections (87). Most GIS's have specific mechanisms that facilitate the conversion of a coverage among specific map projections (e.g. universal transverse mercator to azimuthal equidistant). This is often important because different projections have different qualities that may be useful for particular types of analyses of a single coverage. For example, an equal-distant projection produces less error in distance measurements but more error in area measurements than an equal-area projection. Lastly, all GIS's provide some mechanism for manipulating the spatial scale of a coverage. Often, an image provides too much spatial detail and a map generalization function is used to translate that coverage to a smaller scale.

Data Reporting

Output from a GIS may be in the form of a graphical image or tabular listing. An example of a tabular listing might be a list of all polygons and their attributes, or it could be a mean of polygon attributes, weighted by their area. There are a variety of modes of graphical output. Perhaps the most common are 2-dimensional map representations. For example, after overlaying hydrology, road, and vegetation coverages, it may be useful to view a map of the combined image. Map representations are typically viewed directly on the system monitor, or paper copies may be generated using a variety

of printers and plotters. Continuous data are often represented using an orthogonal projection or contours.

Entomological Applications

GIS software is described most correctly as "enabling technology". A GIS provides insect ecologists and pest managers with the capabilities to store, retrieve, process, and display spatially referenced data. It is likely that entomologists will rapidly embrace emerging GIS technology because so many questions from insect ecology to pest management have a spatial component. Whether studying the patch dynamics of host and herbivore or predicting regional hazard, GIS technology can provide entomologists with the ability to answer questions that frustrated their predecessors. At present it is possible to identify two general areas where a GIS has been used in applied insect ecology: characterization of habitat susceptibility to outbreaks and compilation of census data.

Probably the major use of GIS technology in applied insect ecology has been for relating insect outbreaks to biological and physiographic features of the landscape (105,8). For example, Shepherd et al. (85) digitized historical maps of defoliation caused by the Douglas-fir tussock moth in British Columbia from 1924-86, and overlaid these images to obtain a map of defoliation frequency. This outbreak frequency map was then overlaid with forest type and biogeoclimatic maps to determine how forest type and climate were related to outbreak frequency. Their characterization of sites most prone to outbreaks can be used to predict where outbreaks will occur in the future. In a similar study, Johnson used a GIS to examine the relationship between historical grasshopper outbreaks and soil characteristics (40) and between weather and survey counts (41). From these geographically referenced data, Johnson (1989b) found that grasshopper abundance in Alberta was related to soil type, but not to soil texture. Furthermore, a significant association was found between rainfall levels and grasshopper densities; populations tended to decline in areas receiving above-average rainfall (41).

In any of these types of studies, the scale of the original data determines the scale at which projections of risk can be made. For example, Liebhold et al. (58) used aerial sketch maps of historical gypsy moth defoliation to determine associations with specific forest types and elevation classes. The defoliation and forest type data were only reliable at 2 x 2 km raster resolution and consequently any use of these habitat classifications was limited to that scale. Sometimes, other methods can be used to improve the spatial resolution of data. Twery et al. (101) used elevation and aspect to predict forest type and consequential susceptibility to gypsy moth defoliation at a 30 m resolution for areas where actual habitat data was not available at that resolution. There is increasing awareness of the importance of spatial scale in the analysis of ecological systems (3,1,65). Parameters and processes important at one scale are frequently not important or predictive at another scale (63,1,54). Care should be taken when aggregating spatial data since bias and spurious relationships can be generated as data are reduced to lower resolution (73).

Future efforts to characterize habitat susceptibility will probably use remotely sensed data extensively because of their high spatial resolution and its availability in virtually every portion of the

globe (for a complete review of remote sensing in entomology, see Riley [78]). For example, Bryceson (7) used Landsat multispectral data to identify areas in New South Wales, Australia, which were likely to have egg beds of the Australian plague locust. Through the use of a normalized difference vegetation index (NDVI) and maximum-likelihood classification, Bryceson (7) was able to predict the location of nymphal bands from changes in NDVI that resulted from rains during March (nymphal bands tend to be associated with "green" areas that result from rain). Similar "greenness mapping" studies have been conducted in Africa for grasshoppers and locusts (97). In addition to illustrating the apparent ecological association between nymphal bands of acridids in Australia and Sahelian Africa and changes in NDVI, studies of Bryceson (7,8) and Tappan et al. (97) have immense practical utility because they produce real-time estimates of the location and extent of potential pest problems. Through such methods, it has been possible to improve the efficiency of sampling for prediction of outbreaks as well as reduce the guess-work involved with planning and execution of pest management programs.

The second major use of GIS technology has been for compilation and analysis of insect census data. An example of this type of application in an agricultural system is the manipulation and display of boll weevil trap counts in USDA eradication activities (106). Several examples of GIS-based monitoring systems can be found in gypsy moth management programs. Gage et al. (27) used counts of male gypsy moths from traps located throughout Michigan to develop interpolated maps of trap capture using a distance-weighting algorithm. These counts were then used to generate maps of predicted defoliation using a linear model that was developed from historical data. These defoliation prediction maps could then be used to delineate areas where suppression activities were warranted. Spears et al. (94) and Ravlin et al. (75) used a GIS to interpolate gypsy moth trap counts and egg mass densities in an integrated pest management demonstration program in the central Appalachians. They showed how map compilations of these data are useful for documenting the range expansion of this insect and planning suppression activities. In yet another gypsy moth study, Liebhold et al. (57) used a GIS to analyze the historical expansion of the range of the gypsy moth as it relates to geographical variation in climate. From this analysis they developed a model that forecasts the future spread into currently uninfested areas.

The compilation and interpretation of spatially referenced insect and habitat data is a complex process, if for no other reason than the large size (in megabytes) of GIS coverages. Although GIS software is designed to successfully handle this complexity, these systems are often not easy to use. In order to make GIS's more accessible to applied problems, they are increasingly being linked as a part of larger decision support systems (DSS). These systems typically use a GIS to manage habitat, geophysical, political, and census data; the DSS uses these geo-referenced data, along with other types of data as input to mathematical models and rule bases to produce useful abstractions or recommendations (72). These outputs might be maps of high-damage hazard or even maps of proposed control areas. DSS's that utilize GIS's exist, or are under development, for the jack pine budworm (60), the southern pine beetle (11), the gypsy moth (25), and rangeland grasshoppers (4). Coulson et al. (12) used the term "intelligent geographical information system" (IGIS) to describe systems that use a GIS and rule based models to integrate landscape data and knowledge from a diversity of scientific disciplines.

GEOSTATISTICS

Insect populations are typically spatially heterogeneous in their densities. This heterogeneity is often of considerable importance to the development of sampling procedures (93), to the understanding of predator-prey relationships (29,5), to the understanding of intraspecific competition (37), and in the development of rational pest management strategies (33).

For the above reasons, a great deal of effort has been invested in characterizing spatial patterns of insect densities. Most earlier studies have attempted to describe spatial patterns with the use of dispersion indices such as s^2/\bar{x} (18), coefficients of Taylor's Power Law (99), I_d (64), Lloyd's Patchiness Index (59), and Iwao's patchiness regression coefficients (38). These indices focus on the frequency distribution of samples (most quantify the relationship of the sample variance to the mean) but ignore the spatial location of samples. This property produces certain undesirable effects: (a) these indices often fail to differentiate among different spatial patterns (50,34) and (a) their descriptions of spatial pattern are highly dependent on the size of sample units (81). What is required is a tool that uses both value and location simultaneously to quantify spatial pattern.

One school of spatial analysis that takes this approach is geostatistics. Geostatistics is a branch of applied statistics that concentrates on the description of spatial patterns and estimating values at unsampled locations. The prefix "geo-" derives from the geological disciplines that provided the main theoretical and application developments over the past two decades. Nevertheless, many of the precursors to modern geostatistics can be traced back over 100 years from such diverse disciplines as forestry, economics, and meteorology (80).

A well-written, clear, introductory text on geostatistics is Isaaks and Srivastava (36). Davis (21) and Hohn (31) are also clear texts that discuss geostatistics with geological applications. More formal texts, ones that require understanding of calculus and matrix algebra and use mining examples exclusively, are Journel and Huijbregts (48), David (19,20) and Rendu (77). Rossi et al. (80) and Legendre & Fortin (53) may be consulted for more thorough treatment of the use of geostatistical tools for interpreting ecological spatial patterns.

Modeling Spatial Variability

Geostatistics quantify and model spatial and temporal correlation. Underlying this approach is the expectation that, on average, samples close together are valued more similarly than those that are farther apart. This makes intuitive sense.

Let $z(x)$ represent the value of a variable at location x and let $z(x+h)$ represent the value of the same variable some h distance, or lag, away. Note that in the temporal domain h represents some unit of time. For the sake of brevity, henceforth examples presented will be spatial problems even though these tools can be applied to temporal and spatio-temporal problems. Typically we have more than just two samples in a data set, so consider the set of all possible combinations of samples that are

separated by h . One quick way to express the similarity or dissimilarity between the paired values is to plot them in a $z(x)$ vs. $z(x+h)$ scattergram. This plot is known as an h -scattergram. If the difference between all the $z(x)$ and $z(x+h)$ is small, then the scatter of points will be close to the 45° line and the variable is described as "autocorrelated". Alternatively, the larger the difference between the pairs, the more diffuse will be the scatter of points around the 45° or $z(x) = z(x+h)$ line. When h is small, the scatter of points will, on average, be "tighter"; when h is large, the scatter is typically more diffuse.

The "tightness" or "diffuseness" of the cloud of points about the 45° line may be thought of as their "moment of inertia" about the line. If x_i and y_i are the coordinates for all $i=1$ to N points in an h -scattergram, then the moment of inertia for all points is defined:

$$\text{Moment of inertia} = \frac{1}{2N} \sum_{i=1}^N (x_i - y_i)^2 \quad 1.$$

(47). In other words, the value of the moment of inertia summarizes the spread of the cloud in an h -scattergram.

The h -scattergrams can be useful models of the degree of similarity or dissimilarity between samples separated by a common distance, but they are not very practical. Because, too many h -scattergrams would be required to adequately characterize the spatial similarity for all samples and for all h , a meaningful summary of these h -scattergrams is required. Intimately related to the moment of inertia is one of the most familiar tools in geostatistics: the "semi-variogram" or simply the "variogram." A variogram summarizes all h -scattergrams for all possible pairings of data for all significant h :

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2 \quad 2.$$

where $\hat{\gamma}(h)$ is the estimated variogram value for lag h and $N(h)$ is the number of pairs of points separated by h . Variograms plot the $\hat{\gamma}(h)$ as a function of distance h (Figure 2). The variogram values can be computed either as averages over all directions, in which case the lag measure is scalar, or specific to a particular direction, in which case the lag measure is a vector.

Two "rules of thumb" apply to variogram construction (48). First, it is only appropriate to plot variogram values out to about half the width of the sampling space in any direction. This is because the variogram should be representative of the whole sampling space. At distances greater than one half the total distance, only the pairs of samples at the boundary of the sampling space are compared. Second, all variogram values must be represented by at least 30-50 pairs of samples to impart minimum credibility. The greater the number of pairs, the greater the statistical reliability in each distance class.

Typically, when variogram values are plotted for all appropriate h , the values are small for low values of h , then they increase with increasing distance, and then usually level off or become constant after some distance (Figure 2). These features are known as the "structure" in a variogram and they reflect the average degree of similarity or dissimilarity between samples. Constant variogram values

imply that the variance between values does not change with distance. Small variogram values at short lags are indicative of data that are autocorrelated or spatially continuous. Large values, on the other hand, indicate that the paired samples are dissimilar, and more spatially discontinuous.

If a variogram displays a leveling-off behavior, then the variogram value at which the plotted points level off is known as the "sill" (Figure 2). The value of the sill is usually equivalent to the traditional sample variance. The distance at which the variogram values level off is known as the "range." The range designates the average distance within which the samples remain correlated spatially. Variograms that do not demonstrate a leveling off imply that the range is beyond the maximum appropriate distance represented.

Notice in Eq. 2 that, strictly speaking, $\hat{\gamma}_k = 0$ when $h = 0$ since there is no variability between a sample and itself. In practice, however, when a variogram's scatter of points are extrapolated to lag zero, they often appear to intercept the ordinate at a value that is greater than zero. The variogram value at which the model appears to intercept the ordinate is known as the "nugget." The term "nugget" was coined by gold mining engineers who would find nuggets of gold apart from the spatially continuous seams of ore. The spatial characteristics of these gold nuggets impart unexplained variability in the modeling of the gold seams.

A nugget represents two, often co-occurring, sources of variability. One source derives from spatial variability at a scale smaller than the minimum lag distance, and hence it cannot be modeled with the present sampling scheme. The other genesis of a nugget is experimental error which is sometimes referred to as the "human nugget." Interpretations made from variograms depend on the size of the nugget because the difference between the nugget and the sill (if there is one) represents the proportion of the total sample variance that can be modeled as spatial variability.

Variograms sometimes appear horizontal. These models have a complete lack of structure and their values are nearly identical to the sample variance over all h . In geostatistics these models are known as "pure nugget" variograms. Pure nugget variograms represent an absence of spatial dependence at the scale sampled. In this instance, the sample variance adequately summarizes the data's variability.

For entomological and environmental variables the similarity or dissimilarity between locations is rarely uniform with direction. For instance, one might expect, a priori, that a natural population of some insect would more often display different densities with different directions due to migration patterns or some environmental cue. When variograms computed for specific directions show different behaviors, the data is described as "anisotropic."

Generally, there are two types of anisotropy: geometric and zonal. Geometric anisotropy is indicated by directional variograms that have different ranges. A longer range in a direction means that the values of the property of interest are more continuous in that direction than for a direction with a shorter range. Zonal anisotropy is indicated by directional variograms that have different sills. Zonal

anisotropy means that the magnitude of spatial variation changes with direction. Often, both forms of anisotropy are evident in directional variograms. Thus, the researcher may need to compute many directional variograms in order to uncover the type and specific direction of any anisotropy.

Because the variogram computes the average *squared* difference between samples separated by a common lag and oriented in a common direction, it is very sensitive to outlier data. A few particularly large or small values can greatly affect the behavior of variograms. Normally, variograms computed from data that contain especially large- and/or small-valued samples will be "noisy." That is, instead of smoothly rising with increasing h , the variograms will be erratic with sharp increases and decreases. Variogram "noise" due to data outliers can even completely mask structure and produce a pure nugget effect.

The h -scattergrams are effective tools for discovering outliers because these data will plot away from the "cloud". However, searching for outliers with h -scattergrams can be tedious. Once a suspected outlier is discovered, it may be removed from variogram analysis only if there is a suitable justification (80). As an alternative, many "resistant" variogram measures (i.e., geostatistical tools that are "resistant" to the influence of unusually large and small data) and outlier detection methods have been proposed (32,30,52,23). Some of the more popular resistant variogram measures are the median absolute deviation estimator (45), generalized distance measures (47), median polish (14,15), the Cressie-Hawkins estimator (16), and Omre's estimator (69).

Variograms also can provide a limited view of spatial variability when the data contain trends. A trend may be thought of as spatial pattern larger than the extant sampling scheme's capability to fully detect. Trends manifest themselves two ways. Sometimes local mean values change over the sampling space while other times it is the local variances that change. Frequently, both local means and local variances change as a function of location within the sampling space. The usefulness of a variogram stems primarily from its ability to model lag-to-lag spatial continuity. If there is a trend, both the underlying lag-to-lag variability and the trend variability will be modeled in a variogram.

In geostatistics there are two additional tools used for quantifying spatial variability that remove mean and variance trend effects so that the underlying lag-to-lag variability can be articulated. These two tools, spatial covariance and lag correlation, filter changes in the local mean and variance and specify the strength of the underlying spatial relationship. Like the variogram, these tools summarize the h -scattergrams computed for various lag distances. The "non-ergodic" or spatial covariance, $\hat{C}(h)$ is estimated:

$$\hat{C}(h) = \frac{1}{N(h)} \sum_{i=1}^{N(h)} [z(x_i) - m_{-h}] [z(x_i + h) - m_{+h}] \quad 3.$$

(35). As before, $z(x_i)$ and $z(x_i+h)$ are two data points separated by the vector h . Datum $z(x_i)$ is the tail and $z(x_i+h)$ is the head of the vector, $N(h)$ are the total number of data pairs separated by lag h , and m_{-h} and m_{+h} are the mean of the points that correspond to the tail and head of the vector, respectively. The formal definition of "ergodicity" is rather involved (see Olea [68]), but the main idea is that the traditional ergodic covariance considers $m_{-h} = m_{+h} = m$. Differences between the head and tail means are thus accounted in the non-ergodic covariance.

The second tool, lag correlation, $\hat{\rho}(h)$, filters both lag means and lag variances. It is related to the non-ergodic covariance and is similarly estimated:

$$\hat{\rho}(h) = \frac{1}{N(h)} \frac{\sum_{i=1}^{N(h)} (z(x_i) - m_{-h})(z(x_i+h) - m_{+h})}{s_{-h}s_{+h}} = \frac{\hat{C}(h)}{s_{-h}s_{+h}} \tag{95}$$

where s_{-h} and s_{+h} are the standard deviations of the tail and head values of the vector, respectively. The correlogram can vary only from +1 to -1 depending upon whether the correlation between locations is positive or negative.

The non-ergodic, or spatial, covariance and correlation values can be plotted as a function of lag distance like a variogram. Note, however, that unlike the variogram which usually contains small values at short h and large values at larger h , the non-ergodic tools' values are large for small h and small for large h . Or, to put it another way, they are "flipped" images of the variogram.

The true variogram, covariance, and correlogram are all related. If the population mean and variance are constant over the sampling space ($\mu_{-h} = \mu_{+h} = \mu$ and $\sigma^2_{-h} = \sigma^2_{+h} = \sigma^2$, i.e., there is no trend) then:

$$\begin{aligned} \gamma(h) &= \sigma^2 - C(h) \\ C(h) &= \sigma^2 - \gamma(h) \\ 1 - \rho(h) &= \gamma(h) / \sigma^2 \end{aligned} \tag{96}$$

For ease of comparison, these relations permit us to re-express the covariance and correlograms in variogram form. When the lag covariance values are subtracted from the sample variance, the resulting plot is equivalent, though not identical, to the variogram. When the correlogram is subtracted from 1, then the resulting plot is in the form of a variogram.

The non-ergodic tools should be computed concurrently with the variogram and then all three should be compared. Differences between the variogram and covariance signal changes in the local means. Plotting m_{-h} and m_{+h} as a function of h provides a description of the magnitude and direction of local mean changes. Differences between the covariance and correlogram indicate varying local variances. Plots of s_{-h} and s_{+h} versus h model the nature of the variance changes.

In addition to furnishing an appreciation for both lag-to-lag and local trends, the non-ergodic tools should be computed along with the variogram because trends can completely obscure structure or falsely impart it. Isaaks and Srivastava (35) provide an example of a gold deposit that has a noisy, near pure nugget variogram, but it displays a well-structured non-ergodic covariance. By appraising only the variogram, one may falsely conclude that there is no spatial dependence. Rossi et al. (80), on the other hand, show an example of a structured variogram with a near-zero nugget, but it had a pure nugget non-ergodic covariance. In this case, interpreting spatial dependence using only the variogram would lead to the false conclusion that there is a small scale, lag-to-lag spatial dependence. Knowing that an organism's spatial pattern occurs on a small and/or large scale and having some idea of the

relative strength of these patterns can be a valuable aid in understanding the distribution of an insect. Moreover, as we will see shortly, the scale of the spatial pattern will influence strongly the success of geostatistical tools that provide estimates for unsampled locations.

Some entomological properties are naturally nominal variables. The presence or absence of an insect and genotype are two examples. Variograms, covariances, and correlograms can be computed for nominal variables after coding presence and absence as "0"s and "1"s. These models are known as indicator variograms, covariances, or correlograms and are interpreted the same way as they are for continuous variables (44,31).

Indicators may also be applied to continuous variables. For instance, say a researcher would like to specify the spatial dependence of a particular size, age, or density class in an entomological data set. Indicator coding may be performed for any subset desired. The indicator transformed variable, $i(x;k)$ is thus a function of both location, x , and cutoff, k . In the simplest nominal case, the cutoff defines a single threshold for a particular subset:

$$i(x;k) = \begin{cases} 1 & \text{if } z(x) \geq k \\ 0 & \text{if } z(x) < k \end{cases} \quad 6.$$

In addition to characterizing nominal ecological variables, indicators may also be used to discretize a continuous variable's cumulative distribution function (cdf) into a series of cutoffs (44,31). These cutoffs may be defined according to some natural or predefined proportions like particular size and age classes, or they may be chosen arbitrarily (eg. at each decile). For each subset or cutoff along the cdf, indicator transforms are made of the data according to Eq. 6. The resulting array of indicator variograms, covariances, and correlograms provides the entomologist with unique models of the spatial dependence for the whole spectrum of an organism's attribute. The greater the number of cutoffs, the more refined will be the discretized cdf. Ultimately, it is the number of samples available to define any one class or subset that will limit this non-parametric approach. For that reason, indicator transforms should rarely be performed on cutoffs smaller than the first or larger than the ninth deciles.

Geostatistical tools are also available for modeling the spatial covariation between variables. This capability can be one of the most useful and informative in geostatistics. These methods, called cross-variograms, cross-covariances, and cross-correlograms, are simply extensions of the variogram (Eq. 2), the covariance (Eq. 3), and the correlogram (Eq. 4). Lack of space prevents an examination of these tools, but Isaaks and Srivastava (36) and Rossi et al. (80) should be consulted for their theoretical development and interpretation using practical examples.

Geostatistical Estimation Tools

Geostatistics offer a variety of methods that provide estimates for unsampled locations. Known generally as "kriging" techniques, they estimate values by taking a weighted linear average of available samples, not unlike multiple linear regression. The term "kriging" was named by Georges Matheron (62) in honor of Danie Krige who first formulated and implemented this form of interpolation in 1951.

Like traditional point interpolation methods (e.g., inverse distance weighting, triangulation, and local sample means), kriging can provide an estimate for a specific location. And like traditional areal interpolation methods (e.g., polygonal weighting and cell declustering), kriging can estimate an average value over an area. Often the traditional methods are as accurate and less time-consuming than kriging, so the researcher should first consider these other methods (36). However, certain characteristics of kriging distinguish it from these other methods.

First, kriging can provide an estimate that is either larger or smaller than any of the sample values. The traditional techniques are restricted to the range of sample values. Second, whereas the traditional methods use Euclidean distance to weight available samples, kriging takes advantage of both distance *and* geometry (i.e., the anisotropic relations) among samples. Third, unlike traditional methods, kriging is designed to minimize the variance of the expected error. The expected error is the difference between the estimate and the true value. Of course, the true value is never actually known, so kriging applies a conceptual, probabilistic random function model of the true values (66,36). Finally, kriging can incorporate alternate forms of information into the analysis. For example, say an entomologist is interested in estimating the density of an insect in unsampled areas, and it is known that soil moisture affects the distribution of the organism. Kriging can use the spatial dependence inherent in both properties as well as their joint spatial dependence to provide estimates that are more accurate than when using only one or the other of the single variables.

The basic idea of kriging is simply an extension of the notion of spatial dependence discussed earlier; on average, samples close together are more similarly valued than those that are farther apart. Suppose we want to estimate the value of a property at some unsampled location and we do have some samples in the vicinity. Directional models (variograms, covariances, or correlograms) provide us with a measure of the strength of correlation for different directions and for different distances. Using this information, kriging weights the known samples to provide a weighted linear estimate for the unsampled location.

The geostatistical interpolation procedure known as "ordinary kriging" (OK) is essentially identical to multiple linear regression with a couple of important twists. In classical multiple linear regression the dependent and independent variables represent different variables usually measured at the same location in space or time. Thus, the matrices used to solve the system of simultaneous equations is inferred only once from the data. In geostatistics, dependent and independent variables represent the same property, only now measured at different locations, and we wish to estimate (i.e., interpolate) values at unsampled locations.

For example, if $z^*(x_0)$ is the value to be estimated at location x_0 , $z(x_i)$ are the sampled values at their respective locations, and λ_i are the weights to be given to each sampled value, then an OK estimate may be expressed as:

$$z^*(x_0) = \sum_{i=1}^N \lambda_i z(x_i) \quad 7.$$

which is a simple modification of a multiple linear regression formulation.

In multiple linear regression, a least-squares variance is minimized with respect to each independent variable's coefficient or weight. Kriging has a parallel requirement which seeks to insure that over the estimation space the expected value of the estimates will equal the expected value of the true (i.e., the random function) values. In other words, we expect that our estimates will be unbiased. Unbiasedness requires that, on average, the difference between our estimates and the true, but unknown, values will be zero:

$$E[Z(x) - Z^*(x)] = 0 \quad 8.$$

To insure unbiasedness, we restrict the sum of weights to equal one:

$$\sum_{i=1}^n \lambda_i = 1 \quad 9.$$

Just like multiple linear regression, in ordinary kriging we wish to find the weights, λ_i , while simultaneously minimizing the quantity $[Z(x) - Z^*(x)]$ for all estimated points and making sure they sum to unity. Analogous to the least-squares variance in regression, kriging minimizes the estimation variance, S_{ev}^2 which is the variance of the error:

$$S_{ev}^2 = \text{Variance}[Z^*(x) - Z(x)] \quad 10.$$

The geostatistical way to do all this is to infer the "true" value from an empirical model of the existing spatial continuity or degree of spatial dependence with distance and direction. These are the variogram, covariance, or correlogram models. There are several forms of linear and nonlinear models that can be used to fit observed variogram values in order to obtain $g(h)$ for all lags (36). We implicitly decide that the model is accurate over the whole estimation area. This so called "stationarity hypothesis" is important in geostatistical estimation because if it is in error, the kriging estimates will also be in error.

Kriging uses matrix algebra to solve a set of simultaneous partial differential equations that minimize the error variance (Eq. 10) with respect to each weight, λ_i , while ensuring unbiasedness (Eq. 9). To accomplish this task, matrices are built from the values of a positive definite model that is fit to the experimental variogram (or covariance or correlogram) points. One matrix, C, itemizes all of the data-to-data values and thus captures data spatial continuity and accounts for any data redundancy or clustering. The other matrix is a vector, D, of all data-to-estimation-location model values; this captures the distances to measured points. The kriging system of equations is then solved: $C^{-1} \cdot D = W$ where W is the vector of sought-after weights, λ_i .

Entomological phenomena are frequently multivariate and the primary variable of interest is expensive and/or time-consuming to sample. A geostatistical interpolation technique known as "co-kriging" offers a way to minimize the number of samples taken of the primary variable by sampling a secondary covariate more intensively, one that is easier or less expensive to sample (36). Co-kriging is just a modification of OK (see Eq. 7) formulation. A co-kriging estimate is a linear combination of both the primary and secondary data. In co-kriging, variograms (or covariances or correlograms) computed on each variable, as well as cross-variograms (or cross-covariances or cross-correlograms), are used to specify the spatial dependence relationships. One advantage of co-kriging

is that since more information is being employed in the estimation, the minimized variance is usually smaller than for OK.

Indicator transforms were introduced above as serving two variography functions. One was a means of encoding nominal variables so that their spatial dependence might be modeled. The other function was to discretize a continuous variable's cumulative distribution function (cdf) and then computing models of the spatial dependence at each cutoff. A geostatistical interpolation method known as "indicator kriging" (IK) can be used to perform estimation on these indicator variables (46,47). IK is simply another modification of the kriging concept: it is OK performed on the indicator transformed data.

OK and co-kriging provide a specific estimated value for a location. In the nominal variable case IK provides an estimate of the probability that the location's value is either a "0" or "1." In the case of a continuous variable's discretized cdf, IK estimates the probability that the location's value is less than or equal to the cutoff value. These results are possible owing to a powerful and simple property of indicator data: the expected value of an indicator-coded data set is identical to the probability that the random variable it represents is less than or equal to the value of the cutoff value.

After performing IK at each cutoff, we have multiple estimates of the probability that a location is greater than various cutoff values. These values define a discretized probability density function for that location. Moreover, the probability density function is conditional to the available sample values. Once inter-cutoff distribution assumptions are made, the conditional probability associated with any cutoff can be assessed. Also, the probabilities may be mapped for the entire sampling space.

Indicator kriging is but one of many means of estimating the conditional probability density function for a location. Other methods include, but are not limited to: lognormal kriging, multi-Gaussian kriging, and disjunctive kriging (47,22). A recent "twist" on the kriging theme is known as conditional or stochastic simulation (43,22). Conditional simulation goes a step further than kriging methods by generating multiple equally probable estimates that are conditional to the samples. These multiple estimates characterize jointly the certainty or uncertainty in the value for a location. Unlike kriging methods, conditional simulations provide the opportunity to estimate the joint probability density function between any two or more locations. This allows for measuring a phenomenon's continuity over a region.

Applications In Entomology

The application of geostatistical methods for quantifying spatial patterns in insect count data is relatively new and there are only a few published applications. Small scale studies (less than 500 m total area) in both agricultural (82,83) and forest (56) systems indicate that localized discontinuity (as measured by the nugget effect) is typically high and some data indicate a pure nugget effect. This high localized discontinuity may be due to either sampling error or it may reflect spatial dependence that occurs at a spatial scale smaller than that sampled in the data. The ubiquity of this phenomenon in insect data probably reflects phenomena in which there exist aggregations at a variety of spatial scales.

Liebhold et al. (56), used variograms of data from a variety of spatial scales to demonstrate that gypsy moth egg masses are aggregated at scales ranging from 25 m to 50 km. Studies of rangeland grasshoppers (41,39,51) indicate substantial spatial dependence at distances ranging from 1-100 km though the magnitude and range of this dependence varies considerably among regions and years. The existence of these vast ranges of spatial dependence illustrates the value of the geostatistical approach in that it provides a mechanism for quantifying spatial dependence over a range of scales; other procedures that use a single index, such as the fractal dimension (96) or dispersion indices (98), do not quantify spatial dependence at multiple scales.

Comparisons among variograms calculated from insect count data taken at different times can be useful for investigation of effects of dispersion and mortality on spatial patterns of insect abundance. Schotzko and O'Keefe (82) used variograms to compare the spatial dependence in within-field *Lygus hesperus* counts and found that early-season counts were generally more clumped than mid-season samples. They hypothesized that early-season aggregations may be caused by aggregation for mating and that mid-season populations are more uniformly distributed because of pre-ovipositional dispersal. Borth and Huber (6) found very different results when they followed within-field variation in densities of the pink bollworm, *Pectinophora gossypiella*, during a single growing season. They found no detectable spatial structure in the parental generation, but increased spatial dependence in the F_1 and F_2 generations; this change was attributed to the expansion of populations into unoccupied space. Setzer (84), in a unique study, used correlograms to quantify the spatial dependence in mortality rates of the gall-forming aphids, *Pemphigus populitransversus* and *P. populicaulis*. Setzer found significant autocorrelation among spatially adjacent galls, indicating a clumped pattern of mortality which was attributed to the foraging habits of dipteran predators. On a much larger scale, Liebhold and Elkinton (55) quantified spatial dependence in yearly maps of gypsy moth defoliation in Massachusetts and found that spatial dependence generally was high in rising populations but was lower when outbreaks declined.

The existence of strong spatial dependence in insect data indicates that there is value in estimating counts at unsampled locations from values at nearby locations. There are many instances in ecological research and pest management where it is necessary to interpolate among spatially stratified samples. The current emphasis on area-wide pest management strategies often entails the use of spatially stratified samples to assess the need for treatment over large areas. The benefit of kriging in these situations is that these estimates provide the "best estimates", and procedures are available for generating confidence intervals of these estimates (43,44).

The gypsy moth, *Lymantria dispar* (L.), is an example of a major pest where management depends heavily on interpolating among spatially stratified samples (74,76,27). Gypsy moth egg masses are present from late summer through early spring of the following year. The availability of egg masses over such a long interval makes this life stage convenient for sampling. Most gypsy moth management programs rely on estimates of egg mass densities for evaluating the necessity of suppression in an area (74). Liebhold et al. (56) modeled semivariograms from gypsy moth egg mass data from Massachusetts and used these models to generate maps of kriged estimates. They also used indicator kriging to generate maps of probabilities of exceeding a threshold density. Because

pest management decisions are usually triggered by exceeding some threshold density (70), maps of outbreak probabilities from indicator kriging can be useful for management decision making.

Rangeland grasshoppers provide another example of insects that are managed on an area-wide basis and considerable effort is invested in collecting census counts that are spatially stratified over large geographical areas. Historically, suppression programs have been large, often resulting in thousands of hectares treated for grasshopper control. Johnson and Worobec (41) used an inverse-distance weighted mean technique to estimate maps of grasshopper abundance in Alberta. Kemp et al. (51) used ordinary kriging to estimate maps of grasshopper counts in Montana. Presumably, kriged estimates result in a lower estimation error than obtained using an inverse-distance method, though results are often very similar (36).

A problem with insect count data is that the random variables that these data represent typically do not approximate a univariate normal distribution. This situation results in substantial bias in the use of the kriging estimation variance as a measure of reliability or confidence in the kriged estimate (Eq. 10) (49). It is because of this problem that methods other than the kriging estimation variance are often more desirable for estimation of confidence intervals of estimates; these other methods include the use of indicator kriging or conditional simulation. Often researchers will perform a nonlinear transform of the data (e.g. $\log(x)$, \sqrt{x}) prior to kriging to make the data more univariate normal. An example of this can be found in a study in which kriging was used to generate interpolated maps of pear thrips densities in Vermont (2). In this study, a $\sqrt{x - 3/8}$ transformation was used to correct the highly skewed nature of the count distribution. The kriged estimates that were presented using a simple back-transformation were biased. Any time a nonlinear transform of the data is made, kriging is performed, and then the results are simply inverse-transformed, the kriged estimates will be biased. The only published, unbiased back-transformation is the logarithmic case (48).

Application of geostatistical tools is not limited to counts of insect numbers, but also can be used to quantify spatial variation in genotypic and phenotypic characteristics of populations. Several studies have used spatial autocorrelograms to quantify within-population spatial variation in insect genotypes (92). Some of these studies have found population attributes that are spatially anisotropic and this has been interpreted as evidence for clinal variation (67, 92). A recent criticism of this work (86) argues that sampling error, stochastic variation, and parametric variation caused by differences among processes governing allele frequencies may be the major sources of variation and will overwhelm any spatial differentiation within populations. Sokal and Oden (91) defended the use of spatial autocorrelation and argued that Slatkin and Arter's (86) conclusion resulted from limiting the values of parameters in their simulations.

THE FUTURE

In many respects, GIS and geostatistics are technologically advanced, yet it is likely that these technologies will evolve and mature considerably over the next decade. For example, geostatistical procedures have generally not been incorporated within currently available GIS software. Furthermore, most GIS and geostatistical software is not easy to use; it is likely that more intuitive user

interfaces will be developed in the future, thereby making these tools available to a wider audience of ecologists.

The advent of GIS and geostatistics has made analysis of complex spatial patterns an attainable reality for ecologists and it is therefore likely that these tools will contribute to major developments in applied insect ecology. However, these future developments may be limited by our current conceptual ecological framework, which until recently has not concentrated on processes operating through space. This theoretical gap is embraced by the new field of "landscape ecology" which emphasizes large area phenomena and the effects of spatial patterning in the analysis of ecological phenomena (104,28). Despite the availability of tools such as GIS and geostatistics, the incorporation of space into ecological theory, ecological models, and pest management practices will not happen overnight because substantial developmental changes in both theory and practice must occur.

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Figure Captions

Figure 1. Methods used for representing spatial data. (A) Raster method. (B) Vector method.

Figure 2. A typical Variogram.