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GEOSTATISTICS IN ECOLOGY: INTERPOLATING WITH KNOWN VARIANCE[1]

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Interpolation is perhaps central to most ecological field studies. Ecologists who infer mean values for particular variables within a given experimental plot or time increment implicitly interpolate values for all points not measured. For example, in systems ecology the mean value for a flux over a landscape unit is usually based on an average value for randomly distributed samples within the unit examined. In plant population ecology, estimated population densities are often based on random small-area samplings within the community. So long as assumptions regarding sample independence and normality are met, parametric statistics for samplings such as these provide optimal estimates of variance about unbiased means, and are widely used to describe attributes of experimental sites and to test hypotheses about ecological processes at these sites.

Often however, assumptions about sample independence cannot be met in field studies because of autocorrelation: samples collected close to one another are often more similar to one another than are samples collected farther away, whether in space or time. Consequently, estimates of variance about interpolated points may differ substantially from overall population variance, resulting in imprecise estimates of sample

values within the unit sampled (Trangmar et al. 1985) and a biased estimate of treatment effects in experimental systems (Sokal and Rohlf 1981). In many field studies such autocorrelation can arise from subtle topographic features of a site that affect a host of other environmental factors such as microclimate or soil nutrient status; in other studies lack of sample independence may reflect distance from a major seed, predator, or herbivore source. In studies that involve sampling through time, autocorrelation can result from underlying temporal features of the system such as diel trends in temperature, radiation, or some other factor not readily identified and thus not readily treated as a covariate.

The recent development of regionalized variable theory (Matherton 1971) for applications in geology (e.g., Journel and Huijbregts 1978, Krige 1981) and soil science (e.g., Burgess and Webster 1980a) provides an elegant means for describing autocorrelation in data, and a means to use knowledge about this autocorrelation to derive precise, unbiased estimates of sample values within the sampling unit and thereby resolve detailed spatial and temporal patterns with known variance for each interpolated point. The development of this theory should be of considerable interest to ecologists. Spatial variability in particular has long been difficult to quantify in ecologically meaningful ways: conventional interpolation techniques such as proximal weighting, trend surface analysis, and spline interpolation do not consistently provide unbiased estimates for the points interpolated, nor do they estimate optimal variances for the interpolated values. Such imprecision leads to questions of statistical confidence and subsequent difficulty with the interpretation of the patterns defined. Geostatistical techniques address these problems directly.

Excellent reviews of regionalized variable theory and its strengths and limitations exist already (Krige 1981, Vieira et al. 1983, Trangmar et al. 1985, Webster 1985). Rather than repeat these discussions, in this note I present an overview of the theory as it applies to the analyses of two ecological data sets. The first data set is from a study of temporal changes in *Rhodomonas* (Cryptophyceae) density in the epilimnion of a temperate hardwater lake; the second is from an investigation of the spatial variability of soil mineral nitrogen in a Michigan old-field community. In addition to descriptions of these analyses I provide a set of FORTRAN algorithms that allow straightforward access to these new statistical tools.

Approach and Examples

In its simplest form, geostatistical analysis is a two-step process: (1) defining the degree of autocorrelation among the measured data points, and (2) interpolating values between measured points based on the degree of autocorrelation encountered. Autocorrelation is evaluated by means of the semi-variance statistic γ (**h**), calculated for each specific distance or time interval **h** in a data set such that

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

where $z(x_i)$ is the measured sample value at point x_i, $z(x_{i+\mathbf{h}})$ is the sample value at point $x_{i+\mathbf{h}}$, and $N(\mathbf{h})$ is the total number of sample point contrasts or couples for the interval in question. The resulting plot of $\hat{\gamma}(\mathbf{h})$ vs. all **h**'s evaluated is termed the semi-variogram; the shape of this plot describes the degree of autocorrelation present.

Once spatial or temporal dependency is established, one can use semi-variogram parameters to interpolate values for points not measured using kriging algorithms. There are several different forms of kriging (Trangmar et al. 1985); the simplest are punctual and block kriging. In punctual kriging, values for exact points within the sampling unit are estimated; block kriging involves estimating values for areas within the unit. Block interpolation (Burgess and Webster 1980b) may be more appropriate than punctual interpolation where average values of properties are more meaningful than exact single-point values, especially where spatial or temporal dependence is weak.

Both forms of kriging provide an error term (estimation variance) for each value estimated, providing a measure of reliability for the interpolations. These error terms are independent of the observed sample values themselves; estimation error depends only on the locations of samples within the range of sample interdependence and on the degree of this dependence as quantified by the semi-variogram. Consequently, kriging can also be used before sampling to design an optimal strategy for sampling an area or time series knowing only something about the degree of sample interdependence (the shape of the semi-variogram) for samples within the interpolation domain. For example, where samples are strongly autocorrelated over small sampling intervals, pre-sample kriging can show where to add sample points to bring estimation precision to a desirable level in sparsely sampled regions. Conversely, where samples are weakly autocorrelated over small intervals, pre-sample kriging can show that additional sampling in a given region will add little additional precision to interpolation estimates.

Fig. 1a is a semi-variogram for the temporal *Rhodomonas* data collected for the study mentioned earlier. These data represent cell counts of *Rhodomonas* sp. in water samples taken from the epilimnion of Law-

γ

h (days)

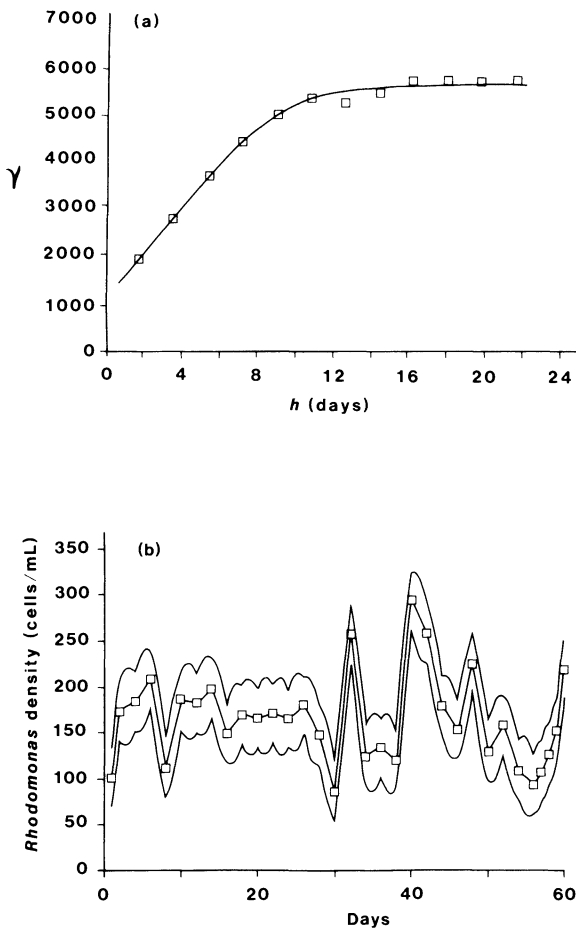Rhodomonas density (cells/mL)

Days

FIG. 1. (a) Semi-variogram of *Rhodomonas* sp. density (cells/mL) in the epilimnion of a southwest Michigan Lake for the period August 1982–August 1983 (Taylor and Wetzel 1984). The solid line describes a spherical function fit by weighted least-squares analysis ($r^2 = 0.977$) such that $\hat{\gamma}(\mathbf{h}) = 6073. [1.5\mathbf{h}/14.2 - 0.5(\mathbf{h}/14.2)^3]$ for $\mathbf{h} \le 14.2$, and $\hat{\gamma}(\mathbf{h}) = 6073.$ for $\mathbf{h} > 14.2$. (b) *Rhodomonas* sp. density interpolated over the first 60 d of the 384-d study period. Measured points appear as boxes. Estimation standard deviations bound the interpolated points.

rence Lake in southwest Michigan at variable sampling intervals (W. D. Taylor and R. D. Wetzel 1984 and *personal communication*). Samples were collected over a 376-d period beginning in August 1982, such that the smallest interval **h** separating any two points in the series was 1 d, and the largest was 375 d. Fig. 1a is a plot of semi-variances for intervals up to 24 d, after which there was no consistent change in the shape of the curve. In this data strong autocorrelation is evident among sample points <15 d apart, with the strongest autocorrelation (the steepest portion of the semi-variogram slope) among points separated by <6-d inter-

vals. Progressively less correlation occurs among points >8 d distant, such that at ≈15-d intervals the variance attributable to autocorrelation becomes approximately equal to the population variance. Thus sample points separated by >15 d appear independent of one another.

The solid line in Fig. 1a describes a spherical model of the semi-variogram obtained by weighted least-squares analysis ($r^2 = 0.997$; SAS Institute 1985). The spherical model is a modified quadratic equation of the form $\hat{\gamma}(\mathbf{h}) = C[1.5\mathbf{h}/a - (\mathbf{h}/a)^3]$ for $\mathbf{h} \le a$, and $\hat{\gamma}(\mathbf{h}) = C$ for $\mathbf{h} \ge a$, where C is semi-variance at the asymptote and a is the interval **h** at the asymptote. Fitting a reasonable model to the semi-variogram is a critical step for subsequent interpolation by kriging, as the technique is sensitive to relatively small changes in semi-variogram parameters, in particular to estimates of y intercept and slope values. Other models that have been found to fit semi-variograms well include linear, exponential, DeWijsian, and segmented models (Trangmar 1985, Webster 1985). The y intercept of semi-variograms should theoretically equal 0, as indicated in Eq. 1; where it does not, as in the *Rhodomonas* example where $\hat{\gamma}(0)$ is ≈15% of the population variance, suggests either measurement error, or that autocorrelation occurs at intervals of less than the smallest interval sampled (<1 d in this example). In most cases this so-called nugget variance is probably a combination of these sources of variation.

With autocorrelation established and a suitable model for the semi-variogram defined, kriging can be used to interpolate between *Rhodomonas* sample points in order to estimate more precisely the values for unsampled locations. Punctual kriging is an exact interpolator (Delhomme 1978), so that where interpolated points coincide with measured points, the estimated values are identical to measured values. Thus interpolated values for a single-dimension data set such as the *Rhodomonas* data will not diverge from a line drawn between all measured sample values (Fig. 1b). Nevertheless, kriging can be valuable for single-dimension data because it can provide estimates of variance about the interpolated points that will be more precise than overall population variance. In the *Rhodomonas* case, for example, these variance estimates can be useful for judging whether temporal patterns of epilimnetic *Rhodomonas* densities differ significantly from patterns for other species or from temporal patterns of environmental variates.

Two-dimensional spatial data present a more complex interpolation problem, chiefly because the degree of autocorrelation among sample points may be a function of their alignment on the interpolation grid in addition to their distance apart. On a grid with topographic relief, for example, points that are downslope or upslope from one another may be differently au-
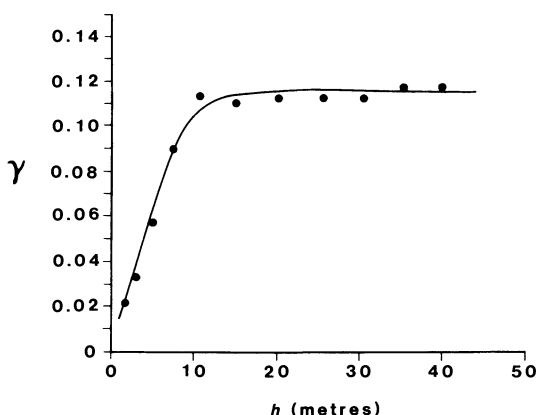
FIG. 2. Semi-variogram of soil mineral-N content (values log-transformed before analysis) in a Michigan old-field community. The solid line is an exponential function fitted by weighted least-squares analysis ($r^2 = 0.968$) such that $\hat{\gamma}(\mathbf{h}) = 0.001 + 0.115(1 - e^{-h/13.1})$.
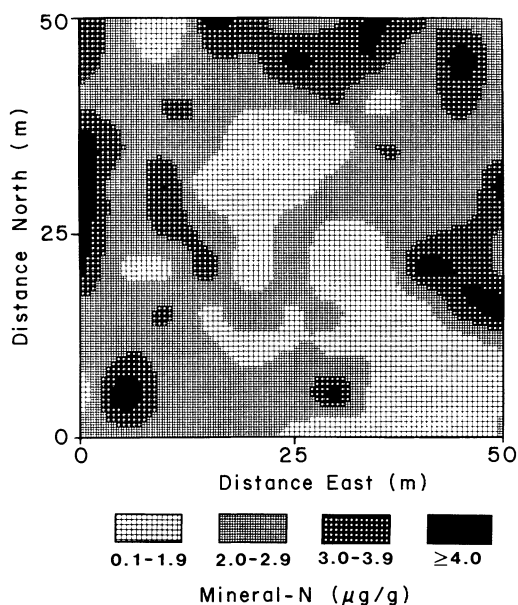

Mineral-N (μg/g)

FIG. 3. Isopleth of soil mineral-N content punctual kriged at 0.6-m intervals across a 0.25-ha portion of the old field. Estimation variances range from 0.004 to 0.296 (μg/g)^2 N.

tocorrelated than points located along the same contour interval. Where such anisotropy exists, a directional component must be included in the semi-variogram model.

Fig. 2 demonstrates an isotropic semi-variogram for two-dimensional spatial data of soil mineral-N content in a Michigan old-field community (G. P. Robertson and J. M. Tiedje, *personal observation*). Soil samples were collected on a regular grid 69 m square at 4.6-m intervals for a total of 256 sample points, with an additional 45 soil cores taken from the northeast quadrant of the field at sample intervals as little as 0.9 m apart. After collection, three replicate subsamples from each of the 301 cores were extracted in 2 mol/L NaCl and extracts were analyzed for total mineral-N (NH_4^+-N + NO_3^- − N) by continuous flow analysis (Technicon 1973). Data for 11 of the 301 cores were lost during sample handling or analysis. As the data were lognormally distributed, all statistical analyses were performed on log-transformed values.

Anisotropy did not appear to be present and the isotropic semi-variogram was fit by weighted least-squares analysis (SAS Institute 1985) to an exponential model (Fig. 2; $r^2 = 0.968$). The shape of this model suggests that some autocorrelation occurs among samples <40 m apart and that points <20 m apart are very strongly autocorrelated. That the y intercept or nugget variance is <10% of the population variance suggests that spatial autocorrelation at the 1–40 m scale accounts for most of the variation in total mineral-N content across the field.

Punctual kriging at 0.6-m intervals across a 50 m square portion of the larger grid produced the isopleth in Fig. 3. Mineral-N content across the 0.25 ha pictured

ranged from 0.1 to 7.9 μg/g soil. Estimation variances for soil N at the points interpolated ranged from 0.004 to 0.296 (μg/g)^2. As noted earlier, estimation variances are highest where interpolated points are farthest from sample locations; thus the highest estimation variances in this data set coincide with locations of the missing cores from this portion of the field.

Discussion

Regionalized variable theory is widely used for interpolating spatial pattern in geological exploration. Its recent adaptation by soil scientists shows clearly its potential in ecological studies for providing precise, unbiased estimates of sample values in sample domains where collected samples are not independent of one other, and for describing temporal and spatial patterns with statistical confidence.

In the *Rhodomonas* study described above, geostatistics allows comparisons of temporal *Rhodomonas* trends with other species densities or environmental variates collected on different dates. Standard parametric statistics are inappropriate for such comparisons because the samples collected are strongly autocorrelated. In the soil mineral-N content example, spatial patterns in the old-field community emerged as interpolated points with known variance for each. The estimation standard deviations for mineral-N at these points ranged from 0.06 to 0.54 μg/g soil; this contrasts with a standard deviation of 1.35 μg/g soil for the mean

mineral-N content (2.67 μg/g soil) of all points sampled.

Ecological studies that produce data not amenable to normal statistical treatment because of spatial or temporal autocorrelation may significantly benefit from geostatistical analysis. Autocorrelation is a potential problem in many if not most field sampling strategies, and its presence should be routinely evaluated. The application of geostatistics to studies with data that exhibit autocorrelation and to studies dealing explicitly with spatial or temporal patterning may substantially aid their interpretation.

FORTRAN Algorithms

The analyses described above were performed using a set of algorithms written for interactive use on microcomputers. The algorithms are written in Microsoft FORTRAN, a subset of the ANSI-77 FORTRAN Standard designed to operate on MS-DOS microcomputers but compatible with most mainframe compilers. Source code listings ($\approx$6000 lines) are available in printed form[3] or on diskette from the W. K. Kellogg Biological Station Computer Lab.[4] Documentation files that accompany the programs provide instructions for their use; users should refer to Vieira et al. (1983), Trangmar et al. (1985), and Webster (1985) for discussions of how to interpret algorithm results.

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[3] See ESA Supplementary Publication Service Document No. 8733 for 90 pages of supplementary material. For a copy of this document, contact the author or order from The Ecological Society of America, 328 E. State, Ithaca, New York 14850-4318 USA.

[4] Source code and documentation on two 5.25-inch, IBM-compatible diskettes are available from the Computer Laboratory, W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060 USA. Please include a $12.00 handling fee payable to Michigan State University.

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