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8

Assessing the Heterogeneity of Belowground Resources: Quantifying Pattern and Scale

G. Philip Robertson and Katherine L. Gross

I. Introduction

That belowground resources in terrestrial plant communities are heterogeneously distributed is very nearly an ecological truism. Whether imposed by geomorphological features of the landscape such as the glacial redistribution of soil parent material (e.g., Walker and Ruhe, 1968), by patchy plant distributions across an otherwise uniform geomorphology such as early sand dune succession (e.g., Olson, 1958), or by microtopographic variation within old fields (e.g., Reader and Best, 1989), water and nutrients are rarely homogeneously distributed in soils. Nevertheless while spatial heterogeneity is well recognized, the scale or extent to which it occurs, and how this might differ among communities, is very poorly understood. Although spatial variation of belowground resource distributions has been the explicit subject of a number of studies in recent decades (e.g., Downes and Beckwith, 1957; Snaydon, 1962; Pigott and Taylor, 1964; Zedler and Zedler, 1969; Allen and MacMahon, 1985; Folorunso and Rolston, 1985; Robertson *et al.*, 1988), our understanding of the scale of variability of belowground resources is in most cases at a qualitative level that does not lend itself well to generalizations about patterns nor—more importantly—to generalizations about controls on or consequences of these patterns.

To at least some degree this lack of understanding is due to a lack of appropriate quantitative tools for detecting and accurately describing spatial patterning. Although variability in resource levels across a site can be assessed by replicated sampling, whether the variability observed

can be interpreted as spatially structured heterogeneity depends on the distribution of the variability. In general, assessments of spatial heterogeneity in resources implicitly address three questions related to variability: (1) How variable is the resource in question; that is, is the range of variability likely to be biologically significant? (2) What proportion of the total variation observed can be accounted for by spatial factors; that is, how predictable is the pattern in space? (3) At what scale or scales is the patterning, if present, expressed?

Answers to the first question—the general degree of sample variability— can be addressed well by standard parametric statistics. Answers to the latter questions, however, presuppose that we can detect spatial patterning of a resource and identify the scales at which it is expressed. From at least a quantitative standpoint this is rarely a straightforward exercise, because parametric statistics are poorly suited for analyses of autocorrelated data and because the sampling effort required to quantify the spatial scale of the variation can be daunting.

At a qualitative level the detection of pattern and scale in soil resources can be relatively easy, especially at large, highly aggregated scales such as the regional or continental (Figure 1). Variation in soil characteristics and fertility at large scales is in general coincident with patterns of climate and vegetation. At smaller scales, however—where variation is likely to affect the local distribution and abundance of plant species and the performance of individual organisms—pattern detection and its implications can be more difficult to address. First, measurements of soil resources at these scales (Figure 2) tend to be more analytically demanding than at larger scales where one can rely on surrogate measures such as slope and soil texture (e.g., Burke, 1989; Schimel *et al.*, 1985). Second, soil resource patterning within communities may be subtle and also temporally variable, with small differences at the scale of individuals having important ecophysiological effects that can be amplified to the community and ecosystem levels (e.g., Snaydon, 1962; Woldendorp, 1983; Jackson and Caldwell, 1989; Tilman and Wedin, 1990).

To rigorously address questions linking variation in plant population and community patterns to soil resource heterogeneity, we need statistically robust, spatially explicit quantitative tools that will allow us (1) to detect and test hypotheses about environmental controls on the patterning and scale of soil resource distributions and (2) to design field sampling programs that capture appropriate levels of variation with a reasonable degree of sampling effort. The development of such methods are important for addressing a broad range of questions in ecology, both from the standpoint of experimental design and rigor—for example, how do we avoid bias due to spatial autocorrelation in field experiments—and from the standpoint of developing a mechanistic under-

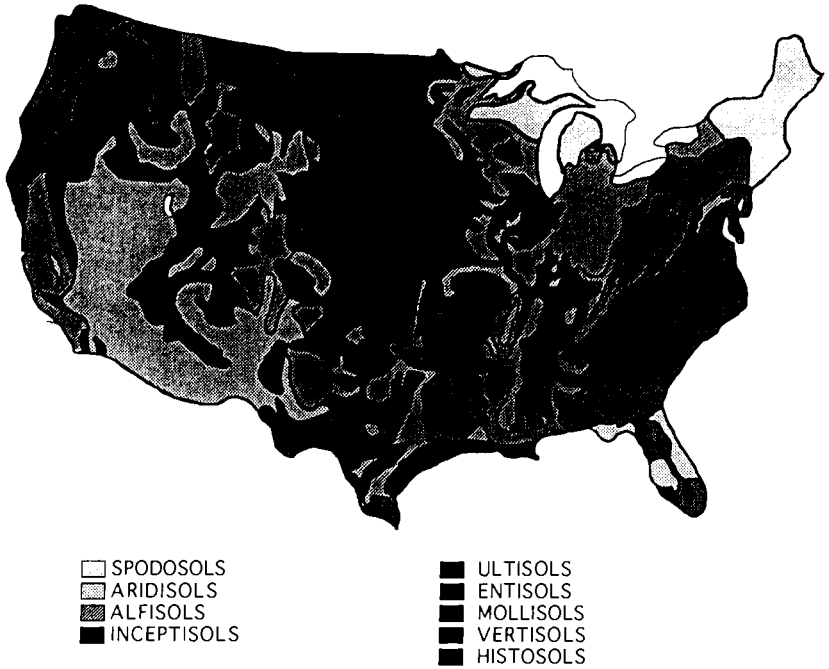


Figure 1 Patterns of soil orders and suborders of the United States. Redrawn from a map provided by the Soil Survey Division, U.S. Soil Conservation Service.

standing of the causes and consequences of these patterns across different levels of ecological organization. In particular, attempts to understand the consequences of global environmental change require that we examine the appropriate levels of aggregation for describing ecological phenomena at regional and global scales.

In this chapter we describe the potential applications of geostatistics for detecting and quantifying spatial heterogeneity in ecological communities, and illustrate how geostatistics might be used to provide ecologically useful information about potential controls on soil processes and their concomitant effects on plant species distributions. Geostatistics is a powerful and readily interpretable technique for quantifying autocorrelation within a spatial domain and for then using this information to identify scales and patterns of spatial heterogeneity. Only recently have these methods been used to quantify soil resources (e.g., Webster, 1985; Trangmar *et al.*, 1985; Webster and Oliver, 1990) or biological processes in the context of plant community patterns (Robertson, 1987; Robertson *et al.*, 1988; Jackson and Caldwell, 1993). Rossi *et al.* (1992) reviewed the

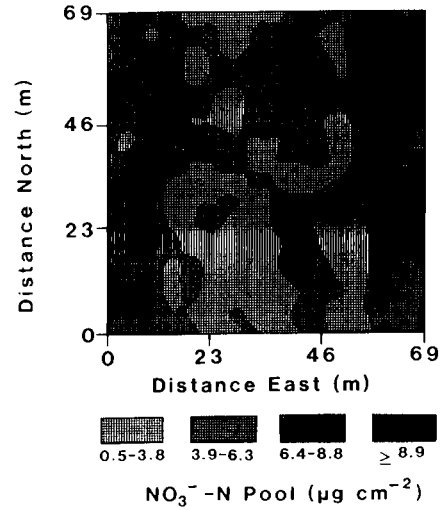


Figure 2 Nitrate nitrogen concentrations in the top 20 cm of soil from a Michigan old field. Values were interpolated by kriging at 1-m intervals across after first establishing spatial dependence (see discussion of kriging in text) to locations. (From Robertson *et al.*, 1988.)

development of geostatistics and potential applications and pitfalls in ecology in general; our goal here is to evaluate the advantages and constraints of using geostatistical approaches to quantify spatial heterogeneity in soil resources and to relate this to ecological patterns at various scales.

II. Detecting Spatial Dependence: Autocorrelation Analysis

Environmental gradients are a basic feature of ecological communities. Few biologically significant resources are either homogeneously or randomly distributed at scales that affect individual organisms. Gases such as CO_2 and O_2, for example, may be more or less uniformly distributed in the earth's boundary layer, but gradients across a leaf surface or through a soil aggregate can profoundly affect rates of biological activity for individual organisms. Likewise, precipitation over a given time interval may be randomly distributed across a semiarid landscape, but localized soil properties and differential uptake rates within communities will quickly result in moisture gradients at scales relevant to individual plants. Detecting such gradients, and in particular detecting over what scales they occur, is a question best addressed by autocorrelation analysis.

Spatial autocorrelation is based on the simple premise that near neighbors are more likely to experience similar environments than are far neighbors; for example, that soil nitrogen levels at a given location are better predicted by nitrogen levels at locations 1 m distant than by levels at locations 100 m distant. Whether this is in fact the case—or whether nitrogen levels are independent of sample location at even 1-m distances—can be determined only by examining changes in the degree of autocorrelation for a property over a range of distance intervals.

There are a number of statistical methods available for detecting autocorrelation in environmental data; these include conventional autocorrelogram approaches (e.g., Webster and Cuanalo, 1975), Moran's I autocorrelation analysis (e.g., Sokal and Oden, 1978; Slatkin and Arter, 1991; Heywood, 1991), Mantell's test (e.g., Heywood, 1991), fractal analysis (e.g., Tyler and Wheatcraft, 1990a,b), spectral analysis (e.g., McBratney and Webster, 1981), and semivariance analysis (e.g., Burgess and Webster, 1980). Of these techniques, semivariance analysis has seen the most application in the study of belowground resources, probably in part because of its robust simplicity, but also because of its now widespread use and rapid development in the geological sciences.

A. Semivariance Analysis

Semivariance analysis provides a versatile and unbiased means for examining autocorrelation in environmental data. Semivariance is evaluated by the statistic

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

where $\gamma(h)$ is the semivariance for all locations in a spatial domain separated by the distance interval h, $z(x_i)$ represents the value of the property at location x_i, and $z(x_{i+h})$ the value at distance interval h from x_i; N is the total number of pairs in the domain that are separated by distance h. In practice, h is defined as a distance class interval, representing all sample locations within a domain that are separated by a specific class of distances such as 0–5 m or 25–30 m.

The primary advantage of the semivariance statistic over other measures of autocorrelation (e.g., Moran's I) is that semivariance does not require second-order stationarity. Regionalized variable theory (Matheron, 1971), from which the semivariance statistic is derived, allows the assumption that variance and covariance are homogeneously distributed throughout the sample region—an assumption central to parametric statistics—to be relaxed; semivariance analysis requires only that covariance among samples be finite and independent of position within

the region (Webster, 1985). This allows the unbiased evaluation of autocorrelation where variance and covariance are heterogeneously distributed throughout a domain—the usual case for environmental variates such as soil properties. Semivariance is, however, sensitive to skewed distributions and clustering (see Krige, 1981; Rossi *et al.*, 1992); often environmental data must be transformed to approach normality before geostatistical analysis.

A secondary advantage of semivariance is its direct use in kriging, a means for optimally interpolating values for locations not sampled across a site. As discussed in the following, semivariance (as a measure of spatial dependence) is used to weight sample points when deriving kriged interpolation estimates.

1. The Semivariogram Calculating semivariance for all possible distance intervals or classes within a domain yields the semivariogram or variogram (Figure 3), a graphical representation of the degree of spatial dependence within a region. Semivariograms are derived by fitting models to the semivariances calculated for the various distance classes (h) in the domain. By modeling semivariance one may estimate autocorrelation

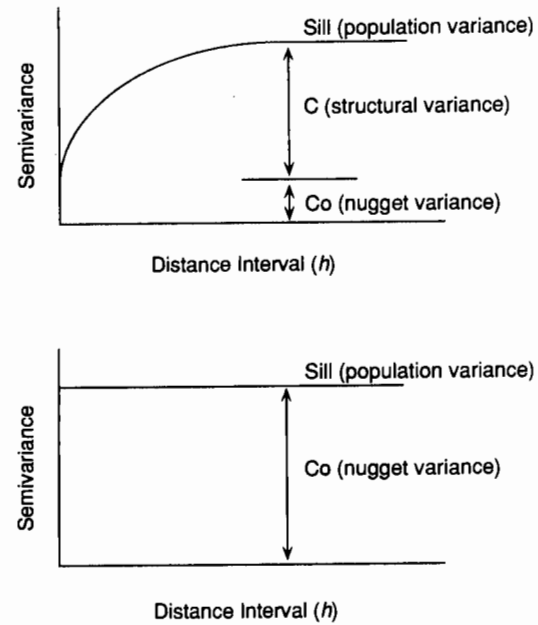


Figure 3 Generalized semivariograms. In the top figure structural or spatially dependent variance makes up a large proportion of total population variance. In the bottom figure there is no spatial dependence at the scales examined.

for all possible distance intervals in a region in spite of the fact that relatively few distance intervals may be available for calculating semivariance.

Where spatial dependence is present (Figure 3, top), γ typically rises to some asymptote (often termed "sill"), which should be roughly equivalent to the population variance. At least theoretically, semivariance should approach zero at a distance interval close to zero—any given sample location should be perfectly autocorrelated with itself—but in practice this is rare. The difference, estimated as the y intercept of the semivariogram (termed "nugget" variance by early geostatisticians because occasional gold nuggests were encountered away from seams), represents either random sampling/analytical error or spatial dependence at distance intervals less than the minimum interval sampled. The proportion of the total variance accounted for by structural or spatially dependent variance ($C/[C + C_0]$; see Figure 3) is a useful index of the spatially dependent predictability of the resource.

From an ecological perspective, then, a semivariogram documents whether there is a spatial component to the variability (is there patchiness) and the robustness of the pattern (how distinct the patches are). In addition, the semivariogram also reveals the spatial scale over which autocorrelation occurs (patch size). These properties can be quantified and compared among sites or experimental treatments by statistically parameterizing semivariogram models. Though variability may be characteristic of all environments, knowing the degree of spatial dependence and its extent is critical for evaluating its ecological significance. For some soil resources, for example, for soil respiration within a 0.5-ha Michigan old field (Figure 4, bottom) (Robertson *et al.*, 1988), there may be no detectable spatial component to the variance at the scales examined—in this case 1 m to 50 m. This suggests that at the time this field was sampled, controls on soil CO_2 fluxes were either randomly distributed (spatially independent) or influenced by ecological processes operating at smaller scales than those examined (in this case 1 m), for instance, at scales of individual plants or even rhizospheres. In most cases reported to date for soil resources, however, structural or spatially dependent variance represents a major proportion of the total population variance. For example, in this same old field over 70% of the variation in nitrogen availability (as indexed by nitrogen mineralization potentials, Figure 4, top) was spatially autocorrelated (Robertson *et al.*, 1988).

Where autocorrelation is present, the semivariogram (and semivariance statistics) will define the range or distance over which spatial dependence is expressed. More specifically, the distance at which the semivariogram reaches an asymptote—approximately equivalent to population variance—is the distance over which geographic points in the community

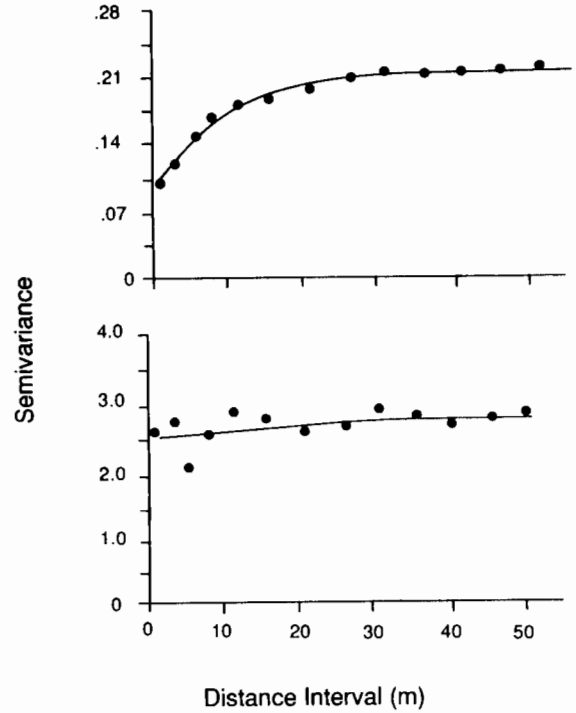


Figure 4 Semivariogram for soil N mineralization potentials (top) and soil respiration (bottom) in the top 20 cm of soil from a Michigan old field community; n = 300 sample locations. (From Robertson *et al.*, 1988.)

are (on average) spatially related. Beyond this range, points are spatially independent of one another. Knowledge of the range for a particular soil resource, and how (or if) it differs among communities, may be equally or more important than the mean level of the resource for understanding the effects on plant population and community patterns. For example, in the old field studied in Michigan, nitrogen mineralization is spatially correlated at points in the field less than ca. 25 m distant of one another (see Figure 4). Moreover, because the slope of the semivariogram is greater at smaller distances, points within 10 m of one another are far more similar to one another than are points within a 10 to 25-m radius.

That semivariance analysis can both quantify the degree of spatial dependence for a resource in a community and explicitly define the scale over which dependence is expressed, makes the analysis especially valuable for inferences about controls on community resources and possible effects on associated plants. The analysis described earlier, for exam-

ple, suggested that controls on soil respiration in early successional old fields may be expressed at spatial scales of <1 m. In a nearby cultivated maize (*Zea mays*) community, spatially dependent respiration was restricted to scales of <0.15 m (Figure 5) (Merrill *et al.*, 1993). This implies that CO_2 fluxes in these communities—and the biological activity associated with these fluxes—may be controlled by factors that operate at the rhizosphere or soil aggregate scale. In other, perhaps even most communities, one might expect spatial patterning for CO_2 fluxes and other soil properties to exist—and be discretely expressed—at rhizosphere, individual plant, microtopographic, and larger scales simultaneously.

2. Nested Structure Multiple-scaling of variability is likely to be a common feature of ecological phenomena because processes that affect patterns operate at different scales (e.g., Burrough, 1981; Wiens, 1989; Milne, 1991; Palmer, 1992). Such multiple scaling can be most clearly inferred from a nested semivariogram model. For example, soil pH across a 43-ha soybean (*Glycine max*) community (Figure 6) (Robertson *et al.*, 1992) appears to be spatially dependent at two scales, suggesting that multiple factors may be influencing the level and distribution of pH at this site. The steep rise in semivariance between 1 and 5 m suggests that local, perhaps microtopographic or plant-based factors influence pH at scales of 5 m or less. A second sharp increase in semivariance at

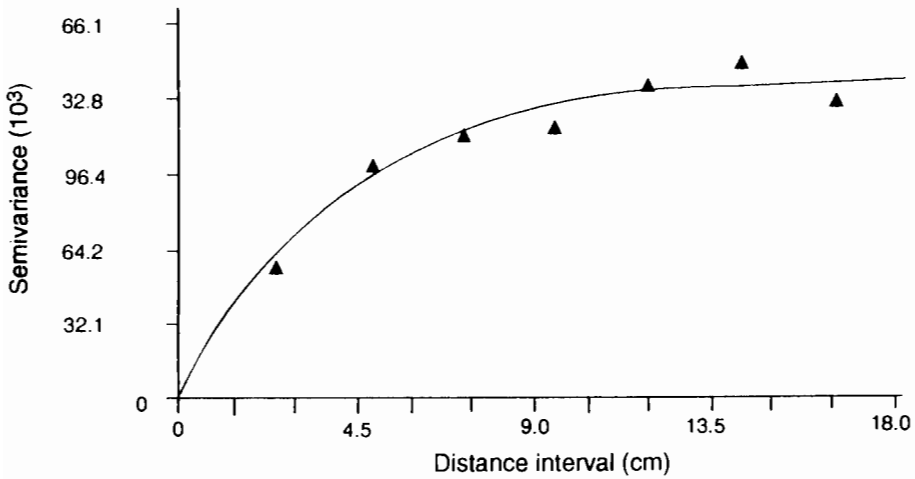


Figure 5 Semivariogram for soil respiration along a 1-m transect in an early-season corn (*Zea mays*) field; n = 40 2.5-cm-diameter soil cores taken immediately adjacent to one another. (From Merrill *et al.*, 1992.)

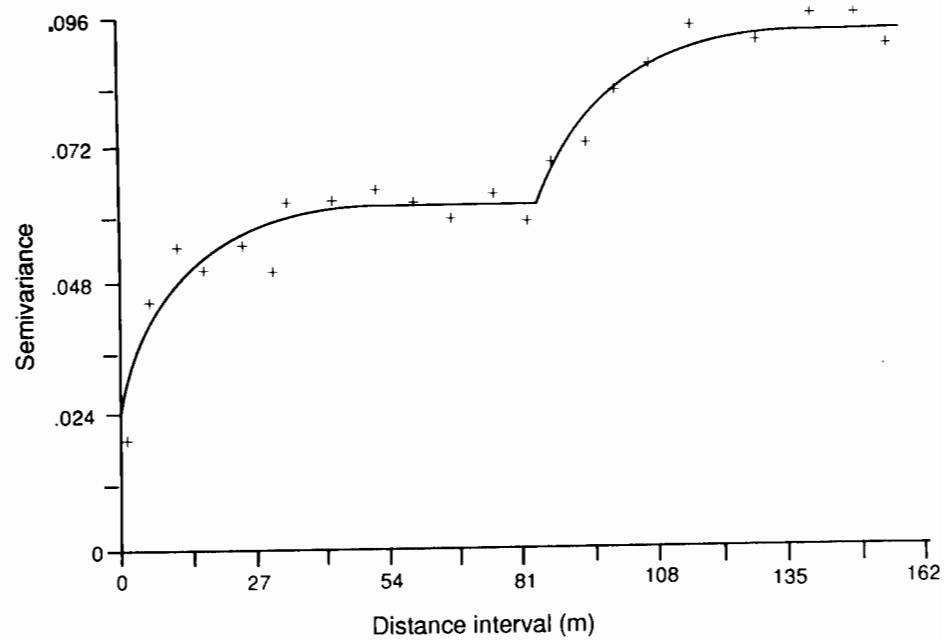


Figure 6 Semivariogram for soil pH from a 42-ha Michigan agricultural field; n = 620 soil cores. Note the nested semivariogram structure with spatial dependence between 0–5 m and again at 80–120 m. (From Robertson *et al.*, 1993.)

ca. 90 m suggests that a different, probably cultural, control is exerted at the larger field scale. One might expect additional jumps in semivariance at still larger scales as geomorphologic and climatic influences come to bear.

Although sampling limitations will in most cases restrict our direct knowledge of nested variation, at least in concept such an approach should be capable of sorting variation into numerous components ranging from the rhizoplane ($<10^{-4}$ m) to the landscape (10^4 m). The nested nature of such a semivariogram (Figure 7) would suggest different controls at different scales for the resource at question. There is some evidence for nested patterns of spatial dependence in terrestrial vegetation, particularly in highly dissected and/or human-altered landscapes (e.g., Sugihara and May, 1990; Milne, 1991; Palmer, 1992). Being able to detect such patterns could be especially valuable for defining appropriate levels of aggregation for estimates of regional- and global-scale soil processes such as CO_2 or other trace gas fluxes (Robertson, 1993).

3. Anisotropy For many soil properties spatial dependence may be strongly directional, that is, spatial dependence in one compass direction

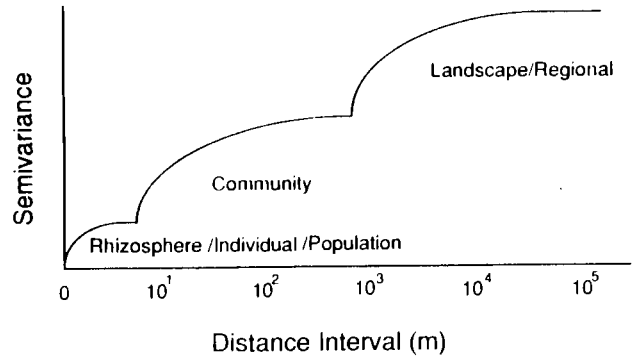


Figure 7 Generalized semivariogram denoting spatial-dependent variation at different (nested) scales ranging from the rhizoplane to the global.

may differ from dependence in another. This can be readily imagined by considering a mountainside plant community in which soil resources (e.g., soil nitrogen pools) might change much more rapidly in an upslope—downslope direction than in a cross-slope direction. One might then expect the semivariogram for the upslope–downslope direction to have a much steeper rise to an asymptote—a much smaller range—than that for the cross-slope direction. Such geometric anisotropy (cf. zonal anisotropy, David, 1977) might also be expressed for other ecological phenomena under less obvious conditions. For example, seed dispersal patterns and consequently seed bank densities may be affected by predominant wind direction, historical cultivation patterns, or topography. Similarly, organic matter distributions and subsurface/lateral water flow that might affect soil moisture can be strongly affected by topographic and subsurface geomorphologic patterns.

Anisotropy can be evaluated by comparing semivariograms calculated for sample points aligned in different individual directions—often 0°, 45°, 90°, and 135° from a central axis. Where present, anisotropy can provide important clues for understanding patterns and underlying controls on belowground resources.

4. Semivariance and Fractal Analysis Fractal analysis provides another means for examining scale-dependent variation, and several recent studies have used fractals to analyze patch characteristics in vegetation at the landscape level (e.g., Burrough, 1981; Naven and Lieberman, 1984; Milne, 1991; Palmer, 1992). In its simplest form, a fractal is an index of self-similarity; that is, an analysis of the degree to which complexity at one scale is repeated at others. In effect, then, the Hausdorff–Besicovich or fractal dimension D is a measure of spatial dependence and in this

sense very similar to the semivariance statistic. In fact, Burrough (1981) points out that semivariance can effectively estimate D such that

$$D = 2 - (m/2),$$

where m = the slope of a log-log semivariogram.

The fractal dimension thus can provide a single-value summary of spatial complexity across a region, and in this respect it can be quite useful. But such a summary may be of limited use for evaluating the spatial complexity of community-level resources—information such as the range of spatial dependence and information about nested variation (Figure 6) can be lost or obscured by expressing complexity as a single value. Analyses of how the fractal dimension shifts at larger scales can indicate whether pattern is being influenced by factors that operate at different scales (Sugihara and May, 1990; Palmer, 1992), but often the spatial scales at which a landscape is homogeneous can be better determined by semivariance analysis. Burrough (1981) suggests avoiding fractal models altogether where controls on environmental properties are complex and may differ at different scales. This is likely to be the case for small-scale variation in soil resources, influenced by a mixture of biological, chemical, and physical features of the environment.

III. Characterizing Pattern: Kriging

Of methods currently available for characterizing pattern, that is, for generating isopleths (maps) of resource levels across spatial domains such as plant communities, none matches kriging for providing optimal, unbiased estimates of locations not sampled. Traditional approaches to such interpolation have included simple linear techniques as well as approaches that weight nearby neighbors using moving averages, localized regression surfaces, cubic splines, and inverse square distributed weights (Webster and Oliver, 1990). Kriging is similar to these in that it is a local averaging technique, but different in that it provides optimal unbiased estimates for interpolated points by calculating and minimizing the estimation error associated with these points. Estimation error is calculated using knowledge about spatial relatedness in the region to weight the neighbors used for the estimate; the semivariogram provides this knowledge. That kriging produces an estimation error term (e.g., standard error) for every interpolated point is in itself a strong advantage of the technique for attempts to understand *in situ* patterning—no other interpolation techniques provide explicit measures of statistical confidence.

The kriging interpolation estimate is defined as

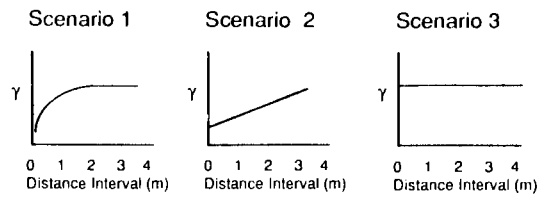
$$z(B) = \sum_{i=1}^{n} \lambda_i z(x_i),$$

where $z(B)$ is the estimated value for the resource over a local area or block B, $z(x_i)$ is the measured sample value at point x_i, n is the number of samples within the defined estimation neighborhood, and λ_i is the weight associated with sample value $z(x_i)$. This weight is based on (1) the distance of B from x_i and (2) the degree to which samples separated by distance $B - x_i$ are spatially dependent (as estimated by the semivariogram). To avoid bias, all weights associated with an estimate sum to 1.0.

A highly simplified, hypothetical example illustrates this weighting in Figure 8. Here four sample points (x_1 . . . x_4) fall within the 4-m-radius estimation neighborhood for interpolation point B. The kriging weights associated with each point are largely determined by the shape of the semivariogram. In scenario 1, points beyond the semivariogram's range of 2.0 m are given weights close to 0 while the closer, more related points x_1 and x_2 are assigned weights of .8 and .2, respectively; x_1's weight is higher because of the relative steepness of the semivariogram curve at 0.5 m distance.

In the second scenario the semivariogram describes a linear model. All sampled points in the neighborhood are used in this estimation, with weights assigned based primarily on proximity.

In the third scenario, no spatial dependence was established over the range of distances sampled (the semivariogram exhibits a "pure nugget" effect) and all neighbors are assigned equal weights. Note that in this scenario the estimation error term for interpolated values will be substantially higher than it would be had the semivariogram exhibited spatial dependence.



Actual Sample	Distance from z_{est} (m)	λ_i	λ_i	λ_i
x_1	1.0	.6	.4	.25
x_2	1.5	.4	.3	.25
x_3	3.0	0	.2	.25
x_4	4.0	0	.1	.25

Figure 8 Hypothetical kriging weights for a single interpolate location with four sample points in its 5-m interpolation neighborhood. Scenarios illustrate different weights as a function of different semivariograms (different levels of spatial dependence).

The procedure for assigning weights to sampled neighbors is not, of course, as simple as these scenarios suggest. In actual practice weights are chosen to minimize estimation variance.

$$\sigma^2(B) = 2\sum_{i=1}^{n}\lambda_i \gamma(x_i,B) - \sum_{i=1}^{n}\sum_{j=1}^{n}\lambda_i\lambda_j \gamma(x_i,x_j) - \gamma(B,B),$$

where $\gamma(x_i,B)$ is the average semivariance between the estimation block B and sample point x_i, $\gamma(x_i,x_j)$ is the semivariance between sample points i and j, and $\gamma(B,B)$ is the average semivariance within the estimation block (for point or punctual kriging this term becomes 0 since $\gamma(X_0,X_0) = 0$). A series of linear equations is used to minimize variance using all sampled points in the interpolation neighborhood; the method is thus computationally intensive because a new set of linear equations must be solved for every interpolated point.

For mapping soil resources, block kriging will usually be more appropriate than punctual kriging. Block kriging provides an average estimate for an area around the interpolation point; punctual kriging provides an estimate for the individual point. As one might expect, the estimation error for punctual-kriged interpolates is usually much higher than that for block kriged, reflecting a greater uncertainty for estimating a value for a single point location as opposed to an average value for a small area around a point. Because of this averaging, block kriging tends to be less sensitive to analytical error than punctual kriging. Punctual kriging is a perfect interpolator such that estimated values for locations that coincide with measured value locations will evaluate to the measured values. This means that outliers will map as outliers, whereas with block kriging outliers will be somewhat smoothed. Nevertheless, even for block kriging it is important to minimize analytical error as much as possible, especially if that error is somehow distance-dependent (e.g., sample carryover during soil sampling). One must thus be careful to replicate appropriately at both the sampling and analytical levels, even though replicate values will not themselves be used directly for kriging.

It is also worth noting that kriging estimation variance is independent of measured values, depending instead only on (1) the distance between interpolation point B and sample point x_i and (2) the shape of the semivariogram. This means that once one has sampled sufficiently to define the semivariogram for a particular community property or resource, this information can be used to design an optimal sampling strategy, that is, a sampling strategy that will provide interpolated values with an acceptable and already-known degree of statistical confidence (e.g., Burgess and Webster, 1981).

The further application of kriging to ecological data should allow us to better and more quantitatively evaluate patterning in ecological communities. The technique is especially well suited to those properties of communities that exhibit high levels of spatial dependence at community-level and smaller scales. This probably includes most if not all belowground resources important to plants.

IV. Conclusions

Belowground resources are distributed heterogeneously but not, in general, at random: recent analyses of the spatial structure of the variability of these resources have shown that many soil properties are significantly autocorrelated at scales that are likely to be significant to individual plants. Moreover, available evidence, though scanty, suggests that autocorrelation in natural communities is scale-dependent, that is, not continuous from the rhizosphere (less than cm) through the landscape (km) levels.

Geostatistics offer a powerful and promising technique for analyzing spatial variability. Semivariance analysis provides a robust means for quantifying autocorrelation or dependence across a spatial (or temporal) domain, and kriging provides an optimal, unbiased means for interpolating with statistical confidence. Interpolations are useful for qualitative visual descriptions of spatial variation, for relating resource levels to the performance of individuals or distribution of species within a community, or for comparing patterns and scales of resource heterogeneity in different communities. Fractals provide an alternate means for summarizing autocorrelation that may be useful for understanding patterns of scaling across landscapes in some circumstances.

Further applications of geostatistical techniques should provide substantial power for determining scales at which controls over specific resources are expressed. Applications should also allow us to identify appropriate levels of aggregation for regional and global models of ecological phenomena.

Acknowledgments

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