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A comparison of quantitative methods for examining landscape pattern and scale

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Abstract

Ecologists have long recognized the importance of spatial and temporal patterns that characterize heterogeneity in landscapes. However, despite the realization that inferences about ecological phenomena are scale dependent, little attention has been paid to determining appropriate scales of measurement (e.g., plot or grain size) in studies of landscape dynamics or ecosystem change. This paper compares the results from three data sets using several quantitative methods available for characterizing landscape heterogeneity and/or for determining scale of measurement. Methods evaluated include tests of non-randomness, estimation of patch size, spectral analysis, fractals, variance ratio analysis, and correlation analysis. The results showed that no one method provides consistently good estimates of scale. Thus, sampling strategies for landscape studies should be derived from estimates of patch size and/or scale of pattern obtained from more than one of these methods.

Introduction

Combining' information from multiple scales of measurement is an essential part of global change and landscape dynamics research. Models and measurements of large-scale phenomena such as the effects of acid precipitation, global carbon and nitrogen cycles, increased desertification, and climate change are scale dependent. In the development of global ecological theory, for example, Gosz (1986) suggests that even our interpretation of the role of consumers in influencing spatial/ternporal variation in the environment depends upon the scale of the data considered. Addicott *et al.* (1987) have further shown that conclusions appropriate to one scale of environmental heterogeneity may be inappropriate when transferred to another scale. Consequently, the level of resolution and, thus, the heterogeneity at all relevant scales must be considered when defining the research goals and sampling design for studies conducted across spatial/temporal scales.

Ecologists have long recognized the importance of spatial and temporal patterns of heterogeneity in landscapes. Such patterns are known or hypothesized to affect many ecological phenomena, including population dynamics, life histories, dispersal patterns, species diversity, predation, and patterns of natural selection (Addicott *et al.* 1987). The influence of spatial/temporal landscape patterns on

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organisms has provided the stimulus for a relatively new area of ecological research called landscape ecology. By definition, landscape ecology involves interpreting a variety of scales to accurately gauge patterns affecting ecological phenomena. Thus, studies in landscape ecology run a larger risk of invalid conclusions than experiments conducted on a single scale that are intended for more limited inferences. A reduction in this risk requires that the resolution needed and methods for assessing pattern be carefully considered.

Risser *et al.* (1984) described four major topics of research in landscape ecology: 1) the development and dynamics of spatial heterogeneity, 2) spatial and temporal interactions and exchanges across heterogeneous landscapes, 3) influences of spatial heterogeneity on biotic and abiotic processes, and 4) management of spatial heterogeneity. All these research topics require knowledge of the appropriate level of resolution before the mechanisms behind the observed spatial heterogeneity can be understood. More directly, these topics require techniques that 1) describe patch size and distribution, 2) quantify spatial variation and correlation, 3) estimate appropriate scales of measure (plot size) to make inference to the landscape on the scale or scales of the ecological phenomena being studied, 4) estimate the lag or distance between sample plots to provide uncorrelated observations, 5) determine a sample size that provides adequate power for testing a prespecified hypothesis, and 6) detect change over time.

O'Neill *et al.* (1986) stress the importance of viewing the world in the space and time scale at which it responds rather than the space and time frame in which humans operate. However, because of the realities of time and money, sampling strategies for ecological studies are often not derived from a preliminary study of the system from which information on the inherent heterogeneity can be obtained. The lack of appreciation for this type of preliminary study indicates that the determination of an apropriate scale on which measurements will be taken has not been adequately or systematically addressed.

Scale is defined here as 1) the extent of coverage and grain (smallest unit of measure) of measurements based on human defined limits, 2) the effective extent (in terms of interaction) of an ecological phenomenon, and 3) a function of covariance between measurements taken further and further apart. These aspects of the definition are not necessarily mutually exclusive. Statistics based on varying window sizes (e.g., block sizes, transect segment lenghts) and lags are considered tools to evaluate scale.

The objectives of this paper are three-fold. We will 1) compare through the illustration of results six quantitative methods available to landscape ecologists for assessing ecological pattern and scale (tests of non-randomness, estimation of patch size, spectral analysis, fractals, variance ratio analysis, and correlation analysis), 2) determine which methods can be used to address the research topics listed by Risser *et al.* (1984), and 3) suggest quantitative problems still needing resolution.

The Data Sets

Three data sets will be analyzed to facilitate comparisons between methods. Comparison criteria is based on detecting patterns when present and negating patterns when data are spatially independent. All three data sets are one-dimensional even though many of the techniques can be used on higher dimensional data. Analysis of a method's strengths and weaknesses on a single dimension should provide insight to a method's capability with higher dimensional data.

Two data sets are generated from a Poisson distribution simulating a 2000-m transect of percent cover of one species. The third data set is a 2050-m line-intercept transect of the percent of the transect covered by bluebunch wheatgrass (*Agropyron spicatum*) from Carlile *et al.* (1989) (Figure 1). For both Poisson-generated data sets, percent cover was calculated from independent identically distributed Poisson ($\mu = 30$) random observations (x) where x was not modified, and thus spatially independent, or modified to produce spatial dependence. The unmodified Poisson-generated data set has a constant mean and variance of 30 (Figure 1A) and should have no detected scales. The modified

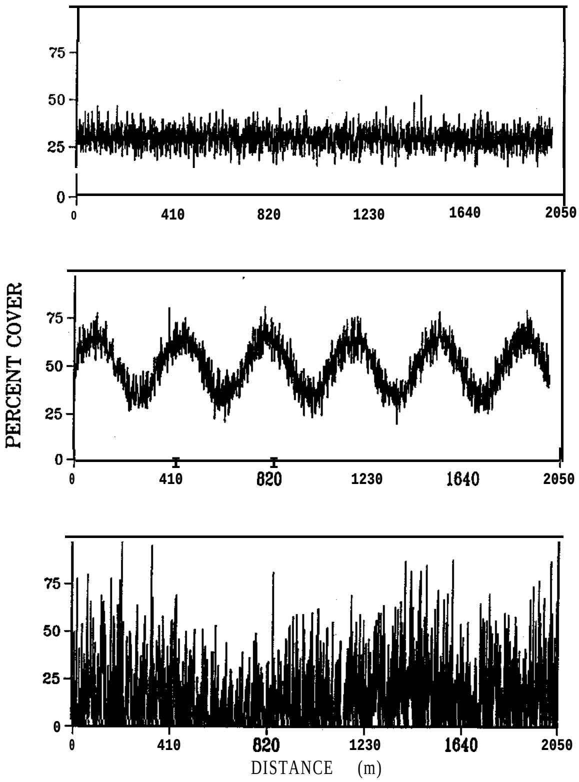

Figure 1. Individual Intersection Lengths of an Independent Poisson Random Variable (A), a Modified Poisson Random Variable (B), and Bluebunch Wheatgrass (*Agripyron spicatum*) (C) Converted into Percent Cover For Each l-m Unit Along a 2050-m Transect.

Poisson-generated data set has observations (y) that have been modified into a sine wave,

$y = [x + 20 + 15*\sin(\theta)]$ for θ (radians) = 0, 5, 10, 15,. . .

with θ changing every 5 m. This produced a sine wave with periodicity of 360 meters and with constant variance of 30 about the wave (Figure 1B). The *A. spicatum* data are the percent cover at l-m intervals and were derived from the length of intersection of every plant along the transect (Figure 1C).

For our purposes, we will define patch size as a window size (> 1 grain unit) that on average contains elements that are more homogeneous than elements in neighboring window sizes. The grain of all three data sets is 1 m, and for the modified Poisson generated data, a patch size should be detected at 90, 180, and higher harmonics. Pattern will be defined as a repetition of elements (> 1 grain unit) consistent over space or time. Thus, the scale of pattern is a window size which on average encompasses more of a pattern than observed in neighboring window sizes. The scales of pattern for the modified Poisson generated data is 360 m. Based on our definition of scale, a periodic effect has a scale but is not in and of itself a scale.

Analysis

Tests of Non-Randomness

A major area of investigation for landscape ecologists is identifying the cause of vegetative distribution across a landscape. Despite the lack of evidence for naturally occurring random distributions, the hypothesis persists that, as area (*i.e.* plot size) decreases, underlying factors that constrain or aid plant dispersal and growth become more similar and approach a constant. Thus, chance governs which individual succeeds at any point, and the resulting individual plant distribution is random (Greig-Smith 1983). Departures from randomness imply that an individual's success is affected by the location of existing vegetation, and/or that minute deviations from a constant in one or more underlying factors determines vegetative distributions.

Many tests for departures from randomness are available in the literature (see Greig-Smith 1983), Chapter 3). However, because plant distribution is likely to be non-random (as suggested above), the detection of non-randomness is almost always ensured. At best, one could hope to show at which plot size randomness is detected and hence define a scale smaller than any causal factor that produces the non-random patterns obtained at larger scales. As Greig-Smith (1983) reported, all methods for detecting non-randomness depend on the size and shape of the study areas used. Hill (1973) argued that failure to detect non-randomness is evidence of strongly homeostatic conditions, and thus (in this case), only effects that are density dependent affect pattern. Hill further pointed out that non-independence of individuals, as would be displayed by density-dependent effects, negates the hypothesis of randomness as defined by the Poisson distribution.

Table 1. Individual Outcomes for Each Method and Data Set

Method	Data Set		
	Independent Poisson	Modified Poisson	*Agropyron spicatum*
Lefkovitch's Index			
1-m cells	−0.02	0.57	0.93
50-m cells	−0.08	0.99	0.98
100-m cells	-0.19	0.99	0.99
Patch Size Analysis			
Peaks	none	100 m	> 200 m
Hill's Method			
Peaks	none	180, 540, 900 m	10, 750 m
Troughs	none	360, 720 m	> 900 m
Spectral Analysis			
Peaks	none	180 m	250 m
Semi-Variogram			
Sill	none	none	10 m
Fractal Dimension	2	2	1.97
Variance Ratio Plot			
Peaks	400 m	360, 720 m	90 m
Correlation versus Transect Segment Length			
Peaks	none	10, 300, 425, 650, 775 m	85 m
Throughs	none	180, 360, 540, 720, 900 m	> 750 m
Correlation versus Lag			
Crosses Zero	noise	90 m	290, 300 m

Some would argue that detecting non-randomness should be the first step in spatial analysis. However, all further tests of hypotheses must then be based on the conditional outcome of first detecting non-randomness. We suggest choosing techniques directed at specific questions regarding patch distribution or spatial variation that by default can negate randomness. Thus, the justification for the use of tests of non-randomness in landscape ecology appears to be limited.

Lefkovitch's (1966) index,

$$L = \frac{4}{a} \tan^{-1}\left(\frac{\text{variance of abundance}}{\text{mean abundance}}\right) - 1,$$

(using radians) provides a means to determine the degree of randomness, regularity, or contagion from abundance data. The mean value of L for random, regular, and contagious distributions is 0, −1, and l'respectively. Because abundance within a sampling unit, or cell, ignores the size of each individual, we can calculate Lefkovitch's index for data on the percent cover by assuming each individual occupies 1% of each cell. Thus, a cell having 30% cover contains 30 individuals. Using this index with cell sizes of 1, 50, and 100 m, we obtained values of 0.93, 0.98, and 0.99 for the A. *spicatum* data, −0.02, −0.08, and −0.19 for the spatially independent Poisson generated data, and 0.57, 0.99, and 0.99 for the modified Poisson data, respectively (Table 1). Thus, as expected, the A. *spicatum* and the modified Poisson data are indicated as having a contagious distribution and the independent Poisson data are indicated as random. Techniques which allow the separation of uniform (regular), random, and clumped (contagious) distributions for two dimensional data are discussed in Clark an Evans (1954), Eberhardt (1967), and Greig-Smith (1983, p. 65-75). Comparisons between actual two dimensional map data and model derived map data is discussed by Gardner *et al.* (1987). The latter technique has the potential for evaluating landscape change (Turner 1989).

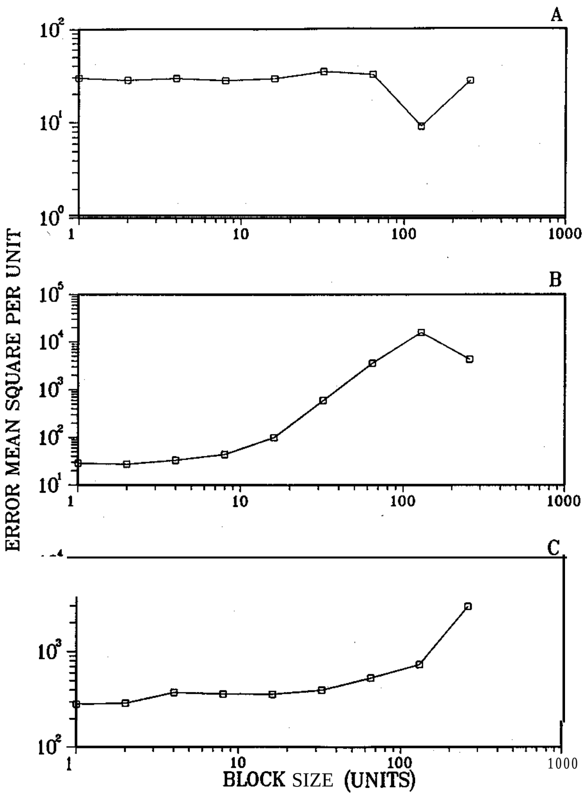

Figure 2. Mean Squared Error of the Independent Poisson (A), Modified Poisson (B), and Bluebunch Wheatgrass (*Agripyron spicatum*) (C) Percent Cover Standardized as 1-m Units Versus the Block Size Using the General Method.

Estimation of Patch Size

Knowledge of the average patch size may make it possible to determine the cause of patches on the landscape and, further, provide information about scales of heterogeneity present (Greig-Smith 1983). Methods for estimating patch size originally defined patches as clumps of vegetation. This definition was later expanded to include areas having a common soil characteristic such as soil pH (Kershaw 1958; Pemadasa *et al.* 1974; Anderson 1965; Morton 1974). A more holistic definition for patch is any place in the environment where the abundance of either resources or organisms is high or low relative to its surroundings (Roughgarden 1977).

The general method for estimating patch size requires a measure of individual plant intersection lengths from a given species along a transect (i.e., the amount of transect covered by each individual plant) (Figure 1) or a count of individuals present within a set of ever increasing contiguous grids (traditionally by powers of 2). One-way analysis of variance among classes defined as blocks of 2, 4, 8, 16, etc., consecutive grid elements (or transect units) is used to estimate the within grid (or unit) variance. For each block size, the within grid variance is made up of the differences between two observations per block composed of the sum of 1, 2, 4, 8, etc., (powers of 2) consecutive grid elements. Plots are made of the within grid variance divided by the number of grid elements per observation (dependent variable) versus the block size (independent variable) (Greig-Smith 1983).

The location and pattern of peaks in the plots of variance versus block size are important. Peak locations estimate the average patch size for each scale of heterogeneity present. Peak patterns can be used to classify, in general, the distribution of individuals within a patch and to classify the distributions of patches into random, uniform, or clumped categories (see Errington 1973; Hill 1973; Usher 1975; Greig-Smith 1983). For independent identically distributed individuals, no peaks should exist in the plot because all block sizes will produce an estimate of the same mean and variance.

As expected, the independent Poisson-generated cover produced noise about the variance of the percent cover (30) (Figure 2A). The dip in the plot at 128 m should be regarded as an indication of the noise possible as the degrees of freedom for the error decrease. The modified Poisson produced a peak at about 100 m (Figure 2B), reflecting the smaller 90-m scale. Analysis of the *A. spicatum* data produced no peaks, but indicated a steady rise in the error mean square, suggesting that a scale of pattern could exist beyond 200 m (Figure 2C and Table 1).

In general, interpretation of these variance versus block size plots can be difficult. As pointed out by Usher (1969) and Errington (1973), shifts in the peaks to the right of the true patch size can be caused by sparse vegetation and to the left of the true patch size by the transect starting position during analysis. Hill (1973) solved the latter prob-

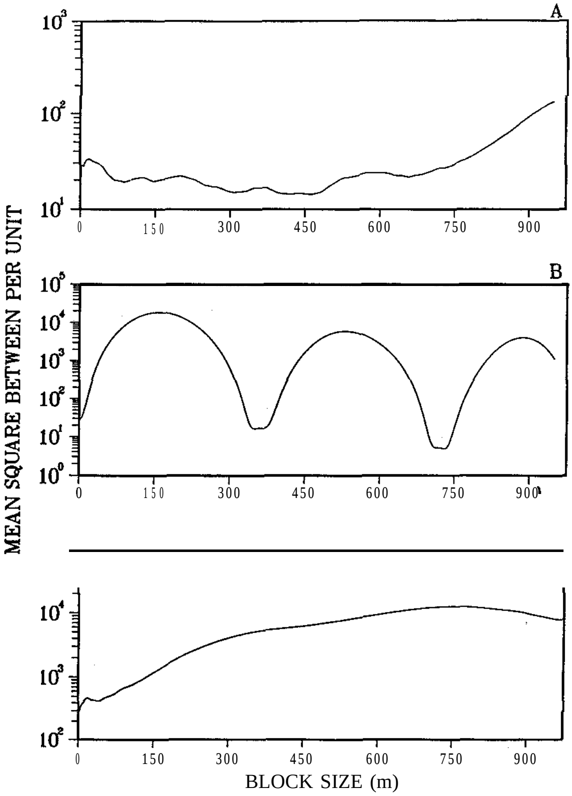

Figure 3. Between Block Mean Square of the Independent Poisson (A), Modified Poisson (B), and Bluebunch Wheatgrass (***Agripyron*** spicatum) (C) Percent Cover Standardized as l-m Units Versus the Block Size Using Hill's Method.

lem by calculating the average mean square derived from all possible starting positions. Although this technique removes the shifts to the left in the resulting plots, it produces plot periodicity (Usher 1975) that sometimes can be mistaken for new scales of heterogeneity.

The location of both the peaks and the troughs in plots using Hill's method provide information. The location of peaks, as in the general method of patch size analysis, are still estimates of the average patch size. The location of troughs, however, estimate the scale of similar pattern. Troughs occur where the differences between blocks are at a minimum compared with the surrounding block sizes. However, if the variance of the cover data increases monotonically with block size, any periodicity in the data is lost, and thus, no troughs will be evident. Thus, the effect of the gradient in the cover variance outweighs periodicity. For data having strong periodicity, the location of peaks is equal to one half of the period (estimated by the distance between troughs), which may or may not be a good estimate of the average patch size.

The independent Poisson-generated data again produced noise about the variance of the percent cover (30) and rose slightly but continuously beyond 750 m as the degrees of freedom diminished (Figure 3A and Table 1). The modified Poisson data produced peaks at 180, 540, and 900 m and troughs at 360 and 720 m (Figure 3B) duplicating the periodicity in the data. For the *A. spicatum* data, the Hill-method confirmed the general analysis and produced no large peaks below 200 m (Figure 3C). A small peak at approximately 10 m and another at 750 m are discernible if one is liberal in the interpretation. The mean square between blocks does not begin decreasing until block sizes are greater than 980 m.

A problem with both the general and Hill's method of estimating patch size is the difficulty in determining when the location of peaks is significantly different, which would suggest that multiple scales of heterogeneity exist. If the estimates of variance for different block sizes are not independent (which is the case in the general method for estimating patch size), standard statistical methods for testing the significance of differences among peak locations are inappropriate. An additional complication in testing for peak location differences arises because the variances for larger block sizes are based on fewer degrees of freedom than those for smaller block sizes (Goodall 1974). Comparisons between multiple transects instead of within a single transect would overcome this objection. Greig-Smith (1983) suggests that interpretation of the significance of peak locations should be made in conjunction with recognition of patterns in the field. If field recognition fails, Greig-Smith continues, other methods of pattern analysis (unspecified) would be required to validate multiple scales of heterogeneity. O'Neill *et al.* (1991) required the detection of each scale of heterogeneity by more than one of the techniques discussed in this paper to accept the existence of multiple scales.

Thus, the block size analysis results in estimates of the average patch size and provides estimates of pattern scale and some indication of multiple scales of heterogeneity. However, arriving at useful conclusions may be difficult because of problems in interpreting the per unit within block variance versus block size plots. Interpretation of multiple scales and patches from mixed distributions becomes difficult at best. We suggest confirmation with multiple techniques as a means of acceptance of patch size and distribution, pattern scale, and multiple scales. Further research efforts in this area could be directed toward estimating the variance associated with the estimate of average patch size and examination of the sensitivity of these methods to landscape changes over time.

Spectral analysis

Spectal analysis (usually concerned with observations at constant time intervals) has also been used to describe pattern (Hill 1973; Usher 1975; Ripley 1978; Fasham 1978). To use this method, plant intersection lengths collected along a transect are expressed as linear equations of sine and cosine functions known as a Fourier transform. Unlike the block size and variance analysis described above, results of this transform are unaffected by the starting position. Smoothed periodograms are generated by plotting the information ($I_j = (c_j^2 + s_j^2)m/8\pi$) as function of the sine and cosine coefficients

$$c_j = \frac{2}{m}\left[\sum_{i=1}^{m} x_i \cos\left(\frac{2\pi ij}{m}\right)\right] \quad \text{and}$$

$$s_j = \frac{2}{m}\left[\sum_{i=1}^{m} x_i \sin\left(\frac{\pi ij}{m}\right)\right]$$

with neighbors averaged against the block size $(m/(2j))$. The value m is the total number of observation units (***i.e.,*** m = 2000 for the Poisson data), and the value j is less than or equal to m/2 – 1. I_j is proportional to the reduction in the sum of squares associated with fitting sine and cosine waves of period m/j. Depending on whether plots are made against the period or block size, the result

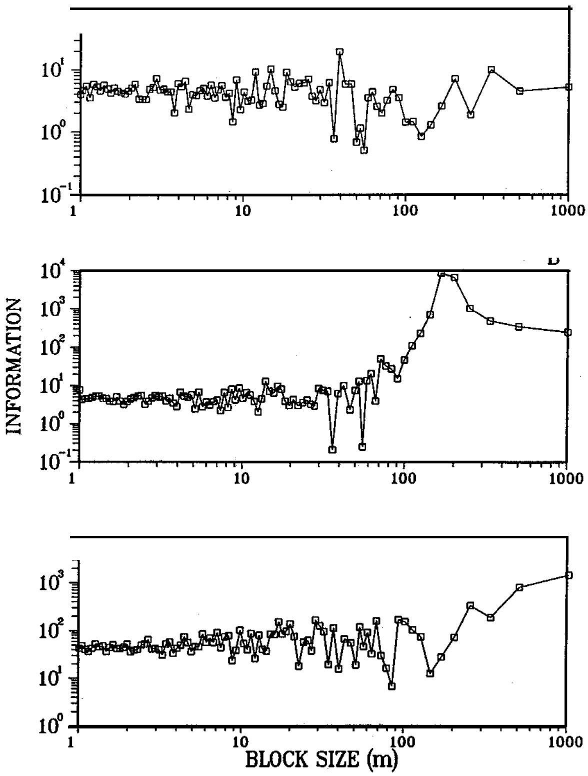

Figure 4. Smoothed Periodgram (Information) of the Independent Poisson (A), Modified Poisson (B), and Bluebunch Wheatgrass (*Agripyron spicatum*) (C) Percent Cover as a Function of Block Size.

is an estimate of scales of pattern (Greig-Smith 1983) or patch size (Ripley 1978) for one or more scales of heterogeneity. The period is defined by the length of the transect required to complete a full cycle of the wave, and the patch size is estimated as one half of the period. If plots are made against the period, the location of the resulting peaks should confirm the troughs in Hill's method, which also indicate the scale of pattern. Alternatively, if plots are made against the block size, the location of the resulting peaks can be multiplied by two to estimate the period.

Plotting against block size, the independent Poisson-generated cover produced noise about the mean information (Figure 4A and Table 1). The modified Poisson produced a large peak at about 180 m, which corresponds to the trough in Hill's plot at 360 m (Figure 4B). The ***A. spicatum*** data

(Figure 4C) has a small peak at 250 m and continues to rise, but this does not correspond with troughs obtained using Hill's method.

This method is sensitive to genuine periodicity, but as with the block size and variance analysis, spectral plots are plagued with spurious peaks that make interpretation difficult. Bartlett (1964) and Greig-Smith (1983) caution against the use of spectral analysis to describe pattern, suggesting that less cumbersome analyses (presumably the analysis of variance method described above) may be more appropriate. Despite this cautionary note, Fasham (1978) argues that spectral analysis coupled with the knowledge of stochastic processes provide the best understanding of plankton patchiness now available. We feel that its use in conjunction with other methods that detect scales of pattern and multiple scales provides some level of assurance that peaks are not spurious. Also, many software packages provide confidence limits about estimates that aid in determining significant signals. Considering the vast amount of literature available on spectral analysis, we suggest that it would be unwise to disregard this method.

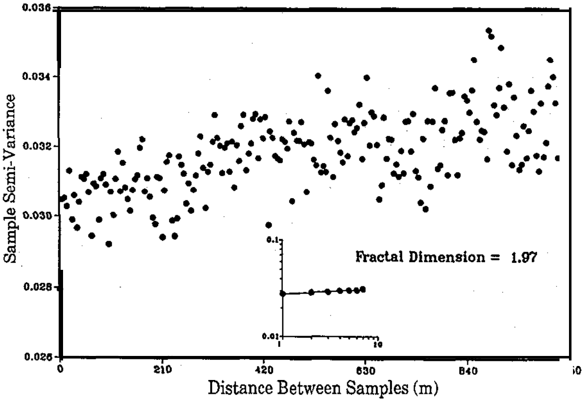

Figure 5. Every 5th Point of the Semi-Variogram of Bluebunch Wheatgrass (*Agripyron spicatum*) Percent Cover. Only the first seven data points are used to calculate the fractal dimension (inset).

Fractals

Fractal geometry brings a new perspective to studying landscape dynamics. Instead of looking at patch size and distribution, fractal geometry provides techniques for quantifying the shape and texture of landscape features (Milne 1990). The term fractal was introduced by Mandelbrot (1983) to denote temporal or spatial phenomena that are continuous but not differentiable and exhibit partial correlations over scale (Burrough 1981). By definition, a fractal has "an incredibly convoluted boundary that when magnified, instead of looking smoother, appears to be equally complicated on every scale" (Peterson 1987). The generalized fractal does not require self-similarity (a constant pattern of irregularity at all scales), but does require increasing variance with decreasing scale (Burrough 1983). Brownian motion was one of the early examples of fractal behavior. The fractal dimension (d) is a real value for linear fractal functions between 1 (completely differentiable; very smooth such as a line or smooth curve) and 2 (so rough and irregular that it effectively covers the whole of a two-dimensional Euclidian space), and for surfaces between 2 (absolutely smooth) and 3 (infinitely convoluted). The value of d is then used quantitatively to describe shape (d between 1 and 2) and texture (d between 2 and 3).

For transect data, the fractal dimension can be estimated from the slope of the observed semi-variogram plotted on logarithmic axes [d = 0.5*(4 slope)] (Burrough 1983; Armstrong 1986). The semi-variogram is a plot of onehalf of the mean squared differences between observations a distance h apart versus the distance h (Clark 1979). The sill (*i.e.*, the area that levels off on the true semi-variogram) of the sample semi-variogram for the *A. spicatum* data was reached very quickly (≈ 8 m). The slope of the first seven data points plotted on logarithmic axes (inset, Figure 5) resulted in a fractal dimension of 1.97 (more data gave values closer to 2), which implies very little spatial dependence in the data (e.g., white noise). Both Poisson distribution-generated covers resulted in fractal dimensions of 2.0 (Table 1).

For well-defined two-dimensional data such as patches observed from satellite imagery, the fractal dimension can be estimated using the area-perimeter (A-P) relationship [P ≈ A**(d/2)] suggested by Mandelbrot (1977). Estimation of d is then achieved by regressing log P on log A and estimating d as two times the slope (Lovejoy 1982; Krummel *et al*. 1987). It is possible that to provide enough data for this method, patches from multiple scales would be sampled. In such a case, splines *(i.e.,* segmented regression connected at join-points) can be fit to the data, and an estimation of dimension at each scale can be carried out in the same manner. Comparisons of the join-points of the splines from different landscapes may provide interesting speculation on patch dynamics and resource flow.

Theoretically, the examination of d over a landscape would be useful in determining separate scales of spatial variation. However, estimating the slope of the observed semi-variogram can be complicated by the subjective elements in determining the beginning of the sill and in determining whether to remove trends from the data before estimating the slope. In addition, a sample of patches close in area but not in perimeter *(i.e.,* a poor fit to the linear model) complicate the interpretation of the estimated slope. Furthermore, currently no information exists on the correlation between ecosystem change (or even landscape change) and changes in fractal dimension other than an expected decrease in fractal dimension with increasing human manipulation as observed by O'Neill *et al.* (1987). Milne (1988) suggests that perhaps the range of scales over which a fractal pattern persists may be more useful for specifying the spatial implications of ecological processes. In short, the meaning of changes in fractal dimension is unclear, and neither the persistence of a fractal pattern in relation to ecological processes, nor the relationship between fractals and scales of heterogeneity and patch dynamics has been explained.

The procedure used to estimate the fractal dimension may cause several interpretative problems. O'Neill (personal communication 1988) indicated that estimates of d generally captured the gross features of landscape pattern from aerial photographs, but that they were ill-behaved *(i.e.,* inconsistent) when based on ground measurements. In this case, O'Neill found that estimates of d were overly sensitive to minute (nuisance) changes, a situation that makes comparisons and interpretation difficult. Only moderate success was achieved by Armstrong (1986) when he used the fractal dimension to describe the spatial variation of soil properties. He suggests that his interpretation difficulties were a result of too small a sample to adequately estimate the semi-variogram and hence, d. Currently, no statistical (or other) means exist for determining an appropriate sample size for estimating d. These problems simply point to the need for additional research on estimation and interpretation of the fractal dimension and its relation to landscape research as discussed by Risser *et al.* (1984).

Sampling strategies, including both the resolution and the number of samples required to provide a chosen level of power for a test of a specific hypothesis, can be obtained from the semi-variogram. The range of the semi-variogram is equal to the lag at 95% of the sill semi-variance and can be used to estimate the scale of pattern or resolution for further sampling purposes (Curran 1988). For lags greater than the range, elements are no longer spatially related, and Curran suggests that the lag equal to the range is suited for determining the resolution of future studies on that landscape. The *A. spicaturn* data suggest a sill at about 10 m, thus implying a scale at 9.5 m (Table 1). This scale is in close agreement to the smallest scale detected by the Hill analysis.

Webster and Burgess (1984) suggest a strategy for estimating the number of samples from the semi-variogram. Under the usual method of sample size calculation, the standard estimate of variance ignores the spatial correlation between sampling units, and the results are often impractical. Instead, Webster and Burgess (1984) use the estimated kriging variance, which is a weighted function of the semi-variance, to determine sample sizes for a desired level of precision. Because this method accounts for the variance structure, it has shown substantial savings in sampling effort.

Spatial Variance and Correlation Analysis

The idea of defining ecological scale as the strength of interrelationships between ecological processes that can be measured by the spatial variation and

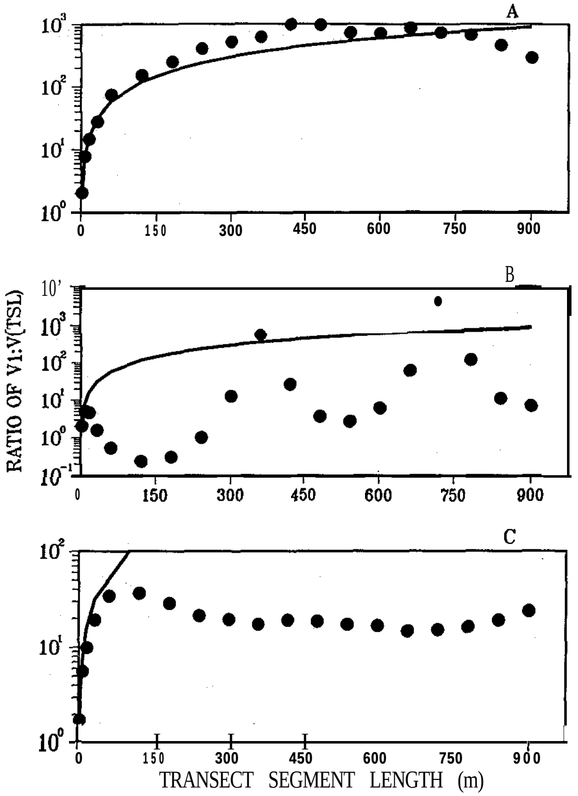

Figure 6. Variance-Ratio of the Independent Poisson (A), Modified Poisson (B), and Bluebunch Wheatgrass (*Agripyron spicatum)(C)* Percent Cover Versus Transect Segment Length (TSL).

correlation across a landscape is suggested by Carlile *et al.* (1989). Their method is used to define the level of resolution (e.g., plot size and dispersion or lag) defined by the estimated spatial variation and correlation. This method can provide a sampling strategy for a continuous study such as the monitoring of a landscape or can be used to examine change over time as reflected by changes in the spatial variation and correlation.

To determine sampling strategies based on the landscape variation or an ecological scale for plant cover requires a measure of individual plant intersection lengths along a sufficiently long transect covering the area of interest. The percent cover for each species is then calculated for each transect segment length (TSL) that is 1, 2, 4, 8. . . m along the transect.

Functions of the sample variance and interclass or simple correlation (Steel and Torrie 1980) estimated from 100 randomly chosen pairs of segments separated by a lag or intersegment distance (ISD) of 0, 1, 2, 4, 8, . . . m for each of the segment lengths are then used to estimate appropriate transect lengths or plot sizes and lag. The choice of this series for both the TSLs and ISDs is merely for convenience, but does limit the resolution of the results. If program run time is not a problem, all TSLs and ISDs can be examined such that two times the greatest TSL plus the greatest ISD is less than one-half of the total transect length.

To estimate appropriate transect lengths, a plot of the ratio of the smallest unit variance (TSL = 1) to the variance at TSL = n for ISD = 0 versus TSL is examined for peaks and troughs. Transects of a given TSL can be viewed as a sum of n segments that under independence introduce no covariance terms to the overall transect variance and, theoretically, would produce a plot of n versus n. Unlike previously discussed methods, peaks in the variance ratio plot correspond to a small spatial covariance between pairs of transects at that TSL. The location of the first dominant peak then provides an estimate of a level of resolution or transect length that approximates the ecological scale of the percent cover of the species observed. Theoretically, TSLs greater than this provide no new information at that level of resolution. The location of peaks can be associated with both the patch size and the scale of pattern in data with strong periodicity. Multiple peaks indicate multiple scales or a result of periodicity in the data. Troughs in this plot are associated with a large covariance term implying spatial dependence between adjacent segments.

The independent Poisson data produced noise about the theoretical variance ratio (indicated by a solid line) for approximately 180 m and then diverged and peaked at 400 m above the theoretical line (Figure 6A and Table 1). This peak indicates that the variance of a single unit is greater than the variance between transects larger than 180 m and smaller than 750 m, implying very little covariance. The modified Poission data produced a first peak in the variance ratio plot at 360 m and another at 720 m mimicking precisely the periodicity in the data (Figure 6B). The *A. spicatum* data had a dominant peak at approximately 90 m in the vari-

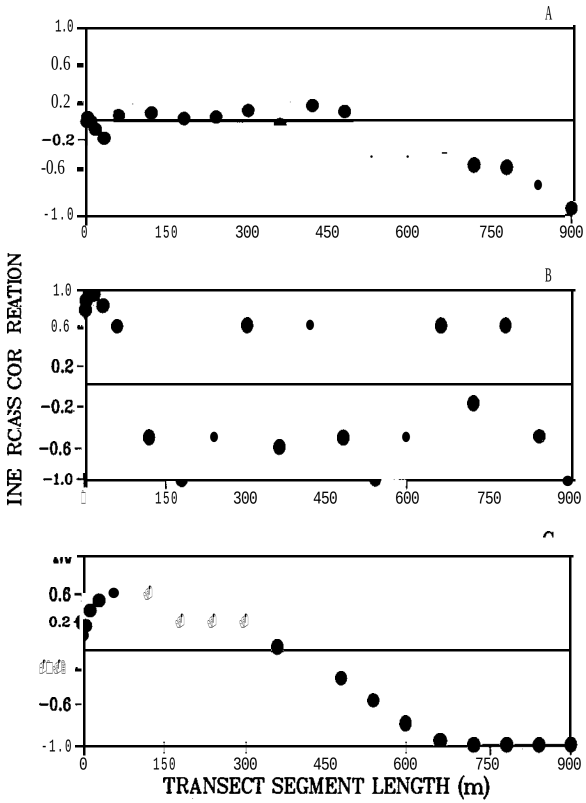

Figure 7. Correlation of the Independent Poisson (A), Modified Poisson (B), and Bluebunch Wheatgrass (*Agripyron spicatum)* (C) Percent Cover Versus Transect Segment Length (TSL).

ance ratio plot (Figure 6C), suggesting study plots or transects should be at least 75 to 90 m.

A plot of the interclass correlation between transect segment pairs as a function of TSL at ISD = 0 corresponds well with the Hill plot producing peaks where the Hill plot produces troughs and vice versa. Peaks in the correlation plot, as expected, designate a high correlation between the transect segment pairs and should correspond with the first dominant peak in the variance ratio plot, suggesting the appropriate transect length.

The decline in the variance ratio for transect lengths greater than 800 m for the independent Poisson data (Figure 6A) can be associated with the increasing correlation between transect segments nearly one half the length of the entire transect (Figure 7A and Table 1). The correlation between segments stayed about 0 and then diverged for transect lengths greater than 450 m. For the modified Poisson data, the correlation versus TSL plot had multiple peaks at 10, 300, 425, 650, and 775 m (Figure 7B). The troughs at 180, 360, 540, 720, and 900 corresponded to both the peaks and troughs in the plots generated by Hill's method (Figure 3B). The *A. spicatum* data again portrayed a dominant peak at approximately 85 m in the correlation versus TSL plot, and a trough centered beyond 750 m (Figure 7C).

Plots of the interclass correlation with increasing ISD and constant TSL are examined to determine an appropriate lag between transect to obtain relatively uncorrelated observations. In these plots, an appropriate lag is determined by the ISD for which the interclass correlation is approximately 0. This will occur at different ISDs for different transect lengths, but in practice, it makes sense to use the TSL chosen from the variance ratio plot for this determination.

The correlation between segments for the independent Poisson data as a function of lag or ISD fluctuated about zero for lags up to 500 m and for transects up to 256 m (not shown) (Figure 8A). Thus, all lags produced relatively uncorrelated observations. The correlation for the modified Poisson crossed 0 at lags of 90 m for small transect lengths (Figure 8B). Thus, a sampling strategy would place transects one-quarter of a wavelength apart. For the *A. spicatum* data, the correlation versus ISD plot (Figure 8C) crossed zero between 200 and 300 m, suggesting this much of a lag is required for relatively uncorrelated replicate plots.

The method of Carlile *et al.* (1989) does not provide a means to determine how long the initial investigative transect should be, but instead averages the data available to determine an appropriate scale of measurement. This scale is more or less appropriate depending on the variability encompassed in the investigative data as compared with the landscape of interest. It is to the researcher's benefit to attempt as long a transect as possible. Variance ratio and correlation analysis does not provide an estimate of the number of transects required for a chosen level of power in testing hypotheses for monitoring change. However, the variation across time in the variable being measured for change is needed in this determination, not the

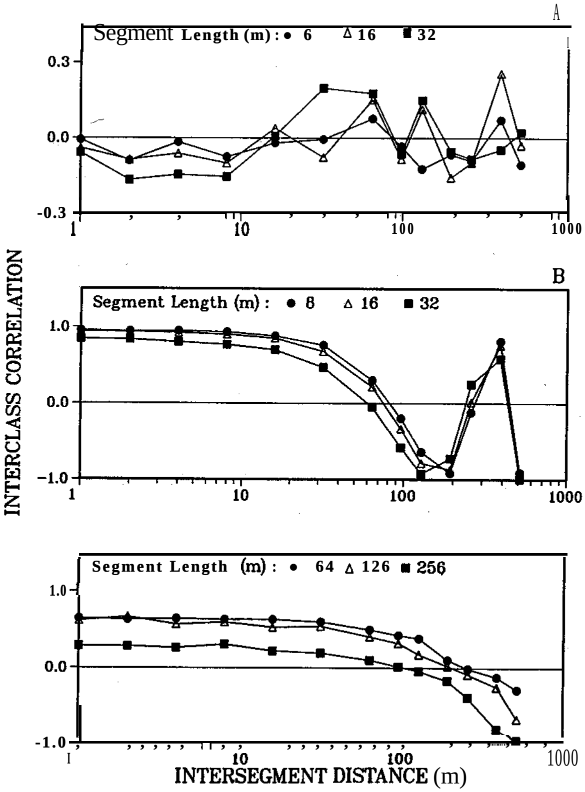

Figure 8. Correlation of the Independent Poisson (A), Modified Poisson (B), and Bluebunch Wheatgrass (*Agripyron spicatum)* (C) Percent Cover Versus Intersegment Distance (ISD).

observed spatial variation during the investigative stage. This analysis also does not provide a means to determine significance between peak locations, and the authors offer no guidance as to whether the correlation as a function of TSL provides a better estimate of ecological scale than the variance ratio plot. This analysis would benefit from the comparison of two or more investigative transects that would allow averaging of results or confirmation.

The relationships between spatial variation, correlation, transect segment lengths, and lag were further reinforced by a follow-up study at another site using another arid-land plant (winter fat, *Eurotia lanata), A. spicatum,* and satellite imagery data on a composite of arid-land vegetation (Simmons *et al.,* accepted). Davidoff and Selim (1988) observed similar patterns with soil moisture and temperature using semi-variograms and autocorrelation. Even though the level of resolution may be landscape specific, these collective results suggest an examination of correlations based on similarities in ecological system parameters and spatial variance before designing either large or small-scale experiments.

Discussion and Conclusions

The research needs of landscape ecologists as implied by the topics of interest described by Risser *et al.* (1984) cannot be met by using any one of the quantitative methods currently available. However, using a combination of methods would potentially allow scientists to establish agreement in their assessment of ecological pattern and scale.

Table 2 outlines the questions examined by each of the methods discussed above (indicated with an X) in relation to landscape pattern and change. Methods are also marked if they have been historically used for a given purpose. This table highlights the important elements of the method associated with each of the questions. Most of these methods use plots of either a function of spatial variance or of correlation. The location of the resulting peaks and troughs are used to indicate scale. The sensitivity of all these methods varies.

As pointed out by O'Neill *et al.* (1991), spectral analysis is more sensitive to small-scale variability while Hill's analysis is more sensitive to larger scale variability. Because only 100 random pairs were sampled, the variance ratio and correlation analysis verses TSL only estimated a neighborhood rather than a precise scale, but they were still more reliable in detecting fine-scale variability than Hill's method. Further, peaks in the Hill plots can also be due to a strong periodicity in the data rather than a scale (indicated when the peak is one-half of the value of a trough).

Because of' the variable sensitivity of each of these methods, the detection of multiple scales and the determination of ecological change must be confirmed by more than one method. Table 2 is not intended to delineate a method's ability to provide a correct answer; rather, it is to provide other methods that may support a possible scale of variability.

A summary of results based on the three data sets

Table 2. Methods Examined By Questions they Address Relevant to Landscape Ecological Research

Method	Estimation of Patch Size or Scale	Examination of Patch Distribution	Examination of Spatial Variation	Examination of Spatial Correlation	Estimation of Scale of Pattern or Period	Estimation of Lag	Estimation of Sample Size	Detection of Multiple Scales	Detection of Ecological Change
Tests of Non-randomness		X	X						
Patch Size Analysis									
Peaks	X	X	x					X	
Hill's Method									
Peaks	X	X	X					X	X
Troughs		X	X		X			X	X
Spectral Analysis									
Peaks			X		X			X	X
Semi-Variogram									
Sill	X		X				X		X
Fractal Dimension			X	X					X
Variance Ratio Analysis									
Peaks.	X		X		X			X	X
Correlation Versus Transect Segment Length									
Peaks	X			X				X	X
Troughs .				X	X			X	X
Correlation Versus Lag				X		X		X	X

used throughout this paper and their correspondences with each other are presented in Tables 1 and 3, respectively. Table 1 presents the results as specific values, while Table 3 indicates the agreement and sensitivity of each of the methods. Together, the two tables can be used to suggest the ranges over which pattern may be observed. For example, for *A. spicatum,* both Hill's patch size analysis and the semi-variogram suggest patches of 8 to 10 m while no other methods produced scales this small. Both the variance ratio analysis and the correlation plot verses TSL produced peaks at 85 to 90 m. The Hill plot and correlation versus TSL analysis suggest another possible scale greater than 750 m, but it is not well defined. Thus, two and possibly three scales can be detected as was found in O'Neill *et al.* (1991).

Hypothesized correspondences between each of the methods based on known patterns and distributions are also indicated in Table 3 for comparison with those between each of the data sets. This is not a complete list of correspondences because all possible patterns have not been investigated. In general, the patch size analysis of Greig-Smith should correspond to both peaks in the Hill plots, the troughs in the correlation versus TSL plots, and the sill in the semi-variogram. For periodic data, the troughs in the plots using Hill's method should correspond to peaks in the spectral analysis, variance ratio, and in the correlation versus TSL plots. For non-periodic data, peaks in the variance ratio plot should correspond to peaks in the correlation versus TSL plot. Finally, the value of the fractal dimension should be < 2 when the correlation versus ISD plot has a distinct pattern and 2 when the plot suggests only noise about zero. Likewise, when the fractal dimension is 2, there should be no sill in the semi-variogram.

For each of the data sets (Table 1), Lefkovitch's index (Test of Non-randomness) produced the expected outcome, approximately 0 for the independent Poisson data, and 1 for both dependent data sets. Variability as a function of cell size was observed and suggests that the index should be calculated for a range of cell sizes. Analysis of the independent Poisson data showed expected results for the patch size analysis, Hill's analysis, spectral analysis, semi-variogram, fractal dimension, and correlation versus TSL and ISD plots. However, we can provide no explanation for the peak in the variance ratio plot at approximately 400 m. Because this peak is above the theoretical line of TSL = TSL, which implies little covariance, we feel that the peak is not indicative of a patch size. The modified Poisson, however, produced all of the expected results with the exception of the patch size analysis. Here, the peak was at 100 m corresponding to the 90 m sine wave cycle. It is interesting that none of the other methods delineated this small scale pattern but did detect the 180-m patch size and 360-m scale of pattern. The remaining peaks and troughs are merely reflections of data periodicity. The differences among estimates is an indication of the sensitivity of the different methods. Results based on the *A. spicatum* data are far more difficult to generalize. As previously stated, patches of 8 to 10 m and another of 750 m are indicated; scales of pattern of 90 to 120 m and 900 to 980 m are also indicated. However, the fractal dimension of approximately 2 is inconsistent with all other results.

In conclusion, our review indicates that tests of non-randomness and nearest-neighbor techniques provide limited information about the distribution of patches and, in general, the results are redundant when any of the other methods is used. Obviously, if a patch size or scale of variability is indicated by other methods, non-randomness has been detected. Uniformity of a pattern can be detected and quantified by all of the methods designated for the examination of spatial variation in Table 2. For similar reasons, testing an average landscape patchiness against a neutral (random) landscape in and of itself is not statistically useful. However, a time series of landscape clusterbehavior may allow prediction of disturbance patterns needed for landscape management.

Patch size analysis methods, including spectral analysis, are useful in identifying multiple scales of heterogeneity and estimating the average patch size, but interpretation of the resulting plots is difficult. Further, one cannot assume that the average patch size is an appropriate level of resolution for the study of landscape dynamics without confirmation with other methods (e.g., variance ratio and corre-

Table 3. Hypothesize and Actual Correspondence Between Individual Outcomes for Each Data Set and Method

Method	Data Set: Independent Poisson			Data Set: Modified Poisson			Data Set: *Agropyron spicatum*			Hypothesized Correspondence		
	Patch Size	Scale of Pattern	Correlation	Patch Size	Scale of Pattern	Correlation	Patch Size	Scale of Pattern	Correlation	Patch Size	Scale of Pattern	Correlation
Patch Size Analysis												
Peaks	X					X				X		
Hill's Method												
Peaks	X			X			X			X		
Troughs		X			X						X	
Spectral Analysis												
Peaks		X			X			X			X	
Semi-Variogram												
Sill	X						X			X		
Fractal Dimension			X									X
Variance Ratio Analysis												
Peaks	X	X			X		X			X	X	
Correlation versus Transect Segment Length												
Peaks	X						X			X		
Troughs	X	X		X	X		X			X	X	
Correlation versus Lag												
Crosses Zero			X			X		X				X

lation analyses). Although fractal dimension has a potential for characterizing landscape heterogeneity, interpreting changes in fractal dimension in relation to ecological change is problematic and requires additional research.

If landscape ecologists wish to make inference to processes that potentially impact organisms or measurements on multiple scales, an appropriate size of study plots or transects specific to the inferences desired needs to be determined. Procedurally, this process may require that the research be carried out in two stages: one stage for determining the level of resolution needed for the desired inference and a second stage for conducting the intended research. We suggest that sampling strategies be consistent with scales of pattern that are estimated by more than one of the methods discussed. It is important to recognize, however, that no one method is correct because each method addresses a different statistical question and each has a different sensitivity over changes in scale. Further, the ecological significance of the patch and/or scale of pattern as estimated here is unknown and requires more research. A patch delineated quantitatively as above may not function as a patch. Conversely, a patch of size x may have an ecological influence of 2x. Finally, an ecologically functional patch may not be quantitatively distinguishable.

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