

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Spatial variance in ecology

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Spatial variance of observed measures such as density is no longer viewed as a statistical annoyance. It is now treated as a biologically important quantity that changes value depending on the scale of measurement. Processes that generate spatial variance are often inferred by matching scales of maximum biological spatial variance to dominant physical processes at the same scale. Success in this approach has been limited to patchiness of plant communities along environmental gradients and to patchiness of passive aquatic organisms relative to physical flow structures. Some progress in formalizing spatial variance has been made using empirical models derived from quantitative descriptions of pattern, but further progress requires theoretical models of spatial variance and processes that generate variance as a function of spatial scale.

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The investigation of spatial variance is nearly a century old. During this time the concept has evolved from being treated as a statistical nuisance (cf. Cassie 1963, Steele 1976) to being recognized as a biologically important quantity (Huffaker 1958, Lasker 1975, Platt and Harrison 1985). Concomitant with this change was the realization that observed patterns of spatial variance are dependent on the scale of measurement (Sawyer 1989, Yamamura 1990, Lepš 1993). Recent developments in computing hardware (speed and memory), the introduction of spatially explicit software (e.g. Geographic Information Systems), and a large increase in scale-sensitive studies (e.g. Wiens 1989, Menge and Olson 1990, Holling 1992, Levin 1992) should accelerate the understanding of spatial

variance patterns in biological quantities such as density, mortality, and recruitment.

The dependence of spatial patterns on measurement scale was first investigated in agricultural experiments. To improve statistical control in agricultural uniformity trials, a variety of plot sizes were used to isolate the "best" scale (Mercer and Hall 1911). Results of these experiments were then used to develop an empirical relation between plot size and variability among plots (Fairfield Smith 1938, Bliss 1941). Characterizing spatial variance as a function of plot size was later applied to naturally distributed plants using nested (Greig-Smith 1952) and contiguous (Kershaw 1957) quadrats.

Development in the analysis of scale-dependent pat-

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tern occurred over the following twenty years but four contributions in 1978 consolidated the concept of scale in ecological observation. First, Smith (1978) explicitly recognized the scale-dependence of measurement and stressed the importance of choosing an appropriate measuring framework relative to the organism of interest. The second contribution was a proposal by Shugart (1978) that the spatial and temporal range of a biological quantity is dependent on its level of organization. This introduced Simon's (1962) concept of hierarchy to ecology. Haury et al. (1978) adapted a schematic diagram by Stommel (1963) to show how variances of biological quantities are linked to the spatial and temporal scales of physical processes. Steele (1978) extended the linkage of spatial and temporal scale to include the mass of an organism.

The treatment of spatial variance in biological quantities is fragmented between the aquatic and terrestrial literature. This review integrates the two fields by examining the quantification of spatial variance at a single scale and then as a function of scale. We summarize progress in the analysis of spatial variance and conclude by speculating where current analytical trends are headed.

Spatial variance at single scales

Certainly the most common use of a variance is to measure the precision of a mean. Variance s^2 of a quantity x is a measure of dispersion and is defined as the average sum of squared deviances from a sample mean \bar{x} :

$$s^2 = \frac{1}{n-1} \sum_{i=1}^n (x_i - \bar{x})^2 \quad (1)$$

The variance of a quantity is used to estimate confidence intervals of sample means for ecological variables. What is not usually considered when making these calculations is that the magnitude of a variance is dependent on the spatial and temporal scale of sampling.

Another common use of variance in ecology has been to quantify the degree to which organisms are aggregated. The most common technique was to compare an observed index of aggregation to an expected value from a Poisson distribution (i.e. events are rare and random occurrences). These indices were largely based on variance to mean ratios (Fisher et al. 1922, Clapham 1936, Blackman 1942). In a Poisson distribution the expected value of the variance is equal to the mean and thereby the ratio of the variance to the mean is expected to be unity. Attributes of a "perfect coefficient" (i.e. index) were compiled by Taylor (1984) who supplemented those listed by Green (1966) and Lefkovich (1966). Curtis and McIntosh (1950) demonstrated the dependence of several indices on measurement scale. Patil and Stiteler (1974) speculated that variance to mean ratios were a function of measurement scale, but developed the idea no further. A

chronologic detailing of the development of variance to mean indices of aggregation and their equivalences can be found in Pielou (1969), Ripley (1981), or Greig-Smith (1983). In stark contrast, Hurlbert (1990) argues that the variance to mean ratio is not a suitable measure of departure from randomness and an uninterpretable measure of aggregation.

Morisita (1954, 1959a) developed an index I_δ based on Simpson's (1949) measure of diversity λ .

$$I_\delta = q \frac{\sum_{i=1}^q n_i(n_i-1)}{N(N-1)} \quad (2)$$

where n_i ($i = 1, 2, 3, \dots, q$) is the number of individuals in q quadrats and N is the total number of individuals observed. Morisita (1959b) recognized the dependence of variance to mean indices on measurement scale and attempted to design I_δ to be independent of sample resolution. Morisita's index compares density variances of organisms among patches. Index values are less than 1 in regular distributions, approach 1 in random distributions, and exceed 1 in contagious distributions. But values of the index are only independent of sample size as long as quadrat sizes are smaller than patches. This index assumes sample quadrats occur within large patches and that the distribution of organisms is random or regular within patches (Patil and Stiteler 1974).

In an attempt to relate spatial distribution to density-dependent behaviour, Lloyd (1967) developed an index of aggregation that measures mean crowding \dot{m} relative to a focal organism:

$$\dot{m} = \frac{s^2}{\bar{x}} + \bar{x} - 1 \quad (3)$$

An index of patchiness was formed by the ratio of mean crowding \dot{m} to average abundance \bar{x} . Lloyd (1967) used the equivalence of \dot{m} to I_δ to claim that the mean crowding index \dot{m} was also independent of sample size, and therefore quadrat size could be set at a spatial scale equivalent to the study organism's 'ambit'. In parallel to Morisita's index, this claim is valid when quadrat size is smaller than patch size. Iwao (1968, 1970) linearly regressed \dot{m} on \bar{x} and used the intercept α as an indicator of aggregation size. Confusion over assumptions of the method have resulted in inappropriate conclusions when applied to field data (e.g. Byerly et al. 1978, Gutierrez et al. 1980).

As an alternative to developing an index from a variance to mean ratio, Taylor (1961) described the variance of a quantity as a function of the mean. Taylor's Power Law states that variance s^2 in the local density of many species is proportional to the mean density \bar{x} , raised to an empirically determined exponent b :

$$s^2 \cong a\bar{x}^b \quad (4)$$

The parameter a was reported as a sampling or computing factor. The magnitude of a is dependent on the size of sampling unit and the method used to calculate variance. The exponent b was proposed as an index of population aggregation. It should be noted that the biological interpretation of b is not independent of the value of a . A regular distribution is indicated by an a value equal to 0. a and b values near unity indicate a random distribution. Values greater than 1 indicate an aggregated distribution. The fit of this relation has been checked in a diverse set of populations (e.g. Taylor 1961, Taylor et al. 1978) and shown to require special treatment at low mean abundances (Taylor and Woiwod 1982, Routledge and Swartz 1991). Taylor and Taylor (1977) postulated that this relation results from a density-dependent balance of attractive and repulsive behaviours among individuals that are attempting to maximize resource consumption. This " Δ -model" was questioned by Hanski (1980, 1982) and Anderson et al. (1982) who showed that the relationship between the variance and mean density can arise from stochastic demographics, rather than complex behaviours. Taylor et al. (1983) rejected the stochastic models on technical and a priori evolutionary grounds. Thórarinnsson (1986) found that Δ -models did not represent individual movement as a response to inter-individual contact.

The detection of a general relation between the variance and the mean of a population retains its appeal. Routledge and Swartz (1991) advocate the use of Bartlett's (1936) quadratic relationship (see below) over Taylor's Power Law to model the variance as a function of the mean. In response, Perry and Woiwod (1992) compare the fit of quadratic, power, split domain (Woiwod and Perry 1989), and generalized linear models (McCullagh and Nelder 1983). Using a ratio of deviances, they found that Taylor's power relationship and the generalized linear model were the best fitting models. The generalized linear model has the added advantage of not requiring stationary variance.

A sixth method to quantify spatial variance in abundance at a single scale is the use of the parameter k from the negative binomial distribution (Waters 1959). The application of k as an index of dispersion was adopted from Bartlett's (1947) general expression of variance:

$$s^2 = c\bar{x} + \frac{\bar{x}^2}{k} \quad (5)$$

where the value of c must be unity to ensure a negative binomial distribution. Low values of k indicate an aggregated distribution while high values are indicative of a more random distribution. The maximum likelihood estimate of k is found by iteration or numerical maximization (Ripley 1981). Results from an aphid density study (Anscombe 1948) instigated an unsuccessful search by many ecologists for a constant k value among populations (e.g. Taylor et al. 1979). If found, a robust index of aggregation such as k could be used to compare popula-

tion distributions at different locations or times. Kuno (1968) and Hill (1973) proposed that random removal of individuals does not change observed patterns or the value of $1/k$. Pielou (1969) provided a proof to show that this is true only when the original population has a negative binomial distribution. Even this result does not apply to count data (Ripley 1981) because counts of organisms can not be less than zero. A random thinning of individuals lowers the mean, creates zero counts, eliminates patches of organisms, and changes the variance. Without an increase in sample resolution to compensate for the increased number of zeros due to thinning, spatial variance will increase at small scales (Horne 1995).

At the same time as these empirical measures were being proposed, there were continuing attempts to use theoretical frequency distributions to describe spatial variance. This line of research has been reviewed by Rogers (1974), Douglas (1979), and Greig-Smith (1983). Motivations for fitting theoretical distributions to empirical observations include population description with a limited number of parameters, and interpretation of parameter values for clues to processes that determine spatial structure. The negative binomial distribution was one of the first theoretical distributions used in ecology (Student 1907, Greenwood and Yule 1920). It is commonly used to describe the degree of aggregation in aquatic organisms (e.g. Taylor 1953, Houser and Dunn 1967), despite criticisms of its biological basis (Williams 1964). The Pólya-Aeppli (Pólya 1931), Neyman A, B, C (Neyman 1939), Thomas double-Poisson (Thomas 1949), and Adès (Perry and Taylor 1985) frequency distributions all assume a Poisson process of clustered organisms, but differ in assumptions concerning the distribution of organisms within clusters. Comparisons of negative binomial distributions to other distributions based on Poisson processes have concluded that the negative binomial distribution is usually the most applicable theoretical frequency distribution, but no single frequency distribution is applicable to all data (Bliss 1941, McGuire et al. 1957, Harcourt and Binns 1980, Brown and Cameron 1982, Wilson et al. 1983).

The dependence of spatial variance on scale of measurement has restricted the application of theoretical frequency distributions to organism density data. Sample resolution was found to influence the fit of any theoretical frequency distribution (Numata and Suzuki 1953, Iwata 1954, Pielou 1957) and to affect the subsequent interpretation of spatial variance patterns. Altering sample resolution may alter the fit of a theoretical frequency distribution to the data, or increase the number of distributions that fit the data equally well. Ambiguous identification of appropriate theoretical frequency distribution models limits their use as descriptive summaries, or as clues to identifying potential variance generating processes.

The criticism that measures of aggregation are dependent on scale of measure applies to all methods of quantifying spatial variance of organism distribution at a single scale. Therefore, comparisons of aggregation in-

dices among populations are only valid if made at the same spatial scale. The next logical step was to examine spatial variance in population dispersion as a function of scale.

Spatial variance at several scales

Pattern analysis (Greig-Smith 1952) was the first formal method to evaluate spatial variance as a function of scale. Organisms are counted in a grid of contiguous quadrats, with the resolution of the grid decreasing by a factor of two at each count iteration. The mean square from an analysis of variance is plotted against sample resolution (i.e. inverse of quadrat size). If the distribution of organisms is random over the entire grid then the mean squared deviation is independent of resolution and the variance will equal the mean. A patchy distribution will produce a peak of the mean square at the quadrat size of a patch. Kershaw (1957) extended this method by using linear transects of rectangular, contiguous quadrats rather than a grid of square, nested quadrats. This alteration of quadrat shape and layout enabled sampling of larger scales with less effort and facilitated analysis along obvious environmental gradients. Kershaw's transect approach was used to examine spatial variance in numerous plant communities (for examples see Greig-Smith 1983) and adapted to other measures of spatial variability (e.g. Morisita 1959a, Iwao 1972). Pattern analysis has the advantage over earlier methods of explicitly including spatial scale in the analysis. The method was used to identify the scale of maximum variability in any quantity of interest. It can be used to set the sampling scale for manipulative experiments, and to provide clues to variance generating processes by matching dominant scales of biological variance to physical processes at the same spatial scale.

Plotting mean squares as a function of quadrat size does have limitations. Pielou (1969) cites five drawbacks of Greig-Smith's method: 1. calculated mean squares are not independent thereby preventing variance-ratio tests (but see Mead 1974), 2. entire sites must be sampled within a grid (but this does not apply to transects), 3. observed peaks in plots are influenced by shape of sample quadrat (rectangular or square), 4. intermediate quadrat sizes between quadrat size doublings are not assessed, and 5. distributional patterns of the presence or absence of organisms are indistinguishable in mean square plots. An important drawback omitted by Pielou was the sensitivity of mean and variance estimates to size of the original quadrat and the location of sample grid (Skellam 1952). Usher (1969) and Hill (1973) proposed two different techniques to compensate for the dependence on sample start location but these have not been widely used. Ripley (1981) and Greig-Smith (1983) provide additional examples and detail studies that examine other caveats on pattern analysis.

One method that simultaneously examines a wide range of spatial scales and is not sensitive to sample start location is spectral analysis. The variance of a continuously recorded variable (e.g. organism density), is represented by a set of sine and cosine waves summed over a range of measurement frequencies. For a full description see Jenkins and Watts (1968), Platt and Denman (1975), or Chatfield (1980). The resulting spectral density estimates are plotted as a function of frequency, the inverse of spatial or temporal scale. Peaks in the spectrum are interpreted as dominant scales of pattern. This technique has been widely used by oceanographers and limnologists to examine scale-dependent spatial variance of passive tracers of the fluid (e.g. surface water temperature – Fasham and Pugh 1976, Richerson et al. 1978) or organisms in fluid environments (e.g. phytoplankton – Platt et al. 1970, Powell et al. 1975). The equivalence of spectral analysis to other indices of aggregation is shown in Ripley (1981) and Schneider (1994b).

Spectral decomposition techniques are not ideally suited to the analysis of patchily distributed, rare organisms. Continuous processes are well described by sine and cosine functions but the non-Gaussian character of point processes, such as mobile organism counts, limits the use of spectral models (Bartlett 1975). Biological density data rarely provide long temporal or spatial series and often violate other assumptions of regular sampling intervals and stationarity of means. The partitioning of variance among frequencies by spectral analysis is sensitive to low means (Fasham 1978) and to the presence of zeros in count data (Horne 1995). Coherence, a frequency-dependent measure of spatial association between two variables, can be lowered by random sampling error in a Poisson process (Mackas 1977), and does not adequately reflect non-linear relationships between two variables (Star and Cullen 1981). Despite these limitations, Ripley (1981) found that spectral analysis was at least as reliable as other methods.

Recently there have been attempts to predict change in spatial variance at a single scale and across scales. Predictions of change in spatial variance are formulated using biological or physical processes that are capable of generating or reducing spatial variance in the quantity of interest. The ability to predict change in scale-dependent spatial variance is important in several ecological contexts including: effects of predators on the stability of prey populations (Pacala et al. 1990, Hassell et al. 1991), effects of habitat fragmentation on population stability (Kareiva 1990); density-dependent effects of crowding on reproduction and growth (Stephen 1929, Connell 1961), and the effects of predator searching (Salt 1974) and encountering resources (Possingham 1989). Schneider (1992) found that changes in spatial density variance of bamboo worms *Clymenella torquata* could be predicted from the foraging dispersion of an avian predator, the short-billed dowitcher *Limnodromus griseus*, at the spatial scale of intertidal flats (0.2–3 km²) but not at the scale of plots (1 ha) within flats. Similarly, Schneider

and Bajdik (1992) attempted to predict changes in spatial variance in counts of gelatinous zooplankton based on wind-induced Langmuir circulation cells. They found that variance in counts was proportional to spatial scale during a wind event, but the magnitude of change was not easily predicted. These two examples illustrate that predicting changes in spatial variance is difficult, and that methods to predict changes in spatial variance across scales require development.

A second application of evaluating spatial variance at several scales is using plots of spatial variance as a function of scale to identify domains of homogeneous spatial variance (Wiens 1989). Boundaries of spatial variance domains can be demarcated using fractal geometry (Mandelbrot 1982). Slopes of spatial variance plots are converted to Hausdorff or fractal dimensions (Bradbury et al. 1984, Sugihara and May 1990, Schroeder 1991) to quantify the degree of self-similarity across spatial scales. A constant or near constant value over a range of scales indicates that observed patterns of spatial variance may be generated by a single process (Sugihara and May 1990). Large changes in fractal dimension (e.g. Krummel et al. 1987, Palmer 1988) mark boundaries and indicate scales where there may be a shift in processes that generate spatial variance (Mandelbrot 1982).

Spatial variance domains have two important implications. First, spatial variance domains limit the range of research conclusions (Sugihara and May 1990). Ecosystem process models should not be extrapolated beyond domain boundaries just as regression models should not be generalized beyond limits of sampled data. A second practical application of spatial variance domains is the reduction of field survey costs. By setting sample resolution equal to the smallest spatial scale within a domain, survey costs are minimized and the results can be extrapolated throughout the domain. A wider application of fractal geometry to spatial variance research may provide clues to processes that influence organism dispersion and be used to delineate the range of scales over which they operate.

The analysis of spatial variance

Progress in assessing spatial variance of ecological quantities has been marked by transitions from verbal acknowledgement to graphical models, and from graphic to formal models of pattern and process. Transitions from verbal to graphical and formal models have not been synchronous in all areas of ecology. However awareness of spatial variance is rapidly spreading. A computer scan of *Current Contents* using keywords 'spatial' and 'variance' in June 1994 resulted in 371 titles from 225 different journals published since September 1992.

A major advance in the analysis of spatial variance was the recognition that measures of variance depend on the scale of observation. This represented a change from

treating variance as a statistical detail to treating it as a biologically important quantity (Steele 1976). One response to this realization was to re-analyze data at a different scale and compare the second set of results to the original. In aquatic systems, Fairweather and colleagues (Fairweather et al. 1984, Fairweather 1988) and Schmitt (1982, 1985) both found that the sign of association between predator and prey changed from negative to positive when the scale of observation was increased. A second response has been to report the analysis of biological quantities at two or more scales (e.g. Pinel-Alloul and Pont 1991, Ives et al. 1993). This approach increases the number and range of observation scales. It does not indicate if observations were set at scales of maximum spatial variance.

The analysis of spatially indexed data has matured from verbal descriptions at discrete scales to graphic representations of spatial variance as a continuous function. This was initiated by the development of pattern analysis (Greig-Smith 1952) and was expanded to include other measures of spatial variance plotted as a function of scale. The computational burden of this approach has been significantly reduced with the wide availability of statistical software packages. Large, spatially explicit data sets are routinely analyzed using geostatistical techniques (e.g. Rossi et al. 1992) which are often incorporated in geographic information systems (GIS). In oceanography spectral analysis is commonly used to describe scale-dependent biological pattern in the frequency domain (e.g. Mackas and Boyd 1979, Weber et al. 1986). The frequency of maximum spatial variance can then be converted to a length scale for biological or physical interpretation.

Efforts to explain biological spatial variance in both terrestrial and aquatic research commonly proceed by matching scales of biological pattern to dominant physical processes at the same scale. This has been successfully used in descriptions of plant communities with reference to environmental gradients (e.g. Greig-Smith 1952, Kershaw 1958), and the coupling of spatial variance patterns of passive tracers to flow structures in fluid environments (e.g. Denman and Powell 1984, Mackas et al. 1985). The key assumption in this matching approach is that pattern is directly coupled to processes acting at the same scale (Horne and Schneider 1994a). This assumption excludes non-linear relationships among ecosystem components, multiple processes influencing pattern at a single scale, and the propagation of effects across spatial or temporal scales (e.g. adult cohort size established at an early life history stage).

A second assumption in this matching approach is that the coupling of biological spatial variance to any variance generating process occurs at a characteristic scale. Characteristic spatial scales have been reported for terrestrial (e.g. Greig-Smith 1952, Kershaw 1957) and aquatic systems (e.g. Grassle et al. 1975, Schneider 1989, Rose and Leggett 1990) at small temporal scales. But in all studies, scales of maximum spatial variance differ among tran-

sects. In the few studies that increase the temporal scale by averaging multiple plots (Weber et al. 1986, Schneider 1994a), these scale-dependent concentrations of spatial variance do not occur. In aquatic systems, the occurrence of characteristic scales of spatial variance among mobile organisms appear to be limited to short temporal scales (Horne and Schneider 1994b).

A third assumption in this matching approach is that the creation of biological spatial variance is generated exclusively by physical processes. Biological processes can also influence spatial variance over a range of scales. Phytoplankton critical patch size is a classic example. One theory is that the size of a phytoplankton patch is determined by the opposing forces of horizontal diffusion and phytoplankton reproductive rates (Skellam 1951, Kierstead and Slobodkin 1953). The critical patch size theory was later expanded to include herbivore grazing (O'Brien and Wroblewski 1973, Wroblewski et al. 1975). The assumption that spatial variance of passive tracers is generated exclusively by physical processes is also contradicted by the idea that the dominating process determining phytoplankton spatial variance switches between physical and biological processes over time (Demers and Legendre 1979, 1981). Reliance on matching biological pattern to physical processes was due, in part, to a lack of analytic tools that quantify the relative importance of variance generating processes.

The most important recent development in the characterization of spatial variance has been the idea of formally expressing biological pattern and processes that generate variance as a function of scale. Empirical indices of spatial variance (e.g. variance to mean ratios, Lloyd's mean crowding index \bar{m} , Morisita's I_b) that were implicitly calculated at single scales are now explicitly calculated as a function of scale (e.g. Schneider and Piatt 1986). Similarly, the exponent b from Taylor's Power Law and slopes of spectral density plots can be used to quantify changes in spatial variance with changes in scale. We could not find any research report in which parameters of a theoretical frequency distribution were expressed as a function of scale in an equation or as a graph. To provide an example, the parameter k from the negative binomial distribution could be estimated using moment ratios (Ord 1972) and expressed as a function of measurement scale L :

$$k = \alpha L^\beta \quad (6)$$

Estimating k at different scales is accomplished by grouping contiguous values in increasing quadrat sizes or comparing values over larger separation distances. This relation could be used to calculate an expected variance at one scale based on an observed variance at another scale. Alternatively, the exponent β could also be used as an index of the dependence of k on measurement scale. If β equals 0 then k is independent of spatial scale. As the value of β approaches 1, k becomes directly proportional to the scale of observation L .

The next steps

The treatment of scale-dependent spatial variance has evolved since its recognition as a biologically important quantity. Increased awareness of the importance of scale in the measurement of spatial or temporal variance will ensure that this progress continues. Further development of quantitative tools will help standardize the analysis of spatial variance. Application of new techniques will improve sample design and subsequent data analysis.

A simple and useful standardization is the explicit treatment of measurement scale in sample design. Explicit treatment eliminates any novelty associated with scale and obligates the reporting of all measurement scales in results (e.g. Kareiva 1994). A second development in the standardization of survey design would be the use of scale-dependent spatial variance to determine the resolution and number (or frequency) of samples needed to obtain a pre-determined precision of parameter estimates. If the variance of a quantity is dependent on scale then precision of parameter estimates also depends on measurement scale. One method to maximize precision of parameter estimates is to confine sampling to established domains of spatial variance. Spatial variance domains minimize changes in spatial variance across scales which maximizes precision of parameter estimates within domains. If domains of spatial variance are very small then the range of sampling should be set to minimize the rate of change in spatial variance across spatial scales. Minimizing the rate of change in spatial variance, by selecting a narrow sample range, also maximizes precision of parameter estimates and potentially increases the ability to theoretically predict sources of spatial variance.

Overall, the standardization of analytic techniques will enhance the comparison of pattern and process among diverse ecosystems. A statistical tool that analyzes continuous or discrete data across a wide range of spatial and temporal scales would reduce problems associated with low means and zeros in count data (Horne 1995), and simplify comparisons among sample locations or scales. Legendre and Fortin (1989) provide a comprehensive summary of techniques used to analyze variance in organism distributions as a function of location or as a function of scale. Despite ambiguity in their use of geographic location and spatial scale, they demonstrate the feasibility of explicitly including spatial variables (location, sample resolution) in the analysis of organism distributions. By including measurement variables, the dependence of observed patterns on measurement scale can be tested directly.

The most challenging task ahead is to develop the theory and quantitative methods needed to predict changes in spatial variance of biological quantities as a function of scale. Successful completion of this goal requires: numerical methods that analyze continuous and discrete density data, additional quantitative descriptions and comparisons of scale-dependent variance patterns, incorporating the temporal dependence of spatial sam-

pling (cf. Gaston and McArdle 1994), tools to quantify the relative importance of variance generating processes, and further attempts to predict changes in spatial variance. In combination these elements will solidify the theory of spatial variance-in ecology.

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