- ter Braak, C.J.F. (1988b). CANOCO an extension of DECORANA to analyze species-environment relationships. *Vegetatio*, **75**, 159–60.
- ter Braak, C.J.F. (1990). Update notes: CANOCO version 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands.
- Vannier, G. (1985). Mode d'exploitation et de partage des ressources alimentaires dans le système saphrophage par les microarthropodes du sol. Bull. d'Écol., 16, 19-34.
- Wauthy, G., Noti, M.-I. and Dufrêne, M. (1989). Geographic ecology of soil oribatid mites in deciduous forests. *Pedobiologia*, 33, 399-416.
- West, C.C. (1984). Micro-arthropod and plant species associations in two subantarctic terrestrial communities. Oikos, 42, 66-73.
- Wiens, J.A. (1984). On understanding a non-equilibrium world: Myth and reality in community patterns and processes. In: *Ecological Communities: Conceptual Issues and the Evidence* (D.R. Strong Jr, D. Simberloff, L.G. Abele and A.B. Thistle, eds) Princeton University Press. pp. 439–57.

Whittaker, R.H. (1956). Vegetation of the Great Smoky Mountains. Ecol. Monographs, 26, 1-80.

## Discussion

DONALD E. MYERS

Department of Mathematics, University of Arizona

#### Overview

Spatial structure, spatial correlation, spatial dependence, spatial heterogeneity and spatial variability are all terms that are used to denote some form of known or presumed relationship between a variate of interest and geographical positioning. That is, the data is spatially located in one of several possible senses. In some instances the variable represents a value for a region and in others it may represent a measure at a point or small area/volume. If the variable of interest is additive then these two perspectives can be merged. It will make some difference whether the variable(s) are categorical, nominative or continuous. In most cases the objective is to quantify the spatial structure or spatial variability. Spatial structure is also related to interpolation methods. Because both of these aspects are central to this paper it is useful to consider other methods for quantifying spatial structure and alternative interpolation methods.

There are at least two ways to characterize spatial structure, one of which is to explicitly incorporate spatial coordinates in the quantification of the spatial correlation. The authors have used a second approach, implicit quantification by a multivariate analysis technique, canonical correspondence analysis (CCA). While CCA does not specifically relate geographical position or distance to correlations it has the potential for identifying factors contributing to the spatial variability. This is especially useful when those factors are not directly observable or measurable. Similar or related techniques include principal components analysis, factor analysis and correspondence analysis. Ordinary, i.e., non-canonical, correspondence analysis was first introduced for categorical variables but has been extended and applied to continuous environmental data by a number of authors. These are all data driven techniques in that there is no model assumed a priori in order to perform the analysis. One disadvantage is that the method does not incorporate an adjustment for the support of the sample; in this particular application the support would correspond to the shape and volume of the cores. In general, variability will decrease as the

support is increased especially in relationship to the geographical extent of the area sampled. Another disadvantage is that the multivariate characterization of spatial structure does not incorporate directional dependence.

### 2. Variograms

Alternatively, spatial correlation can be quantified by the use of a (spatial) autocorrelation function. The variogram, first introduced in the context of ore reserve estimation problems in mining, has certain advantages over the autocorrelation function but is essentially comparable. The variogram explicitly relates spatial correlation of a variable to itself in terms of the separation vector between sample locations; it is also adaptable to changes in sample support. A further advantage is that the variogram can then be used in the spatial interpolation stage. Estimation and modeling of variograms is described in a number of standard references on geostatistics. The variogram also can incorporate directional dependence.

### 3. Inverse distance weighting

Contour maps, using irregularly spaced data, are produced in two stages. First the data is interpolated to a regular grid and then the contouring algorithm produces the contour lines from the gridded data. There are a variety of techniques that can be used to interpolate from irregularly spaced data (locations) to a grid. Inverse distance weighting, IWD, was used by the authors. While it is common to use the square of the distance in determining the weights, there is no intrinsic reason for doing so. As was shown in Kane et al. (1982) the results may or may not be sensitive to the choice of the exponent. IWD has a number of disadvantages. First of all it only incorporates the spatial correlation between individual sample locations and the location to be interpolated. Secondly IWD only incorporates distance and not direction in assigning weights to sample data. It does not incorporate non-punctual sample support and does not provide for direct estimation of spatial averages. Finally it is not an exact interpolator. It does have the advantage of not requiring any model assumptions. While the geostatistical interpolator (kriging) does require some model assumptions it does not have the disadvantages noted for IWD. For an overview of geostatistical methods and available public domain software see Myers (1991).

## 4. Interpolation and contouring

Interpolation methods nearly always result in smoothing the data and hence reduce the variability. In appraising the goodness of a contour map one may be tempted to assume smoothness is a desirable characteristic but this may also be misleading. Some measures of the interpolation errors would provide a better gauge of the goodness of a contour map. In particular when the data locations are irregularly spaced the contour map will not be equally reliable in all parts. Unfortunately IWD does not incorporate any measure of the interpolation errors and hence does not provide a measure of goodness for the resulting contour maps. When contour maps are produced from irregularly spaced data the reliability of any portion of a map is directly related to the density of the data locations used in producing the map as well as the interpolation method. Geostatistical techniques have the advantage of providing a measure of the variability of the interpolation errors; other well-known techniques such as thin-plate splines are incorporated as special cases of the

geostatistical interpolators. Geostatistical techniques have been extended to multivariate data and incorporate intervariable as well as spatial correlations.

#### Additional references

Kane, V., Butz, T., Begovich, C. and Myers, D.E. (1982). Interpretation of Regional Geochemistry. *Comp. Geosci.*, 8(2), 117-36.

Myers, D.E. (1991). Interpolation and Estimation with Spatially Located Data. *Chemomet. Intell. Lab. Syst.*, 11, 209-28.

Myers, D.E. (1992). Correspondence Analysis applied to Environmental data sets. In: *Multivariate Environmental Statistics* (G.P. Patil and C.R. Rao, eds) North Holland/Elsevier Science Publishers, Amsterdam. (To appear).

# Discussion

H.J.B. BIRKS

Botanical Institute, University of Bergen

As an ecologist, I was particularly pleased to read Borcard and Legendre (1994) (hereafter B&L) for several reasons. First, it provides a novel and exciting way of identifying and exploring, for the purposes of hypothesis-generation, possible causes of ecological variation operative at a variety of spatial scales. Second, it brings some ecological and geographical life into the display of ordination results, so frequently presented in ecological papers as rather lifeless two-dimensional scatter plots of site scores on axes 1 and 2, etc. Third, it shows that ordination and contour mapping, commonly regarded by many ecologists as totally separate activities (but see, for example, MacDonald and Waters, 1988) can be usefully combined to provide new, effective, and revealing displays of ecological patterns. Fourth, B&L is a fine example of empirical environmental modelling in community ecology. It starts with a simple ecological species-substrate model and progressively improves on this by incorporating further explanatory variables to generate new and increasingly more precise and realistic ecological hypotheses. It is thus a clear example of 'the method of successive approximation' in statistical ecology.

The idea of using constrained ordination techniques such as canonical correspondence analysis or redundancy analysis to detect spatial gradients in ecological data was first presented by ter Braak (1987) and developed by Legendre (1990) and Hill (1991) with the use of quadratic or cubic terms of the basic geographical coordinates. Borcard et al. (1992) exploited this type of analysis, along with ter Braak's (1988) partial constrained ordination techniques, to decompose the variance in species-abundance data into four independent, additive components — a purely environmental component (fraction a in Figure 4 of B&L), a spatially covarying environmental component (fraction b), a purely spatial component (fraction c), and an unexplained component (fraction d). This general variance-partitioning procedure for multivariate ecological 'response variable-type' data has wide potential applicability in statistical ecology (Legendre, 1993). For example, it has now been used to decompose the variance of plant abundances over a 10-year-period into spatial and temporal components (ter Braak and Wiertz, 1993), the variation in late-glacial-pollen stratigraphical data from several sequences into within-sequence temporal and between-sequence