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LOCATING DISCONTINUITIES ALONG ECOLOGICAL GRADIENTS[1]

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Cost-efficient ecological and natural resource surveys need: (1) flexible, logistically simple, and statistically sound sampling methods, and (2) sensitive, computationally simple, and ecologically robust data analysis methods. "Gradsects" (gradient-oriented transects) have recently been shown to be a more efficient sampling method than random sampling using nongradient-oriented transects, especially when surveying large, biologically diverse areas (Gillison and Brewer 1985). If biotic (e.g., vegetation) sampling is oriented along a defined environmental gradient, and the purpose is classification, then simple, efficient analysis techniques are needed. This note briefly reviews appropriate analysis techniques in order to identify ecotones or boundaries along gradsects.

If the vegetation survey or resource inventory is made by sampling at fixed intervals along a steep gradient, then the sampling units (e.g., plots, quadrats, lines) may traverse different biotic zones reflecting underlying environmental (e.g., topographic, soil) discontinuities. And, if the data set obtained at each sampling unit is multivariate (e.g., many species are observed), then these data can be used to locate ecotones separating different biotic zones along the gradsect.

A simple but robust method for locating the boundaries or ecotones between communities sampled along gradsects is the computation of moving split-window distances, a procedure described by Whittaker (1960) who was working on "... quantitative methods by which relative discontinuities ... might be objectively revealed from the transect tables" for his Siskiyou Mountains gradsect data. The basic procedure is: (1) obtain multivariate gradsect data by sampling along a defined gradient; (2) bracket or block a set of sampling positions into a window of preassigned width (i.e., including the data for two or more adjacent sampling positions, as for calculating moving averages; Legendre and Legendre 1983:344); (3) split this window of transect samples into two equal groups; (4) average the data for each variate within each group; (5) compute a distance or dissimilarity between these two groups (Legendre and Legendre 1983:Chapter 6); (6) move the window one position further along the gradsect and compute another distance; and (7) after moving the split-window along the gradsect from one end to the other, with a distance computed for each window midpoint position, plot distances (ordinate) against gradsect positions (abscissa). Sharp, high peaks identify the location of boundaries between adjacent biotic community zones. For continuous gradations the expected graph would be "... points generally at the same level, but with some zig-zag up and down due to chance variations in stand composition" (Whittaker 1960).

As an example, Wierenga et al. (1987) used both squared Euclidean distances (SED) and Hotelling-Lawley trace F values (HLF) with the moving split-window procedure to examine the coincidence of boundaries separating vegetation zones and soil zones along a gradsect in the northern Chihuahuan Desert. Seven vegetation zones were revealed by distance peaks (Fig. 1), which were strongly coincident with eight soil series zones. These results substantiated earlier vegetation–soil studies in the area (Stein and Ludwig 1979). A window width of 10 revealed a smoother pattern of distance peaks, whereas a width of 2 (the SED between adjacent gradsect positions) had greater sample-to-sample noise, as expected. Although SED was used, several other distance coefficients were examined and gave similar results. Any one of several association, similarity, distance, or dependence coefficients (Legendre and Legendre 1983:Chapter 6) could have been used.

When defining soil zones using HLF, Wierenga et al. (1987) reduced the original data set to a smaller set with principal components analysis, as described by Webster (1973). Relative to the simple computation of SED, the HLF calculation is more powerful, but HLF is more complex and is limited to fewer variables (e.g., principal components) and to wider window widths (Wierenga et al. 1987). Many variables can be used to compute SEDs, with a larger number of variables likely to produce a more accurate distance. If a large number of variables is used to compute HLF, window width must also be large, which may obscure boundaries because the window may include two or more boundaries (Webster 1973). In our analysis, varying window width from 6 to 10 did not appreciably affect the interpretation of boundary locations, only the emphasis of certain peaks. Abrupt shifts in community types are evident as high, narrow peaks (e.g., as between zones 5 and 6 in Fig. 1), whereas gradual ecotone shifts or fuzzy community boundaries are evident by wider and lower SED peaks (e.g., as between zones 3 and 4 in Fig. 1).

The technique described above is generally similar, but differs in detail from, other boundary analysis techniques described in the literature. Beals (1969) used the coefficient of dissimilarity or percentage difference (Legendre and Legendre 1983:201) to compare successive adjacent segments of five samples (a split-window with a window width of 10) for two altitudinal gradients in Ethiopia. The vegetation was similar over the two transects. Beals found significant (chi-square test) peaks (dissimilarity), indicating marked vegetation zonation along a 20-km steep gradient, but not along a 300-km gentle slope.

Bratton (1975) used a diversity function and plotted the percentage difference between the first plot and every other plot along a moisture gradient in the Great Smoky Mountains, where abrupt changes in diversity may indicate the location of discontinuities in the gradient, that is, a shift from one zone into another. However, this approach of comparing the very first plot of a gradient with all the other plots along the gradient could lead to the situation where two adjacent, but different, plots could be of about equal dissimilarity to the first plot, and no abrupt change would occur to indicate a shift between the two different communities.

Wilson and Mohler (1983) used a method that measures rates of species turnover along gradients to locate those points that have high rates of turnover. Their method (gradient rescaling) estimates rates of change in beta diversity by computing diversity for pairs of adjacent samples and summing over different intervals (details are provided by Wilson and Mohler 1983). Although they did not specifically examine their gradient rescaling method with the aim of locating ecotones along their simulated gradients, their procedure should accurately locate the presence (or absence) of such discontinuities.

Lange and Sparrow (1985) used interspecific association to measure the homogeneity within sampled blocks (windows), sequentially positioned (moved) across heath and mallee–heath vegetation in South Australia, where "a graph of block associations (ordinate) against sequential block positions (abscissa) reveals intersected homogeneous communities as horizontal low sections separated by sharp peaks." Their results defined four plant communities, substantiating earlier studies in the area (Lange 1966).

The basic moving split-window distance technique (and its variants described above) is specifically aimed at locating discontinuities along gradsects using multivariate data. It differs in aim and detail of computation from related methods aimed at: (1) searching for *repetitive* patterns of response in *one* variable along a *one-dimensional* transect, e.g., spectral analysis, semivariograms, correlograms, periodgrams, etc. (see Legendre and Legendre 1983:Chapter 10; Ludwig and Goodall 1978), (2) predicting, smoothing, or interpolating the response pattern of *one* variable across a *two-dimensional* grid, e.g., Laplacian smoothing splines, kriging, etc. (see Laslett et al. 1986), or (3) classifying community data that repeat due to *multivariate* sampling along *random* transects (or by gradsect sampling along gently undulating gradients), e.g., cluster analysis, association analysis, etc. (Legendre and Legendre 1983:Chapter 7).

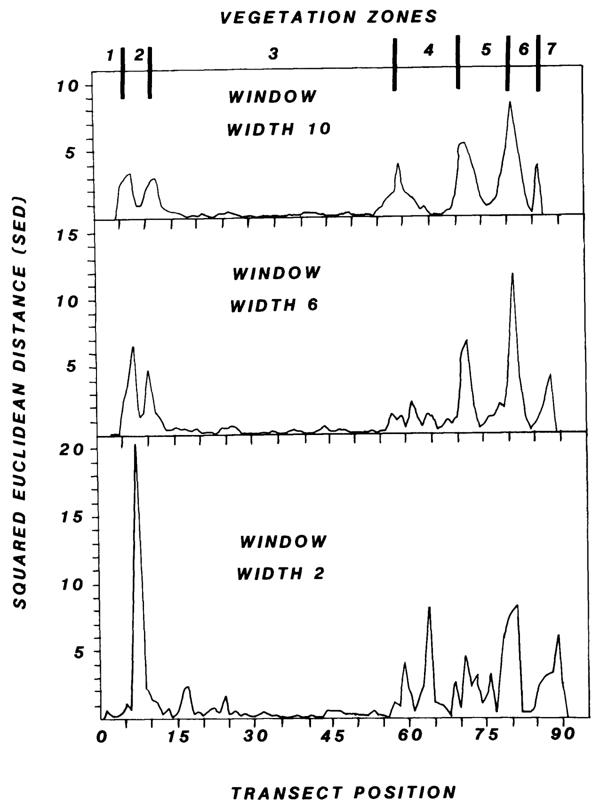

FIG. 1. Peaks of squared Euclidean distance (SED) across 91 positions (starting at position zero with positions 30 m apart) for a 2700-m gradsect in the northern Chihuahuan Desert (the Jornada Long-Term Ecological Research transect) at window widths of 2, 6, and 10 positions, which locate six discontinuities defining seven vegetation zones.

In summary, when gradsect data with many variables measured at fixed intervals are available, the calculation of moving split-window distances provides a sensitive method for locating discontinuities that may exist, thereby defining different zones. The method is applicable to any such multivariate gradsect data, biotic or abiotic (e.g., plant cover, animal abundances, soil properties). In fact, the data need not be from sampling units at fixed intervals along a transect as long as the transect position is known for computing and plotting the split-window distances against transect position. Indeed, the data need not even be strictly from a transect as long as the sampling units can be assigned to a gradient position defined by some factor (e.g., elevation) or some method (e.g., ordination). Further, the technique could be applied to two-dimensional grids of sample stations, where distance peaks or ridges on a surface could reveal discontinuities within two-dimensional space. The technique could also be applied to spatial transect data with repeated observations through time, where distance peaks or ridges on the space–time surface could reveal temporal shifts in spatial boundaries.

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