

Spectral analysis of hummock-hollow pattern in a weakly minerotrophic mire

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Abstract

Periodogram and spectral analyses are used to investigate spatial patterning of vegetation and microelevation in a weakly minerotrophic mire in boreal Ontario, Canada. The results indicate strong deviation from a random series for both patterns, reflecting an underlying hummock-hollow complex of periodicity 1.8 m. Hummocks in the mire appear to have arisen through the accumulation of *Sphagnum* species about the branches of the shrub *Chamaedaphne calyculata*. It is suggested that the mire pattern reflects intraspecific competition in *Chamaedaphne*, and that this pattern is perpetuated through a combination of autogenic and allogenic factors. The results also indicate that the vegetation closely tracks microelevational variation, suggesting habitat partitioning by mire species. The importance of combining descriptive investigations with competition studies and manipulative experiments to further our understanding of vegetation structure and dynamics in mires is discussed.

Nomenclature: for vascular plants follows Gleason, H. A., 1968. The new Britton and Brown flora of the northeastern United States and Canada, Hafner, New York, and for bryophytes Ireland, R. R., Bird, C. D., Brassard, G. R., Schofield, W. B. & Vitt, D. H., 1980. Checklist of the mosses of Canada, Nat. Mus. Can. Publ. Bot. 8.

Introduction

Nutrient-poor mires of northern latitudes are characterized by patterned hummock-hollow complexes (Sjörs 1961). Microtopographic surface patterns result in a habitat mosaic reflecting differences in moisture status, nutrient availability, and acidity (Jasieniuk & Johnson 1982), which in turn underly a complex environmental gradient of elevation above water level (Bellamy & Rieley 1967; Rydin 1985). While individual species of *Sphagnum* have been shown to partition mire habitats according to microelevation (e.g. Sjörs 1948; Vitt *et al.* 1975;

Rydin & McDonald 1985), the overall response of vegetation to this complex gradient remains poorly documented.

Various mechanisms have been proposed to account for the development and dynamics of hummock-hollow complexes in mires (Tallis 1983). Von Post & Sernander (1910) first proposed the idea that hummock-hollow dynamics involves a 'regeneration sequence', in which differential peat accumulation results in cyclical replacement of hummocks and hollows over time. This essentially autogenic model, later formalized by Osvald (1923), appeared to be supported by early studies of peat cores from

various European mires. More exhaustive investigations have often refuted the regeneration cycle model, however, and it is now generally accepted that no single mechanism can account for the diversity of dynamic processes observed in mire habitats (Walker & Walker 1961; Tallis 1983). Studies in northern mires have usually concluded that while hummock-hollow complexes tend to be perpetuated over time, cyclical changes are rather uncommon (e.g. Björk-bäck 1965; Moore 1977). A recent study in Sweden (Svensson 1988) found no evidence for the cyclical regeneration of hummock and hollow communities. Instead, it was suggested that hollows are 'secondary features' which arise following an increase in water level; thus, hummock-hollow dynamics is attributable more to allogenic than autogenic factors.

Whatever the mechanism, the development and perpetuation of hummock-hollow complexes result in the distinctive patterning of mire habitats. While such periodic patterns have often been described (e.g. Sjörs 1961), I am unaware of any studies which have attempted to quantify the description of vegetation pattern in mires. Such an approach can lead to a more complete understanding of the structure and dynamics of hummock-hollow complexes.

A number of methods based on a grid or transect of plots are available for quantifying the description of spatial pattern (Greig-Smith 1983; Upton & Fingleton 1985). The 'quadrat variance' methods accomplish this by examining the variance between plots at different block sizes (or different spacings). The original method proposed was hierarchical ANOVA or grid analysis (Greig-Smith 1952), which was later modified by Kershaw (1957) for use with transect data. This method has a number of drawbacks: it is limited to examining pattern only in powers of two, the results are dependent upon starting position, variance estimates are not independent, and patches and gaps are not distinguished (Pielou 1977). Various methods have been developed to overcome one or more of these problems, including two-term local variance (Hill 1973), random-pairs (Goodall 1974), and stepped block-quadrat analysis (Usher 1975). Comparisons have indicated that no method completely overcomes the problems outlined above (e.g. Ludwig & Goodall 1978; Carpenter & Chaney 1983). Goodall & West (1979) have suggested

that the choice of an appropriate test will depend on the type of pattern analyzed and the questions asked.

Spectral analysis is an alternative to the quadrat variance methods which examines a spatial or temporal trend by Fourier transformation of spatial autocorrelation functions (Ripley 1978). The method is particularly suited to the analysis of a continuous oscillating pattern, such as temporal fluctuations in phytoplankton abundance (Platt & Denman 1975); here, pattern is examined by partitioning an observed trend into a set of additive sine and cosine waves. The method appears to be less suited to the detection of patch size in discrete data (Usher 1975; Carpenter & Chaney 1983). Classical spectral analysis is based on one-dimensional data (e.g. a set of measurements over time, or a transect of contiguous plots). The directional (anisotropic) trends in a spatial pattern must be addressed using two-dimensional spectral analysis (Renshaw & Ford 1984). Unfortunately, two-dimensional grid data could not be obtained in the present study without severely disturbing the fragile peat substrate and its associated vegetation.

In this paper I examine the spatial pattern of vegetation in a weakly minerotrophic basin mire, located in the boreal forest of east-central Ontario, Canada. A continuous, periodically patterned hummock-hollow complex characterizes the site; such a periodic organization in space is typical of many mire habitats (Watt 1947; Sjörs 1961). It was therefore felt that spectral analysis was the appropriate method for investigating spatial pattern in mire systems. The objective of this paper is to quantify the description of community spatial pattern in the mire, and to relate the observed trends to micro-habitat variation at the site.

Methods

Study area

A weakly minerotrophic, undisturbed basin mire near Matatchewan, Ontario, Canada, was chosen for study. The region occurs in the southern portion of the North American boreal forest, and falls with-

in the 'low boreal' wetland region (Zoltai & Pollett 1983). Although drained by the Montreal River, the region contains extensive poorly-drained areas dominated by *Sphagnum* peat. *Picea mariana* (black spruce) is the major tree of these peatlands, while *Pinus banksiana* (jack pine), *Populus tremuloides* (trembling aspen), and *Abies balsamea* (balsam fir) are characteristic of upland habitats.

The climate of the study area is continental. Mean annual precipitation is 780 mm, approximately half of which falls between May and September. Mean annual temperature is 2 °C, with January and July means of -16 °C and +17 °C, respectively.

The vegetation of the study area is typical of the continental North American *Sphagnum* 'lawns' described by Glaser *et al.* (1981). The major peat-forming species include *Sphagnum cuspidatum*, *S. nemoreum*, *S. magellanicum*, and *S. fuscum*. The shrub layer, which consists mainly of the ericaceous species *Chamaedaphne calyculata*, *Kalmia polifolia*, and *Oxycoccus microcarpon*, is interspersed with the sedges *Carex oligosperma*, *C. limosa*, and *Eriophorum angustifolium*. Small, actively layering black spruce are common on higher ground, though they do not occur within the area investigated.

The study site is a 'basin bog' according to the Canadian wetland classification system (Zoltai & Pollett 1983); here, a bog is defined as any peat-covered area with a high water table, overlain by a carpet of *Sphagnum* and often including ericaceous shrubs and sedges. The composition of the vegetation and the groundwater acidity (mean pH = 4.27, $n = 10$) suggest that weakly minerotrophic conditions prevail (Jasieniuk & Johnson 1982; Kenkel 1987). This indicates classification of the site as an acidic, weakly minerotrophic ('poor') fen according to the Swedish classification system (Sjörs 1983). Peat accumulations are greater than 1 m throughout the area studied. During the sampling period (July 30–Aug. 12, 1987), the water table was at the surface of the lowest hollows. Mean elevation above water table for the hummock-hollow complex studied is approximately 17 cm, with a mean hummock height of approximately 33 cm. Maximum hummock height is 45 cm above the water table. The hummocks appear to have arisen as a result of *Sphagnum* accumulation about the branches of

Chamaedaphne calyculata (c.f. Dansereau & Segadas-Vianna 1952).

Sampling

A 100 m transect was located at random within the central (non-treed) portion of the open *Sphagnum* lawn. On July 27, 1987, a surveyor's transit was used to locate stakes at 10 m intervals along the transect, and to position a string 55 cm above the water level. 1000 contiguous 10 × 10 cm plots were located along the transect, and percent cover of all vascular plants and bryophytes recorded in each. In addition, the perpendicular distance from string level to the plot center was measured (later converted to height above water table), and the slopes and aspect of each plot noted. Throughout the sampling period great care was taken to avoid disturbance to the vegetation and substrate along the transect.

Spectral analysis

The methods of pattern analysis used here decompose a spatial series into a set of sine and cosine waves of different amplitudes and wavelengths (Platt & Denman 1975; Ripley 1978). In periodogram analysis, a trended series is partitioned into a set of discrete components, each with a unique angular frequency. A closely related method, spectral analysis, differs in that the sample power density spectrum is assumed to be continuous. In this study the spectral density functions were estimated using the fast Fourier transform (Kendall *et al.* 1983).

Periodogram and spectral analysis methods were applied to both the microelevation and vegetation data. Since these are univariate analytical methods, the microelevation data could be examined directly but the vegetation data (with 18 species) could not. One possible solution is to perform a separate analysis for each species. However, such an approach ignores the complexity of species interactions. The alternative is to first employ a seriation procedure (c.f. Kendall 1971) to obtain an ordering of plots according to their overall species composition. Similar strategies for studying community pattern have been

advocated by Goodman (1979) and Gibson & Greig-Smith (1986). In this study the seriation was obtained through the use of plot scores along the principal axis of correspondence analysis (Benzécri 1969). Unlike other eigenvector methods, the first axis of correspondence analysis normally gives a monotonic ordering of plots with respect to a major underlying gradient (Hill 1974).

In this study, the cumulative periodogram was used to test for deviation from a random pattern (c.f. Ripley 1978), while spectral analysis was used to assess the nature of spatial patterning. Spectral analysis results are generally plotted as the log of the estimated spectral density function against frequency of the series. Peaks in the spectral density function correspond to major periodic trends present over the entire series. In addition to performing spectral analysis on the complete transect series (1000 plots), analyses were also undertaken on each of four 250 plot sectors of the original series. This was done to determine the degree of consistency in the pattern revealed across the entire series (E. D. Ford, pers. comm.).

Correspondence between the spatial trends in vegetation and microelevation was examined by plotting their spectral density estimates together. In addition, cross-spectral analysis (Koopmans 1974) was used to examine the relationship between the two spectral series. Since the density estimates at

each frequency are independent, the analysis must be accomplished component by component. Two values are required to describe spectral density relationships at each frequency: the coherence is a squared correlation specifying amplitude correspondence, while the phase describes lead-lag relationships. Together, the coherence and phase spectra provide a complete description of the relationship between the two spectral series across the entire frequency domain (Koopmans 1974). To further aid in the interpretation of vegetation-elevation relationships, responses of selected species to microelevation were summarized by plotting mean species cover against height above the water table.

Results

The first correspondence analysis axis for the vegetation data ($R^2 = 0.822$, $p < 0.001$) appears to reflect an underlying gradient in microelevation, with a correlation $r = 0.806$ ($p < 0.001$) between the plot component scores and microelevation. Microhabitat occupation with respect to height above the water table for the 12 most abundant species (Fig. 1) reinforces the importance of microelevation in determining species distributions in these hummock-hollow complexes. Species characteristic of lower elevations (close to the water table) such as *Sphag-*

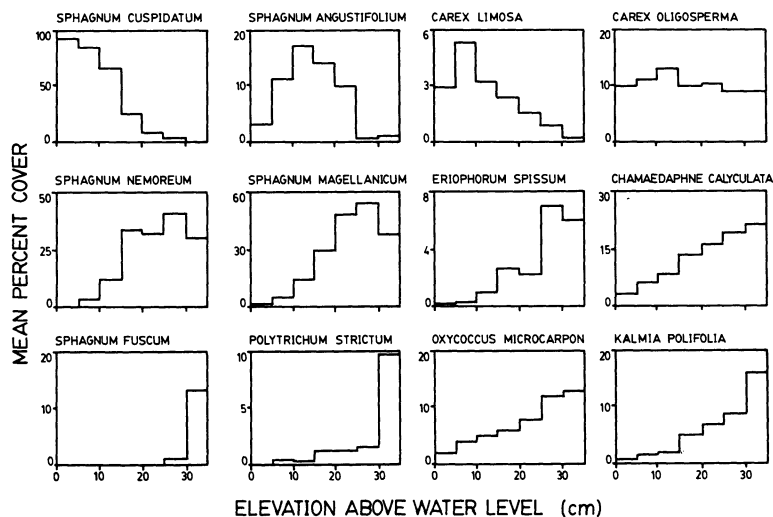


Fig. 1. Mean percent cover of twelve mire species relative to elevation above the July 27, 1987 water level.

num cuspidatum, *S. angustifolium*, and *Carex limosa* had high positive loadings on the first correspondence analysis axis. Conversely, those species occupying higher microelevations (*S. nemoreum*, *S. magellanicum*, *S. fuscum*, *Polytrichum strictum*, *Eriophorum spissum*, *Chamaedaphne calyculata*, *Oxycoccus microcarpon*, and *Kalmia polifolia*) had high negative scores.

The estimated spectral density functions for both the microelevation and vegetation data are shown in Fig. 2a. The corresponding cumulative periodograms (Fig. 2b) indicate strong deviation from a random series, reflecting the presence of regular oscillations in both the microelevation and community spatial patterns. For both patterns, four major peaks in the estimated spectral density functions corresponding to periodicities of approximately 1.8,

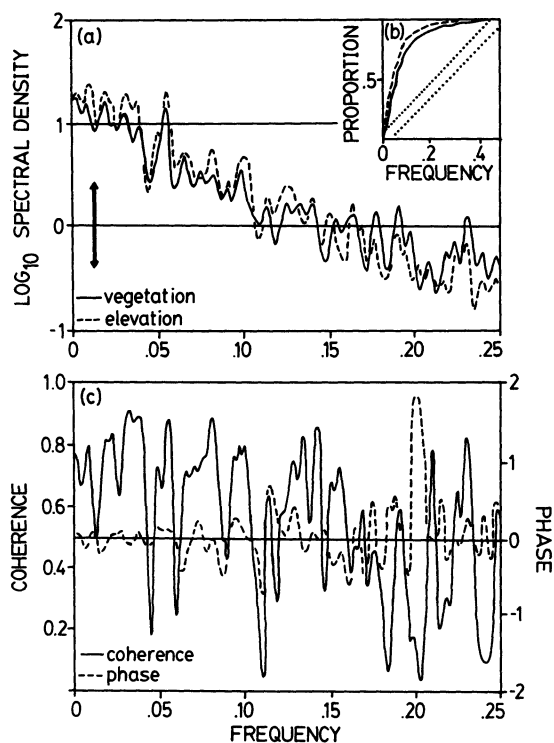


Fig. 2. Pattern analyses of microelevation and vegetation along a transect of 1000 quadrats. For clarity, only the frequency range 0–0.25 is shown, as the remaining portions of the spectra were negligibly small. (a) spectral density function estimates, with 95% confidence interval for each frequency (double arrow), (b) cumulative periodogram, with 95% confidence band (dotted lines), and (c) cross-spectral analysis results, showing the coherence and phase spectra.

2.8–3.3, 5.2, and 12.0 m can be recognized. Three much smaller peaks (spectral density estimates 3–4 times smaller than the four major peaks) corresponding to periods in the 1.0–1.5 m range are also present. The coherence values associated with all peaks exceed 0.8 (Fig. 2c), indicating that the community pattern closely tracks microtopographic variability. Phase spectra values corresponding to the major peaks are close to zero (Fig. 2c), which indicates that the two patterns are closely synchronous.

Spectral analyses of the four 250 plot series (not shown) also indicated peaks at approximately 1.8 and 3.0 m, and three showed a peak in the 5.3–5.6 m range. None showed a strong peak at 12.0 m, presumably because this large period is close to the Nyquist frequency of the 25 m series (Koopmans 1974). These analyses suggest that the major peaks revealed through analysis of the entire series (Fig. 2a) are consistently present.

Perusal of the raw data suggested that the four major peaks are indicative of true spatial trends; none appeared to be an artifact of the spectral decomposition. The smallest major period (1.8 m) is indicative of hummocks which result from the growth of *Sphagnum* species about the branches of a single, large *Chamaedaphne* shrub. Peaks corresponding to the 2.8–3.3 and 5.2 m periods indicate larger hummocks, which appear to have resulted from *Sphagnum* growth about the branches of two or more adjacent *Chamaedaphne* shrubs. Finally, the 12.0 m period is indicative of regions of alternating high and low shrub density along the transect.

Discussion

This study has used spectral analysis to quantify the description of spatial pattern in a mire, and has verified previous qualitative statements regarding the presence of a regular, repeating pattern in such ecosystems (Sjörs 1961). The hummock-hollow complex studied appears to have developed through the establishment and growth of *Sphagnum* about the branches of *Chamaedaphne calyculata*, the most abundant large shrub in the mire. Peat excavations in eastern North America have previously demon-

strated the importance of a branch 'framework' of this species to hummock development (Dansereau & Segadas-Vianna 1952). A similar phenomenon involving *Calluna vulgaris* occurs in European mires (Clymo & Hayward 1982).

The characteristic patterning of mire vegetation has long fascinated ecologists, and various mechanisms have been proposed to explain the development and perpetuation of such a pattern (Tallis 1983). Given that the presence of a regular spatial pattern normally offers strong empirical evidence for competition (Antonovics & Levin 1980), the results of this study suggest that autogenic factors may be important in explaining the development of *Chamaedaphne-Sphagnum* hummock-hollow complexes. Specifically, a regular spatial pattern resulting from competitive interactions between individuals of *Chamaedaphne calyculata* could be an important determinant of patterning in mire vegetation. Accumulation of *Sphagnum* peat about the branches of *Chamaedaphne* shrubs would serve to attenuate this pattern, and would eventually result in the isolation of hummocks from direct ground-water influence (Bellamy & Rieley 1967; Karlin & Bliss 1982).

Once a pattern is established in the mire, both autogenic and allogenic factors could conceivably play a role in its perpetuation. Possible autogenic factors include continued intraspecific competition in *Chamaedaphne*, together with interspecific interactions among *Sphagnum* species (Clymo & Hayward 1982; Rydin & McDonald 1985). In addition, a dynamic degeneration-regeneration process involving the *Chamaedaphne-Sphagnum* hummocks may occur (c.f. von Post & Sernander 1910; Watt 1947). Of the possible allogenic factors, the role of long-term fluctuations in water level has received the greatest attention (e.g. Walker & Walker 1961; Svensson 1988). In boreal regions, seasonal water level fluctuations may also be important. In the study area, sub-surface peat remains frozen throughout the spring snowmelt; this reflects the strong insulating properties of peat (Crampton 1974). As a result water ponds above the frozen peat, accumulating in the hollows. The effect of ponding may be to check the advancement of *Chamaedaphne-Sphagnum* hummocks, thereby maintaining the established mire

pattern (Boatman & Armstrong 1968).

A distinction between the vegetation of hummocks and hollows has long been recognized (Osvald 1923; Du Rietz 1954), and is thought to reflect the response of species to a complex microenvironmental gradient of increasing dryness, acidity, and nutrient deficiency from hollow to hummock top (Clymo & Hayward 1982). That the vegetation closely tracks microenvironmental variation (Fig. 2) is testament to the importance of this gradient in determining community pattern. Experimental evidence indicates that *Sphagnum* species differ in their tolerance to desiccation (e.g. Rydin 1985); all grow well when water is readily available, but few can survive excessive drying (Clymo 1973). Because desiccation tolerance of species is generally uncorrelated with their vertical distribution, it has been suggested that interspecific competition is more important in the hollows, and that hummock species (e.g. *Sphagnum fuscum*) are restricted to drier habitats through competitive displacement (Clymo & Hayward 1982; Rydin 1985; Rydin & McDonald 1985).

The partitioning of microhabitat by *Sphagnum* species found in this study (Fig. 1) largely confirms previous studies in both Europe and North America (e.g. Vitt *et al.* 1975; Clymo & Hayward 1982). The vascular plant species also exhibit microelevational preferences; the only exception is *Carex oligosperma*, a clonal species which forms long, creeping rhizomes. *Oxycoccus microcarpon*, *Eriophorum spissum*, and *Kalmia polifolia*, all of which root in the top few cm of peat (Karlin & Bliss 1982), are found most frequently on hummock tops. *Chamaedaphne calyculata* shows a similar distribution; in this case, however, the plant roots deeply in the peat with only the young shoot tips exposed. *Carex limosa* is the only vascular species showing a preference for hollows. These results suggest that the accentuation of habitat variability following hummock development leads to a concomitant increase in species diversity.

This study has emphasized the importance of quantifying the description of mire pattern in obtaining a more complete understanding of the development and dynamics of hummock-hollow complexes. Spectral analysis has proven to be a useful technique for examining such patterns. Unlike the quadrat variance methods, which assume a 'square

wave' pattern, spectral analysis assumes that a pattern is composed of a series of continuous, oscillating waves (Ripley 1978). This latter model appears to be more in keeping with the observed pattern in mires. A further advantage of spectral analysis is that the relationship between two spectra can be examined using the cross-spectral method.

Additional studies of spatial pattern in mire systems should be undertaken to verify the results presented here. Examination of the anisotropic aspects of mire pattern through the use of two-dimensional spectral analysis (Renshaw & Ford 1984) would be particularly enlightening. Furthermore, detailed field experiments to study competitive interactions among *Sphagnum* species are long overdue, as are investigations of intraspecific competition in *Chamaedaphne calyculata* and the other large shrubs characteristic of mires. The role of fluctuating water levels on mire dynamics is also deserving of greater attention; this should involve both long-term surveys, and controlled experimental manipulation of water levels. It is clear that a complete understanding of the structure and dynamics of mire ecosystems can only come through a pluralistic approach involving both descriptive and experimental investigations.

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