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Multiple landscape scales: An intersite comparison

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Abstract

Vegetation transect data from three locations were analyzed to determine if multiple scales of pattern could be detected. The sites included a semiarid grassland in New Mexico, a series of calcareous openings in a deciduous forest in Tennessee, and a shrub-steppe system in Washington. The data were explored with four statistical techniques. A scale of pattern was accepted if detected by more than one analytical method or located by a single method in multiple taxa. The analyses indicated 3 – 5 scales of pattern on all three sites, as predicted by Hierarchy Theory.

Introduction

Early papers by Watt (1925, 1947) drew attention to the relationship between spatial patterns and ecological processes operating at many spatiotemporal scales. Recent developments in terrestrial (Wiens 1986) and aquatic (Powell 1989) ecology have generated renewed interest in questions of scale (Delcourt *et al.* 1983). Jeffers (1988) has pointed out the need for careful design in data sets and statistical analyses in order to study ecological scales.

Hierarchy theory (Allen and Starr 1982, O'Neill *et al.* 1986) represents a comprehensive theory of ecological scale. The theory proposes that spatial and temporal scales are the natural consequence of nonlinear biotic and abiotic interactions in complex ecological systems (O'Neill 1988). Interacting components operate at similar dynamic rates and are relatively isolated from higher or lower levels (O'Neill *et al.* 1986). As a result, dynamics will tend to be grouped into distinct scales or levels, rather than being uniformly distributed between the fastest and slowest rates (O'Neill 1989).

Since ecological processes help determine spatial patterns in vegetation (Turner, in press), the theory predicts that the hierarchy of process rates should be reflected in a hierarchy of spatial scales on the landscape (O'Neill 1989). Biotic interactions, such as competition and grazing, can generate spatial patterns at scales characteristic of the underlying processes. Levin (1976, 1978) has shown that predator-prey interactions, combined with spatial movement of the populations, can result in a patchy spatial distribution. The scale of the distribution, i.e., size and distance between patches, is determined by the feeding and migration rates. Paine and Levin (1981) showed theoretically and empirically that disturbance-recovery dynamics result in a patchy spatial distribution. The size and distribution of the patches determine the scale of the spatial pattern, and result from the underlying disturbance and recolonization processes. Abiotic constraints, such as topography and soil, can impose additional patterns (Forman and Godron 1986). It is reasonable to expect that this complex organization would be reflected in multiple scales of vegetation pattern on the landscape.

A first step in determining the utility of the theoretical framework, therefore, is the detection of multiple scales of pattern. However, detection of multiple scales cannot be considered a rigorous test of hierarchy theory. A number of landscape scales could result from independent abiotic factors, with climate imposing large patterns and substrate imposing smaller patterns. Therefore, the detection of multiple scales does not demonstrate an underlying hierarchical organization. Nevertheless, the ability to detect multiple scales through field data and statistical analysis is a prerequisite to application and testing of the theory.

Our approach was to examine vegetation transect data from 3 sites in North America using a suite of statistical analyses previously established as useful for detecting spatial scales (Turner *et al.*, in press). The sites included a semiarid grassland in New Mexico, a series of calcareous openings in a deciduous forest in Tennessee, and a shrubsteppe grassland in Washington. The intersite comparison was designed to test the hypothesis that multiple spatial scales could be detected across a variety of ecological systems.

The data

The vegetation data for the semiarid grassland in New Mexico were gathered in 1989 along a 1600-m transect at the Sevilleta National Wildlife Refuge Long Term Ecological Research (LTER) Site, Bernardo, New Mexico by S.J. Turner. The site is a mixture of C_4 perennial and annual species. The data are line-intercept at decimeter resolution, i.e., at each decimeter interval, a plant was recorded if it lay in a vertical slice above or below a stretched measuring tape. The presence-absence data can be converted to canopy cover by summing values over each meter interval and dividing by 10. Data were recorded in four categories, representing the two dominant grasses, ***Boutelouagracilis*** and ***B. eriopoda,*** as well as forbs, and gaps representing bare ground between plants.

The second data set was gathered in April 1989 on the Boeing Tennessee, Inc. property adjacent to the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee by S.J. Turner, M. Cunningham, L. Pounds, L. Mann, and V.H. Dale. The data were collected along a 1319-m line transect through a deciduous forest that included several calcareous opening communities. The protocol for data collection was identical to that used at Sevilleta. The resulting data are composed of taxa characteristic of the calcareous opening communities. Data are reported for various grasses, considered as a single taxon, ***Fragaria virginiana, Juniperus virginiana,*** and gaps representing bare ground between plants.

The third data set was collected at Hanford, Washington from the Arid Lands Ecology Reserve, a shrub-steppe grassland on the Department' of Energy's Hanford Site in south central Washington State. Cover for ***Agropyron spicatum,*** bluebunch wheatgrass, was measured along a NW-SE 2050-m line-intercept transect at an elevation of about 370 m (Carlisle ***et al.*** 1989). Points along the transect where a measuring tape intercepted the beginning and end of discrete bunches of ***A. spicatum*** were recorded. ***A. spicatum*** was chosen because it is the dominant plant species on the study site and grows in discrete bunches with well-defined crowns suitable for measurement with line-intercept methods.

Although the data is extensive, there is only a single transect for each site. Additional transects taken, for example, at right angles, would more adequately sample total site characteristics. Our analyses, therefore, reveal scales of patterns within the sampled transects but may not adequately describe all the spatial processes operating on the landscape.

Analyses

The selection of analytic methods was based on a review of statistical approaches suitable for identifying spatial scale (Turner *et al.*, in press). Based on the review, we chose four methods that we will identify as (1) Hill analysis, (2) Correlation analysis, (3) Ratio analysis, and (4) Spectral analysis. Turner *et al.* (in press) should be consulted for details of the four methods briefly outlined below.

Each technique has weaknesses, but the suite of four analyses complement each other. The strengths of one tend to compensate for the weaknesses of others. Our approach was to accept a scale of pattern only if it was detected by more than one technique and/or located by a single technique in multiple taxa. Our desire to examine each taxon separately precluded the use of multivariate approaches (e.g., Ver Hoef and Glenn-Lewis 1989, Ver Hoef *et al.* 1989).

We also tried to make conservative interpretations. Since our objective was to detect multiple scales, we combined similar scales of pattern. For example, when three different techniques indicated patterns at 20, 22, and 26 m, we assumed these patterns were not generated by different processes but indicated a single pattern in the range of 20-26 m. This approach seems warranted since some of the techniques are imprecise in locating a periodicity, and indicate a neighborhood rather than a precise scale.

The Hill (1973) analysis calculates the mean square error between adjacent transect segments (MSB). All possible pairs of adjacent segments are considered, and the segment length is varied up to 1/2 the total transect length. The MSB reaches local maxima or peaks at segment lengths where the pairs are most different from each other, and local minima or troughs where the pairs are most similar.

Ludwig (1979) noted that when two scales of pattern exist, the Hill technique emphasizes the larger. In our analyses, the Hill technique often missed fine-scaled patterns, *i.e.*, patterns less than 100 m, that were evident from other techniques. The approach detects large-scaled patterns although these patterns often result in broad peaks and troughs. These broad features clearly indicate a pattern, but their breadth makes it difficult to assign a specific periodicity to the pattern (Turner *et al.*, in press). In summary, the Hill analysis may fail to detect fine-scale patterns and is reliable, yet imprecise, for larger scales.

There is a further ambiguity in interpreting results based on the Hill technique (Ripley 1978). In a regularly repeating pattern of solid patches and gaps (e.g., 30 m present, 30 m absent, 30 m present), a peak appears at 30 m and a trough at 60 m. If the repeating pattern is 20-40-20-40 . . ., the trough still appears at 60 m but, surprisingly, the peak remains at 30 m, *i.e.*, one half the periodicity (Errington 1973). Therefore, the trough represents the scale of repetitive pattern, and little credence can be given to peaks at 1/2 the scale of a trough unless the scale is confirmed by other techniques.

To complement the Hill analysis, the Correlation analysis calculates the correlation or similarity between adjacent segments rather than the differences (Carlile *et al.* 1989). The sampling differs from the Hill technique in that 100 random pairs of adjacent segments are chosen for a specified set of segment lengths. This sampling is repeated six times, and the results are averaged to produce the final estimate of correlation for each segment length. For most applications, the Correlation analysis produces results that confirm the Hill analysis. We consistently observed a trough in the Correlation analysis where a peak was observed in the Hill analysis. However, this approach was more reliable than the Hill analysis in detecting fine-scale patterns.

The variance Ratio analysis compares the variance calculated for unit segment lengths with the variance calculated at various longer segment lengths (Carlile *et al.* 1989). Assuming Poisson independence, the ratio should follow a linear relationship with segment length. However, as segment length increases, covariance causes the ratio to deviate from the linear relationship, reach a peak, and then decline. The peak represents a scale at which covariance begins to dominate the calculated ratio. The Ratio analysis results in a single peak, and, therefore, it is only capable of indicating a single scale of pattern. The analysis is very conservative and can result in a flat line with no peak so that no scale can be inferred. Nevertheless, whenever this approach did show a peak, this scale was invariably confirmed by other analyses, particularly at scales between 50 and 150 m.

Spectral analysis (Ripley 1978) fits the spatial data to a model composed of sinecosine pairs of various periods. A regular pattern is indicated when an unusual amount of the total variance is explained by the model term of corresponding period. This technique provides very precise identification of small periodicities because the analysis examines a large number of periodicities at small scales. At the same time, the analysis is very sensitive at small scales, often producing peaks that are not confirmed by other methods. These unconfirmed peaks were not considered in our interpretations. On the other hand, spectral analysis makes few, widely separated estimates at large scales and is relatively imprecise at pinpointing the periodicity of larger-scale patterns.

The transect data can be interpreted either as very fine-scaled (millimeter to decimeter) presence-absence data or as percentage cover if aggregated to slightly larger scales (e.g., one meter). The spectral analysis results differ, depending on the data representation. Thus, the technique was used on both forms of the data.

In general, we accepted scales of pattern for a site that were confirmed across two or more of these analytical methods. The interpretation is complicated, however, when a peak in the Hill analysis falls at the same scale as a peak in the spectral analysis. As stated previously, a peak in the Hill analysis is not reliable for regularly repeating patterns. However, the spectral analysis peaks are reliable, and we retained these scales in our interpretations although, at present, it is unclear what type of underlying pattern would generate these results.

Results

Table 1 presents the scale analyses for the Sevilleta LTER data. Beginning at the smallest scales, the spectral analysis of presence-absence data indicates a pattern at 8–10 m for ***B. gracilis,*** forbs, and ***B. eriopoda.*** Because spectral analysis is very sensitive at small scales, it is not surprising that the 8-10-m pattern is not identified by other analyses. However, the pattern is not spurious since it is evident in three taxa.

The ***B. gracilis*** data show small-scale patterns at 25-26 m and 60 m. The smaller pattern is confirmed by a 20-m peak in the correlation analysis and by 25-m and 26-m peaks in the spectral analyses. Since the spectral analysis is more precise than the Correlation analysis at small scales, we conclude that the data show a peak at 25-26 m. The second confirmed peak at 60 m appears in both the spectral and the Ratio analyses.

The largest pattern in the ***B. gracilis*** data occurs in the neighborhood of 600 m as indicated by a 525-600-m peak in the Hill analysis, a trough at 575 m using Correlation, and a peak at 580-780 m in the Spectral Analysis of percent cover. As noted previously, peaks in the Hill analysis may not accurately reflect data periodicities. However, in this case, the corresponding peak in the Spectral Analysis indicates a pattern at about 600 m.

The forbs show a small scale pattern at 50-60 m (Correlation, Spectral, and Ratio analyses) that is similar to the 60 m pattern in the ***B. gracilis*** data. Because Spectral Analysis is relatively precise at small scales, the 50-53-m pattern (Table 1) could be distinct. However, we will remain conservative and conclude that the data show a single pattern in the 50-60 m range. The forbs also show a pattern between 350 and 650 m based on the Hill and Correlation analyses. This pattern probably cannot be distinguished from the 600-m pattern in ***B. gracilis.*** The Spectral Analysis indicates a peak at 177 m that is unconfirmed by the other methods but may be the same as the 180-200-m pattern in the bareground data. The spectral analysis also indicated peaks at 80, 114, and 300 m that are not confirmed by other analyses or other species and must, for present purposes, be considered as spurious.

Patterns at 10, 22, and 60 m in the Spectral analysis of ***B. eriopoda*** data appear to match the patterns in ***B. gracilis.*** The 60-m pattern is confirmed by the Spectral analyses for both presence/absence and percentage cover and by a peak in the Correlation analysis. The large-scale pattern at 670-680 m appears as a well-defined trough in the Hill analysis,

Table 1. Scale analyses of transect data for ***Bouteloua gracilis, Bouteloua eriopoda,*** Forbs, and Bare Ground at Sevilleta Long Term Ecological Research Site, New Mexico. The analyses are based on four statistical methods and values are expressed in meters.

		B. gracilis	Forbs	***B. eriopoda***	Bare Ground
Hill	peak	525-600	350-650	400-500	200, 500-600
	trough	–	–	680	230
Correlation	peak	20	50	60, 670	60, 230
	trough	575	550	550	180, 600
Spectral	p/a’	< 10, 25, 60	8, 50	10, 22, 60	50
	cover	26, 60, > 580	53, 80, 114, 177, 300	60, 550	65, 400
Ratio		60	60		

‘Presence/absence

Table 2. Scale analyses of transect data for grasses, ***Fragaria virginiana, Juniperus virginiana,*** and Bare Ground at Oak Ridge National Laboratory Environmental Research Park. ,

		Grasses	*F. virginiana*	*J. virginiana*	Bare Ground
Hill	peak	300, 600	300, 600	300, 600, 650	180, 320, 550
	trough	500	100, 350	400, 620	410, 600
Correlation	peak	< 100, 450	120, 350	60, 420	20,410
	trough	300	300	20, 300	300
Spectral	p/a’	80, 180	15, 20, 120	22, 260	18, 24, 200
	cover	87, 180, > 580	27, 125, 650	16, 400	**15, 70, 200**
Ratio			120	60	60

‘Presence/absence.

and is confirmed by a well-defined peak in the Correlation analysis. Since these analyses are relatively precise in locating large-scale patterns, we conclude that the imprecisely located 550-m peak in the Spectral analysis represents the same pattern.

The bareground data show patterns at 50-60 m (Correlation and Spectral analyses) and 400-600 m (Hill, Correlation, and Spectral analyses). In addition there is a pattern in the range of 180 to 230 m. This pattern is confirmed by a peak/trough combination in both the Hill and Correlation analyses.

Table 2 shows the analyses for the Oak Ridge site. The grasses have a pattern at 80-87 m (Spectral Analysis of presence-absence and cover) that probably corresponds to the Correlation peak at < 100 m. The Spectral Analyses indicate another peak in the grasses at 180 m that is confirmed by Hill and Spectral analyses of bareground data. A pattern at 450-500 m is evident from the trough of the Hill analysis and the peak of the Correlation. Finally, there is 600-m peak in the Hill analysis for grasses that is confirmed by a similarly placed peak in the Spectral analysis.

The Spectral Analyses of ***Fragaria virginiana*** indicate one or more small-scale patterns in the 15-27-m range. These patterns are confirmed in the Correlation and Spectral analyses of ***J. virginiana*** and bare ground. A second scale in the range of **100**– 125 m appears in all four analyses of ***F. virginiana*** but appears to be unique to this species. A third pattern appears at 350 m (Hill and Correlation analyses). Finally, there is a pattern in ***E. virginiana*** at 600-650 m that appears as a peak in the Hill analysis and as a peak in the spectral analysis of cover data.

The ***J. virginiana*** data repeat most of the patterns of ***F. virginiana.*** Patterns appear at 16-22 m (Correlation and Spectral analyses, 400-420 m (Hill, Correlation, and Spectral analyses), and 600 m (Hill analysis). An additional peak appears in ***J. vir-***

Table 3. Spatial analyses for transect data on ***Agropyron spicatum*** at the Battelle Pacific Northwest Laboratories Environmental Research Park.

		A. spicatum
Hill	peak	750
	trough	950
Correlation	peak	60
	trough	725
Spectral	p/a’	450
	cover	75, 105, 1000
Ratio		125

‘Presence/absence.

giniana at 60 m (Correlation and Ratio analyses) and is also evident in the bareground data.

The bareground data introduce no additional scales but reflect most of the scales found in the three taxa. There are five scales: 15-24-m (Correlation and Spectral analyses), 60-70-m (Spectral and Ratio analyses), 180-200-m (Hill and Spectral analyses), 410-m (Hill and Correlation analyses), and 600-m that once again shows up as a trough in the Hill analysis.

Table 3 presents the spatial analyses for the A. *spicatum* landscape in Washington. The Correlation analysis indicates a scale at 60 m that probably cannot be differentiated from the 75-m peak in the Spectral analysis of cover. Similarly, the 125-m peak in the Ratio analysis is probably the same as the 105-m peak in the spectral analysis. The largest pattern, at 950– 1000 m (Hill and Spectral analyses) appears to be confirmed but must be considered to be very imprecisely located.

Table 4 summarizes our interpretations across the sites. An asterisk in the table indicates that a scale of pattern was confirmed across methods and/or taxa. In general, every taxon is associated with 3-5 scales. No single scale is found on all sites confirming that there is no artifact introduced by the similar method of data collection or by the analyses.

An additional confirmation of the results is given by the pattern in bareground data at Sevilleta and Oak Ridge. Assuming there we no disturbances, one would not expect bareground to show unique scales, but rather to be “left over space” and reflect patterns determined by the vegetation. Table 4 shows that, as expected, the bareground category mimics scales set by the vegetation and, for the most part, is restricted to the characteristic scales at each site (Table 4).

Each site has three characteristic scales that can be observed in all or most of the taxa. Sevilleta shows scales at 8– 10 m, 50-60 m, and 500-700 m. Oak Ridge shows scales at 15-26 m, 350-500 m, and 500-700 m. Hanford shows scales at 60-75 m, 100– 120 m, and 950– 1000 m.

Conclusions

Based on our analyses, we conclude that multiple scales of vegetation pattern can be detected in transect data from these three sites. Thus, the hierarchical hypothesis of multiple scales of pattern in landscape data is confirmed. Notice, however, that field data over 4 orders of magnitude (mm to decimeter resolution and total extent of 1319 to 2050 m) were required to detect patterns ranging over 2 orders of magnitude (10 m to 1000 m).

The criterion of confirming a scale across several analytical methods and taxa seems a reasonable approach to data exploration and avoids the weaknesses of individual techniques. Because we were exploring patterns, rather than testing hypotheses, it is difficult to make statements about the relative statistical power of the methods. However, examination of Tables l-4 indicates that use of any single statistical technique could produce misleading results. Previous efforts to analyze multi-scaled data (Burrough 1983a, b, Ver Hoef and Glenn-Lewis 1989, Ver Hoef *et al.* 1989) utilized single methods. Our results indicate that explorations with a single method may miss some scales of pattern.

Even though our approach is reasonable, data interpretion requires a significant amount of subjective judgment. The investigator is left to decide if a 60-m pattern detected by one technique is, indeed, the same as a 53-m pattern detected by another approach. As a result, the exact number of scales and their precise periodicity must be considered as preliminary estimates rather than final determina-

Table 4. Summary of scale analyses across sites. Asterisks in the table indicate a specific scale of pattern that is confirmed across analyses and/or taxa.

	8–10	15-26	50-60	60-75	80-87	100–120	170-230	350 500	500–700	950–1000
Sevilleta										
B. gracilis	*	*	*						*	
B. eriopoda	*	*	*						*	
Forbs	*		*				*		*	
Bare Ground			*				*		*	
Oak Ridge										
Grasses					*		*	*	*	
F. virginiana		*				*		*	*	
J. virginiana		*		*				*	*	
Bare Ground		*		*			*	*	*	
Hanford										
A. spicatum				*		*				*

tions. Clearly, exploration must be followed by data collections specifically designed to test hypotheses about individual scales.

Unfortunately, our analyses do not immediately reveal the underlying processes that produced the vegetation patterns. Nevertheless, a close examination of Table 4 and criteria from Hierarchy Theory encourage speculations about potential causes.

According to Hierarchy Theory, we would expect large-scale patterns to result from constraints imposed by higher levels in the system. Patterns could result, for example, from large-scale geomorphological processes patterns in soils. Scaled patterns have been demonstrated in soils (Burrough 1983a), probably caused by abrupt changes in parent materials (Burrough 1983b). Higher level constraints would impose a scale of pattern across the entire plant community and would be seen in all species. Table 4 indicates that scales of pattern about 300 meters satisfy these criteria and may be due to higher level constraints, possibly reflected in soil patterns.

The theory would lead us to expect smaller scale patterns resulting from interactions within the community. Roughgarden (1974) has shown that competition combined with dispersal can interact with small-scale heterogenity to produce pattern. Scales of pattern due to competitive interactions would be shared by two or three competing species, but not necessarily by every population in the community. Table 4 shows that the majority of patterns in this study are shared across two or three species and might, therefore, be caused by competitive interactions.

Patterns can also be caused by “local uniqueness” (Levin 1976). Patches of a single species result when the species is uniquely suited to local conditions. We would expect this mechanism to result in pattern only in the well adapted species. Table 4 suggests that local uniqueness might be the cause of pattern in the monospecific. ***A. spicatum*** system, and in grasses and ***F. virginiana*** in the Oak Ridge data.

Pattern can also result from “phase difference” (Levin 1976). Disturbances open a gap in the community that subsequently undergoes recovery. At any point in time, there will be a mosaic of patches undergoing different stages of recovery. Disturbance processes would cause intermediate scale patterns that would be seen across all species in the community, such as the 50-60 meter pattern in the Sevilleta data (Table 4).

Thus, scales patterns can be caused by patterns in soils, competitive interactions, unique adaptations to local conditions, and disturbance-recovery processes. Each of these processes would lead to specific “signatures” in terms of the scale of the pattern and the number of species involved. The present study (Table 4) leads us to speculate that all of these processes may be involved in the complex patterns detected on the landscape.

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