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5. Heterogeneity and Spatial Hierarchies

Robert V. O’Neill, Robert H. Gardner, Bruce T. Milne, Monica G. Turner, and Barbara Jackson

To apply the traditional scientific method, ecologists ordinarily focus on the mean or central tendency of a data set. For example, a typical hypothesis test would involve demonstrating that the mean is significantly different from a control measurement. However, ecological systems are heterogeneous, and much information may be lost if the variance of a data set is ignored. This chapter shows that a specific prediction of hierarchy theory can be tested by examining how variance changes as measurements are taken across a range of scales.

A number of authors (e.g., MacMahon et al., 1978; Webster, 1979; Eldredge, 1985; SaltAli, 1985) have suggested that hierarchy theory can make significant contributions to the study of ecological systems. The theory views system dynamics as isolated into discrete scales. Interacting entities, such as organisms and populations, operate at a similar spatiotemporal scale and are relatively isolated from dynamics at much larger or smaller scales (Allen and Starr, 1982).

The theory does not maintain that every ecological system must necessarily be hierarchical (O’Neill, 1989). Rather, it points out that stable complex systems often take on such a structure. O’Neill et al. (1986) developed the concept that hierarchical structuring permits complex systems to develop by combining relatively stable lower level systems. Though hierarchical structuring is not the only way to achieve stable complex systems, such structure appears to be common in physical, chemical, and biological
systems (O'Neill et al., 1986). When a level structure is found, the investigator can take advantage of this fact to simplify the investigation of complex systems (Overton, 1972; Allen et al., 1987).

Although the theory shows considerable promise for organizing the study of ecological systems, it is difficult to test theory predictions. As pointed out below, the simplest test requires estimates of heterogeneity of a broad spectrum of time-space scales, and most ecological investigations focus on one or a few scales. However, as McIntosh (1985) pointed out, much of the current interest in scale and hierarchy builds on a considerable tradition of work on vegetation analysis on landscapes (e.g., Greig-Smith, 1957). Therefore it is not surprising that it is at the landscape scale that test data are available.

In the present study the data were available in the form of digitized maps. A digitized map can be sampled at consecutive scales from the finest resolution to the extent of the total map. It provides one of the few sources of data that is virtually continuous over a significant range of scales.

The purpose of this study was to test predictions about how heterogeneity varies with scale on a landscape. First, theoretical predictions were developed on how heterogeneity should change if the landscape is hierarchically structured. Then the predictions were tested by analyzing the patterns sampled on digitized maps of land cover.

### Theoretical Development

The analysis begins with the simple observation that the variance \( S^2 \) associated with an estimate of the mean is inversely proportional to sample size.

\[
S^2 \sim 1/n \quad (1)
\]

Where \( n \) = the number of samples or the size of a sample quadrat. Taking the logarithm of both sides of equation (1) and introducing a proportionality constant \( a \) we find

\[
\ln S^2 = a - \ln n \quad (2)
\]

which is a form of the equation for a straight line. Therefore if \( \ln S^2 \) is plotted as a function of \( \ln n \), the result is a straight line with a slope of \(-1\). This result holds whenever the sample population is randomly distributed in space so that each new sample is independent. However, if spatial correlations exist with correlation coefficient \( r \), the next sample will not be independent and the slope of the log-log plot will lie between \(-1 \) and \( 0 \) \((r = 0)\) and \( 0 \) \((r = 1)\) (Smith, 1938). Wiegert (1962) used this approach to study vegetation on quadrats of different scales. Levin and Buttel (1986) proposed that the deviation of the slope from \(-1\) is a measure of the spatial scale or patchiness of the landscape.

In previous studies it has been assumed that the landscape has no scale structure; i.e., the same structure or pattern occurs at all scales. In contrast, hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986) predicts that complex dynamic systems such as landscapes often have a hierarchical structure. For a hierarchically structured landscape, we would expect processes that affect pattern to be isolated at discrete scales. At these scales, the slope of the \( \ln S^2/\ln n \) relation should be significantly less than \(-1.0\). At intermediate scales, we would expect no pattern, i.e., slopes of \(-1.0\). The expectation, then, is that the log-log plot would appear like a staircase, having discrete scales with shallow slopes (steps) alternating with slopes of \(-1.0\) (risers).

### Materials and Methods

To test the hypothesis we used the land use and land cover digital data produced by the US Geological Survey (Fgegas et al., 1983). Six data tapes were made available through the Oak Ridge Geographic Data Systems Group. The tapes are at a resolution of \(1:250,000\) and contain land use information on a \(200\)-m grid. Each landscape tape contains \(525 \times 850\) grid points. The tapes and land uses used for this study are shown in Table 5.1.

The sampling design involved a set of radiating transects. Starting near the center of the map, 32 line transects radiated outward, separated by approximately \(11.25^\circ\). The shortest transects were 5 grid points (\(1000\) m) in length and the longest was 150 (\(30,000\) m). At each of 30 transect lengths, it was assumed that the 32 transects sampled an area equal to a circle with radius equal to the transect length. The percentage of the grid points along each transect in a specific land use (Table 5.1) was recorded. This method permitted 32 samples at each of 30 scales for estimating mean and variance.

### Table 5.1. Landscape Scenes and Land Uses Used for the Analysis of Heterogeneity

<table>
<thead>
<tr>
<th>Landscape Scene</th>
<th>Abbreviation</th>
<th>Land Use</th>
<th>% Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goodland, Kansas</td>
<td>GD</td>
<td>Grasslands</td>
<td>29</td>
</tr>
<tr>
<td>West Palm Beach, Florida</td>
<td>WP</td>
<td>Grasslands</td>
<td>18</td>
</tr>
<tr>
<td>Macon, Georgia</td>
<td>MC</td>
<td>Forest</td>
<td>54</td>
</tr>
<tr>
<td>Greenville, South Carolina</td>
<td>GV</td>
<td>Forest</td>
<td>62</td>
</tr>
<tr>
<td>Natchez, Mississippi</td>
<td>NZ</td>
<td>Forest</td>
<td>55</td>
</tr>
<tr>
<td>Knoxville, Tennessee</td>
<td>KK</td>
<td>Forest</td>
<td>76</td>
</tr>
</tbody>
</table>

The abbreviations are those used in Table 5.3. Percent cover refers to the percentage of the grid points on the total landscape scene covered by the land use in the third column.
2. More than a single scale (ideally many consecutive scales) would be found on each step and riser. It is possible that a discrete level or the interval between levels could be represented by a single slope (i.e., three consecutive points). However, confidence is increased if there is a series of points representing each step or riser.

For landscapes that satisfied these criteria, a further analysis was applied in the form of piece-wise linear regression. In essence, the analysis takes the first two points and fits them with a straight line. It then estimates the next point. If the estimate is within a criterion supplied by the user (in our case 0.05), the point is lumped with the first two and a new regression calculated. This process continues until the linear regression fails to predict the next data point ± 0.05. At this point a break is defined, and the process begins anew. In this way the fitted curve is a series of linear segments. According to the hierarchical hypothesis, the linear segments should alternate between line segments with slopes close to $-1.0$ and line segments with much shallower slopes.

### Results

The first task was to determine the range of scales that would accurately reflect any hierarchical structuring on the landscape. We are interested in the pattern over the range where the variance behaves according to equation (2). This expected pattern, in fact, occurs only over intermediate scales on the maps. At the smallest scales, i.e., transect lengths between 5 and 10, variance tends to increase with scale. Each successive sample moves into new pattern elements, and the variance increases until a scale is reached that integrates across the microheterogeneity. In general, variance began to follow equation 2 at transect lengths of 10 and larger, but the general criterion was to begin the analysis when the variance turned downward.

At the opposite extreme, variance would rise at the largest scales sampled. Imagine, for example, that you are sampling an area of mixed agriculture and grassland. At the next larger scale, you suddenly cross a barrier such as a river, estuary, or topographical barrier. For subsequent samples, the variance increases until you reach a scale at which both the old and new patterns are being adequately sampled. For most maps, the variance began to increase at transect lengths of about 45. For purposes of our analysis, we ignored scales beyond 45 that showed increased variance. In general, we considered transects from 10 grid points (1,257 hectares) to 45 grid points (25,447 hectares).

There is a potential bias that results from the radial design. At small scales, the transects are close to each other and may show greater correlation than would be expected. If this bias exists, the smallest scales should show shallow slopes. In fact, the variance increases, as explained above.
<table>
<thead>
<tr>
<th>Linear Regression (L2) Range (area)</th>
<th>GD</th>
<th>WP</th>
<th>MC</th>
<th>NZ</th>
<th>KX</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7.14-7.50</td>
<td>7.33-7.66</td>
<td>7.50-7.88</td>
<td>7.68-8.08</td>
<td>7.88-8.28</td>
</tr>
<tr>
<td></td>
<td>0.07</td>
<td>0.03</td>
<td>0.12</td>
<td>0.20</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>0.04</td>
<td>0.09</td>
<td>0.14</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0.60*</td>
<td>0.82*</td>
<td>0.83*</td>
<td>0.81*</td>
</tr>
<tr>
<td></td>
<td>+0.14</td>
<td>+0.07</td>
<td>+0.17</td>
<td>+0.03</td>
<td>+0.17</td>
</tr>
<tr>
<td></td>
<td>-0.07</td>
<td>-0.07</td>
<td>-0.11</td>
<td>-0.12</td>
<td>-0.11</td>
</tr>
<tr>
<td></td>
<td>-1.01*</td>
<td>-0.87*</td>
<td>-0.80*</td>
<td>-0.73*</td>
<td>-0.72*</td>
</tr>
<tr>
<td></td>
<td>+0.44</td>
<td>+0.61*</td>
<td>+0.59*</td>
<td>+0.66*</td>
<td>+0.70*</td>
</tr>
</tbody>
</table>

Each entry represents the slope of three successive samples, covering the range indicated in the first column. Slopes greater than +0.65 are indicated by an asterisk.
Even after the variance begins to decrease, the first slope might be shallow because of this bias. However, on at least one scene, Natchez Table 5.2), the initial slope is steep rather than shallow. Furthermore, for land uses that are distributed randomly, e.g., barren ground at Goodland (Fig. 5.1), the slope of the line is exactly $-1.0$, indicating no bias due to the sample design. It seems, therefore, that the potential bias at small scales does not seriously affect the results presented. Nevertheless, some bias is possible on the first slope after the variance starts to decrease, and it may not be circumstantial that most maps show shallow slopes first. Some caution is necessary when interpreting the first shallow slope as indicating a clear hierarchical level.

An additional source of potential bias is the lack of independence of successive samples, a problem shared by all nested quadrat designs. However, this bias tends to make it more difficult to find breaks in the line, as successive points tend to be similar. Therefore this bias works to make the analysis conservative and increases the confidence one can place in changes in slope when they are located.

As a preliminary indication of the hierarchical structuring discovered in this study, Figure 5.2 shows the data for Goodland, Kansas with line segments fitted by piece-wise linear regression. The data appear to break into six line segments with slopes that alternate from shallow to steep. The curve is in marked contrast to the random, unpatterned data in Figure 5.1. The piece-wise regressions for six landscape scenes are given in Table 5.2. The pattern that most closely matches the expected hierarchical structuring is that of Goodland, Kansas (GD). On this landscape, from 7.14 (1257 ha) to 8.08 (3217 ha) there is a sequence of seven windows showing shallow slopes with the smallest at $-0.03$, followed by an abrupt change over the range from 8.20 (3631 ha) to 8.80 (6648 ha), with seven windows having large slopes, the largest being $-0.93$. This grouping followed by three windows with the smallest slope being 0.27, five windows with slopes reaching $-1.05$, three windows with a smallest slope of $-0.04$, and six windows with slopes up to $=1.07$. There appears clear evidence here of three levels of scale separated by scales showing random distributions.

A multilevel structure also is evident in the data for Macon, Georgia (MC). Here, a set of shallow slopes is followed by a set of steep slopes, then by another set of shallow slopes. The shallow slopes approach 0 and the steep slopes approach $-1.0$.

In the case of West Palm Beach (WP) and Greenville (GV), a similar pattern is evident: shallow, steep, shallow, steep. However, in both cases, the intermediate steep slopes do not approach $-1.0$ ($-0.6$ to $-0.65$). Furthermore, the steep slope is found only over two or three windows. Thus the evidence that there are two distinct scales separated by a random interval is not strong. Nevertheless, the evidence is clear that there is at least one set of patterned scales and another distinct region where the data appear to be random.

For Natchez and Knoxville, there is clear evidence only for one level, either preceded or followed by a random section. There is no clear evidence for a multilevel structure, but there is evidence that pattern exists at one set of scales with conditions approaching randomness at other scales.

Table 5.3 shows the results of the piecewise linear analysis of the four landscape scenes that indicate multiple levels in Table 5.2 Goodland and Macon clearly show the pattern of alternating shallow slopes and slopes approaching $-1.0$. Greenville and West Palm Beach show the predicted pattern, but the steep line segments are far from $-1.0$. The piecewise linear analysis confirms the results obtained by the sliding window analysis: There are line segments that alternate between shallow (correlated or patterned) and steep (uncorrelated or random) slopes.

**Discussion**

The present study demonstrates the importance of analyzing heterogeneity in ecological systems. The analysis permits a test of the prediction of hierarchy theory that complex systems, such as landscapes, are often structured into discrete levels. There is evidence of a multilevel structure on
Table 5.3. Piecewise Linear Regression of Landscape Pattern

<table>
<thead>
<tr>
<th>Landscape</th>
<th>Line Segments</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Begin</td>
<td>End</td>
</tr>
<tr>
<td>Goodland</td>
<td>7.14</td>
<td>8.32</td>
</tr>
<tr>
<td></td>
<td>8.32</td>
<td>9.02</td>
</tr>
<tr>
<td></td>
<td>9.02</td>
<td>9.26</td>
</tr>
<tr>
<td></td>
<td>9.25</td>
<td>9.52</td>
</tr>
<tr>
<td></td>
<td>9.52</td>
<td>9.91</td>
</tr>
<tr>
<td></td>
<td>9.91</td>
<td>10.00</td>
</tr>
<tr>
<td>West Palm Beach</td>
<td>7.81</td>
<td>8.42</td>
</tr>
<tr>
<td></td>
<td>8.42</td>
<td>8.89</td>
</tr>
<tr>
<td></td>
<td>8.89</td>
<td>9.52</td>
</tr>
<tr>
<td></td>
<td>9.52</td>
<td>9.91</td>
</tr>
<tr>
<td></td>
<td>9.91</td>
<td>10.14</td>
</tr>
<tr>
<td>Macon</td>
<td>7.14</td>
<td>8.20</td>
</tr>
<tr>
<td></td>
<td>8.20</td>
<td>8.97</td>
</tr>
<tr>
<td>Greenville</td>
<td>7.33</td>
<td>8.31</td>
</tr>
<tr>
<td></td>
<td>8.31</td>
<td>8.62</td>
</tr>
<tr>
<td></td>
<td>8.62</td>
<td>8.97</td>
</tr>
<tr>
<td></td>
<td>8.97</td>
<td>9.70</td>
</tr>
<tr>
<td>Natchez</td>
<td>7.95</td>
<td>8.89</td>
</tr>
<tr>
<td></td>
<td>8.89</td>
<td>9.12</td>
</tr>
<tr>
<td></td>
<td>9.12</td>
<td>9.26</td>
</tr>
<tr>
<td></td>
<td>9.26</td>
<td>9.40</td>
</tr>
</tbody>
</table>

four of the six landscapes examined, and the evidence appears using two methods for analyzing the data. The conclusion that the levels are not artifacts is confirmed by the fact that the levels do not appear in such land uses, as barren ground (Fig. 5.1), which is unlikely to be hierarchically structured.

The theory does not predict that every landscape must be hierarchically structured, and indeed two of the landscapes examined do not show convincing evidence of a multilevel structure. At the present time we are unable to identify any simple criterion that predicts a priori whether a landscape scene will or will not show a hierarchical pattern. This question seems to be an important one to be addressed by hierarchy theoreticians.

The current analysis raises additional questions for hierarchy theory. For example, it would be interesting to have a prediction of how many hierarchical levels to expect over a given range of scales, e.g., 1,257 to 25,447 hectares. If the theoretical expectation was that the levels should be separated by an order of magnitude, it is not surprising that some of our scenes showed only one level.

One of the most unsatisfying aspects of the current study is that the analysis gives no hint of what is causing the level structure on the land-

scapes. In nested hierarchies, dynamics and pattern at larger scales are the result of interactions among lower level systems. Thus the level structure is generated by dynamics intrinsic to the nested system. There is some evidence that larger-scaled patterns in vegetation can result from such lower level interactions (Anderson, 1971). However, this interaction is not the only way a level structure can be produced. In the case of landscape ecology, it is not at all clear that higher level structure is due to intrinsic dynamics. Each level may represent a new level of constraints imposed on the system from outside. In the present study one suspects, at least, that larger scale patterns are being imposed by topography, coastlines, or patterns in geological variables such as soil. The question of what is causing the level structure detected in our analyses must await further research for resolution.

Summary

Ecologists often focus on controlled experiments in which the central tendency of a data set is of primary interest. However, patterns in the heterogeneity of the data can reveal much about the structure of the system. For example, hierarchy theory predicts that variance will decrease slowly at scales corresponding to hierarchical levels and more rapidly at intermediate scales. This prediction is tested on data for cover types at the landscape scale. On several landscapes, the analysis of heterogeneity revealed the underlying spatial structure of the system.

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References

6. Communities in Patchy Environments: A Model of Disturbance, Competition, and Heterogeneity

Hal Caswell and Joel E. Cohen

All landscapes are to some extent patchy. The biological heterogeneity of communities on patchy landscapes reflects the time scales of local biotic interactions and abiotic disturbance, the time and space scales of dispersal, and (especially) the interaction of these scales. To investigate these factors, we examine here a simple model that provides a framework for building models of patchy communities directly from hypotheses about time scales. The model has numerous applications (Caswell and Cohen, 1991, in preparation); here we focus on the interplay of competition and disturbance as well as the kinds of biological heterogeneity that can be maintained by that interplay.

Our model describes a landscape composed of an effectively infinite set of effectively identical patches. Species colonize these patches, interact, are affected by abiotic disturbance, and eventually become locally extinct. Each of these processes has a characteristic temporal scale, in terms of which we describe the stochastic dynamics of individual patches and the resulting statistical properties of the landscape. Because we assume that all patches are identical, we are providing only the bare minimum of environmental heterogeneity—that produced by the independence of the patches. Our focus is on heterogeneity generated by the biological processes.

Consideration of the interaction of competition and disturbance has led to two important ecological concepts. The first is the idea of fugitive species...