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Spatial and temporal analysis of landscape patterns

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Abstract

A variety of ecological questions now require the study of large regions and the understanding of spatial heterogeneity. Methods for spatial-temporal analyses are becoming increasingly important for ecological studies. A grid cell based spatial analysis program (SPAN) is described and results of landscape pattern analysis using SPAN are presentedd. Several ecological topics in which geographic information systems (GIS) can play an important role (landscape pattern analysis, neutral models of pattern and process, and extrapolation across spatial scales) are reviewed. To study the relationship between observed landscape patterns and ecological processes, a neutral model approach is recommended. For example, the expected pattern *(i.e.,* neutral model) of the spread of disturbance across a landscape can be generated and then tested using actual landscape data that are stored in a GIS. Observed spatial or temporal patterns in ecological data may also be influenced by scale. Creating a spatial data base frequently requires integrating data at different scales. Spatial scale is shown to influence landscape pattern analyses, but extrapolation of data across spatial scales may be possible if the grain and extent of the data are specified. The continued development and testing of new methods for spatial-temporal analysis will contribute to a general understanding of landscape dynamics.

Introduction

A variety of ecological questions now require the study of large regions and the understanding of spatial heterogeneity. Landscape ecology seeks to understand the ecological function of large areas and hypothesizes that the spatial arrangement of ecosystems, habitats, or communities has ecological implications. For example, landscape patterns may influence the spread of disturbance (e.g., Romme and Knight 1982; Franklin and Forman 1987; Turner 1987a), the distribution and persistence of populations (e.g., Van Dorp and Opdam 1987; Fahrig and Paloheimo 1988), 'large herbivore foraging (e.g., Senft *et al.* 1987), the horizontal flow of materials such as sediment or nutrients (e.g., Peterjohn and Correll 1984; Ryszkowski and Kedziora 1987), and other ecologically important processes such as net primary production (e.g., Turner 1987b; Sala *et* al. 1988). Landscape-level phenomena are also receiving increasing attention as questions of global change become more prominent. Therefore, methods to analyze and interpret heterogeneity at broad spatial scales are becoming increasingly important for ecological studies.

The need to consider spatial and temporal scale in ecological analyses has often been noted (e.g., Allen and Starr 1982; Delcourt *et al.* 1983; O'Neill *et al.* 1986; Addicott *et al.* 1987; Getis and Franklin 1987; Meentemeyer and Box 1987; Morris 1987;

Urban *et al.* 1987). Given the dramatic expansion of the range of scales at which ecological problems are posed, this need may be greater than ever. Parameters and processes important at one scale are frequently not important or predictive at another scale, and information is often lost as spatial data are considered at ‘coarser scales of resolution (Henderson-Sellers *et al.* 1985; Meentemeyer and Box 1987). Ecological problems may also require the extrapolation of fine-scale measurement for the analysis of broad-scale phenomena. Therefore, the development of methods that will preserve information across scales or quantify the loss of information with changing scales has become a critical task. Such methods are necessary before ecological insights can be extrapolated between spatial and temporal scales.

Geographical information systems (GIS) of varying complexity have emerged as useful tools in addressing landscape-level research questions. Many current ecological problems can be addressed more easily by using some type of GIS. Such questions might include: How has landscape structure changed through time? What factors control landscape patterns? How does landscape pattern affect ecological processes? Can measures of landscape pattern be directly related to ecological function? How does landscape pattern affect the spread of disturbance? Can landscape changes be predicted using simulation models? How does spatial scale influence the analysis of landscape pattern?

The objectives of this paper are to review several topics in which GIS can play an important role and to highlight current research results. In particular, I will focus on the analysis of landscape data, the use of neutral models of pattern and process, and extrapolation across spatial scales.

Landscape pattern analysis

Before the interaction between landscape structure and ecological processes can be understood, landscape patterns must be identified and quantified in meaningful ways. Landscape mosaics are mixtures of natural and human-managed patches that vary in size, shape, and arrangement (e.g., Burgess and Sharpe 198 1; Forman and Godron 1981, 1986; Krummel *et al.* 1987; Turner and Ruscher 1988). Considerable progress has been made in landscape pattern analysis (e.g., Milne 1988; O’Neill *et al.* 1988; Turner and Ruscher 1988). Many studies employ user-generated computer programs to perform the analyses rather than commercially available GIS. User-generated programs allow the inclusion of customized analytical methods and easy linkages to other programs such as spatial simulation models. Such programs generally lack the advanced graphics capabilities of commercially available GIS, but may have the ability to run on almost any computer. I will describe a spatial analysis program that I developed in FORTRAN and briefly review some of its applications.

Spatial analysis program (SPAN)

SPAN is a grid-cell based analysis program that can be applied to any kind of categorical data (note that SPAN is not related to the commercially available geographic information system, SPANS). The program was developed to quantify landscape patterns and their changes in an ecologically meaningful manner (Turner and Ruscher 1988) and to evaluate the predictions of a spatial simulation model (Turner 1987c, 1988). SPAN can be used with any kind of categorical data that can be rasterized at an appropriate level of resolution. The program provides printed output with some summary statistics and computerized output in the form of data files that can be statistically analyzed using SAS.

SPAN incorporates a series of measures of spatial pattern (Table 1). The fraction of the landscape, p, occupied by each type of data (e.g., cover type) is calculated. Nearest neighbor probabilities, q_{ij} are then calculated, representing the probability of cells of land use type i being adjacent to cells of land use type j. The q_{ij} values are calculated by dividing the number of cells of type i that are adjacent to typej by the total number of cells of type i. Nearest neighbor probabilities can be calculated both vertically and horizontally (even diagonally) such that anisotropism, or directionality, in the spatial pattern can be measured. The degree of

Table 1. Measurements of landscape pattern that are calculated in SPAN.

Variable	Description
P_k	Proportion of the landscape occupied by each category
s, l	Size and perimeter of each patch
d	Fractal dimension of patch perimeters
$E_{i,j}$	Edges between each pair of categories
$q_{i,j}$	Probabilities of adjacency (vertical and horizontal) between categories
H	Diversity index
D	Dominance index
C	Contagion index

anisotropism in a landscape may depend upon topographic or other physical constraints and may also vary with the extent of human influence. The differences between the horizontal and vertical probabilities of adjacency can indicate this directional alignment of spatial components.

The amount of edge between each land use is determined by summing the number of interfaces between adjacent cells of different land uses, then multiplying by the length of a cell (e.g., 100 m for l-ha cells). The amount of edge between all categories is printed, and the edge data files can be statistically analyzed using SAS.

Each patch in the landscape matrix is then identified. A patch is defined as contiguous, adjacent (horizontally or vertically) cells of the same land cover; diagonal cells are not considered to be contiguous. Each patch in the landscape matrix is located, and its size (s) and perimeter (l) are recorded. The number and mean size of patches by any category can then be calculated for each matrix using SAS (SAS Institute 1982). The complexity of patch perimeters is measured using fractal dimensions (Mandelbrot 1983), which can be used to compare the geometry of landscape mosaics (Milne 1988). The fractal is calculated for grid cell data using an edge to area relationship (Burrough 1986; Gardner et *al.* 1987) in which ($l/4$) is the length scale used in measuring the perimeter. To calculate an overall fractal dimension for each or all data categories in a matrix, linear regression analysis of log (N4) against log(s) is done using SAS. The fractal dimension of the patch perimeters is equal to twice the slope of the regression line. In this analysis, the fractal dimension can theoretically range from 1 .O to 2.0, with 1.0 representing the linear perimeter of a perfect square and 2.0 representing a very complex perimeter encompassing the same area.

Three indices (O'Neill et *al.* 1988) based on information theory (Shannon and Weaver 1962) are also included in SPAN. The first index, H, is a measure of diversity:

$$H = - \sum_{k=1}^{m} (P_k) \log(P_k), \qquad (1)$$

where P_k is the proportion of the landscape in cover type k, and m is the number of land cover types observed. The larger the value of H, the more diverse the landscape.

The second index, D, is a measure of dominance, calculated as the deviation from the maximum possible diversity:

$$D = H_{\max} + \sum_{i=1}^{m} (P_k) \log(P_k), \qquad (2)$$

where m = number of land use types observed on the map, P_k is the proportion of the landscape in land use k, and $H_{\max}$ in Eq. 2 normalizes the index for differences in number of land cover types between different landscapes; the terms in the summation are negative, so Eq. 2 expresses the deviation from the maximum. Large values of D indicate a landscape that is dominated by one or a few land uses, and low values indicate a landscape that has many land uses represented in approximately equal proportions. However, the index is not useful in a completely homogeneous landscape (i.e., m = 1) because D then equals zero.

The third index, C, measures contagion, or the adjacency of land cover types. The index is calculated from an adjacency matrix, Q, in which $Q_{i,j}$ is the proportion of cells of type i that are adjacent to cells of typej, such that:

$$c = K_{max} + \sum_{i=1}^{m} \sum_{j=1}^{m} (Q_{i,j}) \log (Q_{i,j}), \quad (3)$$

where K_{max} = 2 m log(m) and is the absolute value of the summation of $(Q_{i,j})\log(Q_{i,j})$ when all possible. The summation term is negative, and Eq. 3 gives the deviation from the maximum possible contagion. K_{max} normalizes landscapes with differing values of m and causes C to be zero when m = 1 or all possible adjacencies occur with equal probability. When $m \geq 2$, large values of C will indicate a landscape with a clumped pattern of land cover types.

Landscape pattern analysis using SPAN

SPAN was used by Turner and Ruscher (1988) to determine how landscape patterns in Georgia (southeastern U.S.) had changed during the past 50 years and whether the patterns varied by physiographic region. Historical aerial photography from the 1930's to the 1980's was digitized in grid cell format and analyzed using SPAN.

Changes in the landscape pattern through time were identified. The Georgia landscape has become less fragmented and more connected, as indicated by a general decrease in edges, fractal dimensions, contagion, and dominance. Forests, the natural vegetative cover, became more connected, increasing in aerial extent and in mean patch size. The dominant types of edge changed qualitatively (from transitional-agricultural and transitional-hardwood to agricultural-pine and pine-hardwood), reflecting the successional changes that followed cropland abandonment. The changes observed in the Georgia landscape contrast with the decreased connectively observed in other areas of the U.S. (Burgess and Sharpe 1981; Whitney and Somerlot 1985; Sharpe *et al.* 1987) and many European countries (e.g., Van Dorp and Opdam 1987).

Regional differences in the Georgia landscape were identified. The piedmont and mountain regions were most-patchy, whereas the coastal plain had fewer and larger patches. Complex patch perimeters, as indicated by higher fractal dimensions, were observed in the mountains and piedmont; simpler shapes were observed in the coastal plain. The highest diversity and most edges were observed in the mountains, and there was a geographic trend of decreasing diversity and increasing dominance and contagion from the mountains to the lower coastal plain. Thus, broad-scale topographic patterns and physiography may be reflected in the landscape patterns. Other studies (e.g., Swanson et *al.* 1988) have also suggested the importance of landforms in controlling landscape pattern.

Landscape components that were less influenced by humans (e.g., hardwood forests) tended to be more complex in shape than those which received greater human influence (e.g., urban or agricultural lands). Similar results have been reported for other sections of the United States (Krummel *et al.* 1987). The observed complexity of patches of transitional land and lower deciduous forest may reflect topographic or edaphic patterns.

Several of these indices may provide different information at different spatial scales. Using a data set that covers most of the eastern U.S., O'Neill *et al.* (1988) used three indices (dominance, contagion, and fractal) to discriminate among major landscape types such as urban coastal landscapes, mountain forest, and agricultural areas at one point in time. In the Georgia study, Turner and Ruscher (1988) observed significant changes in the diversity and dominance indices through time but not among physiographic regions. In contrast, contagion, which identifies finer-scaled aspects of pattern (O'Neill *et al.* 1988) differed significantly among physiographic regions but not through time. Edges and patch sizes, which describe even finer detail, varied significantly in Georgia both through time and among regions. Thus, broad-scale measures of pattern may be useful to detect large temporal changes but may be less useful to differentiate spatial patterns within a biotic province.

Neutral models of landscape pattern

Once landscape patterns have been quantified, understanding their causes and potential effects on ecological processes is of tremendous interest. Geographic information systems can play an important role in such studies if explanatory variables are included in the spatial data base; However, the relationship between observed landscape patterns and an ecological process can only be rigorously tested if the expected pattern in the absence of the process is known (Gardner *et al.* 1987). This type of expected pattern has been termed a 'neutral model' (Caswell 1976). Neutral models can be used to measure the improvement in predictability which may be achieved by modeling topographic, climatic, and disturbance effects, for which data are frequently contained in a GIS.

The movement of disturbances across landscapes is being studied in a neutral model context by Turner *et al.* (1988, 1989a) using percolation theory (Stauffer 1985; Orbach 1986; Gardner *et al.* 1987). A landscape can be characterized in terms of habitat that is susceptible to a particular disturbance (e.g., pine forests susceptible to bark beetle infestations) and habitat that is not susceptible to the disturbance (e.g., hardwood forests, grasslands, etc.). The spatial arrangement of the disturbance-susceptible habitat can be randomly generated at' probability p on an appropriately scaled percolation map, and the propagation of disturbances that spread within the susceptible habitat may then be studied. Turner *et al.* focused on two disturbance characteristics, intensity and frequency, as they interact with landscape pattern. Disturbance frequency is defined as the probability that a new disturbance will be initiated in a unit of susceptible habitat at the beginning of the simulation. Intensity is defined as the probability that the disturbance, once initiated, will spread to adjacent sites of the same habitat. The spread of a disturbance across a landscape is then predicted as a function of (1) the proportionof the landscape occupied by the disturbance-prone cover type, (2) disturbance intensity, and (3) disturbance frequency.

The neutral model of disturbance quantitatively predicted the spread and effects of disturbance on the susceptible habitat and identified a critical threshold in the spatial pattern. Disturbance propagation and effects on landscape pattern were qualitatively different when the proportion (p) of the landscape occupied by disturbance-susceptible habitat was above or below the percolation threshold (p_c) (Fig. 1). (The percolation threshold is the probability at which the largest patch or cluster can span the entire grid and is approximately 0.5928). The distribution and spatial arrangement of the susceptible habitats helps explain these differences. Habitats occupying less than p_c tend to be fragmented, with numerous, small patches, and low connectivity (Gardner *et al.* 1987). The spread of a disturbance was constrained by this fragmented spatial pattern, and the sizes and numbers of clusters were not substantially affected by the intensity (i) of disturbance. Habitats occupying more than p_c tend to be highly connected, forming continuous clusters (Gardner *et al.* 1987). Disturbance could spread through the landscape even when frequency was relatively low.

The neutral model of disturbance propagation can be tested using landscape pattern and disturbance data for actual landscapes. A digitized map of the habitat types in the landscape would be required, and a temporal sequence of landscape patterns before and after disturbances would be particularly useful. Data for landscapes that have different spatial patterns but are susceptible to the same disturbance (e.g., fire or pest outbreak) might also be used. In addition, data on the number of initiations, the rate of spread, and the spatial extent of disturbance would be necessary. Knowledge of a few parameters that describe landscape heterogeneity and the propagation of disturbance may provide useful insights for predicting landscape effects.

The expected patterns of a variety of ecological phenomena (e.g., spatial distribution of species) can also be studied using a neutral model approach. For example, the suitability of a landscape for particular species (e.g., Palmeirim 1988) could be predicted, and boundary phenomena (e.g., Wiens *et al.* 1985; Schonewald-Cox 1988) could be studied. As the use of GIS becomes increasingly widespread, it will become more important to consider expected patterns in the absence of specific processes before the observed patterns can be explained.

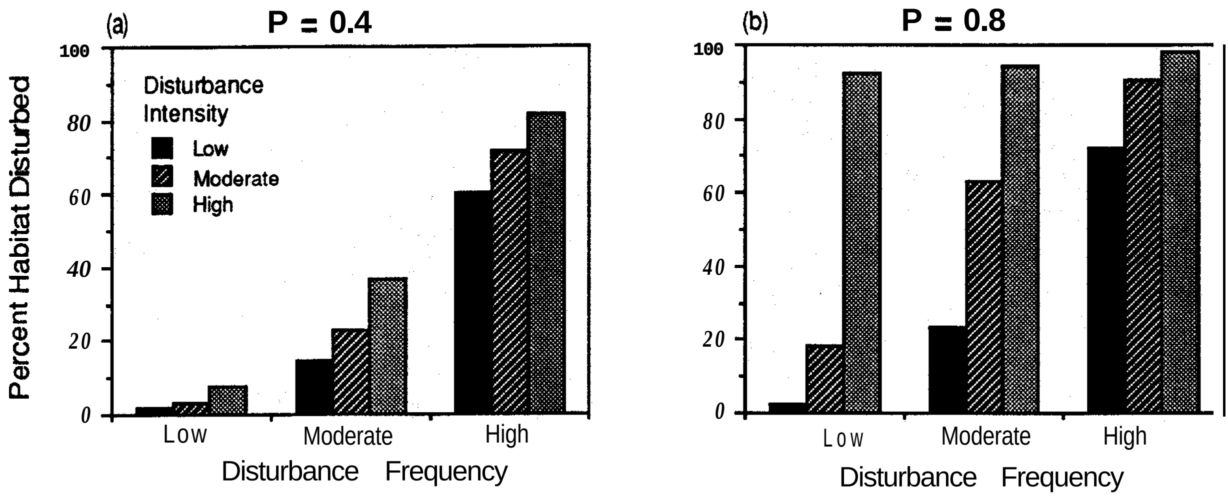

Fig. 1. The percent of susceptible habitat on a random landscape that is affected by disturbances of different frequency and intensity when the proportion of susceptible habitat was (a) below or (b) above the critical threshold (p_c = 0.5928). When $p < p_c$, disturbances frequency has a greater influence than intensity, whereas when $p > p_c$, disturbance intensity is very important even when frequency is low. (Adapted from Turner et al. 1989a).

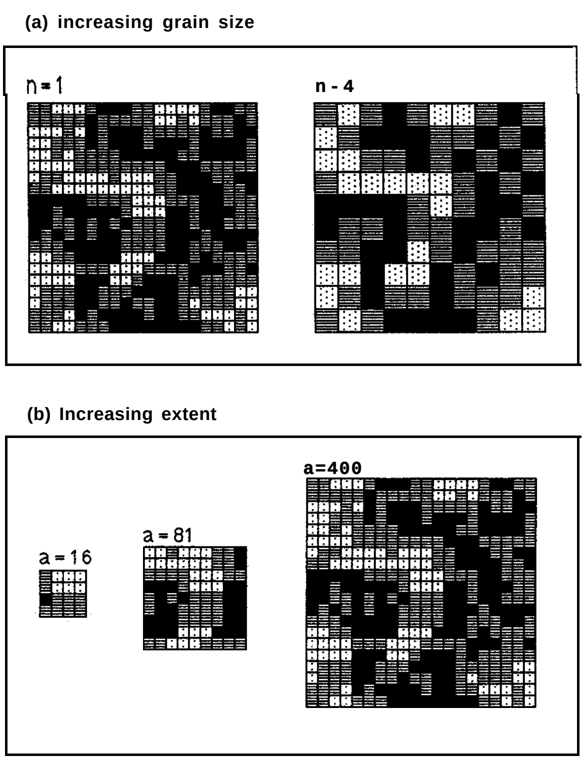

Fig. 2. Illustration of changing two components of spatial scale, grain and extent. (a) Grain size refers to the resolution, *n*, of each data unit. (b) Extent refers to the size of the study area, a. Changes in grain and extent affect the measurement of landscape pattern in different ways. (from Turner et al. 1989b).

Extrapolation across spatial scales

The patterns observed in ecological data may be influenced by spatial scale. In studies of landscape structure or function, information may be available at a variety of levels of resolution, data must often be compared across large geographic regions, and it may be necessary to extrapolate information from local to regional scales. Applications of GIS also frequently require the integration of data obtained at different spatial scales. It is therefore important to develop an understanding of and ability to predict changes in ecological phenomena with changes in scale.

The spatial scale of ecological data encompasses both grain and extent (Fig. 2). Grain refers to the resolution of the data, *i.e.*, the area represented by each data unit. For example, a fine-grain map might organize information into l-ha units, whereas a map with an order of magnitude coarser resolution would have information organized into 10-ha units. Extent refers to the overall size of the study area. For example, maps of 100 km^2 and 100,000 km^2 differ in extent by a factor of 1000. The effects of grain and extent are of particular concern, and the responses of ecological parameters measured on the landscape to changes in spatial scale are not known. It has been suggested (Allen et *al.* 1987) that information can be transferred across scales if both grain and extent are specified.

Turner et *al.* (1989b) used an experimental approach to study the effects of spatial scale on landscape pattern. The purpose of the study was to observe the effects of changing the grain (the finest level of spatial resolution possible with a given data set) and extent (the total area of the study) of landscape data on observed spatial patterns and to identify some general rules for comparing measures obtained at different scales. Simple random maps, maps with contagion (i.e., clusters of the same land cover type), and actual landscape data from USGS land use (LUDA) data maps were used in the analyses. Landscape patterns were compared using indices measuring diversity (*H*), dominance (*D*) and contagion (*C*). Rare land cover types were lost as grain became coarser. This loss could be predicted analytically for random maps with two land cover types, and it was observed in actual landscapes as grain was increased experimentally. What was particularly interesting, however, was the manner in which the spatial pattern influenced the rate at wwhich information was lost as grain became coarser. Although less dominant cover types always declined, cover types that were dispersed were lost most rapidly and cover types that were clumped were lost most slowly. The diversity index decreased linearly with increasing grain size, but D and C did not show a linear relationship. The indices *D* and *C* increased with increasing extent, but *H* exhibited a variable response. The indices were sensitive to the number (m) of cover types observed in the data set and the fraction of the landscape occupied by each cover type (P_k); both m and P_k varied with grain and extent.

The results demonstrated how the spatial scale at which landscape patterns are quantified can influence the result, and that measurements made at different scales may not be comparable. Qualitative and quantitative changes in measurement across spatial scales will differ according to how scale is defined. Therefore, the definition and methods of changing scale must always be explicitly stated. It is important to define the scale of ecological data in terms of both grain, S_g, and extent, S_e. The identification of properties that do not change or change predictably across scales would simplify the extrapolation of measurements from fine scales to broad scales. Characterizing the relationships between ecological measurements and the grain and extent of the data may make it possible to predict or correct for the loss of information with changes in spatial scale. More importantly, the ability to predict how ecological variables change with scale may open the door to extrapolating information to larger scales and to comparing data measured in different regions.

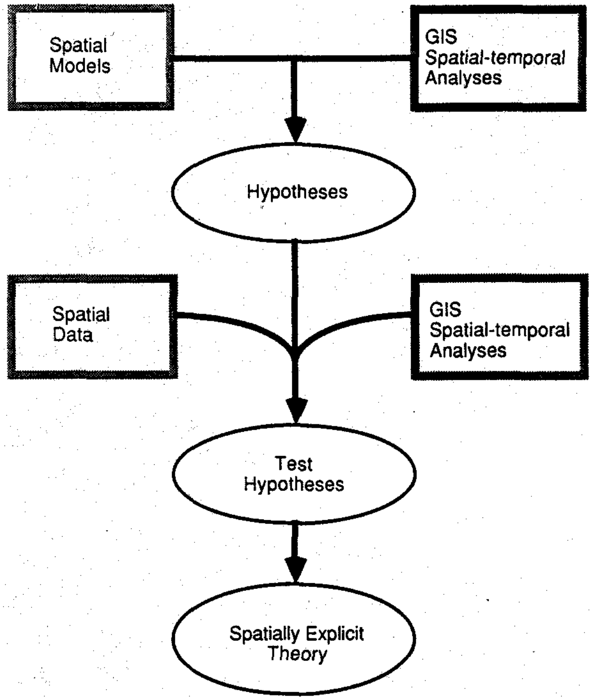

Fig. 3. Illustration of how models, GIS, and data can contribute to the development of theory that addresses the ecological implications of spatial patterns. These methods make it possible to generate and test landscape-level hypotheses.

Conclusion

Spatial-temporal analysis in ecology promises to provide additional insight into ecological processes at a variety of scales. Hypotheses at the landscape level can now be generated and tested by combining models, spatial-temporal analyses, and spatially explicit data (Fig. 3). Analytical methods are neces-

Table 2. General hypotheses that can now be tested by using models, data, and spatio-temporal analyses.

Measures of landscape pattern can be directly related to ecological processes at different scales.
Landscape patterns can be predicted using a small set of ecological variables.
Predictive variables differ with’ spatial and temporal scale.
Landscape effects on ecologically important parameters can be detected by comparing expected patterns (i.e., neutral models) and observed patterns.
There are critical thresholds in the spatial patterns in the landscape at which ecological processes will qualitatively change.
The spatial spread of disturbance can be predicted using a few parameters describing landscape heterogeneity and disturbance characteristics.
Information may be extrapolated across spatial scales if the grain, extent, and contagion of the data are known.

sary for changes or differences in spatial patterns to be identified. Therefore, these methods are also necessary for the development of ecological theory that incorporates the implications of spatial arrangement. Models’can be constructed to improve our theoretical understanding of spatially influenced phenomena, just as experiments are conducted to improve understanding of an empirical problem (Caswell 1988). Combining spatial-temporal analyses with models permits the development of hypotheses that can then be empirically tested using spatial data.

The selection of particular methods of analysis (e.g., user-generated programs or the many commercial GIS systems) depends upon the objectives of a particular study and the available equipment. The analysis programs described in this paper are relatively simple and were developed to answer specific landscape-level questions. The programs are easy to run and interpret and can be applied to any categorical data that are in raster format. Analysis programs such as SPAN can also be linked with spatial simulation models and used to test the goodness-of-fit between model predictions and landscape data.

The results reviewed in this paper suggest some directions for future research. Simple indices and measures such as those presented here can capture aspects of landscape pattern at different scales. Significant changes in landscape patterns through time and differences across regions can be identified. These analyses could be applied to a variety of data in a GIS to determine how the patterns of different variables were related. The measures also show promise of relating to ecological processes (e.g., disturbance), but more research is required to elucidate the linkage between pattern and process.

Neutral models may be extremely useful in identifying the factors causing landscape patterns or the effects of ecological processes. The disturbance model presented here is one example of a neutral model relating pattern and process; many others could be developed. Data that are in a GIS can be used to test neutral models and determine how the addition of ecological factors improves predictability. The existence of critical thresholds (e.g., p_c) beyond which dramatic changes occur could also be tested using a GIS.

Spatial scale influences the analysis of landscape data, and the comparison of data obtained at different scales may not be straightforward. Rules for extrapolating across spatial scales may be possible, but scale must be defined and specified in terms of grain and extent. Considerable additional research is required to develop a more complete understanding of the relationship between scale and the patterns and processes observed on the landscape.

With the availability of GIS and other methods of spatial-temporal analysis, hypotheses can now be tested at broad spatial scales. Some general hypotheses that emerge from the research reviewed here are presented in Table 2. These hypotheses could be tested using appropriate ecological processes in actual landscapes. New methods of analysis will continue to be developed and tested as ecological research focuses on broader spatial and temporal scales. The development of robust analytical methods, models, and experiments that provide unique insights into ecological processes will contribute to a general theory of landscape dynamics.

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Literature cited

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. and Soluk, D.A. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340-346.

Allen, T.F.H. and Starr, T.B. 1982. Hierarchy. University of Chicago Press, Chicago.

Allen, T.F.H., O'Neill, R.V. and Hoekstra, T.W. 1987. Interlevel relations in ecological research and management: some working principles from hierarchy theory. Journal of Applied Systems Analysis 14: 63-79.

Burgess, R.L. and Sharpe, D.M., eds. 1981. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

Burrough, P.A. 1986. Principles of geographic information systems for land resources assessment. Clarendon Press, Oxford.

Caswell, H. 1976. Community structure: a neutral model analysis. Ecol. Monogr. 46: 327-354.

Caswell, H. 1988. Theory and models in ecology: a different perspective. Bull. Ecol. Soc. Amer. 69: 102-109.

Delcourt, H.R., Delcourt, P.A. and Webb, T., III. 1983. Dynamic plant ecology: The spectrum of vegetation change in space and time. Quaternary Science Review 1: 153-175.

Fahrig, L. and Paloheimo, J. 1988. Effect of spatial arrangement of habitat patches on local population size. Ecology 69: 468-475.

Forman, R.T.T. and Godron, M. 1981. Patches and structural components for a landscape ecology. Bioscience 3 1: 733-740.

Forman, R.T.T. and Godron, M. 1986. Landscape Ecology, John Wiley & Sons, New York.

Franklin, J.F. and Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1: 5-18.

Gardner, R.H., Milne, B.T., Turner, M.G. and O'Neill, R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology 1: 19-28.

Getis, A. and Franklin, J. 1987. Second-order neighborhood analysis of mapped point patterns. Ecology

Henderson-Sellers, A., Wilson, M.F. and Thomas, G. 1985. The effect of spatial resolution on archives of land cover type. Climatic Change 7: 391-402.

Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V. and Coleman, P.R. 1987. Landscape patterns in a disturbed environment. Oikos 48: 321-324.

Mandelbrot, B.B. 1983. The fractal geometry of nature. W.H. Freeman and Co., San Francisco, CA.

Meentemeyer, V. and Box, E.O. 1987. Scale effects in landscape studies. In: Landscape heterogeneity and disturbance. pp. 15-34. Edited by M.G. Turner. Springer-Verlag, New York.

Milne, B.T. 1988. Measuring the fractal dimension of landscapes. Appl. Math. Comp. 27: 67-79.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology 68: 362-369.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B. and Allen, T.F.H. 1986. A hierarchical concept of ecosystems. Princeton University Press, New Jersey.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H. and Graham, R.L. 1988. Indices of landscape pattern. Landscape Ecology 1: 153-162.

Orbach, R. 1986. Dynamics of fractal networks. Science 231: 814-819.

Palmeirim, J.M. 1988. Automatic mapping of avian species habitat using satellite imagery. Oikos 52: 59-68.

Peterjohn, W.T. and Correll, D.L. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65: 1466-1475.

Romme, W. and Knight, D.H. 1982. Landscape diversity: the concept applied to Yellowstone Park. Bioscience 32: 664-670.

Ryszkowski, L. and Kedziora, A. 1987. Impact of agricultural landscape structure on energy flow and water cycling. Landscape Ecology 1: 85-94.

Sala, O.E., Parton, W.J., Joyce, L.A. and Lauenroth, W.K. 1988. Primary production of the central grassland region of the United States. Ecology 69: 40-45.

SAS Institute. 1982. User's guide: statistics. SAS Institute, Cary, North Carolina.

Schonewald-Cox, C. 1988. Boundaries in the protection of nature reserves. Bioscience 38: 480-486.

Senft, R.L., Coughenour, M .B., Bailey, D. W., Rittenhouse, L.R., Sala, O.E., and Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37: 789-799.

Shannon, C.E. and Weaver, W. 1962. The mathematical theory of communication. University of Illinois Press, Urbana.

Sharpe, D.M., Guntenspergen, G.R., Dunn, C.P., Leitner, L.A. and Stearns, F. 1987. Vegetation dynamics in a southern Wisconsin agricultural landscape. In: Landscape heterogeneity and disturbance. pp. 139–158. Edited by M.G. Turner. Springer-Verlag, New York.

Stauffer, D. 1985. Introduction to percolation theory. Taylor and Francis, London.

Swanson, F. J., Kratz, T.K., Caine, N. and Woodmansee, R.G. 1988. Landform effects on ecosystem patterns and processes. Bioscience 38: 92-98.

Turner, M.G., ed. 1987a. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

Turner, M.G. 1987b. Land use changes and net primary production in the Georgia landscape: 1935 to 1982. Environ. Manage. 11: 237-247.

Turner, M.G. 1987c. Spatial simulation of landscape changes in Georgia: a comparison of 3 transition models. Landscape Ecology 1: 29-36.

Turner, M.G. 1988. A spatial simulation model of land use changes in Georgia. Appl. Math. Comp. 27: 39-51.

Turner, M.G. and Ruscher, C.L. 1988. Changes in the spatial patterns of land use in Georgia. Landscape Ecology 1: 241-251.

Turner, M.G., Gardner, R.H., Dale, V.H. and O'Neill, R.V. 1988. Landscape pattern and the spread of disturbance. *In:* Proc. VIIIth Intl. Symp. Probs. Landsc. Ecol. Res., Vol. 1. pp. 373-382. Edited by M. Ruzicka, T. Hrnciarova, and L. Miklos. Institute of Experimental Biology and Ecology, CBES SAS, Bratislava, Czechoslovakia.

Turner, M.G., Gardner, R.H., Dale, V.H. and O'Neill, R.V. 1989a. Predicting the spread of disturbance in heterogeneous landscapes. Oikos. 55: 121-129.

Turner, M.G., O'Neill, R.V., Gardner, R.H. and Milne, B.T. 1989b. Effects of changing spatial scale on the analysis of, landscape pattern. Landscape Ecology 3(3/4): 153-163.

Urban, D.L., O'Neill, R.V. and Shugart, H.H. 1987. Landscape ecology. Bioscience 37: 119– 127.

Van Dorp, D. and Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landscape Ecology 1: 59-73.

Whitney, G.T. and Somerlot, W.J. 1985. A case study of woodland continuity and change in the American midwest. Biol. Conserv. 31: 265-287.

Wiens, J.A., Crawford, C.S. and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421-427.