20. Future Directions in Quantitative Landscape Ecology[1]

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20.1 Introduction

Landscape studies have always posed difficult quantitative problems for ecologists. Although many different variables may be measured, repeated observations in time and space are not often available at the landscape scale. This situation results in what Allen and Starr (1982) refer to as the dilemma of middle number systems, which lack a clear means of identifying cause and effect relationships. While these issues are not new to ecology (Hurlbert 1984), the traditional solution is the controlled experiment, which may be difficult or impossible at the landscape scale. When one is embarking on a landscape-level study, therefore, it is prudent to examine the broad spectrum of analysis and simulation methods available and choose those which best address the problem at hand and have the most quantitative rigor.

20.2 Quantitative Analyses and Models in Landscape Ecology

This book presents a diversity of tools and techniques from a variety of fields, offering new methods and approaches to the quantitative analysis problem at the landscape scale. This comes at an appropriate juncture in ecological research

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because the availability of key techniques affects the kinds of questions that are asked. This feedback is important—the advent of new techniques helps stimulate new avenues of research, which, in turn, generate new questions. However, a note of caution is appropriate regarding new approaches. It is important to recognize that the inappropriate application of a technique can result in incorrect answers to important questions. Thus, as with any analysis, the method must be suited to the question being addressed.

Technological improvements have greatly broadened the scope of questions that can be addressed in landscape studies. The revolutions in computer and remote sensing technologies have reduced computational expenses and provided new sources of spatially extensive data. This is fortuitous because many current environmental issues demand information and analysis at broad spatial scales. For example, projecting the spread of a disturbance or the ecological effects of climatic change at the regional scale requires landscape-level data and sophisticated analysis methods. Current methods presented in this book now allow rapid answers to many questions (e.g., what are the land cover patterns in a region? how has the landscape changed through time?) and provide a foundation for more complex investigations concerning the nature of landscape change and potential interaction among the multiple factors that contribute to these changes. As demonstrated in this book, theory and models are now available to predict the relationship between landscape pattern and ecological processes, and many specific hypotheses can be tested against available data.

Landscape processes occur in a spatially heterogeneous context. The multispectral information provided by remote sensing (Quattrochi and Pelletier, Chapter 3; Musick and Grover, Chapter 4; and Luvall and Holbo, Chapter 6) has altered the way that we view and quantify this heterogeneity. The possibility of taking repeated measures at broad scales, combined with methods that are able to handle extensive data sets, has only begun to influence the type and scale of ecological problems that can be tackled. The necessary remote sensing techniques to measure specific processes, such as evapotranspiration, across landscapes (Luvall and Holbo, Chapter 6) will allow fine-grained physiological responses to be projected through time and space.

A host of statistical methods for the analysis of broad-scale data are now available (S.J. Turner et al., Chapter 2). These techniques, combined with an understanding of the key components relating pattern and process, will allow us to determine the appropriate spatial and temporal scales for study. In addition, new methods based on photogrammetric techniques of textural analysis by Musick and Grover (Chapter 4) provide an especially nice method for analyzing edges in continuous gradient data.

Geographic Information Systems (GISs) have become an invaluable tool for the analysis of landscape data. The development of GISs for microcomputers has reduced costs and increased the availability of methods to store, retrieve, and analyze spatial data. The evolution of these methods has resulted in a suite of computer-based tools for problem solving and decision making (Coulson et al., Chapter 7), adding needed power and speed to the processes of data analysis and

hypothesis testing. Because the GIS allows a massive amount of information to be manipulated and key landscape attributes to be viewed easily, species-specific questions can be addressed at landscape scales (Dunn et al., Chapter 8).

The quantitative difficulties posed by the problem of assessing the ecological effects of landscape heterogeneity on biogeochemical cycling mandates a simple approach to empirical studies. Shaver et al. (Chapter 5) found that the effect of spatial heterogeneity in element cycling at the landscape level is best studied in simple systems, such as the arctic. The result of these empirical studies is a conceptual model for analyzing and quantifying the importance of element transport between landscape "units," and the approach could be applied to other landscapes.

Methods for spatial analysis of empirical data are also important as tools for the development and testing of landscape models. Although models differ greatly in their representation of space (links and nodes, grids, geometric shapes, etc.) and the complexity of feedbacks between components, all spatial models show that space and time are intertwined and cannot be reduced to two independent components (Sklar and Costanza, Chapter 10). Models of animal population dynamics (Merriam et al., Chapter 16) and herbivory (Hyman et al., Chapter 18) nicely demonstrate that landscape pattern and habitat connectivity affect the spatial and temporal scales at which the problem can be considered.

Gardner and O'Neill (Chapter 11) make the argument that the most effective model for understanding cause and effect relationships at the landscape scale is the simplest model. Several theoretical approaches are suggested, including percolation theory, epidemiology theory, and diffusion-reaction theory. Fahrig (Chapter 17) carries this argument further in the development of spatial population models, giving several examples of a general model for simulating population dynamics in a patchy landscape.

The use of landscape models for testing interactions of biotic and abiotic factors at landscape scales is illustrated with vegetation-soil-water interactions on a barrier island (Rastetter, Chapter 14). A profile through the dune allows a two-dimensional image of a three-dimensional problem to be constructed. Results show that the abiotic processes of dune formation are an integral and dynamic part of succession, demonstrating spatially interactive elements that form the landscape. Therefore, it is necessary to measure and incorporate large-scale processes as dynamic parts of the system, not as extrinsic controlling factors.

Economic factors are often the dominant forces affecting landscape change (Parks, Chapter 12). Conversely, the pattern of resources in a landscape often dominates economic development. However, ecologists often ignore the links between economic theory and ecological studies. Parks's review of economic approaches and examples of their use is helpful for choosing a model for particular questions linking ecology and economics. It is clear that much remains to be done in this area; the interactions among economic factors and landscape patterns should be a fruitful new area for study.

The temporal and spatial scales necessary for understanding disturbance-landscape interactions make models a useful tool for analysis (M.G. Turner and Dale, Chapter 13). Nearly all landscapes are disturbed in some way, but new models and analysis methods are again needed at the broad scales. Turner and Dale provide a summary of approaches to simulating landscape disturbances, including the advantages and limitations of each approach. Elucidating the relationship between landscape heterogeneity and disturbance remains a challenging research area.

Methods derived from fractal geometry have useful landscape applications (Milne, Chapter 9). The importance of fractals in determining scale-related effects is particularly germane to many landscape studies. The effect of fractal patterns on diffusive movement and the existence of critical landscape phenomena can be treated in a general fashion by fractal analysis. Although simple combinations of variables in spatial models can produce complex results that can be difficult to analyze, Milne shows that equally simple methods of analysis can "decompose" these complex patterns into simpler forms.

Bartell and Brenkert (Chapter 15) provide an interesting example of the interface between models and empirical data that is well suited to the quantitative testing of predicted effects. Using a finite difference model of nutrient movement in the vegetation and soil of a watershed, the chapter explores the implications of heterogeneities in vegetation type and topography on the accumulation of nutrients in a forested watershed. Sensitivity analyses demonstrate the time dependence of model processes, with short-term effects due to the internal cycling of nutrients and long-term effect dominated by changes in topography. Because aggregation in space distorts watershed topography, the spatial and temporal scales adopted for model simulations can be critical.

The issues and problems posed by the various spatial and temporal scales of ecological analyses pervade this book. Therefore, it is appropriate that the final chapter discusses in depth the quantitative issues associated with scale, with particular emphasis on translating information across scales (King, Chapter 19). The challenge of developing a rigorous conceptual framework for addressing multiple scales and the quantitative methods for implementing them is a serious and timely challenge. Success in this area will allow us to: (1) identify where critical fine-grain detail is required, (2) develop reliable simulation tools, (3) recommend new information and/or measurements, (4) and extrapolate this information in a rigorous and reliable fashion. Chapter 19 provides new impetus (and theory) to expand the theoretical foundation of landscape ecology as our tools and data base also expand.

20.3 Future Directions

New methods are usually developed to address a particular set of questions. The successes and failures in answering these questions often stimulates the development of the next generation of techniques. A review of the chapters in this book indicates several areas where the development of new techniques would be immediately useful.

The difficulty in quantifying the effects of landscape heterogeneity stems largely from our inability to distinguish, a priori, important relationships from merely interesting ones. The diversity of species, the variety of their responses to changes in resources, and the complex mechanisms needed to explain these interactions demonstrate that all landscape studies must limit the scope and scale of their measurements. But how can this be accomplished without sacrificing our ability to make reliable (and interesting) predictions? New techniques—similar to sensitivity and uncertainty analysis—that allow the importance of different variables and mechanisms to be evaluated before additional measurements are taken would be extremely useful for establishing realistic limits for landscape studies. Although sensitivity methods have been successfully applied in a variety of ecological studies (see Gardner et al., 1990, for a review and Chapter 15 for an example), these methods have yet to be generally and rigorously applied to spatial systems.

Theoretical studies of spatial effects in physical and chemical systems offer several new concepts that may be useful for landscape studies. For instance, the "backbone" is defined in percolation theory as the critical set of sites through which there is flow of material or energy (Stauffer 1985). The concept of a backbone is of interest to landscape studies because it suggests that disturbance of specific sites may have landscape-scale consequences. For instance, removal of sites adjacent to the backbone will not affect the movement of organisms, but the removal of a single site from the backbone itself can effectively disconnect the cluster and thus disrupt both pattern and process at the landscape scale.

Another statistic that might be adapted from percolation theory is the "correlation" or "connectivity length." The correlation length is estimated by taking the landscape average of the distances between similar sites that belong to the same cluster. Theoretical studies show that sudden increases in the correlation length occur near the critical thresholds in landscape connectivity (Stauffer 1985). Because the abundance of many species can be related to the number, size, and connectivity of suitable habitat sites, the correlation length should provide a useful index describing landscape-scale changes in abundance and diversity of organisms. For instance, sudden reductions in the correlation length as a result of change in landscape heterogeneity (i.e., disturbance) should indicate equally sudden changes in species abundances.

Although much work has been performed in cellular automata (see Casti 1989 for a recent review), these theoretical methods have not been applied to the problem of spatial heterogeneity at landscape scales. Recent simulations of cellular automata that allow the spatial and temporal scales of effects to be varied (Gerhardt et al. 1990) indicate real potential for estimating the broad-scale effects of changes in fine-grained details.

If one could make a single quantitative wish, one might request the development of a technique (or techniques) that would establish, a priori, what the relevant spatial and temporal scales of measurement and prediction should be. Continued interest in this problem is evident (see Dale et al. 1989), and progress is being made in a variety of disciplines (e.g., Chapter 9). Hierarchy theory (Allen and Starr, 1982; O'Neill et al. 1986) predicts that complex systems, including landscapes (Urban et al. 1987) should develop structures that are hierarchically organized—that is, patterns that show significant shifts with changes in scale. Although this effect has been observed in several empirical studies (Anderson 1971; Krummel et al., 1987; O'Neill et al., submitted), it remains a challenge to establish the spatial and temporal scales at which specific mechanisms (e.g., variability in soils, topography, climate, economics, species life-history attributes, etc.) will have the most influence on our ability to measure and predict.

Spatial models must be tested with spatial data. We expect to see rapid progress in the integration of models with GISs, which will allow predictions to be compared with landscape data. This development is both exciting and quantitatively challenging. If the power of the GIS is used to develop a "best fit" between data and predictions, then the spatial display of prediction errors will not be useful. However, if data are divided into separate sets for model development, calibration, and testing, then the spatial attributes of model errors will be extremely interesting. An analysis of these errors, similar to the analysis of regression residuals, should establish confidence limits for predictions and indicate where new measurements will most improve our understanding and prediction of spatial phenomena.

The general relationships between landscape indices, ecological processes, and scale need more study to provide understanding of both the factors that create pattern and the ecological effects of changing patterns on processes. Quantitative measures of landscape heterogeneity can provide appropriate metrics for monitoring regional ecological changes. These applications are of particular importance because changes in landscape patterns (e.g., in response to global change) can be measured with remote-sensing technology, and an understanding of the pattern-process relationship will allow functional changes to be inferred.

Future research should be oriented toward testing hypotheses in actual landscapes. Methods for characterizing landscape structure and predicting changes are now available, but the landscape questions require creative solutions to experimental design. Theoretical and empirical work should progress jointly, ideally through an iterative sequence of model and field experiments. Natural experiments, such as disturbances that occur over large areas or regional development, also provide opportunities for hypothesis testing. Of paramount importance is the development and testing of a general body of theory relating pattern and process at a variety of spatial and temporal scales (Turner 1989).

20.4 Guidelines for Obtaining Robust Results

Studies of spatial systems show that even simple interactions can display a bewildering variety of behaviors dependent upon the spatial arrangement of the component parts. Because landscapes are spatially heterogeneous, it is necessary to understand not only the mechanisms of interaction among the individual components but also how these components are spatially arrayed. In the past this has been difficult because of insufficient data, limitations of equipment, and inadequacies of theory. These objections are now being met to produce a revolution in the way we think about and deal with the great diversity of landscape issues.

We believe that landscape studies will continue to develop and apply new methods for quantifying spatial heterogeneity, comparing patterns and processes in different landscapes, and predicting the broad-scale effects of changes in pattern and process. Because landscape ecology is complex, the development and use of new and untried quantitative methods can lead to spurious results. Therefore, we encourage the continued development of methods that: (1) result in the identification of key landscape components, (2) quantify the spatial and temporal scales over which reliable predictions can be made, (3) use simulation methods to indicate where critical information and measurements are required, and (4) verify predictions by comparison with existing data.

20.5 Summary

This book presents a diversity of tools and techniques from a variety of fields, offering new methods and approaches to the quantitative analysis problem at the landscape scale. In this chapter, we present an overview of these approaches along with caveats for their application. Future directions in both quantitative methods development and landscape studies are identified. Research needs that are of particular importance include the application and testing of available theory and the identification of appropriate scales for measurement and prediction.

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