16

LANDSCAPE ECOLOGY
Directions and Approaches

Paul G. Risser
Illinois Natural History Survey

James R. Karr
University of Illinois

Richard T. T. Forman
Rutgers University

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CONTENTS

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INTRODUCTION

In recent years, several attempts have been made to define a field of science entitled "regional ecology" or "landscape ecology." These initiatives have originated from a number of scientific points of view (Watt 1947; Whittaker and Levin 1977), yet no clear set of general principles has emerged.

Current ideas about landscape ecology (e.g., Burgess and Sharpe 1981; Forman 1981; Forman and Godron 1981; Luder 1981; Minnich 1983; Naveh 1982; Romme and Knight 1982; Sharpe et al. 1981) are influenced by (a) a preoccupation with the extension of island biogeography theory to continental landscape patches, (b) the presumption that ecosystem-level characteristics are adequate to address landscape-level characteristics, (c) a recognition of the need to address landscape issues in land and resource management, (d) a belief that map-overlay methodology is sufficient to capture the essential attributes of multiunit landscapes, (e) the realization that human activities are an integral part of any meaningful concept of landscape ecology, and (f) the recognition that the inclusion of many appropriate scientific disciplines results in an exceedingly complex field. Collectively, these influences appear to have stalled the crystallization and communication of current understanding of "landscape ecology," especially as the concept might facilitate basic and applied research on natural resources.

A landscape perspective in ecology is not new (Neef 1967; Troll 1968); indeed, this is the perspective embodied in *A Sand County Almanac* (Leopold 1949) and in many early writings in ecology, natural history, and wildlife biology. Similarly, this landscape perspective is represented in related disciplines, such as landscape planning, economic geography, and cultural anthropology. However, these ideas have never been coalesced, organized, and confronted rigorously to produce a theoretically sound basis for understanding landscape-scale interactions. Further, the ecological base of this disciplinary integration is especially weak, and so developing definitive and ecologically based methods and models for managing natural resources is essential.

In spite of this conceptual bottleneck, ideas and concepts are developing (albeit slowly), research is being designed, and resource managers are grasping at even fragments of generalizations about the ecology of landscapes that can focus research efforts and guide resource management decisions (Forman 1979; Hansson 1977; Isard 1975; Klopatek et al. 1983; Naveh and Lieberman 1984; Samson and Knopf 1982). A mechanism for speeding the integration of a landscape ecology approach was to gather together experienced individuals with different viewpoints but with a strong desire to examine landscapes through the ideas of ecology and related disciplines. This report summarizes the deliberations of the 25 individuals (see List of Participants) who spent three days attempting to outline the disciplinary area of landscape ecology, to evaluate the potential of such a discipline, and to describe its application to basic and applied natural-resource issues. Although the group represented diverse points of view, an ecological perspective prevailed. Ideas contained in this report represent the collective efforts of the group, and no attempt has been made to identify specific thoughts with any particular individual.

DEFINITION AND CONCEPT OF LANDSCAPE ECOLOGY

Ecology deals with the understanding of fundamental processes and consequences of management of spatially and temporally homogeneous and heterogeneous geomorphic and living systems.

Landscape ecology differs from subdisciplines of ecology, such as population, community, and ecosystem ecology, in matters of primary emphasis. Landscape ecology focuses explicitly upon spatial pattern. Specifically, *landscape ecology considers the development and dynamics of spatial heterogeneity, spatial and temporal interactions and exchanges across heterogeneous landscapes, influences of spatial heterogeneity on biotic and abiotic processes, and management of spatial heterogeneity.* Thus, the primary focus of landscape ecology is on (a) spatially heterogeneous geographic areas, e.g., pine barrens, regions of row crop agriculture, Mediterranean woodland landscapes, and areas of urban and suburban development; (b) fluxes or redistribution among landscape elements; and (c) human actions as responses to, and their reciprocal influences on, ecological processes. Principles of landscape ecology help to provide theoretical and empirical underpinnings for a variety of applied sciences, e.g., regional planning, landscape architecture, and natural-resource management.

The relationship between spatial pattern and ecological processes is not restricted to a particular scale. One's understanding of landscape ecology issues focused at one scale may profit from experiments and observations on the effects of pattern at both finer and broader spatial scales. In turn, results from landscape studies may find application in understanding the way organisms interact with patterned environments at other levels of scale (Wiens in press).

Ecological processes vary in their effects or importance at different scales. Thus, biogeographic processes may be relatively unimportant in determining local patterns but may have major effects upon regional patterns. Processes leading to population decline may produce extinction at a local scale, but may only appear as spatial redistributions or alterations in age structure at broader levels.

Different species and groups of organisms (e.g., plants, herbivores, predators, parasitoids) may operate at different spatial scales, and thus, investigations undertaken at a given scale may not treat such components with equivalent resolution. Operationally, scales of landscape elements are defined arbitrarily, using spatial "filters" of specified sizes determined by the specific objectives of the investigation. At the landscape level, there may be spatial units or elements, such as fields, woodlots, clearings, or hedgerows. With some well-exercised caution, patterns and processes studied at other levels of scale, e.g., within a simple, relatively homogeneous landscape element, such as an old field, may provide concepts useful in understanding the landscape level, and vice versa. Processes and patterns occurring at much finer scales are not always perceived because of filtering or averaging effects, whereas those occurring at much broader scales may be missed simply because the investigation is focused within a single landscape unit. Although hierarchical approaches may offer some thoughtful insights (Allen and Starr 1982), there are few simple answers to ecological questions regardless of scale, and there will be no substitute for carefully constructed experiments and tests of ideas drawn from many disciplines.

Because of the spatial patterning of landscapes, flows and transfers among spatial components assume special importance. The process of the redistribution of materials, energy, and/or individuals among landscape elements is an essential feature of landscape ecology. Redistribution among landscape elements thus represents a dynamic in ecological systems that has largely been ignored by ecologists; until very recently dynamics of heterogeneous environments were largely ignored by the ecological sciences.

Traditionally, ecological studies have operated with the assumption that systems are more or less homogeneous and, in some cases, at approximate equilibrium. These considerations, primarily made for convenience, emphasized relatively undisturbed, "natural" habitats for study. Adoption of a perspective that admits the importance of spatial and temporal heterogeneity creates a major argument for the merger of the more or less independently developing European school of landscape geography and the growing body of ecological theory resulting from the study of heterogeneity and instability in ecological systems. Thus, the need to consider spatial pattern in ecological systems and the consequences of pattern on the dynamics and persistence of landscapes is clear.

At present, the theoretical treatment of these patterns and even the measurement of pattern is possible, but too little basic empirical information exists to document the phenomena and their consequences for landscapes. Thus, a clear need exists to focus basic ecological investigation on the patterns and interrelationships among the elements of landscapes to provide the empirical base from which to test and refine current models and societal policies. Ultimately, this approach will contribute to the development of general principles of landscape ecology.

A major forcing function of landscapes is the activity of mankind, especially associated cultural, economic, and political phenomena. Given the history of ecology, it may be tempting to draw a sharp line between landscape ecology and the applied management of landscapes. This distinction is not sharp, however, particularly since management practices of the past had much to do with the structure of landscapes that have developed today. Understanding landscapes requires that we deal with human impacts contributing to the landscape phenomenon, without attempting to draw the traditional distinction between basic and applied ecological science or ignoring the social sciences.

Landscape ecology could be viewed as the intersection of many disciplines, as a separate discipline, or as one branch of ecology. The first option is intellectually and practically the most persuasive. Arguments can be made for the inclusion of concepts and methods from such disciplines as terrestrial and aquatic ecology, geography, history, agricultural economics, civil engineering, landscape architecture, and wildlife management. To be recognized as a distinct scientific discipline, an area of activity must have a set of general, guiding principles, a conceptual framework of its own. Landscape ecology cannot now be viewed as a discipline because principles developed by practitioners (landscape ecologists) are few; most applicable principles have been developed in other established disciplines. In time, new principles should emerge and landscape ecology will develop its own body of theory. The third option, viewing landscape ecology as a branch of ecology, would emphasize natural spatial processes and patterns and, at least by tradition, would tend to exclude the formal analysis of human cultural processes that form landscapes. Viewing landscape ecology as an interdisciplinary area of research avoids the issue of which discipline "owns" landscape ecology. In human ecology (Young 1974), several disciplines (i.e., geography, sociology, anthropology) have claimed ownership, which has been a futile exercise, because human ecology, like landscape ecology, is also inherently interdisciplinary.

REPRESENTATIVE QUESTIONS ADDRESSED BY LANDSCAPE ECOLOGY

What does landscape ecology, so defined, have to offer? To test this potential, we must be able to frame fundamental questions concerning the development, maintenance, and effects of temporal and spatial heterogeneity of the landscape. Four examples follow.

How are fluxes of organisms, of material, and of energy related to landscape heterogeneity?

Thoughtful observation and experimentation indicate that units of landscape are not ecologically independent. Patches in a landscape mosaic are coupled by fluxes of organisms, biotic and abiotic energy, and nutrients. Understanding the fundamental behavior of such operationally defined units requires specific study of the fluxes at the landscape scale and a recognition that anthropocentrically defined landscape patches are differentially significant to different species. Fluxes of organisms among landscape patches include an array of organisms along a wide spectrum of size, mobility, developmental rates, and resource requirements. Each species views the landscape differently, and what appears as a homogeneous patch to one species may comprise a very heterogeneous, patchy environment to another. At each species-specific scale of reference, species survival often depends on interpatch fluxes. For example, some populations of small vertebrates survive in agricultural landscapes of the north-central United States and central Canada only because they can move between wooded patches along fencerow corridors through intervening farmland. Both white-footed mice (*Peromyscus leucopus*) and chipmunk (*Tamias* sp.) suffer frequent local extinctions and, lacking a durable source area, depend for survival at the landscape scale on fluxes of colonists among patches (Fahrig, Lefkovitch, and Merriam 1983; Henderson, Merriam, and Wegner submitted; Middleton and Merriam 1981; Wegner and Merriam 1979). In a comparison of avian distribution in Australia and Wisconsin, Howe (in press) concluded that the regional mosaic in Australia with a larger proportion of its landscape in forest as compared with Wisconsin, may account for the differing species-area relations for birds in isolated woodlots.

These examples demonstrate the dynamics of populations in the farmland mosaic. There is also evidence that even within continuous forests, bird species may require a mosaic of habitat patches (Karr 1982a, b; Karr and Freemark 1983; Middleton and Merriam 1983). This dependency of many terrestrial and aquatic vertebrates on habitat mosaics seems to be a general phenomenon (Karr and Freemark in press). Comprehension of this dependency may yield new insights into species survival and local population phenomena as they relate to patch dynamics in general as elements in the ecology of regions.

Grazing systems offer an opportunity to evaluate the transport of nutrients across the landscape pattern (Woodmansee 1979). Nutrients in rangelands are transported among patches by four principal agents: large animals, water, wind, and man (via supplemental feeding). Large animals are important transport mechanisms because they typically graze from patches (remove material) that contain relatively large amounts of high-quality forage. Usually these grazing areas (patches) are separated spatially from areas (patches) where the animals water, rest, bed down, and ruminate. Overall, material is removed from the grazed areas and accumulates in resting areas via defecation and urination. Most behaviors of animals in western rangelands (except watering, which may be partially determined by the manager) are determined primarily by soil type and fertility, plant community relationships, and topography. Though these studies have been conducted with cattle, the results should be generalizable to many large and small herbivores and are demonstrated from the Serengeti (McNaughton 1979). Historically, spatial and temporal heterogeneity in species attributes and population characteristics have been a problem for ecologists as they searched for communities that were homogeneous in space and time. Recognition of the role of spatial and temporal dynamics on the integrity and continuity of ecosystem processes may be essential to our understanding of basic ecology and of the problems that derive from landscape ecology (McNaughton 1983; Karr and Freemark in press).

Many species of insects require resources in two or more landscape units (patches) to complete their complex life cycles. For example, many herbivorous species feeding within crop units must move to wooded areas for overwintering, and many predaceous insects, such as vespid wasps, colonize hedgerows but forage in cultivated fields. Thus, crop mix and phenology, as well as natural events, have major influences on the flow of insect herbivores. Similar patterns also occur in unmanaged landscapes, such as those of the western tent caterpillar in Canada (Wellington et al. 1975; Thompson, Vertinsky, and Wellington 1979) and *Heliothis zea* in North Carolina (Stinner, Rabb, and Bradley 1977). Indeed, managing elk herds and waterfowl habitats also represent classic examples which are implicitly concerned with patch dynamics.

Plant breeders and pest control scientists are finding it desirable to use a landscape approach in choosing strategies for developing and using the different types of resistance. For example, if antibiosis is introduced into a crop variety that represents the chief food biomass of an insect herbivore and this variety is used uniformly over the area representing the habitat of an isolated population of the herbivore species, the population of insects develops tolerance to the antibiotic properties of the crop variety. However, if the crop variety represents but a small fraction of the food biomass of the ambient herbivore population, insect resistance does not decrease so readily (Kennedy 1983).

These paragraphs introduced three topics of significance at the landscape level, all involving redistribution of populations, energy, and materials: habitat selection by small mammals and birds, grazing system transfer of materials, and management of insect pests. Other examples could have been chosen, e.g., acid precipitation (Krug and Fink 1983). The point, however, is importance of the common theme of spatial heterogeneity and of redistribution processes.

What formative processes, both historical and present, are responsible for the existing pattern in a landscape?

Formative processes in the landscape can be organized in various ways. At the broadest level, virtually all processes of climate, geology, vegetation, animals, microorganisms, and human culture could be included. Both natural and man-created processes are important. For example, the natural movement of water is an important formative process in a landscape, but as man alters water movement through such means as dam construction or extensive irrigation of cropland, a new landscape may be created.

No clear method has emerged as a conceptual framework to organize the study of formative processes. Such a framework must transcend a complexity of dynamics in physical and biological processes at a variety of spatial and temporal scales and, for biology, at individual, population, community, and ecosystem levels.

One framework proposed during the workshop places organized "processes" into several general categories. Conserving processes tend to restrict change, while expanding processes promote growth and development of a landscape attribute. In conserving processes, for example, competitively superior organisms resist colonization by other species. Expanding processes occur when organisms or groups of organisms significantly expand the geographic area that they occupy within a landscape. Resisting processes protect the landscape from outside forces. In a biological context, these are analogous to resilience (Holling 1973). To a major extent, these types of "processes" are not really synthetic system-level processes. Rather, each seems to be a passive result of an accumulation of dynamics of physical and biological components of landscape systems.

These and other dynamics interact to create pattern on the landscape. Consider a landscape composed of two types of land systems. Assume that both types are exceptional in their ability to maintain themselves at a site (conservative processes) and that each type is able to hold the space against the other. A landscape composed of such subsystems would be a fixed mosaic of unchanging patches. Change made in the number or areal extent of such patches would not equilibrate to the initial state. Such a landscape might have a self-sustaining natural system (such as a forest) and an equivalently self-sustaining man-made system (cropland). This landscape dominated by conservative processes could be quite static.

As a second example, consider system types that are extreme in their expansive processes. If the two types are exactly at parity with respect to their ability to hold space, the landscape could appear quite unchanging like the "conservative-conservative" landscape just described.

Levin (1978) discusses the range of landscape system behavior for landscapes composed of expansive systems (*diffusion* is the word used for expanding processes). With regular disturbance, these "expansive-expansive" land systems can behave as a shifting dynamic mosaic. At a finer scale, the dynamic sorting due to erosion and silt deposition in stream channels is an example; the locations of pools and riffles, sand bars, and woody debris shift. At a broader scale, the natural vegetation of the northern hardwood forest with waves of disturbance (Sprugel 1976; Sprugel and Bormann 1981) or the role of fire in the regional pattern of vegetation of southern California (Minnich 1983) are examples.

Landscapes with interacting processes, perhaps with one type of land system expansive-process dominated and the other conservative-process dominated, would respond in the manner of classic succession theory. With regular disturbance, such a landscape would tend to have a replacement sequence and would require regular disturbance to maintain both land-system types in the mosaic.

The strong need for an integrative framework to organize the disparate set of processes and dynamics that influence landscape pattern is clear from these few examples. Other examples that might be cited include the feedback between landscape elements (such as natural and man-disturbed), dynamics due to disturbances that are either acute or chronic in intensity, the distinction between landscape processes that operate at evolutionary and ecological time scales, and processes mediated by global control, such as climatic pattern.

How does landscape heterogeneity affect the spread of disturbances?

The complexity of types of disturbances, their spatial and temporal scales, and their differential effects on biological processes (due to variations among taxa and levels, e.g., individual, population) defy simple comprehension (Karr and Freemark in press). As a generality, homogeneity often enhances the spread of disturbance. Examples include the spread of pests in agroecosystems, wildfire perpetuation, the spread of Dutch elm disease, and erosional patterns. Indeed, the effects of disturbance may increase the heterogeneity of the environment and, thus, alter the impact of a later disturbance of the same magnitude.

Heterogeneity also may enhance the spread of disturbance, as, for example, is the case where small woodlots harbor white-tailed deer populations that disturb surrounding crops. Heterogeneity may act as a stabilizing factor (e.g., by the spreading of risk) as well as fostering disturbance.

Many species require two or more landscape elements to complete their life cycle, and the impact of a specific disturbance (e.g., a severe dry period) may be a function of the spatial pattern of landscape elements. Of course, temporal and spatial heterogeneity may also affect or limit the perpetuation of disturbance. Finally, landscape heterogeneity may impact the rate of recovery of landscapes from disturbance by providing refuges for recolonizing organisms.

Again, we emphasize the complexity of responses of organisms (and the biota) at the landscape level to perturbations, both large (= disturbance) and small. Indeed, a given perturbation may be a disturbance to one organism occupying a landscape, yet it may not be perceived by another organism in the same landscape (Karr and Freemark in press). Similarly, the same organism in two different landscapes may be affected differently by the same disturbance.

How can natural resource management be enhanced by a landscape ecology approach?

Natural resource managers, by necessity, often implement landscape ecology from an observational rather than an empirical or theoretical approach. For example, silviculturists have traditionally been concerned with the size, shape, distribution, and timing of timber harvests for the regeneration of forest stands. Agricultural grassland, shrub land, and aquatic ecosystems have been managed with similar single-resource objectives and multiresource consequences.

Ruffed grouse (*Bonasa umbellus*) use timber stands of various ages for feeding (mature forest), breeding (pole size), and brooding (regeneration stands). As a result, habitat managers manage forest stands to include these age classes in close proximity (Gullion 1977). Similarly, pheasants (*Phasianus colchicus*) use agricultural cropland for feeding, but populations are enhanced if 10–15 percent of the habitat is in hay crops to provide nesting and roosting cover (Warner 1981). The same principles are employed when managing habitat for wildlife that migrates over long distances, e.g., elk and waterfowl. Both breeding and overwintering requirements must be met, but in addition, a habitat mosaic may be important in each season. For example, migrating and overwintering geese (*Branta canadensis*) and mallard ducks (*Anas platyrhynchos*) require agricultural crop residue and forage, while canvasback (*Aythya valisineria*) and redhead ducks (*A. americana*) require aquatic vegetation and invertebrates, such as the fingernail clam (*Musculium transversum*), for food (Bellrose et al. 1979). The management of recreation resources also requires a mosaic of landscape classes that support different types or combinations of dispersed recreation (Driver and Brown 1978).

No body of ecological theory exists by which to evaluate or alter current management programs that result in various production levels of wildlife, timber, or recreation. As a result, decisions about the size, shape, distribution, and timing of resource management actions are based on observations. Landscape ecology, by defining responses to management apparent at the landscape scale, together with appropriate characterizations of heterogeneity, can provide a unifying framework for developing consistent predictive models of utility in resource management.

The recognition that informed resource management decisions often cannot be made exclusively at the site level is essential. A shift to regional and national decisions will place greater emphasis on landscape ecology concepts (Joyce et al. 1983). The realization of this fact is expressed in regional consortia, such as the Ohio River Basin Commission in water resource management and the Flyway Council concept in migratory waterfowl management. Multiple or joint resource production interactions inherent in landscape management must consider: (a) optimizing trade-offs in production, since not all natural values can be maximized simultaneously, (b) imposing economic values in deciding among trade-offs between alternative landscape management actions, and (c) considering the socio-economic impacts, as well as the production of natural values, in choices of alternative landscape management actions.

Clearly, the evaluation of the trade-offs, when accomplished comprehensively, demands a set of principles based on landscape ecology issues discussed in this paper.

METHODOLOGIES APPLICABLE TO LANDSCAPE ECOLOGY

In earlier sections of this report we have discussed the concept of landscape ecology, and have presented examples of fundamental ecological questions that require the application of landscape ecology concepts. In developing a framework for landscape ecology, it is necessary to consider techniques and methods that are particularly appropriate and how these techniques will provide for the needs of landscape ecology. The following paragraphs address four methodological questions which may demonstrate the value of a variety of appropriate techniques.

Methods for Measuring Landscape Heterogeneity

Many issues in landscape ecology require quantification of spatial heterogeneity or landscape pattern. Currently, several descriptive techniques exist for quantifying the spatial relationships among entities, such as individuals in populations, habitats, and land-use types. In addition, there are schemes or terms for describing landscape pattern, e.g., species-dependent patch, matrix, corridor, and mosaic.

However, some problems require modifications or extensions of these methods to include (a) human cultural and demographic characteristics, (b) capture of the dynamics of changes in patterns over time, and (c) incorporation of value judgments with empirical data associated with landscape pattern. The following paragraphs discuss useful techniques and describe additional methods from other fields of science that might be effective in addressing the required modifications.

Topological Measure of Spatial Heterogeneity. A variety of graph theoretical methods, as well as statistical, metric, and topological methods, could be applied to landscape ecology (Haggett, Cliff, and Frey 1977; Lowe and Moryadas 1975; Mandelbrot 1977; Sugihara 1983). Movement of migrants or propagules among elements of the mosaic can be expressed in graph theoretic measures of connectivity. Experimental manipulation (e.g., introducing corridors or barriers) can be used to test hypotheses about the importance of connectance in landscape dynamics (Fahrig, Lefkovitch, and Merriam 1983). Statistical methods employ a basic distribution model for the whole population of spatially distributed characters (e.g., Poisson model) and test the observed distribution against the model. In probabilistic methods, heterogeneity is measured as the probability of obtaining the observed spatial distribution by a random process. Macroheterogeneity and microheterogeneity can also be distinguished as functions of scale, and results are often expressed by information theory terms or concepts to emphasize the progression of knowledge given by each successive step in the analysis (e.g., Batty and Sikdar 1982).

Spectral Analysis. Techniques used in spectral analysis have most often been applied to time series, generally with the hope of associating underlying processes with pattern. That is, spectral analysis is a technique to elucidate the autocorrelation structure of the underlying process. These techniques have also been used to quantify patterns in space. For example, Denman and Platt (1976) used spectral analysis to study the patch structure of marine phytoplankton fields.

Spectral analysis (Shugart 1978) techniques often require treatment of the data (e.g., detrending, filtering to reduce noise) and require considerable amounts of data collected at regular intervals. Analysis is in the form of a graph of variance accounted for plotted against the log of the frequency of a sine function. The power of the method is in quantification of pattern in a precise mathematical way coupled with a tradition of interpreting patterns in terms of functional characteristics.

Artificial Intelligence Methods. The problem of recognizing and classifying patterns embedded in heterogeneous, spatial, and temporal arrays has become a prime focus of the emerging field of artificial intelligence (Michalski and Chilausky 1980). The term "pattern" is closely allied with "concept." This is not a single technique, but the application of several related techniques to the synthetic problem of pattern analysis. Landscape ecology may benefit from and ultimately contribute to this effort.

Data Acquisition Approaches

Data bases with spatial components useful in landscape ecology are available from several sources. Many of these sources are conventional, e.g., aerial photography, multispectral scanner imagery, and biological sampling schemes as well as various statistical measures of demography. Several problems require particular attention in acquisition, management, and display of spatial data in the context of landscape ecology: merging data from multiple sources with various levels of precision, resolution, and timing; introduction of distortions when reporting and displaying mapped information; decisions about the appropriate resolution for a particular problem; and choice of display formats for particular uses and users. Field samples may result in statistical replications in a universe that is assumed to be homogeneous. If the universe is heterogeneous, use of systematic sampling or stratified sampling, which takes into account the heterogeneity, becomes necessary. Also there is the need to determine the "grain" of heterogeneity to know the mean radius of validity of any physical or biological measure. A traditional approach has been to collect a cumulative series of measures such that the magnitude of the variances in the sampled parameters corresponds to the grain size.

Useful Modelling Approaches

Purposes and Applications. Modelling techniques are useful for the static description of spatial heterogeneity and for the elaboration of the dynamics of pattern. In the former category are such well-established methodologies as direct and indirect gradient analysis and other multivariate statistical methodologies as well as more recent approaches to pattern analysis, noted above. The focus of this section is on the dynamics of pattern, primarily in ecological time, and on their consequences for the species and systems on the landscape.

Models serve many purposes: as predictive tools, allowing estimation of future consequences of past, present, and future events; as vehicles for the design of management schemes in which an adaptive or feedback component may be central; as descriptors and explainers of historic patterns; and as general frameworks for arranging ideas, defining research priorities, and understanding natural systems. In an applied context, a spectrum of models ranging from generic ones, which serve as preliminary screens, to site-specific ones, which serve as the basis for solving more detailed problems, is needed.

When using models, one must also recognize the multiplicity of interrelated scales—hierarchical, spatial, and temporal—on which processes take place.

Such models as the JABOWA-FORET class of forest growth descriptors (Shugart and West 1980) and patch models of intertidal zones (Levin and Paine 1974; Paine and Levin 1981) treat a spatial scale small enough that recruitment may be regarded as independent of internal dynamics. Such models exhibit the importance of an explicit consideration of spatial scale.

Individual and Population-Level Models. Spatial effects often can be appraised from individual or population-level models (Levin 1974, 1978). Considerable attention has been devoted to patch effects upon the foraging behavior of individuals, generally in the context of optimization. Such models consider the effects of patchy distributions of resources upon proximate features of behavior (capture rates, patch residency times, etc.) but generally do not consider (but see Stinner, Rabb, and Bradley 1977) the dynamics of the patches themselves (e.g., resource depletion, disturbance, succession) or patch interrelationships (e.g., patch position effects). A variation on this theme addresses central-place foraging behavior (Orians and Pearson 1978), in which the key landscapelike components are a central place from which individuals forage (e.g., den, nest site, colony) and the surrounding area, which is often assumed to be homogeneous. However, one application of such central-place ideas has considered patchiness in resource distributions in the foraging zone. Ford et al. (1982) modeled the distribution of foraging seabirds in the oceanic areas about a colony, assigning various areas different resource production levels. In this model the landscape components had internal dynamics (depletion and renewal of resources) that had effects on population structure and persistence, but patch interactions or position effects were not included in the model. Another model by Fahrig, Lefkovitch, and Merriam (1983) considering the rate of exchange between patches showed that interpatch connectiveness was capable of stabilizing population levels in patches.

Other population-level attributes may also be affected in the spatial configuration of the landscape, and these attributes are candidates for spatial modelling approaches (Schluter 1981). The probability of the persistence of a single-species population, for example, may be affected by spatial heterogeneity (Chesson 1981). At a basic level, the concept has been envisioned as "spreading of risk" (den Boer 1968, 1981) in which a population distributed among patches in a landscape has patch-specific probabilities for growth, extinction, and recolonization, and the population as a whole persists because of the spatial subdivision of these probabilities. These processes have been modelled by applying conventional population-dynamics models to individual patches and then aggregating the responses over the population (landscape) as a whole.

Elements of island biogeography theory predict that as patch size decreases and isolation increases, the probability of local extinction should increase and that of recolonization should decrease. Such theoretical expectations have not been integrated into a landscape perspective that would consider the effects of patch dynamics (including fragmentation and patch regeneration) in a mosaic landscape rather than an island setting.

Simple extensions of single-species population systems to two-species systems permit incorporation of the effects of processes, such as predation and competition, and consideration of their relationship to environmental patchiness (Noy-Meir 1981). However, a modelling approach that simply aggregates or sums within-patch population dynamics over the various patch types displayed in a landscape will be inadequate (Wiens 1984). Spatial relationships and patch configuration must be considered in such models, perhaps capturing the redistribution process by variations of diffusion-reaction approaches that are cast in terms of the dynamics of various populations.

JABOWA-FORET Models. One class of models that has been useful in some aspects of the landscape are the forest vegetation models based on the reproduction behavior of species populations. These temporally dynamic models are based on sets of individual patches. The patches are not connected to each other, but each patch is connected to a universal pool of seeds. These models can reproduce temporal changes in a heterogeneous environment, because each patch is characterized by a specific soil, climate, elevation, slope, aspect, and disturbance regime (e.g., Weinstein 1982; Harwell and Weinstein 1982).

Other Patch Models. Other models have been developed based on a paradigm similar to the JABOWA-FORET models—that patchiness is important but that specific spatial position is not, because a common seed or larval source, or both, is available. These models include the simple Markov transition matrices describing forest secondary succession (Horn 1976) and the patch dynamics models of Levin and Paine (1974), which allow patches to change in size and which consider explicitly changes in the age-size distribution of patches in relation to disturbance. Position is not explicitly considered, except for a causal relation of successional patterns to physical characteristics. Nonequilibrium island biogeographical models (Faaborg 1979; Williamson 1981) represent an intermediate class in which some aspects of position are considered, e.g., distance to source.

Interaction-Redistribution Models. The most generically important class of models is those which examine growth, interaction, and spatial redistribution on a common time scale. These are extensions of the prototypical diffusion-advection-reaction models, which, though they have limitations (Chesson 1981), have played a fundamental role in a wide spectrum of fields (e.g., Levin 1974). In these models (possibly stochastic), local dynamics are coupled with movement either within and among a mosaic of cells or patches or in a continuum. More recent work has developed the mathematical detail to sophisticated levels, including density-dependent and space-dependent movement patterns, aggregation, the effects of geometry, and interacting populations with diffusion and long-distance transport (e.g., Haggett, Cliff, and Frey 1977). Much current biological work examines the applicability of the generally used descriptors of movement, including especially insect mark-and-recapture experiments, radio tracking of vertebrates, and comparison of model predictions with data on seed, pollen, and particulate dispersal. In general, this approach has increasingly proved to be an adaptable, realistic, and accurate basis for describing movement of many organisms (e.g., Gunn and Rainey 1979; Rabb and Kennedy 1979).

Optimization Models. Optimization models that consider landscape features have been employed in integrated pest management programs operative at the regional level, controlled burning of forests, optimizing clear-cut settings, land allocation strategies, resource management, and optimal design of reserves. Optimization techniques build on a combination of the diffusion-reaction approach described earlier, dynamic programming, and control theory, which includes stochastic and econometric methods. Frequently used approaches blend ecology and economics; consider costs and benefits, such as yield; and present net worth.

Other Approaches. Not explicitly covered in this report, but of recognized potential importance and highly developed, are:

the influence of spatial heterogeneity upon the generation and maintenance of genetic diversity and the implications for the development of resistance to pesticides, heavy metals, and other anthropogenic stresses

the development of physical models (e.g., microcosms) and experimental field studies coupled with mathematical models (Physical models are extremely important when site-specific information is necessary, as contrasted with the generic approaches emphasized in this report.)

relationships to techniques in geography (It would be profitable to develop interactions among ecologists, epidemiologists, and geographers interested in similar landscape problems and analyses to develop common methodologies.)

Landscape Ecology Procedures Useful in the Solutions of Pest Management Problems

It has been more traditional to follow landscape approaches to forest pest problems (e.g., spruce budworm in North America) and to pests of man and animals (e.g., tsetse flies in Africa) than it has been in attacking agricultural problems, although there are exceptions (e.g., locusts in Africa and Asia and beet leafhoppers in North America). In contrast, most agricultural pest management studies in the past have been site specific (i.e., they relate to one crop in one habitat). In recent years, however, emphasis on wide-area population studies has increased and greater recognition has been given the need for manipulating landscape heterogeneity (e.g., see many papers in Proceedings of the Tall Timbers Conference on Ecology and Animal Control by Habitat Management, No. 1-6, 1969-1974, Tallahassee, Florida).

Ecotones have been recognized as sources of agricultural pests (e.g., weeds, plant pathogens, invertebrate and vertebrate herbivores) and their natural enemies for many years (van den Bosch and Telford 1964; Southwood and Way 1970; and Rabb et al. 1976). The potential for enhancing natural control of agricultural insect pests through managing field borders (ditch banks, fence rows, and wood edges) has been noted by many researchers; however, little overt management has resulted. Price (1976) drew fresh attention to this potential in his attempt to apply island biogeography theory in studying fluxes of insect pests and their natural enemies in soybean fields. Stinner et al. (1974) modelled the role of spatial and temporal patterns of several crops in the population dynamics of *Heliothis zea*. They computed the movement of moths among field types as a function of an attraction index of hosts for adults for each crop-maturity combination and the average distance between fields of different types (immature stages do not disperse among fields). Agricultural landscapes can be designed to reduce *H. zea* density in the most susceptible crops.

As yet, no studies have been designed to measure and specifically evaluate for pest management purposes a significant portion of the landscape (i.e., the interaction of several habitat types). Such studies are strongly recommended. These long-term investigations would aid our understanding of long-range dispersal patterns of pest species, how the landscape mosaic impacts their life histories, and how the landscape can be managed for purposes of biological control.

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PARTICIPANTS

Landscape Ecology Workshop

Allerton Park, Piatt County, Illinois

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Gary W. Barrett
Environmental Institute
Miami University
Oxford, Ohio 45056
(513) 529-5811

Carl Becker
Illinois Department of Conservation
Forest Research and Natural Resources
600 North Grant Avenue, West
Springfield, Illinois 62706
(217) 782-2361

Daniel B. Botkin
Environmental Studies
University of California
Santa Barbara, California 93196
(805) 961-2968

Robert Costanza
Coastal Ecology Laboratory
Center for Wetlands Research
Louisiana State University
Baton Rouge, Louisiana 70803
(504) 388-1558

Richard T. T. Forman
Department of Biological Sciences, Botany
Rutgers University
New Brunswick, New Jersey 08903
(201) 932-2363

Michel Godron
Centre d'Etudes Phytosociologiques et Ecologiques
CNRS, B.P. 5051
Route de Mende
34033 Montpellier, France

Frank B. Golley
Institute of Ecology
University of Georgia
Athens, Georgia 30602
(404) 542-2968

Thomas Hoekstra
U.S. Department of Agriculture
Rocky Mountain Forest and Range Experiment Station
240 West Prospect Street
Fort Collins, Colorado 80526
(303)221-4390 Extension 489

Louis R. Iverson
Illinois Natural History Survey
607 East Peabody Drive
Champaign, Illinois 61820
(217) 333-0914

James R. Karr
Department of Ecology, Ethology, and Evolution
University of Illinois
606 East Healey
Champaign, Illinois 61820
(217) 333-1633

Simon A. Levin
Section of Ecology and Systematics
Cornell University
Ithaca, New York 14853
(607) 256-4617

Gray Merriam
Biology Department
Carleton University Laboratory
Colonel by Drive
Ottawa, Ontario K1S 5B6
Canada
(613) 231-3662

Robert V. O'Neill
Oak Ridge National Laboratory
Environmental Sciences Division
Post Office Box X
Oak Ridge, Tennessee 37830
(615) 574-7301

William J. Parton
Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523
(303) 491-5571

Robert L. Rabb
Entomology Department
North Carolina State University
Raleigh, North Carolina 27650
(929) 737-2638

Paul G. Risser
Illinois Natural History Survey
607 East Peabody Drive
Champaign, Illinois 61820
(217) 333-6830

William G. Ruesink
Illinois Natural History Survey
607 East Peabody Drive
Champaign, Illinois 61820
(217) 333-6820

Glen C. Sanderson
Illinois Natural History Survey
607 East Peabody Drive
Champaign, Illinois 61820
(217) 333-6870

David M. Sharpe
Department of Geography
Southern Illinois University
Carbondale, Illinois 62901
(618) 536-3375

H. Henry Shugart
Environmental Sciences Division
1505 Oak Ridge National Laboratory
Oak Ridge, Tennessee 37830
(615) 574-7371

Carl Steinitz
Department of Landscape Architecture
Graduate School of Design
Harvard University
Cambridge, Massachusetts 02114
(617) 495-2573

Jack Ward Thomas
U.S. Department of Agriculture Forest Service
Range and Wildlife Habitat Laboratory
Route 2, Box 2315
La Grande, Oregon 97850
(503) 963-7122

John A. Wiens
Department of Biology
University of New Mexico
Albuquerque, New Mexico 87131
(505) 277-5355

Michael Wiley
Illinois Natural History Survey
607 East Peabody Drive
Champaign, Illinois 61820
(217) 333-6889

Bob Woodmansee
Ecosystem Studies
National Science Foundation
1800 G Street, N.W.
Washington, D.C. 20550
(202) 357-9596

Landscape ecology workshop participants (left to right): R. V. O'Neill, J. R. Karr, P. G. Risser, M. Wiley, S. A. Levin, W. G. Ruesink, M. Godron, H. H. Shugart, R. L. Rabb, F. B. Golley, R. Woodmansee, R. Costanza, J. A. Wiens, C. Steinitz, G. W. Barrett (back row), T. Hoekstra (middle row), W. J. Parton (middle row), D. B. Botkin (front row), J. W. Thomas (back row), G. Merriam, D. M. Sharpe, L. R. Iverson, G. C. Sanderson, C. Becker, R. T. T. Forman.

CONCLUSIONS

A. Although the need for a set of coherent principles about the ecological characteristics and behavior of landscape units has arisen from diverse theoretical and practical viewpoints, no unifying theory has been developed and communicated.

B. Landscape ecology is not a distinct discipline or simply a branch of ecology, but rather is the synthetic intersection of many related disciplines that focus on the spatial-temporal pattern of the landscape.

C. Conceptually, landscape ecology considers the development and maintenance of spatial heterogeneity, the spatial and temporal interactions and exchanges across heterogeneous landscapes, the influences of heterogeneity on biotic and abiotic processes, and the management of that heterogeneity.

D. Because of the spatial patterning of landscapes, flows and transfers between spatial components assume special importance, and the process of redistribution of organisms, materials, and/or energy among landscape components is thus an essential feature of landscape ecology.

E. A special need exists for research in numerous aspects of spatial patterning and its effects on redistribution processes. Building the requisite data base has begun, but a significant increase in effort is required. Specific hypotheses, tests, and empirical studies conducted by single investigators or within single disciplines are likely to provide the bases for most principles of landscape ecology and the requisite scientific base for development.

F. Many fundamental questions in both basic ecology and resource management issues require understanding and application of a landscape perspective. Examples include: How are fluxes of organisms and of materials and energy related to landscape heterogeneity? What formative processes, both historical and present, are responsible for the existing pattern in a landscape? How does landscape heterogeneity affect the spread of disturbance? How can conventional natural resource management be enhanced through a landscape ecology approach?

G. Quantitative methods currently available provide many of the analytical tools necessary for progress in landscape ecology. Further, models, geographic information systems, and data-base management methods are developing rapidly in ecology and related disciplines. Continuing advances in the development of analytical tools will further aid the conceptual base of landscape ecology.

H. Clearly enunciating principles of landscape ecology will catalyze a convergence of developing methodology and theory and will provide practical improvements in existing methodologies, such as inserting ecological processes more forcefully in geographic information systems used for planning purposes.

I. Addressing issues of landscape ecology will result in critical consideration of several conventional and restrictive ecological assumptions, such as homogeneity and equilibrium. Further, the importance of spatial and temporal pattern and the role of disturbance as integral parts of ecological systems will be emphasized.

J. Principles of landscape ecology will be identified in part by intellectual exchanges, such as illustrated by this workshop, and also by examination of previous studies in ecology and related fields. The development of a specific theory that addresses issues of landscape heterogeneity will be expedited by collecting and analyzing empirical data, using model simulations, and searching for similarities in related disciplines from which to extract and formalize theory.

K. Improvement in the conceptual base of landscape ecology will also assist in the communication of ideas between and among groups that now suffer from the absence of a common framework. Examples include the information produced by scientists and needed by resource managers, data and interpretations used to resolve regulatory (legal) conflicts associated with management at the landscape scale, and the bases on which this country recommends an international policy for management of natural resources.

RECOMMENDATIONS

The deliberations of the workshop provide a basis for a number of recommendations concerning the current and future status and the importance of landscape ecology. Landscape ecology is fundamental to a broad range of issues and scientific questions, yet no conceptual framework has developed and matured. This fact strongly suggests that the present intellectual and monetary support system is insufficient or not sharply focused. In retrospect, the reasons for the slow growth are clear:

A. By definition, landscape ecology depends upon data and ideas from diverse fields such as ecology, geography, and wildlife management. The historical separation of these disciplines produced a communication barrier and limited funding opportunities.

B. Ideas about ecology are based on studies of more or less natural systems, whereas landscape ecology expands to consider managed systems as well and specifically includes resource management activities. Furthermore, many ideas about landscape ecology are based on maturing concepts about population dynamics and ecosystem processes and on a recently developing awareness of the importance of the spatial, as well as temporal, patterning of systems. The development of landscape ecology has thus depended upon the maturation of several related fields and of new insights in those disciplines.

C. Many early resource decisions, made in the absence of real pressure from advancing society, were based largely on empirical observation without a theoretical basis. Now, however, decisions must be realistically predictive, withstand the scrutiny of interest groups, and be generalizable over large geographical areas. A firmer theoretical foundation is essential.

D. Addressing some questions in landscape ecology requires the ability to acquire and manage large quantities of data. The availability and relatively low cost of computing power and mass storage will facilitate the development of landscape ecology.

E. Training of individuals in landscape ecology involves numerous disciplines, and in the normal post-secondary education system, institutional and departmental boundaries are especially discouraging to such a synthetic interdisciplinary approach.

F. Many formative ideas about landscape ecology developed in Europe from a geographical perspective. More recently, North American ideas about landscape ecology have matured from advances in ecological science. An integration of these independent pathways is essential to the development of the landscape approach.

Based on this analysis, these recommendations are made to expedite development of landscape ecology.

A. That the interdisciplinary nature of landscape ecology be recognized and dealt with.

1. Funding should be provided for high-quality basic research that clearly addresses the spatial patterning of landscapes and its effects, especially emphasizing redistribution processes. Furthermore, funding agencies must develop mechanisms through which funding can be solicited for multidisciplinary research that is outside of the conventional boundaries of funding programs.

2. Colleges and universities should specifically contemplate the scope of curricula and training programs required to educate landscape ecologists and should provide appropriate courses. Further, funding agencies should support educational research in landscape ecology with dissertation grants, fellowships, etc.

B. That resource agencies (e.g., state conservation departments, U.S. Fish and Wildlife Service) recognize the need for developing the necessary data bases, as well as a strong conceptual and theoretical basis for management studies, and seek to incorporate components in individual studies as well as in programmatic planning and funding.

C. That the relevant disciplines and professional societies eschew parochial views about landscape ecology and

1. Encourage the intellectual development of this complex, interdisciplinary field through symposia, journal review guidelines, etc.

2. Work cooperatively to establish training courses to acquaint scientists of all relevant disciplines with the approaches and techniques applicable to landscape ecology.

D. That because landscape ecology investigates questions that transcend traditional boundaries of agencies and disciplines and have direct application to regional issues, land management agencies cooperate in supporting programs in landscape ecology.

E. That as many landscape ecology issues are global in nature and because a full understanding of similar ideas from elsewhere will facilitate the maturation of landscape ecology, several activities should specifically focus on international interactions. These interactions could include joint symposia, workshops combined with field excursions (perhaps supported by organizations such as the International Association of Landscape Ecology), and cooperative research and management projects with multinational support.