CHAPTER 1

INTRODUCTION TO LANDSCAPE ECOLOGY

LANDSCAPE ECOLOGY OFFERS NEW CONCEPTS, theory, and methods that are revealing the importance of spatial patterning on the dynamics of interacting ecosystems. Landscape ecology has come to the forefront of ecology and land management and is still expanding very rapidly. The last decade has seen a dramatic growth in the number of studies and variety of topics that fall under the broad banner of landscape ecology. Interest in landscape studies has been fueled by many factors, the most important being the critical need to assess the impact of rapid, broad-scale changes in our environment.

Most of us have an intuitive sense of the term *landscape*; we think of the expanse of land and water that we observe from a prominent point and distinguish between agricultural and urban landscapes, lowland and mountainous landscapes, natural and developed landscapes. Any of us could list components of these landscapes, for example, farms, fields, forests, wetlands, and the like. If we consider how organisms other than humans may see their landscape, our own sense of landscape may be broadened to encompass components relevant to a honey bee, beetle, vole, or bison. In all cases, our intuitive sense includes a variety of different elements that comprise the landscape, change through time, and influence ecological dynamics. In his 1983 editorial in *BioScience*, Richard T. T. Forman used tangible examples to bring these ideas to the attention of ecologists:

> What do the following have in common? Dust-bowl sediments from the western plains bury eastern prairies, introduced species run rampant through native ecosystems, habitat destruction upriver causes widespread flooding down river, and acid rain originating from distant emissions wipes out Canadian fish. Or closer to home: a forest showers an adjacent pasture with seed, fire from a fire-prone ecosystem sweeps through a residential area, wetland drainage decimates nearby wildlife populations, and heat from a surrounding desert desiccates an oasis. In each case, two or more ecosystems are linked and interacting. (Forman, 1983)

In this chapter, we define landscape ecology, discuss the importance of landscape studies within ecology, briefly review the intellectual roots of landscape, and present an overview of the remainder of the book. In addition, some commonly used terms in landscape ecology are defined in Table 1.1.

WHAT IS LANDSCAPE ECOLOGY?

Landscape ecology emphasizes the interaction between spatial pattern and ecological process, that is, the causes and consequences of spatial heterogeneity across a range of scales. The term *landscape ecology* was introduced by the German biogeographer Carl Troll (1939), arising from the European traditions of regional geography and vegetation science and motivated particularly by the novel perspective offered by aerial photography. Landscape ecology essentially combined the spatial approach of the geographer with the functional approach of the ecologist (Naveh and Lieberman, 1984; Forman and Godron, 1986). During the past two decades, the focus of landscape ecology has been defined in various ways:

> Landscape ecology . . . focuses on (1) the spatial relationships among landscape elements, or ecosystems, (2) the flows of energy, mineral nutrients, and species among the elements, and (3) the ecological dynamics of the landscape mosaic through time. (Forman, 1983)
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> Landscape ecology focuses explicitly upon spatial patterns. Specifically, landscape ecology considers the development and dynamics of spatial hetero-

TABLE 1.1.
DEFINITION OF COMMONLY USED TERMS IN LANDSCAPE ECOLOGY

Configuration: Specific arrangement of spatial elements; often used synonymously with spatial structure or patch structure.

Connectivity: Spatial continuity of a habitat or cover type across a landscape.

Corridor: Relatively narrow strip of a particular type that differs from the areas adjacent on both sides.

Cover type: Category within a classification scheme defined by the user that distinguishes among the different habitats, ecosystems, or vegetation types on a landscape.

Edge: Portion of an ecosystem or cover type near its perimeter and within which environmental conditions may differ from interior locations in the ecosystem; also used as a measure of the length of adjacency between cover types on a landscape.

Fragmentation: Breaking up of a habitat or cover type into smaller, disconnected parcels.

Heterogeneity: Quality or state of consisting of dissimilar elements, as with mixed habitats or cover types occurring on a landscape; opposite of homogeneity, in which elements are the same.

Landscape: Area that is spatially heterogeneous in at least one factor of interest.

Matrix: Background cover type in a landscape, characterized by extensive cover and high connectivity; not all landscapes have a definable matrix.

Patch: Surface area that differs from its surroundings in nature or appearance.

Scale: Spatial or temporal dimension of an object or process, characterized by both grain and extent.

ADAPTED FROM FORMAN, 1995.

geneity, spatial and temporal interactions and exchanges across heterogeneous landscape, influences of spatial heterogeneity on biotic and abiotic processes, and management of spatial heterogeneity. (Risser et al., 1984)

Landscape ecology is motivated by a need to understand the development and dynamics of pattern in ecological phenomena, the role of disturbance in ecosystems, and characteristic spatial and temporal scales of ecological events. (Urban et al., 1987)

Landscape ecology emphasizes broad spatial scales and the ecological effects of the spatial patterning of ecosystems. (Turner, 1989)

> Landscape ecology deals with the effects of the spatial configuration of mosaics on a wide variety of ecological phenomena. (Wiens et al., 1993)
>
> Landscape ecology is the study of the reciprocal effects of spatial pattern on ecological processes; it promotes the development of models and theories of spatial relationships, the collection of new types of data on spatial pattern and dynamics, and the examination of spatial scales rarely addressed in ecology. (Pickett and Cadenasso, 1995)

Collectively, this set of definitions clearly emphasizes two important aspects of landscape ecology that distinguish it from other subdisciplines within ecology. First, *landscape ecology explicitly addresses the importance of spatial configuration for ecological processes.* Landscape ecology is not only concerned with how much there is of a particular component, but also with how it is arranged. The underlying premise of landscape ecology is that the explicit composition and spatial form of a landscape mosaic affect ecological systems in ways that would be different if the mosaic composition or arrangement were different (Wiens, 1995). Most ecological understanding previously had implicitly assumed an ability to average or extrapolate over spatially homogeneous areas. Ecological studies often attempted to achieve a predictive knowledge about a particular type of system, such as a salt marsh or forest stand, without consideration of its size or position in a broader mosaic. Considered in this way, with its emphasis on spatial heterogeneity, landscape ecology is applied across a wide range of scales (Figure 1.1). Studies might address the response of a beetle to the patch structure of its environment within square meters (e.g., Johnson et al., 1992a), the influence of topography and vegetation patterns on ungulate foraging patterns (e.g., Pearson et al., 1995), or the effects of land-use arrangements on nitrogen dynamics in a watershed (e.g., Kesner and Meentemeyer, 1989).

Second, *landscape ecology often focuses on spatial extents that are much larger than those traditionally studied in ecology,* often, the landscape as seen by a human observer (Figure 1.2). In this sense, landscape ecology addresses many kinds of ecological dynamics across large areas such as the Southern Appalachian Mountains, Yellowstone National Park, the Mediterranean, or the rain forests of Rondonia, Brazil. However, it is important to note that, although these areas are typically larger than those used in most community- or ecosystem-level studies, the spatial scales are not absolutes. We deal with issues of scale in the next chapter and throughout this book, but suffice it to say here that landscape ecology does not define, a priori, specific spatial scales that may be universally applied; rather, the emphasis is to identify scales that best characterize relationships between spatial heterogeneity and the processes of interest. These two aspects, explicit treat-

FIGURE 1.1.

The concept of landscape as a spatial mosaic at various spatial scales: (a) An example of a microlandscape, or landscape complexity from the perspective of a grasshopper. Grass cover is *Bouteloua gracilis* and *Buchloe dactyloides*, and vegetation cover in the ~4 m^2 microlandscape is occasionally disrupted by bare ground. (Photo by Kimberly A. With.) (b) Set of experimental microlandscapes used to explore relative effects of habitat abundance and fragmentation on arthropod communities in an agroecosystem. System consists of a replicated series of 12 plots (each 16 m^2) that vary in habitat abundance and spatial contagion based on fractal neutral landscape models (With et al., 1999). (Photo by Kimberly A. With.) (c) Clones of Gambel oak (*Quercus gambelii*) in Colorado illustrating heterogeneity within approximately 1 km^2. (Photo by Sally A. Tinker.) (d) Aerial view of a muskeg and string bog landscape, Alaska. (Photo by John A. Wiens.) (Refer to the CD-ROM for a four-color reproduction of this figure.)

FIGURE 1.2.
Different types of landscapes across relatively large areas in the western United States: (a) Undeveloped mountainous landscape in the Front Range of Colorado, USA. (Photo by Monica G. Turner.) (b) Landscape mosaic of forest and agricultural land south of Santiago, Chile. (Photo by John A. Wiens.) (c) Urbanizing landscape outside Denver, Colorado. (Photo by John A. Wiens.) (d) Aerial view of clear-cuts in a coniferous (lodgepole pine, *Pinus contorta*) landscape, Targhee National Forest, Idaho. Postharvest slash piles scheduled for burning can be seen in the clear-cuts. (Photo by Dennis H. Knight.) (Refer to the CD-ROm for a four-color reproduction of this figure.)

ment of spatial heterogeneity and a focus on broad spatial scales, are not mutually exclusive and encompass much of the breadth of landscape ecology.

The role of humans, obviously a dominant influence on landscape patterns worldwide, is sometimes considered an important component of a definition of landscape ecology. Indeed, in the landscape ecology approaches characteristic of China, Europe, and the Mediterranean region, human activity is perhaps the central factor in landscape ecological studies. Landscape ecology is sometimes considered to be an interdisciplinary science dealing with the interrelation between human society and its living space—its open and built up landscapes (Naveh and Lieberman, 1984). Landscape ecology draws from a variety of disciplines, many of which emphasize social sciences, including geography, landscape architecture, regional planning, economics, forestry, and wildlife ecology. Throughout this book, the role of humans in shaping and responding to landscapes will be considered in many ways. The scientific contributions of landscape ecology are essential for land-management and land-use planning. However, we do not think it necessary to include a human component explicitly in the definition of landscape ecology, because humans are but one of the factors creating and responding to spatial heterogeneity.

What, then, is a landscape? We suggest a general definition that does not require an absolute scale: ***a landscape is an area that is spatially heterogeneous in at least one factor of interest.*** Although at the human scale we may observe "a kilometers-wide mosaic over which local ecosystems recur" (Forman, 1995), it is important to recognize that landscape ecology may deal with landscapes that extend over tens of meters rather than kilometers, and a landscape may even be defined in an aquatic system. In addition, we might observe a landscape represented by a gradient across which ecosystems do not necessarily repeat or recur. Thus our definition is general enough to permit consideration of both aspects of landscape ecology described above.

WHY LANDSCAPE ECOLOGY HAS EMERGED AS A DISTINCT AREA OF STUDY

The recent emergence of landscapes as appropriate subjects for ecological study resulted from three main factors: (1) broad-scale environmental issues and land-management problems, (2) the development of new scale-related concepts in ecology, and (3) technological advances, including the widespread availability of spatial data, the computers and software to manipulate these data, and the rapid rise in computational power.

Broad-Scale Environmental Issues

Demand for the scientific underpinnings of managing large areas and incorporating the consequences of spatial heterogeneity into land-management decisions has been growing since the 1970s and is now enormous. The paradigm of *ecosystem management*, for example, carries with it an implicit focus on the landscape (Agee and Johnson, 1988; Slocombe, 1993; Christensen et al., 1996). Applied problems and resource-management needs have clearly helped to catalyze the development and emergence of landscape ecology. For example, questions of how to manage populations of native plants and animals over large areas as land use or climate changes, how to mediate the effects of habitat fragmentation or loss, how to plan for human settlement in areas that experience a particular natural disturbance regime, and how to reduce the deleterious effects of nonpoint source pollution in aquatic ecosystems all demand basic understanding and management solutions at landscape scales. Federal agencies concerned with conservation in the United States are faced with many of these challenges. The cumulative loss of wetlands and riparian forests from many landscapes poses challenges for the management of animal populations and of water flow and quality. The U.S. Forest Service continues to wrestle with resource-management questions regarding fragmentation of contiguous old-growth forests in the northwestern United States. The patchwork quilt of overgrazed lands in the western United States poses management difficulties for the Bureau of Land Management that extend over multiple states. The National Park Service must attempt to determine whether existing parklands are of sufficient size to sustain biotic populations and natural processes over the long term. These problems require a spatially explicit, broad-scale approach, yet much of ecology had focused on mechanistic studies in relatively small homogeneous areas over relatively short time periods. Landscape ecology provides concepts and methods that complement those that have been traditionally employed in ecology.

Concepts of Scale

The importance of scale (see Chapter 2) became widely recognized in ecology only in the 1980s, despite a long history of attention to the effect of quadrat size on measurements and recognition of species–area relationships. The development of conceptual frameworks focused on scale (Allen and Starr, 1982; Delcourt et al., 1983; O'Neill et al., 1986; Allen and Hoekstra, 1992) prompted ecologists to think hard about the patterns and processes that were important at different scales of space and time. It became clear that no single scale was appropriate for the study of all ecological problems. Some problems required focus on an individual organism and its physiological response to environmental changes. Other problems required study of how numbers of individuals or species change with competition for a limited resource. Still other problems required study of communities and the potential for stable configurations of interacting populations. And still other problems required focus on the arrangement of communities in space and how they interact with heterogeneous patterns of resources on the landscape.

The theory of scale and hierarchy that emerged in the 1980s emphasized that attention should be focused directly on the scale at which a phenomenon of interest occurs. It demonstrated that the insights gained at one scale could not necessarily be translated directly to another scale, hence questioning the applicability of results from numerous fine-scale studies in ecology to the broad-scale problems that were so pressing. Scale theory mandated that the understanding of landscape-level dynamics should be obtained from direct study of the landscape. Finer-scale processes could be considered ***mechanisms*** that explain the landscape dynamics. Broader-scale patterns could be viewed as ***constraints*** that limit the potential range of rate processes. The critical factor was, and remains, identifying the proper scale at which to address the problem.

Thus, land-management problems and hierarchy, or scale, theory encouraged ecologists to address the landscape as a distinct area of study. Landscape ecology recognizes that ecological systems are arrayed in space in response to gradients of topography, temperature, moisture, and soils. Additional pattern is imposed by disturbances, biotic interactions, and human use of the land. Spatial arrangement, in turn, influences many ecological processes, such as the movement patterns of organisms, the spread of disturbances, and the movement of matter or energy. Landscape ecology, focusing on spatial pattern and the ecological responses to this pattern, leads to a new set of principles, distinct from the principles that govern ecosystem and population dynamics at finer scales.

Technological Advances

Technological developments have also contributed to the emergence of landscape ecology. These developments include rapid advances in desktop computing power, availability of remotely sensed data such as satellite images, and development of powerful computer software packages called geographic information systems (GIS) for storing, manipulating, and displaying spatial data. New research techniques are required in landscape ecology because of the focus on spatial pattern and dynamics and on large areas that simply cannot be thoroughly sampled or easily manipulated. For example, laboratory and plot experiments are appropriate at fine scales, but broad-scale experiments are logistically difficult, and replication is often impossible. Landscape ecologists have needed to incorporate new sources of data into their studies and creatively study *natural experiments.* For example, large disturbance events (e.g., hurricanes, forest fires, and volcanic eruptions) as well as land-management practices (e.g., timber harvest and land-use change) create opportunities for studying ecological phenomena at the landscape scale. The availability of remote imagery has made it possible to study spatial pattern over large areas and its change through time, opening new horizons for landscape analysis. With the development of powerful GIS software, scientists can work with spatial data in ways that were not even imagined two decades ago. In addition, quantitative approaches such as spatial statistics and neutral modeling (discussed in Chapters 5 and 6) offer new possibilities for statistical analysis of spatial pattern and associated processes.

THE INTELLECTUAL ROOTS OF LANDSCAPE ECOLOGY

Although landscape ecology became more prominent within ecology in North America beginning in about 1980, it did not begin de novo at that time, but drew upon a rich history. Landscape ecology had its roots in Central and Eastern Europe. European biogeographers viewed the landscape as the total spatial and visual entity of human living space, thereby integrating the environment, the biota, and the human-created components of an area (Naveh and Lieberman, 1984). Troll, who coined the term *landscape ecology,* studied biology and then became a geographer. He was impressed by the ecosystem concept as defined by Tansley (1935) and fascinated by the comprehensive view of landscape units depicted on aerial photographs (Zonneveld, 1990; Schreiber, 1990). He viewed landscape ecology not as a new science, but as a special viewpoint for understanding complex natural phenomena (Schreiber, 1990). Troll (1968) wrote (as translated by Schreiber, 1990), "Aerial photo research is to a great extent landscape ecology, even if it is used, for instance, for archaeology or soil science. In reality, it is the consideration of the geographical landscape and of the ecological cause–effect network in the landscape." At about the same time, the Russian scientist Sukachef (1944, 1945) also developed a very similar concept of a biogeocenology.

Landscape ecology gained wider acceptance and appreciation in the German-speaking countries of Europe throughout the 1950s and 1960s, and it became closely linked with land planning and landscape architecture (Haber, 1990; Ruzicka and Miklos, 1990; Schreiber, 1990; Zonneveld, 1995). There was a strong emphasis on land evaluation, classification, and mapping as the basis from which land-use recommendations could be developed (Figure 1.3). A Society of Landscape Ecology was founded in The Netherlands in 1972; its members included a wide variety of scientists and practitioners whose concerns ranged from conservation to planning (Zonneveld, 1982, 1995). The major literature of landscape ecology from its inception until the early 1980s was predominantly in German and Dutch.

Despite the development of landscape ecology in Europe, the term was virtually absent from North American literature in the mid 1970s (Naveh and Lieberman, 1984). A handful of scientists from North America began attending European symposia and workshops on landscape ecology in the early 1980s (Forman, 1990) and disseminating these new ideas. Several influential publications in the early 1980s helped to introduce the developing field of landscape ecology to English-speaking scientists. Forman and Godron's (1981) article in *BioScience* asked whether the land-

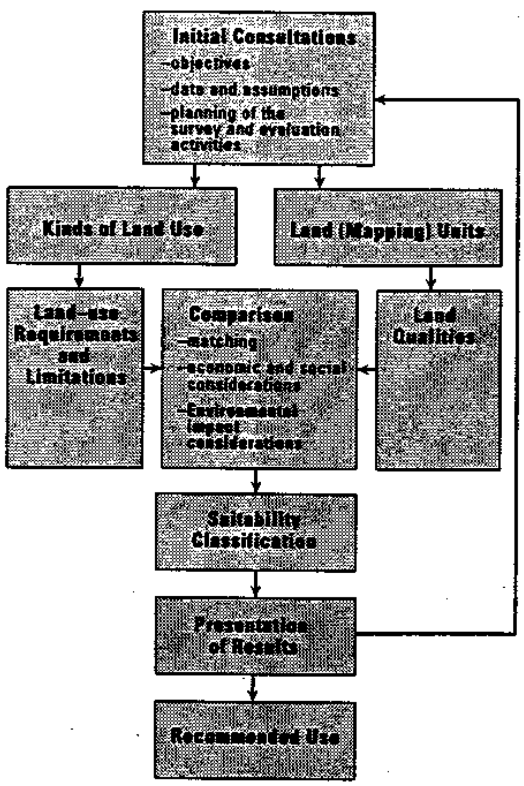


FIGURE 1.3.
Landscape classification and mapping approach developed by Dutch landscape ecologists. Note that the objective was to develop recommended uses of the land.

ADAPTED FROM ZONNEVELD, 1995.

scape was a recognizable and useful unit in ecology and provided a set of terms, such as patch, corridor, and matrix, that remain within the common parlance of landscape ecology. Naveh, an ecologist who focused on vegetation science, fire ecology, and landscape restoration, largely in Mediterranean climates, published a review that laid out a conceptual basis for landscape ecology (Naveh, 1982); his writing emphasized the integral relationship between humans and the landscape and the importance of a systems approach. These ideas were developed further as a book (Naveh and Lieberman, 1984) that delved into both concepts and applications of landscape ecology and stimulated much discussion among ecologists. Forman's (1983) editorial in *BioScience*, from which we quoted earlier, identified landscape ecology as the candidate idea for the decade, with a richness of empirical study, emergent theory, and applications lying ahead. And although not part of the infusion of ideas from Europe to North America, Romme's study of fire history in Yellowstone National Park (Romme, 1982; Romme and Knight, 1982) offered a breakthrough in the development of new metrics to quantify changes in the landscape through time.

Two pivotal meetings in the early 1980s helped to define the current scope of landscape ecology. A 1983 workshop held at Allerton Park, Illinois, brought together a group of North American ecologists to explore the ideas and potential of landscape ecology concepts (Risser et al., 1984). This meeting came soon after an influential meeting in The Netherlands that drew together landscape ecologists in Europe (Tjallingii and de Veer, 1982), and it represented the coalescence of several independent lines of research in the United States. The report that emerged (Risser et al., 1984) still makes for good reading. In many respects, the organized search for principles governing the interaction of pattern and process at the landscape scale began at these two meetings. The emphasis of landscape ecology in North American is somewhat different from Europe, where the association with land planning is so much closer and where the landscape itself has been more intensively managed for a much longer time. However, landscape ecology has grown out of intellectual developments that extended back many decades. The questions addressed by landscape ecologists typically couple the observation that landscape mosaics have spatial structure with topics that have interested ecologists for a long time (Wiens, 1995). Next we highlight several of the important precursors to the concepts of landscape ecology.

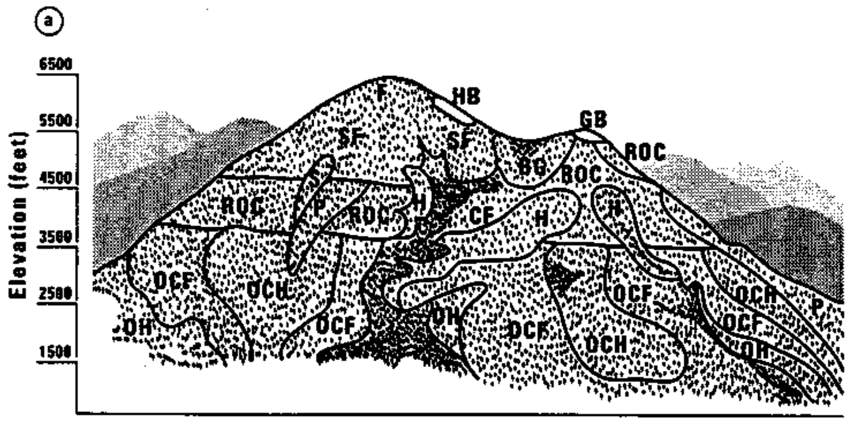
Phytosociology and Biogeography

Phytosociologists in Europe and the United States had long studied the spatial distribution of major plant associations (Braun-Blanquet, 1932), even going back to the observations of von Humboldt (1807) and Warming (1925). For example, it was well known that vegetation distributions in space responded to the north–south gradient of temperature combined with an east–west gradient of moisture. Vegetation pattern was further determined by topographic gradients in moisture, temperature, soils, and exposure. Thus, at broad scales, it was well established that ecological systems interacted with spatially distributed environmental factors to form distinct patterns.

Gradient analysis, an approach similar to the European phytosociology methods, developed in the United States as a means for explaining vegetation patterns; Robert Whittaker's analysis of communities in the Great Smoky Mountains provides an excellent example (e.g., Whittaker, 1952, 1956). In these eastern mountains, distinct patterns have formed with elevation, due to temperature, and with exposure, due to moisture. In a classic analysis, Whittaker was able to decipher the environmental signals creating the pattern. The complex vegetation system was arrayed on a vertical axis of elevation and a horizontal axis representing exposure from moist sites (mesic) to dry, exposed sites (xeric) (Figure 1.4). This simple two-dimensional diagram permits us to predict the vegetation type at any spatial location on the landscape based on its elevation and exposure.

One line of theory was particularly influential in the development of landscape ecology: island biogeography, the analogy between patches of natural vegetation and oceanic islands. The British biogeographer Lack (1942) had early observed that smaller and more remote offshore islands had fewer bird species. From this and similar observations, MacArthur and Wilson (1963, 1967) developed a general theory of island biogeography. The theory has two basic parts: (1) the probability of a species reaching an island is inversely proportional to the distance between the island and the source (mainland or source patch) and directly proportional to island size, and (2) the probability of extinction of a species on the invaded island is a function of island size.

The original theory of island biogeography has been subjected to considerable criticism (e.g., Simberloff, 1974) because of its simplifying assumptions. Nevertheless, it has proved useful as a heuristic construct in designing nature reserves (e.g., Burkey, 1989), and dozens of empirical studies have validated at least some general features of the model. Current efforts in landscape biogeography, dealing with population and community responses to fragmented landscapes, owe much to this body of theory. Nonetheless, metapopulation models (Hanski, 1998) have largely replaced island biogeography models as the theoretical framework within which issues of habitat fragmentation are considered.



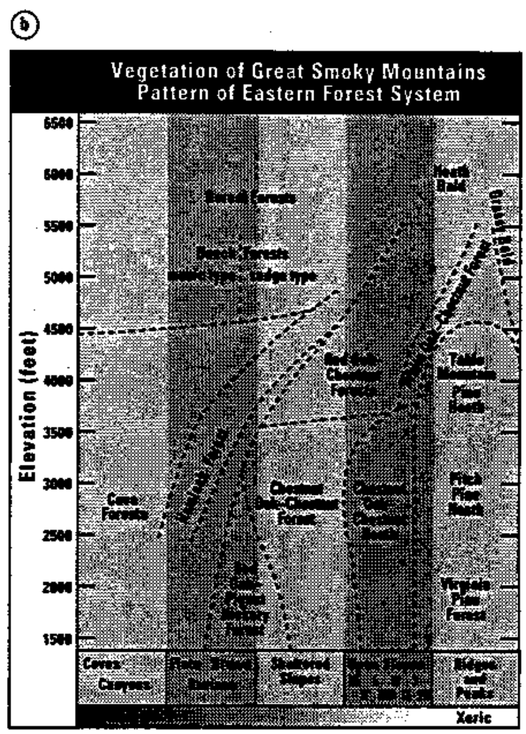


FIGURE 1.4.

(a) Topographic distribution of vegetation types on an idealized west-facing mountain and valley in the Great Smoky Mountains. Vegetation types are: BG, beech gap; CF, cove forest; F, fraser fir; G, grassy balk; H, hemlock forest; HB, heath bald; OCF, chestnut oak–chestnut forest; OCH, chestnut–oak–chestnut heath; OH, oak–hickory forest; P, pine forest and pine heath; ROC, red oak–chestnut oak; S, spruce; SF, spruce–fir; WOC, white oak–chestnut forest. (b) Vegetation of the Great Smoky Mountains, below the subalpine conifer forests, with respect to gradients of elevation and topography.

ADAPTED FROM WHITTAKER, 1956.

Landscape Planning, Design, and Management

The relationship between human societies and landscape change has been a fundamental concern of ecologists in Europe for many years (see Naveh, 1982). Indeed, the history of human-induced change is clearly apparent throughout Europe, with roads and viaducts constructed during the Roman Empire still having a visible effect in many regions (Marc Antrop, personal communication). The emphasis of ecological studies in North American has been on relatively undisturbed systems (Risser et al., 1984), but an awareness of human effects on landscapes has been evident for more than 140 years (Marsh, 1864, as cited by Turner and Meyer, 1993). The writings of a number of authors have provided an important context for integrating ecological effects with landscape planning, including the development of map overlay techniques (a precursor to current GIS methods) by McHarg (1969), the studies of Watt (1947) that focused on patch structure as fundamental to understanding vegetation pattern, an overview of the effects of ecosystem fragmentation in human-dominated landscapes edited by Burgess and Sharpe (1981), and the development of concepts of adaptive management by Holling (1978).

The goals of landscape planning, design, and management include the identification and protection of ecological resources and control of their use through plans that ensure the sustainability of these resources (Fabos, 1985). The result is that landscape planning is a primary basis for collaboration and knowledge exchange between landscape planners and landscape ecologists (Ahern, 1999). Perhaps the best examples of the integration of landscape planning, design, and management can be found in The Netherlands, where a national plan for a sustainable landscape is being implemented (Vos and Opdam, 1993). In North America, the best examples include the current plans for ecosystem management of national forests (Bartuska, 1999) and studies aimed at conservation design (Diamond and May, 1976; Mladenoff et al., 1994; Ando et al., 1998).

Multidisciplinary Studies and Regional Modeling

The geographic sciences have made important contributions to the methodology of landscape ecology. Satellite imagery, classified to cover type, has been an invaluable resource. Software developments (e.g., GIS and image analysis programs, spatial statistics) provide computer capabilities for displaying, superimposing, and analyzing spatial patterns. These analytical tools and the geographer's experience in handling large spatial databases have been a stimulus and critical resource for landscape ecologists.

During the 1960s, a number of diverse projects resulted in the development of large regional models. The result was the application of systems analysis and computer modeling at landscape scales that clearly established the broad-scale impact of human development. These models were often associated with urban development programs (Lowry, 1967) concerned with the interaction of spatial patterns and socioeconomic processes, a topic that remains important today. Transportation models were developed to link human activities at different positions on the landscape. Large-scale urban renewal programs (Pittsburgh Community Renewal Project, 1962) theorized about the optimal spatial arrangement of economic activities on the urban landscape. The central theme of these studies was the interactions by which socioeconomic processes produced spatial pattern and the patterns, in turn, encouraged or constrained human activities (Hemens, 1970). By the end of the 1960s, studies on pattern–process interactions had resulted in a considerable body of theory. Much of the development was synthesized under the titles of *urban dynamics* (Forester, 1969) and *regional science* (Isard, 1960, 1972, 1975). Considerable effort was expended toward linking spatial activities on the landscape with socioeconomic theory (Smith, 1976).

An important set of studies considered the spatial allocation of processes from the perspective of central place theory (Herbert and Stevens, 1960; Steger, 1964), which predicts that human activities will radiate outward from a center of economic activity, such as a city, transportation center, or highway intersection. This theory was later applied to the spatial pattern of foraging by animals (Aronson and Givnish, 1983), including ants (Harkness and Maroudas, 1985) and birds (Andersson, 1981) that forage outward from a nest. Central place theory was also used to predict land-use change following the installation of a sawmill in a rural area (Hett, 1971).

In subsequent years, regional modeling became concerned with predicting the effects of socioeconomic activities on the environment. Example applications with a strong spatial component included studies of the impact of large-scale energy developments (Basta and Bower 1982; Krummel et al., 1984) and the planning of riverbasin systems (Hamilton et al., 1969). These studies resulted in new theoretical constructs to link socioeconomic and ecological variables in the same model (Klopatek et al., 1983), which were later applied to such diverse problems as modeling oil and gas extraction in the western United States (Mankin et al., 1981) and cattle herding societies in Africa (Krummel et al., 1986). All these studies focused on the interaction between landscape pattern and ecological processes and emphasized the need to include socioeconomic processes in landscape analyses, long before the principles of landscape ecology were articulated in Europe or North America.

Spatial Pattern and Theoretical Ecology

A number of theoretical population studies have considered the interaction between spatial patterning and ecological dynamics for terrestrial (Clark et al., 1978, 1979; Johnson et al., 1992a) and aquatic (Steele, 1974a; Harris, 1998) ecosystems. These studies demonstrated that unstable population interactions can sometimes be stabilized by spreading the interaction across a heterogeneous landscape (e.g., Reddingius and Den Boer, 1970; Roff, 1974a; Hastings, 1977; Scheffer and de Boer, 1995). At the same time, ecological processes alone can generate complex patterns in an otherwise homogeneous landscape (Dubois, 1975; McLaughlin and Roughgarden, 1991; Molofsky, 1994). Clark (1980) has pointed out that management practices that reduce heterogeneity to produce more stable dynamics are often counterproductive, because destruction of pattern can interfere with ecological mechanisms for persistence.

Many developments in population theory can be traced to the classic experiments of Huffaker (Huffaker, 1958; Huffaker et al., 1963), who studied the interactions of fructiverous and predatory mites in experimentally manipulated arrays of oranges. The oranges provided food for the fructivorous mites, which, in turn, were consumed by predatory mites. Spatial manipulation of the oranges could shift dynamics between unstable (oranges placed close together, allowing predators to locate and eliminate all prey) and stable (oranges formed into patches, preventing predators from locating and eliminating all prey). These experiments helped to define the importance of the spatial relationships among local populations that had been previously pointed out by Andrewartha and Birch (1954).

The interplay between spatial heterogeneity with species-specific patterns of dispersal has been extensively studied (e.g., Bradford and Philip, 1970; Caswell and Cohen, 1995; Cohen and Levin, 1991; Epperson, 1994; Hastings, 1996a; Kareiva, 1990; Levins, 1970; Levins and Culver, 1971). Spatial pattern of resources provides refuges (Comins and Blatt, 1974) that permit individuals to escape unfavorable conditions. The degree to which heterogeneity stabilizes relationships depends on the relative dispersal ability of predator and prey (Vandermeer, 1973; Taylor, 1990) and differences in their reproductive rates (Hilborn, 1975). Ziegler (1977) has also shown that dispersal or migration at discrete times can lead to a stable system even if continuous dispersal does not. The ability to disperse over a gradually changing environment could enable a population to survive extreme conditions (Roff, 1974b; Hamilton and May, 1977). It seemed clear that spatial pattern could affect both the stability of populations (Jones, 1975) and the total population size that could be supported (Steele, 1974b). Importantly, spatial pattern and the ability to disperse could spread the utilization of a resource over space so that it is not exhausted (Myers, 1976).

Another series of theoretical studies has been concerned with the biotic (Sprugel, 1976) and abiotic (Levin and Paine, 1974a, b) factors that cause the observed patterns on the landscape. Levin (1976a) provided an excellent general treatment of the subject, identifying three factors: (1) local uniqueness of sites on the landscape caused by variations in microhabitat, soils, and the likes, (2) phase differences, such that different points on the landscape are at different stages of development or different stages of recovery from localized disturbances, and (3) dispersal effects in which differential movement by organisms across landscapes leads to patchiness (e.g., Criminale and Winter, 1974).

Theoretical studies have suggested a number of specific mechanisms to explain landscape patterns. In areas where two species overlap, competitive interactions may produce sharp boundaries (Yamamura, 1976). Several workers (e.g., Kierstead and Slobodkin, 1953) have empirically demonstrated that spatial patterning in biota may reflect spatial patterning in abiotic factors such as water turbulence or topography. If a system has multiple stable states, a distinct spatial pattern may result simply by differences in microhabitat, which may be sufficient to structure phytoplankton communities (Powell et al., 1975). Even without microhabitat heterogeneity, Okubo (1974) has shown that the combination of competitive interaction and dispersal can result in patchiness. Segal and Levin (1976) reach a similar conclusion, particularly if there are mutualistic relationships among the prey.

Two important conclusions can be drawn from this brief survey of theoretical studies on spatial patterning: (1) it is clear that patterning is an important ecological phenomenon, with disruption of the pattern possibly resulting in the eruption of pests and subsequent population extinction events; (2) spatial patterns are the result of complex interplay between abiotic constraints, biotic interactions, and disturbances. The pattern is not simply a constraint imposed on the ecological system by topography and soils. Instead, there is an intimate tie between pattern and process that forms an important core for the understanding of landscape ecology.

Recent Theoretical Developments

New developments in theory are continuing to provide a stimulus for landscape ecology. We illustrate this with examples taken from fractal geometry, percolation theory, and self-organized criticality.

Fractal geometry (Burrough, 1981; Mandelbrot, 1983), which has identified classes of pattern that remain similar over a wide range of scales, has had intriguing applications in ecology (Sugihara and May, 1990). If the assumptions of the fractal theory are satisfied, extrapolation of spatial pattern across scales becomes possible, allowing broad-scale patterns to be predicted from fine-scale measurements. An early application of fractal geometry for landscape studies was the use of the fractal dimension as an index of human interference with landscape pattern (Krummel et al., 1987). Other applications include studies of insect movement (Johnson et al., 1992b; Wiens et al., 1995), measures of landscape texture (Plotnick et al., 1993), species perception of landscape structure (With, 1994a), generation of artificial landscapes (Palmer, 1992; With et al., 1997), characterizing landscape pattern (Milne, 1988; Overpeck et al., 1990), and using fractal theory for landscape design (Milne, 1991a).

Percolation theory (Stauffer and Aharony, 1992) deals with spatial patterns in randomly assembled systems. The application of percolation theory to landscape studies has addressed a series of questions dealing with the size, shape, and connectivity of habitats as a function of the percentage of a landscape occupied by that habitat type. Because percolation theory generates pattern in the absence of specific processes, the comparison of random maps with actual landscapes provides a neutral model capable of defining significant departures from randomness (Gardner et al., 1987a; With and King, 1997) of patterned landscapes. This theory has offered important insights into the nature of connectivity (or its inverse, fragmentation) on landscapes (Gardner et al., 1992a; Fonseca et al., 1996; Milne et al., 1996).

Descriptions of landscape pattern and process are beginning to benefit from insights provided by the theory of self-organized criticality (Bak et al., 1988). This theory states that open, complex systems (that is, systems with many independent components) may be described by power-law statistics over many orders of magnitude. Because these systems are self-similar (Grumbacher et al., 1993), a fundamental understanding of scale-dependent phenomena can emerge from studies of self-organized criticality. Well-studied examples of physical systems that display the properties of self-organized criticality include avalanches in sandpiles (Grumbacher et al., 1993), earthquakes (Ceva, 1998) and ferromagnetic systems (Tadic, 1998). Recently, these concepts have been applied to ecosystems (Milne, 1998), with examples that include canopy gaps in rain-forests (Katori et al., 1998), river flows (Pandey et al., 1998), and coevolution in multispecies communities (Caldarelli et al., 1998). The importance of these results has recently been confirmed by using power-law statistics to estimate the risk of large fires from measurements taken from small to medium fires (Malamud et al., 1998).

OBJECTIVES OF THIS BOOK

It is clear that landscape ecology has a rich intellectual history and that it draws on a wide range of natural and social science. The remainder of this book will deal with the concepts, questions, methods, and applications of landscape ecology, with an emphasis on the ecological approach. This in no way diminishes the importance of the social sciences in the interdisciplinary study of landscapes; however, this text is written by ecologists, and our biases and expertise fall within the science of ecology. We hope that the book will be useful not only to students in ecology, but also to students in disciplines such as conservation biology, resource management, landscape architecture, land planning, geography, and regional studies who wish to delve more deeply into landscape ecology as an ecological science. In addition, we hope that this volume will complement other recent landscape ecology books that have somewhat different emphases (e.g., Haines-Young et al., 1993; Forman, 1995; Hansson et al., 1995; Bissonette, 1997; Farina, 1998; Klopatek and Gardner, 1999).

Landscape ecology may also serve as a source of new ideas for other disciplines within ecology. For example, aquatic ecologists have applied a landscape ecological approach to the study of riffle, cobble, and sandy substrates within streams (e.g., Wohl et al., 1995), patch distributions of fishes as measured by echolocation (e.g, Magnuson et al., 1991; Nero and Magnuson, 1992), patterns and processes of rocky benthic communities (e.g., Garrabou et al., 1998), and spatial variation in coral bleaching (Rowan et al., 1997). Thus, landscape ecology benefits from and contributes toward intellectual developments in other disciplines.

The development and application of models has emerged as an important component of landscape ecology, as in other areas of science. In particular, spatially explicit models of ecological dynamics have become widely used in landscape-level studies. There remains a strong need for enhanced integration of models with appropriate field or empirical studies. The combination of models, which provide a rigorous representation of our hypotheses or best understanding of the dynamics of a systems, and empirical data, which keep us firmly rooted in the ecological systems that we seek to understand, offers a powerful approach likely to result in greater insight than either approach applied alone. Nevertheless, we include a chapter on modeling to familiarize readers with the fundamental concepts of this important topic.

This is also not a textbook for geographic information systems (GIS) or remote sensing, although landscape ecology makes extensive use of these technologies. Often, landscape ecologists use the final products of GIS manipulations or the interpretation of spectral data, but many are not technically proficient in all the intricacies of the processes involved. Many fine texts are excellent resources for the landscape ecologist who needs a more thorough introduction to these subjects. For GIS, we suggest Burrough (1986), Bonham-Carter (1994), Fotheringham and Rogerson (1994), and Burrough and McDonnell (1998); for remote sensing, we suggest Lillesand and Kiefer (1994) or Jensen (1996).

We have organized the book in a sequence comparable to what we teach in a landscape ecology course. The first three chapters provide an introduction to the subject and its development (Chapter 1), a treatment of scale (Chapter 2), which influences everything that follows, and an introduction to basic modeling concepts (Chapter 3). We then examine the causes of landscape pattern (Chapter 4), including both biotic and abiotic factors, and consider observed changes over extended temporal scales. The quantification of landscape pattern, which is a necessary component of understanding the interaction between pattern and process, is presented in detail in Chapter 5. The use of neutral models in landscape ecology, which is closely related to quantification of pattern and to linkages of pattern with process, is considered in Chapter 6. The next three chapters deal with particular phenomena that have received considerable attention in landscape studies during the past two decades: disturbance dynamics (Chapter 7), the responses of organisms to spatial heterogeneity (Chapter 8), and ecosystem processes at landscape scales (Chapter 9). We then deal explicitly with the many applications of landscape ecology (Chapter 10) and, finally, suggest conclusions and future directions for the field (Chapter 11).

SUMMARY

Landscape ecology has come to the forefront of ecology and land management in recent decades, and it is still expanding very rapidly. Landscape ecology emphasizes the interaction between spatial pattern and ecological process, that is, the causes and consequences of spatial heterogeneity across a range of scales. Two important aspects of landscape ecology distinguish it from other subdisciplines

within ecology. First, landscape ecology explicitly addresses the importance of spatial configuration for ecological processes. Second, landscape ecology often focuses on spatial extents that are much larger than those traditionally studied in ecology. These two aspects, explicit treatment of spatial heterogeneity and a focus on broad spatial scales, are complementary and encompass much of the breadth of landscape ecology.

The recent emergence of landscapes as an appropriate scale for ecological study resulted from (1) broad-scale environmental issues and land-management problems, (2) the development of new scale-related concepts in ecology, and (3) technological advances, including the widespread availability of spatial data, the software to manipulate these data, and the rapid rise in computational power. However, landscape ecology has a history, with its roots in Central and Eastern Europe. The major literature of landscape ecology from its inception in the late 1930s through the early 1980s was predominantly in German and Dutch; the term *landscape ecology* was virtually absent from North American literature in the mid 1970s. The recent search for principles governing the interaction of pattern and process at the landscape scale began with two influential workshops in the early 1980s in Europe and North America. The questions addressed by landscape ecologists typically couple the observation that landscape mosaics have spatial structure with topics that have interested ecologists for a long time. Landscape ecology has grown out of intellectual developments that extended back many decades and include phytosociology and biogeography, landscape design and management, geography, regional modeling, theoretical ecology, island biogeography, and mathematical theory.

DISCUSSION QUESTIONS

1. Reconcile the two different ways in which ecologists use the concept of landscape: as a relatively large area composed of elements that we recognize and as a theoretical construct for considering spatial heterogeneity at any scale (see Pickett and Cadenasso, 1995). Are these notions mutually exclusive or complementary? Do they confuse or enhance our understanding of landscape ecology?
2. Describe three current environmental issues that require consideration of the landscape, either as a causal factor or a response. What information or understanding is lost if a landscape perspective is not taken?
3. How has landscape ecology been influenced by the historical development of ideas in ecology? In landscape design and management?

4. Is landscape ecology defined by its questions or by its techniques? Do you consider it to be a broad or narrow avenue of inquiry within ecology?

RECOMMENDED READINGS

PICKETT, S. T. A., AND M. L. CADENASSO. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269:331–334.

TURNER, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171–197.

URBAN, D. L., R. V. O'NEILL, AND H. H. SHUGART. 1987. Landscape ecology. *BioScience* 37:119–127.

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IN THEORY AND PRACTICE

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