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LANDSCAPE ECOLOGY

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Spatial heterogeneity is ubiquitous in all ecological systems, underlining the significance of the pattern–process relationship and the scale of observation and analysis. Landscape ecology focuses on the relationship between spatial pattern and ecological processes on multiple scales. On the one hand, it represents a spatially explicit perspective on ecological phenomena. On the other hand, it is a highly interdisciplinary field that integrates biophysical and socioeconomic perspectives to understand and improve the ecology and sustainability of landscapes. Landscape ecology is still rapidly evolving, with a diversity of emerging ideas and a plurality of methods and applications.

DEFINING LANDSCAPE ECOLOGY

Landscapes are spatially heterogeneous geographic areas characterized by diverse interacting patches or ecosystems, ranging from relatively natural terrestrial and aquatic systems such as forests, grasslands, and lakes to human-dominated environments including agricultural and urban settings (Fig. 1). Landscape is an ecological criterion whose essence is not its absolute spatial scale but rather its heterogeneity relevant to a particular research question. As such, the "landscape" view is equally applicable to aquatic systems. This multiple-scale concept of landscape is more appropriate because it accommodates the scale multiplicity of patterns and processes occurring in real landscapes, and because it facilitates theoretical and methodological developments by recognizing the importance of micro-, meso-, macro-, and cross-scale approaches.

The term landscape ecology was coined in 1939 by the German geographer Carl Troll, who was inspired by the spatial patterning of landscapes revealed in aerial photographs and the ecosystem concept developed in 1935 by the British ecologist Arthur Tansley. Troll originally defined landscape ecology as the study of the relationship between biological communities and their environment in a landscape mosaic. Today, landscape ecology is widely recognized as the science of studying and improving the relationship between spatial pattern and ecological processes on a multitude of scales and organizational levels. Heterogeneity, scale, pattern–process relationships, disturbance, hierarchy, and sustainability are among the key concepts in contemporary landscape ecology. Landscape ecological studies typically involve the use of geospatial data from various sources (e.g., field survey, aerial photography, and remote sensing) and spatial analysis of different kinds (e.g., pattern indices and spatial statistics). The intellectual thrust of this highly interdisciplinary field is to understand the causes, mechanisms, and consequences of spatial heterogeneity in landscapes.

Heterogeneity refers to the spatial variation of the composition and configuration of landscape, which often manifests itself in the form of patchiness and gradient. In landscape ecology, scale usually refers to grain (the finest spatial or temporal resolution of a dataset) and/or extent (the total study area or duration). When heterogeneity becomes the focus of study, scale matters inevitably because the characterization and understanding of heterogeneity are scale dependent. Landscape

FIGURE 1 Landscapes of the real world. The study objects of landscape ecology range from natural, to agricultural, to urban landscapes. Not only may they be dominated by different vegetation types (e.g., forests, grasslands, and deserts), but they also may have either a terrestrial or an aquatic matrix (e.g., a lakescape, seascape, or oceanscape). Photographs by J. Wu.

pattern involves both the composition of landscape elements and their spatial arrangement, and the relationship between pattern and process also varies with scale. Disturbance—a temporally discrete natural or anthropogenic event that directly damages ecosystem structure—is a primary source of spatial heterogeneity or pattern. Like pattern and process, disturbance is also scale dependent—meaning that the kind, intensity, and consequences of disturbance will change with scale in space across a landscape. This scale multiplicity of patterns and processes frequently results in the hierarchical structure of landscapes—that is, landscapes are spatially nested patches of different size, content, and history. The goal of landscape ecology is not only to understand the relationship between spatial pattern and ecological processes but also to achieve the sustainability of landscapes. Landscape sustainability is the long-term ability of a landscape to support biodiversity and ecosystem processes and provide ecosystem services in face of various disturbances.

EVOLVING PERSPECTIVES

Two dominant perspectives in landscape ecology are commonly compared and contrasted: the European perspective and the North American perspective. The European perspective traditionally has been more humanistic and holistic in that it emphasizes a society-centered view that promotes place-based and solution-driven research. It has focused on landscape mapping, evaluation, conservation, planning, design, and management. In contrast, the North American approach is more biophysical and analytical in that it has been dominated by a biological ecology–centered view that is driven primarily by scientific questions. It has had a distinct emphasis on the effects of spatial pattern on population and ecosystem processes in a heterogeneous area. This research emphasis is practically motivated by the fact that previously contiguous landscapes have rapidly been replaced by a patchwork of diverse land uses (landscape fragmentation) and conceptually linked to the theory of island biogeography developed in the 1960s and the perspective of patch dynamics that began to take shape in the 1970s.

However, this dichotomy most definitely oversimplifies the reality because such geographic division conceals the diverse and continuously evolving perspectives within each region. In fact, many ecologists in North America have recognized the importance of humans in shaping landscapes for several decades (especially since the dust bowl in the 1930s). Although humans and their activities have been treated only as one of many factors interacting with spatial heterogeneity, more integrative studies have been emerging rapidly in the past few decades with the surging interest in urban ecology and sustainability science in North America. On the other hand, the perspective of spatial heterogeneity has increasingly been recognized by landscape ecologists in Europe and the rest of the world. Thus, the current development of landscape ecology around the world suggests a transition from a stage of diversification to one of consolidation (if not unification) of key ideas and approaches.

Both the European and North American perspectives are essential to the development of landscape ecology as a truly interdisciplinary science. To move landscape ecology forward, however, one of the major challenges is to develop comprehensive and operational theories to unite the biophysical and holistic perspectives. Viewing landscapes as complex adaptive systems (CAS) or coupled human–environmental systems provides new opportunities toward this end. In addition, spatial resilience—which explores how the spatial configuration of landscape elements affects landscape sustainability—may also serve as a nexus to integrate a number of key concepts, including diversity, heterogeneity, pattern and process, disturbance, scale, landscape connectivity, and sustainability.

KEY RESEARCH TOPICS

Although landscape ecology is an extremely diverse field (Fig. 2), a set of key research areas can be identified. These include quantifying landscape pattern and its ecological effects; the mechanisms of flows of organisms, energy, and materials in landscape mosaics; behavioral landscape ecology, which focuses on how the behavior of organisms

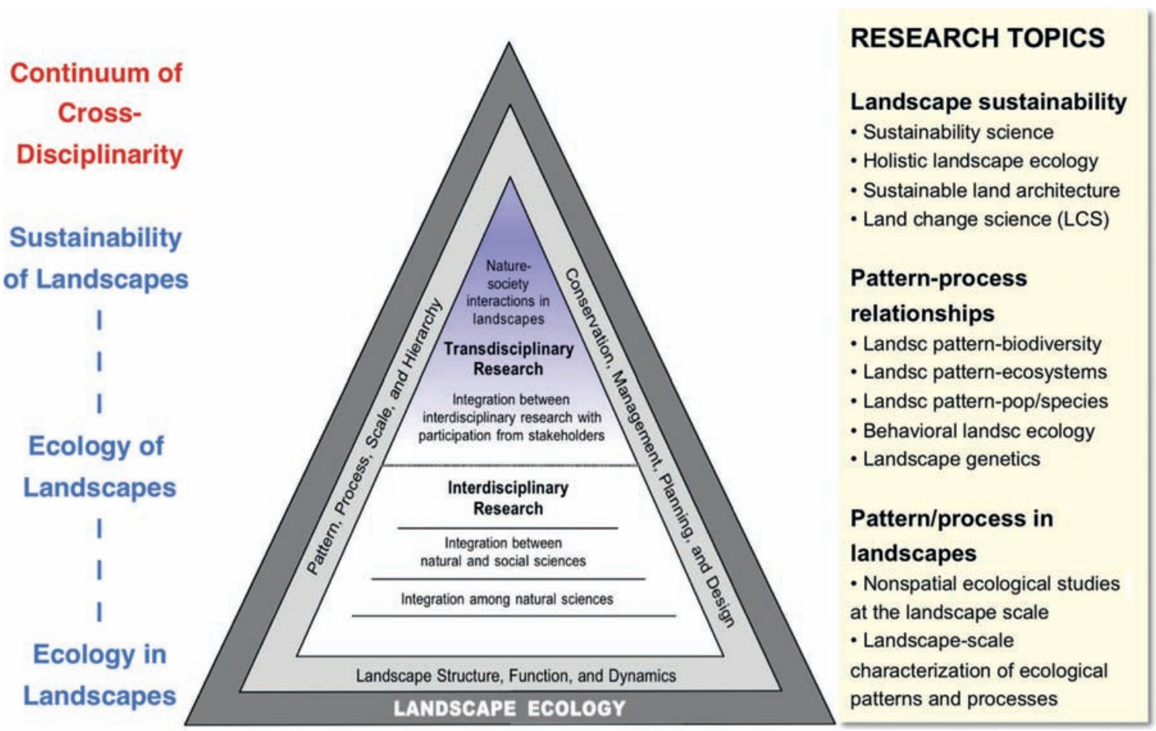

FIGURE 2 A hierarchical and pluralistic view of landscape ecology (modified from Wu, 2006). "Hierarchical" refers to the multiplicity of organizational levels, spatiotemporal scales, and degrees of cross-disciplinarity in landscape ecological research. "Pluralistic" emphasizes the values of different perspectives and methods in landscape ecology derived from its diverse origins and goals.

interacts with landscape structure; landscape genetics, which aims to understand how landscape heterogeneity affects population genetics; causes and consequences of land use and land cover change; spatial scaling, which deals with translation of information across heterogeneous landscapes; and optimization of landscape pattern for conservation or sustainability. A number of theoretical challenges exist in the study of these key topics. These challenges hinge on the spatialization of processes of interest—i.e., explicitly describing where processes take place and how they relate to each other in space. Mathematically, spatialization introduces heterogeneity, nonlinearity, and delays into models.

Thus, spatial explicitness is a salient characteristic of landscape ecological studies. Metapopulations and metacommunities have been fair game in landscape ecology. In general, however, a landscape mosaic approach considers more than the network of patches. For example, in contrast with metapopulations, landscape populations emphasize not only the dynamics of, and interactions between, local populations but also the effects of the heterogeneity of the landscape matrix. Thus, landscape population models explicitly consider the size, shape, and spatial arrangement of all habitat and nonhabitat elements. Also, the landscape population approach allows for explicit examination of how idiosyncratic features of habitat patches and the landscape matrix affect the dispersal of organisms or propagules. In general, the theory of island biogeography, metapopulation theory, and most population viability analysis (PVA) models focus mainly on the islands in a homogeneous matrix, whereas the landscape population approach explicitly considers all landscape elements and their spatial configuration in relation to population dynamics across a heterogeneous geographic area.

In the study of ecosystem processes in a heterogeneous area, the landscape mosaic approach is characterized by the explicit consideration of the effects of spatial heterogeneity, lateral flows, and scale on the pools and fluxes of energy and matter within an ecosystem and across a fragmented landscape. While models of ecosystem processes have been well developed in the past several decades, landscape-scale ecosystem models are still in their infancy. The primary difference between these two kinds of models lies in the fact that landscape models explicitly account for the locations of pools and rates, and in many cases multiple interactive ecosystems are considered together. The landscape approach to ecosystem dynamics promotes the use of remote sensing and GIS in dealing with spatial heterogeneity and scaling in addition to more traditional methods of measuring pools and fluxes commonly used in ecosystem ecology. It also integrates the pattern-based horizontal methods of landscape ecology with the process-based vertical methods of ecosystem ecology and promotes the coupling between the organism-centered population perspective and the flux-centered ecosystem perspective.

FUTURE DIRECTIONS

Emphasis on heterogeneity begs questions of the relationship between pattern and process. Heterogeneity is about structural and functional patterns that deviate from uniform and random arrangements. It is this pervasively common nonhomogeneous characteristic that makes spatial patterns ecologically important. Thus, studying pattern without getting to process is superficial, and understanding process without reference to pattern is incomplete. Emphasis on heterogeneity also makes scale a critically important issue because heterogeneity, as well as the relationship between pattern and process, may vary as the scale of observation or analysis is changed. Thus, whenever heterogeneity is emphasized, spatial structures, underlying processes, and scale inevitably become essential objects of study. From this perspective, landscape ecology is a science of heterogeneity and scale. On the other hand, with increasing human dominance in the biosphere, emphasis on broad spatial scales makes inevitable to deal with humans and their activities. As a consequence, humanistic and holistic perspectives have been and will continue to be central in landscape ecological research.

Various effects of the compositional diversity and spatial configuration of landscape elements have been well documented, and a great number of landscape metrics (synoptic measures of landscape pattern) and spatial analysis methods have been developed in the past decades. The greatest challenge, however, is to relate the measures of spatial pattern to the processes and properties of biodiversity and ecosystem functioning. To address this challenge, well-designed field-based observational and experimental studies are indispensable, and remote sensing techniques, geographic information systems (GIS), spatial statistics, and simulation modeling are also necessary. Landscape ecology is leading the way in developing the theory and methods of scaling that is essential to all natural and social sciences. However, many challenges still remain, including establishing scaling relations for a variety of landscape patterns and processes as well as integrating ecological and socioeconomic dimensions in a coherent scaling framework. Massive data collection efforts (e.g., NEON) are expected to provide both opportunities and challenges to

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landscape ecology to develop and test models and theories using detailed data spanning from local to regional scales. Mathematical theory and modeling are critically important for the development of a science of spatial scale.

Overall, landscape ecology is expected to provide not only the scientific understanding of the structure and functioning of various landscapes but also the pragmatic guidelines and tools with which resilience and sustainability can be created and maintained for the ever-changing landscapes (Fig. 2). The rapid developments and advances in landscape ecology are best reflected in the pages of the flagship journal of the field, *Landscape Ecology* (http://www.springeronline.com/journal/10980/).

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