00007 Landscape Ecology ☆

Jianguo Wu Ph.D.[1,*], Arizona State University, Tempe, AZ, United States

*Jianguo Wu

Abstract

Ecological systems are spatially heterogeneous on a wide range of scales. Landscapes usually refer to broad geographic areas that comprise multiple ecosystems or land use/land cover types, which are human-environmental systems with varying degrees of anthropogenic dominance. Landscape ecology is the science of studying and improving the relationship between spatial pattern and ecological processes across scales and organizational levels. In a broad sense, landscape ecology represents both a field of study and a new ecological paradigm. As a highly interdisciplinary research field, landscape ecology integrates biophysical and analytical approaches with humanistic and holistic perspectives across natural and social sciences. As a scientific paradigm, landscape ecology is characterized by its explicit emphasis on the causes, processes, and ecological consequences of spatial heterogeneity on multiple scales. Thus, the relationship between pattern, process and scale has been a dominant theme of landscape ecological studies since the 1980s. Ecological flows in landscape mosaics, land use and land cover change, scaling, relating landscape pattern analysis with ecological processes, biodiversity conservation, ecosystem services, and landscape sustainability are among the key research topics in modern landscape ecology. During the past several decades, the landscape ecology perspective has become pervasive in almost all areas of ecology, and increasingly important to biodiversity conservation, landscape and urban planning, and sustainability research and practice.

Key Points

- Landscapes are spatially heterogeneous areas in which multiple ecosystems interact.
- Spatial heterogeneity is ubiquitous and matters to ecological processes across scales.
- Heterogeneity leads to patterns which in turn make the scale of analysis critically important.
- Landscape ecology focuses on the relationship between spatial pattern and ecological processes on broad geographical scales.
- The ultimate goal of landscape ecology is to understand how landscape composition and configuration affect ecosystem processes, so that landscapes can be made more sustainable.
- Landscape ecology emphasizes spatially explicit methods, relying heavily on remote sensing data, GIS, and spatial analysis tools.
- Landscape ecology is highly interdisciplinary, and closely related to geographical and planning sciences in particular.

Introduction

The natural world is amazingly beautiful and full of wonders in many ways. That is because neither abiotic nor biotic entities are distributed completely randomly or regularly in space, but rather they form patterns and organize into ecosystems and landscapes. This is a manifestation of spatial autocorrelation – things that are closer tend to be more similar – the so-called first law in geography. Spatial pattern, or spatial heterogeneity, exists on all scales (from local ecosystems to the entire biosphere) and across all systems (including physical, ecological, and socioeconomic systems). Does spatial pattern or heterogeneity matter to biodiversity and ecological processes? The answer is yes in general, but it may not sometimes. Ecology as a term was coined in 1866, but no ecological discipline had focused on this essential question before the rise of modern landscape ecology in the 1980s. Traditional “ecologies” assume away spatial heterogeneity and focus on “systems”, albeit systems of interacting individuals (populations), systems of interacting species (communities), or systems of interacting organisms and their environment. In contrast, landscape ecology embraces spatial heterogeneity as its core idea.

Explicitly considering spatial heterogeneity in ecological studies requires new conceptual frameworks, methods, and technologies. Although the term “landscape ecology” was coined in 1939, the field had made only limited progress before the 1980s when nonequilibrium ecological concepts, remote sensing, GIS, personal computers, and other spatial analysis tools began to reshape the fields of ecology and geography. Because spatial heterogeneity is ubiquitous and because landscapes are where people interact with ecosystems, landscape ecology has become an increasingly relevant and important research field for understanding both how “nature” works and how it ought to

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work. This chapter provides an overview of landscape ecology as a highly interdisciplinary field. It covers the definitions of landscape and landscape ecology, evolving perspectives in the field, key research topics, and future directions.

What Is Landscape Ecology?

Landscapes are spatial mosaics of interacting local ecosystems and other entities, which are frequently considered as human-environmental systems (**Fig. 1**). Landscape ecology has been defined in various ways partly because the word, "landscape," means different things to people with different scientific and cultural backgrounds. The diversity of perspectives can often be related to the philosophical underpinnings of reductionism versus holism, as well as different disciplinary traditions and practical considerations. Although a spectrum of views exists as to what landscape and landscape ecology are, few would disagree that landscapes are compositionally diverse and spatially heterogeneous. Modern landscape ecology is highly interdisciplinary, and may be defined as the integration of science and art of studying and improving the relationship between spatial pattern and ecological processes on multiple scales over broad geographic areas. Land-

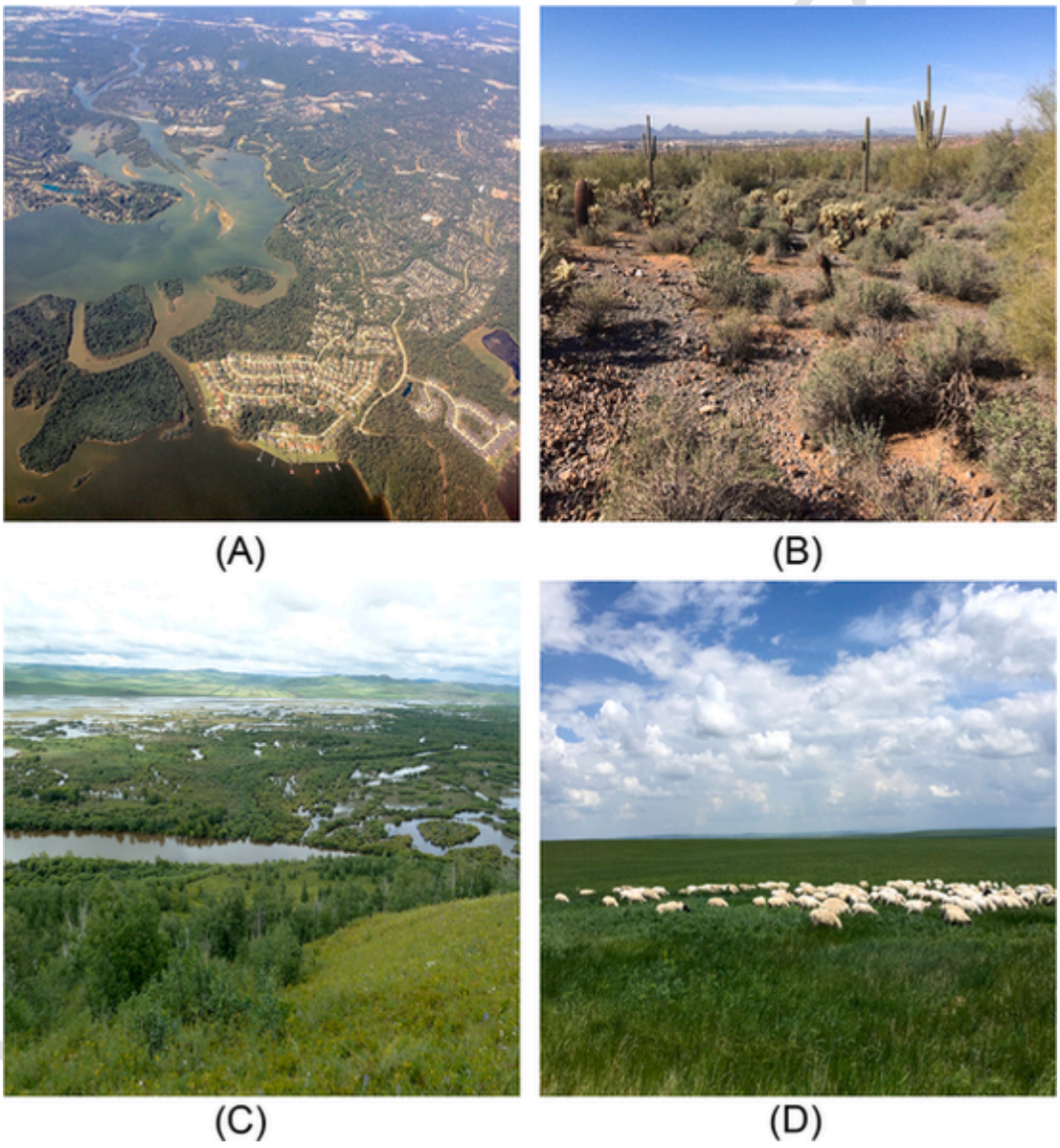

Fig. 1 Different kinds of landscapes as spatial mosaics of various patches on a range of scales. (A) An urbanizing forest landscape, (B) a Sonoran desert landscape, (C) a wetland landscape, and (D) a grassland landscape. All photos by Jianguo Wu.

scape ecology is not only a field of study, but also represents a new scientific perspective or paradigm that is relevant to a range of ecological, geophysical, and social sciences.

Heterogeneity, scale, pattern–process relationships, hierarchy, disturbance, coupled social-ecological dynamics, and sustainability are among the key concepts in landscape ecology. Typical research questions include: How can spatial heterogeneity be quantified so that it can be related to relevant ecological processes? What are the processes and mechanisms responsible for existing landscape patterns? How does spatial heterogeneity influence the flows of organisms, material, and energy, and vice versa? How does landscape pattern affect the spread of disturbances such as pest outbreaks, diseases, fires, and invasive species? How do patterns and processes on different scales relate to each other? How can ecological information be translated across scales in space and time? How can the knowledge of spatial heterogeneity help improve biodiversity conservation, management and planning? How can sustainable landscapes be developed and maintained?

Studies in landscape ecology usually involve extensive use of spatial information from field survey, aerial photography, and satellite remote sensing, as well as pattern indices, spatial statistics, and computer simulation modeling. The intellectual thrust of this highly interdisciplinary science is to understand the causes, mechanisms, and consequences of spatial heterogeneity, while its ultimate goal is to provide a scientific basis and practical guidelines for developing and maintaining sustainable landscapes (**Fig. 2**).

Evolving Perspectives in Landscape Ecology

Modern landscape ecology is characterized by a flux of concepts and perspectives that reflect the differences in the origins of ideas and the ways of thinking, both of which are shaped by physical and cultural landscapes. 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 saw the need for combining the more structurally-oriented geographical approach with the more functionally-centered ecosystem approach, in order to allow for geography to acquire ecologi-

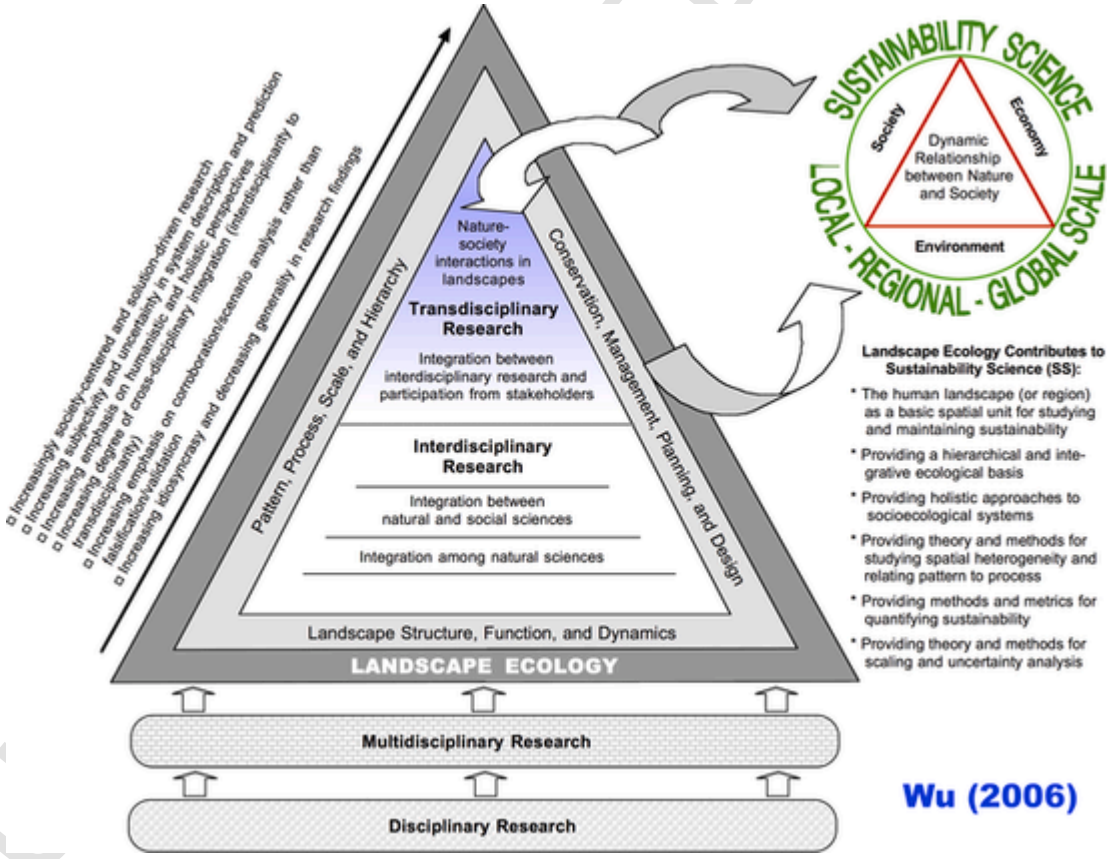

Fig. 2 A hierarchical and pluralistic view of landscape ecology. "Hierarchical" refers to the multiplicity of organizational levels, spatiotemporal scales, and degrees of cross-disciplinarity in landscape ecological research. "Pluralistic" indicates the necessity to recognize the values of different perspectives and methods in landscape ecology dictated by its diverse origins and goals. Reproduced from *Landscape Ecology*, 21, 2006, 1–6, Cross-disciplinarity, landscape ecology, and sustainability science, Wu J, with kind permission of Springer Science and Business Media.

cal knowledge of land units and for ecology to expand its analysis from local sites to larger regions. Thus, he defined landscape ecology as the study of the relationship between biological communities and their environment in a landscape mosaic on various spatial scales. In the same time, Troll also emphasized the holistic totality of the landscape that was perceived as something of a Gestalt (an integrated system organized in such a way that the whole cannot be described merely as the sum of its parts). This holistic and humanistic landscape perspective, focusing on landscape mapping, evaluation, conservation, planning, design, and management, has often been termed the European approach or the European school of thought, but it is now widely embraced worldwide.

Landscape ecology in North America occurred independently of the European root around the late 1970s and the early 1980s, inspired primarily by the theory of island biogeography, with an explicit emphasis on spatial heterogeneity. Not until the first International Congress on Landscape Ecology in the Netherlands in 1981 did landscape ecologists from the two continents begin to communicate with each other about their science. In 1983, twenty-five ecologists and geographers gathered at a workshop in Allerton Park, Illinois of USA to discuss landscape ecology's directions and approaches. This workshop has played an instrumental role in the development of modern landscape ecology. With its burgeoning growth in North America – especially in the development of new theories and methods – landscape ecology became a widely-recognized scientific discipline by the mid-1990s around the world. Although a landscape can be generally defined as a spatially heterogeneous area whose spatial extent varies according to research questions and processes of interest, most landscape ecological studies have focused on broad scales, ranging from tens to thousands of square kilometers. A multiple-scale concept of landscape is meaningful and necessary as it facilitates the theoretical and methodological developments by promoting micro-, meso-, and macro-scale approaches. Despite their variations in details, landscape ecology in North America has traditionally had a more explicit emphasis on spatial heterogeneity or spatial pattern, with the primary goal of understanding the causes, mechanisms, and ecological consequences of spatial heterogeneity. For example, many studies focus more on the relationship between spatial pattern and ecological processes on scales ranging from tens of square meters to thousands of square kilometers in space.

For decades, North American landscape ecology has had a distinct emphasis on the effects of spatial pattern on biodiversity, population dynamics, and ecosystem processes. This research emphasis has been 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. Island biogeographic theory relates the equilibrium-state species diversity of islands to their size (area effect on species extinction rate) and distance to the mainland (distance effect on species immigration rate). The heuristic value of the theory is apparent for understanding the ecology of habitat patches submerged in a sea of human land uses. The patch dynamics perspective, on the other hand, treats ecological systems as mosaics of interacting patches of different size, shape, kinds, and history, emphasizing the transient dynamics and cross-scale linkages of such patchy systems. In this view, a forest is a dynamic mosaic of tree gaps of various age, species composition, and biophysical properties; thus, the dynamics of the forest can be adequately predicted by aggregating the behavior of individual tree gaps. The perspective of patch dynamics has been evident in the conceptual development of modern landscape ecology.

In summary, the European approach is more humanistic and holistic in that it emphasizes a society-centered view that promotes place-based and solution-driven research. 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. Here I hasten to point out that 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 recent decades with surging interests in urban ecology and landscape sustainability in North America and the rest of the world. On the other hand, the perspective of spatial heterogeneity has been increasingly recognized by landscape ecologists in Europe and the rest of the world. Thus, the current development of landscape ecology around the world seems to suggest a transition from a stage of diversification to one of consolidation of key topics and approaches.

Indeed, both the European and North American approaches can be traced back to the original definition of landscape ecology. Carl Troll′s proposal to integrate the geographical and structural approach with the ecological and functional approach is best reflected in the pattern–process–scale perspective, which enhances the scientific rigor of landscape ecology. The holistic and humanistic perspective, on the other hand, epitomizes the idea of landscape as a coupled nature-society system embraced by Troll and others. This perspective is entailed by any attempt to tackle practical problems in real landscapes on broad scales. Both the European and North American perspectives are essential to the development of landscape ecology as a truly interdisciplinary science.

Key Topics in Landscape Ecology

The scope of modern landscape ecology is quite comprehensive and dynamic. As with other interdisciplinary fields, it is impossible to define precisely the domain of landscape ecological studies. To get a sense of what the scientific core of landscape ecology is, here I discuss a series of key research topics based on the collective view of leading landscape ecologists and relevant publications, mainly in the flagship journal of the field, Landscape Ecology (see "Relevant Websites" section). These include: (1) pattern–process–scale relationships of landscapes; (2) landscape connectivity and fragmentation; (3) scale and scaling; (4) spatial analysis and landscape modeling; (5) land use and land cover change; (6) landscape history and legacy effects; (7) landscape and climate change interactions; (8) ecosystem services in changing landscapes; (9) landscape sustainability; and (10) accuracy assessment and uncertainty analysis. Here I highlight six of these key

topics, and more in-depth discussions of these key issues can be found in Further Reading at the end of this article.

(1) Pattern–process–scale relationships and ecological flows in landscapes. Understanding how organisms, matter, and energy affect, and are affected by, the spatial pattern of landscape mosaics is a fundamental problem in landscape ecology. Much progress has been made in unraveling the effect of spatial heterogeneity on the spread of disturbances (e.g., fires and diseases) and the influence of landscape fragmentation on population dynamics, particularly, through studies of metapopulations (structurally discrete and functionally connected population ensembles). Research into the effects of landscape pattern on ecological processes across scales is still a rapidly developing area. Important areas for future research also include the spread of invasive species, the effects of landscape structure on population genetics (known as landscape genetics), and the effects of socioeconomic processes on ecological flows in landscape mosaics on multiple scales.

(2) Mechanisms and consequences of land use and land cover change. Land use and land cover change, driven primarily by socioeconomic processes, exerts the most pervasive and profound influences on the structure and functioning of landscapes. Thus, quantifying the spatiotemporal pattern of landscape change and understanding its underlying driving forces are essential. More effort is needed to couple biophysical with socioeconomic approaches and to integrate ecological with historical methods in the study of land change.

(3) Scale and scaling. Spatial pattern and ecological and socioeconomic processes in heterogeneous landscapes operate on multiple scales, and thus understanding the totality of landscapes requires relating different phenomena across domains in space and time. The process of translating information from one scale or organizational level to another is referred to as scaling. Landscape ecologists are leading the way in developing the theory and methods of scaling that is essential to all natural and social sciences. However, many challenges 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.

(4) Coupling landscape pattern analysis with ecological processes through spatial analysis and landscape modeling. Quantifying spatial heterogeneity is the necessary first step to understanding the effects of landscape pattern on ecological processes. 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 two decades. The greatest challenge, however, is to relate the measures of spatial pattern directly to the processes and properties of biodiversity and ecosystem functioning. To address these challenges, 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.

(5) Ecosystem services in changing landscapes. Ecosystem services are benefits that people derive from ecosystems. As a concept, ecosystem services bridges ecology and economy and has been increasingly used in the science and practice of conservation, resource management, and sustainable development. All ecosystem services are generated and used in landscapes that continue to change; the flows of ecosystem services are affected by landscape patterns; and certain spatial configurations of multiple ecosystems may synergistically render services (or disservices) that single ecosystems cannot produce. Thus, it is crucial to quantify spatiotemporal patterns, source-sink dynamics, trade-offs, and synergistic interactions of provisioning, regulating, and cultural ecosystem services at the landscape and regional scales. Place-based landscape theories of ecosystem services are needed.

(6) Landscape sustainability. We may define landscape sustainability as the adaptive process of simultaneously maintaining and improving biodiversity, ecosystem services, and human well-being in a landscape. Because of the emphasis on broad- and multi-scale patterns and processes with interdisciplinary approaches, landscape ecology is uniquely positioned to provide a comprehensive theoretical basis and pragmatic guidelines for biodiversity conservation, ecosystem management, and sustainable development. These real-world problems cannot be adequately addressed by species-centered or individual ecosystem-based approaches. How do spatial processes occurring in landscapes (e.g., urbanization, agriculture, flooding, fires, biological invasion) affect the biodiversity, ecosystem functioning, ecosystem services, and human-wellbeing altogether? How do ecological, economic, and social processes interact to determine landscape resilience and sustainability? What are the design principles for sustainable landscapes? These are only a few of many challenging questions landscape ecology will continue to address in decades to come.

Concluding Remarks

Emphasizing spatial heterogeneity begs questions of the relationship between pattern and process. Simply put, heterogeneity is about structural and functional patterns that deviate from uniform and random arrangements. It is this pervasively common non-homogeneous characteristic that makes spatial patterns ecologically important as it suggests nontrivial relationship with underlying processes. Thus, studying pattern without getting to process is superficial, and understanding process without reference to pattern is incomplete. Emphasizing 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. Consequently, humanistic and holistic perspectives have been and will continue to be central in landscape ecological research.

The above arguments also, in part, explain the two seemingly disparate views that have become known as the European and North American perspectives in landscape ecology. The world is already too fragmented ecologically, economically, and socially, and we cer-

tainly do not need a landscape ecology for each continent. As discussed earlier, the two perspectives should be viewed as being complementary rather than contradictory. To increase the synergies between the two approaches, not only do we need to appreciate the values of each, but also to develop an appropriate framework by which different perspectives and methods can be integrated. This requires a pluralistic and multi-scale perspective (**Fig. 2**). Landscape ecology not only is expected to provide the scientific understanding of the structure and functioning of various landscapes, but also practical guidelines and tools with which sustainability can be created and maintained for the ever-changing landscapes. Thus, the ultimate goal of landscape ecology has to be improving the sustainability of landscapes of all kinds. Thus, landscape ecology is intrinsically related to the emerging field of landscape sustainability science.

Further Reading

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Further Reading

Relevant Websites

http://www.landscape-ecology.org – International Association of Landscape Ecology.
https://link.springer.com/journal/10980 – Landscape Ecology, the flagship journal of the field of landscape ecology and sustainability, Springer.