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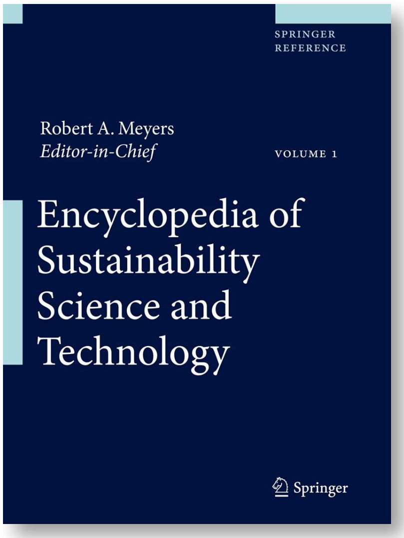

2012, 2012, L, 14869 p. 2500 illus. in color.

SPRINGER REFERENCE

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eReference

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- ***7.140,00 € (D) | 7.200,00 € (A) | CHF 9'038.50**

Print + eReference

- **7.500,00 € | £6,750.00 | $10,150.00**
- ***8.025,00 € (D) | 8.250,00 € (A) | CHF 10'752.00**

R.A. Meyers, RAMTECH Ltd., Larkspur, CA, USA (Ed.)

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Metadata of the chapter that will be visualized online

Chapter Title	Landscape Ecology	
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Abstract

Landscapes are spatially heterogeneous areas characterized by diverse patches that differ in size, shape, contents, and history. When spatial heterogeneity is considered, scale matters and hierarchy emerges. Landscape ecology is the science and art of studying and improving the relationship between spatial pattern and ecological processes on a multitude of scales and organizational levels. In a broad sense, landscape ecology represents both a field of study and a scientific paradigm. As a highly interdisciplinary and transdisciplinary enterprise, landscape ecology integrates biophysical and analytical approaches with humanistic and holistic perspectives across natural and social sciences. Landscape ecology was initially developed in Europe. With theoretical developments in spatial ecology and technological advances in remote sensing and geospatial information processing, landscape ecology became an internationally recognized field of study in the 1980s. The most salient characteristics of landscape ecology are its emphasis on the pattern-process relationship and its focus on broad-scale ecological and environmental issues. Key research topics in landscape ecology include ecological flows in landscape mosaics, land use and land cover change, scaling, relating landscape pattern analysis with ecological processes, and landscape conservation and sustainability.

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Landscape Ecology

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Article Outline

Glossary

Landscape A geographic area in which at least one variable of interest is spatially heterogeneous. The boundary of a landscape may be delineated based on geographic, ecological, or administrative units (e.g., watersheds, ecosystem mosaics, or metropolitan regions) which are relevant to the research questions and objectives.

Landscape connectivity The degree of a landscape to facilitate or impede the flows of organisms, energy, material, and information among landscape elements. This is sometimes referred to as landscape functional connectivity, which is a function of both landscape structural connectivity and the movement characteristics of the species or process under consideration. Landscape structural connectivity is simply a measure of how spatially connected the elements in a landscape are, without reference to any particular ecological process.

Landscape ecology The science of studying and improving the relationship between spatial pattern and ecological processes on multiple scales. Landscape ecology studies the structure, function, and dynamics of landscapes of different kinds, including natural, seminatural, agricultural, and urban landscapes.

Landscape fragmentation The breaking-up of landscape into smaller patches by anthropogenic activities, or the human introduction of barriers that impede flows of organisms, energy, material, and information across a landscape. Habitat fragmentation is a similar term to landscape fragmentation, but has a more explicit focus on changes in habitat of organisms of interest.

Landscape pattern The composition (diversity and relative abundances) and configuration (shape, size, and spatial arrangement) of landscape elements, including both spatial patchiness and gradients.

Landscape function The horizontal and vertical flows of organisms, energy, material, and information in a landscape.

Landscape structure The composition and spatial arrangement of landscape elements – including patches, corridors, and the matrix.

Landscape dynamics Temporal changes in the structure and function of a landscape, driven by natural and anthropogenic processes.

Landscape sustainability The ability of a landscape to maintain its basic environmental, economic, and social functions under ever-changing conditions driven by human activities and climate change. Landscape sustainability emphasizes scale-multiplicity, self-organization, and spatial optimization of landscape pattern so as to achieve a high level of resilience and metastability.

Metapopulation The total population system that is composed of multiple local populations geographically separated but functionally connected through dispersal.

Patch dynamics A perspective that ecological systems are mosaics of patches, each exhibiting

Robert A. Meyers (ed.), *Encyclopedia of Sustainability Science and Technology*, DOI 10.1007/978-1-4419-0851-3,

nonequilibrium dynamics and together determining the system-level behavior.

Pattern analysis The procedures with which landscape pattern is quantified using synoptic indices and spatial statistical methods.

Scale The spatial or temporal dimension of a phenomenon in landscape ecology scale usually refers to grain and extent. Grain is the finest resolution of a data set in space or time within which homogeneity is assumed whereas extent is the total spatial or temporal expanse of a study.

Scaling The translation of information between or across spatial and temporal scales or organizational levels.

Spatial heterogeneity The discrete or continuous variations of one or more variables in a landscape, which can be characterized as patchiness, gradients, or a mixture of both.

Spatially explicit models Models that explicitly take account of the locations of events in a two- or three-dimensional space so that not only landscape composition but also landscape configuration matters.

Definition of the Subject

Landscapes are spatially heterogeneous areas characterized by diverse patches that differ in size, shape, contents, and history. When spatial heterogeneity is considered, scale matters and hierarchy emerges. Landscape ecology is the science and art of studying and improving the relationship between spatial pattern and ecological processes on a multitude of scales and organizational levels. In a broad sense, landscape ecology represents both a field of study and a scientific paradigm. As a highly interdisciplinary and transdisciplinary enterprise, landscape ecology integrates biophysical and analytical approaches with humanistic and holistic perspectives across natural and social sciences. Landscape ecology was initially developed in Europe. With theoretical developments in spatial ecology and technological advances in remote sensing and geospatial information processing, landscape ecology became an internationally recognized field of study in the 1980s. The most salient characteristics of landscape ecology are its emphasis on the pattern-process relationship and its focus on broad-scale ecological and environmental issues. Key research topics in landscape ecology include ecological flows in landscape mosaics, land use and land cover change, scaling, relating landscape pattern analysis with ecological processes, and landscape conservation and sustainability.

Introduction

Landscape ecology is an interdisciplinary field that aims to understand and improve the relationship between spatial pattern and ecological processes on a range of scales [1]. Although the term appeared in the 1930s, landscape ecology was not a recognized scientific field of global reach until the 1980s when remote sensing data and computers became widely accessible to ecologists and geographers. The 1980s was also a time period when ecological ideas of spatial heterogeneity and nonequilibrium dynamics flourished, and when landscape ecology took roots in North America. Today, landscape ecology is a well-established field of study, with active participation of ecological, geographical, and social scientists from around the world.

Landscape ecology has been dominated by two schools of thought: the European perspective and the North American perspective. At the risk of oversimplification, the European landscape ecology perspective may be considered as being characterized by a more holistic, humanistic, and society-centered view, with a focus on user-inspired and solution-driven research. The North American landscape ecology perspective, on the other hand, has been dominated by a more analytical and biological ecology–centered view, with a focus on basic science-oriented and question-driven studies. Cautions must be exercised, however, to avoid overinterpretation of such dichotomous characterization [2]. The two perspectives are neither inclusive nor exclusive; they are not contradictory but complementary. There are, and should be, other approaches to landscape ecology. For example, one may argue for an Australian landscape ecology perspective that focuses on pragmatic and functional approaches, typically, tied with land management, restoration, and conservation issues (e.g., [3]).

Landscape ecology is now a well-established interdisciplinary field of study, which is evidenced by several characteristics. These include an evolving but identifiable system of concepts, theories, principles, methods, and applications, a hierarchy of professional organizations from the international association to local chapters, a flagship journal (http://www.springerlink.com/content/0921-2973), the adoption in educational and training programs by major universities and research institutes around the world, and an increasing number of publications in mainstream scientific journals which indicate its recognized status as well as its expanding impacts on related disciplines.

In this entry, I focus on the key concepts, research topics, and quantitative methods in landscape ecology. A number of textbooks on landscape ecology are available where more details on the contents covered here can be found [4–8].

What is Landscape Ecology?

Diverse Concepts of Landscape

The term, "landscape," is a key concept in a number of fields, from social to geographical and ecological sciences. With the rise of landscape ecology in the past several decades, the concept of landscape has achieved a prominent status in the interdisciplinary literature. However, because of the plurality of its origins and interpretations, landscape has acquired various connotations. For example, the same word may refer to a natural landscape, a cultural landscape, a political landscape, an economic landscape, a mental landscape, an adaptive landscape, a landscape view, landscaping, or landscape painting [9, 10].

Even within the field of landscape ecology, the word, "landscape," has different meanings, and the differences usually hinge on the spatial scale and the contents of a landscape. For example, landscape has been defined as a kilometers-wide geographic area [11, 12], which corresponds to the "human-scale" landscape. This is the scale at which the field of landscape ecology was originally developed in Europe, and at which most landscape studies have been conducted around the world ever since. The human-scale landscape, in general, seems to coincide well with geographic units such as watersheds and urban regions [4], as well as spatial domains of human perception [13]. Thus, it resonates with the public, the decision makers, and researchers who are conscious about the environmental setting in which they live, work, and engage in recreation.

Many other landscape ecologists, however, have treated landscape as a multi-scale or hierarchical concept, meaning that a landscape is a spatially heterogeneous area that may be of various sizes, depending on the subject of study and the research questions at hand [6, 14, 15]. In this case, landscape is an "ecological criterion" [14], and its essence does not lie in its absolute scale but in its internal heterogeneity. Different plant and animal species perceive, experience, and respond to spatial heterogeneity at different scales, and patterns and processes in landscapes tend to have different characteristic scales [16]. Thus, a hierarchical concept of landscape, of course also encompassing the human-scale, is both sensible and necessary. Apparently, one does not need to consider a landscape of tens of square kilometers to study how grassland vegetation pattern affects the movement of beetles [17] or is affected by gophers [18].

The contents that constitute a landscape vary greatly in landscape ecological research. For simplicity, the components of a landscape may be classified as tangible versus intangible and biophysical versus cultural. This is not intended to represent a dichotomous view, but rather a continuum within which a variety of components coexist. Tress and Tress [10] proposed a "transdisciplinary landscape concept" that encompasses five dimensions: (1) landscape as a spatial entity, (2) landscape as a mental entity, (3) landscape as a temporal dimension, (4) landscape as a nexus of nature and culture, and (5) landscape as a complex system. Landscape ecological studies often have focused on some but not all of these dimensions. The concept of landscape provides a meeting ground for a number of disciplines, including archaeology, ecology, geography, geology, history, landscape architecture, and regional economics. To achieve its interdisciplinary and transdisciplinary goals, landscape ecology needs to appreciate and integrate the multifaceted perspectives on the culture-nature/people-place relationships that are offered by these diverse disciplines.

Evolving Concepts of Landscape Ecology

The definitions of landscape ecology are also diverse, although they are not quite as numerous as those of landscape (Table 1). Images can be powerfully inspiring, and this is especially true to someone who has a special interest in landscape patterns. Partly inspired by the conspicuous spatial patterns revealed in aerial photographs, the German geographer and botanist Carl Troll [19] coined the term “landscape ecology” and defined it later as “the study of the main complex causal relationships between the life communities and their environment in a given section of a landscape” [20, 21]. Carl Troll’s training and research in multiple disciplines endowed him with the abilities to synthesize across, and innovate at the interface between, different fields. He was trained as a botanist; did his doctoral dissertation in plant physiology; and then spent decades working on the climatic, geologic, geographical, and ecological aspects of various landscapes in Europe, South America, and Africa. It is not difficult to understand why Troll could simultaneously appreciate the then-new idea of “ecosystem” put forward by Arthur Tansley [28], as well as the great potential for geospatial analysis presented by aerophotography. As a result of his attempt to integrate the “vertical” ecological approach with the “horizontal” geographical approach, a new field of study was born.

In the past several decades, landscape ecology has acquired a number of definitions which all are, in some way, related to Carl Troll’s original definition. For example, Zonneveld [22] defined landscape ecology as “an aspect of geographical study which considers the landscape as a holistic entity, made up of different elements, all influencing each other.” He advocated that the landscape should be studied as the “total character of a region,” not “in terms of the separate aspects of its component elements” [22, 29]. This holistic landscape perspective continues and culminates in the work by Naveh [30], who described landscape ecology as the study of “the total spatial and functional entity of natural and cultural living space.”

Some key ideas of contemporary landscape ecology, such as patch dynamics [31–33] and the patch-corridor-matrix model [11, 12], began to emerge in North America in the late 1970s, apparently with little connection to the European root. The early ideas of landscape ecology in North America were inspired by the theory of island biogeography [34], with an explicit focus on spatial heterogeneity. The first major communication between North American and European landscape ecologists occurred in 1981 when five American ecologists attended the first International Congress on Landscape Ecology in the Netherlands. Two years later, 25 ecologists (23 Americans, 1 Canadian, and 1 French) gathered at Allerton Park, Illinois of USA, to discuss the nature and future directions of landscape ecology. The report of this historic work, published in the following year [24], became an important guide to the incipient landscape ecologists in North America [35].

Why was such discussion necessary after landscape ecological research had been practiced for more than 40 years in Europe? The answer seems clear from Forman [36]: “What theory explains the spatial heterogeneity of energy, nutrients, water, plants, and animals at the level of a landscape, the setting in which we live? Alas, none.” To develop such a landscape theory, broader scales that encompass multiple ecosystems need to be considered, and horizontal interactions have to be a focus of study. Thus, Forman and Godron [11, 12] defined landscape ecology as the study of the structure (spatial relationships among the distinctive landscape elements), function (flows of energy, materials, and species among landscape elements), and dynamics (temporal change in landscape structure and function) of landscapes. The main theme of landscape ecology in North America, with an unmistakable focus on spatial heterogeneity, was set in Risser et al. [24]:

- 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.

Is landscape ecology a subdiscipline of ecology? The term itself apparently suggests that it is. Many ecologists do consider landscape ecology as a branch of ecology (e.g., [6]), and most ecology programs of major research universities worldwide now offer courses in landscape ecology. On the other hand, Zonneveld [22] indicated that landscape ecology is not part of biological sciences, but a branch of geography. Risser et al. [24] contemplated three ways in which landscape ecology may be viewed: as an intersection of many disciplines, as a separate discipline, or as a branch of ecology. They concluded that only the first option was "intellectually and practically the most persuasive." They further pointed out that "viewing landscape ecology as an interdisciplinary field of research avoids the issue of which discipline 'owns' landscape ecology" (a problem that may have hindered the healthy development of some interdisciplinary fields, such as human ecology, for which geography, sociology, and anthropology all have claimed ownership). The Allerton workshop report clearly recognized the importance of the multidimensionality of landscapes and the cross-disciplinarity of landscape ecology:

▸ A major forcing function of landscapes is the activity of mankind, especially associated cultural, economic, and political phenomena. ... 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" [24].

Today, a general consensus seems to have emerged that landscape ecology is not simply an academic discipline, but rather a highly interdisciplinary field of study [2, 37]. Landscape ecology is an interdisciplinary and transdisciplinary science that focuses on the relationship between spatial pattern and ecological processes across scales. The goal of landscape ecology is not only to understand this relationship but also to influence it so as to help achieve landscape sustainability [38–40]. As such, a pluralistic and hierarchical framework has been proposed to facilitate synergistic interactions between biophysical/pattern-process and holistic/humanistic perspectives (Fig. 1) [37, 38]. "Hierarchical" here refers to the varying degrees of cross-disciplinary, the hierarchy of organizational levels, and the multiplicity of spatiotemporal scales of landscape ecological studies. "Pluralistic" indicates the necessity and importance of recognizing and valuing the different perspectives and methods in landscape ecology due to its diverse origins and goals.

Key Research Topics Landscape Ecology

Based on the suggestions by a group of leading landscape ecologists (Table 2), Wu and Hobbs [2] identified six key issues that characterize landscape ecology: (1) interdisciplinarity or transdisciplinarity, (2) integration between basic research and applications, (3) Conceptual and theoretical development, (4) education and training, (5) international scholarly communication and collaborations, and (6) outreach and communication with the public and decision makers. Wu and Hobbs [2] also summarized ten key research topics and priorities as follows:

1. Ecological flows in landscape mosaics: A primary goal of landscape ecology is to understand the reciprocal relationship between spatial pattern and ecological processes [14]. Understanding the mechanisms of flows of organisms, energy, material, and information in landscape mosaics is central to landscape ecology. In particular, the study of the effects of spatial pattern on population and ecosystem processes has made much progress in the past several decades. There is a need to integrate socioeconomic theory of landscape change into metapopulation models to make them more relevant to the issues of biodiversity conservation and landscape sustainability. The spread of invading species has become an increasingly important ecological and economic problem which deserves more research efforts.
2. Causes, processes, and consequences of land use and land cover change: Land use and land cover change is arguably the most important driver for changes in the structure and function of landscapes. Land use and land cover change is driven primarily by socioeconomic forces, and is one of the most important and challenging research areas in landscape ecology. Numerous studies have been carried out to investigate the effects of land use and land cover change on biodiversity and ecological flows in human-dominated landscapes. More research efforts are needed to incorporate the insights of economic geography which studies how economic activity is distributed in space and resource economics which determines how land will be used [41]. Long-term landscape changes induced by economic activities and climate

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change, as well as "land use legacies" (i.e., the types, extents, and durations of persistent effects of prior land use on ecological patterns and processes) need to be emphasized in future research.

3. Nonlinear dynamics and landscape complexity: Landscapes are spatially extended complex systems which exhibit emergent properties, phase transitions, and threshold behavior. To understand the complexity of landscapes, concepts and methods from the science of complexity and nonlinear dynamics should be helpful. For example, self-organization, percolation theory, complex adaptive systems (CAS), fractal geometry, cellular automata, and genetic algorithms have been used in the study of spatiotemporal dynamics of landscapes (e.g., [42–46]). However, the theoretical potential and practical implications of these concepts and methods are yet to be fully explored.
4. Scaling: Scaling refers to the translation of information from one scale to another across space, time, or organizational levels. Spatial scaling, in particular, is essential in both the theory and practice of landscape ecology because spatial heterogeneity does not make any sense without the consideration of scale [47]. While scale effects are widely recognized in landscape ecology, scaling-up or scaling-down across heterogeneous landscapes remains a grand challenge in landscape ecology and beyond [48]. General rules and pragmatic methods for scaling landscape patterns and processes need to be developed and tested.
5. Methodological advances: Landscape variables are often spatially autocorrelated and spatially dependent, which poses serious challenges for using traditional statistical methods based on the assumption of independence of observations. The spatial autocorrelation and dependence that traditional statistical methods try to get rid of are usually what landscape analyses intend to get at. Thus, spatial statistical methods that directly deal with spatial autocorrelation and dependence have increasingly been used in landscape ecology. Also, most landscape ecological problems need to be studied over large and multiple scales in a spatially explicit manner. This need poses problems such as the lack of replicability or "pseudoreplication" [49]. To get to the processes and mechanisms of landscape phenomena, landscape ecology has developed a suite of spatially explicit modeling approaches [50, 51]. In both spatial analysis and modeling of landscapes, remote sensing and GIS (geographic information systems) have become indispensable.
6. Relating spatial pattern measures to ecological processes: To understand the relationship between pattern and process, quantifying landscape pattern is necessary. Indeed, landscape pattern analysis has been a major part of landscape ecological research for the last few decades. A number of landscape metrics (Table 3) and spatial statistical methods have been developed and applied for describing and comparing the spatial patterns of landscapes, monitoring and predicting changes in landscape patterns, and relating spatial pattern to ecological processes at a particular scale or across a range of scales [47, 53, 54]. Nevertheless, a sound ecological understanding of these spatial analysis methods is yet to be fully developed [55].
7. Integrating humans and their activities into landscape ecology: Socioeconomic processes are the primary drivers for land use and land cover change which in turn determines the structure, function, and dynamics of most landscapes. Social and economic processes have increasingly been integrated into landscape ecological studies. The need for incorporating humans, including their perceptions, value systems, cultural traditions, and socioeconomic activities, into landscape ecology has made it a highly interdisciplinary and transdisciplinary enterprise [38, 56]. That said, effectively integrating human-related processes into ecology may remain one of the ultimate challenges for landscape ecologists in years to come.
8. Optimization of landscape pattern: If spatial pattern significantly influences ecological flows in the landscape, then there must be certain patterns that are better than others. This is a question of landscape pattern optimization (e.g., optimization of land use pattern, optimal landscape management, optimal landscape design, and planning). For example, can landscape patterns be optimized in terms of both the composition and configuration of patches and matrix

characteristics to maximize biodiversity and ecosystem services? Are there optimal ways of "spatially meshing nature and culture" to promote landscape sustainability? These are some of the challenging questions that landscape ecologists ought to address now and in the future. Spatial optimization of landscape pattern for ecological processes presents exciting research opportunities and requires interdisciplinary approaches.

9. Landscape conservation and sustainability: Biodiversity, ecosystem functions, and human activities, all take place in landscapes. Landscape fragmentation profoundly alters ecological and socioeconomic processes. Thus, the importance of applying landscape ecological principles in biodiversity conservation and sustainable development has been increasingly recognized. However, specific landscape ecological guidelines for biodiversity conservation are needed, and a comprehensive and operational definition of landscape sustainability is yet to be developed.
10. Data acquisition and accuracy assessment: Landscape ecological studies use large-scale and multiscale data. A suite of advanced technologies are readily available, including various remote sensing techniques, GIS, GPS (global positioning systems), and spatial analysis and modeling approaches. However, ecological understanding of species and ecosystems is essential in landscape ecology, and this requires the collection of basic biological data of landscapes. Also, to ensure the quality of landscape data, error analysis, uncertainty analysis, and accuracy assessment have become a key issue in landscape ecological research.

Future Directions

Landscape ecology is a highly interdisciplinary field of study which is characterized, most conspicuously, by its spatial explicitness in dealing with ecological problems in theory and practice. Emphasis on spatial heterogeneity begs questions of the pattern-process relationships and scale. Studying spatial pattern without relating it to ecological processes is superficial, and investigating ecological processes without consideration of spatial pattern is incomplete. From this perspective, landscape ecology is a science of heterogeneity and scale, providing a new scientific paradigm for ecology and other related fields.

On the other hand, with increasing human dominance in the biosphere, emphasis on broad spatial scales makes it 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. Thus, landscape ecology has become increasingly relevant to sustainability research and practice [38, 56]. First, landscape ecology provides a hierarchical and integrative ecological basis for dealing with issues of biodiversity and ecosystem functioning from fine to broad scales. Second, landscape ecology has already developed a number of holistic and humanistic approaches to studying nature–society interactions. Third, landscape ecology offers theory and methods for studying the effects of spatial configuration of biophysical and socioeconomic component on the sustainability of a place. Fourth, landscape ecology has developed a suite of pattern metrics and indicators which can be used for quantifying sustainability in a geospatially explicit manner. Finally, landscape ecology provides both theoretical and methodological tools for dealing with scaling and uncertainty issues that are fundamental to most nature–society interactions.

To move forward, future landscape ecological studies need to further address the key research topics as discussed earlier in this entry. In addition, concerted efforts need to be made to focus on sustainability-related research questions. For example, what theories, principles, and methods of landscape ecology are pertinent to sustainability and how can they be operationalized? How does landscape pattern or spatial heterogeneity affect sustainability? How do ecological, economic, and social patterns and processes in landscapes change with scale and interact to influence sustainability? How is landscape sustainability measured and what roles can landscape metrics play in all this? How can landscape models to project sustainability trajectories in response to environmental, economic, social, and institutional changes be developed? And finally, how can landscape ecology help design sustainable landscapes?

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t1.1 **Landscape Ecology. Table 1** A list of definitions of landscape ecology

	Definition	Source
t1.2, t1.3	The German geographer Carl Troll coined the term "landscape ecology" in 1939, and defined it in 1968 as "the study of the main complex causal relationships between the life communities and their environment in a given section of a landscape. These relationships are expressed regionally in a definite distribution pattern (landscape mosaic, landscape pattern) and in a natural regionalization at various orders of magnitude" (Troll 1968; cited in Troll 1971)	• Troll [19] • Troll [20] • Troll [21]
t1.4	"Landscape ecology is an aspect of geographical study which considers the landscape as a holistic entity, made up of different elements, all influencing each other. This means that land is studied as the 'total character of a region', and not in terms of the separate aspects of its component elements" (Zonneveld 1972)	• Zonneveld [22]
t1.5	"Landscape ecology is a young branch of modern ecology that deals with the interrelationship between man and his open and built-up landscapes" based on general systems theory, biocybernetics, and ecosystemology (Naveh and Liberman 1984). "Landscapes can be recognized as tangible and heterogeneous but closely interwoven natural and cultural entities of our total living space," and landscape ecology is "a holistic and transdisciplinary science of landscape study, appraisal, history, planning and management, conservation, and restoration" (Naveh and Liberman 1994)	• Naveh and Lieberman [5] • Naveh and Lieberman [23]
t1.6	"A landscape is a kilometers-wide area where a cluster of interacting stands or ecosystems is repeated in similar form; landscape ecology, thus, studies the structure, function and development of landscapes" (Forman 1981). Landscape structure refers to "the spatial relationships among the distinctive ecosystems;" landscape function refers to "the flows of energy, materials, and species among the component ecosystems;" and landscape change refers to "the alteration in the structure and function of the ecological mosaic over time" (Forman and Godron 1986).	• Forman [11] • Forman [12]
t1.7	"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" (Risser et al. 1984). "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" (Risser et al. 1984).	• Risser et al. [24]
t1.8	"Landscape ecology emphasizes broad spatial scales and the ecological effects of the spatial patterning of ecosystems" (Turner 1989).	• Turner [25]
t1.9	"Landscape ecology is the study of the reciprocal effects of the spatial pattern on ecological processes," and "concerns spatial dynamics (including fluxes of organisms, materials, and energy) and the ways in which fluxes are controlled within heterogeneous matrices" (Pickett and Cadenasso 1995).	• Pickett and Cadenasso [14]
t1.10	"Landscape ecology investigates landscape structure and ecological function at a scale that encompasses the ordinary elements of human landscape experience: yards, forests, fields, streams, and streets" (Nassauer 1997).	• Nassauer [26]
t1.11	Landscape ecology is "ecology that is spatially explicit or locational; it is the study of the structure and dynamics of spatial mosaics and their ecological causes and consequences" and "may apply to any level of an organizational hierarchy, or at any of a great many scales of resolution" (Wiens 1999).	• Wiens [27]

Landscape Ecology. Table 1 (Continued)

	Definition	Source
t1.12	"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" (Turner et al. 2001). "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" and "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" (Turner et al. 2001).	• Turner [6]
t1.13	"Landscape ecology is the science and art of studying and influencing the relationship between spatial pattern and ecological processes across hierarchical levels of biological organization and different scales in space and time."	• Wu and Hobbs [1]

t2.1 **Landscape Ecology. Table 2** A list of major research topics in landscape ecology suggested by a group of leading landscape ecologists from around the world at the 16th Annual Symposium of the US Regional Association of the International Association for Landscape Ecology, held at Arizona State University, Tempe, in April 2001 [2]

t2.2	Development of theory and principles	• Landscape mosaics and ecological flows • Land transformations • Landscape sustainability • Landscape complexity
t2.3	Landscape metrics	• Norms or standards for metric selection, change detection, etc. • Integration of metrics with holistic landscape properties • Relating metrics to ecological processes • Sensitivity to scale change
t2.4	Ecological flows in landscape mosaics	• Flows of organisms, material, energy, and information • Effects of connectivity, edges, and boundaries • Spread of invading species • Spatial heterogeneity and ecosystem processes • Disturbances and patch dynamics
t2.5	Optimization of landscape pattern	• Optimization of land use pattern • Optimal management • Optimal design and planning • New methods spatial optimization
t2.6	Metapopulation theory	• Integration of the view of landscape mosaics • Integration of economic theory of land use change and cellular automata
t2.7	Scaling	• Extrapolating information across heterogeneous landscapes • Development of scaling theory and methods • Derivation of empirical scaling relations for landscape pattern and processes
t2.8	Complexity and nonlinear dynamics of landscapes	• Landscapes as spatially extended complex systems • Landscapes as complex adaptive systems • Thresholds, criticality, and phase transitions • Self-organization in landscape structure and dynamics
t2.9	Land use and land cover change	• Biophysical and socioeconomic drivers and mechanisms • Ecological consequences and feedbacks • Long-term landscape changes driven by economies and climate changes
t2.10	Spatial heterogeneity in aquatic systems	• The relationship between spatial pattern and ecological processes in lakes, rivers, and oceans • Terrestrial and aquatic comparisons
t2.11	Landscape-scale experiments	• Experimental landscape systems • Field manipulative studies • Scale effects in experimental studies
t2.12	New methodological developments	• Integration among observation, experimentation, and modeling • New statistical and modeling methods for spatially explicit studies • Interdisciplinary and transdisciplinary approaches
t2.13	Data collection and accuracy assessment	• Multiple-scale landscape data • More emphasis on collecting data on organisms and processes • Data quality control • Metadata and accuracy assessment
t2.14	Fast changing and chaotic landscapes	• Rapidly urbanizing landscapes • War zones • Other highly dynamic landscapes

Landscape Ecology. Table 2 (Continued)

	Landscape sustainability	• Developing operational definitions and measures that integrate ecological, social, cultural, economic, and aesthetic components • Practical strategies for creating and maintaining landscape sustainability
t2.15	Human activities in landscapes	• The role of humans in shaping landscape pattern and processes • Effects of socioeconomic and cultural processes on landscape structure and functioning
t2.16	Holistic landscape ecology	• Landscape ecology as an anticipative and prescriptive environmental science • Development of holistic and systems approaches

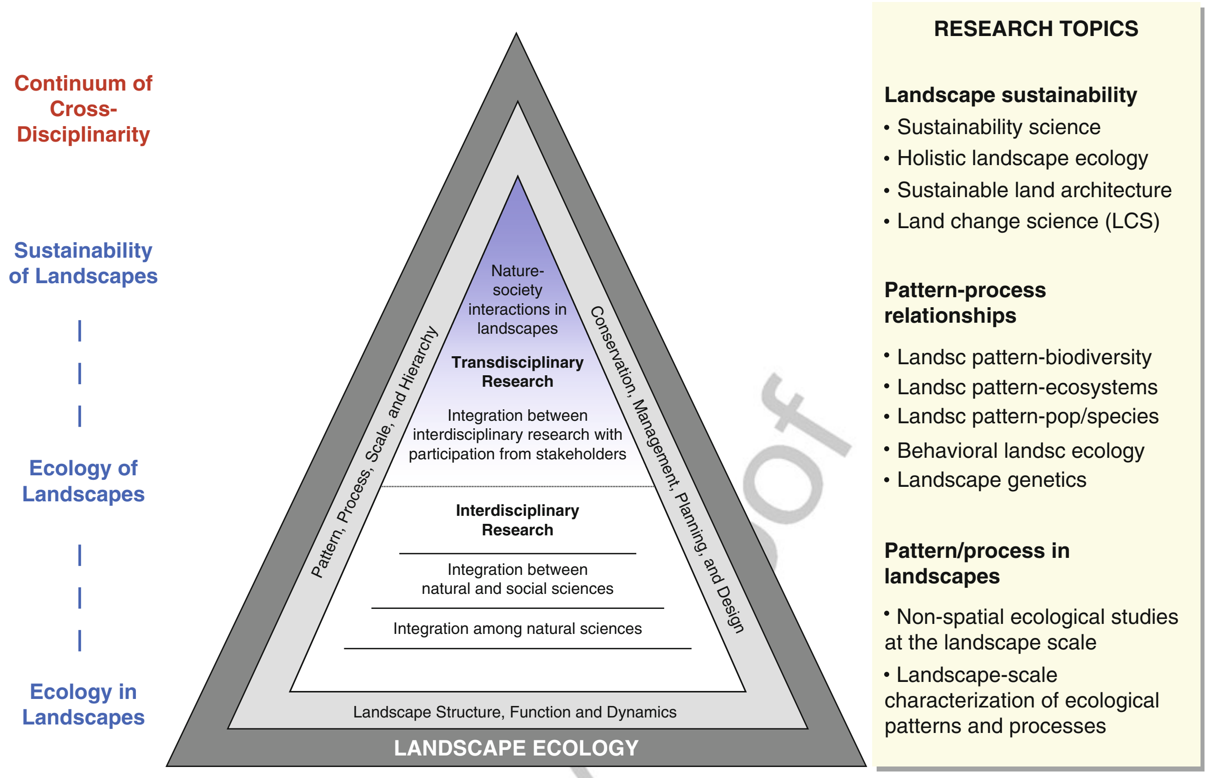
t3.1 **Landscape Ecology. Table 3** Some commonly used landscape metrics [4, 52]

	Landscape metric	Abbreviation	Description
t3.2			
t3.3	Patch shape index	PSI	A measure of the shape complexity of an individual patch: $PSI = \frac{P}{2\sqrt{A\pi}}$ where P is the perimeter of a patch, and A is the area of the patch. $D = 1$ for circles; $D = 1.1283$ for squares; and $D = 1.1968$ for a rectangle (2 L by L). $1/D$ is called "compactness" (see Forman [4]).
t3.4	Perimeter/area ratio	PAR	A measure of the shape complexity of an individual patch: $PAR = P/A$ where P is the perimeter of a patch, and A is the area of the patch.
t3.5	Number of patches	NP	The total number of patches in the landscape.
t3.6	Patch density	PD	The number of patches per square kilometer (i.e., 100 ha).
t3.7	Total edge	TE	The sum of the lengths of all edge segments (unit: meter).
t3.8	Edge density	ED	The total length of all edge segments per hectare for the class or landscape of consideration (unit: m/ha).
t3.9	Patch richness	PR	The number of different patch types in the landscape.
t3.10	Patch richness density	PRD	The number of patch types per square kilometer (or 100 ha).
t3.11	Shannon's diversity index	SHDI	A measure of patch diversity in a landscape that is determined by both the number of different patch types and the proportional distribution of area among patch types: $H = -\sum_{i=1}^{m} p_i \ln(p_i)$ where m is the total number of patch types and p_i is the proportion of the landscape area occupied by patch type i.
t3.12	Dominance index	D	A measure of the degree of dominance by one or a few patch types in a landscape: $D = H_{max} + \sum_{i=1}^{m} p_i \ln p_i$ where H_{max} is the maximum diversity when all patch types are present in equal proportions, m is the total number of patch types, and p_i is the proportion of the landscape area occupied by patch type i. Small values of D tend to indicate that landscapes with numerous land use types of similar proportions.
t3.13	Largest patch index	LPI	The ratio of the area of the largest patch to the total area of the landscape (unit: percentage).
t3.14	Mean patch size	MPS	The average area of all patches in the landscape (unit: ha).
t3.15	Patch size standard deviation	PSSD	The standard deviation of patch size in the entire landscape (unit: ha).
t3.16	Patch size coefficient of variation	PSCV	The standard deviation of patch size divided by mean patch size for the entire landscape (unit: percentage).
Au2 t3.17	Landscape shape index	LSI	A modified perimeter/area ratio of the form: $LSI = \frac{0.25E}{\sqrt{A}}$ where E is the total length of patch edges and A is the total area of the landscape (unitless).

Landscape Ecology. Table 3 (Continued)

Landscape metric	Abbreviation	Description
Mean patch shape index	MSI	A patch-level shape index averaged over all patches in the landscape: $MSI = \dfrac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left[\dfrac{0.25P_{ij}}{\sqrt{a_{ij}}}\right]}{N}$ where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, and N is the total number of patches in the landscape (unitless).
Area-weighted mean patch shape index	AWMSI	Mean patch shape index weighted by relative patch size: $AWMSI = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[\left(\dfrac{0.25P_{ij}}{\sqrt{a_{ij}}}\right)\left(\dfrac{a_{ij}}{A}\right)\right]$ where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, A is the total area of the landscape, m is the number of patch types, and n is the total number of patches of type i (unitless).
Double-log fractal dimension	DLFD	The fractal dimension for the entire landscape which is equal to 2 divided by the slope of the regression line between the logarithm of patch area and the logarithm of patch perimeter: $DLFD = \dfrac{2}{\left[\dfrac{\left[N\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\ln(P_{ij})\ln(a_{ij})\right)\right] - \left[\left(\sum_{i=1}^{m}\sum_{j=1}^{n}\ln(a_{ij})\right)\right]}{\left(N\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\ln(P_{ij}^{2})\right)\right) - \left(\sum_{i=1}^{m}\sum_{j=1}^{n}\ln(P_{ij})\right)^{2}}\right]}$ where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, m is the number of patch types, n is the total number of patches of type i, and N is the total number of patches in the landscape (unitless).
Mean patch fractal dimension	MPFD	The average fractal dimension of individual patches in the landscape, which is the summation of fractal dimension for all patches divided by the total number of patches in the landscape: $FD = \dfrac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\dfrac{2\ln(0.25P_{ij})}{\ln(a_{ij})}\right)}{N}$ where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, m is the number of patch types, n is the total number of patches of type i, and N is the total number of patches in the landscape (unitless).
Area-weighted mean patch fractal dimension	AWMFD	The patch fractal dimension weighted by relative patch area: $AWMPED = \sum_{i=1}^{m}\sum_{j=1}^{n}\left(\dfrac{2\ln(0.25P_{ij})}{\ln(a_{ij})}\left(\dfrac{a_{ij}}{A}\right)\right)$ where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, m is the number of patch types, n is the total number of patches of type i, and A is the total area of the landscape (unitless).
Contagion	CONT	An information theory–based index that measures the extent to which patches are spatially aggregated in the landscape (Li and Reynolds 1993): $CONT = \left[1 + \sum_{i=1}^{m}\sum_{j=1}^{m} p_{ij}\ln(p_{ij})/2\ln(m)\right](100)$ where p_{ij} is the probability that two randomly chosen adjacent pixels belong to patch type i and j, m is the total number of patch types in the landscape (unitless).

t3.18 t3.19 t3.20 t3.21 t3.22 t3.23 Au3



Landscape Ecology. Figure 1
A schematic representation of a hierarchical and pluralistic view of landscape ecology (Modified from [38])

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