



Landscape Ecology of Wetlands: Overview 10

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Contents

Introduction	80
Historical Background	80
Key Topics in Landscape Ecology	81
Pattern and Process	81
Spatial Heterogeneity	81
Scale and Scaling Issues	83
Connectivity and Fragmentation	84
The Human Element	85
Future Directions	86
References	87

Abstract

Landscapes are heterogeneous areas consisting of interacting biotic and abiotic components. Landscape ecology emphasizes landscape pattern, connectivity within the landscape, and the interaction between landscape pattern and ecological process. The interaction of people with the landscape is also an integral component of landscape ecology due to the significant reciprocal nature of the relationship between humans and the environment. The section, *Landscape Ecology of Wetlands*, describes common landscape ecology principles and how they are being applied by wetland scientists and practitioners.

Keywords

Connectivity · Disturbance · Fragmentation · Landscape Ecology · Metacommunity · Metapopulation · Patch/Gap Dynamics · Pattern · Process ·

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79

Restoration · Riparian Buffer · Scale · Scaling Issues · Source-Sink Dynamics · Spatial Heterogeneity

Introduction

Landscapes are heterogeneous areas consisting of interacting biotic and abiotic components. Landscape ecology emphasizes landscape pattern, connectivity within the landscape, and the interaction between landscape pattern and ecological process. The interaction of people with the landscape is also an integral component of landscape ecology due to the significant reciprocal nature of the relationship between humans and the environment. Many landscape ecologists seek to apply research results to improve landscape management, conservation, and restoration. Wetland ecologists have also been applying landscape ecology principles explicitly or implicitly to answer basic questions concerning wetland landscapes and to improve wetland conservation and management. The section, *Landscape Ecology of Wetlands*, describes common landscape ecology principles and how they are being applied by wetland scientists and practitioners.

Historical Background

Landscape ecology has a relatively recent history. It was founded by Carl Troll, a German biogeographer, in the late 1930s as he sought to integrate ecology with geography to form one holistic branch of science. His effort culminated with the publication of *The Geographic Landscape and Its Investigation* in 1950. As a new discipline in Europe, landscape ecology focused on the landscape as mosaic of interacting abiotic and biotic features and also on the interaction between humans and the environment. It is through this holistic view of the environment that European landscape ecologists saw the applied sciences such as landscape management and conservation as vital to the discipline.

Landscape ecology was introduced to North America 30+ years after Troll's seminal work (Forman and Godron 1981, 1986; Risser et al. 1984). North American scientists dove into this emerging field, but rendered a slightly different form of the discipline. Rather than focusing on the applied sciences, North American scientists took a more basic and theoretical approach to landscape ecology and concentrated on spatial and temporal heterogeneity, the interaction of pattern and process, and scaling issues within the landscape. In response to these seemingly divergent paths, landscape ecologists on both sides of the world called for unification of the European and North American visions of the new emerging field of landscape ecology (Farina 2007; Wu and Hobbs 2002; Wu 2009a).

While landscape ecology was emerging as its own distinct interdisciplinary field, the principles of landscape ecology were being applied by wetland scientists and

practitioners. Certainly, many of the central topics within landscape ecology were not unique to the field. In the following section, common principles and topics of landscape ecology are explained and how they are applied within the field of wetland ecology as described by section contributors is introduced.

Key Topics in Landscape Ecology

Pattern and Process

Spatial patterns across the landscape, and how processes influence and are influenced by patterns within the landscape, are a central focus of landscape ecology (Turner 1989; Turner et al. 2001). Spatial patterns describe the distribution of elements such as ecosystems, communities, species, nutrients, and water across the landscape. Processes such as species dispersal, natural disturbances, human land use, nutrient movement, and water flow influence the spatial patterns of the aforementioned landscape elements, but they are also influenced by the arrangement of the elements across the landscape. Emergent from the relationship between pattern and process are the principle topics of landscape ecology.

Spatial Heterogeneity

Landscapes are mosaics of elements that compose the landscape itself (Fig. 1). The *spatial heterogeneity* that emerges from the mosaic influences multiple ecological processes within the landscape and arises from the processes operating within the landscape (Pickett and Cadenasso 1995). The process of moving water creates rivers and associated riparian ecosystems that are elements of watersheds and contribute to landscape heterogeneity. Watersheds, in turn, affect multiple processes within the landscape such as nutrient movement as dissolved nutrients flow towards streams in watersheds and influence, and are influenced by, nutrient cycling in riparian zones. Wetlands also contribute to landscape heterogeneity and, like riparian ecosystems (Ward et al. 2002), are heterogeneous in space and time. Larkin (2017) describes types and sources of wetland heterogeneity and how wetland heterogeneity impacts community dynamics and ecosystem functions such as carbon sequestration and denitrification.

Disturbance also contributes to landscape heterogeneity (Levin and Paine 1974), and disturbance parameters such as severity, duration, and frequency are influenced by the patterns and locations of elements within the landscape. For example, natural disturbances such as floods can scour soil and vegetation, sculpting the floodplain and creating a patchy environment (Fig. 2). Watershed size and shape, relief ratio, and depth to bedrock are some landscape elements that impact flood disturbance parameters. A steep fan-shaped watershed with a high relief ratio increases flood magnitude and shallow bedrock decreases the time it takes for a flooding stream to reach bankfull stage.

Fig. 1 Heterogeneous riparian landscape consisting of abiotic and biotic components such as stream, soil, boulders, vegetation, and other organisms (Photo by Jere Boudell)



Fig. 2 Flooding of the San Pedro River, Arizona USA (Photo by Juliet Stromberg)



One of the functional outcomes of disturbance is that it produces areas, or patches, of newly available resources. This creates an opportunity for *patch/gap dynamics* (Levin and Paine 1974; Pickett and White 1987), further contributing to landscape heterogeneity. Patch/gap dynamics occur as species take advantage of the

Fig. 3 Regeneration from the seed bank after simulated flood scour (Photo by Jere Boudell)



newly available resources released by the disturbance by dispersing or immigrating into gaps and successfully inhabiting the previously occupied space. For instance, in response to floods, buried and dispersed wetland seeds once exposed to light and water can germinate and occupy the space created when floods scour vegetation and surface soils (Fig. 3).

Scale and Scaling Issues

The issue of *scale* is integral to the discipline of landscape ecology, and ecology in general (Wiens 1989; Levin 1992). Pattern, process, and scale are interrelated concepts. Phenomena can change spatially from millimeters to kilometers and temporally from seconds to centuries. Phenomena can also change through levels of organization from cells to ecosystems. For example, the pattern and process of nutrient cycling varies over the scale of meters to kilometers, minutes to eons, and from individual organisms to the ecosphere. Hierarchy theory incorporates scale and describes a system and its components. Within a hierarchical system, the top level of the system constrains the focus level and the lower level components impact and provide the mechanism that explains what is happening at the focus level (Turner et al. 2001). An investigator incorporating hierarchy theory into his/her investigation of plant productivity in wetlands needs to be cognizant of the top or broad scale controls on plant productivity such as climate and the bottom or finer scale controls such as light, water, and nutrient availability in plant microenvironments.

Scaling issues arise when investigators seek to understand phenomena and must pick the appropriate spatial and temporal scale and organizational level at which to study the phenomena. They can be confounded by scaling issues if they seek to apply their understanding of the phenomena to other scales and levels. Knowledge and application of scaling theory and methods can help investigators cope with scaling issues (Peterson and Parker 1998; Wu 2009b).

Connectivity and Fragmentation

Connectivity links landscape elements (Taylor et al. 1993). Connectivity also describes the flows of materials, such as water and nutrients, across landscapes as well as species dispersal and migration (Fig. 4). Research on connectivity typically focuses on the patterns and dynamics that significantly impact organisms that are reliant upon functional links through the landscape. The movement of water between wetlands, between groundwater and wetlands, and of migratory birds and amphibians among wetlands requires, and effectively constitutes, functional links between wetlands. Connectivity between wetlands and the role of connectivity in migration and wetland protection is discussed by Rittenhouse and Peterman. *Landscape genetics* focuses on the movement and interaction of elements and species within the landscape and the resulting effects on gene flow (Holderegger and Wagner 2008). Spear describes this newly emerging field in an essay on landscape genetics in wetlands and how it is being applied to understand in what way landscape elements and configurations impact gene flow of wetland species.

Metapopulations (Hanski and Gilpin 1997) and *metacommunities* (Holyoak et al. 2005) describe networks of populations and communities, respectively, whose members disperse between constituent populations and communities and potentially interact. Without linkage between populations and communities within the networks, these systems become fragmented, and metapopulations and metacommunities fall apart. Schooley and Cosentino discuss metapopulation theory and its application in the conservation of wetland species. A natural extension of metapopulation theory, metacommunity theory, is described by Boudell in an essay on metacommunity dynamics in riparian and lotic ecosystems. *Source-sink dynamics* of species, a component of metapopulation and metacommunity theory, occur as individuals migrate or disperse from robust populations to sparse populations. These dispersal dynamics ultimately help prevent local extinction of smaller, less successful populations (Pulliam 1988). Peterman and Rittenhouse follow up their essay on

Fig. 4 Wetland hydrologically connected to a nearby stream (Photo by Jere Boudell)



connectivity with an essay on source-sink dynamics in wetlands. Here they focus on source-sink dynamics of amphibians and reptiles and on the variety of methods used to study these dynamics.

Fragmentation of the landscape whether created by natural perturbations such as landslides or more commonly by humans through road construction and other activities disrupt connectivity within the landscape (Fisher and Lindenmayer 2007) (Fig. 5). As a consequence, fragmentation impacts landscape elements and interrupts ecological processes such as metapopulation and source-sink dynamics that are dependent on robust connections. Indeed, it is challenging to describe the many ecological processes that require connectivity without discussing fragmentation impacts. Thus, many of the aforementioned essays include discussions of fragmentation impacts. Cosentino and Schooley explicitly describe the effects of fragmentation on wetlands and specifically, the impact of fragmentation on dispersal and its outcome on biodiversity.

The Human Element

Humans are profoundly connected to the landscape they inhabit. Like other animals, our lives are significantly influenced by the environment affecting where and how we live. As a successful dominant species and as ecosystem engineers we, in turn, affect our environment. In recognition of the reciprocal nature of our relationship with the environment, landscape ecologists have explicitly included the human element within the discipline. Landscape ecology, particularly as it is practiced in Europe, has focused on how our surrounding landscape



Fig. 5 Riparian landscape fragmentation caused by repeated mowing (Photo by Jere Boudell)

influences where live, where we grow our food, where we recreate, and how these factors impact us culturally (Farina 2007). Its principles have been included in the applied sciences of conservation, management, restoration, sustainable agriculture, and landscape design. For example, maintaining connectivity and understanding how fragmentation disrupts landscape genetics, source-sink dynamics, and metacommunities are essential in order to manage and conserve species and allows managers to predict how species will react to the fragmented landscapes they inhabit.

In many of the contributed essays in the *Landscape Ecology of Wetlands* section, authors describe how to manage to maintain connectivity and/or mitigate the outcomes of disruption to the myriad dynamics occurring within the landscape. Several contributors solely focus on conservation and attempts to ameliorate anthropogenic impact on the environment through management and restoration of wetlands and riparian areas. Zedler and Miller describe the need for, and efforts to, restore degraded wetlands at the landscape scale. Ma focuses on the role of riparian buffers, the interface between streams and impacted lands such as agricultural fields, not only in wetland protection and water quality maintenance but also as habitat for many species.

Future Directions

Landscape ecology, as a relatively new discipline, is still evolving and defining itself. Many of the early issues that arose as the field was developing have been partially resolved through attempts to unify the European and North American perspectives on landscape ecology. And yet, there is room for further integration of the basic and the applied sciences within the discipline (Wu and Hobbs 2002; Wu 2009a). There are still topics to be investigated within the field such as interactions between the varying causes of spatial patterns, further exploration of heterogeneity, and looking beyond the typical temporal scale of many studies (Turner 2005). Our changing climate and its impact on disturbance regimes and species migration and dispersal are important topics that can benefit from the holistic approach of landscape ecology.

Landscape ecology has great potential to improve conservation and management. Indeed, the call was issued for applied landscape ecology as a subdiscipline in hopes that landscape ecology principles can be tested and incorporated into conservation, management, and restoration (Turner 2005). Wetland ecology can benefit from incorporating a broader view of the landscape by including both individual wetlands and surrounding environments and how patterns and processes can interact to influence ecological phenomena at multiple spatial and temporal scales. Wetland science can only improve and become more effective at solving pressing issues such as species conservation in the face of a continually fragmented and changing environment by incorporating landscape ecology principles and methods.

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