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Landscape Ecology, Use and Application in Forestry

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Introduction

Many ecological processes result in or are affected by spatial patterns. However, the relative importance of different processes is very sensitive to the scale of analysis. For example, at a very local scale, species diversity is often strongly affected by competition and trophic interactions between species. In contrast, at the regional scale species diversity is more strongly influenced by habitat dynamics and biogeography. The majority of ecological studies in the past has focused on local level processes, probably because they are less daunting to measure and are more amenable to experimental manipulation. The recognition that the important processes acting at a landscape level are often different from those at a local level has led to the development of landscape ecology as a distinct approach with its own paradigms and methodologies.

Ecologists have traditionally been interested in the spatial patterns of organisms. Charles Darwin's *On The Origin of Species* contains an entire chapter discussing the geographical distribution of species. However, the focus of his chapter, like much of the ecological literature since, is on the processes that create spatial patterns or biogeography. In contrast, an area of prime interest in landscape ecology is the way that spatial patterns affect ecological processes. This article reviews some of the ideas that this perspective has generated and looks at their relevance to forestry.

Why Landscape Scale?

The question of which is the appropriate scale for a particular analysis will largely depend on its objectives. Many issues in applied ecology and particularly those concerning environmental management are most appropriately addressed at a landscape scale. This is certainly true of forestry where many of the key management issues concern processes that operate over large areas. Environmental change, conservation, sustainability concerns, recreation, and public participation all involve considering forests in their landscape context.

The term 'landscape' has no precise definition. It implies an area that is perceived to have some coherence of natural or cultural entities. In practice the lack of a formal description of what constitutes a landscape is no more problematic than the similarly vague definition of the term 'population' in ecology. Both are useful because they demarcate biologically meaningful groups. Just like landscapes, populations can be identified at a scale that is appropriate to the objectives of the study.

The need for a large-scale perspective is not a new one but it is only recently that ecologists have acquired the tools that permit them to carry out this type of analysis efficiently. Remote sensing and geographic information systems (GIS) have permitted the collection and analysis of large quantities of spatial data. Although ecologists use experimental approaches more frequently than many environmental scientists, the possibilities for experimental landscape ecology research are severely limited. It is usually impractical to deliberately manipulate landscapes for experimental purposes and even in those situations where a treatment occurs as a consequence of other action it is usually impossible to replicate or control. Hence landscape ecologists typically measure rather than manipulate; patterns and processes are described rather than being experimentally controlled. Although purely descriptive studies in ecology are often criticized it is only by having accurate quantitative descriptions of landscape patterns that testable hypotheses can subsequently be developed.

Simulation modeling can be used as an alternative to the descriptive–inductive approach to landscape ecology. Aided by huge advances in computing, simulation modeling has permitted landscape ecology to throw off some of the constraints of studying region-specific, observable phenomena. Modeling has been used to identify the ecological implications of changing landscape patterns and of alternative management regimes applied to existing land use configurations. The combination of ecological models with GIS and, more recently, computer-generated visualization have provided a powerful planning tool.

One area that has proved to be a consistent challenge in landscape ecology has been the development of accurate, consistent, and ecologically meaningful measures of spatial pattern. The measurement of spatial pattern is often strongly scale-dependent. The types of pattern that can be recognized depend very much on the scale at which they are viewed. For example features that appear clustered at a small scale can be dispersed when viewed at a large one. Connectivity can change too. Small patches of woodland and wooded corridors between patches can disappear when a landscape is viewed at a small scale (**Figure 1**).

In 1967, Benoit Mandelbrot published a paper in which he concluded that the length of the coastline of Britain depended on the scale of measurement. He pointed out that each increase in scale reveals a new level of roughness and thus an increase in its length. He termed such patterns, which reveal greater complexity as they are enlarged, fractals. Many of the measures that are used to quantify shape and complexity in landscape ecology are similarly dependent on the scale of the analysis. This implies that it is crucial when investigating the impacts of spatial pattern on ecological processes to make sure that pattern is measured at a scale that matches the way the study organism perceives the landscape. A region in which woodland is highly fragmented from the point of view of a wood mouse (*Apodemus sylvaticus*) can be well connected for a more mobile organism like a jay (*Garrulus glandarius*). A further dimension to this problem is the difficulty of obtaining a consistent quality of information over space and time. Some types of measures of spatial pattern are sensitive to the quality of input maps. Very large differences have been found in a number of measures used to quantify landscape structure when the same region is analyzed on different map products.

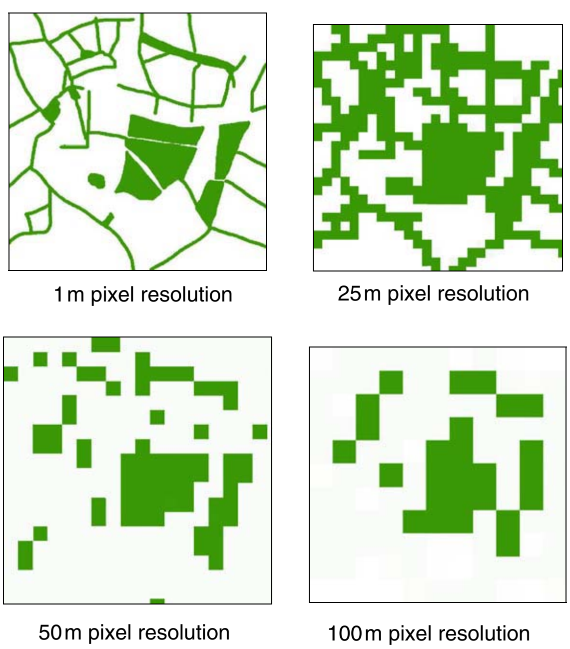

Figure 1 The connectivity of wooded areas in an Oxfordshire landscape changes with the resolution of the image used for the analysis.

Landscape Ecology and Forestry

Both forestry activities and deforestation alter landscape structure in ways that have significant effects on organisms. In many parts of the world different components of the landscape are managed virtually in isolation, with little or no account taken of surrounding land use or landscape context. Such components include forested blocks, agricultural fields, urban areas, and waterways. A consequence of this is that management objectives are often frustrated by the functional dependence of one land area on those around it. For example, recent research in Costa Rica has shown that the diversity of moths in sites outside forest is most correlated with forest cover within 1–1.5 km of the surveyed site. Fragmented management often results in resource use conflicts and environmental stress.

Growing interest in sustainable forest management systems over the last decade has resulted in efforts to apply ideas from landscape ecology to forest management practices, particularly timber harvesting and new woodland creation. A guiding principle has been the emulation of natural patterns. Landscape ecology provides useful ways in which natural patterns can be described and compared with those in the managed landscape.

There are four landscape characteristics that have important implications for forest management.

Fragmentation

Fragmentation occurs when a large area of forest is broken up into smaller, less connected patches. In many tropical landscapes fragmentation of natural forest is occurring rapidly and efforts to protect biodiversity and to understand the ecological processes that determine its survival are becoming increasingly important. In contrast, in many temperate countries, an excess of agricultural land and a concern to increase the area of woodland for aesthetic, conservation, and recreation reasons, have prompted interest in the potential benefits of defragmentation. There have been two types of approach to understanding patterns in fragmented landscapes; those that address issues of community composition and those that examine single species population dynamics. Here, both approaches are described.

The equilibrium theory of island biogeography (advanced in the 1960s by MacArthur and Wilson) has been a cornerstone of our understanding of the processes that determine community composition in a fragmented environment for nearly 40 years. Their theory proposed that the diversity of organisms on an island should decrease as its size decreases and isolation from the mainland increases. This concept has been widely applied to habitat fragments on the assumption that they function like islands surrounded by a 'sea' of more hostile environment. However, it has not generally proved to be a useful tool for predicting species diversity in habitat patches within a matrix of other land uses. This is because the community of species in a patch of habitat will be strongly influenced by the nature of the landscape around it and the sorts of species that inhabit that landscape. The management regimes used in open countryside have been found to influence both bird and invertebrate diversity in adjacent forest patches. Species that inhabit forest patches can be affected by competition and predation from species that inhabit surrounding land use types. For example, in the Midwest of the USA the replacement of forest by agricultural and suburban landscapes has resulted in a substantial expansion in the range of the brown-headed cowbird *(Molothrus ater)*. A relationship has been found between songbird nest predation and parasitism by cowbirds and the degree of forest fragmentation. The implication of studies such as this is that two fragments of forests may have identical areas and be equally isolated but their species composition may be very different as a consequence of their interactions with surrounding land use types.

Models of single-species population dynamics at a landscape level are a much more recent development. A variety of models has been formulated to describe the dynamics of a range of organisms with very different ecologies. Metapopulation theory envisages that a landscape is divided into habitable patches separated by unsuitable habitat and that as a consequence a species population will actually consist of a series of interacting local populations each occupying a patch. Changes that occur in one local population do not necessarily occur in other patches at the same time. This can mean that one local population may go extinct whilst others are thriving. Migration between patches can re-establish a local population should it go extinct. Metapopulation theory predicts that a threshold number of patches is needed in order that the species persists at a landscape level. The dynamics of the metapopulation are not simply a function of local population dynamics since larger-scale factors such as the distribution of patches in the landscape and migration rates between patches are important. The metapopulation concept has important implications for the management of fragmented forests. Silvicultural operations such as felling and coppicing can drastically alter habitat quality and unless there are enough similar habitat patches within migration distance it may be impossible for a local population to re-establish should it go extinct. Many rare UK butterflies are found exclusively in large and non-isolated habitat patches, while small or isolated patches of suitable habitat remain vacant. This distribution pattern is the result of local extinction and colonization processes and implies that long-term population persistence requires networks of suitable habitats, sufficiently close to allow natural dispersal. An extension of metapopulation theory considers the landscape to consist of habitat of variable quality rather than a simple division into habitable and uninhabitable areas. An area in which a species population thrives (with births exceeding deaths) may become a source of colonists whereas poor quality habitat may be a sink (deaths exceeding births). An important implication is that the decline of a local population in one forest may result in declines in adjacent forest patches as mobile species move out to recolonize vacant areas. This may make it difficult to diagnose the cause of a population decline and it emphasizes the importance of conserving habitat networks rather than focusing on the protection of a single site.

The fragmented nature of management planning in many patchy landscapes can make management of conservation networks difficult. Numerous owners and a variety of organizations may be responsible for taking decisions with the result that forest operations are planned on a case-by-case basis with no account taken of what is happening to adjacent forest areas. Landscape ecology has highlighted the importance of making sure that land use policies are aligned across owners and government agencies when sustainability is an essential goal.

Edge Effects

As patch size decreases so a progressively larger proportion of the remaining forest is influenced by edge effects. These can include increases in light and temperature and decreases in humidity. Increases in light have often been found to result in higher density and faster growth of natural regeneration of light-demanding trees along forest edges but also in the proliferation of herb and vine species. In tropical rain forest in the Brazilian Amazon significant increases in liana density have been detected up to 100 m from a forest edge. There is often an increased risk of windthrow on exposed forest edges. This has encouraged the development of special treatments for stand edges in areas that suffer from a high risk of wind damage. These include establishing shelterbelts of wind-resistant species or heavy thinning regimes to encourage well-tapered stems. It is also clear that the pattern of felling at a landscape level can have a significant effect on both the total length of exposed forest edge and wind turbulence.

Small woods have a high proportion of edge to core area. One reason for the creation of new forests in landscapes that have lost most of their forest area is to provide new niches that are not currently available. Large forests offer opportunities for species that require large forested territories, use large home ranges, or which thrive in forest interior habitats (i.e., are disadvantaged in forest edge habitats).

Connectivity

Connectivity refers to the degree to which habitat patches are linked so that organisms can move from one patch to another. Little is yet understood about colonization processes and rates and landscape use by many forest organisms but it is clear that connections in a landscape are organism-specific.

It has often been claimed that connectivity can be increased by the creation of habitat corridors. Strips of habitat connecting patches were assumed to facilitate migration and reduce the risks of local population extinction. However, empirical studies have shown that it is often the structure of the entire landscape matrix (the 'habitat network') that determines whether organisms can move. Many organisms can migrate through a landscape using a variety of habitats that they would not live in. Conversely, the provision of habitat corridors does not guarantee movement. Patches that are physically linked by a narrow corridor may not be connected for an organism that only occupies forest interior habitats. Indeed, it has even been proposed that corridors may facilitate colonization by invasive species and species tolerant of disturbed conditions.

Direct physical connections may be necessary for movement of organisms that inhabit old-growth forest and that have highly specific habitat requirements. Such species typically have extremely slow colonization rates. Even with an adjacent source of colonization, the number of such poorly dispersed species that will establish in newly forested areas may be low. Forest management systems need to be designed to maximize the opportunities for the dispersal of old-growth forest specialist species. This may include leaving substantial areas without any form of management intervention, avoiding excessive edge effects by minimizing the amount of harvesting around unmanaged core areas and distributing harvesting to ensure that regenerating forest is not isolated from old-growth areas.

Disturbance

Disturbance regimes determine the structure and composition of natural forests. Large or frequent disturbances (such as wildfires or hurricanes) create forests that have a uniform structure and a predominance of pioneer or colonizing species. In contrast, climax or shade-tolerant species will dominate forests that have only small or infrequent disturbances (such as those caused by the collapse of an old tree). As many of the organisms in a natural forest will be adapted to the prevailing disturbance regime, natural forest management systems that intend to sustain this biological diversity have attempted to match natural patterns. This includes matching the design of harvesting blocks to the pattern and distribution of natural disturbances across a landscape in terms of their size, shape, and frequency.

Natural forest management systems were abandoned during the twentieth century in many European and North American countries as markets for traditional woodland products declined. As a consequence, many seminatural forests have lost the diversity of ages and hence structures that management maintained and that were important for wildlife. There are a number of initiatives to bring neglected woodlands back into management with the primary objective of enhancing their wildlife value. Techniques such as thinning, coppicing, and the introduction of group selection felling systems have begun to re-establish a variety of woodland habitats. An important task is to decide how these different management regimes should be distributed at a landscape scale. Studies of natural disturbance regimes can help in the design of appropriate silvicultural systems but one of the greatest challenges remains the coordination of actions at a landscape scale particularly where this involves a number of different landowners.

See also: **Biodiversity**: Biodiversity in Forests; Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Entomology**:

Population Dynamics of Forest Insects. **Environment**: Environmental Impacts. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Landscape Ecology, the Concepts. **Resource Assessment**: GIS and Remote Sensing. **Silviculture**: Natural Stand Regeneration.

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Landscape Ecology, the Concepts

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Introduction

Landscape ecology is an emerging discipline that aims to understand the environmental processes and patterns influencing habitats and species beyond the site level. It arose independently in the latter part of the twentieth century in central and Eastern Europe and in North America as geographers, planners, and ecologists began to push the boundaries of their subject interests in the search for integrated approaches to land management of sensitive areas. They combined intellectual forces in the International Association of Landscape Ecology (IALE), formed in 1982.

Landscape ecology is based on the initial premise that a landscape can be viewed as a series of patches within an overall background matrix; taken together, patches and matrix make up a heterogeneous landscape mosaic. The significance for forestry is that it can take the focus up a level from the management of stands within a forest to forests within a landscape. Each forest or woodland can be viewed as a patch, within a matrix of other land use. The power of landscape ecology is that its principles can apply at vastly different scales, depending on the landscape or the research question. It has been used equally effectively by natural resource managers in conservation planning of large protected areas such as watersheds or national parks and by those undertaking local-scale restoration projects consisting of a few sites. In Europe the challenge is often to mitigate the effects of development, but landscape ecology can be used more proactively to design for conservation and related benefits. It is equally applicable to temperate and tropical landscapes, and although data constraints are significant, it is more often the speed of landscape change that prevents the full application of the discipline to landscape problems.

Landscape ecology is a broad discipline, with spatial planning at its heart, but it is much more than just mapping, as its twin concern is the time dimension of both natural and human-induced effects. Timescales from hours to years are used to understand more fully the effects of landscape-scale processes such as habitat fragmentation, loss, or restoration. In multifunctional landscape management many concerns can be taken on board in an approach based on landscape ecology, although there are criticisms that, because it is focused primarily on biodiversity issues, it currently fails to elaborate or model fully socioeconomic and cultural issues.

Underlying Thories

The patch/matrix model is in part an extrapolation of the theory of island biogeography in which the patches are islands in an archipelago, and their size and proximity to sources of biodiversity are critical factors in determining their own species load. Larger islands tend to contain more species than smaller islands and those nearer the mainland more than distant islands. Relative rates of colonization and extinction were invoked to explain these findings. It