

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 ap-

proaches 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 Theories

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

is now recognized that the theory is too simplistic for most landscapes as the critical factors for species and populations in land-locked patches are often more numerous and complex. Landscape ecology addresses the many variables involved, such as the composition of the patches themselves and the nature of the surrounding land use, which can be overriding factors in species dispersal in a landscape.

The notion of functional connectivity between patches, e.g., the flow of genes or energy, is still critical, as in island biogeography, but landscape ecologists consider this in a temporal as well as spatial context. Dispersal of organisms between habitat patches is explained in terms of metapopulation theory, dependent on identifying a series of interlinked subpopulations making up a functional population unit, and the related source–sink theory, in which patches are either net providers or net absorbers of migrating individuals.

Discrete landscape elements do not exist in isolation and there are different ways in which the linkages between elements can be understood. Hierarchy theory views the landscape elements as nested,

Thus a forested landscape might be hierarchically composed of drainage basins, which in turn are composed of local ecosystems or stands, which in turn are composed of individual trees and tree gaps. The landscape system is a nested hierarchy with each level containing the levels below it (Forman RTT (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge: Cambridge University Press).

The linkages that need to be understood between landscape elements are those disrupted, or created by changes in the processes and pattern in the immediate and wider landscape. They include those to landscape elements at the scale below and above the element under consideration and the landscape

ecologist should consider these in addressing research or management questions (Table 1).

### Interpreting Landscape Pattern

Landscape metrics are used to compare different landscapes or the same landscape over time (Table 2). It is important to remember that many metrics are correlated with or derived from each other, e.g., edge length and edge density, and care should be taken to choose a metric appropriate to available data and the conclusions or decisions that will flow from the data analysis. Knowledge of landscape structure and composition may become the basis for making assumptions about landscape-scale processes, e.g., erosion.

### Issues of Scale

Selecting the appropriate scale at which to work is fundamental to the success of a landscape ecology approach. Anthropocentric bias must be minimized when considering scale. It is vital to acknowledge the scale at which the target organism(s) themselves are operating: is it tens of meters in the case of a woodland butterfly or is it kilometers in the case of a raptor? This leads us to an understanding that ‘patches’ overlap, and may even be nested, i.e., the patch for species A may be wholly incorporated within the patch for species B. It is likely that these species will be experiencing a different level of detail or grain in the landscape.

### Data Constraints

The principal limitation to a more widespread application of landscape ecology is the availability of robust data sets at the appropriate scale. There are issues of comparability between data sets recorded at

**Table 1** The landscape ecology approach

	<i>Action</i>	<i>Check</i>
Step 1	Crystallize the research or management need	Consult widely, with stakeholders, subject experts, and policy-makers
Step 2	Identify the appropriate scale at which to work	This must relate to the issue or species but is often dictated by data availability
Step 3	Define the landscape and the time frame	Make transparent the reasons for selection of both the landscape boundaries and the time scale
Step 4	Design optimum data capture strategy	Historical data Fieldwork at what scale and intensity? Design of geographic information systems?
Step 5	Gather data	Check scale and comparability of data sets
Step 6	Analyze data	Focus on identifying the spatial/temporal relationships between data sets
Step 7	Relate data analysis to research or management question and draw conclusions	Review limitations of data and analyses

**Table 2** Landscape metrics

<i>Metric</i>	<i>Notes</i>
<b>Landscape configuration metrics</b>	
Patch size	The average size of a particular type of patch, e.g., woodland. In general, greater variability in patch size indicates less uniformity in landscape pattern
Patch core area	May be critical to certain species, e.g., those dependent on the more stable conditions in the interior of a forest patch
Patch shape = $0.25 \text{ perimeter} / \sqrt{\text{area}}$	With this equation a simple shape such as a square has a shape index = 1. A more complex shape has shape index > 1 Altering the shape of a habitat patch may influence many different processes within it, not least because edge and core measurements may change, and so may have advantages or disadvantages depending on the conservation priorities
For individual patches in the landscape: $FD = 2(\ln 0.25P / \ln A)$	Fractal dimension (FD) may also be used as a measure of shape complexity. $FD = 1$ for square and 2 for complex shape. FD can be computed for each patch and then averaged for the landscape. Because the patches are not usually equal sizes, this metric should be weighted, i.e., obtain the FD for each patch, then weight each value by the ratio of the patch area to the landscape area. This weighted average addresses patch evenness
Nearest neighbor = distance (m) to the nearest patch of the same type	This can be either to the patch perimeter or center
Edge metrics	If these are high it implies greater spatial heterogeneity
Total patch edge and patch edge density: these are not spatially explicit but fit best within landscape configuration	Changes in the total length of edge of an important cover type, e.g., forest, may be the most significant measure of fragmentation available. Many other metrics depend on edge or perimeter data. (In a raster GIS data set, the length of all edges is biased upwards because of the “stair-step” effect when the edge is composed of a series of squares. Edge indices change with the resolution of the image, with finer resolutions giving longer measures of edge)
Contagion If there are $s$ cover types then the probability $P$ can be calculated that in a raster data set, two randomly selected adjacent cells or pixels will belong to cover types $i$ and $j$ respectively	A high $P$ -value indicates a clumped pattern of cover types over the landscape
Adjacency What is the probability that a grid cell of cover type $i$ is adjacent to cover type $j$ ?	This can be calculated directionally – to find directionality in the pattern (anisotropy) or the average value calculated. High values indicate clumping of cells of the same cover type, i.e., they are likely to be found aggregated together
<b>Landscape composition metrics</b>	
This second group of metrics is concerned with the relative proportions of the patch types present and not with their spatial arrangement. However, taken together with the configuration metrics above, they help to explain landscape pattern	
Proportion of landscape	This is the proportion $p$ of the landscape that is occupied by each cover type. $p$ is used in other metrics which may then be correlated
Relative richness $R = s/s_{max} \times 100$	If there are data available for a similar landscape which allows one to estimate the maximum number of cover types present ( $s_{max}$ ) then it is possible to describe a second landscape with number of cover types $s$ as having relative richness $R$
Diversity and dominance indices: dominance is the deviation from the maximum possible diversity for a landscape having $s$ cover types; a high value indicates that the landscape is dominated by one or very few cover types	These are similar to the measures of plant and animal diversity. There are two parts to each index: richness, i.e., number of cover or patch types present, and evenness or the distribution of the total area among these different types. Different indices are more sensitive to one or other of these, e.g., the Shannon–Wiener diversity index which is more sensitive to richness than evenness, so rare cover types are disproportionately influential. A high level of the index $H$ indicates high diversity in the landscape, although the absolute value is not meaningful except where appropriate comparisons are being made between landscapes These metrics are most useful when comparing change in a known landscape; even then, if the number of cover types and relative proportions remain the same, with a shift in the nature of the cover types between the proportions, then the indices will give similar values and be of limited value. Only one or other should be used as they give the same information about the landscape and they may not be useful where separate information is required on richness and evenness

GIS, geographic information system.

After McGarigal K (1996) *Fragstats Manual*. Corvallis, OR: Oregon State University, with permission.

different times and often for different purposes which are drawn on to cover as many variables as possible within the landscape. Analysis of such data sets has become possible with the advent of more user-friendly software tools applicable to natural resource management. Many ecologists, planners, and policy-makers now use geographic information systems (GIS) to analyze and present data and these support a variety of landscape ecology tools. Historic and contemporary maps of infrastructure, vegetation, or soils all provide a useful basis for understanding a landscape's structure but often the corresponding biotic data are lacking.

If, for example, the conservation of a particular forest bird species was paramount, data would be needed on the spatial and temporal variants in the life cycle of the bird, its population, and its habitat needs. It is unlikely that fully comprehensive data will be available to the forest manager but key facts on bird and habitat distribution, breeding cycles, and foraging patterns would be needed to implement landscape-scale management. The minimum level of data required will vary depending on the question addressed. To some extent, this single-species approach is the simplest application of landscape ecology but its success is still dependent on quality data.

At an early stage in a landscape ecological study the landscape boundary must be defined. There are parallels with the ecosystem approach – the concept of an ecosystem is itself abstract – and in some respects it is more straightforward to identify the boundaries of a landscape of interest, acknowledging that these might be arbitrarily influenced by land-ownership or management. The scale of the landscape however must be informed by the requirements of the target organisms.

### **A Key Challenge for Landscape Ecology: Reducing Fragmentation**

Irreversible habitat loss is the greatest threat to biodiversity worldwide but this is closely followed by the fragmentation of habitats, and ecosystems, within landscapes. In the Brazilian Amazon it has been estimated in 2003 that the area of forest land affected by fragmentation was three times that which had been deforested. Combating fragmentation is a key action for biodiversity conservation both because many landscapes have become degraded as a result of habitat fragmentation and because many nature reserves and other important protected areas have become isolated fragments, with the associated pressures on the biodiversity under protection.

Fragmentation occurs when formerly extensive areas of natural habitat are divided into smaller fragments as a result of human activities, including the building of roads, railways, pipelines, and other communication lines. It may accompany larger-scale habitat destruction due to housing, industrial, or agricultural development. As a result, the remaining fragments of habitat may be separated by a highly modified or degraded landscape that may be inhospitable to species movements beyond or between fragments. As habitats become fragmented, the increased 'edge' is also exposed to a greater variety of microclimatic and biotic influences and human disturbance that typically have a detrimental effect on the remaining biodiversity. As patches of habitat become smaller, so the ratio of edge to interior, or core, increases disproportionately and edge effects may dominate the remaining fragment. The magnitude of edge effects is related to the nature of the matrix surrounding the habitat fragment. The greater the contrast in habitat type and structure, the greater the intensity of edge effect in most ecosystems. Thus an area of forest surrounded by scrubby vegetation is likely to suffer less severely from edge effects in comparison to a fragment surrounded by intensively managed farmland.

As well as the loss or reduction in movement of biota from and between fragmented habitats, the impact of external biota such as domestic stock, predators, or nonnative plant species may severely threaten the integrity of ecosystem fragments. These effects are typically strongest at habitat edges. For example, levels of nest predation by predators such as domestic cats, crows, squirrels, or opossums on birds dwelling in forest fragments have been shown in a number of studies to be strongly linked to distance from habitat edge. Equally, increased light availability, nutrient enrichment and disturbance as a result of habitat fragmentation may encourage the colonization of invasive, often nonnative species at the expense of the less competitive native flora.

In forested landscapes roads are often a cause of fragmentation. The impacts have been shown to be highly significant for many organisms. Large mammals can be adversely affected by a reduction in the integrity of their domain; others, e.g., deer species, may exploit the increased patchiness of the landscape, and species operating at smaller spatial scales may be influenced by the change in the forest interior to edge ratio or by the fragmentation of other habitats around the wooded areas. Isolation may cause local extinctions within the metapopulation, which will be threatened if these subpopulations are not replaced. Overall, there is an increase in edge habitat and a reduction in core area – this may be

offset by road closure when no longer needed but more often the cost of installing forest roads is so high they remain a permanent influence in the landscape.

### Population Isolation and Barriers to Movement

The continued viability of populations in fragmented ecosystems may often be reliant on movement beyond the fragment to fulfill resource or habitat requirements (e.g., for hunting or seasonal feeding) and between fragments to maintain greater genetic diversity. Species' perception of 'barriers' will vary from species to species. For example, for small organisms such as invertebrates and some bird species, 100 m across an agricultural habitat may form a total barrier to dispersal, while for other bird species, small intervening areas of inhospitable habitat, such as a road or even a small development, may not radically affect movement between fragments. For small mammals, a road may form a significant barrier to movement due to road kills, while for larger mammals a fence may form a significant barrier to movement. A plant which is dispersed by wind or by birds may be able to disperse across small areas of inhospitable habitat, whereas a plant species with no such dispersal adaptations may be unable to disperse to other areas of suitable habitat.

If the surrounding matrix is an adverse environment for species dispersal, the landscape is described as 'resistant.' It is unlikely that the matrix is made up of one land use and so this heterogeneity must be analyzed to identify the key contributors to resistance where feasible. Resistance can potentially be improved by altering the intensity of the land use adjacent to the forest or by planting different vegetation between wooded patches, but often such intervention is outwith the scope of a forest manager.

### The Role of Corridors

To ease the dispersal of organisms and to counteract the adverse effects of isolation, landscape ecologists

often identify corridors in the landscape where they exist and propose them where they do not. The designation of corridors within a landscape is usually done in a spatial context and it assumes that linear movement is relevant to target organisms and other matter such as water. It is acknowledged that there are many assumptions made in identifying corridors, as there is little empirical evidence for their role in the majority of landscapes and for the majority of species.

In some landscapes potential corridors may be obvious; watercourses creating riparian corridors would be a good example of this. Corridors may actually have more functions than just acting as conduits (Table 3). It is also often forgotten that the corridor functions can vary considerably over different timescales, e.g., within a day, season, or year.

Unexpected effects of corridors can include the transport and spread of seeds by vehicles; this may be problematic if the species are invasive. Disease-causing organisms or pests, e.g., long-horned beetles, may be dispersed via corridors and a forester would need to assess the risk of increasing connectivity in a landscape-scale forest management scheme. It is also necessary to attempt to predict corridors that will be created – often unintentionally – from forest management practices.

### Survival Within a Patch

When does a patch become too small or modified to retain its full range of species and habitats and to cease to function as a patch? Accumulating evidence shows that edge effects can significantly reduce the recruitment of new seedlings and aboveground biomass in small fragments drops sharply. Microclimatic changes and elevated wind turbulence are the most significant edge effects – posing a risk to large established trees as well as new recruits. Broken crowns and snapped trunks cause significant loss of biomass even in surviving trees, indicating that fragments may be less efficient as carbon sinks than previously predicted.

Bird richness and abundance also decline in small forest fragments, though guilds differ in their

**Table 3** The functions of corridors between patches

<i>Function<sup>a</sup></i>	
Conduit	Organisms or propagules move along or adjacent to the corridor
Barrier	Resists passage between patches
Habitat	Species, usually generalists or edge species, which use the corridor as habitat for part or whole of their life cycle
Source	A reservoir of propagules or organisms
Sink	Absorbs water, nutrients, and species from the matrix

<sup>a</sup>Function varies with species.

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response to fragmentation. In tropical forests this has been shown to be due to adverse impacts on food supplies; nectarivores such as hummingbirds may be less affected by fragmentation than insectivores or frugivores. Critical patch size varies as some species are better at exploiting the increased heterogeneity of a disturbed forest. The nature of the surrounding vegetation is critical to minimize edge effects; in some cases secondary growth creates effective links between forest patches.

Fragmentation therefore does not cause an immediate crash in overall biodiversity but it does affect the relative abundance of different species and endemics are particularly vulnerable to its adverse effects.

**Woodland Planting to Counteract Fragmentation**

What if you are considering planting to consolidate an existing woodland resource? How much is needed to maximize proximity and hence the interchange of species? Thirty percent woodland cover is currently suggested as an appropriate target based on a model which randomly added a 1 ha block to a landscape. However, it is not until this figure is doubled that a substantial increase in woodland core area occurs and this is highly relevant for the conservation of forest interior species (Table 4).

In the UK the Woodland Trust (the principal forest nongovernment organization) has considered the evidence for connecting ancient woodland sites to increase biodiversity but has concluded that there is less value in this than in consolidating the significance of individual sites by increasing their area. In

**Table 4** The effect on core area of adding 1 ha seminatural habitat blocks to a 2 x 2 km landscape

Cover %	Cumulative core area (ha)	Critical threshold
1	0	
10	10	
20	20	
30	40	Level at which connectivity is potentially optimal
40	60	
50	100	
60	220	Level at which core area significantly increases
70	260	
80	310	
90	355	
100	400	

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turn, they considered the need to target areas where ancient woodlands are already concentrated for new planting of native woodlands to achieve 30% woodland cover. In such areas, the Trust recommended that this should be matched by 30% cover of seminatural habitats and a reduced intensity of management of the remaining land. The England National Forest also has a target of 30% tree cover but development pressure is such that it is not possible to match this with a similar area of seminatural habitat. The principle is sound however; woodland biodiversity gains are maximized when the adjacent land uses are benign.

**The Challenge of Managing Whole Landscapes**

Landscape ecology is only one component of an integrated landscape management approach. If applied to the exclusion of other interests, it will not provide sustainable solutions. However, its emphasis on spatial and time-related variables makes it a contender to provide the framework to integrate biodiversity conservation with socioeconomic and cultural concerns.

*See also: Ecology:* Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; 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, Use and Application in Forestry.

**Further Reading**

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## Spatial Information

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### Introduction

A common representation of forest characteristics within spatial analysis and geographic information systems (GIS) can often be found in native objects whose interactions are based on simple distance and connectivity relationships. The spatial description of forest objects can be understood as a continuous two-dimensional process as an intensity field, or a collection of discrete locations of spatial objects. Geometrical features, such as points, lines, polygons, and raster cells, are commonly used to describe real-world objects and their characteristics in computerized mapping systems. Data modeling is a process that simplifies and defines real-world objects as database objects. Further spatial analysis may be engaged in when database objects have sufficient characteristics for spatial analysis.

The quantification of heterogeneity in forest areas has long been an objective of forest inventory and management. Heterogeneity depends highly on scale. The spatial and temporal variation of the property that can be detected will often depend on the spatial and temporal scale at which the property was sampled, and the size of the mapping unit. The information levels used in forestry reporting are hierarchically divided into: (1) tree level; (2) stand level; (3) farm level; (4) region level; and (5) country level. The data collection is normally based on measured sample units or subjective field observations that come from reporting units. The spatial pattern of reporting units can be mapped using remote sensing techniques or field observations.

The relative spatial distribution of forests and trees varies, because of changing land use practices, differences in the fertility of soil, and the hydrology,

and size distribution of trees. It is well known that the spatial distribution of seedlings in stands of natural generation depends highly on the location of mother trees and soil preparation affects the probability of survival of seedlings. Spatial information is used in forest inventory planning, and the construction of growth models and problems relating to forest regeneration and thinning. For example, the predictors of a spatial growth model for drained peatlands normally include variables such as the distance between the tree and the nearest ditch. The optimal sampling design of forest inventory can be defined if a spatial pattern of large variation is known and the size of a sample unit can be determined when the probability of tree occurrence can be modeled. Different indices and techniques have traditionally been applied to seedling surveys, in order to find out if the spatial distribution of seedling and saplings is regular. In addition, the effectivity of thinning and stand growth estimates depends highly on spatial regularity.

There are many forestry variables that are spatially sparse and scattered. This is often the case when one is assessing coarse woody debris in managed forests, or surveying threatened species. The spatial description of sparse populations can also be problematic. On the landscape level, information about spatial distribution of different key habitats and areas with a high ecological value has also been used to assess the probability of existing rare species. Field data about indicator species and remote sensing data about landscape features are valuable a priori information for estimating the presence/absence probability and for stratifying areas of interest.

### Spatiality of Trees

The simplest point process model that can be used for the spatial pattern of trees is the Poisson process, which is typically used to produce random Poisson forests and when there is no interaction between the locations of trees. There are several modifications that stem from the basic model, such as the inhomogeneous Poisson processes, the Poisson cluster processes, and the doubly stochastic Poisson processes. The location of seedlings after natural regeneration is often generated using the Poisson cluster processes. Lattice-based processes are suitable models for spatial patterns of trees in plantations. Pair correlation processes produce patterns in which points either 'reject' (regular) or 'attract' (clustered) other trees to each other. Hard-core processes reject other trees with such a high intensity that other trees cannot exist closer than the radius of the core area. The Markov point processes and the Gibbs process