LANDSCAPE ECOLOGY: AN ECLECTIC SCIENCE FOR THE TIMES

Thomas R. Crow[1]

Abstract.--The primary focus in landscape ecology is on spatial (and temporal) patterns and how this heterogeneity affects biotic and abiotic interactions. These interactions vary depending on spatial scale and so problems of scale are an integral part of landscape studies. Principles of landscape ecology are beginning to emerge that should help provide the theoretical and empirical basis for a variety of applied sciences -- including regional planning and natural resource management.

INTRODUCTION

A field of scientific inquiry entitled "landscape ecology" has emerged in recent years that has significance for a variety of applied sciences including regional planning and natural resource management. Still in its infancy, landscape ecology lacks the rigor and definition of a well-established scientific discipline; however, as it matures, its concepts and paradigms will provide a useful theoretical and empirical basis for many resource management decisions.

Landscape ecology can best be considered as the intersection of numerous related disciplines, including ecology, geography, forestry, landscape design, wildlife biology, genetics, and sociology (Risser et al. 1983, Naveh and Lieberman 1984, Forman and Godron 1986, Risser 1987, Urban et al. 1987). It is composed of elements drawn from many sources, an eclectic science, as opposed to being a distinct discipline or simply a branch of ecology. More specifically, landscape ecology focuses primarily on the relationships between spatial and temporal patterns and ecological processes. Landscape patterns have often been described as dynamic mosaics, changing in time and space, and these patterns reflect both human impacts as well as physical features such as climate, physiography, and soils. The redistribution of materials, energy, and organisms among landscape elements in both time and space is an essential feature of landscape ecology.

CHARACTERISTICS OF LANDSCAPES

Patches and corridors, two conspicuous features of the landscape, are critical structural and functional units. The characteristics of these units -- size, shape, width, connectivity -- can be easily quantified (Milne 1988) and incorporated into studies of how the spatial arrangement of forests, bogs, roads, and cities, for example, affects the movement of insect pests, the spread of fire, the colonization of woodlots by animals, or the movement of people.

The grain size of a landscape mosaic is a measure of the average size or patchiness of the landscape. A landscape with fine grain has many small patches, compared with a landscape that has only a few large patches or course grain. Patch size is a major control over the physical and biological characteristics of an individual ecosystem. For many bird species, for example, patch size is an important habitat characteristic (table 1) that affects where a species will occur, and more importantly, whether a patch will support

Table 1.--Minimum size of woodlot that has at least a 50 percent chance of supporting a breeding population (from Temple 1988).

Species	Woodlot Size
Hairy Woodpecker	40 acres
Pileated Woodpecker	240 acres
Acadian Flycatcher	240 acres
Least Flycatcher	160 acres
Tufted Titmouse	80 acres
Blue-gray Gnatcatcher	80 acres
Veery	60 acres
Wood Thrush	20 acres
Yellow-throated Vireo	40 acres
Chestnut-sided Warbler	160 acres
Cerulean Warbler	200 acres
American Redstart	240 acres
Ovenbird	80 acres
Mourning Warbler	160 acres
Hooded Warbler	240 acres
Scarlet Tanager	40 acres

[1]Thomas R. Crow, Research Plant Ecologist, USDA-Forest Service, North Central Forest Experiment Station, Rhinelander, Wisc. 54501

a breeding population. The average woodlot size of only 47 acres in Temple's study area has significant implications for maintaining breeding populations of many species.

Many species require two or more patches to complete their life cycles. Amphibians, for example, need aquatic systems such as small ponds to complete their early larval stage, but spend much of their adult life in the uplands near the pond. The aquatic and terrestrial habitats need to be in close proximity. The use of different-aged stands by ruffed grouse (Bonasa umbellus) has been well documented (Gullion 1977). This species uses mature forests for feeding, intermediate-aged (pole size) stands for breeding, and young regenerating stands for brooding. Again, spatial proximity of these three stand conditions is an important requirement.

Corridors play at least four major functional roles. They act as conduits for the movement of materials and organisms, they act as filters or in some cases as barriers, they provide habitats for edge species, and they act as sources of biological and environmental effects upon adjacent areas (Forman 1986). Width and connectivity are two important structural attributes of corridors that, in turn, affect their functional characteristics. The availability of critical habitat within a patch can be enhanced by connecting similar patches with corridors. In Maryland, forest interior birds were able to maintain themselves in small woodlots when the woodlots were connected to much larger forested areas by corridors (MacClintock et al. 1977).

In the Midwest, fencerows serve as important travel corridors between forest fragments. Small mammals and birds common to the forest are more likely to traverse along the woody cover provided by fencerows than across open agricultural fields (Harris 1984). Influencing the travel patterns of seed-dispersing animal species affects the dispersal of plant species.

Streams, and the riparian zones associated with them, are good examples of corridors. A first-, second-, and third-order stream system forms a dendritic network that links components of the landscape. The various kinds of drainage densities and patterns present form a distinctive imprint that greatly affects the movement of water, nutrients, sediments, and animals within the watershed (Forman 1986). Major river corridors often serve as important flyways for migratory waterfowl and raptors. In areas greatly modified by humans, stream corridors are likely to be the only linkage among remnant patches of natural vegetation.

Edges have always been of interest to ecologists because of the concentration of ecological interactions that occur at the interface between two different ecosystems. It is not unusual to find species from both habitats at the edge along with species that are especially adapted to edge environments. Wildlife managers have always taken a special interest in edges because many important game species are edge species. The abundance of species brings an abundance of biological interactions. Animal activity, including herbivory and predation, is often greater along edges than in patch interiors (Wilcove 1985, Temple 1987). Increased predation along edges is thought to be related to increased prey densities and to the natural travel lanes created by abrupt changes in the vertical structure of vegetation (Reese and Ratti 1988).

In studying the development of an old growth beech-maple forest in Ohio, Whitney and Runkle (1981) concluded that position within the stand had greater impact on overstory composition than did the age of the stand. For example, while northern red oak (Quercus rubra) was abundant along the stand margins, it was virtually absent from the interior of the old growth forest. This conclusion is significant because of the conversion of midwestern forests to small, fragmented woodlots with high edge-to-area ratios.

IMPORTANCE OF SCALE

Problems of scale are important to landscape ecology. The relations between spatial pattern, temporal change, and ecological processes depend largely on scale (Risser et al. 1983, Allen and Hoekstra 1987, Meentemeyer and Box 1987). Ecological processes differ in their effects and importance at different scales, and different species and groups of organisms operate at different scales. The appropriate scales at which to conduct landscape studies depends on the question being asked. Too often, however, the temporal or spatial scale used in a study is based more on the investigators' perceptions than on the organism(s) and ecological process(es) under consideration.

Including variation in both time and space can be challenging when considering landscape patterns. Many population models, for example, assume a homogeneous environment and a uniform distribution of individuals within that environment. Obviously, such simplicity severely restricts the utility of the models; more recently, ecologists have begun to consider population dynamics in heterogeneous environments (e.g., Wiens 1976, Levin 1976, Seagle and Shugart 1985, Lande 1987). In addition to linking time and space, landscape studies are likely to require shifting across several spatial and/or temporal scales. Because biological systems are hierarchical organizations, hierarchy theory offers some promising ideas for addressing complex biological questions at different scales (Allen and Starr 1982, Allen et al. 1984, Allen and Hoekstra 1987). The science of scale needs to develop in concert with landscape ecology, and much additional work remains in both areas. However, any general principles developed for landscapes will have to apply at all relevant spatial and temporal scales.

APPLYING LANDSCAPE ECOLOGY TO MANAGEMENT - EXAMPLES

Landscape ecology, with its emphasis on spatial and temporal heterogeneity, provides a useful context for studying problems related to conserving biological diversity. There is increased recognition that human activities are inextricably linked to the accelerating loss of biological diversity (Myers 1979, Wilson 1985, 1988). Although direct impacts, such as the loss of species due to overexploitation, are a factor in some cases, indirect impacts such as habitat destruction are more important for most endangered species. Habitat destruction not only involves the loss of the original habitat, but even more insidious, it also increases the isolation of populations that required the original habitat. This process of fragmentation is common to growing societies where once large blocks of contiguous habitat are repeatedly divided into smaller and smaller blocks and separated by urban, agricultural, and industrial developments, and their accompanying infrastructures (e.g., roads, utility rights-of-way). Under these land-use patterns, opportunistic species that benefit from disturbance will prosper. These are often exotic "weed" species such as the introduced European starling (Sturnus vulgaris) or edge species such as the blue jay (Cyanocitta cristata) or raccoon (Procyon lotor) that adapt well to fragmented landscapes. In turn, area-sensitive species that require large tracts of habitat decline or even become locally extinct.

Changing landscape patterns between 1939 and 1974 on a 1,117 ha tract in southeastern Illinois resulted in the extirpation of prairie chickens (Tympanuchus pinnatus) from the area in 1969 and substantial declines in bobwhite (Colinus virginianus) and cottontail (Sylvilagus floridanus) populations (Vance 1976). Rapid intensification of cash-grain farming during that time eliminated grasslands and reduced woody cover along fencerows and in woodlots. Because prairie chickens require extensive grasslands, it is not surprising that the major factor limiting prairie chicken populations in Illinois and elsewhere is the lack of suitable grasslands for nesting. The loss of brushy fencerows was especially detrimental to bobwhite and cottontails (Vance 1976).

Pest management can be improved by understanding how landscape patterns affect pest movements and rates of infestations. In general, landscape homogeneity increases the spread of pests. Certainly this is true with agricultural systems, and examples can be also found in natural systems. Fire suppression in western conifers increases forest homogenization and forest maturity, and large stands of mature timber increase the frequency, intensity, and rate of spread of bark beetle infestations (Forman 1987).

Landscape patterns can significantly affect the potential for major forest disturbances. For example, forest cutting patterns and cutting intensities greatly affect susceptibility to windthrow. Franklin and Forman (1987) found the checkerboard cutting pattern commonly applied to Douglas fir forests in the Pacific Northwest greatly increased the frequency and severity of blowdown. Such a cutting pattern increases the contrast between adjacent units, increases the amount of exposed edges in the landscape, and isolates forest patches in cutover areas. Windthrow occurs most frequenly along exposed edges and at the corners of the residual blocks (Franklin and Forman 1987).

Road densities are a measure of landscape "mesh" and road densities have been shown to be an important landscape feature related to the distribution of the timber wolf (Canis lupus) in Wisconsin (Thiel 1985), Ontario (Jensen et al. 1986), and Minnesota (Mech et al. 1988). Wolves in the Great Lakes regions generally do not occur where densities of roads passable by 2-wheel-drive vehicles exceed 0.58 km/km^2. Roads themselves do not inhibit colonization by wolves; instead, human contact is the critical factor. Roads provide accessibility for humans, and humans, either deliberately or accidentally, kill wolves (Mech et al. 1988).

METHODOLOGIES FOR LANDSCAPE ECOLOGY

Techniques and methods currently used in resource management and research can also be used in landscape ecology. Computers, mathematical models, geographic information systems, data-base management, remote sensing, and radiotracking are some of the practical tools available to landscape ecologists.

New methodologies are being applied as well. The development of fractual geometry has made it possible to quantify complex boundaries and patch shapes (Mandelbrot 1983, Milne 1988). Indices are also available for quantifying the degree of connectivity among landscape components (e.g., Pielou 1979).

SUMMARY

Resource managers and planners increasingly recognize that informed management decisions cannot be made exclusively at the site or stand levels. The opportunities associated with a particular management unit are not only determined by the content of that unit, but also to a great extent by the context in which the unit exists. Regardless if the primary management object is producing timber, creating suitable habitats for common game species, protecting a watershed, or providing a wilderness experience, assessing these opportunities requires considerations that extend beyond the boundaries of the specific management unit. An increased emphasis on regional analyses requires a landscape perspective (Joyce et al. 1983, Evans 1986).

Although a landscape perspective is not unique to landscape ecology, (a landscape

perspective has been frequently embodied in many early writings in ecology, natural history, and wildlife biology, e.g., Leopold's Sand Country Almanac), the eclectic character of landscape ecology is unique and provides a potentially useful framework for many fundamental problems in resource management. While a theoretical base for landscape ecology is only beginning to emerge, the application of that theory is likely to soon follow. Indeed, incorporating spatial (and temporal) considerations into resource planning and management remains one of the greatest challenges facing our profession.

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