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SPATIAL CHARACTERISTICS
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LOWER MICHIGAN'S FOREST PATCHES:
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By

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ABSTRACT

LOWER MICHIGAN'S FOREST PATCHES: SPATIAL CHARACTERISTICS AND ECOLOGICAL IMPLICATIONS

BY

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Forest fragmentation in Lower Michigan is the result of patchwork conversion and development of the most accessible and/or productive land. The purpose of this study was primarily to describe the structure of Lower Michigan's forest patches with respect to natural and human-induced landscape processes. Forest patches within seven townships were digitized from topographic maps using C-Map; ERDAS (GIS) was used in data analysis. Size and shape of forest patches are related to topography, patterns of soil fertility and human activities. Fractal analyses and complexity ratios reveal that riparian forests and wetlands have highly irregular edges compared to upland patches. About 62% of all upland patches studied can potentially sustain a near full complement of all plant species found in a mixed deciduous forest. There was a net increase in forestland between 1938 and 1976. More patches within the seven townships are considered to be isolated for *Acer saccharum* compared with *Quercus* spp..

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INTRODUCTION

Lower Michigan was largely a region of deciduous forest at the time of European settlement (Braun, 1950). The presettlement forest was diverse. Yellow birch and hemlock were major components in the Upper Peninsula while the Lower Peninsula was predominantly covered by beech, maple and various pines and oak species. Today, the Upper Peninsula and the northern part of the Lower Peninsula lie within the hemlock-white pine-northern hardwoods region whereas beech-maple and oak-hickory are the dominant species association found in southern Lower Michigan (Braun, 1950; Kuchler, 1964).

Like other parts of the United States, the landscape of Michigan has received both intensive anthropogenic and natural impact. Furthermore, the climate has been changing in a continuous manner since the recession of Wisconsin glaciers. Years of burning have converted the mixed pine forests on sandy soils and mixed hardwood stands on heavier loamy soils to stands of oak sprouts, aspen suckers, white birch, second-growth maple and pine plantations (Whitney, 1987).

Selective logging in Lower Michigan, which began in the mid-19th century (Denton and Barnes, 1987), caused most of the white pine-hemlock-northern hardwoods forests to be replaced by sugar maple (Whitney, 1987). All these disturbances have created a new set of shifting mosaic conditions for some 53% of Michigan's landscape characterized by vegetation under the influence of natural processes and that has not been converted to other land-uses (Klopatek et al., 1979; Whitney, 1987).

The forests of Lower Michigan, which are part of the Eastern Deciduous Forest Biome (Auclair, 1976), have now largely been reduced to fragments. Forest fragmentation in Lower Michigan can be seen as the result of patchwork conversion and development of the most accessible and/or more productive sites to urban areas, cropland and pastures (Whitney, 1987).

The fragmented landscape can thus be characterized by recognizable and repeated groups of ecosystems and disturbance regimes which are simply known as patches (Forman and Godron, 1981, 1986). The "patch" has been a central focus in landscape ecology because it can be visualized as a structural attribute of landscapes. It is highly identifiable because the components that make up a patch are each spatially autocorrelated with one another and are surrounded by a matrix that consists of a community structure or composition that is dissimilar from that of a patch (Forman and Godron, 1986; Risser, 1987). The matrix is characterized by its heterogeneity and degree of connectivity. Previous landscape studies have focused on three important characteristics: structure (Hoover, 1986;

Gardner et al., 1987; Turner, 1987a); function (Wegner and Merriam, 1979; Forman, 1982; Harris, 1984; Gardner et al., 1987); and change (Delcourt and Delcourt, 1987; Turner, 1987a; Turner and Ruscher, 1988; Iverson, 1988; Swanson et al., 1988; Baker, 1989).

In this study, I will focus on structure, in particular on patch distribution, size, number, configuration and kind. The relevance of these structural features to the distribution, movement and persistance of plant and animal species will be examined. Forest patches in the landscape have been found to take on characteristics of habitat islands in proportion to their degree and length of time of isolation. Habitat islands play an important role as stepping stones, corridors or reservoirs in human-populated landscapes (Davis and Glick, 1978; Harris, 1984, 1988).

It is also known that habitat fragmentation leads fundamentally to two consequences (Wilcove et al., 1986). First, a reduction in total habitat area and second, a redistribution of the remaining area into disjunct fragments. These two occurrences can influence a number of ecological phenomena, such as, species extinction (Wilcove et al., 1986); species diversity (Johnson and Raven, 1970; Parsons and Cameron, 1974; Harris, 1984; Wilcox and Murphy, 1985); species richness (van Balgooy, 1969; Davis and Glick, 1978; Dickman, 1987; Hobbs, 1988); turnover rates of bird species (Wright, 1985); species composition, rates and patterns of succession (Sharpe et al., 1981); animal emigration (Stamps et al., 1987) and immigration (Wegner and Merriam, 1979; Darley-Hill and Johnson, 1981; Harris, 1988); and immigration of plant species (Darley-Hill and Johnson, 1981; Wilcox and Murphy, 1985; Johnson and Adkisson, 1985; Hill, 1985; Davis et al., 1986; Johnson, 1988).

The increasing fragmentation of the forest has also been accompanied by an increase in the edge-to-area ratio of remaining woodlots. This results in a loss of interior species (Davis and Glick, 1978) and an increase in weedy species (Levenson, 1981; Ranney et al., 1981; Whitney and Runkle, 1981; Harris, 1988). This in turn can lead to a decrease in migratory bird species that require interior plant species of a forest patch (Whitcomb, 1977).

As shown by these studies, an understanding of the ecology and structure of patches is vital because so much is affected by human-induced changes in the landscape. Several studies on landscape fragmentation (Levenson, 1981; Harris, 1984, 1988; Hill, 1985; Whitney and Somerlot, 1985; Sharpe et al., 1986; Wilcove et al., 1986; Bennett, 1990) and landscape pattern (Bowen, 1981; Gardner et al., 1987; Krummel et al., 1987; Iverson, 1988; O'Neill et al., 1988; Turner and Ruscher, 1988; Turner, 1989, 1990; Pastor and Broschart, 1990) have been carried out in different parts of the United States. Quantification of patch structure has been carried out in Ohio (Bowen 1981) and Georgia

(Hoover 1986). To date, no study has yet documented the patch structure of the fragmented landscape in Lower Michigan.

The primary purpose of this study is to describe the characteristics of Lower Michigan's forest patches with respect to natural and human-induced landscape processes through the application of geographical information system (GIS) techniques. The information obtained is compared with that of other regions for which there are data, and will be used to make a preliminary assessment of the overall adequacy of Michigan's landscape to support indigenous populations of plants and animals. Issues relating to the presence or absence of suitable dispersal pathways for key forest tree species are also considered.

The study involves two scales of investigation. The first, a micro-scale analysis of forest patches within two transects, is a sample of patches in the landscape (Goals 1 through 6) and the second, is a macro-scale analysis of statewide data sets for Michigan (Goal 7). The specific goals of this study are as follows:

1. determine the types of forest patches (i.e. composition) in the landscape of central Lower Michigan;
2. quantify forest patch characteristics such as number, size and geometry;
3. determine whether relationships exist between patch

size and geometry and human population density of nearby areas;

4. determine the co-occurrence of forest patches and preferred agricultural soil types;
5. determine whether a change in number and size of forest patches found on prime farmland soil types has occurred over the past 26-38 years;
6. review pertinent literature on minimum areas for plant and animal species and assess the overall adequacy of Lower Michigan's landscape in supporting indigenous populations of plant and animal species; and
7. evaluate the presence or absence of suitable dispersal pathways for key forest tree species, such as sugar maple (_Acer saccharum_) and oak (_Quercus_ spp.), based on present forest cover and soil texture.

LITERATURE REVIEW

This review describes the role of landscape ecology in the study of landscape pattern and processes. The main focus of this review is on the characterization of landscape patterns and their effects on ecological processes such as dispersal of plant and animal species. Advancing computer technology has made large scale spatial and temporal studies feasible. This is especially beneficial to studies that involve the manipulation of voluminous databases such as in landscape ecology.

Landscape ecology

Landscape ecology can be described as the study of the earth's heterogeneous land area and its clusters of interacting ecosystems that are repeated throughout the whole landscape. Landscapes are usually on the order of kilometers in size. Landscape ecology is an emerging new sub-discipline and emphasizes broad scale spatial patterning of ecosystems and the ecological effects of the patterns (Risser et al., 1983; Naveh and Lieberman, 1984; Forman and Godron, 1986; Zonneveld, 1990). The concept of landscape ecology in Europe dates back to the 1930's when Carl Troll, a geologist and ecologist, defined landscape ecology as the study of the relationship between biotic and abiotic factors that prevail in specific spatial units in the landscape (Schreiber, 1990). In North America, the focus has been mainly on trying to attain a balance between theory and application (Forman, 1990).

Landscape ecology emphasizes 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 (Forman and Godron, 1981, 1986; Risser et al., 1983; Naveh and Lieberman, 1984; Turner, 1987b).

Three landscape characteristics that are central in many studies are structure, function and change. The structural approach to landscape ecology elucidates how species, energy and materials are distributed in relation to the sizes, shapes, numbers, kinds and configuration of the ecosystems or landscape elements present. The functional approach on the other hand builds on the structure and investigates the interactions among the landscape elements, that is, the flows of species and materials between adjacent ecosystems or through the mosaic of ecosystems in the landscape. Interactions between two separated patches of the same community type or between connected patch and corridor, may have diverse fluxes in both directions (Forman, 1982, 1988; Iverson et al., 1989).

The dynamic or change approach focuses on the alteration in structure and function of the ecological mosaic over time. Geographic information systems and satellite image technology, as well as quantitative modeling, have contributed significantly in this aspect (Forman, 1982, 1988; Iverson et al., 1989).

Consideration of scale in landscape ecology

Extrapolation of fine-scale measurements for the analysis of broad-scale phenomena is often carried out in ecological studies, including those at the landscape level. The scale dependency of structure, function and change in a heterogeneous landscape has been pointed out by Meentemeyer and Box (1987); Turner (1989, 1990); Gosz and Sharpe (1989); and Turner et al. (1989a, b). This suggests that measurements of spatial patterns made at one scale cannot necessarily be translated to another because processes and parameters important at one scale may not be as important and predictive at another scale (Gardner et al., 1987; Turner 1989). However, it may be possible to predict or correct for the loss of information with changes in spatial scale if the relationship between ecological measurements and the finest spatial and temporal resolution available in a given data set is characterized (Turner et al., 1989a, b).

Characterization of landscape structure

The spatial landscape pattern observed is the result of complex interactions among physical, biotic and social factors. The basic elements in landscapes include patches, corridors and matrix. Although there are different types of patches produced by different causal mechanisms, remnant patches seem to predominate. This type of patch is caused by widespread disturbance surrounding a small area (patch). It is a remnant of the previous community embedded in a matrix that has been disturbed. Examples of remnant patches are woodlots in an agricultural area. These patches vary from being short-lived, as produced by a single natural or human disturbance followed by recovery around the patch, to long-lived, resulting from chronic human disturbances. Remnant patches occur in various sizes, shapes and degree of isolation (Forman and Godron, 1981, 1986). Rex and Malanson (1990) found that human impact is more significant in its effects on the shape of remnant forest patches than on other characteristics. Size, shape and nature of the edge are important patch characteristics. The functions of corridors are affected by their width, connectivity, breaks, narrows and curvilinearity. The matrix is the most extensive and connected landscape element type and it plays a predominant role in the landscape (Forman and Godron, 1986).

Landscape structure must be quantified in meaningful ways before the interactions between landscape patterns and ecological processes can be understood. Bowen (1981) quantitatively described forest island structure and the distribution patterns of forest islands in the landscape of Ohio. The forest island structures of landscapes in Georgia were examined quantitatively across a continuum of physiographic factors by Hoover (1986).

Shapes and boundaries have been quantified using fractals. Fractals as defined by Mandelbrot (1977), are "a set of objects for which the Hausdorff-Besicovitch dimension strictly exceeds the topological or Euclidean dimension." A fractal also refers to an object that has irregular edges or boundaries (Mandelbrot, 1977; Burrough, 1986). Fractals have been used to compare the geometry of different landscape elements (Gardner et al., 1987; Krummel et al., 1987; Milne, 1988; O'Neill et al., 1988; Turner and Ruscher, 1988). Studies of Krummel et al. (1987), Iverson (1988), and O'Neill et al. (1988) have suggested that natural disturbances caused an increase in landscape complexity while anthropogenic disturbances produced patches that were simpler in shape.

Patch size and arrangement may also reflect environmental factors, such as topography or soil type. Small patches of forest have also been studied as biogeographic islands for both flora and fauna (Burgess and Sharpe, 1981; Bowen, 1981; Whitney and Somerlot, 1985;

Harris 1988). Franklin and Forman (1987) have shown that forest-clearing patterns cause changes in patch structure. This change can potentially affect the persistance of interior and edge species.

Other measures of spatial pattern that have been applied in the analysis of landscape pattern include relative richness, relative evenness and relative patchiness (Romme, 1982); diversity, dominance and contagion (O'Neill et al., 1988); and the width of edges or transitional zones between adjacent land cover types (Gardner et al., 1987; Turner, 1987a; Turner and Ruscher, 1988).

Effects of changes in landscape structure on ecological parameters

Fragmentation in forested landscapes often leaves forest patches of relatively small size which are distributed as disjunct fragments. These patches exist in a matrix that has been culturally modified (Burgess and Sharpe, 1981; Noss, 1983; Sharpe et al., 1986; Delcourt and Delcourt, 1988; Gibson et al., 1988) and can be portrayed as habitat islands (Burgess and Sharpe, 1981; Levenson, 1981).

According to the equilibrium theory of island biogeography (MacArthur and Wilson, 1967), a reduction in size of habitat islands will cause a reduction in habitat heterogeneity within a patch. Conversely, an increase in forest area can lead to an increase in environmental heterogeneity and, consequently, number of species. This is true for breeding bird species where the number appears to double for every 7.25-fold increase in area. Disjunct forest patches of 30 ha do not support a large proportion of bird species characteristic of the Northern Florida hardwood forest (Harris, 1984). A patch of 3.8 ha was found to be the smallest size at which a mature southern mesic forest can perpetuate its interior conditions while sustaining limited random perturbations in Wisconsin (Levenson, 1981). Loss of habitat area has threatened the existence and caused the extirpation of some plant species in Michigan such as the netted chain fern and green trillium (Michigan Endangered, Threatened and Special Concern Plant and Animal Species, 1987).

Forest patch size has been a focus of study because it is an environmental determinant of species diversity, as are patch isolation and age (Preston, 1960; Kilburn, 1966, MacArthur and Wilson, 1967; Johnson et al., 1968; van Balgooy, 1969; Johnson and Raven, 1970; Werger, 1972). Relationships among areas of different sizes and the number of species found in those areas have been demonstrated using species-area curves. A species-area curve may be used to determine minimum area of a community type, defined by Braun-Blanquet (1938) as "the smallest area which can contain an adequate representation of an association." The minimum area is indicated at the point where the curve flattens strongly and tends to become asymptotic with the x-axis. This information is important as it gives an idea to the size of a patch that can sustain a near full complement of species. Du Rietz, later defined minimum area of a plant community as the point where the constancy-area curve became approximately horizontal. The constant represented a species of frequency 90% or more (Hopkins, 1956). There is still yet to be an agreement or consensus on one criterion whereby the minimum area can be determined objectively.

Vestal's (1949) published minimum areas for different vegetation ty es of the world will be used as a reference in this study. According to Vestal, the minimum area is "the minimum statement of composition with approximate ranking of species as to a number of trees and as to some measure of bulk or of ground space occupied." Two points were determined on the species-log area curve so that the ratio of their number of species was 1:2 and their areas 1:50. The former represented the smallest representative area while the latter, the fair-sized stand. The fair-sized stand is 50 times the smallest representative area or 10 times the minimum area. The minimum area is then expressed as five times the smallest representative area and consists 1.5 times the number of species present within the smallest representative area (Vestal, 1945).

The concept of minimum area has been used to help design nature reserves or conservation areas, where viable tracts of forest which are of sufficient size to allow regenerative processes of both plant and animal species to continue, can be maintained (Vestal, 1949; Simberloff and Abele, 1976; Pickett and Thompson, 1978; Harris, 1988). This is important because populations that have been reduced in size or subdivided are more vulnerable to extinction (Wilcox and Murphy, 1985). The minimum dynamic area of a reserve can be defined by the most extinction-prone taxon (Pickett and Thompson, 1978). Larger reserves, or reserves located close to other reserves, can hold more species (Diamond, 1975; Moore and Hooper, 1975; Wilson and Willis, 1975).

Patch shape as a patch characteristic, indirectly describes the amount of edge-to-area for a patch. Shape affects dispersal or home range suitability (Ranney and Johnson, 1977), immigration rates of animal species (Game, 1980) and can alter the connectivity within the patch. A circle, for example, has all points within a minimum distance (Rex and Malanson, 1990). Edge permeability, as a patch characteristic reflects the tendency of a disperser reaching the edge of a habitat patch to cross the boundary and emigrate. Edge permeability and edge-to-size ratios have been shown to relate positively to emigration (Stamps et al., 1987). Some wildlife species require more edge habitat than others. Since community and population characteristics differ between the edge and interior, comparing these characteristics with the interior-to-edge ratio of patches may be useful in evaluating the importance of patch shape in a landscape. Understanding how the geometric shape and size of patches are related to natural and human processes can help in determining the appropriate spatial scales to use in studying ecological systems (Wilson and Willis, 1975; Loehle, 1983).

Fragmentation often leads to an increase in interpatch distance. When this occurs, distance between patches will pose a barrier to species migration and can cause higher rates of extinction and a reduction in species richness (MacArthur and Wilson, 1967; Davis and Glick, 1978; Burgess and Sharpe, 1981;). Isolation among forest patches has caused a loss in bird species from Barro Colorado Island, Panama (Willis, 1974), extinction of some bird species in Connecticut (Butcher et al., 1981) and a decrease in neotropical migratory birds that were dominant in forest interiors in Maryland (Whitcomb, 1977). A distance of 500 m or more between forest patches has caused a decline in the number of wind-dispersed plant species (Hill, 1985), while roads greater than 20 m in width have deterred small mammals from venturing across them (Oxley et al., 1974). Isolation may also cause the increased restriction and isolation of large, wide-ranging species such as the black bear (Ursus americanus) (Harris, 1988); loss of genetic integrity and viability within the species (Harris, 1988, 1989); loss of forest interior species (e.g. birds that depend on a specific size of habitat area for breeding success and existence) (Harris, 1988, 1989; Robbins et al., 1989); and an increase in disturbance-prone species such as raccoon (Procyon lotor) or opossum (Didelphus virgiana) (Harris 1988a), and intolerant plant genera (Quercus and Carya) associated with the open habitat of forest edges (Whitney and Somerlot, 1985).

Animal immigration may be impeded by conversion of natural habitat between patches. Wilcox and Murphy (1985) have shown that mammalian species-richness within patches has decreased with an increase in percent of barren ground per patch, with proximity to buildings and with patchiness in the total vegetation cover. But species-richness has increased with increasing density of vegetation in the layer 25-50 cm aboveground (Wilcox and Murphy, 1985). Beech and sugar maple, with low degree of mobility (Davis and Zabinski, in press; Johnson, 1988) were found to be the last to invade isolated secondary woodlots in northern Ohio following deforestation in the 19th century (Whitney and Somerlot, 1985). For some species, an expansive clearcut or a second-growth forest may be a barrier (Harris, 1984). This suggests that the value of a patch of habitat is dependent not only upon its structural characteristics, but also the matrix within which it occurs.

Interpatch distances can be reduced either by increasing the effective size of individual patches or by increasing their numbers. These two factors enable patches to be linked with corridors or have a higher degree of connectiveness which enhances dispersal and immigration of species, genetic interchange (especially in small breeding populations), and increases stability of patch populations and whole landscapes (Forman and Godron, 1981; Forman, 1982; Middleton and Merriam, 1983; Merriam, 1984; Noss and Harris, 1989; Bennett, 1990). Smaller patches need to be identified and located, so that they can serve as "stepping stone" islands, corridors or reservoirs between the larger centers of dispersal (Diamond, 1975; Diamond and May, 1976; Forman et al., 1976; Davis and Glick, 1978; Harris, 1984).

Corridors and forest patches are both habitat and transition pathways for both plant and animal species (Wegner and Merriam, 1979; Forman, 1982; Forman and Godron, 1986; Schrieber, 1987; van Dorp and Opdam, 1987; Harris, 1988). Forested corridors or stepping stones have been shown to encourage dispersal of interrelated species between forest islands (Willis, 1974; Diamond, 1975; Butcher et al., 1981; Bennett, 1990; Dmowski and Kozakiewiez, 1990. MacClintock et al. (1977) demonstrated the value of connectivity in the fragmented landscape for preservation of biotic diversity. Quality of corridors have been shown to affect the demographics of populations (Kringen and Merriam, 1990; Verboom and van Apeldoorn, 1990). This brief overview shows that landscape structure and pattern does have an influence on the dispersal of species across the landscape and upon the maintenance of biodiversity.

Dispersal of plant and animal species

Dispersal is a mechanism that increases the range, survival and persistance of a species. Dispersal of seeds limits the disproportionate seed and seedling mortality near the parent but increases the chance for seeds to encounter favorable site conditions or remain in the soil or understory until a suitable environment exists for germination and establishment. There have been attempts to study dispersal but most have encountered conceptual and methodological difficulties in sorting out advantages to dispersal modes and processes (Howe and Smallwood, 1982). Seed production depends on the maturity and vigor of the source trees, and the environmental conditions (Baldwin, 1942). The quantity of seeds dispersed to a given distance from a source is dependent upon the seed contribution of source plants at their respective distances from the target point. Small patches tend to have higher edge-to-interior ratios, thus increasing the opportunity for more seeds to be dispersed away from the edge of the patch to the surrounding area.

If the seeds are animal-dispersed, the factors that affect faunal vectors are important, such as attractiveness of forest patches as faunal food sources, and habitat modification through time and space caused by natural or human-induced disturbance to the forest. These factors will indirectly influence propagule germination and survival. Wind-dispersed seeds such as those of maple and birch are able to disperse up to 500 m. Relatively few wind-dispersed species are able to disperse greater than 500 m (van der Pijl, 1972). Dispersal distances of sugar maple derived from models range from 110 m to 400 m in the direction of prevailing winds (Sharpe et al., 1981). In stormy conditions, maple and birch seeds can disperse 4 km and 1.6 km, respectively (van der Pijl, 1972). Heavy-seeded trees such as beech and oaks depend on animals, including blue jays, as dispersal vectors. Blue jays can transport beech nuts up to 4 km (Johnson and Adkisson, 1985) and acorns to 1.1 km (Darley-Hill and Johnson, 1981).

Migration rates based on paleobotanical studies have been increasingly used to predict the ability of various taxa to shift distribution in the face of possible global climate change. Climatic fluctuations can be considered as a disturbance regime at the meso-scale that can affect species migration (Delcourt and Delcourt, 1987).

A warming trend, as part of global climatic change, would have severe implications for the forests. It is expected that global temperatures will increase between 2° and 5°C in the next century and each 1°C rise in temperature translates into a range shift of between 100 and 150 kilometers (Roberts, 1989; Davis, 1990; Peters, 1990). Average rates of Holocene range extensions in eastern North America estimated by Davis (1981) show that oak migrates on average 350 m yr^{-1}, beech 200 m yr^{-1} and maple 200 m yr^{-1}. These estimates are based on fossil pollen in sediments and they reflect vegetation responses to climatic changes during the post-glacial periods. Fossil records show that trees can migrate long distances but if global climatic change is unusually rapid, these species would have to migrate at a faster rate. The reestablishment of forests requires the availability of seeds and other propagules that may not disperse rapidly enough to keep up with climatic change (Woodwell, 1986). Davis (1989) predicts that the ranges of tree species will shift northward approximately 100 kilometers per °C warming while southern populations are eliminated. The rate of change in global average temperature for a middle scenario has been estimated to be 3°C per century (Jaeger, 1988). With this in mind, projections by Davis (1990) show that tree species would need to extend their ranges 300 km per century, an order of magnitude faster than the documented range expansion for trees within a century. The risk of warming faced by tree species depends on the distances that regions of suitable climate are displaced northward and also the rate of displacement. The current spatial distribution and abundance of a species is expected to influence its ability to migrate successfully to regions of suitable climate and soils (Peters and Darling, 1985; Graham et al., 1990).

Davis and Zabinski (in press) suggest that many species may not be able to track climate change rapidly enough, resulting in reductions in geographical range and population sizes. Disjunct colonies in the fragmented landscape can exacerbate the situation when distance becomes a barrier to migration (Davis, 1989). Therefore, it is important to preserve extant forest patches so that they can be seed sources serving to revegetate the surrounding landscape. Understory herbs may be affected more than overtory species as they may not be able to disperse rapidly enough to track climate (Davis, 1990). It has also been predicted that mature natural forest could be reduced in area by 25-50% in the Great Lakes region and New England and that there will be more grassland or scrub growth on poorer sites which are not suitable for tree growth (Winjum and Neilson, 1989). The warming trends may cause droughts that can lead to a reduction in timber production in present forested areas (Winjum and Neilson, 1989). Clearly, changes in the structure and pattern of the heterogeneous landscape may affect species movement and persistance and, consequently, biological diversity. The study of structure and pattern of the fragmented landscape is therefore important and pertinent.

Applications of GIS techniques in landscape ecology

Recent emphasis on large scale data acquisition over a long span of time has coincided with the development of geographical information systems (GIS). GIS is a set of computer hardware and software designed for analyzing and displaying referenced features such as points, lines and polygons with their attributes (Burrough, 1986).

GIS enables the manipulation and analysis of spatially-distributed data. Information can be stored either in a raster or vector database. The former approach stores all mapped, spatial information in the form of a regular grid cell, whereas the latter stores information described by lines and polygons, expressing magnitude, direction and connectivity. The data layers can be synthesized automatically and a spatial database can be updated from time to time (Berry, 1987; Cowen, 1988). One of the functions of GIS and/or databases includes reclassification of polygon or area attributes. Areal measurements are standard output in any type of GIS and are an essential component of an ecological database. Size of patches within a landscape can be obtained from GIS data in both the raster and vector format. The areal data can be expressed in either the original unit or as a proportion of the total landscape. Perimeters of patches can also be measured and the area-to-perimeter ratio has been used to relate forest and landscape patch shape to substrate type and disturbance (Krummel et al., 1987; Iverson, 1988; O'Neill et al., 1988; Pastor and Broschart, 1990).

Number, type and diversity of forest patches have been determined using GIS capabilities (Turner, 1987a, 1990; Iverson, 1988; Turner and Ruscher, 1988; Johnston and Naiman, 1990; Pastor and Broschart, 1990). Area and measures of length of frequency derived from a GIS are being used in spatial studies such as percolation theory

(O'Neill et al., 1988) and neutral models (Gardner et al., 1987). Patch variables such as habitat composition, spatial arrangement and human use have been incorporated in wildlife habitat models and studies (Donovan et al., 1987).

One of the capabilities of GIS is the ability to synthesize information from the overlay of spatially distributed data. The purposes of doing so are to merge separate spatial databases, analyze spatial intersections between data layers or to analyze temporal changes. An example of the analysis of spatial interactions among data is a study carried out by Pastor and Broschart (1990) where the distribution of hemlock and hardwood species in an old growth forest was mapped and analyzed with respect to soil types, topographic slope and aspect, and landscape features such as bogs and lakes. Other studies demonstrated temporal change with emphasis on the effects of anthropogenic and natural processes (Turner and Ruscher, 1988, Turner, 1990) and as correlation with physiographic provinces (Turner and Ruscher, 1988) and soil associations (Iverson, 1988).

Proximity or neighborhood analyses were used to examine spatial interrelationships in a horizontal plane; quantify inter- and intraspecific relationships by examining the selective juxtaposition of hemlock and hardwood tree species (Pastor and Broschart, 1990); determine contiguity of landscape patches (O'Neill et al., 1988; Turner and Ruscher, 1988; Pastor and Broschart, 1990;

Turner, 1990) and to predict susceptibility and/or results of disturbance in the landscape (Gardner et al., 1987). The challenge faced by ecologists is to explore the capabilities of GIS in spatial analyses and the development of simulation studies and models.

MATERIALS AND METHODS

The landscape plays a central role where a dynamic relationship between two characteristics exists - natural landforms, or physiographic regions, and human cultural groups. An objective of this study is to describe the structure of Lower Michigan's forested landscape with emphasis on the nature of the forest patches and their role in the overall landscape.

The study involved two scales of investigation: a micro-scale level analysis of forest patches within Ingham and Clinton Counties of central Lower Michigan, and a macro-scale level analysis of statewide data sets of Michigan.

Micro-scale features

Study area

The study area consisted of two transects situated north and south of the city of Lansing. The north transect encompassed an area of 413.76 km^2 (latitude 42°45′N to 43°7′30″)while the south transect was 492.18 km^2 (latitude 42°15′N to 42°40′N). The width of both transects was 10.3 km (Figure 1).

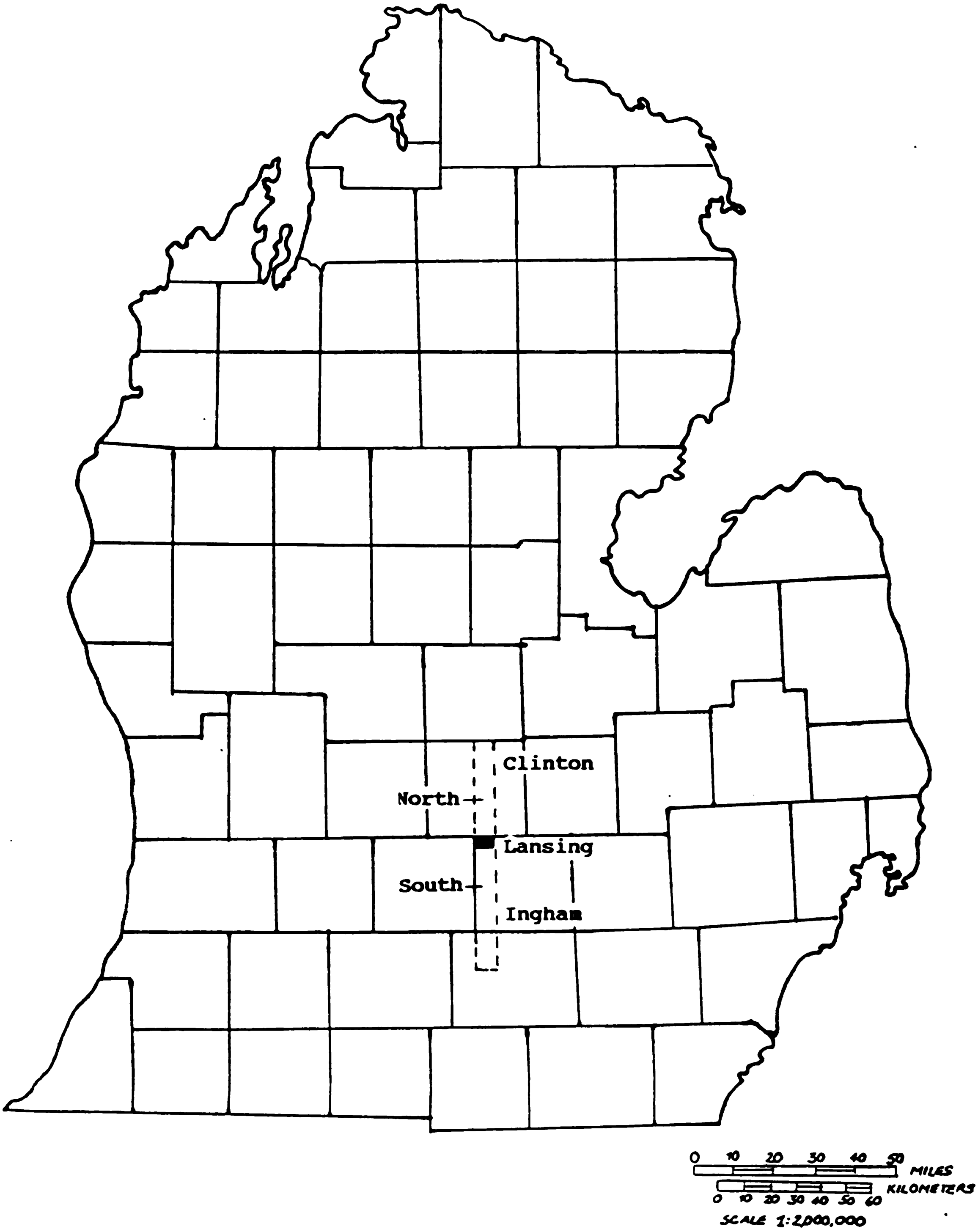

Figure 1 : Location of north and south transects in Clinton and Ingham Counties, Lower Michigan

Only 2 transects in south-central Michigan were used in this study because this was a pilot project on landscape ecology in Michigan and the main emphasis of the study was to develop and utilize Geographic Information System techniques in answering ecological questions. As the acquisition of data through manual digitizing proceeded, it became apparent that time was a constraining factor in being able to include more transects in other locations in the landscape of Michigan as part of the study. It took at least 100 hours to digitize and process the forest patches before analyses could be carried out on them. Therefore, the micro-scale analysis in this study only involved 2 transects.

The south-central part of Michigan experiences a temperate-continental climate in which the summers are humid and hot but winters are cold (Trewartha, 1968). Mean annual temperature for this area ranges from 8 to 9°C (47-48°F). The length of the annual growing season is about 146 days. The area receives an average of 762 to 787 mm (30-31 in) of rain annually; snowfall averages 762 to 1016 mm (Dodge, 1984; Albert et al., 1986).

Beech-maple and oak-hickory forest associations are the dominant vegetation of the two counties. The present day landforms are the result of glacial activity and consist mostly of moraines, till plains and outwash plains (Albert et al., 1986).

Primary data source

The locations of forest patches were taken directly from United States Geological Survey (U.S.G.S.) topographic quadrangles (7.5 minute series, 1:24,000). These maps, published between 1973 and 1981, were based on black and white aerial photographs taken in 1964 and 1976 (1:20,000; United States Department of Agriculture, Agricultural Stabilization and Conservation Service (U.S.D.A. ASCS)) (Table 1). U.S.G.S mapping criteria designate a woodland on these maps if the crown cover for vegetation is > 20% (Thompson, 1987). Hence, for the purpose of description and classification, a woodland or forest patch is an uncultivated area that is covered with vegetation (Thompson, 1987) and situated within a matrix of agricultural or urban land uses.

Table 1. Data sources for this study

U.S.G.S. topographic quadrangles	Date published	Compiled from aerial photographs taken in year
St. Johns North	1973	1964
St. Johns South	1973	1964
Lansing North	1973	1964
Lansing South	1973	1964
Aurelius	1973	1964
Onondaga	1981	1976
Parma	1981	1976

To verify that these maps are a valid source of data for this study and that forest patches have been compiled accurately, the quadrangles for the Clinton County transect were examined. Thus, using the U.S.G.S. criterion, black and white aerial photographs taken in 1964 (1:20,000, U.S.D.A. ASCS) were examined with a stereoscope and a transparent crown-cover template (School of Natural Resources, University of Michigan).

Forest patches within the seven topographic quadrangles were manually digitized, beginning from the boundary of the city of Lansing, using C-Map software (Enslin, 1991). C-Map is a collection of programs designed to facilitate spatial and non-spatial data entry, retrieval, update and analysis at the microcomputer level. C-Map data files are compatible with dBase III Plus database management system by Ashton-Tate, 1986. The seven modules in C-Map include Display, Analyze, Digitize, Convert, Manage, Utilities and Print. While digitizing, a patch was defined as contiguous if adjacent polygons were either touching along a horizontal or vertical line segment, diagonal, corner-touching polygons were not considered as contiguous (Turner and Ruscher, 1988). The data were captured in vector form, where point, line and polygon data could be obtained as such and not distorted. The database consisted of values for parameters calculated by C-Map such as area, perimeter, and geographically referenced locations of points describing the outlines of individual patches in State Plane coordinates. Fractal dimension, complexity ratio and distance from the edge of the city for all patches were also enumerated.

The following is a description of the methods used to satisfy each of the objectives of this study.

Forest patch taxonomic composition

Although a digitized map of forest associations for the whole state of Michigan is available (Center for Remote Sensing, Michigan State University, 1982/1983), it could not be used to accurately determine the forest composition of each patch by means of polygon overlaying. This is because the forest associations map has a small scale (1:1,000,000) and low resolution (100 ha). In contrast, the digitized patch map has a scale of 1:24,000 and a resolution of 1 hectare. This difference in scale would cause an inherently large error if an overlay were attempted (Walsh et al., 1987). Therefore, in this landscape-level study, each patch was assigned to one of three broad categories of forest at the time it was digitized:

a. Upland forest - Deciduous and coniferous forests not found along stream courses.

b. Riparian forest - Deciduous and associated forest vegetation found along or in stream and river courses.

c. Wetland forest - Deciduous and coniferous forests present in marshes and bogs (as indicated by the marsh symbol on the quadrangle maps).

Forest patch structural characteristics and spatial distribution

The number of forest patches and their sizes were determined and stored in a relational database (dBase III Plus, 1986) using C-Map (Enslin, 1991). The patch sizes were listed in ascending order with corresponding geographical reference points. The smallest, largest, mean size and standard deviation values were computed using univariate analysis (SAS Institute Inc., 1985).

Mandelbrot's theory of fractals (Mandelbrot, 1977) allows the quantification of patch shapes. The area-perimeter relation has been used to calculate the fractal dimension of various patch shapes and to determine how patches relate to substrate, disturbance and other processes (Lovejoy, 1982; Krummel et al., 1987; Turner and Ruscher, 1988; Pastor and Broschart, 1990). Fractal dimension (D) measures the spatial complexity of the perimeter of a closed polygon. Area and perimeter measurements from the vector database were used to compute the fractal dimension based on the following equation (Lovejoy, 1982; Gardner et al., 1987; Krummel et al., 1987),

$$D = 2 \log P / \log A$$

where, P = patch perimeter

A = patch area

D = fractal dimension

D-values for each of the forest categories were estimated using linear regression (SAS Institute Inc., 1985). Log area was regressed against log perimeter and D was estimated by halving the slope of the regression line (Lovejoy, 1982; Burrough, 1986). D ranges between 1.00 and 2.00 with 1.00 representing a perfect square or circle and 2.00 representing a very complex perimeter of the same area. According to Krummel et al. (1987), a value of D estimated by this method that is less than 1.5 indicates simpler shapes than obtained by randomly assigning covertypes to individual polygons. Conversely, values of D greater than 1.5 indicate more complex shapes than would be obtained from random polygons. As a comparison, D-values for individual patches were computed (rather than estimated) using the above equation.

The perimeter data were also subjected to another test of shape, the Complexity Ratio (Hole, 1978; Hoover, 1986). The Complexity Ratio (S) is calculated by dividing the perimeter of each forest patch by the perimeter of a circle having an area equal to the area of that element:

$$S = P/P_c$$

where, P = perimeter of a landscape element

P_c = perimeter of a circle with an area equal to that of the landscape element.

A ratio value (S) of 1.00 suggests that the patch resembles the shape of a circle. As the ratio value increases, the more non-circular the patch and the more convoluted the edge or boundary. The categorical limits for the Complexity Ratio were :

$S \leq 1.50$	simple
$1.50 < S \leq 2.00$	intermediate
$S > 2.00$	complex

Patch size-human population density relationship

In order to examine the relationship between patch size and geometry and proximity to a large urbanized area, area and complexity ratios of forest patches in both the north and south transects were regressed independently with distance using linear regression (SAS Institute Inc., 1985). The distance for individual patches was computed by subtracting the y-coordinates of individual patches from the edge of the transects that border the city of Lansing. Regression coefficient (R^2) and slope values were noted for each of the regression analyses.

Co-occurrence of forest patches and preferred agricultural soil types

Agricultural land-use can be used to indicate the degree of human impact on the landscape. It is typically based upon soil type and is extensive in areas of rich and fertile soil. Iverson (1988) found that cropland and pastureland were correlated with the amount of soil organic matter and productivity index whereas the converse was true for deciduous and coniferous forest. To study this relationship, digital, vector-based soil series data at the township level were obtained from the Michigan Resource Information System (Michigan Department of Natural Resources), processed in C-map and exported for analysis in ERDAS (Earth Resources Data Analysis System). ERDAS is one of the major raster-based Geographic Information Systems (GIS) available for use on microcomputers (ERDAS Inc., 1987, 1990). Each soil type found in Delhi, Aurelius, Onondaga, Bingham and Greenbush townships was classified by the Soil Conservation Service into one of three categories based on its suitability for agriculture: prime farmland, prime farmland with drainage, and other soil types. Prime farmland includes cropland, pasture, range, forest, or other land uses, but not urban built-up land or water bodies since these two are considered irreversible uses. Prime farmland soil types are those that have the best combination of physical and chemical characteristics for producing food, forage, fiber and oilseed crops. Additionally, these areas have an adequate and dependable moisture supply from precipitation or irrigation as well as a growing season length sufficient to economically produce sustained high yields when treated and managed according to modern farming methods. The results of this classification were then displayed spatially on a map. The upland forest patch map was then digitally superimposed upon the agricultural-suitability soil map using the "Matrix" command in ERDAS. "Matrix" creates an output file containing classes r presenting the spatial coincidence of the sets of classes from two input files. Resulting class values can be unique for each coincidence of two input class values. The output file provided percentages of the study area and absolute area covered by forest patches on each prime farmland soil category. The upland forest patch cover map and the agricultural-suitability soil maps do not overlap totally over the same area. Only the area where the 2 maps coincided were used in the analysis. An example of the "Matrix" routine is provided here (Table 2).

Table 2 : Example of a "Matrix" routine (GIS).

Input files

Column - Preferred-agricultural soil types

Class code	Description
1	Prime farmland with drainage
2	Prime farmland
3	Other soil types

Row - Upland forest

Class code	Description
1	Non-forested land
2	Upland forest

Output file

Class code	Description
0	Non-forested land
1	Forest on prime farmland with drainage
2	Forest on prime farmland
3	Forest on other soil types

"Matrix" carried out on soil types and forests.

$$\underline{\text{Input file}} \qquad\qquad\qquad\qquad \underline{\text{Output file}}$$

$$\begin{array}{cc|ccc} & & & \text{Column} & \\ & & 1 & 2 & 3 \\ \hline & 1 & 1 & 2 & 3 \\ \text{Row} & & & & \\ & 2 & 4 & 5 & 6 \end{array} \qquad \underline{\text{recode}} \qquad \begin{array}{cc|ccc} & & & \text{Column} & \\ & & 1 & 2 & 3 \\ \hline & 1 & 0 & 0 & 0 \\ \text{Row} & & & & \\ & 2 & 1 & 2 & 3 \end{array}$$

Temporal change in patch pattern

Measurements were made to determine whether a change in number and size of forest patches found on prime farmland has occurred over the past 26-38 years. The current distribution of upland forest patches on prime farmland soil types in Ingham County was compared with black and white aerial photographs taken in 1938 (1: 20,000, U.S.D.A. ASCS). The rationale for using upland forest patches on prime farmland was that these patches would be most vulnerable to clearing for agricultural purposes when more land was needed. An increase of 131.2% in population size was recorded in Clinton County between the period of 1930 to 1980 while an increase of 136.3% was recorded for Ingham county during the same period (Census of Population 1980).

The map of preferred agricultural soil types based on soil series was plotted by townships and physically overlain on the U.S.G.S. topographic quadrangles. Upland patches found on prime farmland soil types were marked on the maps and a sample of 70 patches was randomly chosen from a total of 220 using a random numbers table (Brower et al., 1990). After the patches were randomly chosen, the 1938 black and white aerial photographs were optically rectified and overlain on the topographic quadrangles using a Zoom Transfer Scope (Bausch and Lomb). Areas of increase or decrease for each chosen patch were drawn on a tracing paper overlay. These areas were then measured using the digitizer and a software program written by William Enslin, Center for Remote Sensing, Michigan State University (personal communication). Cumulative total change was calculated and percent change for each patch was computed.

Forest patch species-area relations and dispersal of plant and animal species

The assessment of the adequacy of Lower Michigan's forest patches to sustain plant and animal populations requires the availability of species-area curves. The information available from species-area curves includes "minimum areas." Minimum area refers to the smallest area that can contain an adequate species representation of an association or community type (Braun-Blanquet, 1938; Vestal, 1949). Vestal (1949) has reported minimum area for different vegetation types of the world. The minimum area for a mixed deciduous forest, based on trees, shrubs and herbs in old growth forest, was used in this study. The number of patches with an area less than the minimum area for a mixed deciduous forest (0.88 ha) was evaluated for the two study transects. The analysis then provides information on the size status of Lower Michigan's forest patches relative to maintaining plant diversity. The number of upland patches ranging from 0.1 ha to greater than 100 ha was determined. The number of bird species that can be found within this range of area can then be assessed from information found in the published literature.

Average dispersal distances for tree species are provided by van der Pijl (1972). In order to assess the ability of species to migrate across the fragmented landscape, interpretation of proximity maps produced through an operation in ERDAS ("Search") was carried out. This command radiates a zone out in all directions from a propagule source to a threshold distance in pixels. The threshold distance used in this analyses (400 m) is the average distance a wind-borne propagule can be dispersed across the landscape. A one-hectare cell size was used throughout these analyses (100x100 m). The proximity zone radiates outward until 1) the threshold limit is reached or 2) it meets another zone that was radiating from a neighboring source (Figure 2).

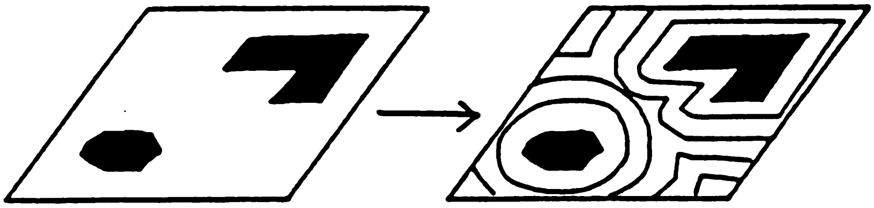

Figure 2. Proximity analysis (GIS) for forest patches.

Any space unoccupied by the proximity zones after a threshold distance for a particular tree species has been exceeded is highlighted on the map. These highlighted areas may be considered as potential barriers to the migration of particular tree species.

Macro-scale features

This analysis involved an evaluation of the presence or absence of suitable dispersal pathways for key forest tree species, such as sugar maple and oak, based on present forest cover and soil texture. Primary statewide data sets used in this study included digitized versions of forest associations and soil texture classes (Center for Remote Sensing, Michigan State University). These maps have a scale of 1:1,000,000 and a resolution of 100 ha. Forest associations that were used in this analysis include maple-birch and oak-hickory. These groupings are part of those used nation-wide by the United States Forest Service (U.S.F.S.) forest inventory nation wide (Raile and Smith, 1983). Although the American beech (*Fagus grandifolia* Ehrh.) is usually associated with maple in Michigan, it is not included in the title of the category as the map has been prepared so that it can be compared with other regions of the United States. According to U.S.F.S., the maple-birch association has sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), upland American elm (*Ulmus americana* L.) and red maple (*Acer rubrum* L.) , occurring either singly or in combination. The oak-hickory forest designation refers to the presence of northern red oak (*Quercus rubra* L.), white oak (*Q. alba* L.), bur oak (*Q. macrocarpa* Michaux), or hickories (*Carya* spp.) which exist either singly or in combination. Sugar maple is generally found on loamy sands, sandy loams and loams, whereas oaks are found on sandy plains, well-drained loamy soils and clay to loamy sands (Fowells, 1965). These textural classes from the soil texture map would be considered as optimal soils for sugar maple and oaks. Other soil textural classes would be referred to as sub-optimal soils.

The next step included an exercise to recode the forest associations map and the soil textures map into fewer categories. Each of the forest association maps intended for study were then digitally compared with its respective optimal and sub-optimal soil texture map using the ERDAS routine "Matrix". The outcome map included areas of sugar maple or oak forests on optimal soils and sub-optimal soils. With this information, a "Search" (ERDAS Inc. 1990) for a number of pixels from propagule sources found on optimal and sub-optimal soils was carried out. A threshold distance of 4 km was used for sugar maple while 1 km was used for oaks (van der Pijl, 1972). The resulting maps from this proximity analysis were then digitally compared with the respective optimal and sub-optimal soil texture maps for the forest type studied. The outcome map shows areas where the 4 km and 1 km - threshold distances co-occur, on optimal and sub-optimal soils. The map produced through this operation provides some insight into the potential germination and establishment capabilities of seeds on the new sites based on dispersal distances and edaphic conditions.

RESULTS

Vegetation in the study transect was categorized as upland forest, riparian forest and wetlands. Upland forests averaged 80.4% of the total forested area in the combined north and south transects. This was followed by riparian forests (15.34%) and wetlands (4.28%). The total land covered by forest was 17,511 ha of the total study area (90,594 ha) (Table 3). In the north transect, 750 upland patches covered an area of 4,533.8 ha, 111 riparian forest patches covered an area of 713.7 ha and 69 wetland patches covered an area of 407.8 ha. In the south transect, 1,137 upland patches covered 9,540.5 ha while 113 riparian patches and 39 wetland patches accounted for 1,973.1 and 341.8 ha, respectively (Table 3) (Figures 3 and 4).

Upland and riparian forests dominate the largest area of vegetated land in the south transect. The area covered by these two forest categories is more than double the area covered by the same forest categories in the north transect. Riparian forests in the south transect are larger in size than riparian forests in the north. In the

Table 3. Categories of vegetation type by number of patches, area and percent cover.

	Number of patches	Area (ha)	Percent of forest cover in the entire state
North Transect			
Upland forest	750	4,533.84	9.59
Riparian forest	111	713.66	1.51
Wetlands	69	407.80	0.86
Non-forested land		41,622.16	88.04
Total	930	47,277.46	
South Transect			
Upland forest	1,137	9,540.45	17.18
Riparian forest	113	1,973.06	3.55
Wetlands	39	341.84	0.62
Non-forested land		43,668.17	78.65
Total	1,289	55,523.52	

Figure 3. Forest patches, North Transect.

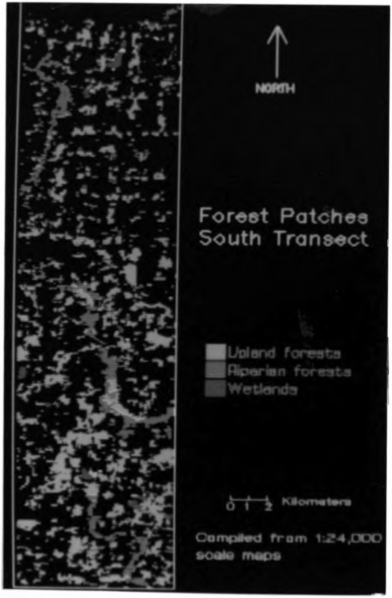

Figure 4. Forest patches, South Transect.

south transect, 113 riparian patches accounted for 1,973.06 ha while 111 riparian forests in the north transect only accounted for 713.66 ha (Table 3).

Forest patch characteristics

Area

The smallest size of a forest patch for all categories of forests included in the north transect is 0.04 ha and ranges up to 72.52 ha. The mean size range for all forest categories within the north transect is between 3.53 - 3.94 ha (Table 4). Forest patches in the south transect are at least 0.05 ha and the range is up to 241.13 ha. The mean size range for all forest categories is 5.65 - 12.00 ha. Riparian forests have the largest mean size (Table 4). In comparing the size of forest patches for both the north and south transects, the mean sizes for all forest categories in the south transect are larger than those in the north (Table 4).

Fractal dimension

Fractal dimension (D) was calculated for forest categories and individual forest patches because both methods have been used in different studies (Rex and Malanson, 1990; Milne, 1991) and there is still contention on the accuracy of each method. In the north transect, D-value of upland forests is the lowest (1.20) while riparian

Table 4. Area of forest patches (ha).

	Upland	Riparian	Wetland
North Transect			
Number of patches	750	111	69
Smallest	0.04	0.12	0.17
Largest	72.23	36.35	72.52
Mean	3.84	3.53	3.94
Std. deviation	6.29	5.95	10.29
South Transect			
Number of patches	1,137	113	39
Smallest	0.05	0.06	0.31
Largest	241.13	104.94	48.07
Mean	5.69	12.00	5.65
Std. deviation	14.62	19.62	10.69

forests have the highest D (1.39) followed by wetlands (1.26) (Table 5; Figure 5, 6 and 7). Upland forests also have a lower D-value in the south transect when compared withrriparian forests and wetlands (Table 5; Figures 8, 9 and 10). Wetlands in the south transect are more complex in shape when compared with riparian forests. Regression coefficients (R^2) are equal to or greater than 0.90 (Table 5).

Mean D-values calculated for individual upland and wetland patches in the two transects are the same, 1.27. Riparian forests in the two transects have higher mean D-values than upland and wetland patches (Table 6).

Complexity ratio

Upland and wetland patches have a lower mean complexity ratio than riparian forests in both the north and south transects. The mean complexity ratio values for riparian forests were 1.96 and 1.95 in the north and south transects respectively compared to 1.42 and 1.59 for upland and wetland patches (Table 7). Using the categorical limits suggested by Hoover (1986), the riparian forests are classified as having complex shapes while the mean complexity ratios of upland and wetland patches indicate that they vary from being simple (near 1.00) to intermediate in shape complexity.

Table 5. Fractal dimension (D)* for forest categories - regression analysis.

	Upland	Riparian	Wetland
North Transect			
Number of patches	750	111	69
D	1.20	1.39	1.26
R^2	0.90	0.91	0.96
South Transect			
Number of patches	1,137	113	39
D	1.26	1.35	1.42
R^2	0.94	0.94	0.96

* $D = 2 \log P / \log A$

where, P = patch perimeter
A = patch area
D = fractal dimension

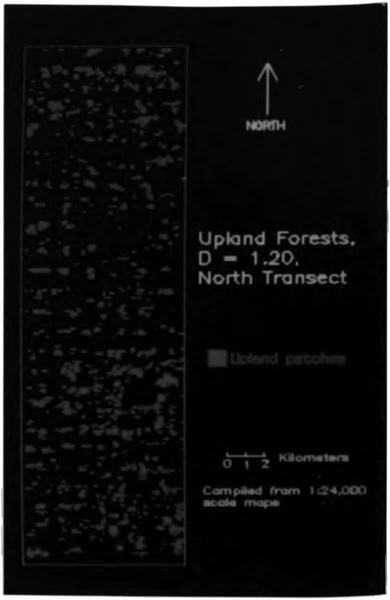

Figure 5. Upland forests, D = 1.20, North Transect.

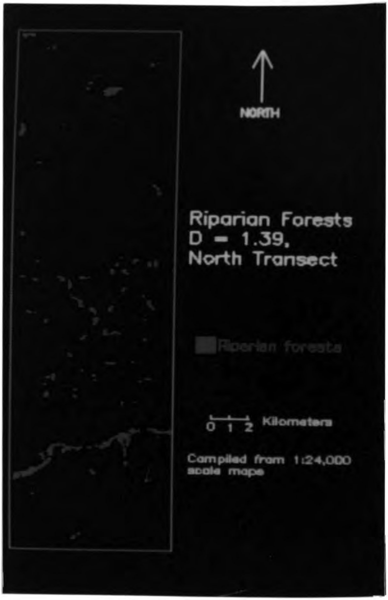

Figure 6. Riparian forests, D = 1.39, North Transect.

Figure 7. Wetlands, D = 1.26, North Transect.

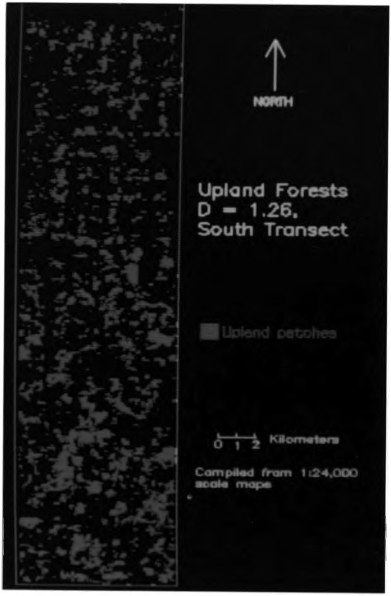

Figure 8. Upland forests, D = 1.26 South Transect.

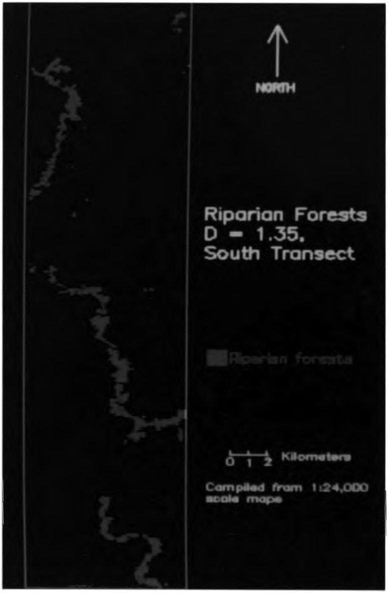

Figure 9. Riparian forests, D = 1.35, South Transect.

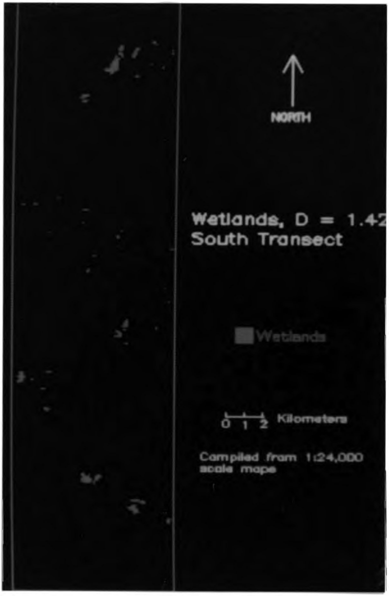

Figure 10. Wetland, D = 1.42, South Transect.

Table 6. Fractal dimension (D)* for individual forest patches.

	Upland	Riparian	Wetland
North Transect			
Lowest	1.19	1.21	1.22
Highest	1.94	1.43	1.35
Mean	1.27	1.31	1.27
Std. deviation	0.05	0.04	0.03
South Transect			
Lowest	1.19	1.20	1.23
Highest	1.46	1.45	1.35
Mean	1.27	1.29	1.27
Std. deviation	0.04	0.04	0.03

* $D = 2 \log P / \log A$

where, P = patch perimeter
A = patch area
D = fractal dimension

Table 7. Complexity ratio* for forest patches.

	Upland	Riparian	Wetland
North Transect			
Lowest	1.05	1.18	1.05
Highest	26.41	5.35	3.09
Mean	1.48	1.96	1.42
Std. deviation	1.08	0.74	0.38
South Transect			
Lowest	1.03	1.05	1.06
Highest	5.04	4.13	3.83
Mean	1.52	1.95	1.59
Std. deviation	0.46	0.75	0.63

* Complexity ratio (S) = P/P_c

where, P = perimeter of a landscape element

P_c = perimeter of a circle with an area equal to that of a landscape element

Relationship of area and shape of patches to human population density

Area and complexity ratios of forest patches in the north transect showed a negative relationship with distance from Lansing. Forest patches located away from Lansing in the north transect were smaller in size and tended to have simpler shapes. The converse was true for forest patches in the south transect. All linear regression analyses yielded low R^2 values (Table 8).

Co-occurrence of forest patches and preferred-agricultural soil types

Delhi, Aurelius and Onondaga Townships (Ingham County) of the south transect and Bingham and Greenbush Townships (Clinton County) of the north transect were the study sites. Prime farmland made up 60.4% of the totalasoil types found within three townships in Ingham County, while the percentage was 72.5% in the two townships of Clinton County (Tables 9 and 10; Figures 11 and 12). Forests on prime farmland soil types and other soil types accounted for 6.92% and 6.86% of total land area, respectively, while forests on prime farmland with drainage soil types accounted for 2.55% of all upland forests in the three townships in Ingham County (Table 11; Figure 13).

Table 8. Relationship between area and complexity ratio of forest patches and distance from the city of Lansing (using linear regression).

	Slope	R^2
North Transect		
Area	-0.5658	0.0010
Complexity Ratio	-9.1×10^{-7}	0.0013
South Transect		
Area	4.3823	0.0138
Complexity Ratio	1.7×10^{-6}	0.0203

Table 9. Prime farmland soil types in Delhi, Aurelius Onondaga Townships, Ingham County (Michigan Resource Information System, Michigan Department of Natural Resources).

	Area (ha)	Percent cover
Prime farmland with drainage soil types	5,691.08	22.91
Prime farmland soil types	9,320.22	37.52
Non-prime farmland soil types	9,829.96	39.58
Total	24,841.26	

Table 10. Prime farmland soil types in Greenbush and Bingham Townships, Clinton County (Michigan Resource Information System, Michigan Department of Natural Resources).

	Area (ha)	Percent cover
Prime farmland with drainage soil types	992.49	5.78
Prime farmland soil types	11,467.12	66.71
Non-prime farmland soil types	4,731.57	27.53
Total	17,191.18	

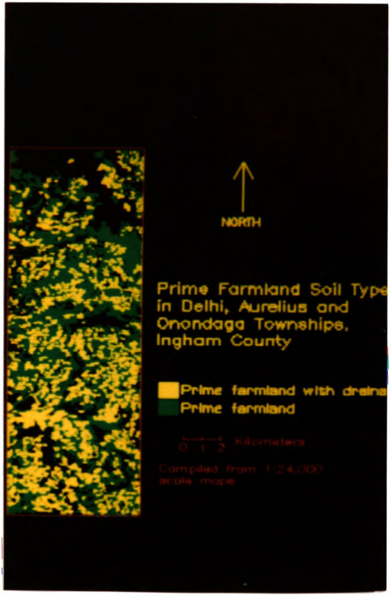

Figure 11. Prime farmland soil types in Delhi, Aurelius and Onondaga Townships, Ingham County.

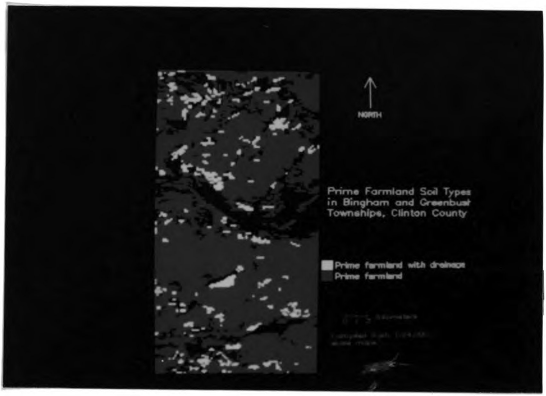

Figure 12. Prime farmland soil types in Bingham and Greenbush Townships, Clinton County.

In Bingham and Greenbush Townships, 5.58% of all upland forests were on prime farmland soil types, while 0.53% were on prime farmland with drainage soil types and 2.76% were on other soil types (Table 11; Figure 14).

Temporal change

There has been a net increase in the areal extent of upland patches on prime farmland soil types over the recent 26-38 years (Table 12). The number of patches within each range of percent increase in patch size are 9 (0-25%), 8 (25-50%), 4 (50-75%), 9 (75-100%) and 8 (> 100%). Although only a random sample of upland patches occurring in the 1938 black and white aerial photographs and topographic maps for Delhi, Aurelius and Onondaga Townships were examined for temporal changes in size, there may have been new upland patches formed over this period of time. However, observations on upland patches in Clinton County (north transect) showed no increase in patch number between the 1930s and 1970s.

Minimum area for plant and animal species

In the north transect, 59.73% of all upland patches have an area larger than the minimum area (0.88 ha) for a mixed deciduous forest while the percentage is 63.3% in the south transect. Percentage of forest patches within the size range of 0.1 - 10.0 ha is 88.16%. Number of breeding

Table 11. Area and percent cover of upland forests on preferred-agricultural soil types - Ingham and Clinton Counties.

	Area (ha)	Percent cover
Ingham County - Delhi, Aurelius and Onondaga Townships.		
Forest on prime farmland with drainage	632.70	2.55
Forest on prime farmland	1,703.19	6.86
Forest on other soil types	1,718.18	6.92
Non-forested land	20,788.09	83.68
Total	24,842.16	
Clinton County - Bingham and Greenbush Townships.		
Forest on prime farmland with drainage	91.96	0.53
Forest on prime farmland	959.54	5.58
Forest on other soil types	473.77	2.76
Non-forested land	15,666.53	91.13
Total	17,191.80	

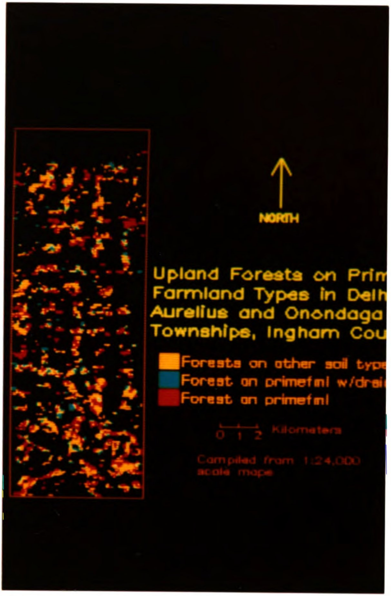

Figure 13. Upland forests on prime farmland soil types in Delhi, Aurelius and Onondaga Townships, Ingham County.

Figure 14. Upland forests on prime farmland soil types, Bingham and Greenbush Townships, Clinton County.

Table 12. Change in area of upland patches over a 38-year period (1938-1976) on prime farmland soil types for Delhi, Aurelius and Onondaga Townships, Ingham County.

	Number of patches	Total change (hectares)
Increase	38	149.36
Decrease	8	19.51
No change	24	0
	Net change	+ 129.85

bird species increases with increase in forest area (Table 13).

Proximity analyses for forest patches

Proximity analysis for upland patches in both the north and south transects show the uniform dispersion pattern of patches and the proximal zones surrounding each patch (Figures 15 and 18). Areas highlighted in red indicate distances of greater than 400 m from individual patches. The city of St. Johns in the north transect exists as the largest area highlighted in red (Figure 15). There is less continuity among riparian forest in the north transect whereas riparian forests are more connected and cover a larger extent in the south transect (Figures 16 and 19). Relative to upland and riparian patches, wetlands are by far fewer in number and more distantly scattered across the landscape in both transects (Figures 17 and 20).

Proximity analyses for sugar maple and oaks in the landscape of Michigan

Sugar maple forests exist in disjunct fragments in the upper and lower peninsulas of Michigan (Figure 21) and cover 11.72% of the total land area in the state and 9.71% of the total forested land area in the state (Table 14). Almost half of the maple dominated forest type is found on optimal edaphic conditions, while the remaining half occurs

Table 13. Number of forest patches within each size range and estimates of area-sensitive forest birds that require these minimum areas for the maintenance of viable breeding populations (based on other studies in other locations).

North and South Transect

Patch area (A) (Ha)	Number of patches	Number of bird species	Location and source
$A = 0.1$	26	-	-
$0.1 < A \leq 1.0$	778	20	New Jersey, Forman et al. (1976); Galli et al. (1976).
$1.0 < A \leq 10.0$	856	30	New Jersey, Forman et al. (1976); Galli et al. (1976).
		22	Virginia, Johnston (1970).
		7	Maryland, Robbins (1979).
$10.0 < A \leq 100.0$	217	35	New Jersey, Forman et al. (1976); Galli et al. (1976).
		13	Maryland, Robbins (1979).
$100.0 < A$	6	13	Maryland, Robbins (1979).

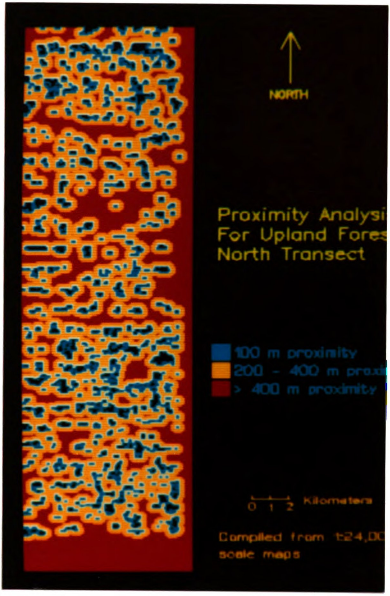

Figure 15. Proximity analysis for upland forests, North Transect.

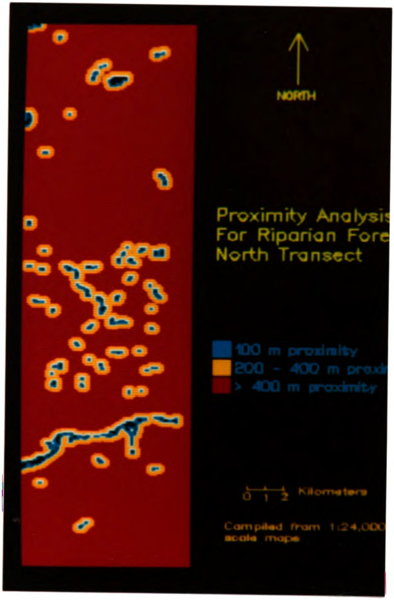

Figure 16. Proximity analysis for riparian forests, North Transect.

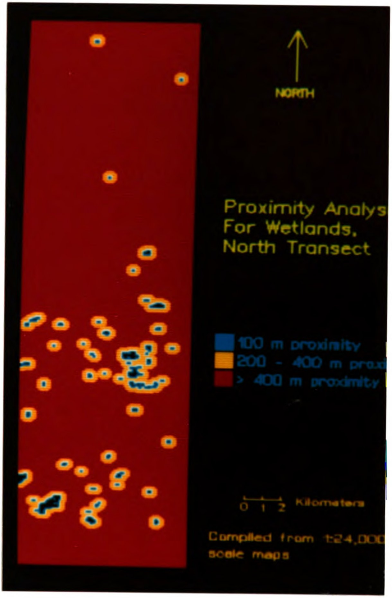

Figure 17. Proximity analysis for wetlands, North Transect.

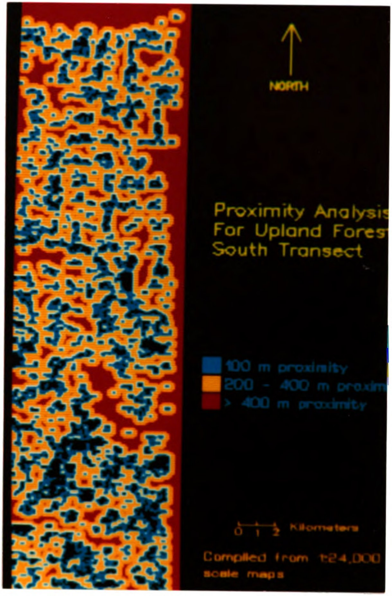

Figure 18. Proximity analysis for upland forests, South Transect.

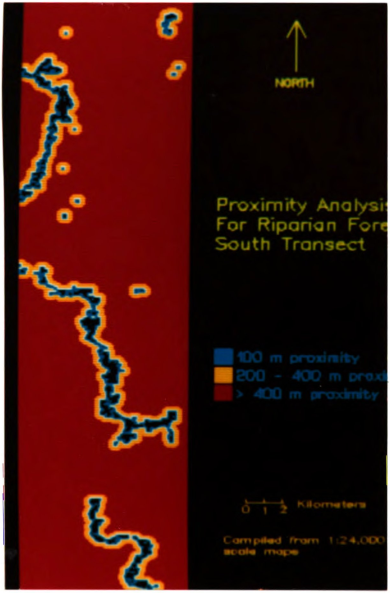

Figure 19. Proximity analysis for riparian forests, South Transect.

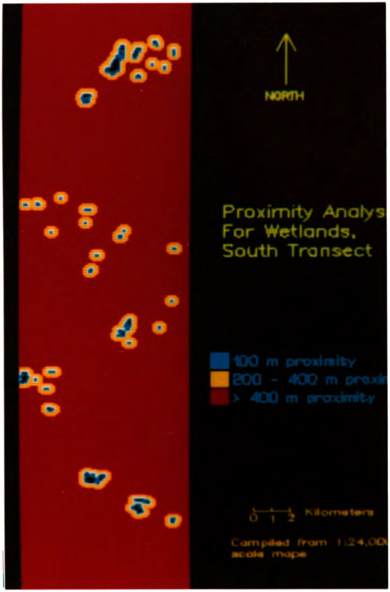

Figure 20. Proximity analysis for wetlands, South Transect.

Table 14. Co-occurrence of sugar maple and other forests and general soil textures, Michigan (Center for Remote Sensing, Michigan State University, 1982/1983).

	Area (Ha)	Percent of forest cover in the entire state
Maple on optimal* soils	769,353	5.10
Maple on sub-optimal* soils	997,868	6.62
Other forests on optimal soils	2,077,642	13.78
Other forests on sub-optimal soils	4,079,479	27.05
Non-forested land	7,156,689	47.45
Total	15,081,030	

* Optimal and sub-optimal soil types are for the species in reference

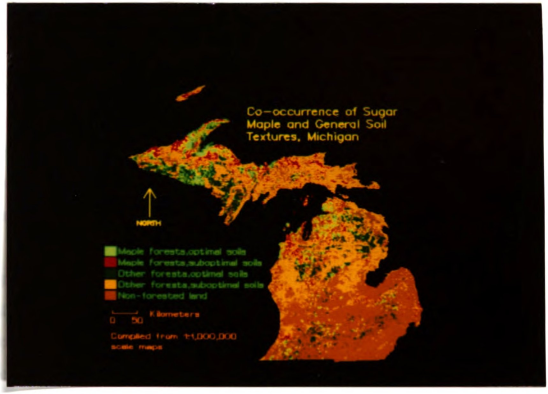

Figure 21. Co-occurrence of sugar maple and general soil textures, Michigan.

on sub-optimal soils. For sugar maple seed sources that occur on optimal soil types, propagules have at least a 50% probability of landing on either optimal soil types or sub-optimal soil types within the 4 km proximity zone (Table 15; Figure 22). However, if the seed source occurs on sub-optimal soils, then there is about a 33.3% probability for seeds to land on optimal soil types within the 4 km proximity zone. More than two-thirds of the 4 km-wide dispersal area has sub-optimal edaphic conditions for the establishment of sugar maple (Table 16; Figure 23).

Most of the oak forest type in Michigan occur on optimal soil types (Table 17; Figure 24). Acorns can be dispersed over a distance of about 1 km (Darley-Hill and Johnson, 1981). The probability of acorns from oak trees occurring on optimal soil types landing in an area of optimal edaphic conditions is 9 times greater than the probability that they will land on sub-optimal soil types (Table 18; Figure 25). For acorns produced from sources on sub-optimal soil types, there is only a 34% probability that they could establish themselves on optimal soil types within the 1 km proximity zone (Table 19; Figure 26).

Table 15. Proximity analysis for sugar maple forests on optimal* soil types, Michigan.

	Area (ha)	Percent cover	Percent of 4 km proximity zone
Maple forests on optimal soils	769,352	5.10	-
1-4 km proximity distance, optimal soils	2,109,544	13.99	56.56
1-4 km proximity distance, sub-optimal soils	1,620,211	10.74	43.44
> 4 km proximity distance	10,581,923	70.17	-
Total	15,081,030		

*Optimal soil types are for species in reference.

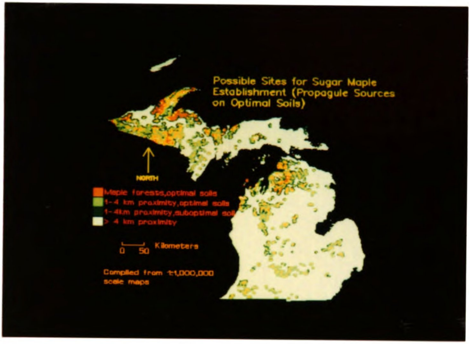

Figure 22. Possible sites for sugar maple establishment (Propagule sources on optimal soils).

Table 16. Proximity analysis for sugar maple forests on sub-optimal* soil types, Michigan.

	Area (ha)	Percent cover	Percent of 4 km proximity zone
Maple forests on sub-optimal soils	997,868	6.62	-
1-4 km proximity distance, optimal soils	1,510,603	10.02	31.25
1-4 km proximity distance, sub-optimal soils	3,322,827	22.03	68.75
> 4 km proximity distance	9,249,732	61.33	-
Total	15,081,030		

* Sub-optimal soil types are for the species in reference.

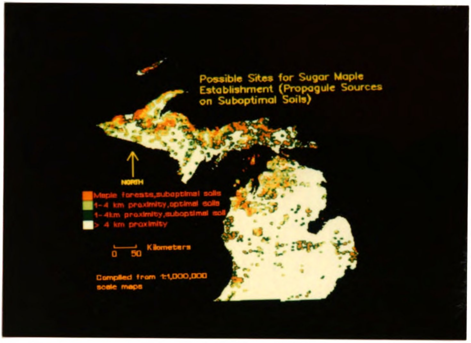

Figure 23. Possible sites for sugar maple establishment (Propagule sources on sub-optimal soils).

Table 17. Co-occurrence of oak forest and other forests and general soil textures, Michigan (Center for Remote Sensing, Michigan State University, 1982/1983).

	Area (ha)	Percent of forest cover in the entire state
Oaks on optimal* soils	916,462	6.08
Oaks on sub-optimal* soils	162,211	1.08
Other forests on optimal soils	4,211,688	27.93
Other forests on sub-optimal soils	2,633,980	17.47
Non-forested land	7,156,689	47.45
Total	15,081,030	

* Optimal and sub-optimal soil types are for the genus in reference

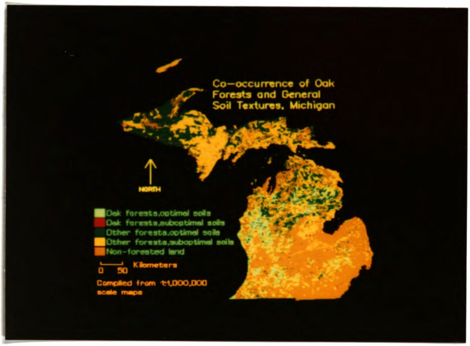

Figure 24. Co-occurrence of oak forests and general soil textures, Michigan.

Table 18. Proximity analysis for oak forests on optimal* soil types, Michigan.

	Area (ha)	Percent cover	Percent of 1 km proximity zone
Oaks on optimal soils	916,462	6.08	-
1 km proximity distance, optimal soils	1,398,596	9.27	90.40
1 km proximity distance, sub-optimal soils	148,510	0.98	9.60
> 1 km proximity distance	12,617,462	83.66	-
Total	15,081,030		

* Optimal soil types are for genus in reference.

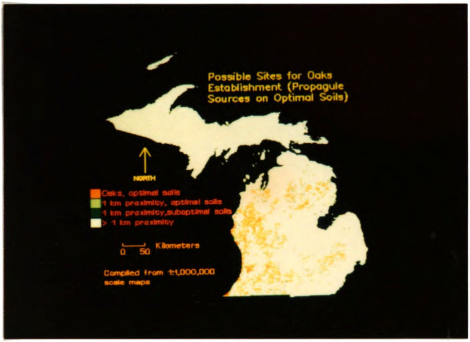

Figure 25. Possible sites for oak establishment (Propagule sources on optimal soils).

Table 19. Proximity analysis for oak forests on sub-optimal* soil types, Michigan.

	Area (ha)	Percent cover	Percent of 1 km proximity zone
Oaks on sub-optimal soils	162,211	1.08	-
1 km proximity distance, optimal soils	143,810	0.95	33.63
1 km proximity distance, sub-optimal soils	283,819	1.88	66.37
> 1 km proximity distance	14,491,190	96.09	-
Total	15,081,030		

* Sub-optimal soil types are for the genus in reference.

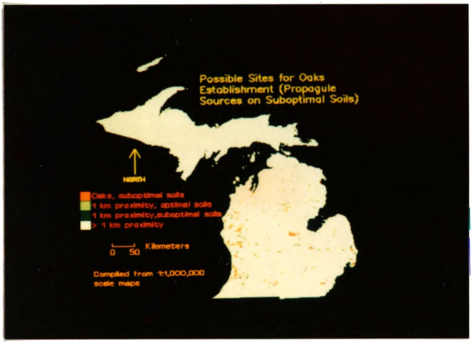

Figure 26. Possible sites for oak establishment (Propagule sources on sub-optimal soils).

DISCUSSION

The purpose of this study was to examine the structure of forest patches in a landscape in Michigan and to consider the underlying causes of patch structure. The study also attempted to evaluate how patch structure may affect ecological processes in the landscape at two levels by applying and developing GIS techniques.

Forest patch structure

The landscape of the southern one-half of Lower Michigan is characterized by forest land existing as patches and corridors that are embedded in a matrix of agriculture land. Forest patches in both the north and south study transects are dispersed uniformly throughout the entire landscape. This distribution of forest patches reflects forest clearing patterns practiced by the early European settlers in the mid-19th century. The economy of Ingham County during this time period was based primarily on subsistence agriculture. Most of the forests in Ingham County were subsequently cleared by 1874 and the subsistence agriculture shifted to cash grain agriculture (Malik, 1960). At this point, the rectangular pattern of roads along section lines that are oriented in the cardinal directions had nearly attained its ultimate development

(Malik, 1960). Most of the productive land in Ingham and Clinton Counties that was easily accesible from roads was by 1874 converted to farmland. Today's forest patches can thus be seen located in the center of rectangular patterns delineated by roads and the patches tend to have regular boundaries.

Upland patches in the north transect (Clinton County) and in the upper half of the south transect (Delhi and Aurelius Townships, Ingham County) clearly demonstrate this pattern of patch arrangement. However, this pattern is not evident in the lower portion of the south transect where upland patches tend to be more varied in size and shape. Cultural and natural factors, such as topography and pattern of soil fertility, lead to landscapes with characteristic features and patch geometry. Patch size and shape within the lower part of the south transect suggest that the patches have not been affected very much by cultural influences but rather by natural factors such as geomorphology and patterns of soil fertility. The topography here is characterized by undulating and uneven terrain while these features are not prominent in the rest of the transect. Therefore, the natural factors such as geomorphology and soils were most likely the underlying causes of patch structure in this part of the landscape.

Riparian forests represent a larger percentage of total forested land in the south transect than in the north. The Grand River and Sandstone Creek traverse the south transect in a north-south direction, therefore covering a larger area (1.79 km^2) within the transect (Figure 4). In contrast, the Looking Glass River and Stony Creek, being the main tracts of riparian forest in the north transect, are oriented in the east-west direction and cover an area of about 0.32 km^2 (Figure 3). All these rivers represent glacial spillways or drainage lines (Sommers, 1977).

All forest categories in the south transect have larger mean sizes when compared to the same categories in the north transect. The largest patches of upland forest in the south transect were found to occur on a variety of muck soils such as Napoleon muck, Palms muck, Houghton muck, Adrian muck, Edwards muck, Henrietta muck and on hydric soils such as Parkhill, Sebewa and Colwood-Brookston loams. These soil types would have made the land unsuitable for farming as drainage ditches would have to be constructed to lower the spring water table. The extra labor and money that needs to be invested in the drainage system would further deter the conversion of forests on muck and hydric soils to farms. Thus, a higher number of large forest patches still exist in the south transect.

Further investigation of the co-occurrence of forests and prime farmland soil types in both Ingham and Clinton Counties supports the above findings. The percent area of upland forest on soil types that are prime farmland if drained in Ingham County is double that of Clinton County.

This might be due to the presence of large upland patches occurring on muck and hydric soil types that are not suitable as prime farmland sites. This could account for the greater occurrence of upland patches on prime farmland with drainage soil types. Thus, soil fertility patterns do influence patch size. Forest patches could have also been left within agricultural fields because they serve as windbreaks and recreational areas, provide hunting grounds and fuelwood, and possess aesthetic values.

Quantification of patch shape using fractal analysis and complexity ratios shows that riparian forests and wetlands within the two transects have more complex shapes than upland patches. Even though there was a significant difference ($p<0.0025$, t-test) between fractal dimensions calculated for forest categories using linear regression and for individual patches, both sets of data support the same trend. Therefore, it is possible to estimate fractal dimension for a category of patches by just using a sample of patches within the category instead of all patches. It has been reported that the regression analysis method (Milne, 1988, 1991) and the least-squares method (Turner et al., 1989c) for calculating fractal dimension are reliable. Data for these respective studies were, however, obtained in a raster format. In contrast, perimeter and area of patches in this study were obtained through a vector-based system and care was taken when digitizing complex perimeters of the polygons. The unique fractal dimension of individual patches could yield a more accurate estimate of its shape, as was supported by Rex and Malanson (1990). The arguments of Milne (1988) and Turner et al. (1989c) indicate that the improvement would, however, be minor. Milne (1991) suggested that fractal dimension of a set of objects allows numerous objects to be treated simultaneously, yields error estimates and best reflects the use of fractal geometry, whereas a fractal for a single object tends to be biased and there is no estimate of error.

It has been reported that patches that have received less anthropogenic influence, such as riparian forests and wetlands, tend to have D-values close to 2.00, the upper limit for D (Turner and Ruscher, 1988; Iverson, 1988; O'Neill et al., 1988, De Cola, 1989). However, D-values for riparian forests and wetlands in this study are not very close to 2.00. This could be due to the fact that all patches in the study area have to some extent received a certain degree of human impact since the whole landscape in central Lower Michigan is largely dominated by human activities. The D-values for riparian forests and wetlands certainly indicate that the patches have received more impact from natural processes than from human-induced processes when compared with D-values for upland patches. The high regression coefficients (R^2) show that area of a patch is strongly dependent on its perimeter.

Human impact, valley width and stream sinuosity were reported to account for 24% of the variance in shape of remnant riparian patches in Iowa (Rex and Malanson, 1990). They reported that human impact was more significant in its effect on patch shapes, but other factors, such as local topography and geomorphology of the area, that could have accounted for the remaining percentage of variance were not investigated in the study. The data from the present investigation suggest that riparian forests and wetlands within the study area have received less human impact compared to upland patches.

Fractal dimension can be used as an index of the intensity of human activities on the landscape. Changes in D-value over time provide valuable information about the degree to which human activities are modifying landscape patterns regardless of specific land uses. Fractal dimension is one indicator that can assist in the analysis of processes that influence the formation of landscape patterns.

Data on patch shape are important in studies of dispersal and foraging. Shape and orientation are critical in the dispersal of animals and plants across a landscape (Forman and Godron, 1986). Enumeration of patch numbers, size and shape would be a beneficial practice as such data can be used to identify patches that are most vulnerable or resistant to disturbance. Large patches that have a high interior-to-edge ratio can be selected for the preservation and maintenance of both plant and animal species that require large interior habitats while small patches tend to promote the perpetuation of edge species. The maintenance of a critical minimum patch size may be an important criterion in the preservation of biodiversity. Hence, data on patch size and shape can be useful in management and conservation programs.

Forest patches tend to decrease in size and in complexity ratios with northward distance from Lansing. This might be attributed to the impact of agricultural activities that are carried out around the city of St. Johns, which is within the study transect. The converse is true of forest patches in the south. Large contiguous tracts of riparian forest and large upland patches in the south transect could have contributed to the positive relationship between size and shape of forest patches and distance from urban centers. The two regression analyses strongly suggest that size and shape of forest patches are not totally dependent on distance from a city or human density centers. The findings show that distance from a city does not influence patch size and shape significantly and there may be other factors such as topography, soil fertility and the way humans have responded through their perception of the landscape that played a greater role in the formation and structure of landscape patches. For example, patterns of soil fertility and topography in the landscape have led to the decision of humans to not use wet sites and rough topography for agricultural activities. Therefore, large tracts of forest with complex shapes have been left unaltered in the landscape. Although humans play an important role in the formation and structure of landscape patches, forest patch structure is not affected by proximity to a city.

The net increase in upland patch size between 1938 and 1976 within the three townships in Ingham County suggests that an increase instead of a decrease in the size of Michigan's forest patches may be occurring. This finding is contrary to the findings of Hill (1985) in New York. Hill (1985) reported that forest patches are decreasing in size and becoming more isolated in human-dominated landscapes such as New York where agricultural intensification and development, industrialization and urbanization are occurring. The findings of this study show that most reduction in forest patch area occurred in the mid-19th century when the most productive and easily accessible forest land was cleared for agriculture. Some forest patches were left uncut because they were on soil types that were not suitable for farming. The census of land area existing as farmland in Ingham and Clinton Counties shows a decline of 0.07% and 0.04%, respectively, in farmland area between 1982 and 1987 (County Food and Agriculture Development Statistics 1990).

The increase in forest patch size in mid-Michigan might be due to the reversion of abandoned farmland to forest over time and the decline in conversion of forest land to other land uses. This trend has been reported for Georgia, where mean size and areal extent of forest has increased between the 1930s and 1980s (Turner and Ruscher, 1988; Brender, 1952). Forest patches could also have been left within agricultural fields because they serve as windbreaks and recreational areas, provide hunting ground and fuelwood, and possess aesthetic value.

Ecological implications of forest patch structure

Forest patch size and the degree of patch isolation are measures for investigating the effects that patch structure and spatial distribution of patches have on the overall status of Michigan's landscape in being able to support an adequate flora and fauna. Upland, riparian, and wetland patches can serve as important genetic reservoirs, "stepping stones" or corridors. More than 50% of all upland patches in the two transects are larger than the minimum area for a highly mixed deciduous forest (Vestal and Heermans, 1945). The minimum area referred to here is large enough to include all important plant species and nearly half of the minor species, and is suggested to show many characteristics of the community type (Vestal and Hermanns, 1945; Vestal, 1949). They have the potential to act as seed sources that can help revegetate the adjacent land and can help reduce interpatch distance. Large patches are capable of preserving interior species. Woodland herbs are vulnerable to loss when changes in habitat occur. Herbaceous plants such as Trillium and trout lilies, unlike weedy herbs that can spread rapidly (Mack, 1984), produce only small numbers of seeds. Many woodland herbs also reproduce vegetatively such as Oxalis spp. and Plantago species (van der Pijl, 1972). This is an effective means to increase locally but not a means for dispersal over discontinuous habitat (Davis, 1990). As shown in Table 20, herbaceous plant species are the largest group among animals and plants to be extirpated in Michigan. About 13% of all plant species that are probably extinct, endangered or threatened occur in woodlands Beaman, 1977). Therefore, it is important to preserve the forest patches that are remaining and to minimize forest fragmentation.

A patch of adequate size to sustain a viable plant population might not be able to serve the same purpose for animals. Forest size has a significant effect on animals, such as the number of bird specie (Galli et al., 1976; Forman et al., 1976; Ambuel and Temple, 1983; Blake and Karr, 1987). Internal environmental heterogeneity within a large forest patch promotes species diversity by providing a greater variety of resources, thus allowing a greater number of bird species to coexist (Blake and Karr, 1987). Minimum areas for bird species range between 0.8 and 10.0 ha and are characteristic for individual species (Galli et al., 1976). It has also been reported in Maryland (Robbins, et al. 1989) that at least one pair of

Table 20. Numbers of animal and plant species that are endangered, threatened, of special concern or extirpated in Michigan (Michigan Endangered, Threatened and Special Concern Plant and Animal Species, 1987).

Group	Number of species				
	Endangered	Threatened	Special Concern	Extirpated	Total
Animals					
Mammals	4	3	2	3	12
Reptiles and amphibians	2	3	6	-	11
Birds	7	9	11	3	30
Insects	2	6	42	-	50
Mollusks	7	5	15	-	27
Plants					
Herbaceous	13	189	23	38	263
Shrubs	1	9	1	-	11
Trees	1	2	1	-	4

red-eyed vireos can be detected from any randomly established observation point within any wooded tract that is larger than 100 ha, regardless of its location and forest composition. Therefore, it is recommended that large patches be used for preservation sites so that they can not only maintain viable populations of birds (Forman et al., 1976; Galli et al., 1976; Lynch and Whigham, 1984; Askins et al., 1990), but also protect rare plant and animal species and help maintain biotic diversity in the region.

The extirpation of plant species as published in 1987 (Tables 20 and 21), has largely been caused by the destruction of their preferred habitats. The landscape exists in a dynamic state where habitats become more or less favorable for the survival of organisms. Although, we know that species are being threatened, endangered or extirpated in Michigan, there is still very little information available on the nature and size of habitats required by individual animal species or the kinds of habitats that are being lost. These gaps in knowledge need to be filled as the information is important for the management of habitat area and the landscape as a whole in order to facilitate the movement and persistance of animal species.

The endangered and threatened status, together with the extirpation of many plant and animal species, has largely been caused by the loss of habitat areas through forest

Table 21. Examples of animal and plant species that have been extirpated in Michigan (Michigan Endangered, Threatened and Special Concern Plant and Animal Species, 1987).

Groups		Species
Mammals -	Bison	*Bison bison*
	Wolverine	*Gulo gulo*
	Wooded caribou	*Rangifer tarandus*
Birds -	Trumpeter swan	*Cygnus buccinator*
	Passenger pigeon	*Ectopistes migratorius*
	Greater prairie chicken	*Tympanuchus cupido*
Fishes -	Longjaw cisco	*Coregonus alpenae*
	Paddlefish	*Polyodon spathula*
	Arctic grayling	*Thymallus arcticus*
Plants -	Fire pink	*Silene virginica*
	Green trillium	*Trillium viride*
	Netted chain fern	*Woodwardia areolata*

clearing for agriculture and urban land uses and draining of wetlands. Wetlands are complex ecosystems that support a variety of fish, insects and other animal and plant life. Frequently, they serve as buffers between lakes and land and can help filter out harmful nutrients before they reach lakes and streams (Forman and Godron, 1986). Wetlands currently exist as very disjunct fragments in the landscape and they are being threatened as pressure for land increases. About 40% of plant species that are probably extinct, endangered, or threatened occur in aquatic and wetland habitats (Table 22). It would be quite impossible to perpetuate wetland plant and animal species if the wetlands are not preserved and continue to be more isolated from one another. Wetlands exist as the smallest percentage (10%) of all forested land in the transects. This ecosystem is very fragile and various plant and animal species would be threatened if these ecosystems are subject to continual human disturbance.

Upland patches and wetlands are important "stepping stones" for plant and animal species. In a fragmented landscape, plant and animal species would encounter barriers when trying to disperse across the landscape. This can lead to a reduction in genetic exchange between the disjunct patches. Riparian forests play an important role at the landscape level as strip corridors for plants and animals along both the terrestrial and aquatic pathways (Forman and Godron, 1981 Mitsch and Gosselink, 1986;

Table 22. Habitats of probably extinct, endangered and threatened plants in Michigan.

	Probably extinct	Endangered	Threatened			Total
			Pteridophytes	Monocots	Dicots	
Aquatic and wetlands	9	3	1	45	33	91
Prairies, open areas, fields	9	3	-	6	24	42
Rock outcrops, bluffs	3	6	6	8	13	36
Woodlands	2	4	2	10	13	31
Dunes and other sandy areas	-	-	-	11	3	14
Unclassified	2	-	3	5	14	24
Total	25	16	12	85	100	238

Source: Reprinted with modifications from Beaman (1977), with permission.

Harris, 1989). The riparian forest is an important ecosystem because of its contribution towards biodiversity at broader scales (Noss and Harris, 1989). This is especially true where there is an abundance of arthropods, vertebrates and over-wintering migrants (Wharton et al., 1981; Harris, 1989). Although upland forest has a higher number in total plant species (Table 23), riparian forests have species that are not common to upland forests and wetlands such as herbaceous bamboo (*Diarrhena americana*), silver maple (*Acer saccharinum* L.), sycamore (*Platanus occidentalis* L.) and black willow (*Salix nigra* Marsh.). The linear, dendritic pattern together with high connectivity that riparian communities offer along stream and river courses, make them ideal pathways for wildlife such as birds, deer, elk and small mammals across regional landscapes (Mitsch and Gosselink, 1986; Harris, 1989). Large tracts of riparian forests are found in the south transect, but not in the north transect. The connectedness of riparian communities needs to be preserved and maintained so that they can function as corridors for wildlife that can move across the landscape.

In the event of global climate change, many plant and animal species would have to migrate long distances to more favorable habitat areas. In regions like Michigan, the biggest concern is whether these organisms will be able to migrate across the fragmented landscape at a rate rapid enough to track global climate change. Ways must be found

Table 23. Total number of plant species in some upland, riparian and wetland forests in Michigan.

	Area (Ha)	Trees	Shrubs	Herbs	Total	Source
Upland forest						
Sanford Natural Area	14.16	56	26	274	356	Beaman, 1970
Baker Woodlot	29.54	45	41	286	372	Stevens and Beach, 1980
Riparian forest						
Red Cedar Natural Area	30.76	35	16	263	314	Kron and Walters, 1986
Wetlands						
North Bog	10.30	10	(woody)	7	17	Keough and Pippen, 1981
South Bog	2.20	2	(woody)	6	8	
Bear Lake Bog	-	26	26	114	166	Hunter, 1975
Summerby Fen	-	9	7	86	102	Weitzman, 1983

to try and mitigate the disjunction of forest patches in the landscape. Possible migratory corridors and "stepping stones" need to be identified and preserved in the landscape to facilitate plant and animal movement. This might help prevent further loss of biotic diversity in the region.

Applications of proximity analysis can give insight as to how current landscape patterns interact to affect dispersal capabilities of selected tree species in the landscape. Isolation of forest patches determines the dispersal success of plant and animal species. Johnson (1988) reported an exponential decrease in sugar maple (*A. saccharum*) seedlings away from isolated seed sources and from a line source along a fencerow in Wisconsin.

Species composition within each patch was not determined in the present study. It was assumed that each patch is capable of acting as a propagule source and that it provides favorable sites for the germination and establishment of seeds. Ignoring the specific locations of individual tree species within forest patches and the exponential decrease in seed fall with distance (Johnson, 1988), a dispersal distance of 400 m for windblown seeds was chosen. It was also assumed that there would not be a significant exchange of windblown seeds beyond this distance. Johnson (1988) found that most green ash (*Fraxinus pennsylvanica*), sugar maple and American basswood (*Tilia americana*) are windblown only a few tens of meters from the seed source and few are dispersed beyond 200 m, while van der Pijl (1972) reported possible dispersal distances of up to 500 m for wind-dispersed higher plants of the world. Dispersal distances of windblown seeds are often found to be reported as approximate distances only. This is because seed dispersal by wind involves a complex of processes and the outcome is difficult to predict (Howe and Smallwood, 1982). Also, several factors influence dispersal of windblown seeds such as local wind turbulence, wind speed, wind direction, seedfall velocities and timing of seed release (Johnson et al., 1981), and the contribution of each plant within a patch (McClanahan, 1986).

Proximity analysis for upland patches in both the north and south transects shows clusters of patches that exist close enough to one another to allow seed exchange between them. Green ash (Fraxinus pennsylvanica) has been estimated to disperse as far as 400 m from seed sources while sugar maple (A. saccharum) has less dispersal capability (Johnson, 1988). Johnson (1988) suggests that d_h, the half distance of dispersal, or the distance where the seedfall is half the quantity of the sources (McClanahan, 1986) is 10 m for A. saccharum. Simulation of A. saccharum using seed fall velocities also provides a similar conclusion concerning the limited dispersibility of Acer species (Johnson et al., 1981). The greater dispersal capability of F. pennsylvanica (three-fold greater than A.

saccharum) gives it the capability to invade patches farther away from seed sources (Johnson, 1988). Consequently, we would expect fewer patches in the transects to be isolated in relation to F. pennsylvanica as compared to A. saccharum. Interpatch distances exceeding 400 m are characteristic of a few parts of the landscape (Figures 15 and 18) and exceed the dispersal capabilities of many other windblown seeds even F. pennsylvanica.

Quercus spp. have the potential to be dispersed over 1 km by birds (Johnson and Adkisson, 1985). This is an example of a zoochore with a dispersal capability that exceeds the dispersal capability of windblown seeds. However, the movement of animals that transport acorns across a landscape can be limited by the type of agricultural matrix. Thus, the landscape within the transects studied in Lower Michigan might be more fragmented for A. saccharum and less so for A. pennsylvanica and Quercus spp.. Using a threshold distance of 200 m in a proximity analysis, Dunn et al. (1991) found that the landscape in Cadiz Township, Wisconsin is less fragmented for Quercus rubra, but more fragmented for A. saccharum and F. americana.

Since the landscape within the transects is fragmented for tree species, it will be fragmented for the understory plants as well, including herbs. Many temperate herbs are animal-dispersed. In a mesic beech-maple forest in New

York, 53% of 45 herbaceous angiosperms are animal-dispersed. Of this, 54% are dispersed by ants (Handel et al., 1981). Similarly, 30% of 23 herb species in 10 mixed hardwood forest sites in West Virginia are ant-dispersed (Beattie and Culver, 1981). This indicates that most of the herb species are dispersed within a local area and even if they are dispersed by small mammals, roads that are greater than 20 m in width could represent significant barriers (Oxley et al., 1974). Therefore the survival capabilities of woodland herbs are much less certain than those of trees and shrubs because the herb population size is frequently very small. Also, woodland herbs are not adapted to long-distance dispersal across a fragmented landscape and often require specific site conditions for establishment (Davis, 1990).

Dispersal capabilities of A. saccharum and Quercus spp. were selected for the macro-level analyses. Sites of seed sources andipossible sites for seed germination and establishment were divided into two categories based on soil textures. This simulation only considered the interactions of distance and suitable soil textures as factors that determine the successful dispersal of seeds. Other factors such as species composition for individual forest patches, microclimate, level of competition, other soil characteristics and disturbance patterns were not accounted for in this study. The dispersal distance of A. saccharum is about 4 km in storm conditions (van der Pijl, 1972; Johnson et al., 1981) and this was the threshold distance used for A. saccharum. Conveniently, it is a multiple of the pixel size (1 km) in the Michigan forest associations data base.

Patches of A. saccharum occurring on optimal and sub-optimal soil types exist as clusters and disjunct fragments in the state of Michigan. Clusters of forest patches that are close enough have the potential to exchange seeds. Interpatch distances can be used to characterize the fragmentation of forested landscapes. A. saccharum on both optimal and sub-optimal soil types in central Lower Michigan is highly fragmented. More than 60% of the landscape of Michigan falls into the category of land that exceeds the dispersal distance of sugar maple and only 10-14% of the whole landscape has the potential to provide suitable establishment sites. This can pose a problem for tree species that need to extend their ranges northward should rapid global warming occur.

Most of the Quercus spp. in Michigan are found on their optimal soil types. These trees can serve as acorn sources and most acorns, if dispersed successfully, have a good chance of surviving and establishing themselves on optimal soils within the 1 km buffer zone. For acorns that originate from trees on sub-optimal soil types, less than 1% of the landscape within the 1 km buffer zone is composed of favorable soil types. No oak sources are shown on the map for the Upper Peninsula. Red, white and black oaks that are common on old dune ridges (Wells and Thompson, 1982; Hazlett, 1986) might be able to follow the corridor found along the west coast of Michigan as a possible migratory pathway northward if these species have to extend their ranges north should climatic change occurs.

Distances among forest patches in the fragmented landscape of Michigan might hinder the successful dispersal of seeds to suitable sites for establishment. The impact of fragmentation is shown to vary with species in this study and is also reported by Dunn et al. (1991). The landscape of mid-Michigan taken at the township or county level might not be fragmented to some wind- and animal-dispersed tree species such as ashes and oaks, but macro-level studies might not support similar results. The results suggest that it is not always possible to make extrapolations of findings across different spatial scales and more studies need to be conducted on the effects of scale on spatial and temporal changes. The impact of landscape fragmentation on ecological processes that take place in the landscape need to be studied in greater detail.

In the event of global climatic change, global temperatures have been predicted to increase between 2° and 5° C in the next century (Davis, 1990; Andrasko, 1990). The broad-scale distribution of terrestrial ecosystem co plexes is determined by climate and can be altered due to climatic change. Climatic change can be caused by natural processes or by human activities such as the burning of fossil fuel which leads to an increase in atmospheric carbon dioxide concentration (Andrasko, 1990).

The impact of climatic change on the geography of major vegetation zones using the Holdridge Life Zone Classification has been evaluated by Emanuel et al. (1985). The Holdridge Life Zone Classification system provides a means for relating the character of natural vegetation associations to climatic indices. The system is determined by average biotemperature (average daily, weekly, or monthly temperature over a year), average annual precipitation, and potential evapotranspiration ratio, the amount of water that would be released to the atmosphere under natural conditions with sufficient but not excessive water available throughout the growing season (Holdridge, 1967).

In order to study the impact of climatic change on vegetation, the Holdridge Life Zones were remapped corresponding to temperature increases caused by a doubling in carbon dioxide concentration under a simulated climatic change (Emanuel et al., 1985). Under this simulation, the Cool Temperate Forest Zone became interspersed with Warm Temperate Dry Forest. All of Michigan would remain as Cool Temperate Moist Forest under this change except for a small portion of the southeastern Lower Peninsula, which will be part of the Warm Temperate Dry Forest (Emanuel et al., 1985).

This simulation is, however, limited by various factors (Emanuel et al., 1985). One of them is the absence of accurate estimates of changes in precipitation, and changes in soil characteristics over a long period of time. There are also inconsistencies between the resolution of simulated climatic change and life-zone maps derived from meteorological data. The use of simulation results from climate models in the analysis of vegetation patterns associated with seasonality, topography and transition zones is restricted by the coarse resolution of climate models. Furthermore, the actual land cover has been modified by human activities, such as that seen in Lower Michigan. Therefore, the impacts of climatic change in regions composed of highly managed ecosystems will depend on human response reflected by altered management practices. Much refinement is required in data sources and climate models before the magnitude of complex vegetation change can be predicted with a high degree of sensitivity. This study has shown some applications of GIS in landscape level analysis. One has to be aware also of the errors that are propagated while using GIS as a tool. Sources of error include: 1) overt errors resulting from the use of outdated source material, and inappropriate or incompatible data format, resolution, and scale; 2) manuscript error derived from georeferencing errors, and 3) processing errors generated by the operator, equipment, or software algorithms (Burrough, 1986; Johnson, 1990). Care was taken to try and minimize the first two sources of error by validating the accuracy of topographic maps, analyzing data of different scales separately, and deriving and calculating forest patch parameters such as area, perimeter, fractal dimension and complexity ratios in the vector format. The third source of error is inherent in many programs. The utility of GIS technology in spatial analyses and simulation models warrants further investigation.

SUMMARY AND CONCLUSIONS

The goal of this study was to describe the structure of Lower Michigan's forest patches, with respect to natural and human-induced landscape processes. The effects of forest patch structure on ecological processes were evaluated at two different spatial scales. Seven topographic maps representing portions of two contiguous counties in Michigan were chosen as representative examples of forest patch structure to be quantified for a micro-level analysis, while already existing statewide data sets were used in the macro-level analysis.

There were 1,887 upland patches, 224 riparian patches and 108 wetland patches in the study transect. Upland patches accounted for the largest area of forested land in the study area followed by riparian and wetland patches. Size of all forest patches ranged between 0.04 and 241.13 ha. Fractal dimensions for all forest categories ranged between 1.20 and 1.42. Complexity ratios indicate that riparian patches have more complex shapes than upland and wetland patches. It has been shown that size and shape of large upland patches, riparian forests and wetlands are related to topography, geomorphologic features and patterns of soil fertility, in addition to anthropogenic activities.

It is appears that in the south transect, that as the roughness of topography increased, the size of forest patches increased.

Patch structure, including such as size and geometry is not strongly influenced by the patches' proximity to a city. Results suggest that patterns of land use in Michigan were somewhat dependent upon the responses of humans to their perception of natural features in the landscape, such as topography and geomorphology, rather than proximity to a city.

This study showed that 57.67% of the total upland patch area in the three townships in Ingham County occurred on prime farmland soil types while the percentage was 68.94 in the two townships of Clinton County. There has been a net increase of 129.85 ha in upland patch area between 1938 and 1976. This increase reflects a slow reversion of farmland to forest land and a decline in the conversion of forest land to other land uses.

About 62% of all upland patches are larger than the minimum area required for trees, shrubs and herbs in a highly mixed deciduous forest. These patches might support a near full complement of plant species, but will not be large enough to support viable populations of large animals.

Quantification of patch size is important because the maintenance of a critical minimum patch size is necessary to preserve biodiversity. Isolation of forest patches determines the dispersal success of plant and animal species and has an impact on the rate that species can migrate across the landscape. Using a buffer zone of 400 m in the proximity analysis on upland patches within the study transects showed that the mid-Michigan landscape is fragmented for sugar maple but not for oak and ash species. However, at the statewide level, proximity analysis using 4 km and 1 km buffer zones for sugar maple and oak species, respectively, demonstrated that the landscape is fragmented for both sugar maple and oak species. Therefore, the findings reveal that the impact of fragmentation varies with species and the scale at which studies are conducted may influence conclusions made about pattern and processes in the landscape. GIS has been demonstrated to be a useful and powerful tool in broad-scale studies of landscape patterns such as conducted in this study.

RECOMMENDATIONS

Changes in the landscape either by natural or anthropogenic processes can lead to landscape fragmentation. It is important to conduct studies on landscape fragmentation because it has serious implications on local and regional patterns of diversity and is recognized as a major conservation issue. Also biodiversity is one of the research priorities of "The Sustainable Biosphere Initiative: an Ecological Research Agenda" (Ecology Vol. 72, No. 2).

Interesting questions that can be addressed concerning biodiversity include the effects of landscape pattern (sizes, shapes, and arrangement of habitat patches) on population size, dispersal, and diversity at the local landscape level, such as that attempted in this study. With this in mind, there needs to be good and reliable data sources for future research. Individual researchers and organizations can avoid the duplication of labor in data acquisition by facilitating the exchange of data materials or creating an archive that can be accessed by contributing and interested researchers. More time can then be used in analyzing and solving research problems. As the amount of research a person can do is often constrained by time and money, the type and availability of data sources for an area intended for study should be taken into consideration before a decision on the number of samples to be taken is made. This is especially true when using remotely-sensed data.

The spatial arrangement of patches, type of matrix and distance between patches are some aspects of landscape structure that were not characterized in this study. These landscape characteristics can provide important information on the effects of pattern on ecological processes such as dispersal of species. Mathematical algorithms will be useful in this aspect when they can be incorporated into the spatial analysis. Simulations and models such as the percolation theory (Gardner et al., 1987) can assist in studies on species dispersal. Field studies involving the quantification of species composition and number together with mapping of species intended for study; and information on the population biology of species will provide a more accurate picture on the dispersal capabilities of species in a fragmented landscape.

Some underlying factors that influence the formation of landscape pattern include geologic features, topography, soil characteristics, and human behavior. Methods need to be developed in order to quantify the relationships among landscape pattern and underlying factors that lead to the formation of the patterns. Of particular importance in ecology is the study of ecological effects of changing processes on patterns. Processes and events at one scale and time have implications for, and may even control processes and patterns at other scales. As shown in this study, landscape structure is scale-dependent. Therefore, a sufficient sample size of local landscape studies is required or variations caused by differences in scale need to be investigated before the results can be used to represent regional landscape patterns.

Landscape level analysis on the statewide level should focus on the acquisition of data bases on the structure of landscape elements and develop methodologies to analyse the function and change of these elements. Basic research that is conducted to gather information on the physical and biological attributes of landscape elements on a broad-scale is necessary for land planning and management purposes. As no individual element exists singly without any interaction with other elements in the landscape, it will be very useful to have a broad view of the structure, function and change of elements in the landscape. This ensures that land-use decisions have been made based on an encompassing view of the landscape and not just a part of it. The coupling of theoretical and empirical work through an iterative sequence of model and field experiments will help achieve these goals.

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