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**A Quantitative Analysis of
Forest Island Pattern
in Selected Ohio Landscapes**

G. W. Bowen
R. L. Burgess

ENVIRONMENTAL SCIENCES DIVISION
Publication No. 1719

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A QUANTITATIVE ANALYSIS OF FOREST ISLAND PATTERN
IN SELECTED OHIO LANDSCAPES^{1,2}

G. W. Bowen and R. L. Burgess

ENVIRONMENTAL SCIENCES DIVISION
Publication No. 1719

¹Submitted as a thesis by G. W. Bowen to the Graduate Council of the University of Tennessee in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

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The purpose of this study was to quantitatively describe the various aspects of regional distribution patterns of forest islands and relate those patterns to other landscape features. Several maps showing the forest cover of various counties in Ohio were selected as representative examples of forest patterns to be quantified. Ten thousand hectare study areas (landscapes) were delineated on each map. A total of 15 landscapes representing a wide variety of forest island patterns was chosen. Landscape placement was dependent upon the grain and intensity inherent in the forest island patterns.

Raw data taken from each landscape included measurements of the perimeter and area of each woodlot and measurements of the distances between woodlots. The raw data were converted into a series of continuous variables which contained information pertinent to the sizes, shapes, numbers, and spacing of woodlots within a landscape. Other features of landscapes (topography, soils, glacial history, original vegetation, and potential natural vegetation) were recorded as non-continuous nominal variables.

The continuous variables were used in a factor analysis to describe the variation among landscapes in terms of forest island pattern. Most of the variation among landscapes was accounted for by two factors. One factor was strongly related to the portion of the

study area covered by forest, as measured by the variable percent forest cover. The other important factor was the degree of forest fragmentation, as measured by either the total number of woodlots in a landscape (island density) or landscape DI (a function of forest perimeter/area ratio).

The factors pertaining to forest cover and fragmentation were used as the basis of a two-dimensional ordination of landscapes. The ordination proved to be a useful graphic summary of landscape variation on which to test hypotheses concerning forest island patterns.

The environmental features of landscapes (as measured by nominal variables) were related to forest island patterns by: (1) overlaying environmental information on to ordination plots; and (2) using discriminant analysis with the environmental features as the criteria of discrimination. The results showed that forest island patterns are related to topography and other environmental features correlated with topography. Landscapes with smooth topography and arable land had but a few percent forest coverage divided among a relatively low number of small woodlots. With increasing topographical roughness, the size and/or density of forest islands increased. The greatest degree of forest fragmentation was associated with 20-30 percent forest cover in hilly topography. Since forest pattern is a result of the cumulative effects of land use over time, these results were interpreted to mean that the patterns of land use in Ohio were somewhat dependent on topography and related factors.

The ability to quantify landscape pattern on a regional basis has applications to regional ecology. Mathematical models can be developed

to predict changes in landscape pattern for given land use scenarios, and parameters of landscape pattern can be analyzed as indicators of habitat and resource distribution and long-term ecosystem stability. The ability to measure forest island pattern and other aspects of landscape pattern can be one part of quantitative approaches to solving regional ecological and land use problems.

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I. INTRODUCTION

Since the arrival of European settlers, the forests of eastern North America have undergone considerable change. The first immigrants brought with them the concepts of agriculture, industry, and the semi-urban environment of the village or town in which to live and work. The natural environment of the new continent was an adversary to be tamed. Land had to be cleared of trees to make it suitable for cropland, pasture, and dwellings. As time passed, the population grew and, with the impetus of the steam engine and the subsequent Industrial Revolution, expanded westward from the original settlements. By 1830, much of the landscape of the eastern United States was dominated by man. In these man-dominated landscapes, the process of settlement, including the growth of agriculture, industry, and urban centers has led to extensive fragmentation of the original forest, creating a landscape characterized by isolated patches, termed "forest islands," set in a variable matrix of non-forest land (Curtis 1956). Concurrent with fragmentation has come the regional or local extinction of species and loss of pristine ecosystems (Burgess 1978). An understanding of these changes in the structure, composition, and dynamics of forests requires quantitative analysis and is important in present and future efforts to maintain local and regional landscape diversity; a diversity that is important not only for the survival of plant and animal populations, but also for the fulfillment of the aesthetic and recreational needs of the human population.

The concept of landscape pattern as used in this thesis needs to be defined. A landscape is defined as "a portion of territory that the eye can comprehend in a single view" (Woolf 1974). An example would be the area of land that would be viewed from the vantage point of a hilltop, an airplane, or an aerial photo. Pattern is simply a "configuration" or "relative arrangement of parts" (Woolf 1974). Some of the distinctive parts or features of a landscape include its vegetation, topography, and soils. Landscape pattern can therefore be defined by the relative arrangement of vegetation, topography, soils or any other features of interest.

Depending upon the purpose of the investigator, one or more landscape features may be emphasized when describing or characterizing an area or region. In ecological research, attention is often focused on vegetation patterns. An analysis of vegetation pattern usually includes a discussion of species composition, spatial arrangement, relation to environmental gradients, climatic history, cultural history, and successional patterns pertinent to the vegetation in question. If an analysis of vegetation is to predict the future and explain the past, as well as describe the present, it must include not only a description of vegetation, but also a consideration of the patterns and processes that influence it, that is, the spatial patterns of environmental factors and the random and deterministic processes associated with the development and maturation of vegetation and with the activities of man. In this thesis, landscapes are quantitatively characterized primarily by one distinctive feature, the spatial arrangement or pattern of forest islands. The forest island patterns

are then related to the topography, soils, glacial history and cultural history of those landscapes.

Topographic, edaphic, and vegetation patterns all affect the processes of settlement, land use (agricultural and urban development), and subsequent landscape change, that are primarily responsible for modern landscape patterns. Auclair (1976) found significant correlations of topographic, edaphic and presettlement vegetation patterns with modern patterns of agricultural land use and forest cover in Dane County, Wisconsin. Modern landscape patterns in turn influence current ecosystem processes by defining one or more biotic components of ecosystems, e.g., vegetation and wildlife. Since ecosystem processes are defined in terms of the interactions of their biotic and abiotic components, a change in the biotic component may influence such ecosystem characteristics as species replacement patterns, species extinction rates, nutrient cycling, productivity, and standing crop biomass. For example, Auclair and Cottam (1971) report that in the highly fragmented forests of southern Wisconsin, sugar maple and basswood (*Acer saccharum* and *Tilia americana*) seem to be decreasing in importance, while black cherry (*Prunus serotina*) has increased [Nomenclature of vascular plants is based on Gray's Manual of Botany (Fernald, 1950)]. Isolated patches of natural habitat in urban areas are also prone to increased rates of species extinction (Greller 1975; Davis and Glick 1978).

Despite evidence that vegetation pattern can markedly affect ecosystem processes, this phenomenon has not become a major area of research concern. For the most part, vegetation studies have been

concerned with describing and classifying plant communities and relating those communities to environmental factors in which the effects of man are considered minimal. A quantitative method for describing the spatial aspects of vegetation pattern must be developed before vegetation pattern can become an object of study to be related to environmental factors and ecosystem processes.

In general, the objectives of this thesis were to develop a methodology for quantitatively describing the forest island patterns of selected Ohio landscapes and then to relate those patterns to environmental factors. The specific goals were to: (1) Review the pertinent literature; (2) Identify and measure a series of several variables suitable for quantifying various aspects of landscape pattern for a single study area. These variables represent properties emergent with the scale of landscape types; (3) Use multivariate statistical techniques to analyze the data; (4) Interpret the variation among landscape patterns in ecologically meaningful terms; and (5) Discuss the implications of this research for other ecological concepts and environmental problems.

II. LITERATURE REVIEW

This review, focused on the broad-leaved deciduous forest of eastern North America, concerns five questions: (1) What have been the approaches to the study of vegetation in the eastern deciduous forest?; (2) What are the current landscape patterns exemplified by the distribution of forest islands on local, regional, and biome scales?; (3) How can landscape pattern, based on forest islands, be quantitatively described?; (4) What environmental, historical, and cultural factors have determined the landscape pattern and how is the pattern changing over time?; and (5) How are the vegetation dynamics of forest islands affected by landscape pattern?

A vegetation analysis is essentially a human creation "serving to order, interrelate, and interpret some of the information about natural communities" (Whittaker 1957). An analysis of vegetation is affected not only by the objectives of the investigator but also by his techniques and his philosophical framework. Those who view vegetation as occurring in discrete units will probably prefer classification techniques for studying vegetation, while those who see plant communities as "vegetational continua" (Curtis and McIntosh 1951) gradually changing over time and distance will probably choose ordination techniques for relating communities to each other (McIntosh 1967; Whittaker 1967).

In classification, the objects of study, e.g., plant communities, are grouped into classes on the basis of their common properties. The best groups are those about which the most numerous, precise, and

important statements can be made concerning the objectives (Cline 1949, Küchler 1967). If the eventual goal of a vegetation study is to produce a vegetation map, then some sort of classification scheme is needed, because mapping requires the delineation of definite boundaries around homogeneous units (Küchler 1973). The works of Braun-Blanquet (1932) best exemplify the school of thought that perceives vegetation as occurring in relatively discrete units termed associations.

Determining the location of boundaries on a vegetation map can be a problem if the transition between vegetation types is gradual (Küchler 1973). Although sharp boundaries do occur between natural vegetation types, the existence of gradual transitions provided the impetus for developing ordination techniques to describe continuous variation. In ordination, the units of study (plant communities) are described by variables exhibiting continuous variation and are arranged in a uni- or multi-dimensional order based on the actual values of the descriptive variables. This arrangement, termed an ordination by Goodall (1952, 1954), is translated directly from the German word "Ordnung" (Ramensky 1930).

The philosophical basis of ordination is firmly rooted in the individualistic concept of species association (Ramensky 1924; Gleason 1917, 1926, 1939). Restated by McIntosh (1975), this concept simply says that each species responds "in its own way to each environmental variable, including other species, which affect it." Therefore, plant communities are individualistic in that they are expressions of their local environments. Early support for Gleason's ideas came from Cooper (1926) who emphasized the dynamic nature of plant communities. But it

was not until the works of Curtis and McIntosh (1951), Whittaker (1956), and Bray and Curtis (1957), that Gleason's concepts began to be reflected in the methodology of vegetation studies. For the first time the objects of study (vegetation stands) were arranged or ordinated in a sequence which was then related to an environmental gradient such as soil moisture or elevation (McIntosh 1967, Whittaker 1967).

Many of the vegetation analyses on a regional or local scale in the United States employ ordination techniques to relate vegetation to environmental factors, whenever the objective involves vegetation mapping, some type of classification scheme is required in order to delineate boundaries. Fortunately there is seldom an intrinsic conflict between ordination and classification approaches, because the map scale and degree of contrast (rapidity of change) between plant communities determine how and where boundaries are drawn (Küchler 1973). In most studies where the goal was to produce small scale maps, e.g., 1:7500000, of the entire eastern deciduous forest, classification of major forest types was the most common approach.

Vegetation Pattern of the Eastern Deciduous Forest

The eastern deciduous forest roughly encompasses the region between the Mississippi Valley and the Atlantic seaboard. It stretches north from the Gulf of Mexico to the vicinity of the Canadian border, and is dominated throughout most of its range by tall, broad-leaved trees that shed their leaves completely in winter. Evergreen trees dominate only where local environmental conditions permit. The topographic, edaphic, and climatic diversity inherent in the region has

led to a correlated diversity of vegetation, and has spawned a variety of classification schemes that attempt to describe the forest as it would appear essentially unaffected by man.

Small scale vegetation maps describing forest patterns have been based on classification schemes developed by Shantz and Zon (1924), Weaver and Clements (1938), Braun (1950), Küchler (1964), Bailey (1976), and Daubenmire (1978). The classifications attempt to organize a coherent body of knowledge from the wealth of information concerning the eastern deciduous forest, and from the body, to extract an understanding of the forest. The classifications are similar in that they often recognize roughly the same areas (e.g., the beech-maple region, the maple-basswood region, the oak-hickory region, etc.). More importantly, these systems differ in their basic philosophical approaches and in their goals as to what is to be understood. These differences, in turn, affect the way in which evidence on natural communities is selected, treated, and interpreted.

Clements (1928), Braun (1950), and Daubenmire (1978) developed hierarchical classification systems based on the plant formation as the major unit of vegetation. The eastern deciduous forest was recognized as a formation expressing the climatic control of vegetation. Within the eastern deciduous forest, lesser units, termed associations or climax communities, were distinguished according to physiognomy, floristic composition, history, and ecological relationships. Dominant plant species provided visible unity and were believed to exert a controlling influence on the rest of the climax community. Braun's classification was intended to serve as the basis of detailed

vegetation studies. The classifications by Clements and Daubenmire were less detailed, serving to summarize, in a general way, the distribution of important plant species and the historical and ecological reasons for their distribution.

Shantz and Zon (1924) and Küchler (1964) developed nonhierarchical classification systems of the vegetation of the United States based solely on physiognomic and floristic characteristics rather than on ecological relations. They were designed to show, in some detail, the potential natural vegetation, that is, the vegetation that would be present if the effects of man were removed and succession were telescoped into a single moment. Küchler's map uses more recent information and is somewhat more accurate and detailed than the Shantz and Zon map. In the area roughly corresponding to the eastern deciduous forest, one can recognize 14 of the vegetation types in Küchler's classification. These classes are thought to represent the best compromise between map scale, the low degree of contrast between vegetation types in the eastern U.S., and the amount of detail to be portrayed.

Bailey (1976, 1978) developed a hierarchical classification system which divides the country into "ecosystem regions." The highest categories (Domain and Division) are based on Köppen's (1931) climate classification. Lower categories (Province and Section) are based on life form, land form, and dominant species. The eastern deciduous forest is classified as one of the provinces within the Hot Continental Division of the Humid Temperate Domain. The Eastern Deciduous Forest Province is further divided into five sections. Other areas

traditionally considered as part of the eastern deciduous forest are contained in eight sections divided among four other provinces. The purpose of this system is to provide a framework for regional land management.

The above schemes attempt to classify the natural vegetation pattern as it would exist when affected primarily by climatic, edaphic, topographic, and pyric conditions. The actual vegetation is often far different from what would be considered the natural vegetation of a region (Klopatek and Olsen et al. 1979). Cultural vegetation, such as crops and orchards, and seminatural vegetation, such as pastures, often exceed natural vegetation in areal extent.

The pattern of the eastern deciduous forest that has evolved is quite complex and ranges from areas of almost complete coverage to areas where the forest has been reduced to isolated island-like entities in a landscape greatly modified by agriculture and urbanization. The pattern of vegetation is now virtually dependent upon the activities of man and his patterns of land use. Landscape utilization is in turn affected by patterns of land ownership and a variety of social and environmental forces.

I have discussed how vegetation pattern has been viewed on a biome scale. Studies of vegetation pattern have also been done on regional scales (Whittaker 1956, McIntosh 1972, del Moral and Denton 1977, del Moral and Watson 1978), and investigations of local vegetation pattern are too numerous to list. A neglected scale of study is the pattern of forest patches or islands in man-dominated landscapes and the relation between pattern and ecosystem processes. This literature review now

shifts to a consideration of forest islands and their relationship to land use and vegetation dynamics.

Occurrence of Forest Islands in Presettlement Times

In presettlement times, the eastern deciduous forest was essentially continuous except for small areas modified by Indians or natural catastrophes (Bromley 1935, Day 1953). Other widely scattered areas were unsuited for forest cover because of peculiar combinations of climatic, edaphic, and topographic conditions, e.g., the heath balds and shale barrens of the Appalachians, the cedar glades of Tennessee, the black belt prairies of Mississippi and Alabama, and the Hempstead plains of Long Island (Burgess 1978). On its western edge, the forest graded into prairie along the prairie-forest transition zone stretching from Texas north through Oklahoma, Missouri, Illinois, Indiana, Wisconsin, and Minnesota into the aspen parklands of Canada. It is along this transition zone that the forest cover was reduced to the point where trees occurred singly or in groves of various sizes and shapes.

The prairie-forest transition zone could be described as a mosaic of forest, grassland, and savanna. Oak-hickory savanna was prevalent from central Texas through central Oklahoma into southern Kansas in an area known as the Cross Timbers. The dominant species were blackjack oak (Quercus marilandica) and post oak (Q. stellata) with lesser amounts of black hickory (Carya texana) (Bruner 1931, Dyksterhuis 1948, Braun 1950, Rice and Penfound 1959). The transition zone from southeast Kansas through northwest Missouri into southeast Iowa, east

across Illinois into northwest Indiana and Ohio (the "Prairie Peninsula") was characterized by prairie and oak scrub on the open uplands and oak-hickory or oak-basswood forests on protected slopes, and in ravines and stream valleys (Gleason 1922; Transeau 1935; Aikman and Smelser 1938; Braun 1950; Hewes 1950; Steyermark 1959, 1963; K uchler 1964). Like its counterpart in Texas and Oklahoma, the transition zone in northwestern Indiana, northern Illinois, southwest Wisconsin, and parts of central Minnesota was dominated by oak savanna and prairie with lesser amounts of oak forest in protected areas (Gleason 1922, Stout 1944, Cottam 1949, Buell and Cantlon 1951, Potzger et al. 1956, Curtis 1959, K uchler 1964). The most common tree in this landscape was bur oak (Quercus macrocarpa) with lesser amounts of white oak (Q. alba), black oak complex (Q. velutina, Q. ellipsoidalis, Q. borealis), and shagbark hickory (Carya ovata). In Minnesota, oak savanna and maple-basswood forest formed a relatively narrow strip between the prairie on the west and conifer forest on the east (Daubenmire 1936). The maple-basswood community sometimes ended abruptly at the prairie, or it graded into the brush prairie composed of isolated stands of bur oak, Corylus americana, Populus tremuloides, and Rhus glabra. Brush prairie was considered by Ewing (1924), to be a stage transitional from prairie to forest in the absence of fire. Brush prairie extends into Canada where it forms the matrix of the aspen parkland (Bird 1961).

The interaction of fire with climatic, topographic, and edaphic conditions controlled the presettlement vegetation pattern (Gleason 1922; Transeau 1935; Daubenmire 1936; Borchert 1950; Wells 1970a,

1970b). With 58 to 102 cm of annual rainfall (Bailey 1978), the region was subject to periodic drought and widespread fires, both natural and manmade. The local edaphic and topographic conditions further affected water relations which influenced plant growth. In the warmer areas, fine-textured soils favored grassland communities, while more porous soils with deep, slowly permeable layers favored the growth of trees (Dyksterhuis 1957). In Minnesota, deep, coarse, sandy soils favored grasslands and heavier soils favored trees (Buell and Facey 1960). Topographic position influenced the degree of exposure to desiccating elements of sun and wind. In general, tree growth was favored by mesic combinations of soils and topography. The occurrence of fire every few years restricted closed forest to protected mesic sites, such as ravines, stream bottoms, and north-facing slopes. On exposed uplands fire maintained grassland, and in large areas it created savanna consisting of large fire-resistant trees (Quercus macrocarpa or Q. stellata and Q. marilandica) scattered in a grass landscape (Rice and Penfound 1950, Gleason 1922, Daubenmire 1936, Stout 1944, Cottam 1949, Steyermark 1963, Buell and Facey 1960).

The pattern of forest islands in the transition zone reflected topography. Forest islands tended to be linear in shape since they followed stream courses and ravines. They varied from a few to hundreds of hectares in size. To the east, individual forest islands lost their character and merged to form increasingly continuous forest cover.

Land Use and Landscape Pattern Following European Colonization

Since European colonization, land use patterns associated with agriculture and urban development have come to supercede natural disturbance in importance as a factor influencing regional ecosystems and landscape pattern. Land use in turn has been strongly influenced by social trends and has become correlated with patterns of land ownership and environmental factors such as topography and soils. Throughout the eastern deciduous forest, a landscape characterized to a greater or lesser degree by forest islands has become evident wherever the land has been suitable for agriculture and urbanization. These conditions may have important consequences for ecosystem dynamics as well as for individual species.

To study the dynamics of changing landscape pattern, it is necessary to study the concurrent changes in land use patterns. One approach to this problem has been to compare presettlement vegetation patterns to modern patterns and relate the changes therein to land use (Auclair 1976). Historical writings by early explorers and settlers and government records are valuable tools for determining original landscape pattern. Other records such as maps and aerial photos can be used to study changes in land use and landscape pattern over time.

An important source of information is the records of the General Land Office Survey. The Congressional Ordinance of 1785 established the General Land Office Survey to divide the public lands of the United States into 6-mile square townships. Each township was further divided into 36 sections, each one mile square (2.59 km^2). Meridians (north-south lines) and baselines (east-west lines) were the basis for

the rectangular coordinate system by which townships were surveyed. At the intersection of section lines and at points halfway between, surveyors marked two or four nearby trees designated as "witness" trees. The survey notes included the common name, diameter, direction, and distance from the corner for each witness tree and commented on soils, vegetation, and other features (Bourdo 1956, Marschner 1959, Stearns 1974). Quantitative and qualitative data from this source and others have enabled investigators to create maps depicting vegetation as it existed at the time of the survey. This has been done for Indiana (Potzger et al. 1956), Wisconsin (Finley 1976), Ohio (Gordon 1969), Minnesota (Marschner 1976), Michigan (Veatch 1959), Nebraska (Kaul 1975), and New Mexico (Gross 1976).

Changes in land use and landscape pattern have been documented for different parts of the eastern deciduous forest. The forests of New England were among the first to feel the effects of agriculture. Raup (1966), in his discussion of the land use history of the area around Petersham, Massachusetts, points out that from 1733 to 1791 only 15 percent of the area had been cleared of its mixed hardwood forests. With an improved road network and resulting prosperity, the proportion of cleared land rose to perhaps as high as 90 percent by 1850. The remnant forest was restricted to ravines, steep slopes and hilltops. The opening of transportation routes from the eastern population centers to the rich farmlands of the midwest meant that crops from Petersham's rocky, hand-labor-intensive farms were no longer competitive. Within 20 years, half the land cleared for farming had been abandoned. Invasion by white pine (Pinus strobus) from the

remnant forests led to the commercial lumbering of this species throughout the region from 1900 to 1920. Today the area is 85 percent forested. This illustrates how natural processes and man's activities work hand in hand to effect changes in the landscape.

A similar story can be told for the South. Much of the Georgia Piedmont had been cleared and put into cultivation by the early 1800's. Destructive farming methods, the Civil War, an agricultural depression, and the boll weevil epidemic resulted in wholesale farm abandonment during the late 1800's and early 1900's (Brender 1974). Nevertheless, by 1920 only 35 percent of the land was covered by forest. By 1972 this percentage had increased to 64 percent (Sharpe and Johnson 1981). Further changes in the composition of the Georgia Piedmont forest are expected because of successional processes leading to an increased importance of hardwoods (Johnson and Sharpe 1976).

The landscape pattern of the Piedmont is kept in a further state of change because of turnover between cleared land and forested land. For instance, in the upper Piedmont of Georgia between 1961 and 1972, approximately 151,000 hectares of forest were cleared while 116,000 hectares of land formerly classed as nonforest reverted back to forest (Knight 1974). In contrast to the Piedmont, where the rate of clearing has almost been balanced with the rate of abandonment, there is a continuing trend of deforestation in the Lower Mississippi Valley. Nearly 75 percent of the bottomland hardwood forests have been cleared in response to agricultural pressures. It is expected that further clearing will leave only 20 percent of the hardwood forests intact (Sternitzke 1976).

Land use change in predominately prairie regions has been documented. Burgess (1964) used General Land Office survey records, aerial photos, field studies, and U.S. Geological Survey topographic maps with vegetation overprint, to document vegetation change in Helendale township in southeastern North Dakota. From 1871 to 1961, agricultural land grew to occupy 89.5 percent of the township. Prairie decreased in areal extent from 81 to 1.5 percent, savanna shrank from 9.13 to 2.77 percent; and forest decreased from 8.41 to 3.50 percent.

Since settlement, agriculture and urban development have changed much of the landscape of Ohio and Wisconsin. At the time of settlement in 1788, about 95 percent of the Ohio territory was forested. This proportion decreased so rapidly that by 1890 only 18 percent of the original forest cover remained. By 1944 only 14.8 percent remained, and most of that was concentrated in the rugged southeastern part of the state (Diller 1944). For instance, in Miami County, Ohio (glacial till plain, once heavily wooded), only 3.4 percent of the county was forested as of 1941, and 87 percent of that was on privately owned farms. The average woodlot size on each farm was 4.1 hectares (Schlemmer 1941). By 1968 forest cover had increased to 24 percent of the state with all of the gains occurring in the hill country of the southeast (Kingsley and Mayer 1970).

Using records from the General Land Office Survey and the Wisconsin Land Economic Inventory, Curtis (1956) showed the change in wooded area (maple-basswood forest) in Cadiz Township, Green County, Wisconsin (Fig. 1). By 1882, 80 percent of the 1831 presettlement

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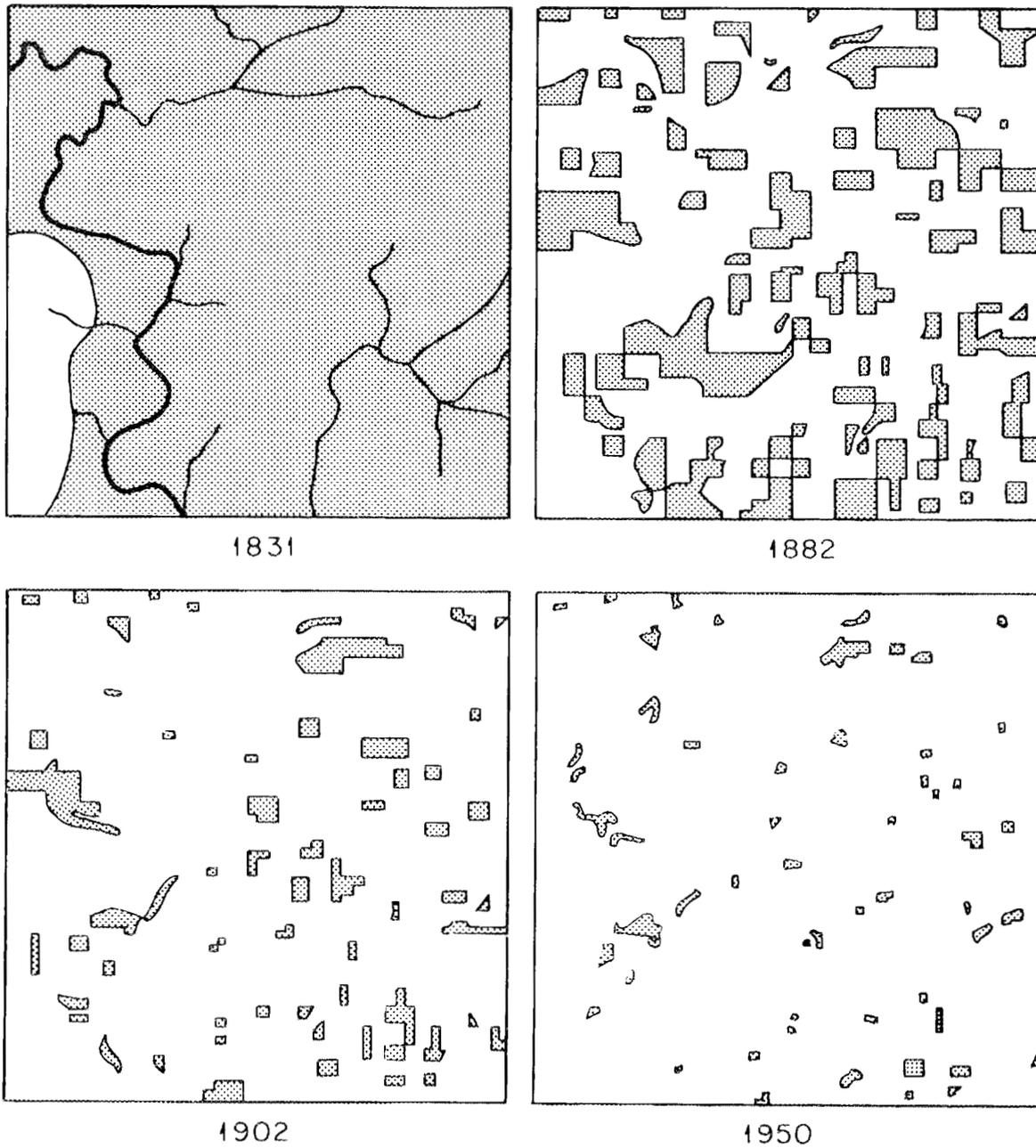


Fig. 1. Changes in wooded area of Cadiz Township, Green County, Wisconsin (89 54' W., 43 30' N.), during the period of European settlement. The shaded areas represent the land remaining in or reverting to forest in 1882, 1902, and 1950.

Source: Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. pp. 721-736. IN W. L. Thomas (ed.), *Man's Role in Changing the Face of the Earth*. Copyright by University of Chicago Press, Chicago, Illinois.

forest had been cleared. This proportion increased to 90 percent by 1935, and to 96 percent by 1950.

The development of forest islands in the prairie-forest transition zone involved more than just the leaving behind of remnant forests. In much of this area forest was excluded or held in savanna condition through the effects of fire. In the absence of fire, savanna usually evolved into closed canopy forest as formerly repressed tree species grew up from seedlings and root sprouts (Stout 1944, Cottam 1949, Dyksterhuis 1957, Rice and Penfound 1959). The appearance of settlers in the mid-1800's heralded a fundamental change in the vegetation dynamics of the region. Agricultural clearing broke up the prairie vegetation and widespread fire ceased to be an important factor affecting vegetation. The land not cleared and put into cultivation or pasture was converted to closed canopy forest stands, which became increasingly isolated as the extent of agricultural clearing grew. This created a landscape pattern where closed canopy forest islands tended to be restricted to soils and topography unsuited for agriculture. In Dane and Iowa counties of Wisconsin, Auclair (1976) showed that by 1934, 98 percent of the original prairie had been converted to cropland or pasture, as was 78 percent of the original oak savanna. The remaining savanna converted to oak forest. From 1934 to 1961, the total area in forest cover increased from 24.3 to 34.9 percent as land marginally suited for intensive agriculture was abandoned. In general, the forest cover is restricted to rocky, thin-soiled hilltops not suited for crops or pasture.

The type of land survey exerts a strong influence on patterns of land ownership and therefore an indirect influence on land use and landscape pattern. The system of metes and bounds (used before 1785) utilized topography and natural features as reference points, resulting in property lines tending to follow the lay of the land (Marschner 1959). In areas covered by the General Land Office Survey, property lines and land use followed the arbitrary grid system. Not until 90 percent of the land in Dane county, Wisconsin had been put into agriculture, did forest islands begin to reflect topography rather than the system of land survey (Curtis 1956). Clearing of woodlands generally began nearest to section line roads, often leaving forest islands in the center of sections and on farms in areas farthest from roads. Forest islands in these areas tend to be square or rectangular and somewhat evenly distributed over the land, unlike those found in areas surveyed by metes and bounds (Diller 1944).

I have discussed some of the factors influencing landscape pattern in man-dominated landscapes. It remains to be shown how landscape pattern itself may affect ecosystem processes.

Dynamics of Forest Islands

Creation of a landscape pattern composed of isolated forest islands in a sea of nonforest lends itself to an application of island biogeography concepts, by analogy if not in quantifiable fact. Island biogeography theory (MacArthur and Wilson 1963, 1967) predicts that species richness of an island at equilibrium is determined by a balance between immigration and extinction rates as affected by island size and

distance from mainland sources. The theory has been expanded to include habitat diversity as another factor directly correlated with species richness (Simberloff 1974). Habitat diversity can be reflected in topography and structural diversity of vegetation (Cody 1975). For example, forest remnants restricted only to hilltops may lack some of the more mesic species found in valleys or bottomlands and heavily grazed or selectively logged forest islands may lack one or more size classes of trees normally important as wildlife habitat. These principles have been applied to the design of wildlife refuges (Diamond 1975, 1976; Faaborg 1979; Simberloff and Abele 1976; Sullivan and Shaffer 1975) and to a study of large mammals in the Rocky Mountains (Picton 1979).

Applying the theory to forest islands, Elfstrom (1974) found that the number of tree species increased rapidly with increasing island size up to one hectare, then more slowly thereafter. Galli et al. (1976), Forman et al. (1976), and Moore and Hooper (1975) showed an increasing relationship between avian diversity and forest island size. Ranney and Johnson (1977) studied the relationship between seed dispersal and interisland distance. Increased isolation of forest islands tends to prevent the easy exchange of propagules between stands, thus the accidental loss of a species may become permanent, as seems to be the case for Acer saccharum and Tilia americana in southern Wisconsin (Curtis 1956, Ward 1956, Auclair and Cottam 1971). Isolation often favors those species with efficient dispersal mechanisms. Auclair and Cottam (1971) partly attributed the ubiquity of black cherry (Prunus serotina Erhr.) in Wisconsin forests to seed dispersal

by birds. Species richness may therefore be inversely related to the degree of island isolation (Levenson 1976).

Species composition and distribution is influenced by island size and shape and by successional processes. The size and shape affect the microclimatic conditions within an island. Forest edge conditions tend to be more xeric than those in the interior and favor pioneer species such as oaks, hickories, and willows, while beech and sugar maple are often confined to the interior (Wales 1972, Levenson 1976). Islands larger than 2.3 hectares are capable of developing relatively mesic interiors by ameliorating the dessicating effects of sun and wind. Islands smaller than 2.3 hectares or with a large perimeter/ area ratio (e.g., Great Plains shelterbelts) are relatively xeric throughout and tend to be all "edge." In small islands or islands restricted to xeric sites, succession may be arrested at a subclimax stage effectively self-insulating the island from the development of more mesic climax species such as beech and maple. In the larger forest islands, tree species richness is greatest along island edges where animal- and wind-dispersed species tend to be concentrated, and decreases in the island interior where a few shade tolerant mesic species become dominant (Levenson 1976, Ranney 1978).

The degree of connectivity between islands has been shown to be a relevant landscape feature. Avian diversity is improved with the presence of corridors between islands (Whitcomb 1977). Habitat corridors such as fence rows are heavily used by birds and small mammals and may relieve (to some degree) the isolating effect of farmland surrounding a forest island (Wegner and Merriam 1979).

Jackson (1979) has suggested that highway rights-of-way be managed as habitat corridors to benefit endangered species such as the red-cockaded woodpecker (Picoides borealis), the Mississippi sandhill crane (Grus canadensis pulla), and Attwater's prairie chicken (Tympanuchus cupido attwateri).

The topographic-edaphic positions occupied by forest islands also affect the local flora and fauna. Forest islands tend to be located on areas unsuited for farming because of rough terrain or poor soils (Curtis 1956, Auclair and Cottam 1971, Auclair 1976). These areas may not generally be representative of the bulk of the region and may be inherently unsuitable for some species due to a lack of proper microsites. This loss of habitat diversity may increase the probability of regional species extinction, especially for those species which were never very numerous or required habitats that were already relatively rare.

Landscape pattern is not static. There is turnover as old forest islands are cut and new ones created from abandoned farm or pasture lands (Johnson and Sharpe 1976, Zeimetz et al. 1976). The rate of turnover can be expected to correlate with the age of forest islands and their composition, in terms of opportunistic and equilibrium species.

Many of the above concepts can be applied to urban areas where continuing fragmentation of natural habitat, disturbance, and increasing isolation of individual habitat islands has brought on a general reduction in species richness. Insensitive species with broad niches dominate, and extinction rates are much higher than colonization

rates. Forest islands and other areas of natural habitat often are restricted to parks, cemeteries, golf courses, and rough terrain. It is expected that continuing urbanization will further reduce island size and increase island isolation (Greller 1975, Davis and Glick 1978).

Land use may also have direct effects on vegetation dynamics. The degree and type of disturbance, e.g., grazing, disease, selective logging and fire strongly affect the composition and structure of forest islands. In Wisconsin, the composition of oak-dominated forest islands shifts toward maple-basswood dominance if left undisturbed (Cottam 1949). Selective logging of oaks and oak wilt disease tend to accelerate this trend, if maple and basswood seeds are available, while grazing tends to maintain the forest in a more xeric pioneer stage (Cottam 1949, Auclair and Cottam 1971). Repeated logging and grazing in Ohio woodlots has resulted in limited tree reproduction or preferential reproduction of prolific seed producers, e.g., American elm, white ash, and sugar maple (Schlemmer 1941, Diller 1944).

Description of Landscape Pattern

One goal of ecology is to organize and explain, within a theoretical framework, the growing body of knowledge concerning ecosystems and their functions. Little is known about how ecosystem processes are affected in man-dominated landscapes. One logical step toward addressing this problem is the identification and measurement of ecologically relevant landscape properties which emphasize the dynamics of forest islands. Quantifiable variables are needed to describe landscape pattern and relate pattern to ecosystem processes. These

variables include measures and indices relating to specific forest islands and their interactions, i.e., island variables; synthesized measures or indices of general landscape attributes, i.e., landscape variables; and measures of how the landscape pattern is changing over time, i.e., spatio-temporal variables.

Island variables relate to specific islands and their interactions. Variables describing individual islands include island size, developmental stage (e.g., young forest vs. mature forest), length/width ratio, perimeter/area ratio, and an edge or diversity index (DI) adapted from limnology by Patton (1975). Patton's index is of the form

$$DI = \frac{TP}{2\sqrt{A\pi}}$$

where TP is the total perimeter and A is the area. DI compares the perimeter of a forest island to the perimeter of a circle of equal area. For instance, DI = 1 indicates the forest island is circular, while a value of 1.5 indicates that the forest has 50 percent more perimeter than a circle of equal area. This index thus provides a method of relating forest island edge to its area.

Island variables relating to island isolation and interactions between islands include average island size, interisland distance, number of corridors between islands, (e.g., fence rows, brushy gullies, etc.), and matrix quality (cover type surrounding each island). Matrix quality is usually some type of natural or cultural vegetation in the sense of Küchler (1969).

Synthesized indices of isolation can be calculated for each island. An average measure of isolation (King 1969) is derived by determining the distance, r_{ij} , between a particular island, j , to a number, n , of its neighbors:

$$r_j = \frac{1}{n} \sum_{i=1}^n r_{ij} .$$

The connectivity between forest islands as measured by the number of interisland linkages or corridors, can be summarized in the accessibility index (A) which formalizes the connectivity between a specific patch, j , and others in its vicinity as:

$$A_j = \sum_{i=1}^n d_{ij} ,$$

where d_{ij} is the presence of a linkage between islands i and j (Lowe and Moryadas 1975).

Other variables which have been used in vegetation and environmental analysis include elevation, aspect, slope percent, landscape topographic position, soilscape position index, soil properties, and soil management classes (Auclair 1976). The variables can be used to describe the location of islands along environmental gradients.

Landscape variables are synthesized measures of general landscape attributes. Some examples include standard distance index, connectivity index, patch distribution (random, uniform, clustered), and patch grain (density per unit area). Table 1 lists landscape

Table 1. Sample landscape pattern variables for Cadiz Township, Green County Wisconsin. Variables 1-3, 7, 12 based on Curtis (1956).

Variables	1831	1882	1902	1950
1. Total forest area (ha)	8720	2582	841	318
2. Number of forest islands	1	70	61	55
3. Average size (ha)	8720	36.9	13.8	5.8
4. Average interisland distance, r_c (m) (centroid to centroid)	-	758	751	760
5. Average interisland distance, r_e (m) (edge to edge)	-	153	332	339
6. Total periphery of woodlots (km)	39.8	159.3	98.5	64.1
7. Amount of edge (m) per ha of forest	4.6	61.7	117	202
8. Amount of edge (m) per ha of study area	4.1	17.1	10.6	6.9
9. Nearest neighbor statistic, R (centroid to centroid)	-	1.31	1.21	1.17
10. Nearest neighbor statistic, R edge to edge	-	0.27	0.45	0.44
11. Percent of study area in forest vegetation	93.5	27.7	9.0	3.4
12. Percent of original forest area	100	29.6	9.6	3.6
13. $\frac{\bar{r}_c}{\bar{r}_e}$		4.85	2.24	2.25
14. Connectivity index	-	32	6	0

Source: Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. pp. 721-736. IN W. L. Thomas (ed.), Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, Illinois.

attributes that have been calculated for the landscape (Fig. 1, p. 18) studied by Curtis (1956).

The standard distance index is a measure of aggregate distance between a series of points, and thus is an indirect measure of the isolation of forest islands:

$$D = \sum_{i=1}^n (\sigma_x^2 + \sigma_y^2) ,$$

in which σ_x^2 and σ_y^2 are the variances of the x and y coordinates of a number of island centroids (Lowe and Moryadas 1975).

The connectivity index (Table 1, row 14) summarizes the number of linkages between points (Lowe and Moryadas 1975). It is based on a tally of linkages between pairs of islands, and involves setting up a connectivity matrix showing this information for all islands in the study area.

One measure of island distribution is the Clark and Evans measure of aggregation (Clark and Evans 1954, 1979; Pielou 1977; Simberloff 1979):

$$R_c = 2\bar{r}_c (\lambda/\pi)$$

in which \bar{r}_c is the average distance from a forest island to its nearest neighbor (centroid to centroid) and λ is the density of forest islands (number per ha). In a randomly distributed population of islands, R_c equals 1; for aggregated populations R_c is less than 1 and for uniformly distributed populations, R_c approaches a maximum

of 2.1491. If the density of forest islands is known with certainty, then deviation from randomness can be tested. R_c can also be computed using the edge to edge distances in calculating the average distance from a forest island to its nearest neighbor (R_e). Computed in this manner, R_e is not a measure of patch distribution, but it can be useful for studying relative change over time. R_e should be correlated with land use patterns and the type of land survey used to divide up the public domain. Changes in R_e over time can give clues concerning the nature of changing landscape pattern (Table 1, rows 9-12).

The ratio $\frac{\bar{r}_c}{\bar{r}_e}$, where \bar{r}_e is the average edge to edge distance from a forest island to its nearest neighbor, gives indirect information concerning the size and distribution of forest islands. A large value indicates large forest islands separated by a small distance while a small value indicates small islands separated by relatively larger distances (Table 1, row 13).

Spatio-temporal variables are measures of how the landscape pattern is changing over time. The changes in landscape can be measured by comparing landscape patterns on old maps to the patterns on newer maps and deriving a matrix of transformation coefficients which describe changes in cover (Hett 1971, Auclair 1976, Zeimetz et al. 1976, Johnson and Sharpe 1976). These transformation coefficients can then be used as rate constants in mathematical models describing the dynamics of landscape pattern. Rates of change in island and landscape variables also can be quantified.

There has been little research addressing the question of how to describe the spatio-temporal pattern of man-dominated landscapes characterized by forest island ecosystems. There is also a lack of understanding about how the landscape pattern affects basic ecosystem processes in these landscapes. There are many questions to be answered concerning ecosystem stability with respect to land use, biological diversity, and species extinction before ecologically oriented information of this nature can be incorporated into resource management decisions on a regional scale. It may be possible that multivariate analysis involving island variables, landscape variables, and spatio-temporal variables can be used to describe and classify forest island landscape pattern in conjunction with mathematical models describing its dynamics. This can lead to a greater understanding of how basic ecosystem functions are affected by landscape pattern and how man can better integrate his activities with the environment.

III. METHODS

Introduction

A primary goal of this study was to develop a methodology to quantitatively describe landscapes in terms of the distribution patterns of forest islands and selected environmental parameters. Accomplishment of this goal required the identification and measurement of variables suitable for representing properties emergent with the scale of a single unit of study (a landscape) and yet capturing the essence of variation among landscapes.

As a first step, the units of study (landscapes) had to be defined in more concrete terms. Although the dictionary defines a landscape as an area of land seen by an observer, it does not state how large that portion must be, because, of course, the size depends upon the vantage point of the observer. For example, an observer on a hilltop can usually see more territory than one in a valley, but less than an airplane pilot flying overhead, and far less than an astronaut in an orbiting capsule. The landscape properties that may be of interest to an investigator are in turn dependent upon landscape scale. Relative density, frequency, and basal area of tree species, indices of similarity, slope, aspect, and soil type are all landscape properties adequately captured from the one-tenth hectare plots normally used in vegetation studies. On the other hand, information pertaining to landscape pattern in terms of the sizes, shapes, and numbers of forest islands, land form classes, and soil mosaics represent properties emergent only at a scale measured in hundreds or thousands of

hectares. The size of a study area is therefore dependent upon the purpose of the investigator. For this investigation, the study areas were several thousand hectares in size.

Data Sources

The ideal sources of forest island information for this study would have been a series of maps showing the extent and location of forest cover at a scale sufficiently large to make distance and area measurements reasonably accurately, but sufficiently small to contain a reasonable number of potentially contrasting landscape types. It was necessary to sample a number of landscapes with contrasting forest island patterns in order to test the feasibility of distinguishing different landscape types on the basis of the selected quantitative measurements. Ideally, the sources of topographic, edaphic, and other environmental information would have been maps at the same scale as those of forest cover. As is often the case, however, the most available and convenient sources of data fell short of the ideal.

The source used for forest island data was a set of county maps of the state of Ohio depicting forest cover on a scale of 1:63,360 (one inch to the mile). The maps, produced by the Ohio Department of Forestry, were based on data collected with Works Projects Administration (WPA) assistance in the late 1930's. The maps present a detailed, large scale, graphic representation of forest island patterns for regions in Ohio that differ in soil, topography, glacial and land use history. Some of the county forest maps are hand-colored, the forest islands coded according to forest type, e.g., Knox and Miami

counties. Others are coded by condition class, e.g., Summit and Franklin counties, while others, e.g., Belmont County, showed only forest shape and location without regard to forest type or condition class. Aerial photos can convey the same information regarding forest island size, shape, and location, but were less readily available and convenient to work with than the county forest vegetation maps. Since the time period of the forest island data was irrelevant, the 1939 county forest vegetation maps were judged adequate for this project.

Aerial photographs were not available for checking the accuracy of the 1939 county vegetation maps. A qualitative evaluation of the accuracy of the Miami County map was accomplished with the aid of a table containing pertinent forest island information (Schlemmer 1941) and aerial photos for the years 1949 and 1968. Twenty woodlots were selected for analysis in Newberry township in the northwest corner of Miami County. These woodlots appeared in the 1939 map and in the aerial photos and were judged to be stable because the trees of the woodlots were mature out to the forest edge and woodlot sizes and shapes were constant throughout the period between 1949 and 1968. Perimeter and area measurements from the 1939 map were compared with those from the aerial photos. The results showed that woodlots on the map were portrayed with larger sizes and rounder shapes than those on the aerial photos. These errors may have been due to a systematic bias associated with drawing the borders of woodlots. The table of forest island information listed a greater density of islands than was found on the map. The aerial photos indicated that woodlots smaller than two hectares were likely to have been omitted from the map. This

observation agrees with the statement by Schlemmer (1941) that only woodlots three acres (1.2 ha) or larger were included in his analysis. These two types of errors were assumed to be systematic, that is, all of the vegetation maps were assumed to omit small islands and portray the rest slightly larger and rounder than should have been the case. The errors were judged small enough not to obscure or distort comparisons made between sample landscapes portrayed on the 1939 maps but were large enough to preclude accurate time series comparisons between the 1939 maps and the aerial photos.

Topographic and edaphic information was obtained from the National Atlas of the United States of America (USDI 1970). Glacial history was determined from a map showing the glacial deposits of Ohio (Ohio Dept. of Natural Resources 1966). Information concerning potential natural vegetation, as defined by Küchler (1964), was obtained from the National Atlas. Gordon (1966) provided data about the natural vegetation of presettlement Ohio.

Data Collection

As a first step in quantifying forest island patterns, study areas (landscapes) were delimited on selected county vegetation maps and assigned a three letter identifier. Because of the time required to measure necessary variables in an area containing possibly hundreds of forest islands, only a limited number of landscapes could be measured. With this constraint in mind, the primary consideration was to obtain a sample of landscapes representing a variety of forest island patterns. Therefore the placement of study areas was based solely on perceived

variation of forest island pattern, both within a single county and among different counties. The goal was to capture as much variation as possible, while minimizing bias toward other considerations. The landscapes were widely distributed throughout Ohio and were located in areas with distinctly different patterns of topography, soils, and glacial history (Fig. 2) even though no special efforts were made toward those ends.

Miami County was initially chosen as a region representing maximum destruction and fragmentation of original forest due to man's activities. Forest covered only about three percent of the county and forest islands were small, more or less square to rectangular, and widely separated. In contrast, Belmont County was chosen for sampling because it contained landscapes with forest island patterns much different from those of Miami County. The county as a whole had much more forest coverage with a larger number of bigger and more irregularly shaped forest islands. Knox, Summit, Holmes, and Coshocton counties were sampled because they contained landscapes that were perceived to be different from landscapes in Miami and Belmont counties in terms of the sizes, shapes, and numbers of forest islands. Figure 3 is an example of the forest island patterns for several of the landscapes used in the study.

The three aspects of forest island pattern governing the size and placement of study areas were density, intensity, and grain. The density of forest islands is simply the number of islands per unit area. Intensity is the "extent to which density varies from place to place" (Pielou 1977), but for the purposes of this project, intensity

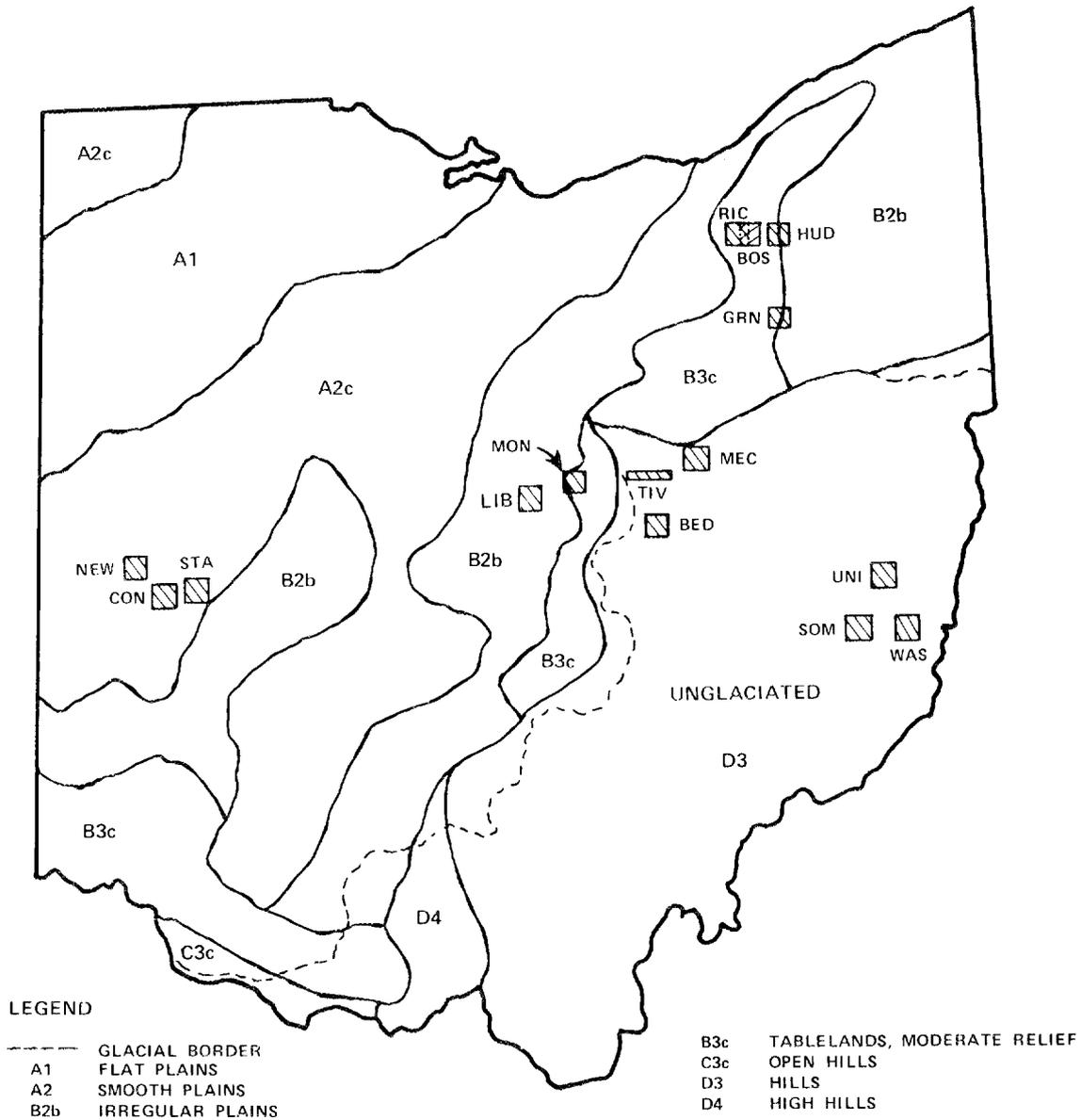


Fig. 2. Distribution of study areas in Ohio with respect to land surface form and glacial history. Study areas are assigned three letter identifiers.

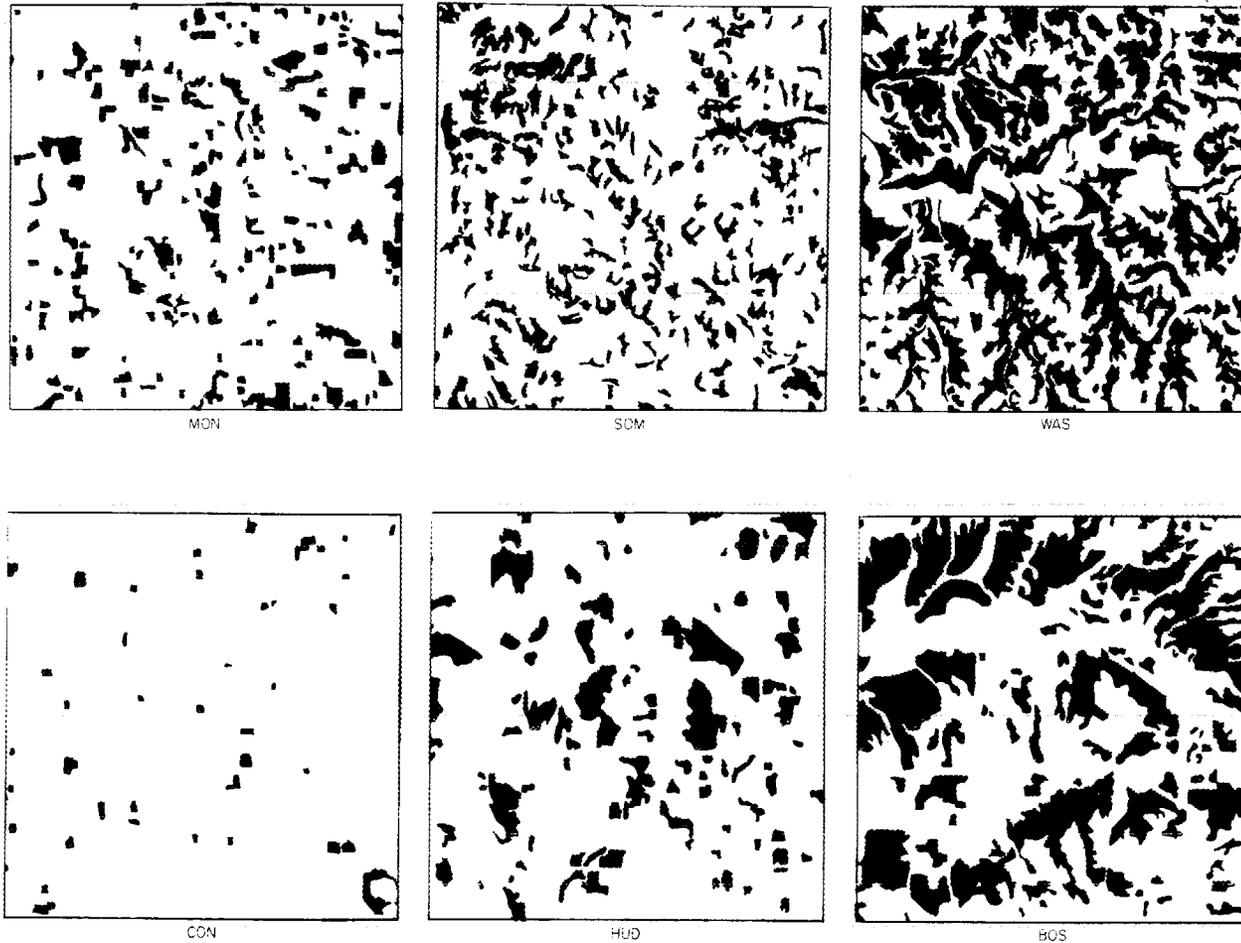


Fig. 3. Forest island patterns of selected Ohio landscapes. The shaded areas represent land remaining in or reverting to forest as of the late 1930's. The landscapes are arranged with increasing forest cover from left to right and increasing island density from bottom to top. Each landscape is approximately 10 km. on a side and has been assigned a three letter identifier.

is generalized to include any noticeable variation of forest pattern in terms of the sizes, shapes, numbers, and spacings of forest islands. Used in this manner, intensity is synonymous with contrast (sensu Küchler 1973). Thus, counties with patterns of high intensity will have areas of sharply contrasting forest island patterns. Counties with low intensity patterns will appear to be somewhat homogeneous throughout. Grain is independent of intensity and refers to the size of the area containing the whole range of pattern intensities (Pielou 1977). Therefore, a region with coarsed-grained pattern will have relatively large contrasting areas compared to a fined-grained region with smaller, but more numerous, areas of contrast.

The density of forest islands governed the initial choice of study area size. The desire (in landscapes with little forest cover) was to have at least 40 forest islands per landscape in order to adequately capture, in one sample, the "essence" of the forest island pattern. For example, a study area that was too small to adequately measure forest island density would be more likely, on the basis of chance alone, to over- or under-represent some landscape property, thus requiring additional samples to compensate for the variation among samples. The initial choice of size was based upon inspection of Miami County, Ohio, where the density and coverage of forest islands were the lowest of all regions studied. An area the size of one township (9324 hectares or 36 square miles) appeared to adequately represent forest island pattern even in the least dense regions of Miami County. But because the boundaries of the townships in Miami County were

somewhat irregular, study areas were conveniently defined as squares ten kilometers on a side (10000 hectares).

Although not quantitatively tested, 10000 hectares was believed to be a sufficiently large landscape to adequately capture the essence of the least dense forest island pattern that was likely to be encountered. For the sake of consistency, 10000 hectare landscapes were delimited in all other counties, except one, even though in some cases a much smaller study area might have sufficed. In Belmont County, the study areas were 9324 hectares and corresponded to the boundaries of conveniently located townships. The relatively small difference between 10000 hectares and 9324 hectares was not believed to be an important source of variation in future analyses because the landscape variables that were eventually calculated were expressed in units independent of study area size. Certain townships (Somerset, Union, and Washington) were used to delineate landscapes in Belmont County for three reasons: (1) The townships were conveniently located; (2) Belmont County had a relatively high density of forest islands that required tedious measurement. Therefore, smaller study areas could be used to obtain the desired information in less time; and (3) Within the county, there was an east-west gradient of large to small islands. This gradient tended to generate a finer grained pattern (compared to the other counties) that was slightly more suited to smaller sized study areas.

Placement of study areas, both within and among counties, was based on perceived pattern intensity. In almost all cases, the grain of the pattern was coarse enough so that 10000 hectare landscapes could

be placed within areas where the internal forest island pattern appeared to be relatively homogeneous. In only one case (TIV) was the shape of the study area changed from a square to a rectangle in order to better fit the grain of the pattern. It was later discovered that an adjacent county had a similar forest island pattern but no study areas were placed there to test that apparent similarity.

In another case, it was discovered, after the measurements were taken, that a landscape in Summit Co. (BOS) appeared to straddle two "types" of forest island pattern. In order to better sample the two types of pattern, two other landscapes (RIC and HUD) were delimited slightly offset from and/or partly overlapping the original landscape. The data from the BOS landscape were retained for comparison with the other landscapes in subsequent analyses.

Within each landscape, the following measurements were made: (1) the perimeter (in meters) and area (in hectares) of each forest island, (2) the total number of islands, and (3) the distance (in meters) between forest island edges. The locations of the landscapes were plotted on the smaller scale topographic, edaphic, and vegetation maps, and each area classified according to land surface form, soil type, glacial history, potential natural vegetation and original presettlement vegetation.

Area measurements were made with a transparent grid overlay whose cells were two millimeters on a side or four mm^2 . The area of an individual island was estimated by counting (to the nearest half cell) the number of grid cells contained within it. A planimeter was used on large, irregularly shaped islands because of the difficulty encountered

when attempting to count large numbers of cells, many of which were only partially filled. The scale of the vegetation maps was 1:63360, meaning that each millimeter represented 63.36 meters. All measurements were converted to metric units on that basis. Each cell represented an area 126.72 meters on a side or 1.606 hectares in areal extent, therefore;

$$\text{No. of hectares} = \text{No. of cells} \times 1.606.$$

Island perimeters were measured with a metric ruler. A hand counter was very useful in keeping track of millimeters. Interisland distances were taken by laying a series of transects across a study area and measuring the distances across the open spaces separating island edges. One hundred such distances were recorded for each landscape. Usually the open spaces were measured between different islands, but in some cases edge to edge distance was measured between different parts of "fingers" of the same island. Perimeter and interisland distance measurements were converted to meters on the basis that each millimeter equaled 63.36 meters thus;

$$\text{No. of meters} = \text{No. of millimeters} \times 63.36.$$

Data Analysis

The goal of quantifying landscape pattern required a mathematical analysis of landscape data. Since many aspects of landscape pattern can be quantitatively measured, the desired techniques of analysis needed to be capable of handling a data matrix whose rows represent individual observations (landscapes) and whose columns represent the

specific types of measures or variables associated with each landscape. With this format in mind, multivariate statistical techniques were chosen to aid in the data analyses.

Prior to performing statistical analyses, the raw data for each landscape had to be converted from the initial form, consisting of hundreds of measurements, to a condensed multivariate form, consisting of a series of continuous "landscape" variables, whose properties were consistent with the scale of the study areas. Multivariate statistical techniques (factor analysis and discriminant analysis) were then used to analyze the variation of forest island pattern among landscapes and relate that variation to environmental patterns of topography, soils, glacial history, potential natural vegetation and original vegetation.

A theoretical model of forest island pattern was used as a conceptual basis for calculating landscape variables from the raw data. The theoretical model considers a hypothetical landscape of finite area that contains a population of circular forest islands, each equal to one unit of area. Such a landscape has a known coverage and density of islands. Both mean and median island size is equal to one unit area, the average island shape is a circle, and the distance between islands is a function of their size, spacing, and density. If we take that landscape and divide each island into two equal circles, then the density doubles but the coverage remains the same. Conversely, if we increase the size of each island but do not create any more islands, then coverage increases while density remains constant. Adding new islands increases both coverage and density.

Figure 4 portrays this concept with hypothetical landscapes, while Figure 5 is a more mathematical representation, i.e., a nomogram.

An actual landscape differs from a hypothetical landscape pattern in two ways. For a given cover and density, the forest islands in a study area have neither uniform sizes nor circular shapes. It is these differences between hypothetical and actual landscapes that can be used to calculate certain landscape variables.

Nine continuous landscape variables were calculated from the set of perimeter, area, and interisland distance measurements for each study area. These included: (1) total forest cover as a percent of the study area; (2) the density of forest islands expressed as a number per 10000 hectares; (3) the median island size in hectares; (4) an average distance between forest edges; (5,6) two indices of island shape; (7) an index of the degree of forest fragmentation; and (8,9) skewness indices of the size and shape distributions for the population of forest island measurements in each landscape. Mean island size can be calculated as cover/density, but the size distribution was consistently skewed toward smaller islands. For that reason, the median island size was considered a better measure of central tendency. An index of this skewness was calculated as the difference between the mean and median island size expressed as a percentage of the mean:

$$\text{Skew-area} = (\text{mean area} - \text{median area})/\text{mean area}.$$

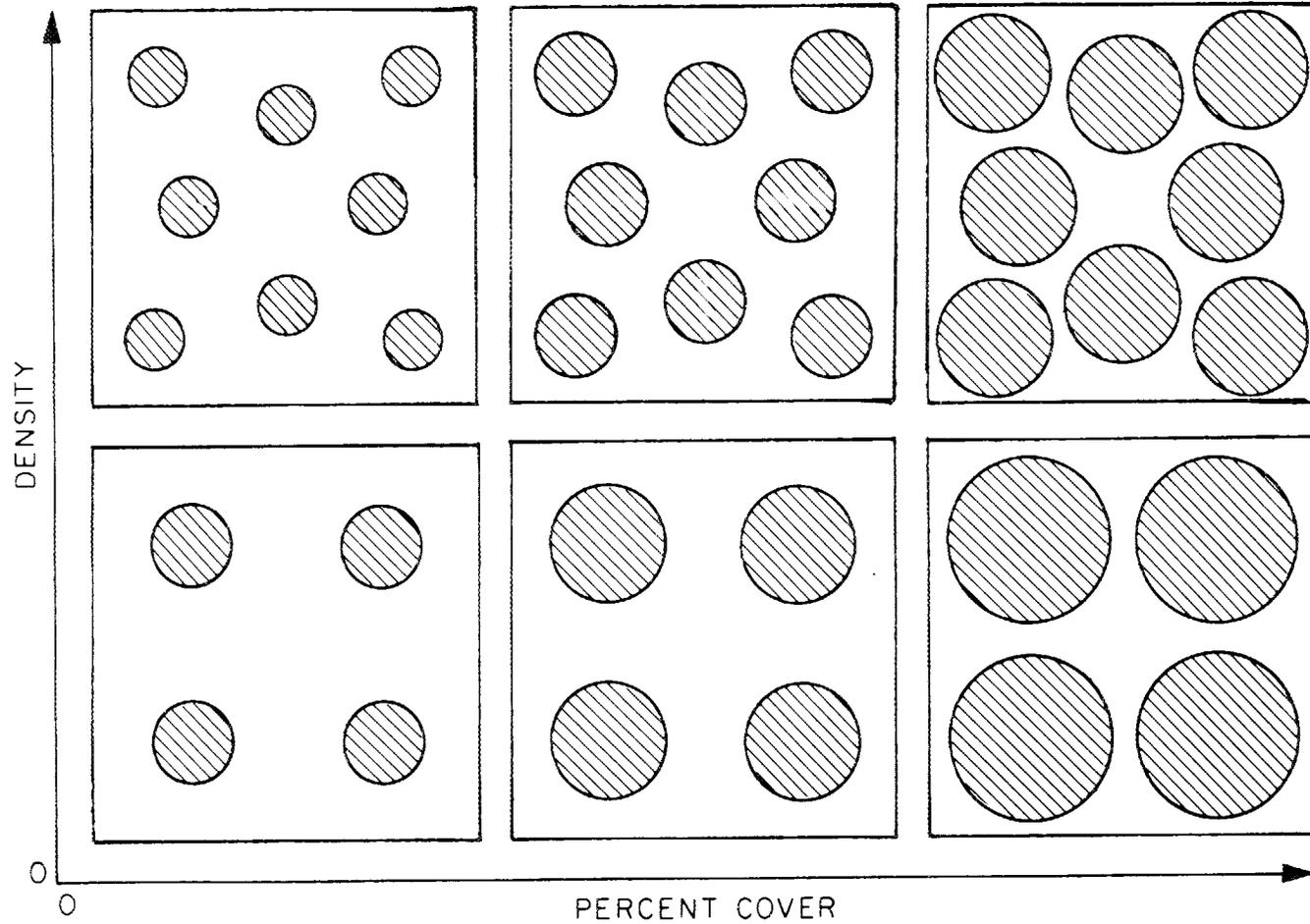


Fig. 4. Hypothetical or "ideal" landscapes populated with circular forest islands. The landscapes are arranged with increasing cover on the horizontal axis and increasing island density on the vertical axis.

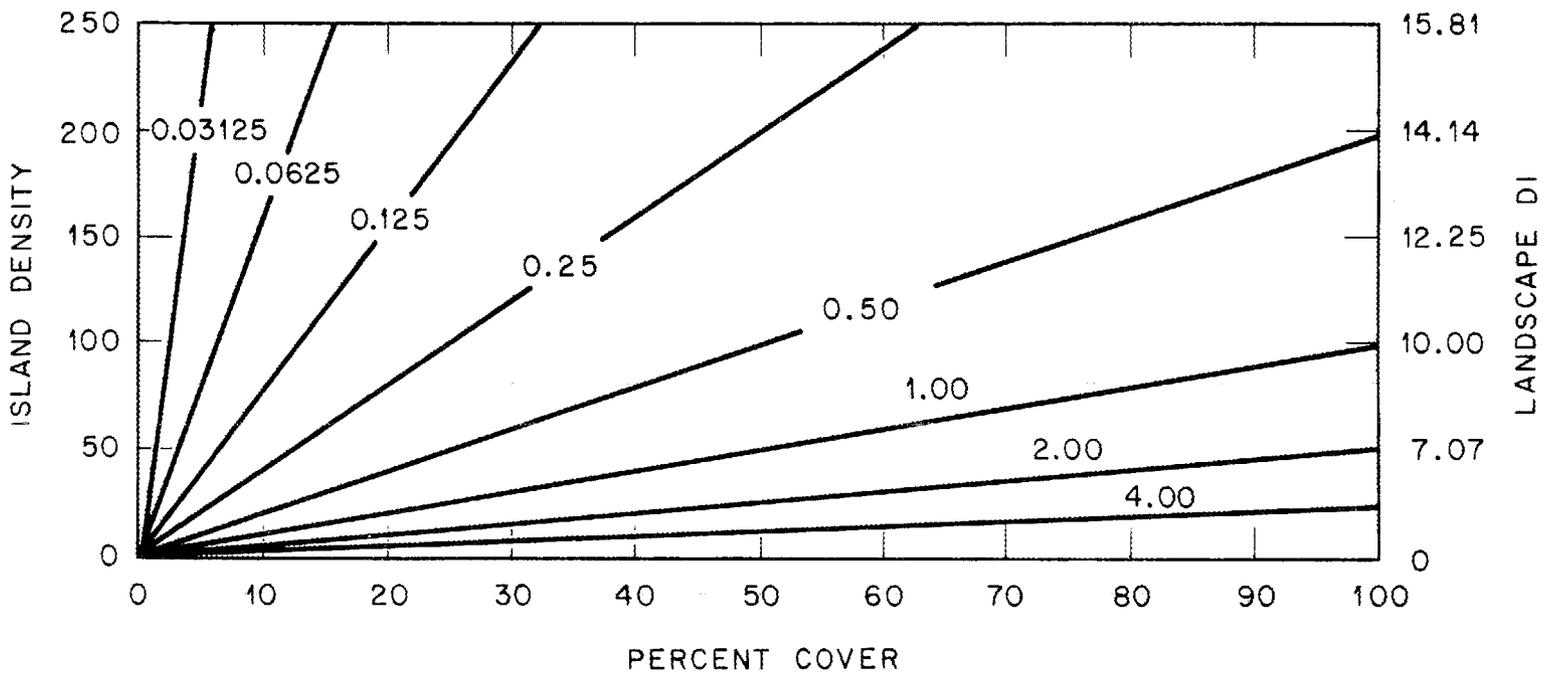


Fig. 5. Nomogram showing the theoretical relationship of mean forest island size to percent cover and island density. Units of the mean forest island size are expressed as a percentage of the total study area. Landscape DI is a function of the total perimeter/area ratio of all islands. For theoretical landscapes populated by forest islands of uniform size and shape, landscape DI is a square root function of island density.

The index of island shape (DI = Dissection Index) for an individual forest island was defined as the perimeter of an island divided by the perimeter of a circle with an area equal to the area of the island:

$$DI = P / (2 \sqrt{\pi A})$$

where P is the perimeter and A is the area expressed as square meters.

The basic DI calculation was originally used in limnology (Wetzel 1975) but was adapted for terrestrial ecology studies as an index of edge habitat (Patton 1975, Thomas et al. 1979) or as an index of shape (Game 1980). When used as an index of edge habitat, DI meant Diversity Index because the amount of edge habitat was considered a component of habitat diversity. In this study, DI stands for Dissection Index because it is primarily used as an index of the irregularity or degree of dissection of island shape.

A landscape with a number of forest islands can be thought of as having a mean and median island DI with some degree of skewness, analogous to the mean, median, and skewness of island size distribution. Mean DI, median DI, and skew-DI were calculated for each landscape:

$$\text{mean DI} = \frac{\sum_{i=1}^n DI}{N} \quad , \text{ and}$$

$$\text{Skew-DI} = (\text{mean DI} - \text{median DI}) / \text{mean DI}.$$

where N = the number of forest islands in a landscape.

The general formula for DI can be applied to the total perimeter and area of all forest islands in a landscape.

$$DI' = \frac{\sum_{i=1}^n P}{2 \sqrt{\pi \sum_{i=1}^n A}}$$

DI' is essentially the same type of measurement as was made by Patton (1975) and Thomas et al. (1979), but it is not entirely suitable for this project because it is not standardized for study area size, that is, landscapes with identical forest island patterns but unequal sizes will have unequal values of DI'. The standardizing transformation was simply to divide the total perimeter and the total forest area by study area size (S) and multiply the resulting formula by a scaling factor (100). This transformation is equivalent to multiplying DI' by $100/\sqrt{S}$. The transformed variable is termed Landscape DI,

$$\text{Landscape DI} = 100 \frac{\sum_{i=1}^n P}{2 \sqrt{\pi S \sum_{i=1}^n A}}$$

An index of interisland distance was calculated as the average of 100 edge-to-edge transect distance measurements taken between islands on each landscape,

$$\text{Mean Distance Index} = \frac{100}{\sum_{i=1}^n d} ,$$

where d is an edge-to-edge distance. This index denotes an average distance between forest island edges.

The computed variables (cover, density, median area, mean DI, landscape DI, and mean distance index) embody an adequate description of forest island distribution patterns. These variables were mathematically continuous. The classifications of landscapes according to topography, soils, glacial history, potential natural vegetation, and original (presettlement) vegetation were considered as variables that described environmental characteristics of landscapes. These were nominal variables, implying neither rank nor continuity.

Factor analysis was used to describe the variation of forest island patterns among the studied landscapes in terms of the differences in sizes, shapes, numbers, and spacings of forest islands. Discriminant analysis was used to determine to what degree forest island patterns could be separated according to the environmental classifications of the landscapes. These classes were then overlaid on factor analysis plots to determine if the variation among forest island patterns was related to environmental gradients. All statistical computer programs were written using SAS (Statistical Analysis System) software (Barr et al. 1979) and submitted to an IBM 360-91 computer. All programs and data were written, stored, and submitted through a PDP-10 interactive computer terminal. Some plots, generated in the course of the research were made with DISPLA - Display Integrated Software System and Plotting Language (Integrated Software Systems Corporation 1978) and plotted on a Calcomp plotter.

The methodology described in this section is the culmination of an evolutionary thought process. Several philosophical and methodological approaches were tried and rejected as inadequate. The first approach

involved using IMGRID - Information Management on a GRID Cell System (Holmes and Jolly 1980) to analyze the landscape patterns of Miami Co., Ohio. A grid (composed of one hectare cells) was laid over portions of the forest vegetation map of Miami Co. and forest island data were digitized on a cell by cell basis. The resulting data matrix could then be manipulated to produce maps and various statistics.

The problem with IMGRID was that it could not easily produce statistics with properties appropriate for the scale of the landscapes about which the research questions were being asked. Its algorithms lacked the flexibility to treat forest islands on an individual basis or calculate parameters that were relevant to the description of forest island pattern. In addition, the high level of resolution of input data (one hectare) required large amounts of time just to encode information for one 10000 ha landscape. The IMGRID approach was eventually abandoned but the questions it raised about the nature of "desirable" data soon led to more fruitful endeavors.

IV. RESULTS AND DISCUSSION

Introduction

Each Ohio landscape chosen for study was described by a series of continuous variables (Table 2). Differences between landscape patterns can be attributed to variation which can be random or systematic, depending upon the nature of the factors underlying pattern formation. If one or more underlying factors, e.g., topography, affect landscape pattern in a definite, non-random fashion, then the variation among landscapes will be systematically correlated with those factors. Factor analysis (a multivariate statistical technique) was chosen to describe the nature of variation among landscapes, that is, whether landscape variables changed randomly or systematically. The environmental information (topography, soils, glacial history, presettlement vegetation, and potential natural vegetation) was then used to explain and interpret the landscape variation.

Description of Study Areas

Throughout this thesis individual landscapes are referred to as if they are definite entities with unique characteristics. Indeed they are. Even though landscape boundaries may be somewhat subjective, that is, they may only exist in the mind of the beholder, the landscapes themselves are nevertheless definite entities with measureable properties existing independent of the mind. Landscapes can be looked at, photographed, and walked upon. The landscapes that are the subject of this thesis were portions of Ohio in the late 1930's represented by designated segments of county vegetation maps and characterized by

Table 2. Continuous variables describing the forest island pattern of 15 Ohio landscapes.

Symbol	County	Percent Cover	Density	Mean Distance Index	Median Island Area	Landscape DI	Median Island DI	Mean Island DI	Skewness Island Area	Skewness Island DI
SOM	Belmont	22.7	244	728	5.6	23.15	1.39	1.50	0.39	0.07
UNI	Belmont	17.7	178	691	6.4	18.84	1.38	1.45	0.35	0.05
WAS	Belmont	43.6	132	403	11.2	20.89	1.60	1.87	0.66	0.14
BED	Coshocton	12.3	175	1153	3.6	18.68	1.32	1.51	0.49	0.13
TIV	Coshocton	32.1	112	627	12.9	16.31	1.49	1.58	0.55	0.06
MEC	Holmes	22.4	243	743	4.8	21.04	1.43	1.45	0.48	0.01
LIB	Knox	7.6	111	1586	3.6	13.81	1.29	1.39	0.47	0.07
MON	Knox	11.8	180	1000	3.6	17.25	1.24	1.36	0.45	0.09
CON	Miami	2.7	46	3520	4.1	7.90	1.15	1.23	0.30	0.07
NEW	Miami	6.0	87	1271	6.0	11.29	1.20	1.26	0.13	0.05
STA	Miami	3.3	48	2923	5.4	8.70	1.17	1.26	0.21	0.07
BOS	Summit	33.8	83	625	8.0	12.52	1.36	1.57	0.80	0.13
GRN	Summit	9.8	135	1513	4.8	15.41	1.28	1.39	0.34	0.08
HUD	Summit	14.5	102	1419	6.4	13.04	1.29	1.42	0.55	0.09
RIC	Summit	25.7	96	1381	9.23	12.85	1.43	1.50	0.66	0.05

certain vegetative and environmental features. The purpose of this section is to briefly describe each landscape in order to provide a better frame of reference.

Landscapes are identified by a three letter code derived from the township name in which the largest percentage of the landscape is located. In three cases (SOM, UNI, and WAS) the landscapes covered 9324 hectares and had boundaries coincident with the civil township boundaries. In all other cases the landscapes were 10000 hectares and included portions of two or more townships.

The landscapes are primarily characterized by certain aspects of forest pattern, that is, sizes, shapes, density, and spacing of woodlots. Density is expressed as the number of woodlots per 10000 hectares. Density is exactly equivalent to the number of forest islands in 10000 hectare landscapes, but in SOM, UNI, and WAS, density is slightly greater than the actual island number. Island size is discussed in terms of the median island size; shape is in terms of the degree of irregularity or dissection; and spacing is in terms of the average interisland distance. The following section is a brief description of each study area.

(1) Somerset landscape, Belmont County (SOM) -- The study area lies in the southwest corner of Belmont County and is characterized by a highly fragmented forest. Over 200 irregularly shaped woodlots account for the 22.7 percent forest coverage. The median island size is 5.62 hectares, although several much larger islands skew the size distribution. The average distance between woodlots is 728 meters. The SOM landscape, like all of Belmont County, is part of the Appalachian Plateau and has nonglaciaded hilly topography.

(2) Union landscape, Belmont County (UNI) -- Union Township lies ten kilometers northeast of SOM in the northwest quarter of Belmont County. It has 17.7 percent cover with a median island size of 6.42 hectares and an average interisland distance of 691 meters. There were 164 woodlots in the township for a density of 178 per 10000 hectares, somewhat less than in SOM.

(3) Washington landscape, Belmont County (WAS) -- WAS lies in the southeast quarter of Belmont County. It has the largest amount of forest coverage (44 percent) of all the study areas and a median island size of 11.24 hectares. Its 129 woodlots are very dissected and the average interisland distance is only 403 meters.

(4) Bedford landscape, Coshocton County (BED) -- The landscape lies in west central Coshocton County, just ten kilometers east of the glacial border. It has 12.3 percent cover and one of the smallest median island sizes at 3.6 hectares. The density was relatively high at 175 woodlots per 10000 hectares, and the average interisland distance was 1153 meters.

(5) Tiverton landscape, Coshocton County (TIV) -- TIV lies eight kilometers north of BED in the northwest corner of Coshocton County. It has the third highest cover at 32 percent, and the largest median island size at 12.85 hectares. Island shape is very irregular; the island density is 112; and the average interisland distance is only 627 meters. TIV lies just east of the glacial border in hilly terrain.

(6) Mechanic landscape, Holmes County (MEC) -- MEC landscape lies on the south central border of Holmes County, four kilometers northeast of the TIV landscape in unglaciated topography. It is similar to the

SOM landscape in that it has a high density of woodlots (243 per 10000 hectares) and an almost identical degree of coverage (22.4 percent) and interisland distance (743 meters). It differs from SOM in having a more pronounced skewness of size distribution. The median island size is 4.82 hectares.

(7) Liberty landscape, Knox County (LIB) -- LIB is in west-central Knox County, two kilometers inside of the Wisconsin glacial border. This landscape is in an irregular plain and has forest islands more characteristic of easily cultivated land. Forest covers 7.6 percent of the landscape, and the median island size is 3.62 hectares. Woodlot shape is less irregular than landscapes in hilly topography because woodlot borders tend to be more linear. Average distance between islands is large (1586 meters) because of a relatively small island size (3.6 hectares) and low density (111 islands).

(8) Monroe landscape, Knox County (MON) -- This landscape lies ten kilometers northeast of LIB, outside of the Wisconsin glaciation but within the older Illinoian glacial topography. MON's tableland topography contributes to an increased cover (11.8 percent) and density (180 islands) compared with that of LIB. Also, MON's woodlots are more dissected. The median island size is 3.6 hectares and the interisland distance is 1000 meters.

(9) Concord landscape, Miami County (CON) -- CON lies in east-central Miami County in smooth glacial topography and is characterized by a forest pattern one would expect to find in agriculturally dominated landscapes. Forest covers only 2.7 percent of

the landscape and is divided among 48 woodlots, the median size being 4.11 hectares. The woodlots tend to have rectangular shapes, unlike those in hilly topography, and the average interisland distance is by far the largest at 3520 meters.

(10) Newberry landscape, Miami County (NEW) -- NEW is the north-west corner of Miami County and has a topography and forest pattern similar to that of CON. It has 6.0 percent forest cover distributed among 87 woodlots, whose median size is 5.97 hectares. Average interisland distance is 1271 meters.

(11) Staunton landscape, Miami County (STA) -- The landscape is one kilometer east of CON and is typical of Miami County landscapes. There are only 48 forest islands totaling 3.3 percent forest cover. The woodlots tend to be rectangular and their median size is 5.42 hectares.

(12) Boston landscape, Summit County (BOS) -- BOS lies in the north-central part of Summit County on glaciated tablelands of moderate relief. It has the second highest coverage at 33.8 percent and a density of 83 woodlots per 10000 hectares. The islands are highly dissected and the median size is 8.03 hectares, but the skewness of the size distribution is more pronounced than in any of the other landscapes, meaning that most of the forest cover is concentrated into a relatively small number of woodlots. Average interisland distance is 625 meters.

(13) Richfield landscape, Summit County (RIC) -- RIC partially overlaps the western portion of the BOS landscape. The landscape has 96 woodlots covering 25.7 percent of the area. Woodlots are highly

dissected and have a median size of 9.23 hectares. The average interisland distance is 1381 meters.

(14) Hudson landscapes, Summit County (HUD) -- This landscape lies one kilometer east of BOS on the border dividing irregular plains from tablelands. It has 14.5 percent cover divided among 102 woodlots. The median island size is 5.42 hectares and the interisland distance is 1419 meters. Like LIB, the island shapes are less irregular than those of hilly landscapes.

(15) Green landscape, Summit County (GRN) -- This landscape is in the southern-most portion of Summit County in glaciated tablelands. There are 135 woodlots covering 9.8 percent of the landscape with forest. Median woodlot size is 4.82 hectares and the average interisland distance is 1513 meters. It is similar to the LIB landscape in many respects.

Forest Island Pattern Description

Factor analysis (a type of principal components analysis) was initially employed to describe the forest island aspect of landscape pattern variation. Principal components analysis is a statistical technique which reduces the dimensionality of a data matrix to a smaller number of orthogonal (independent) components or factors. These factors are linear combinations of the original variables, and there are as many factors as there are variables. The generated factors decrease in order of importance, that is, the first factor accounts for more variation than the second and so on. Theoretically, a factor analysis of the landscape variables could account for most of the variation between landscapes in the first one or two factors.

A landscape can be located in a hyperspace whose dimensions are defined by the values of the landscape variables. A factor analysis of landscapes creates a hyperspace whose dimensions are the factors themselves. The advantage of factor space lies in the ability of the first few dimensions to capture most of the variation among landscape variables. This reduces dimensionality so that one or two factors may account for most of the variation found in six or seven landscape variables. Two factors (the first two principal components) can then be used as the axes of a plot, graphically depicting the relative arrangement of landscapes, an array based solely on the characteristics of the forest islands within the landscapes. This type of arrangement is analogous to an indirect ordination of vegetation stands, e.g., Curtis and McIntosh (1951) and Bray and Curtis (1957).

A factor analysis was performed on the data using cover, density, landscape DI, mean DI, median DI, median area, and the logarithm of the mean distance index (\ln -mean-distance) as the variables. The logarithm transformation of the mean distance index linearizes the relationship between cover and interisland distance and was used because nonlinear intercorrelations of the variables used in a factor analysis tend to distort the results (Pimentel 1979). The skewness of island size distribution (skew-area) was not used because it is a function of cover, density, and median area. Variables that are functions of other variables in the data are termed linear dependencies and should not be used in a factor analysis because they represent redundant information (Pimentel 1979). The skewness of island shape distribution (skew-DI)

was not used for that same reason, since skew-DI is a function of the mean and median island DI.

The results of the factor analysis showed that 90 percent of the variation among landscape variables was accounted for in the first two factors. These first two factors best discriminate (produce the maximum distances) among landscapes and were therefore used as axes in an ordination (Fig. 6). This ordination proved to be a useful visual summary of landscape variation.

Interpretation of a factor analysis is somewhat subjective and often confusing, but in this project it was straightforward and productive. Inspection of the eigenvector coefficients of the first two factors (Table 3) revealed the nature of the interplay between variables. The magnitude of the coefficient for a particular variable was interpreted as the relative importance or weight of that variable in a given factor. The coefficient's sign indicates whether a variable adds to or subtracts from the factor. Variables with the same sign increase or decrease together. For these data, factor 1 was interpreted as an axis weighted, in decreasing order of importance, toward cover, mean DI, median area, and median DI. Factor 2 was an axis composed primarily of density and landscape DI. Ln-mean-distance was of intermediate importance in both factors.

Another, perhaps more straightforward approach, is to run linear regressions (Proc RSQUARE of SAS) of the landscape variables on factors 1 and 2 (Table 4). Inspection of the square of the multiple correlation coefficient (R^2) revealed how much variation in a variable was explained by a given factor or conversely, how much

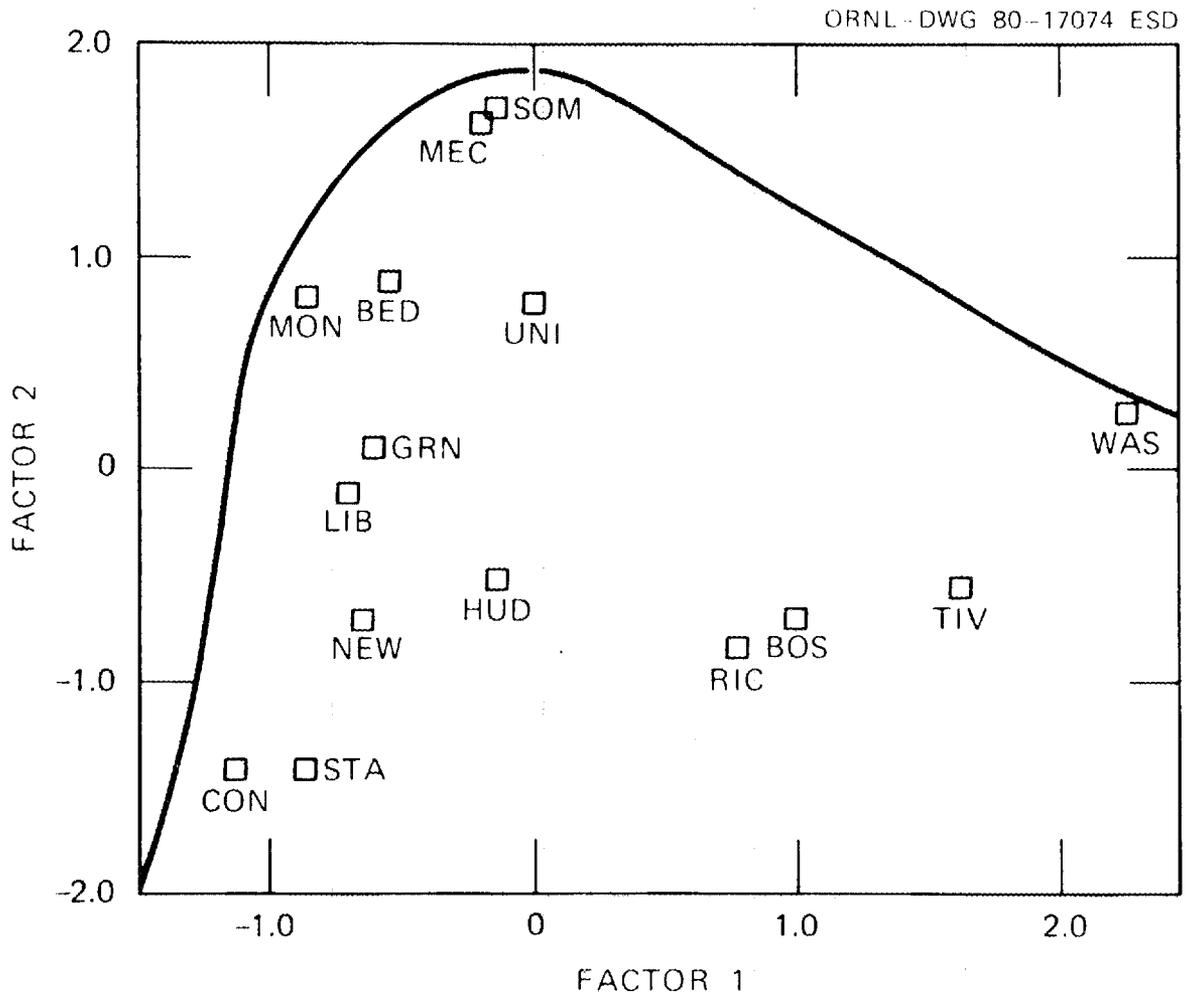


Fig. 6. Basic site ordination of 15 Ohio landscapes. Axes are derived from a factor analysis using seven continuous variables relating to forest island pattern. The solid line delimits the region where landscapes are possible. The existence of landscapes in the upper right and upper left corners is unlikely.

Table 3. Eigenvector coefficients for the first two factors of a factor analysis of 15 Ohio landscapes. The seven landscape variables describe forest island pattern.

Variable	Factor 1	Factor 2
Mean DI	0.89532	0.32295
Median area	0.92681	-0.23417
Median DI	0.88637	0.40420
Cover	0.95011	0.23579
Density	0.00278	0.98788
Landscape DI	0.34398	0.92869
Ln-mean-distance	-0.74605	-0.57897

Table 4. Coefficients of determination (R^2) for the regression of seven landscape variables on the first two factors of a factor analysis of 15 Ohio landscapes.

	Factor 1	Factor 2	Factor 1 and Factor 2
Density	0.0000	0.9759	0.9759
Landscape DI	0.1183	0.8625	0.9808
Ln-mean-distance	0.5566	0.3352	0.8918
Median DI	0.7856	0.1634	0.9490
Mean DI	0.8016	0.1043	0.9059
Median Area	0.8590	0.0548	0.9138
Cover	0.9027	0.0556	0.9583

variation in a factor was explained by one or more variables. Table 4 lists R^2 values for the regression models in which landscape variables are dependent variables and factors 1 and 2 are independent variables. Much of the variation in cover, median area, mean DI and median DI was accounted for in factor 1. The variables skew-area, skew-DI, and ln-mean-distance are correlated to a lesser degree, and density and landscape DI are virtually independent of factor 1. Density and landscape DI were highly correlated with factor 2 and are its primary components. Ln-mean-distance was only moderately correlated with factor 2. Taken together though, the first two factors accounted for 88 percent of the variation in ln-mean-distance. The third column of Table 4 lists how much variation in each landscape variable is accounted for by the first two factors.

The interpretation of a factor analysis in terms of eigenvector coefficients and correlation coefficients is a necessary but insufficient step. It is also necessary to express the meaning of the factors in verbal, nonmathematical terms easily understood by those not familiar with multivariate statistics. In this example, interpretation of the factor plot was straightforward for two reasons: (1) Most of the variation in the data was accounted for in the first two factors; (2) Except for ln-mean-distance, most of the weighting of the landscape variables fell into one factor or the other, i.e., the factors were primarily composed of equally weighted, covarying variables.

Factor 1 was interpreted as a gradient correlated with cover, mean DI, median DI, skewness of size and shape distributions, and inversely correlated with interisland distance. Values for factor 1 ranged from

-1.1 to 2.3. The second axis (factor 2) was correlated with density and landscape DI. It ranged from -1.4 to 1.7. Landscapes with low values (less than -0.5 for factor 1 and -0.6 for factor 2) for both factors, such as CON, STA, and NEW, had less than ten percent forest cover, divided among a relatively low density (<100) of small (4-6 hectare), somewhat rectangular forest islands. As factor 1 increased, the pattern (exemplified by WAS) became one of greater coverage with larger, more irregularly shaped islands and an increasingly skewed island size distribution. As factor 2 increased, the pattern became one of increasing density and landscape DI, e.g., SOM. Landscapes with low values for factor 1 but with relatively higher factor 2 values (<-0.3) had the smallest median woodlot sizes, e.g., MON, BED, and LIB. The mean distance index is dependent upon both factors. The mean distance index is large in landscapes with low numbers of small, widely scattered islands, such as CON, and is small in landscapes, such as WAS, having a high number of large islands, just as would be expected from the hypothetical model of landscape pattern.

The intercorrelated nature of the variables composing each factor is shown in a matrix of Pearson product-moment correlation coefficients (Table 5). Cover, median area, median DI, ln-mean-distance, skew-area, and skew-DI were highly correlated as were density and landscape DI. Some correlations were intuitively expected. For example, one would not expect mean and median DI to be totally independent. In another case, landscape DI is simply the square root of density in the hypothetical landscapes of circular islands. In reality, landscape DI is an integrator of fragmentation (density), island shape, and, to some

Table 5. Matrix of Pearson product-moment correlation coefficients for seven variables used to describe the forest island patterns of 15 Ohio landscapes.

	Mean DI	Median Area	Median DI	Cover	Density	Landscape DI
Median area	0.68455*					
Median DI	0.92643**	0.73070**				
Cover	0.92683**	0.79822**	0.92413**			
Density	0.28441	-0.19574	0.41064	0.24025		
Landscape DI	0.61679*	0.11831	0.68566**	0.52563*	0.91657**	
Ln-mean-distance	-0.82171**	-0.55433**	-0.84160**	-0.85104**	-0.56181**	-0.77293**

*Significant at the 0.05 level.

**Significant at the 0.01 level.

degree, island size distribution. Increasing fragmentation and irregularity of island shapes inflate landscape DI, while a skewed size distribution reduces it. A landscape with one large island and several much, much smaller islands would have a smaller DI than expected on the basis of density alone. Other correlations were not expected. For example, there was no a priori reason for expecting landscapes with relatively high coverage to have increasingly skewed island size distributions.

The significance of high intercorrelations among the variables composing factors 1 and 2 is that some of the variables can be dropped with little loss of ability to discriminate among landscapes. For example, the plots of density vs. cover and DI vs. cover (Figs. 7, 8) look much like the factor plot (Fig. 6). This phenomenon is discussed in greater depth later.

These plots (Figs. 6, 7, 8) are two dimensional representations of the distribution of landscapes in hyperspace. The distribution is based on only 15 landscapes and has gaps or empty regions that need explaining. One gap, located roughly between the SOM and WAS landscapes, is an unsampled region simply because of chance and not because the forest patterns of that region are inherently unlikely. SOM and WAS landscapes are in Belmont County and appear to lie on an east-west gradient of increasing forest fragmentation and decreasing forest cover. They are separated from each other only by Wayne township. Although not tested, it is likely that the Wayne landscape, had it been measured, would have been located between SOM and WAS in the hyperspace describing forest pattern.

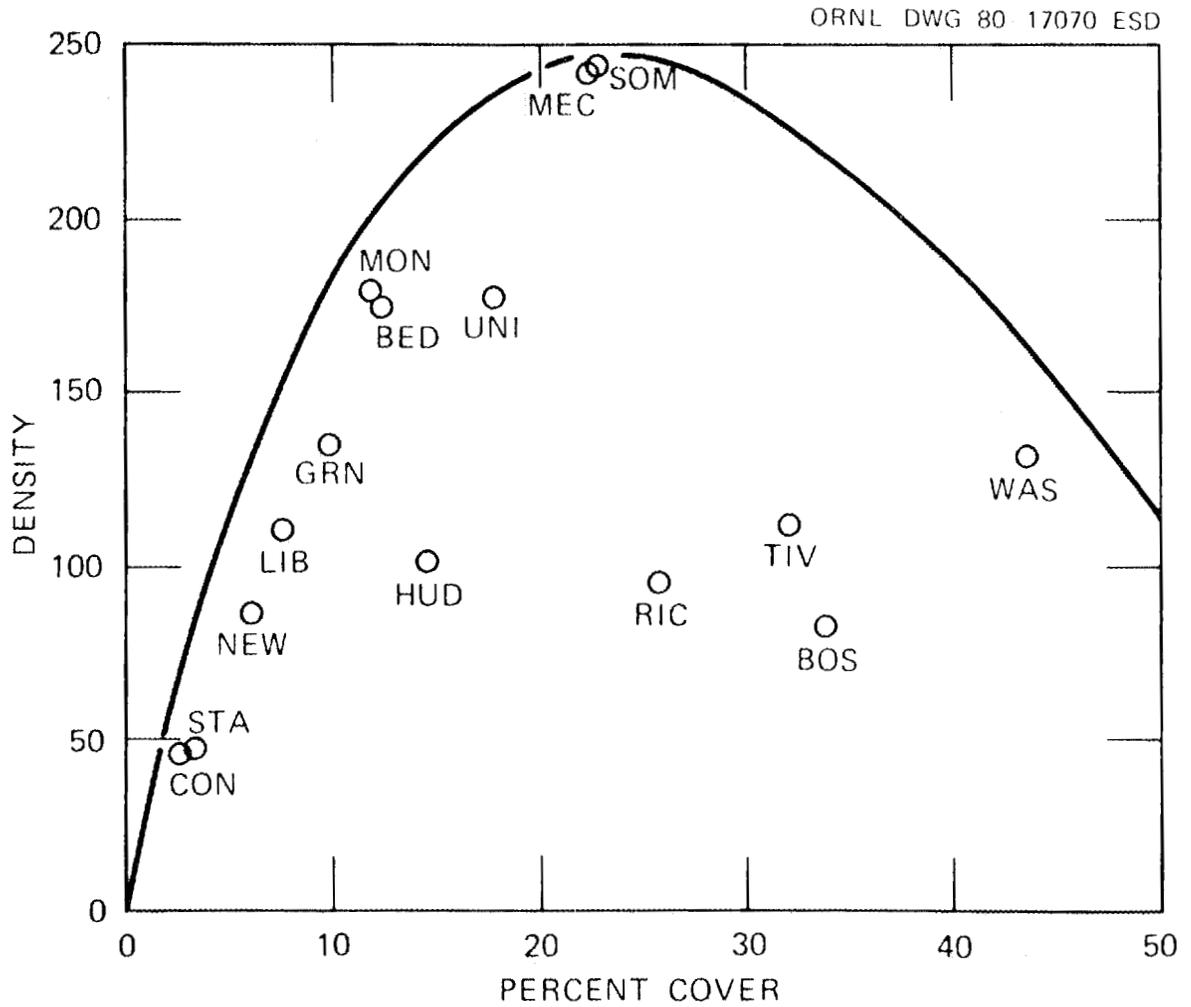


Fig. 7. First alternative site ordination of 15 Ohio landscapes. Axes are the variables percent cover and island density. The solid line delimits the region where landscapes are possible. The existence of landscapes in the upper right and upper left corners is unlikely.

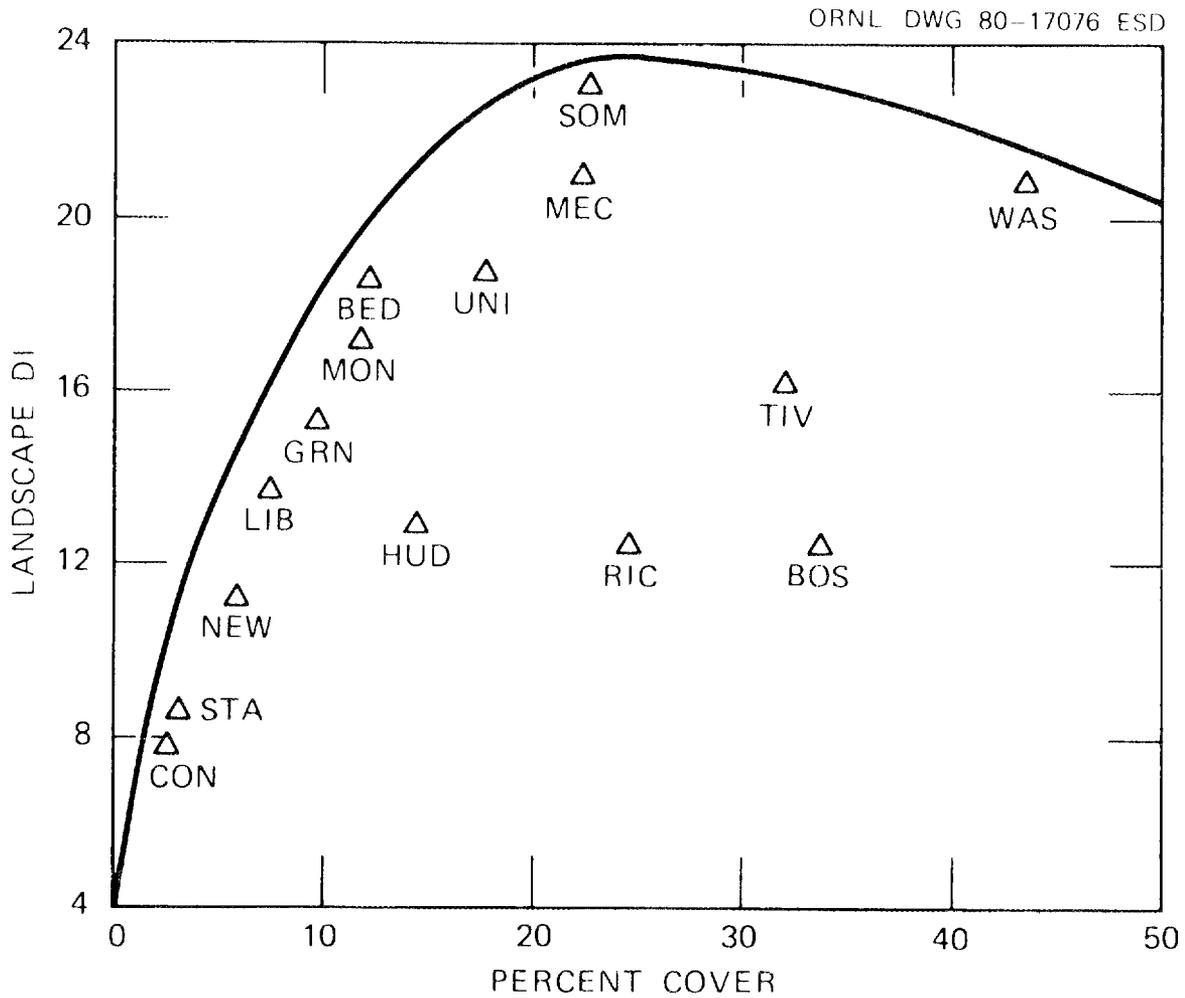


Fig. 8. Second alternative site ordination of 15 Ohio landscapes. Axes are the variables percent cover and landscape DI. The solid line delimits the region where landscapes are possible. The existence of landscapes in the upper right and upper left corners is unlikely.

Empty regions appear in the upper right and left corners of all three plots. These regions represent landscapes with theoretically possible but highly unlikely forest patterns. A landscape appearing in the upper left corner would have a low coverage and be populated by a large number of very small islands. In reality, the size distribution of forest islands is truncated below approximately two hectares, thus restricting the range of probable landscapes to those with a mean or median island size greater than two hectares. A landscape appearing in the upper right corner would have high coverage and a large number of forest islands. This is an unlikely situation because as coverage approaches 100 percent, the distance between woodlots approaches zero. Forest islands begin to coalesce into fewer and fewer units, thereby depressing density and landscape DI, the parameters measuring fragmentation. The WAS landscape (Fig. 2) is a good example of this concept. It has the highest cover (44 percent) and the lowest mean distance index (403 meters) of all the landscapes studied, yet its density is less than several of the others (SOM, UNI, BED, MEC). The forest pattern of WAS is probably close to the upper limits of fragmentation likely to be found in a landscape with that degree of forest cover.

The phenomenon of empty regions in the hyperspace describing forest pattern restricts the range of probable existing landscapes to a hump-shaped region in which peak forest fragmentation (as measured by density and landscape DI) corresponds with 20-30 percent forest cover. It remains to be shown what factors account for the variation within that region.

Environmental Factors and Forest Island Patterns

Land use practices, especially the clearing of forests for cropland and pastureland, were responsible for the patterns of forest islands evident in Ohio during the late 1930's. Presumably, the underlying patterns of topography and soils strongly influenced these land use practices. A farmer would be less inclined to clear forest, plow the ground, and plant crops on a steep, rocky hillside than on a smooth, fertile plain. One would therefore expect forest island patterns to be related to environmental patterns of topography, soils, and glacial history. Specifically, landscapes with rough topography and soils of low farming capability would have greater forest coverage than landscapes with smooth topography and fertile soils.

To test this hypothesis, all landscapes were initially classified according to land surface form, soils glacial history, original presettlement vegetation, and potential natural vegetation (Table 6). The classifications were then recorded beside each landscape on a factor analysis plot (Figs. 9, 10, 11, 12, 13), and the results interpreted.

Land surface form classification was used as an index of topographical variation. It is composed of three parts (Table 7). The first part is a letter (A,B,C,D) referring to the percentage of land area classed as having a surface of gentle inclination (less than eight percent slope angle). The second component is a number measuring local relief, i.e., the maximum difference in elevation within an area the size of a township. The third letter designates profile type, which is the percentage of gently inclined surface lying in the lower half of local relief. Sometimes the third letter is not used.

Table 6. Nominal (noncontinuous) variables used to describe 15 selected Ohio landscapes^a

Symbol	County	Land Surface Form ^b	Soil Type ^b	Glacial History ^c	Original Vegetation ^d	Potential Natural Vegetation ^e
SOM	Belmont	D3	I84	UNGL	MOF	AOF
UNI	Belmont	D3	I84	UNGL	MOF	AOF
WAS	Belmont	D3	I84	UNGL	MOF	AOF
BED	Coshocton	D3	I84	UNGL	MMF	BMF
TIV	Coshocton	D3	I84	UNGL	MOF	AOF
MEC	Holmes	D3	I84	UNGL	MOF	AOF
LIB	Knox	B2B	A74	WISC	BF	BMF
MON	Knox	B3C	A74_I84	ILLI	MMF	BMF-AOF
CON	Miami	A2C	A74	WISC	BF	BMF
NEW	Miami	A2C	A74	WISC	BF	BMF
STA	Miami	A2C	A74	WISC	BF	BMF
BOS	Summit	B3C	A715	WISC	MMF	BMF
GRN	Summit	B3C	A69	WISC	MOF	AOF
HUD	Summit	B2B	A69	WISC	MMF	BMF
RIC	Summit	B3C	A715	WISC	MOF	BMF

^aFor definitions of variations see "Key to Nominal Landscape Variables in Table 6."

^bSource: U.S.D.I. 1970. The national atlas of the United States of America. Washington, D.C. 417 pp.

^cSource: Ohio Department of Natural Resources. 1966. Division of geological survey. U.S.G.S. Misc. Geol. Inv. Map I-316.

^dSource: Gordon, R. B. 1966. Natural vegetation of Ohio, at the time of the earliest surveys. Ohio Biological Survey, Columbus.

^eSource: Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geog. Soc. Spec. Publ. No. 36. New York.

Key to the Nominal Landscape Variables in Table 6

Land surface form classes

- A2c Smooth plains - greater than 80% gently sloping (less than 8% slope angle); relief 30-91 m; 50-75% of gentle slope is on uplands.
- B2b Irregular plains - 50-80% gently sloping; relief 30-91 m; 50-75% of gentle slope is on lowland.
- B3c Tablelands moderate relief - 50-80% gently sloping; relief 91-152 m; 50-75% of gentle slope is on uplands.
- D3 Hills - less than 20% gently sloping; relief 91-152 m.

Soil classes

- A74 Hapludalfs plus Argiaquolls, gently sloping (less than 10% slope angle).
- A69 Fragiudalfs plus Ochraqualfs and Fragiaqualfs, gentle sloping.
- A715 Hapludalfs plus Ochraqualfs, gentle sloping.
- I84 Dystrochrepts, steep slopes (greater than 25% slope angle) plus Hapludalfs and Hapludults both moderately sloping (10-25%).

Glacial history

- UNGL Area was unglaciated throughout its history.
- ILLI Area was most recently covered by the Illinoian glaciation.
- WISC Area was most recently covered by the Wisconsin glaciation.

Original (presettlement) vegetation

- BF Beech forests
- MOF Mixed oak forests
- MMF Mixed Mesophytic forests

Potential natural vegetation

- BMF Beech-maple forests
- AOF Appalachian oak forests

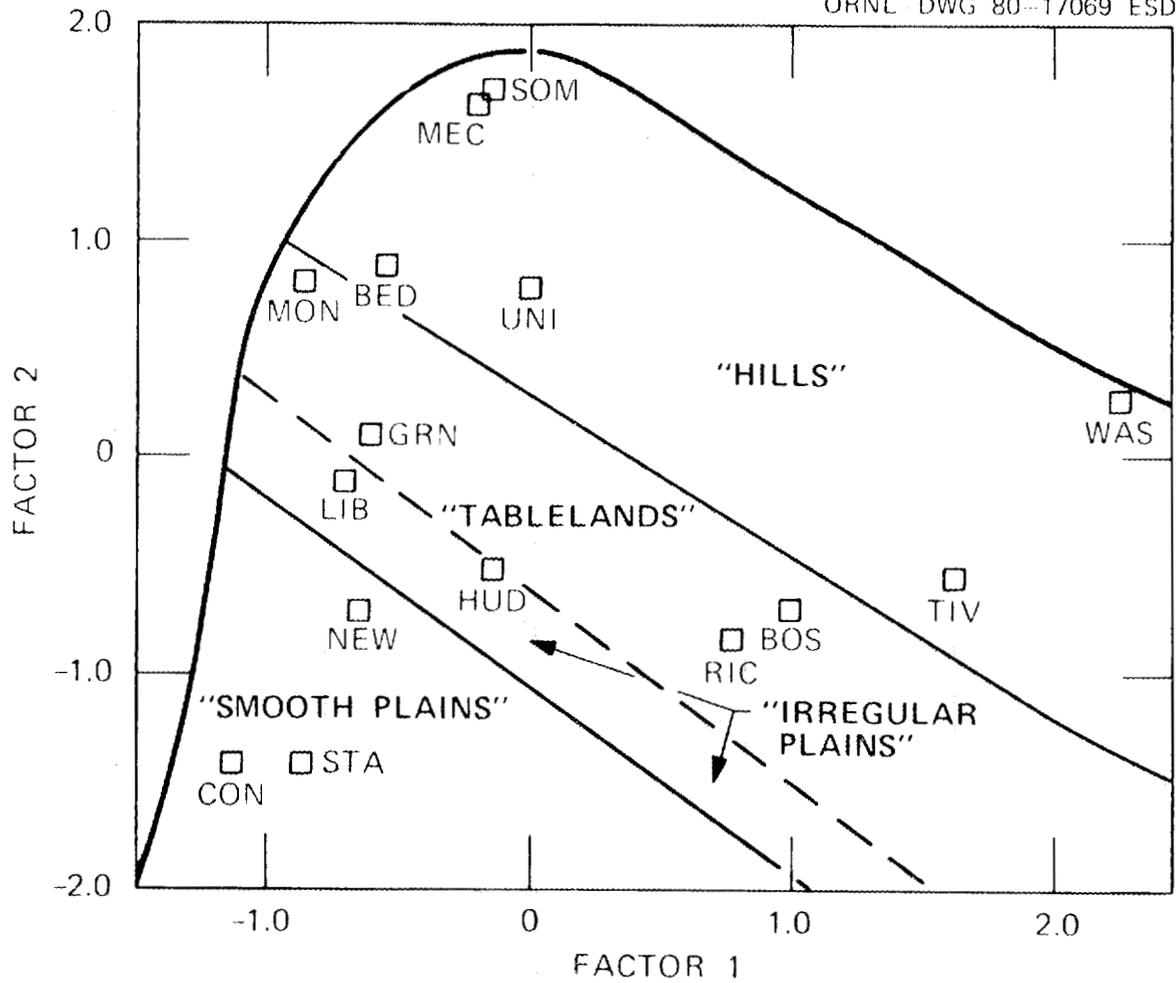


Fig. 9. Overlay of land surface form classes on the basic site ordination of Ohio landscapes.

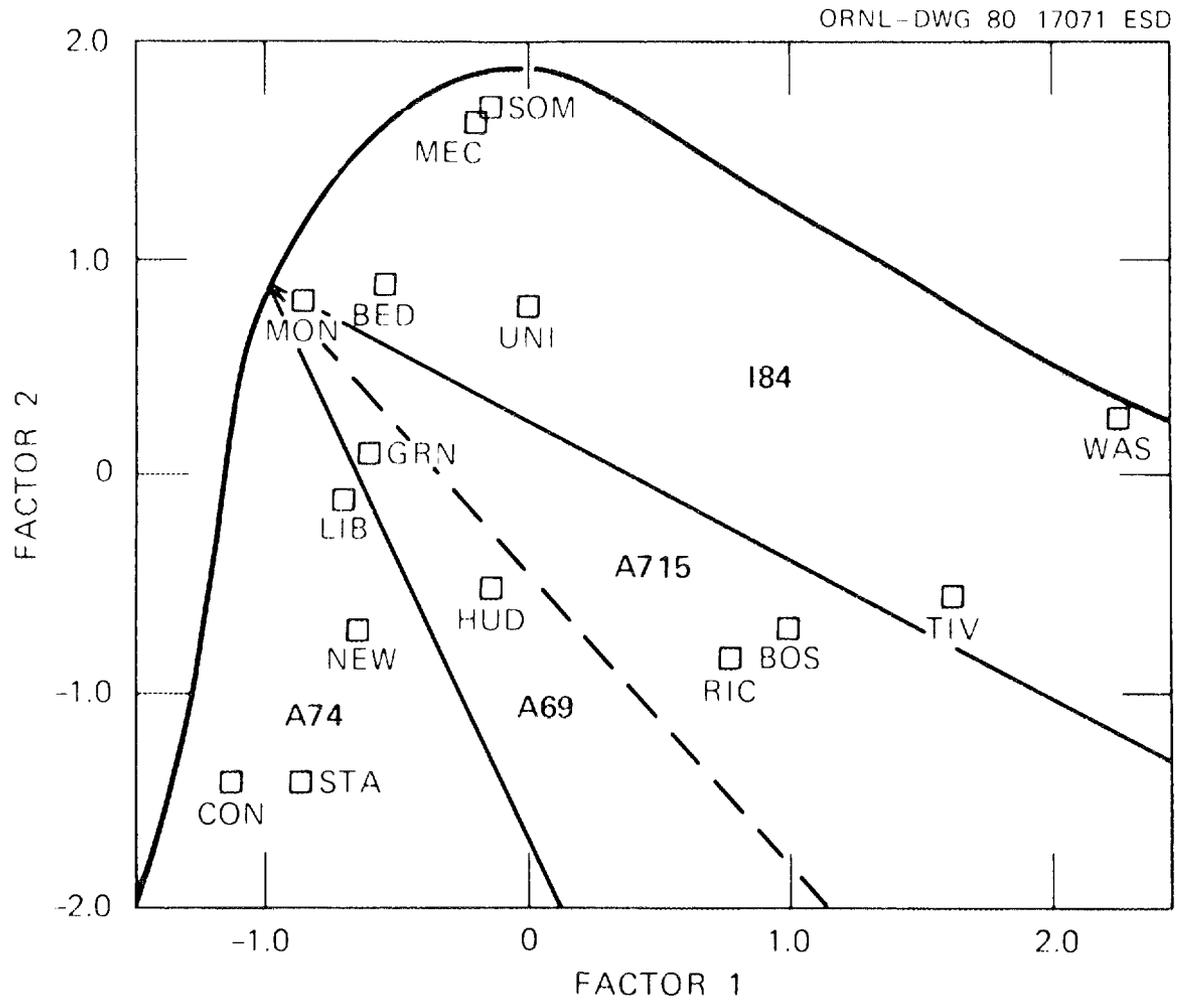


Fig. 10. Overlay of soil type on the basic site ordination of Ohio landscapes.

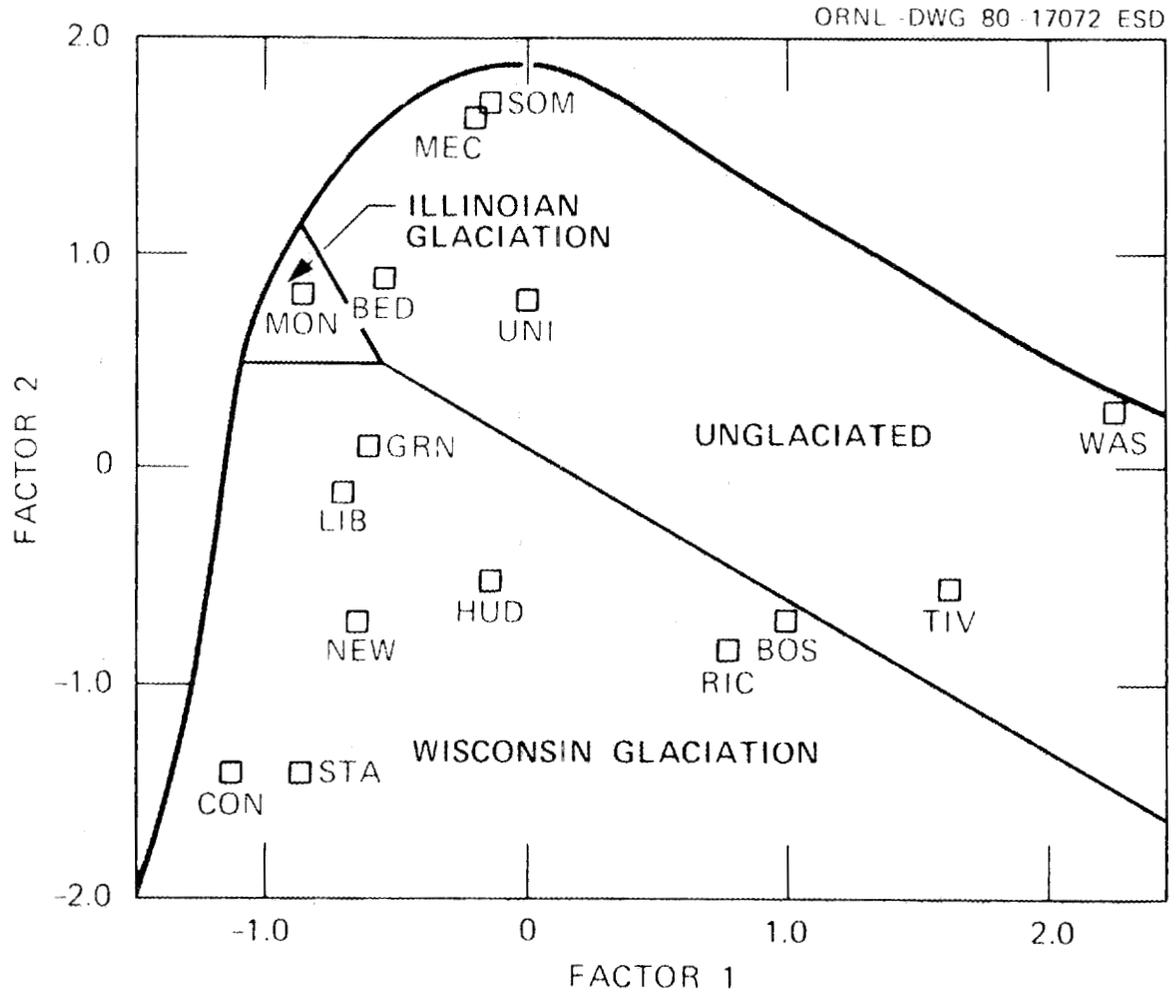


Fig. 11. Overlay of glacial history on the basic site ordination of Ohio landscapes.

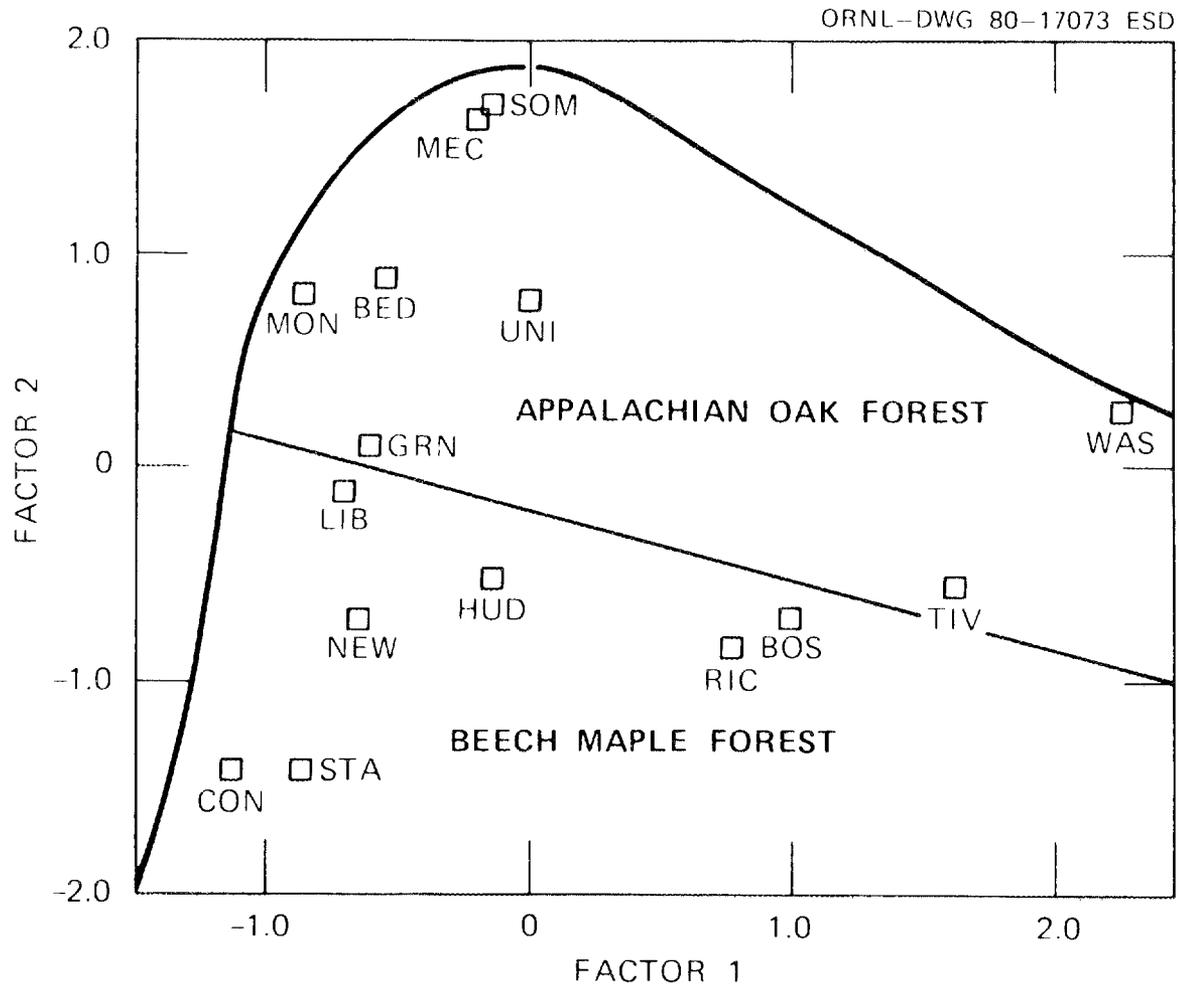


Fig. 12. Overlay of potential natural vegetation types on the basic site ordination of Ohio landscapes.

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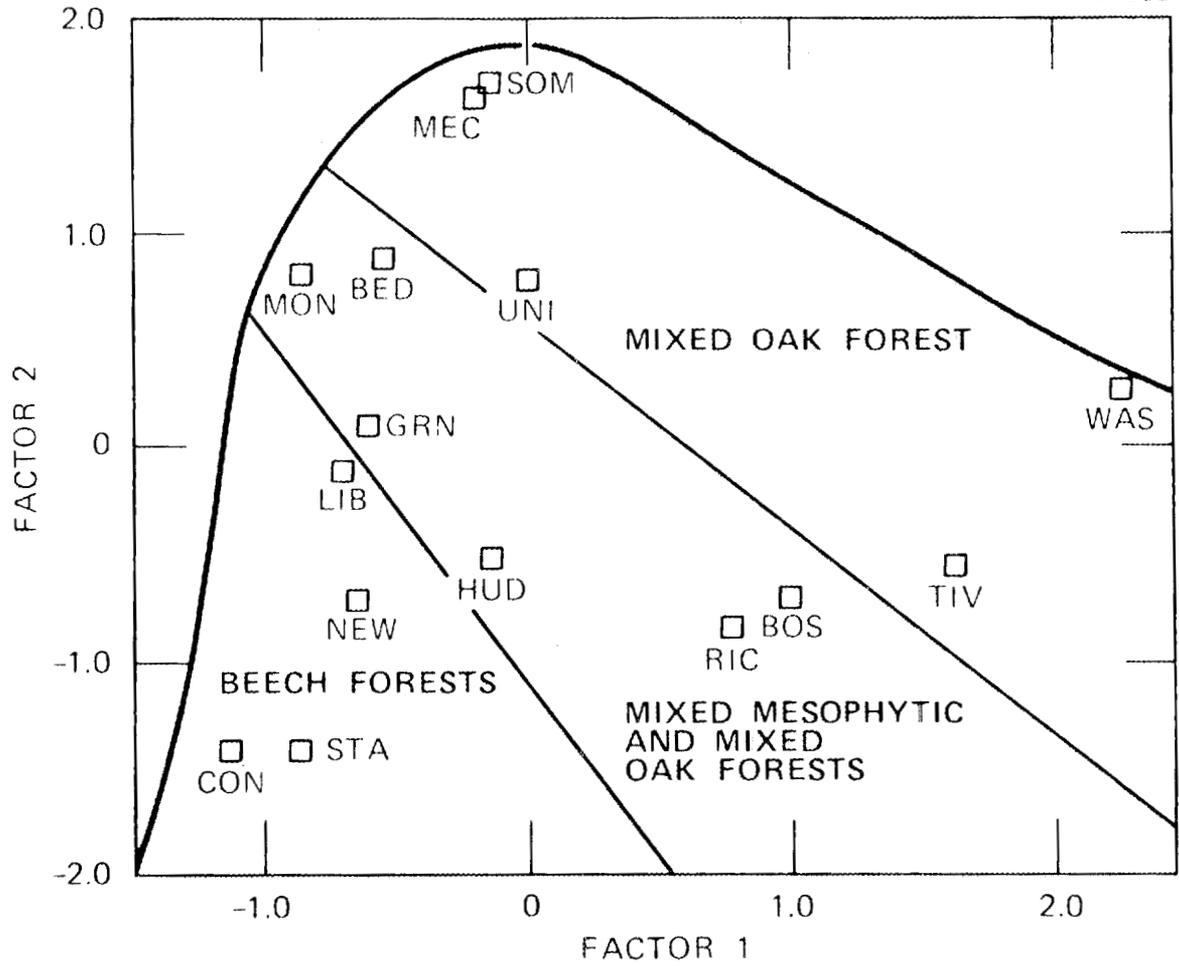


Fig. 13. Overlay of original forest types on the basic site ordination of Ohio landscapes.

Table 7. Classification scheme for the land surface form index. The index has three components corresponding to slope, local relief, and profile type, e.g., A2C.

SLOPE (Capital letter)

- A More than 80 percent of area gently sloping
- B 50-80 percent of area gently sloping
- C 20-50 percent of area gently sloping
- D Less than 20 percent of area gently sloping

LOCAL RELIEF (Numeral)

- 1 0-100 feet
- 2 100-300 feet
- 3 300-500 feet
- 4 500-1000 feet
- 5 1000-3000 feet
- 6 Over 3000 feet

PROFILE TYPE (Lower case letter)

- a More than 75 percent of gentle slope is in lowland
- b 50-75 percent of gentle slope is in lowland
- c 50-75 percent of gentle slope is on upland
- d More than 75 percent of gentle slope is on upland

Source: U.S.D.I. 1970. The national atlas of the United States of America. Washington D.C. 417 pp.

Together, the three components produce an index that integrates information pertinent to slope, local relief, and profile. For example, land classed A2c is more than 80 percent gently sloping, with most of the gentle slope in the uplands, and it has a relief of only 30 to 91 meters (100 to 300 feet). Land designated B2b is 50-80 percent gently sloping (mostly in the lowlands) and has a relief of 10-31 meters. Land classed D3 is less than 20 percent gently sloping, but it has a relief of 31 to 152 meters.

The description of the four land surface form classes found in this study (Table 6) suggests a gradient of topographical ruggedness starting with smooth plains, progressing through irregular plains with low relief to tablelands of moderate relief and culminating in hill country. This gradient is reflected in the overlay of topographical information onto the factor analysis plot (Fig. 9), thus confirming the hypothesis that forest island pattern is related to topography. The two dimensional factor space can be broken down into a sequence of regions corresponding to a topographical gradient aligned obliquely with respect to the factor axes.

Landscapes with gentle topography (CON, STA, NEW) also have a relatively low number of small rectangular islands. All three of these landscapes are in intensively agricultural Miami County, where there are few limitations to farming. As the percentage of relatively flat land decreases to between 50 and 80 percent (classes B2b and B3c), and the relief increases to between 91 and 152 meters, the forest coverage increases. The increased coverage is due to both an increase in the density of islands, e.g., LIB, GRN, MON, and in the size of islands,

e.g., HUD, RIC, and BOS. In addition, island shapes become progressively more irregular and the skewness of woodlot size distributions more pronounced. These trends continued as the percentage of flat land dropped below 20 percent. Hilly landscapes had the highest density of woodlots (SOM, MEC), the largest islands (TIV), the most skewed island size and shape distribution (BOS, WAS) and the most dissected island shapes (WAS) of all landscapes studied.

Glacial history, soils, and original or potential natural vegetation are related to topography and therefore to certain regions in the factor space describing landscapes (Figs. 9, 10, 11, 12, 13). For example, glacial history exerts its effects on landscape pattern by dividing Ohio topography into two sections; the nonglaciaded hills in the southeast and the glaciaded plains or tablelands in the remaining portion of the state (Fig. 2). Landscapes in the glaciaded sections of the state have forest island patterns characteristic of smooth to slightly irregular topography, while the nonglaciaded landscapes have forest island patterns characteristic of the rough, hilly topography (Figs. 9, 11). One landscape (MON) was in the older Illinoian glaciaded, rather than in the more recent Wisconsin glaciaded topography. It has a topography intermediate between the flatter glaciaded west and the nonglaciaded east, and its forest island pattern reflects this condition by having higher density, cover, and median DI than its neighbor, LIB, only seven kilometers to the southwest in the Wisconsin glaciaded.

Given that pedogenic processes are strongly influenced by topography, parent material, and plant cover, it is entirely consistent

to expect soil classes to be related to forest island pattern (Fig. 10). For example, the soil mosaic of the nonglaciaded hills in southeast Ohio is characterized by having a large proportion of dystrochrepts, (soils with weakly differentiated horizons and low base saturation, formed on steep slopes) and is classified I84. The soil type (A74) of the glaciaded plains of Miami County and western Knox County is a mosaic of hapludalfs and argiaquols. Hapludalfs are a type of alfisol (soils marked by grey to brown surface horizons and medium to high base saturation) that are seasonally dry and have a horizon of clay accumulation. Argiaquols are a type of aquol (seasonally wet soils with dark, organic-rich, base-saturated surface horizons) that have a horizon of clay accumulation.

High base saturation is characteristic of young, glacially derived soils, because insufficient time has passed for the carbonate content of the parent material laid down by the glaciers to have been leached away by weathering. The seasonally wet or dry nature of a soil is a function of topography and climate. Seasonally wet soils are usually found in low places with poor drainage, and summer-dry soils are usually found on well drained slopes. High organic matter content in the surface horizons of argiaquols results from the input of plant material and may signify a past history of wet prairie since grasses usually add more organic matter to the soil than trees.

Again, the MON landscape exhibited its intermediate nature by lying on the boundary dividing the I84 class from the A74 class. It was not possible to assign MON to either soil type because of the small scale of the map, so it was classed as a combination of the two (A74-I84).

The remaining landscapes (RIC, BOS, HUD, and GRN) have somewhat different soils. The partially overlapping landscapes of RIC and BOS have a mosaic of hapludalfs and ochraqualfs (poorly-drained, seasonally wet alfisols). The soil type in GRN and HUD landscapes (A69) is marked by ochraqualfs, fragiudalfs (seasonally dry alfisols with a fragipan) and fragiaqualfs (seasonally wet alfisols with a fragipan). The lack of dystrochrepts is evidence of an absence of steep hilly topography, and the absence of argiaquolls distinguishes these soils from the soils found in other parts of glaciated Ohio.

The original presettlement vegetation as described by Gordon (1966) and Küchler's (1964) potential natural vegetation classes are also related to regions in factor space (Figs. 12, 13). Küchler's map is on a smaller scale and has fewer vegetation classes (in Ohio) than Gordon's but both present essentially the same relationships between vegetation, topography, and forest island pattern. In both cases, beech-maple forests were thought to inhabit the glaciated portions of Ohio, while oak forests occupied the unglaciated hills (Forsyth 1970). Three of the forest types recognized by Gordon (beech, mixed mesophytic, and mixed oak) were associated with the study areas. Beech forests were associated with forest island patterns characteristic of the glaciated plains while mixed oak forests were associated with forest patterns found mostly in the unglaciated hills. All three forest types inhabited the glaciated sites of intermediate topographical ruggedness. Only two of Küchler's forest types were assigned to the landscapes. The glacial boundary proved very important in separating Appalachian oak forests from beech-maple forests. MON

and GRN were the only glaciated landscapes not classified into the beech-maple forest type.

Because of the intercorrelations between variables, the plots of cover versus density (Fig. 8, p. 66) and cover versus landscape DI (Fig. 7, p. 65) are very similar to the plot of factor 1 versus factor 2. In a similar fashion, overlaying an environmental class, e.g., land surface form, on these plots (Figs. 14, 15) presents essentially the same information depicted in Fig. 9, p. 71. This was a parsimony in the analysis, since only two variables (instead of seven) were sufficient to distinguish among the forest island patterns of Ohio landscapes and relate them to environmental factors. In other circumstances, the variables pertaining directly to size, shape, and interisland distance might be required to satisfactorily investigate a problem.

The decisions as to what variables to use will depend upon the purposes of the investigator and the time, effort, and expense required to make appropriate measurements. Some of the measurements in this project were easier to make than others. For example, density was easier to measure than landscape DI, yet it contained much the same information. Conversely, once the required measurements of cover and landscape DI were taken, it was a relatively easy task to calculate mean island DI, median island DI, and median island size.

Discriminant Analysis

In this project, the variation in forest island pattern among landscapes was believed to reflect the inherently continuous

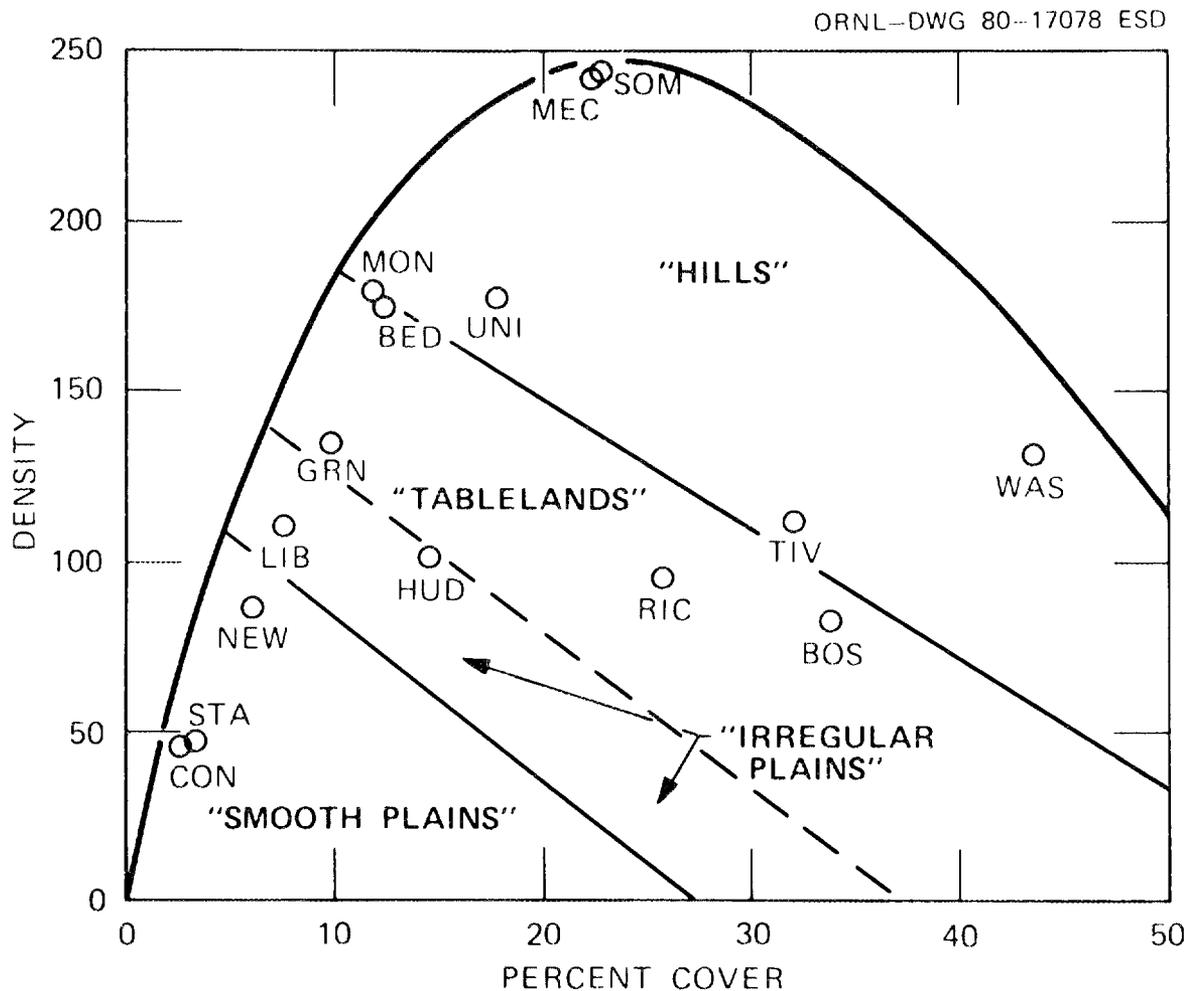


Fig. 14. Overlay of land surface form classes on the first alternative site ordination of Ohio landscapes. Axes are the variables percent cover and island density.

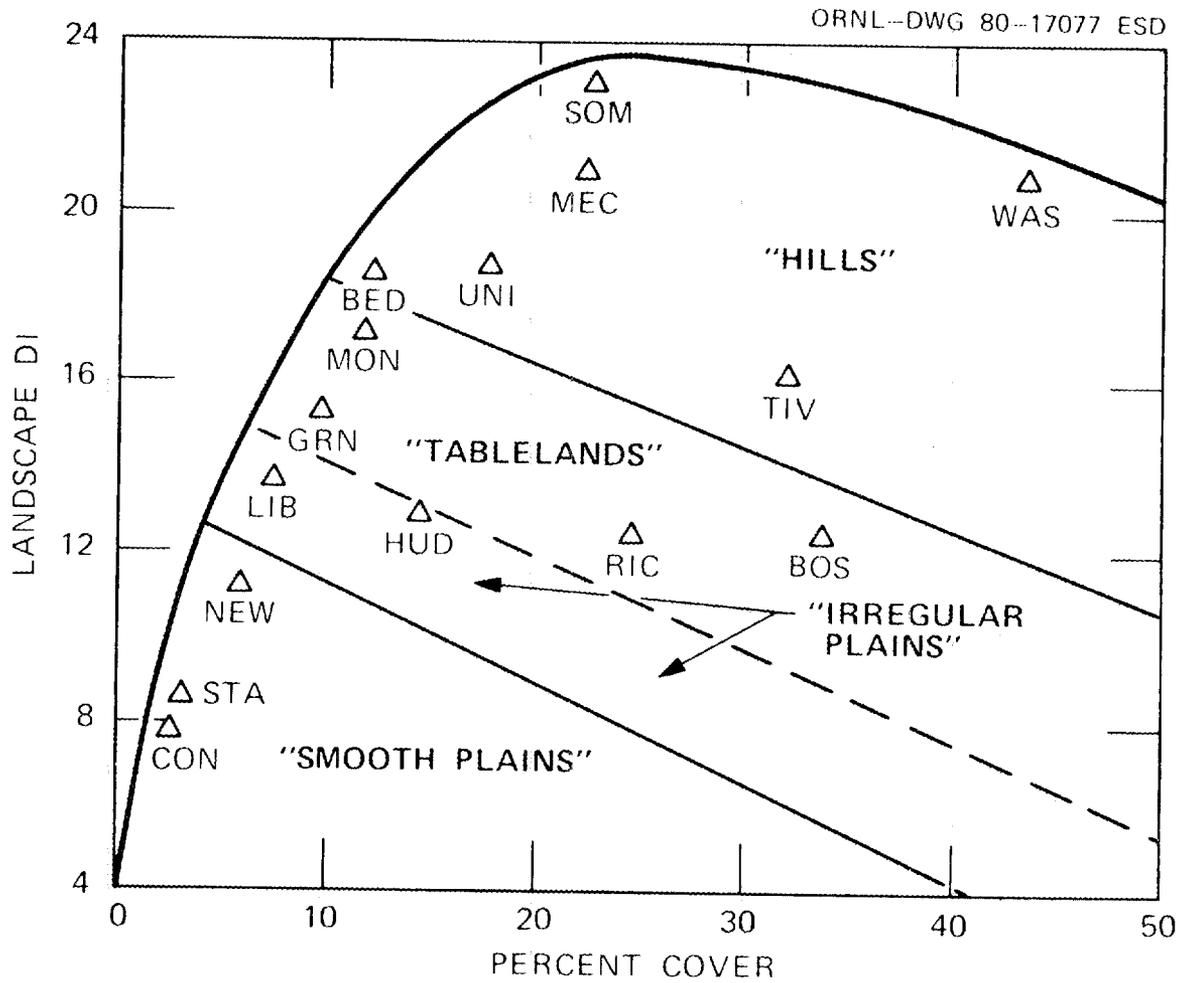


Fig. 15. Overlay of land surface form classes on the second alternative site ordination of Ohio landscapes. Axes are the variables percent cover and landscape DI.

variability of topography and soils. Land use was assumed to be constant in that most land suitable for cultivation or pasture was used for those purposes and therefore landscapes with similar topography and soils would have similar forest island patterns. In accordance with this model, certain aspects of forest pattern were measured with continuous variables and differences among landscapes were graphically portrayed and interpreted with the aid of factor analysis.

Unfortunately, available data on topography and soils were not directly interpretable in terms of the model because the variables were nominal instead of continuous. With noncontinuous variables, it was impossible to quantitatively explain forest island pattern in terms of continuous variation in the topographic and edaphic features of landscapes.

Overlay of the land surface form classes on the factor analysis plot crudely defined a series of groups or regions which could be interpreted as a gradient of topographical ruggedness. Even though the model assumes continuous variation, the land surface form classes were, for the moment, considered as discrete groups. Stepwise discriminant analysis was then employed to determine to what degree landscapes could be separated into topographic classes, solely on the basis of forest island patterns.

The philosophical emphasis of discriminant analysis differs from that of factor analysis, even though both techniques use continuous data and rely on some of the same matrix algebra procedures. Factor analysis seeks to condense the variation among observations into a few independent axes. Conversely, discriminant analysis seeks to define axes maximizing the statistical distance between groups of

observations. The distance between groups in the space defined by the discriminant functions can be used as a measure of group integrity and, in some cases the axes themselves may be explainable. Discriminant analysis emphasizes discrete classes and factor analysis does not, though both define axes that may be subject to interpretation.

The same set of data can often be analyzed in a number of different ways depending upon the investigator's model of the nature of variation within the data set. If the model assumes that observations fall into classes, then techniques like discriminant analysis are used, but if the variation among observations is believed to be continuous, then techniques like factor analysis or canonical correlation are used.

The seven variables employed in the factor analysis (cover, density, landscape DI, mean DI, median DI, median area, and ln-mean-distance) were used in a discriminant analysis with land surface form as the classification variable. The first discriminant function was generated. Distance between group centroids was interpreted as a measure of class integrity, and the relative order of the groups was interpreted as the placement along the topographical gradient. Since the groups representing landscapes with similar topography were arranged serially, albeit obliquely, with respect to the factor axes, the expectation was that the first discriminant axis would pass through these groups. Landscapes with forest patterns characteristic of smooth topography (class A2c) and landscapes with forest patterns characteristic of rough topography (class D3) would be at opposing ends of the axis. The intermediate groups (B2b and B3c) would occupy an intermediate position and would probably be poorly separated from each other.

Because the model of landscape pattern was founded on the concept of continuous variation among landscapes, discriminant analysis was meant only to support and illuminate the interpretations of the factor analysis and its related plots, and not stand as the primary means of investigating the relationships between forest island pattern and environmental factors.

The results of the discriminant analysis indicated no statistically significant differences between the land surface form classes, probably because of the small sample size and the continuous nature of the data. As expected, landscapes were arranged along the first discriminant function according to topographic class (Fig. 16). Cover and landscape DI were best suited for classifying landscapes. Addition of the other variables did not greatly enhance classification ability because they were highly correlated with either cover or landscape DI. No meaningful interpretations could be made for the second discriminant function.

The discriminant analysis was simply another way of presenting the same information found in the overlay of land surface form classes on the factor analysis plot. By collapsing most of the topographic variation among landscapes into a single dimension, it achieved a certain parsimony for explaining forest island pattern in terms of topography. Some information was hidden, because the separation of landscapes within groups was reduced as a result of maximizing separation between groups.

Discriminant analysis using glacial history as the classification variable gave results similar to those for topography. Glaciated

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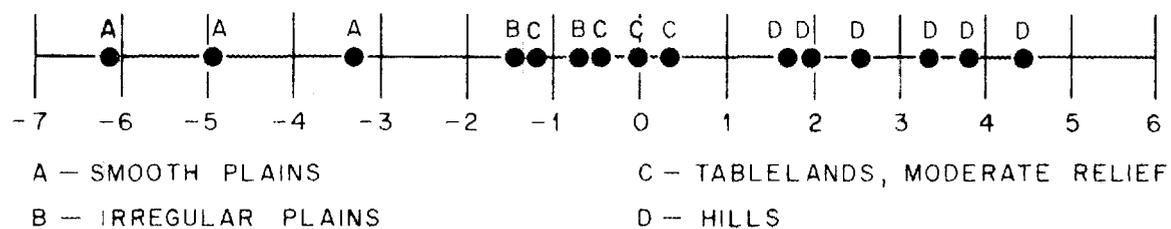


Fig. 16. One dimensional site ordination of 15 Ohio landscapes. Axes are derived from a discriminant analysis based on seven landscape variables and using land form as the discriminant criterion.

landscapes were separated from unglaciated landscapes on the first discriminant function, but the separation was not statistically significant.

Desirability of Continuous Data

Topographic and edaphic data were taken because topography and soils are the most important factors influencing the agricultural land uses that determined forest distributional patterns in Ohio. Because of a lack of time and appropriate maps, the data were discrete (classificatory). If the data had been continuous, then other statistical techniques could have been employed to explain the relationships between forest patterns and topography. For example, the three components of land surface form can be measured directly from topographic maps. Functions derived from the values for relief and percent of land with gentle slope could then be regressed on the factor scores describing forest island patterns or used as the predictor variables in a canonical correlation analysis. Another set of potentially useful measurements could be derived from maps showing land capability classes. Land capability classes integrate topography and soils and show agricultural limitations of a landscape. The percentages of a landscape in the various capability classes should be a good predictor of forest patterns.

There was considerable variability in the forest island patterns of hilly landscapes not explained by the soils or land surface form. Perhaps continuous measurements or indices of topography and soils could better explain why some hilly landscapes had many small islands

(UNI, BED) while others had fewer but larger islands (TIV, WAS). As in any project, the extra time and effort required to collect detailed measurements has to be weighed against the desired resolution of the results. The extra effort needed to make continuous measurements of topography and soils may not have resulted in greater understanding of landscape pattern.

Integration with Other Ecological Concepts

This study focused on a methodology for quantifying different aspects of landscape pattern. Important differences between landscapes can be measured with variables reflecting the ecologically important structures and processes that occur at a landscape scale. As one goal of regional ecology is to quantify the various spatial, temporal, and functional aspects of landscapes (Klopatek, Shugart et al. 1979), the methods are applicable to the study of the forest component of regional systems.

"Man's role is an integral part or functional component of a regional system--" (Klopatek, Shugart et al. 1979). His cultural and technological systems affect all levels of environmental systems and need to be included in any evaluation. Forests are but one aspect of man's environment affected by culture and technology. Large scale forest patterns can provide an index for assessing man's impacts on forests in general. Other aspects of the environment may modify the impact of cultural and technological systems on forests, e.g., topography and soils. A quantitative evaluation of the impacts of culture and technology on large scale forest patterns therefore

requires the measurement, at an appropriate scale, of several landscape variables, some describing forest pattern and some describing other environmental features such as topography and soils.

This study is a specific example of how the response of regional landscape properties to man's activities can be measured. By relating forest island distribution patterns to certain topographic and edaphic landscape features, this project, in effect, measured the cumulative regional response of Ohio forests to the impacts associated with agricultural development and related that response to topography and correlated features. Other examples of how landscape variables can be used to approach regional problems are conceivable. For example, landscape variables could be used to develop data bases for evaluating and anticipating regional environmental impacts of activities associated with land use which singly or in unison have far reaching effects. The similarities and differences between different parts of the eastern deciduous forest could be quantified in terms of forest island distribution patterns and other environmental attributes. Areas having similar landscape attributes can be designated as special regions and portrayed as homogeneous map units. Because these regions have similar characteristics, they would be expected to exhibit a characteristic response to a given disturbance.

Another example using landscape variables involves the evaluation of how a species population responds to the dissection and fragmentation of its forest habitat (Whitcomb 1977). Landscape variables could describe forest island patterns and relate these to the

abundance of a species in the region as a whole and, in doing so, test concepts of island biogeography theory.

Island biogeography has been used to explain the dynamics of semi-isolated populations. The first application was to oceanic islands (MacArthur and Wilson 1963, 1967), but the concepts have since been generalized to include terrestrial habitats such as caves, mountain tops, and woodlots (Culver 1970, Picton 1979, Brown 1971, Elfstrom 1974, Patterson 1980, Forman and Elfstrom 1975, Suhweir 1976, Levenson 1976, Ranney and Johnson 1977). Several parameters associated with island biogeography concepts can be included as landscape variables, e.g., measures of forest island size, shape, and interisland distance. The possibility exists to use some measures of species abundance and persistence as dependent variables and a series of landscape variables as independent variables in an effort to relate species populations to landscape patterns. This approach can be used to determine the optimal configuration of nature reserves (as discussed by Diamond 1975, 1976; Sullivan and Shaffer 1975; Simberloff and Abele 1976; Terborgh 1974, 1976; Whitcomb et al. 1976; Faaborg 1979; Game 1980) or the impacts of forest fragmentation on bird populations (as discussed by Moore and Hooper 1975, Forman et al. 1976, Galli et al. 1976, and Whitcomb 1977).

The advantage of using landscape variables in some studies is that the properties of ecosystems emergent at that scale may influence populations in ways not easily detected with studies made at smaller scales. For example, a landscape with a few large forest islands might support a larger population density of a certain bird species than a

nearby landscape with a larger number of smaller islands, even though the forests of both areas are composed of the same tree species and cover the same total area.

This study was concerned with only one point in time and in essence presented a "snapshot" of the forest island patterns in Ohio during the late 1930's. But landscape patterns are not static. The nature of the disturbance regimes associated with changing land use and the inherent successional properties of forests combine to bring about changes in the distribution patterns of forest cover. Data from Curtis (1956) chronicle the history of change in the forest island pattern of Cadiz township, Green County, Wisconsin from 1831 (the year of the General Land Office Survey) up to 1950 (Fig. 1, p. 18). Except for a prairie opening, forest cover was continuous across Cadiz township in 1831. Subsequent settlement led to the forest's destruction and fragmentation. Forest coverage decreased rapidly from 1831 until 1882, then more slowly afterwards, so that by 1950, only four percent of the township remained in forest (Fig. 17a). Meanwhile, the degree of forest fragmentation, as measured by landscape DI, increased rapidly until 1882 then more slowly afterwards (Fig. 17b).

Examples like Cadiz township illustrate how changes in landscape pattern over time can trace a vector through the n-dimensional hyperspace describing that landscape (Fig. 18). Given enough information, it should be possible to predict the direction and velocity of the vector. Consequently, for certain scenarios of land use, it should be possible to develop mathematical models of how landscape features change over time.

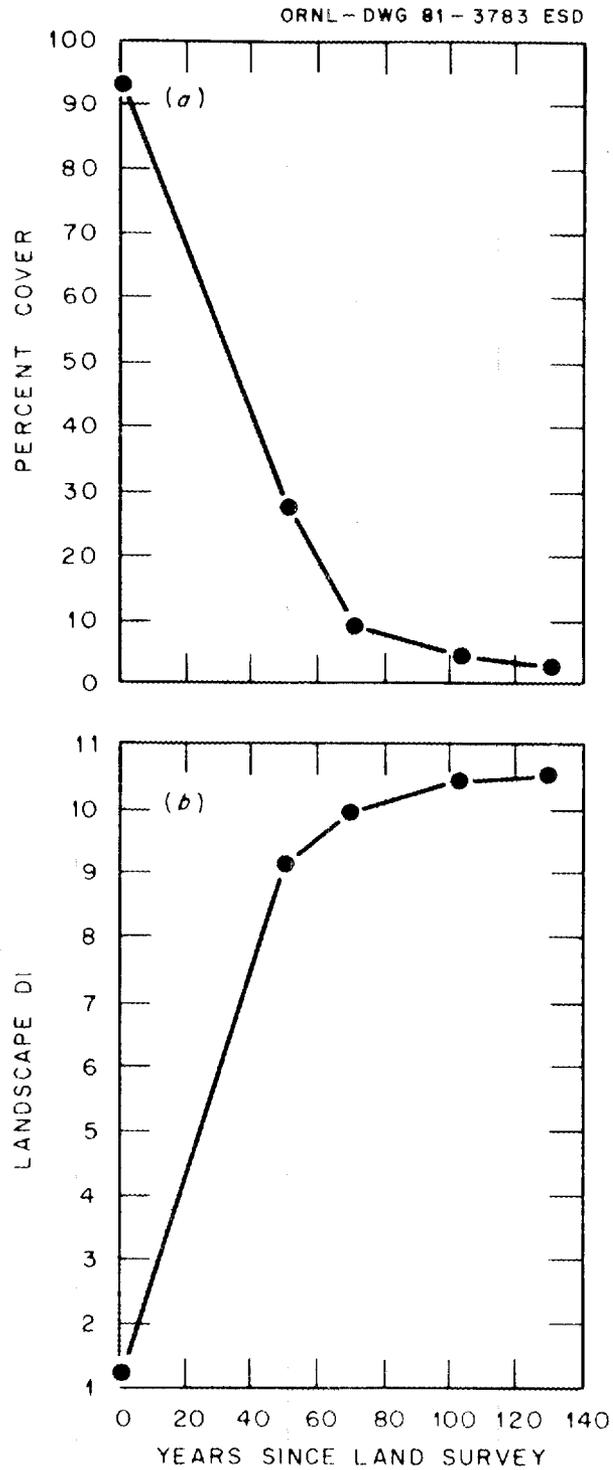


Fig. 17. Changes in two landscape parameters of Cadiz township, Green County, Wisconsin after the General Land Office Survey of 1831.

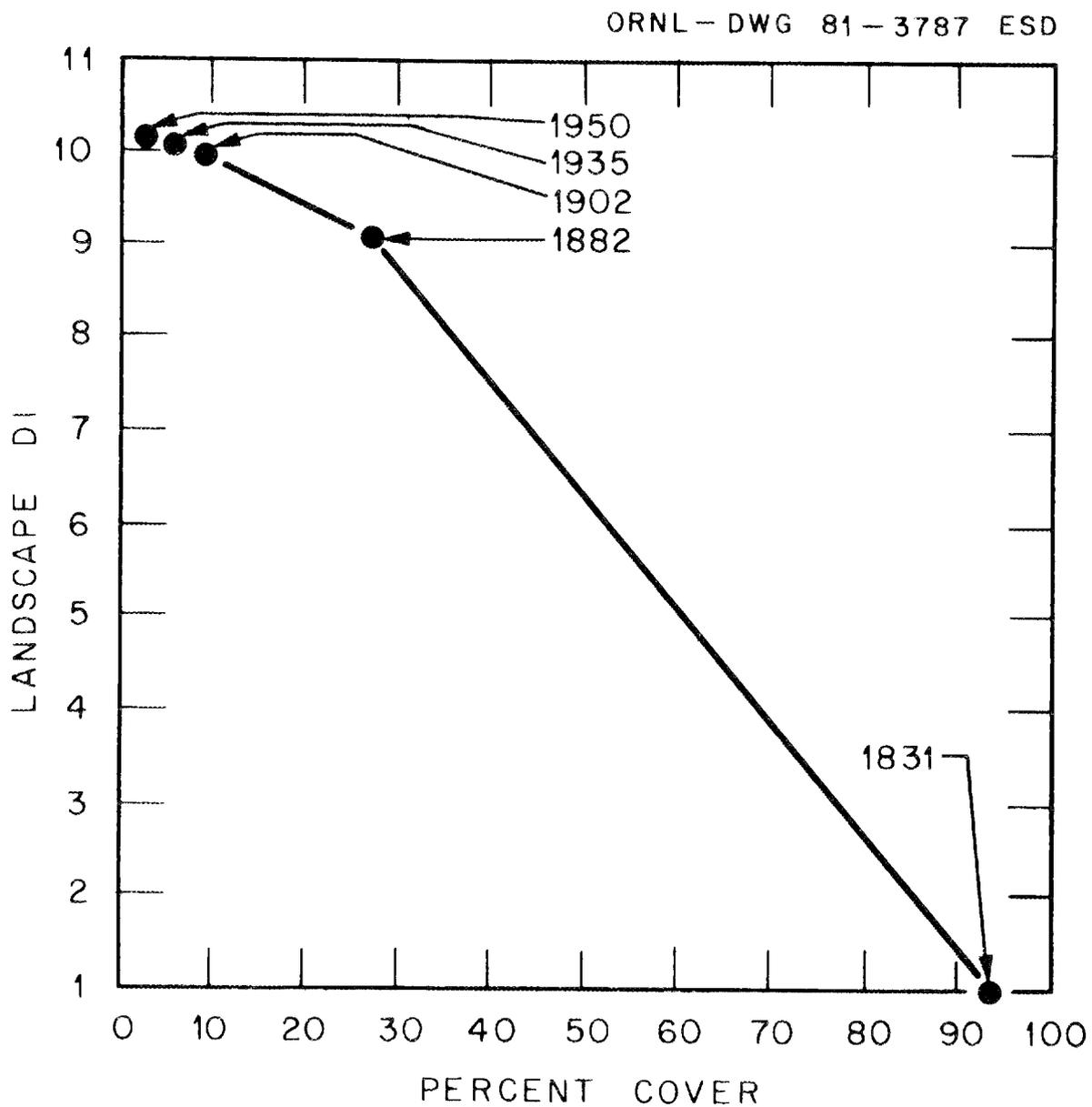


Fig. 18. Changes in the forest pattern of Cadiz township, Green County, Wisconsin portrayed as a vector in a two dimensional space defined by the variables percent cover and landscape DI.

One feature of landscapes that has been successfully modeled is cover type, that is, the type of vegetation (or types of land use) that are associated with a region. Changes in landscape patterns can be modeled by measuring the areal extent of the cover types on old maps and comparing them to measurements taken from newer maps. From those measurements, a matrix of transformation coefficients can then be used as rate constants in dynamic mathematical models that predict changes in landscape cover (Hett 1971; Auclair 1976; Zeimetz et al. 1976; Johnson and Sharpe 1976). Models of this type are similar to Markov models of forest succession (Horn 1976), in the fact that the actual sizes, shapes, and locations of cover types, e.g., forests, are unknown but are integrated into a limited number of measurements. Markov models are possible because of the mathematical properties of cover type as a variable. Other variables, such as median island size and interisland distance, do not have these properties and would have to be modeled using nonlinear techniques.

V. SUMMARY AND CONCLUSIONS

The goal of this study was to quantify various aspects of forest island distribution patterns and relate those patterns to other landscape features. Toward that end, literature pertinent to concepts of landscape pattern in general and to forest pattern in particular was reviewed. Several maps showing the forest cover of various counties in Ohio were chosen as representative examples of forest patterns to be quantified. Ten thousand hectare study areas (landscapes) were delineated on each map. The landscapes were chosen to represent a wide variety of forest island patterns. Their placement was dependent upon the grain and intensity inherent in the forest island patterns.

The raw data taken from each landscape included measurements of the perimeter and area of each woodlot and measurements of the distances between woodlots. The raw data were then converted into a series of continuous landscape variables representing properties appropriate for the scale of landscapes. These landscape variables contained information pertinent to the sizes, shapes, numbers, and spacing of woodlots within a landscape.

The landscape variables were used in a factor analysis to describe the variation among landscapes in terms of forest island pattern. Most of the variation among landscapes was accounted for by the first two factors. An inspection of the factor loadings indicated that the first factor was weighted toward the percent of the study area covered by forest as measured by the variable percent cover. The second factor was interpreted as an axis of forest fragmentation as

measured by the variables island density and landscape DI (the two were highly correlated). An ordination of landscapes was then derived from first two axes of the factor analysis. The ordination proved to be an effective graphic summary of landscape variation and it became the basis of a theoretical framework on which to test hypotheses concerning forest island patterns.

Other features of the landscapes (topography, soils, glacial history, original vegetation, and potential natural vegetation) were measured with non-continuous nominal variables. These environmental features were related to the forest island patterns by: (1) overlaying environmental information on to the ordination plots; and (2) using discriminant analysis with the environmental features as the criteria of discrimination. The results showed that forest island patterns are related to topography and other environmental features correlated with topography. Landscapes with smooth topography and arable land had but a few percent forest coverage divided among a relatively low number of small woodlots. As the roughness of topography increased, the size and/or number of forest islands increased. The greatest degree of forest fragmentation was associated with 20-30 percent cover in hilly topography. Since forest pattern is a result of the cumulative effects of land use over time, these results were interpreted to mean that the patterns of land use in Ohio were somewhat dependent upon topography and related factors.

The ability to quantify landscape pattern on a regional basis has applications to regional ecology. Mathematical models can be developed to predict changes in landscape patterns for given land use scenarios,

and parameters of landscape pattern can be analyzed as indicators of habitat and resource distribution and long-term ecosystem stability. The ability to measure forest island pattern and other aspects of landscape pattern can be one part of quantitative approaches to solving regional problems.

LITERATURE CITED

- Aikman, J. M., and A. W. Smelser. 1938. The structure and environment of forest communities in central Iowa. *Ecology* 19(1):141-148.
- Auclair, A. N. 1976. Ecological factors in the development of intensive-management ecosystems in the midwestern United States. *Ecology* 57:431-444.
- Auclair, A. N., and G. Cottam. 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in southern Wisconsin oak forests. *Ecol. Monogr.* 41(2):153-175.
- Bailey, R. G. 1976. Ecoregions of the United States. U.S. Forest Service, Ogden, Utah.
- Bailey, R. G. 1978. Description of the ecoregions of the United States. USDA Forest Service Intermtn. Reg. Ogedn, Utah. 77 pp.
- Barr, A. J., J. H. Goodnight, J. P. Sall, W. H. Blair, D. M. Chilko, and J. T. Helwig. 1970. SAS user's guide, 1979 edition. SAS Institute, Inc., Sparks Press, Raleigh, North Carolina. 494 pp.
- Bird, R. D. 1961. Ecology of the aspen parkland of western Canada. Canada Dept. Agr., Res. Br. Pub. 1066. Ottawa. 155 pp.
- Borchert, J. R. 1950. The climate of the central North American grassland. *Ann. Assoc. Am. Geog.* 40:40-57.
- Bourdo, E. A. 1956. A review of the general land office survey and of its use in quantitative studies of former forests. *Ecology* 37(4):754-768.
- Braun, E. L. 1950. Deciduous Forests of Eastern North America. Blakiston Co., Philadelphia. 596 pp.
- Braun-Blanquet, J. 1932. Plant Sociology (Translated by G. D. Fuller and H. S. Conard). McGraw-Hill Book Co., New York. 439 pp.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27:325-349.
- Brender, E. V. 1974. Impact of past land use on the lower Piedmont forest. *J. For.* 72:34-36.
- Bromley, S. W. 1935. The original forest types of southern New England. *Ecol. Monogr.* 5(1):61-89.
- Brown, J. H. 1971. Mammals on mountain tops: Nonequilibrium insular biogeography. *Am. Nat.* 105:467-478.

- Bruner, W. E. 1931. The vegetation of Oklahoma. *Ecol. Monogr.* 1:99-188.
- Buell, M. F., and H. F. Buell. 1959. Aspen invasion of prairie. *Bull. Torrey Bot. Club* 86:264-265.
- Buell, M. F., and J. E. Cantlon. 1951. A study of two forest stands in Minnesota with an interpretation of the forest-prairie margin. *Ecology* 32:294-316.
- Buell, M. F., and Vera Facey. 1960. Forest-prairie transition west of Itasca Park, Minnesota. *Bull. Torrey Bot. Club* 87:46-58.
- Burgess, R. L. 1964. Ninety years of vegetational change in a township in southeastern North Dakota. *Proc. N.D. Acad. Sci.* 18:84-94.
- Burgess, R. L. 1978. The changing face of eastern North America. *Frontiers* 42(3):8-11.
- Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35(4):445-453.
- Clark, P. J., and F. C. Evans. 1979. Generalization of a neighbor measure of dispersion for use in K dimensions. *Ecology* 60(2):316-317.
- Clements, F. E. 1928. *Plant Succession and Indicators*. Hafner Press, New York. 453 pp.
- Cline, M. G. 1949. Basic principles of soil classification. *Soil Sci.* 67:81-91.
- Cody, M. L. 1975. Towards a theory of continental species diversities: Bird distributions over mediterranean habitat gradients. pp. 214-257. IN M. L. Cody and J. M. Diamond (eds.), *Ecology and Evolution of Communities*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Copper, W. S. 1926. The fundamentals of vegetational change. *Ecology* 7:247-390.
- Cottam, G. 1949. The phytosociology of an oak woods in southwestern Wisconsin. *Ecology* 30(3):271-287.
- Culver, D. C. 1970. Analysis of simple cave communities I: Caves as islands. *Evolution* 24:463-474.
- Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. pp. 721-736. IN W. L. Thomas (ed.), *Man's Role in Changing the Face of the Earth*. University of Chicago Press, Chicago, Illinois.

- Curtis, J. T. 1959. The Vegetation of Wisconsin - An Ordination of Plant Communities. University of Wisconsin Press, Madison. 657 pp.
- Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476-496.
- Daubenmire, R. F. 1936. The "Big Woods" of Minnesota: Its structure, and relation to climate, fire, and soils. *Ecol. Monogr.* 6(2):234-268.
- Daubenmire, R. 1978. *Plant Geography*. Academic Press, New York. 338 pp.
- Davis, A. M., and T. F. Glock. 1978. Urban ecosystems and island biogeography. *Environ. Conserv.* 5:299-304.
- Day, G. M. 1953. The Indian as an ecological factor in the northeastern forest. *Ecology* 34:329-346.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7:129-146.
- Diamond, J. M. 1976. Island biogeography and conservation: Strategy and limitations. *Science* 193:1027-1029.
- Diller, O. D. 1944. Ohio's forest resources. Forestry Publ. No. 76. Ohio Agricultural Exp. Sta., Woodster, Ohio. 109 pp.
- Dyksterhuis, E. J. 1948. The vegetation of the western cross timbers. *Ecol. Monogr.* 18:325-376.
- Dyksterhuis, E. J. 1957. The savannah concept and its use. *Ecology* 38:435-442.
- Elfstrom, B. A. 1974. Tree species diversity and forest island size on the Piedmont of New Jersey. MS Thesis, Rutgers University, New Brunswick, New Jersey. 55 pp.
- Ewing, J. 1924. Plant successions of the brush prairie in northwestern Minnesota. *J. Ecol.* 12:238-266.
- Faaborg, J. 1979. Qualitative patterns of avian extinction on neotropical land bridge islands: Lessons for conservation. *J. Appl. Ecol.* 16:99-107.
- Fernald, M. L. 1950. *Gray's Manual of Botany* 8th ed. American Book Co., New York. 1632 pp.
- Finley, R. W. 1976. Original vegetation cover of Wisconsin. Compiled from U.S. General Land Office Notes. North Central For. Exp. Sta., USDA Forest Service, St. Paul, Minnesota.

- Forman, R. T. T., and B. A. Elfstrom. 1975. Forest structure comparison of Hutcheson Memorial Forest and eight old woods on the New Jersey Piedmont. *William L. Hutcheson Mem. For. Bull.* 3:44-51.
- Forman, R. T. T., A. E. Galli, and C. F. Leck. 1976. Forest size and avian diversity in New Jersey woodlots and some land-use implications. *Oecologia* 26:1-8.
- Forsyth, J. L. 1970. A geologist looks at the natural vegetation map of Ohio. *Ohio J. Sci.* 70:180-191.
- Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* 93:356-64.
- Game, M. 1980. Best shape for nature reserves. *Nature* 287:630-632.
- Gleason, H. A. 1917. The structure and development of the plant association. *Bull. Torrey Bot. Club* 47:21-33.
- Gleason, H. A. 1922. The vegetational history of the middle West. *Ann. Assoc. Am. Geog.* 12:39-85.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53:7-26.
- Gleason, H. A. 1939. The individualistic concept of the plant association. *Am. Midl. Nat.* 21:92-110.
- Goodall, D. W. 1952. Quantitative aspects of plant distribution. *Biol. Rev.* 27:194-245.
- Goodall, D. W. 1954. Vegetational classification and vegetational continua. *Angew. Pflanzensoziologie, Wien. Festschrift Aichinger* 1:168-192.
- Gordon, R. B. 1966. Natural vegetation of Ohio, at the time of the earliest surveys. *Ohio Biological Survey, Columbus* (map).
- Gordon, R. B. 1969. The natural vegetation of Ohio in pioneer days. *Ohio Biological Survey, Columbus.* 109 pp.
- Greller, A. M. 1975. Persisting natural vegetation in Queens County, New York, with proposals for its conservation. *Environ. Conserv.* 2:61-69.
- Gross, F. A., III. 1976. Primeval Vegetation Types of New Mexico. *New Mexico State University, Las Cruces, New Mexico.* [Reprinted, much reduced and in four parts, in] Gross, F.A., and W. A. Dick-Peddie, 1979. A map of primeral vegetation in New Mexico. *S.W. Nat.* 24:115-122.

- Hett, J. M. 1971. Land-use changes in east Tennessee and a simulation model which describes these changes for three counties. ORNL/IBP-71/8. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 56 pp.
- Hewes, L. 1950. Some features of early woodland and prairie settlement in a central Iowa county. *Ann. Assoc. Am. Geog.* 40:40-57.
- Holmes, D. D., and R. L. Jolly. 1980. IMGRID version 3.5. Tennessee Valley Authority, Norris, Tennessee. 494 pp.
- Horn, H. S. 1976. Succession. pp. 187-204. IN R. M. May (ed.), *Theoretical Ecology: Principles and Applications*. Blackwell Scientific Publishers, Oxford.
- Integrated Software Systems Corporation. 1979. DISSPLA: User's Manual, Version 8.0. San Diego, California.
- Jackson, J. A. 1979. Highways and wildlife - some challenges and opportunities for management. pp. 566-571. IN *The Mitigation Symposium: A national workshop on mitigating losses of fish and wildlife habitats*. Gen. Tech. Rep. Rm-65. Rocky Mtn. For. and Range Exp. Sta., Fort Collins, Colorado.
- Johnson, W. C., and D. M. Sharpe. 1976. An analysis of forest dynamics in the northern Georgia Piedmont. *For. Sci.* 22:307-322.
- Kaul, R. B. 1975. *Vegetation of Nebraska (Circa 1850)*. Conservation and Survey Division, Institute of Agriculture and Natural Resources, Univ. Neb., Lincoln.
- Kingsley, N. P., and C. E. Mayer. 1970. The timber resources of Ohio. U.S.D.A. For. Serv. Res. Bull. NE-19. N.E. For. Exp. Sta. Upper Darby, PA. 137 pp.
- Klopatek, J. M., R. J. Olson, C. J. Emerson, and J. L. Joness. 1979. Land-use conflicts with natural vegetation in the United States. *Environ. Conserv.* 6:191-199.
- Klopatek, J. M., H. H. Shugart, Jr., W. F. Harris, and R. W. Brocksen. 1979. The need for regional ecology. ORNL/TM-6799. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 33 pp.
- Knight, H. A. 1974. Land-use changes which affected Georgia's forest land, 1961-1972. USDA For. Serv. Res. Note SE-189, Asheville, North Carolina. 4 pp.
- Köppen, W. 1931. *Grundriss der Klimakunde*. Walter de Gruyter Co., Berlin.
- Küchler, A. W. 1964. *Potential natural vegetation of the conterminous United States*. Amer. Geog. Soc. Spec. Publ. No. 36. New York. Map plus manual (150 pp.).

- Küchler, A. W. 1967. *Vegetation Mapping*. The Ronald Press Company, New York. 472 pp.
- Küchler, A. W. 1969. Natural and cultural vegetation. *Prof. Geogr.* 21:383-385.
- Küchler, A. W. 1973. Problems in classifying and mapping vegetation for ecological regionalization. *Ecology* 54:512-523.
- Levenson, J. B. 1976. Forested woodlots as biogeographic islands in an urban-agricultural matrix. PhD Thesis, University of Wisconsin. 101 pp.
- Lowe, J. C., and S. Moryadas. 1975. *The geography of movement*. Houghton Mifflin Co., Boston, Massachusetts. 333 pp.
- MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-378.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey. 203 pp.
- Marschner, F. J. 1959. Land use and its pattern in the United States. USDA Agric. Handbook No. 153, Washington, D.C. 227 pp.
- Marschner, F. J. 1976. The original vegetation of Minnesota, 1:500,000, 48 x 66 in. With M. L. Heinselman's interpretation of F. J. Marschner's map of the original vegetation of Minnesota. USDA Forest Service North Central For. Exp. Sta., St. Paul, Minnesota. 24 pp.
- McIntosh, R. P. 1957. The York Woods, a case history of forest succession in southern Wisconsin. *Ecology* 38:29-37.
- McIntosh, R. P. 1967. The continuum concept of vegetation. *Bot. Rev.* 33:131-187.
- McIntosh, R. P. 1972. Forests of the Catskill Mountains, New York. *Ecol. Monogr.* 42:143-161.
- McIntosh, R. P. 1975. H. A. Gleason - "Individualistic Ecologist" 1882-1975: His contributions to ecological theory. *Bull. Torr. Bot. Club* 102:253-273.
- Moore, N. W., and M. D. Hooper. 1975. On the number of bird species in British woods. *Biol. Conserv.* 8:239-250.
- Moral, R. del, and M. F. Denton. 1977. Analysis and classification of vegetation based on family composition. *Vegetatio* 34:155-166.
- Moral, R. del, and A. F. Watson. 1978. Gradient structure of forest vegetation in central Washington Cascades. *Vegetatio* 38(1):29-48.

- Ohio Division of Geological Survey. 1966. Glacial Deposits of Ohio. (Adapted from Glacial Map of Ohio, U.S. Geol. Survey Misc. Geol. Inv. Map I-316). Ohio Div. Geol. Sur., Dept. Nat. Res., Columbus, Ohio.
- Patterson, B. D. 1980. Montane mammalian biogeography in New Mexico. *S.W. Nat.* 25:33-40.
- Patton, D. R. 1975. A diversity index for quantifying habitat "edge." *Wildl. Soc. Bull.* 3(4):171-173.
- Picton, H. D. 1979. The application of insular biogeographic theory to the conservation of large mammals in the northern Rocky Mountains. *Biol. Conserv.* 15:73-79.
- Pielou, E. C. 1977. *Mathematical Ecology*. John Wiley and Sons, Inc., New York. 385 pp.
- Pimentel, R. A. 1979. *Morphometrics the Multivariate analysis of Biological Data*. Kendall/Hunt, Dubuque. 276 pp.
- Potzger, J. E., M. E. Potzger, and J. McCormick. 1956. The forest primeval of Indiana as recorded in the original U.S. Land Surveys and an evaluation of previous interpretations of Indiana vegetation. *Butler Univ. Bot. Studies* 13(1):95-109.
- Ramensky, L. G. 1924. Die Grundgesetzmässigkeiten im Aufbau der Vegetationsdecke. *Bot. Centbl., N. F.* 7:453-455.
- Ramensky, L. G. 1930. Zur Methodik der vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und anderen Objekten, die durch mehrere verschiedenartig wirkende Faktoren bestimmt werden *Beitr. Biol. Pfl.*, 18:269-304.
- Ranney, J. W. 1978. Edges of forest islands: Structure, composition, and importance to regional forest dynamics. PhD Thesis. University of Tennessee, Knoxville, Tennessee. 193 pp.
- Ranney, J. W., and W. C. Johnson. 1977. Propagule dispersal among forest islands in southeastern South Dakota. *Prairie Nat.* 9:17-24.
- Raup, H. M. 1966. The view from John Sanderson's farm: A perspective for the use of the land. *For. Hist.* April:2-11.
- Rice, E. L., and W. T. Penfound. 1959. The upland forests of Oklahoma. *Ecology* 40(4):593-608.
- Schlemmer, N. 1941. Forest resources of Miami County, Ohio. Ohio Forest Survey Report No. 5, Ohio Agricultural Exp. Sta., Wooster, Ohio. 39 pp.
- Shantz, H. L. and R. Zon. 1924. The physical basis of agriculture: Natural vegetation. *USDA Atlas of American Agriculture. Part 1, Section E.* Washington, D.C. pp. 1-29.

- Sharpe, D. M., and W. C. Johnson. 1981. The carbon dynamics of forests in Georgia. *J. Environ. Manage.* (in press).
- Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. *Ann. Rev. Ecol. Syst.* 5:161-182.
- Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. *Science* 191:285-286.
- Simberloff, D. 1979. Nearest neighbor assessment of spatial configurations of circles rather than points. *Ecology* 60:679-685.
- Stearns, F. W. 1949. Ninety years of change in a northern hardwood forest in Wisconsin. *Ecology* 30:350-358.
- Stearns, F. 1974. The use of the American General Land Office Survey in syndynamical vegetation analysis. pp. 75-80. IN R. Knapp (ed.), *Handbook of vegetation science part VIII: Vegetation dynamics.* Junk Publishers, The Hague. 356 pp.
- Sternitzke. 1976. Eastern hardwood resources: Trends and prospects. *For. Prod. J.* 24(3):13-16.
- Steyermark, J. A. 1959. *Vegetational History of the Ozark Forest.* University of Missouri Studies, Columbia, Missouri. 138 pp.
- Steyermark, J. A. 1963. *Flora of Missouri.* Iowa State University Press, Ames, Iowa.
- Stout, A. B. 1944. The bur oak openings in southern Wisconsin. *Trans. Wis. Acad. Sci.* 36:141-161.
- Strong, D. R., Jr. 1979. Biogeographic dynamics of insect-host plant communities. *Ann. Rev. Entomol.* 42:89-119.
- Suhweir, D. E. 1976. *Tree species richness: Farm woodlots as biogeographic islands.* MS thesis, University of Toledo, Toledo, Ohio. 33 pp.
- Sullivan, A. L., and M. L. Shaffer. 1975. Biogeography of the megazoo. *Science* 189:13-17.
- Terborgh, J. 1974. Preservation of natural diversity: The problem of extinction prone species. *BioScience* 24:715-722.
- Terborgh, J. 1976. Island biogeography and conservation: Strategy and limitations, a reply. *Science* 193:1028-1029.
- Transeau, E. N. 1935. The prairie peninsula. *Ecology* 16(3):423-437. USDA Yearbook of Agriculture. 1941. *Climate and man.* Washington, D.C.

- U.S.D.I. 1970. The national atlas of the United States of America. Washington, D.C. 417 pp.
- Veatch, J. O. 1959. Presettlement forest in Michigan. Dept. of Resource Development, Michigan State University, East Lansing.
- Wales, B. A. 1972. Vegetation analysis of north and south edges in a mature Oak-hickory forest. *Ecol. Monogr.* 42:451-471.
- Ward, R. T. 1956. The beech forests of Wisconsin. Changes in forest composition and the nature of the beech border. *Ecology* 37:407-419.
- Weaver, J. E., and F. E. Clements. 1938. *Plant Ecology*, 2nd ed. McGraw-Hill, New York and London.
- Wegner, J. F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. *J. Appl. Ecol.* 16:349-357.
- Wells, P. V. 1970. Post glacial vegetational history of the Great Plains. *Science* 167:1574-1582.
- Wells, P. V. 1970. Historical factors controlling vegetation patterns in floristic distributions in the central plains region of North America. pp. 211-221. IN W. Dort, Jr., and J. K. Jones, Jr. (eds.), *Pleistocene and Recent Environments of the Central Great Plains*. University Press of Kansas, Lawrence.
- Wetzel, R. G. 1975. *Limnology*. W. B. Saunders Co., Philadelphia. 743 pp.
- Whitcomb, R. F. 1977. Island biogeography and habitat islands of eastern forests. *Am. Birds* 31(1):3-23, 91-93.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26:1-80.
- Whittaker, R. H. 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. *Am. J. Bot.* 44:197-206.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42:207-264.
- Woolf, H. B. (Ed.) 1975. *Webster's new collegiate dictionary*. G. and C. Merriam Co. Springfield, Mass. 1536 pp.
- Zeimetz, K. A., I. E. Pillon, E. E. Hardy, and R. C. Otte. 1976. Dynamics of land use in fast growth areas. *Agricultural Economic Report No. 325*. USDA Economic Research Service, Washington, D.C. 48 pp.

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