LANDSCAPE ECOSYSTEMS OF THE MACK LAKE BURN, NORTHERN LOWER MICHIGAN, AND THE OCCURRENCE OF THE KIRTLAND'S WARBLER

by

Wayne S. Walker

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Thesis Committee:
Professor Burton V. Barnes, Chair
Professor Gary W. Fowler
Associate Professor Donald R. Zak

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…desolate reaches of fire-scarred land covered with little pine trees – has an austere charm of its own, as well as moments of beauty when the dew sparkles on the fresh leaves and the ground is sprinkled with the blossoms of shadbush, bird's-foot violet, hare-bell, wood lily, and puccoon.

--Harold Mayfield

To the Walker's and the Woskoski's

ABSTRACT

The Kirtland's warbler (*Dendroica kirtlandii* Baird) is a federally endangered songbird that nests only in ecosystems dominated by young jack pine (*Pinus banksiana* Lamb.) in north central Lower Michigan. Wildfire once maintained large areas of early-successional habitat for this neo-tropical migrant. However, fire suppression and forest fragmentation reduced the availability of suitable breeding habitat such that the warbler population declined to less than 400 individuals in the mid-1970s. Although considerable research has focused on the bird itself, comparatively little information was available on the specific landscape ecosystems occupied by the warbler. The 9,700-ha Mack Lake burn of 1980 provided an opportunity to study the pattern of Kirtland's warbler occurrence in relation to the landscape ecosystems of a highly diverse and productive area of its breeding grounds. Using a multiscale, multifactor landscape ecosystem approach, two high-elevation and four low-elevation landform-level ecosystems were identified, described, and mapped by reconnaissance, line transects, and permanent sample plots (n = 49). Multivariate statistical analyses (i.e., principal components and discriminant analyses) integrating physiographic, soil, and vegetative variables confirmed the ecological distinctness of five jack pine-dominated landforms. A study of microclimate using paired thermometers (n = 14) also showed significant differences in maximum and minimum air temperature among major physiographic levels. Annual census records from 1986 to 1997 were used to examine the spatial pattern of colonization and occupancy of landforms by Kirtland's warbler. The spatial pattern of warbler occurrence over time was strongly mediated by the physical and biotic components of the ecosystems. During the first three years of warbler occupation

(1986-1988), the high-elevation landforms, characterized by warmer temperatures, moister, more fertile soils, and faster-growing jack pines, supported 62% of the population. However, a major shift from the high to the low-elevation terrain occurred thereafter. During the last three years of record (1995-97), the low-elevation landforms, characterized by colder temperatures, drier, less fertile soils, and slow-growing jack pine, supported 86% of the population. A significant decreasing relationship (r^2 = 0.90; $p < 0.00001$) between the average elevation of the warbler population and the year of occupancy further demonstrated the extent of the high- to low-elevation shift. The diversity of high- and low-elevation landscape ecosystems prolonged the duration of warbler occupancy well beyond what would be expected if the burn were characterized by less heterogeneous site conditions. As applied, the landscape ecosystem approach provides a sound ecological framework and practical tool for understanding patterns of Kirtland's warbler occurrence, and for assisting managers in determining appropriate management areas for the continued recovery of this endangered species.

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I. INTRODUCTION

Background

Kirtland's warbler (*Dendroica kirtlandii* Baird) is a federally endangered songbird, and the rarest member of the wood warbler family (Parulidae) in North America. The species was first described by Spencer F. Baird (1852) following its discovery in 1851, but remained relatively unknown until 1879 when the wintering grounds were discovered in the Bahama islands (Cory 1879). The breeding grounds were not discovered until 1903 when Norman A. Wood of the University of Michigan found the first Kirtland's warbler nest in western Oscoda County, Michigan (Wood 1904).

Since the discovery of the first nest, the known breeding range of Kirtland's warbler has been limited to the sand outwash plain, jack pine-northern pin oak forest ecosystems of northern Michigan (Figure 1.1). Overwintering in the Bahamas, warblers migrate to the breeding range in early May and remain until late August (Mayfield 1960, p. 39; Walkinshaw 1983, p. 28), although birds have been observed as late as mid-October (Sykes and Munson 1989, Sykes et al. 1989). Nesting is largely restricted to 13 counties in the northern part of the Lower Peninsula, an area approximately 120 x 160 km (Mayfield 1960, p. 9; Probst 1986; Figure 1.1). Four counties in the central portion of the breeding range (Crawford, Kalkaska, Ogemaw, Oscoda) – all within the drainage of the Au Sable River – have supported 85% or more of the total population for over 25 years (Mayfield 1972, 1973a, 1973b, 1975; Ryel 1976a 1976b, 1979a, 1980a, 1980b, 1981a, 1982, 1983, 1984; Burgoyne and Ryel 1978; Weise 1987; Weinrich 1988a, 1988b, 1989, 1990a, 1990b, 1991, 1993, 1994, 1995, 1996). Although numerous specimens and sight records of Kirtland's warbler exist for the North

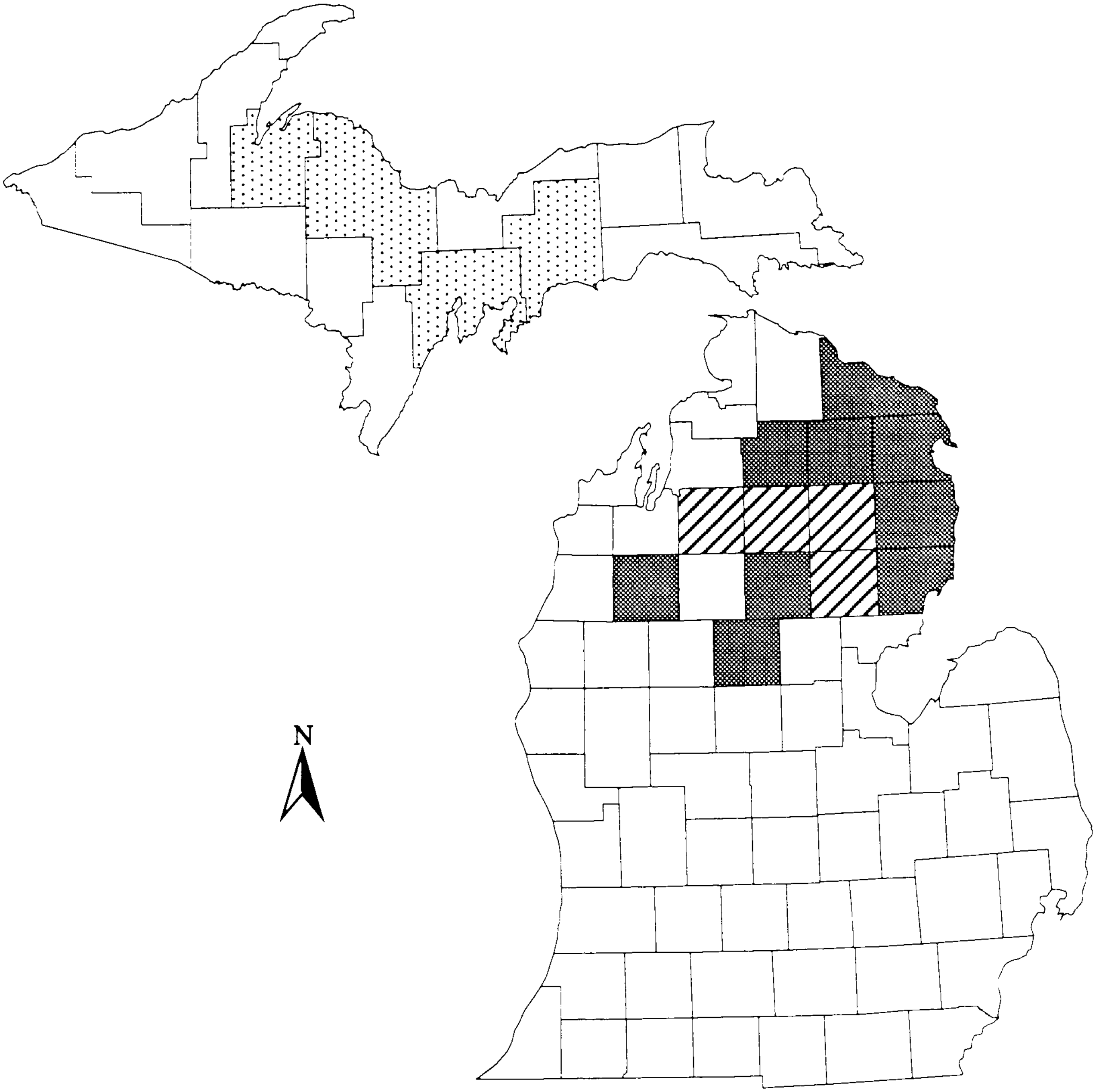

Figure 1.1. Map of the known breeding range of Kirtland's warbler: Four counties in the northern Lower Peninsula of Michigan (cross-hatched) have supported 85% of the Kirtland's warbler population over the last 25 years. Four counties in the Upper Peninsula (stippled) have only recently (since 1993) supported small breeding colonies.

Central states and parts of Canada (Tilghman 1979; Walkinshaw 1983, p. 17; Probst 1986), breeding has never been documented outside of northern Michigan (Probst 1986).

The ecosystems that constitute the breeding range of Kirtland's warbler are characterized by flat to gently rolling, dry, glacial outwash plains and, to a lesser extent, hilly ice-contact terrain (Zou et al. 1992, Barnes 1993). Soils occurring on these sites are primarily the excessively drained, nutrient-poor sands of the Grayling and Rubicon series. In addition, nesting has been observed where sand soils exhibit pedogenic and depositional bands of fine texture (Graycalm and Montcalm soil series) (Zou et al. 1992). Warblers nest only in areas where young (5 to 23 years old), fire-prone stands of jack pine (*Pinus Banksiana* Lamb.), or jack pine mixed with northern pin oak (*Quercus ellipsoidallis* E. J. Hill) occur as the dominant vegetation (Mayfield 1960, p. 14; Probst and Weinrich 1993). Nesting is largely restricted to stands greater than 32 ha in size characterized by relatively dense jack pine canopy cover (20 to 60%) growing in a patchy (contagious) pattern interspersed with numerous small openings (Zou 1988, Probst and Weinrich 1993). Historically, this characteristic pattern of vegetation was maintained by wildfire, which periodically regenerates young pine-oak stands (Barnes et al. 1998, p. 631).

Warblers delay colonization of an area until the pines reach a height of ca 1.4 m (Probst and Weinrich 1993). Nests are built on the ground in small depressions, often at or near the edges of openings, sheltered beneath living pine branches and dense ground vegetation (Mayfield 1960, p. 73; Walkinshaw 1983, p. 77). Warblers typically abandon an area when the tree crowns begin to close in on the openings (height ca 5.0 m), shading out the vegetative cover (Mayfield 1960, p. 15; Buech 1980; Probst and Weinrich 1993). As a result, the effective lifetime of a particular stand as Kirtland's warbler habitat depends largely on the growth rate of jack pine, which in turn depends on the physical site factors of physiography, climate, and soil (Walkinshaw 1983, p. 65).

The first attempt to estimate Kirtland's warbler numbers was made in 1951, 100 years after its discovery. The census, organized and conducted by Harold Mayfield (1953), was the first complete census of a songbird population in the world. Twelve-hundred square miles of young jack pine were identified and systematically searched; 432 singing male warblers were counted, and the total population was estimated at ca 1,000 individuals (Figure 1.2). Ten years later the census was repeated with similar results, suggesting the population was maintaining itself (Mayfield 1962). However, the third census in 1971 revealed a 60% decline in the male count (502 to 201); the total warbler population had dropped to ca 400 individuals (Mayfield 1972; Figure 1.2). The principal reason for the decline appeared to be nest parasitism by the brown-headed cowbird (*Molothrus ater*) (Mayfield 1960, p. 144; Ryel 1981b; Walkinshaw 1983, p. 145). Walkinshaw (1983, p. 148) estimated that from 1966 to 1971, 69% of warbler nests were parasitized. In response to the perceived threat, the U.S. Fish and Wildlife Service (FWS) implemented a program to trap and remove cowbirds from Kirtland's warbler breeding areas. Although nest parasitism was reduced to 3.4% during the first 10 years of cowbird control (1972-1982) (Kelly and DeCapita 1982), warbler numbers showed virtually no response, remaining at ca 400 individuals through 1989 (Figure 1.2). In addition, the FWS appointed a Kirtland's warbler recovery team in 1975 and a formal recovery plan was adopted. The primary objective of the plan was to re-establish a self-sustaining Kirtland's warbler population throughout its known range at a minimum level of 1,000 pairs (Byelich 1976).

Because the warbler population failed to rebound in spite of the significant reduction

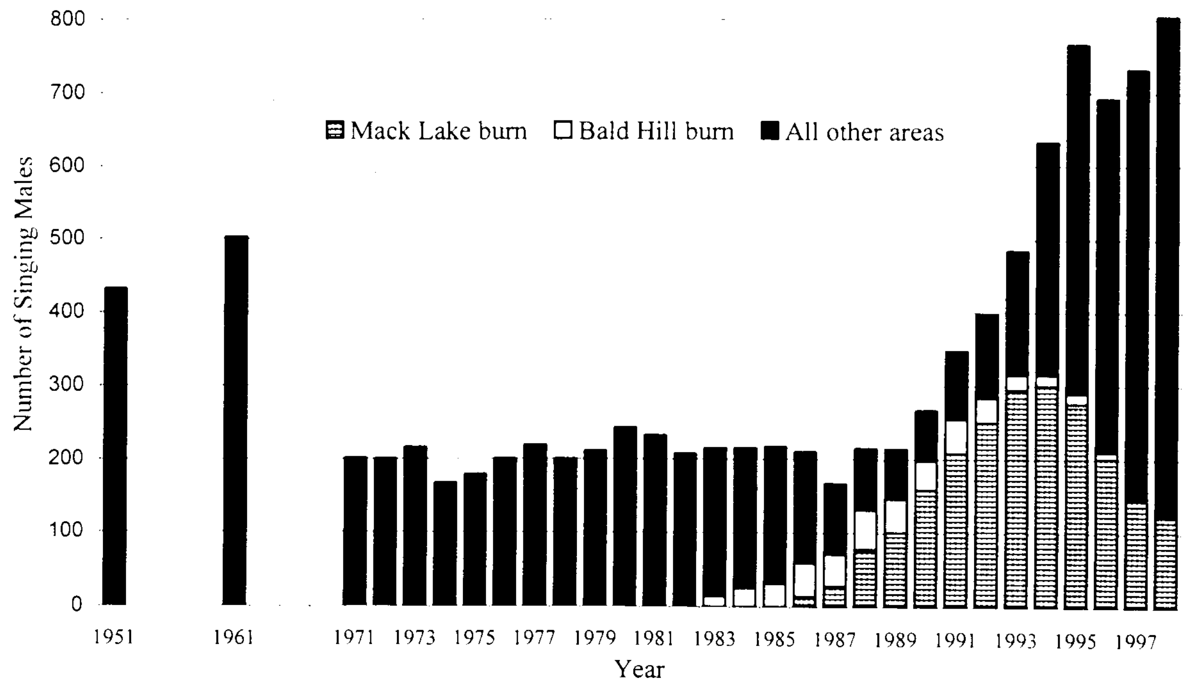

Figure 1.2. Abundance of Kirtland's warblers from 1951 (year of first census) to present based on the annual census of singing males. The 1971 census revealed a 60% decline in the total population. The population remained at or near the 1971 level through 1989. The increase in population beginning in 1990 coincided with the major increase in suitable habitat (ca. 4,500 ha) observed following the Bald Hill (1975) and Mack Lake (1980) burns.

in cowbird parasitism, the ensuing recovery effort became focused instead on the availability of suitable breeding habitat (Ryel 1981b; Probst 1986, 1988). The amount of suitable habitat, and thus the number of Kirtland's warblers, is thought to have been greatest following the lumbering boom of the late 1800s when extensive forest fires regenerated large tracts of jack pine across northern Lower Michigan (Van Tyne 1951; Mayfield 1960, 1983). By the mid 1930s, however, advances in fire detection and control had greatly reduced the number of large fires, which in turn reduced the amount of available habitat (Radtke and Byelich 1963, Ryel 1981b). During the decade 1961-1971 when the warbler population declined by 60%, there was a corresponding decline of 44% in suitable habitat, primarily a result of fire suppression (Ryel 1981b). The adoption of the Kirtland's warbler recovery plan in 1976 greatly hastened efforts to develop and maintain, continuously, tracts of jack pine to provide for the habitat requirements of the bird (Byelich 1976). Jack pine plantations, configured to mimic, in so far as possible, the dense contagious pattern of natural regeneration created by wildfire, were planted extensively across the breeding range. Although the amount of available habitat (primarily plantations) increased to 88% of 1961 levels by 1979, no appreciable increase in the warbler population was observed (Ryel 1981b).

Despite the rapid evolution of management programs directed toward Kirtland's warbler recovery during the late 1970s, it was not until the late 1980s that the warbler population began to rebound (Figure 1.2). The rebound coincided with marked increases in suitable habitat following two major wildfires – the 600-ha Bald Hill burn of 1975 and the 9,700-ha Mack Lake burn of 1980. The Mack Lake burn alone produced nearly 4,000 ha of high-quality habitat which, by 1990, nearly tripled the amount of suitable habitat available

(Kepler et al. 1996). In the years that followed, the warbler population exhibited dramatic growth, increasing at an average annual rate of 24% from 1990 to 1995 (Weinrich 1996, Solomon 1998). In 1991, 70% of Kirtland's warbler singing males occupied the Mack Lake and Bald Hill burns; fewer than 25% occupied plantation habitat (Weinrich 1991). Currently, over 57,000 ha of jack pine are managed for the Kirtland's warbler. Despite the increased reliance on managed plantations, however, over 70% of birds censused in the past 15 years have occupied habitat created by wildfires (Kepler et al. 1996).

The Landscape Ecosystem Approach and Kirtland's Warbler

Rationale

Although significant past and current efforts have been directed to preserve individual species and populations (Scott et al. 1987, LaRoe 1993, Franklin 1993), much less consideration has been given to the maintenance of entire landscape ecosystems – the source and support for all organisms (Rowe 1997). A landscape ecosystem is a single, perceptible topographic unit, a volumetric segment of air and land (physiography and soil) plus organic contents (biota) extended areally over a particular part of the Earth's surface (Rowe 1961). Rare and endangered species such as Kirtland's warbler are notable parts of landscape ecosystems (Barnes 1993), but as Rowe (1989) emphasizes:

> Organisms do not stand on their own; they evolve and exist in the context of ecological systems that confer those properties called life. The panda is part of the mountain bamboo-forest ecosystem and can only be preserved as such. The polar bear is a vital part of the arctic marine ecosystem and will not survive without it. Ducks are creatures born of marshes. Biology without its ecological context is dead.

Rowe's point of view – from *outside* rather than from *inside* – makes clear the dependence of organisms on Earth-surface ecosystems. Recognition among scientists of the inseparability of organisms and ecosystems has prompted recent calls to shift emphasis from organism-based conservation efforts toward a more holistic landscape ecosystem approach (Scott et al. 1987; Scott 1990; Rowe 1992, 1997; Barnes 1993; Franklin 1993; LaRoe 1993; Orians 1993)

The landscape ecosystem approach, as applied in Michigan, is modified from a method of ecological site classification and mapping developed in the southwestern German State of Baden Württemburg (Spurr and Barnes 1980, p. 324-329). Operationally, the approach is a multiscale, multifactor, hierarchical method whereby physiography, climate, soil, and late-successional vegetation are used together to identify, classify, describe, and map entire landscape ecosystems (Barnes et al. 1982; Pregitzer and Barnes 1984, Spies and Barnes 1985, Simpson et al. 1990, Pearsall et al. 1995). The process of delineation and mapping proceeds in a "top down" fashion from more complex and heterogeneous units to less complex and relatively homogenous units (Barnes et al. 1998, p. 24). Through this process of regionalization, the landscape is progressively divided into a series of ecosystems, large and small, nested within one another in a hierarchy of spatial sizes (Rowe and Sheard 1981)

The Ecosphere is the largest, most all-inclusive ecosystem known (Barnes et al. 1998, p. 24). Nested within the Ecosphere, ecosystems are recognized at three general levels: 1) macro-level units at the scale of continents and oceans, 2) meso-level units (regional ecosystems) at the scale of major physiographic features, e.g., mountain ranges and broad plains, and 3) micro-level units at the scale of landforms supporting upland forests, swamps, bogs, etc. (Rowe and Sheard 1981; Rowe 1992; Bailey 1996, p. 24; Barnes et al. 1998, p. 24).

The regional (mesoecosystem scale) landscape ecosystem classification of Michigan was developed by Albert et al. (1986; Figure 1.3) and has since been extended to the states of Minnesota and Wisconsin (Albert 1995). This ecological framework segments the state into three hierarchical ecosystem units: *Regions*, *Districts*, and *Subdistricts*. Boundaries of Regions and Districts were determined primarily by integrating macroclimate and physiographic factors. At the Subdistrict level, where macroclimate is relatively homogenous, boundaries reflect marked differences in the physiography and soil of the respective units. Below the Subdistrict level, regional macroclimate becomes relatively homogenous and similar physiographic features and recurrent vegetation patterns dominate (Barnes et al. 1998, p. 38). At this local or microecosystem level, three hierarchical ecosystem units are defined (Barnes et al. 1998): *Physiographic Systems*, *Landform-level Ecosystems*, and *Landscape-Ecosystem Types*. Physiographic systems are complexes of landforms typically of one recognizable, generic kind (e.g., outwash plain, moraine, ice-contact terrain, etc.). Physiographic systems can be subdivided into their constituent landform-level ecosystems. For example, ice-contact terrain is a complex of distinctive landforms termed kettles and kames, each of which can be identified, described, and mapped. Within a particular landform, at the finest level of ecosystem delineation, a mosaic of landscape-ecosystem types exists. At this microscale, multiple factors including physiography, microclimate, soil, and vegetation are integrated to delineate and map unit boundaries. This process of regionalization results in a hierarchical framework of ecosystem units at different scales of resolution. Thus, researchers and decision-makers have the flexibility to focus their efforts on the hierarchical level that most appropriately serves their objectives.

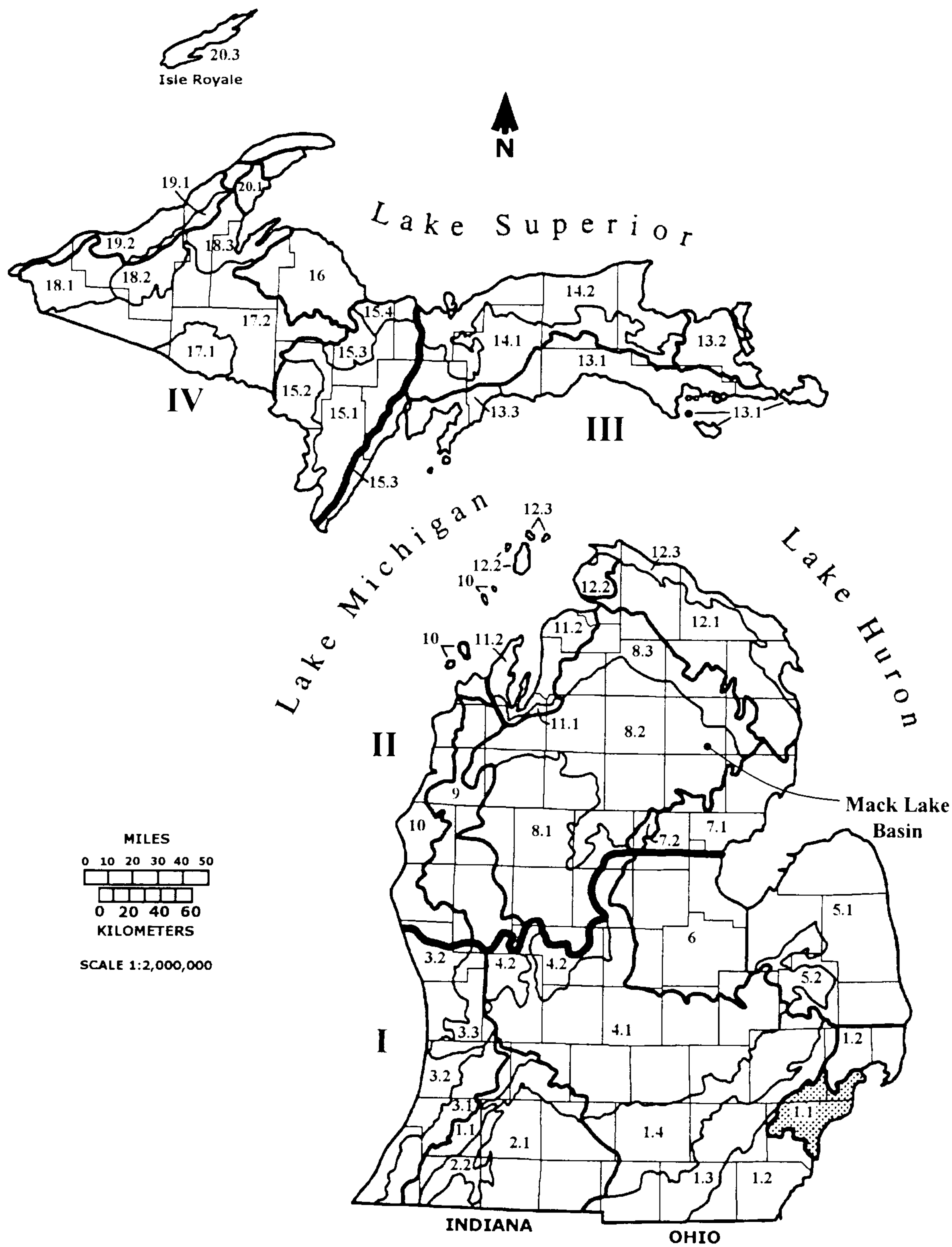

Figure 1.3. Map of regional landscape ecosystems of Michigan. Three hierarchical levels are mapped: Regions I-IV, Districts 1 to 20, and Subdistricts within many Districts. (After Albert et al. 1986.)

Previous Application

On May 5, 1980, the Mack Lake burn consumed ca 9,700 ha of sandy, glacial outwash-plain, jack pine-dominated ecosystems surrounding Mack Lake, in southeastern Oscoda County, Michigan (Simard et al. 1983; see Chapter II). The burn, the largest ever recorded on the Huron-Manistee National Forest, created nearly 4,000 ha of Kirtland's warbler breeding habitat which became suitable in the late 1980s (Kepler et al. 1996). Although considerable research has focused on the bird itself (Mayfield 1960, Walkinshaw 1983), comparatively little detailed information was available on the landscape ecosystems of which Kirtland's warbler is a part (Barnes et al. 1998, p. 633). However, the Mack Lake burn provided an opportunity to study Kirtland's warbler occurrence in relation to the landscape ecosystems of a highly diverse and productive area of the breeding grounds (Barnes 1993).

Research was conducted on the site of the Mack Lake burn from 1986 to 1988 (Barnes et al. 1989, Zou et al. 1992). The objective of the three-year study was to develop a framework of local landscape ecosystems as a basis for understanding the spatial and temporal pattern of Kirtland's warbler colonization and occupancy. Landscape ecosystems were distinguished and classified for a portion of the burned-over area encompassing ca 7,000 ha. The burn was confined to a broad, glacial outwash basin surrounded on three sides by high moraines and ice-contact terrain (Barnes 1993). Within the burn, two physiographically distinct features were identified: 1) a broad, pitted outwash plain in the lower, central part of the basin surrounding Mack Lake, and 2) outwash terraces and hilly ice-contact terrain in the higher, southern part of the basin. Figure 1.4 illustrates the relative positions of these features, hereafter referred to as the *high-elevation* and the *low-elevation*

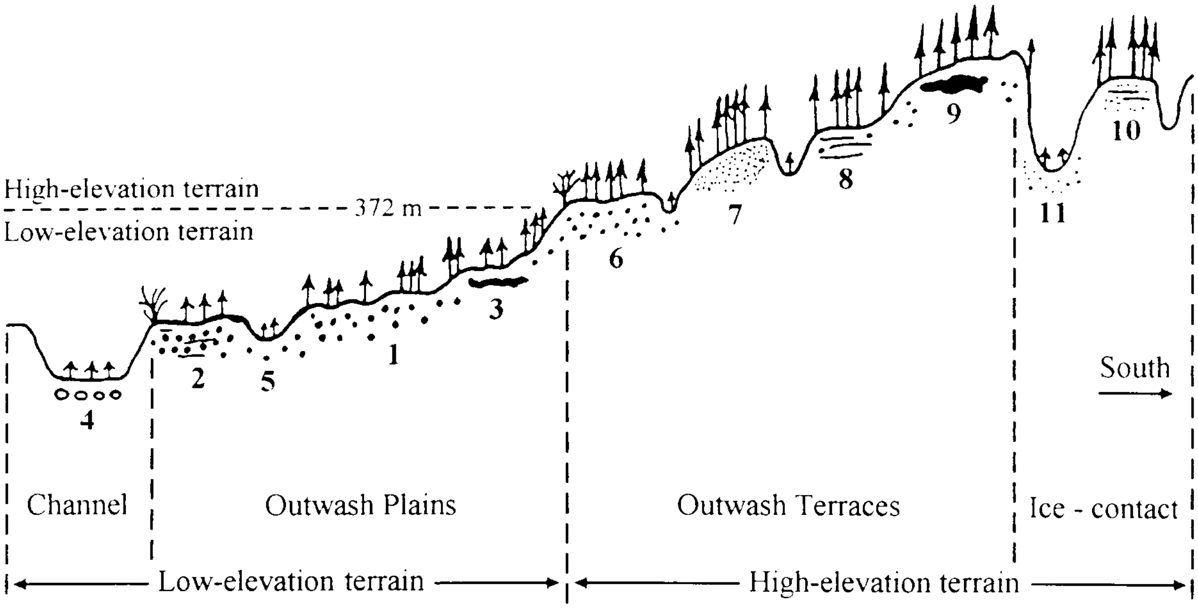

Figure 1.4. Physiographic diagram of part of the Mack Lake burn, Oscoda Co., northern Lower Michigan illustrating the spatial arrangement of high- and low-elevation terrain features and constituent landscape ecosystem types (1-11). The boundary between the high- and low-elevation terrain was arbitrarily distinguished at 372 m. Poorer soils (primarily medium sand), a colder microclimate, and shorter, slow-growing trees characterized the low-elevation terrain. Better soils (fine-textured sand and sand with bands of heavy texture), a warmer microclimate, and taller, fast-growing trees characterized the high-elevation terrain. (After Barnes et al. 1998, p. 634.)

terrain. The two features were further distinguished by marked differences in microclimate and soil (Barnes et al. 1989; Zou et al. 1992; Barnes et al. 1998, p. 633). Air drainage was observed to follow the high-to-low pattern of the landscape; cold air flowed from the high outwash terraces and ice-contact terrain (elev. 385 m) into the low outwash plains and channels (elev. 365 m) (Barnes et al. 1998; Figure 1.3). As a result, the high-elevation terrain was warmer during the growing season than the low-elevation terrain. Soils followed a similar gradient; fine-textured sand and sand with bands of heavy texture occurred in the high-elevation terrain, but were virtually absent in the low-elevation terrain (Zou et al. 1992, Barnes et al. 1998). In turn, the vegetation was observed to follow the landform-based pattern of microclimate and soil. In 1986, young jack pines and northern pin oaks in the high-elevation terrain were, in general, markedly taller, denser, and of a more patchy (i.e., contagious) distribution than those in the low-elevation terrain (Zou et al. 1992, Barnes 1993). Major differences in the presence and abundance of ground-cover species between the two features were also observed. Six ecological species groups, unique groups of plant species repeatedly occurring together and exhibiting similar environmental requirements or tolerances, were identified (Barnes et al. 1989). A description of each ecological species group, including a list of member species, is presented in Appendix A.

Within the high- and low-elevation terrain, 11 individual landscape ecosystem types were distinguished based on local differences in physiography, microclimate, soil, and vegetation (Barnes et al. 1989, Zou et al. 1992; Figure 1.4). The landscape-ecosystem type classification of the Mack Lake burn is presented in Table 1.1; a detailed description of each ecosystem type is presented in Appendix B.

From 1986 to 1988, the colonization of the Mack Lake burn by Kirtland's warbler

Table 1.1 Classification of landscape ecosystems of the Mack Lake burn, Oscoda Co., northern Lower Michigan (Barnes et al. 1989).

Low-elevation Outwash Plains (Elevation 350-372 m)

Level to gently sloping terrain; excessively to somewhat excessively drained (depressions < 1.5 m deep)

1. Outwash plain; medium to medium-fine sand, very infertile
2. Outwash plain; medium sand, infertile (areas of higher relative elevation between glacial meltwater drainage channels)
3. Outwash plain; sand to loamy sand over bands of fine texture; infertile

Channels and depressions; excessively to somewhat excessively drained

4. Glacial meltwater drainage channels (6-15 m deep) with a distinct pebble/cobble layer
5. Depressions (1.5-6 m deep) with extreme microclimate; soil as in ecosystems 1-3

High-elevation Outwash Plains and Ice-contact Terrain (Elevation 372-390 m)

Level to moderately steep slopes; excessively to somewhat excessively drained

6. Outwash plain; gently sloping topography, medium sand; very infertile
7. Outwash plain; level topography, >25% fine sand in top 50-70 cm; infertile
8. Outwash plain; loamy sand to sand, 5-10 cm (cumulative) of fine-textured bands; slightly infertile
9. Outwash plain; loamy sand and/or a relatively thick textural band (> 10 cm); slightly to moderately infertile
10. Ice-contact terrain; sandy kamic hills; infertile

Depressions; excessively to well drained

11. Depressions (3-15 m deep) with extreme microclimate; soils as in ecosystems 6-10

was studied in relation to the high- and low-elevation terrain features and constituent landscape ecosystem types. Of the 14 singing-male warblers to colonize the burn in 1986, 71% of the birds occupied the high-elevation terrain; the remaining 29% occupied the low-elevation terrain (Barnes et al. 1989). This pattern of initial occurrence favoring the high-elevation terrain was attributed to the markedly different physiography that is characterized by warmer temperatures and moister, more nutrient rich soil (Barnes 1993). These factors were in turn responsible for the faster growth of jack pine and northern pin oak. Because tree growth was faster in the high-elevation terrain, the trees reached heights suitable for warbler colonization (ca 1.4 m) more rapidly than those in the low-elevation terrain. Research conducted in 1987 and 1988 indicated that warblers also preferentially colonized specific landscape ecosystem types (Zou et al. 1992, Barnes 1993). Additional findings related to the patchiness of jack pine and the occurrence of warbler territories in relation to landscape ecosystems have been reported by Barnes et al. (1989), Zou (1988), and Zou et al. (1992).

From 1989 through the present, Barnes and coworkers continued to track the annual distribution and abundance of the Mack Lake Kirtland's warbler populations (for methods see Chapter III). During this period, as more of the trees in the low-elevation terrain reached heights suitable for warbler colonization, a shift occurred in the pattern of warbler occupancy from the high-elevation to the low-elevation terrain. By 1993, 75% of the population occupied the low-elevation terrain, a complete reversal in the pattern of occupancy observed in 1986. As a result, the presence of two adjacent physiographic features, and the diversity of landscape ecosystem types within them, appears to have prolonged the duration of warbler occupancy beyond what would be expected if the area were characterized by more homogenous site conditions.

Problem Statement

Since 1971, the Kirtland's has been the focus of an intensive cooperative monitoring effort that includes an annual census of the singing-male warbler population and, more recently, a major biannual banding program (Mayfield 1972, Sykes et al. 1989). During this period, warblers have been censused and/or banded in well over 80 different nesting areas across 17 northern Michigan counties. This long-term monitoring has provided biologists and land managers with critical demographic information, as well as key data on the dynamics and annual distribution of the warbler population. In particular, the annual census has yielded a wealth of data (e.g., census maps, bird locations, etc.) documenting spatial change in the occurrence of the Kirtland's warbler population across the breeding range over time. The enormous potential for such unique data lies in the understanding to be gained from the study of the patterns that underlie, and the factors that drive both spatial and temporal changes in warbler occurrence. At no time, however, has a research effort focused on investigating and interpreting patterns of spatial change underlying the timing of colonization and/or the duration of occupancy of specific nesting areas by Kirtland's warbler populations.

The three-year study (1986-1988) of the Mack Lake burn (Barnes et al. 1989, Zou et al. 1992), coupled with continued monitoring of the Kirtland's warbler population at Mack Lake from 1989-1994, provides a key baseline for a detailed study of the spatial and temporal pattern of Kirtland's warbler occurrence. The benefits of such research include: 1) a complete and detailed record of the spatial pattern of Kirtland's warbler colonization and occupancy in an area of highly productive wildfire habitat beginning with initial site colonization and ending with site abandonment, and 2) an understanding of the interrelated physical and biotic factors (e.g., physiography, microclimate, soil, and vegetation) that drive observed changes in the spatial pattern of warbler occurrence over time. Thus, the focus of my research has been to: 1) track the progression of the spatial shift in the pattern of Kirtland's warbler occurrence originally described by Barnes et al. (1989, Zou et al. 1992), and 2) explain ecologically why this shift in pattern of occurrence has progressed in the way that it has. Tracking the spatial pattern of warbler occupancy necessarily requires an underlying spatial framework to which the pattern can be referenced. To explain the progression of this spatial pattern ecologically, however, requires that the framework consist of 1) units that are reasonably distinct spatially (i.e., mappable), and 2) units that are ecologically unique (i.e., landscape ecosystems). The original landscape ecosystem classification of the Mack Lake burn (Table 1.1; Figure 1.4) provided the initial framework. The major physiographic divisions of high- and low-elevation were indeed mappable, as are the glacial meltwater drainage channels and the ice-contact terrain (ecosystem types 4 and 10; Table 1.1). However, the majority of ecosystem types that occur in a fine-scale mosaic are too costly to map and monitor given the current level of land management. Thus, a broader-scale ecosystem unit (i.e., at the landform-level), nested within the high- and low-elevation terrain features, provides the ecological basis for my research. The position of this landform-level ecosystem unit in the landscape ecosystem hierarchy of the Mack Lake burn is shown (shaded) in Figure 1.5.

Objectives

The research described herein was part of a larger project to study patterns of Kirtland's warbler occurrence in relation to the physical and biotic components

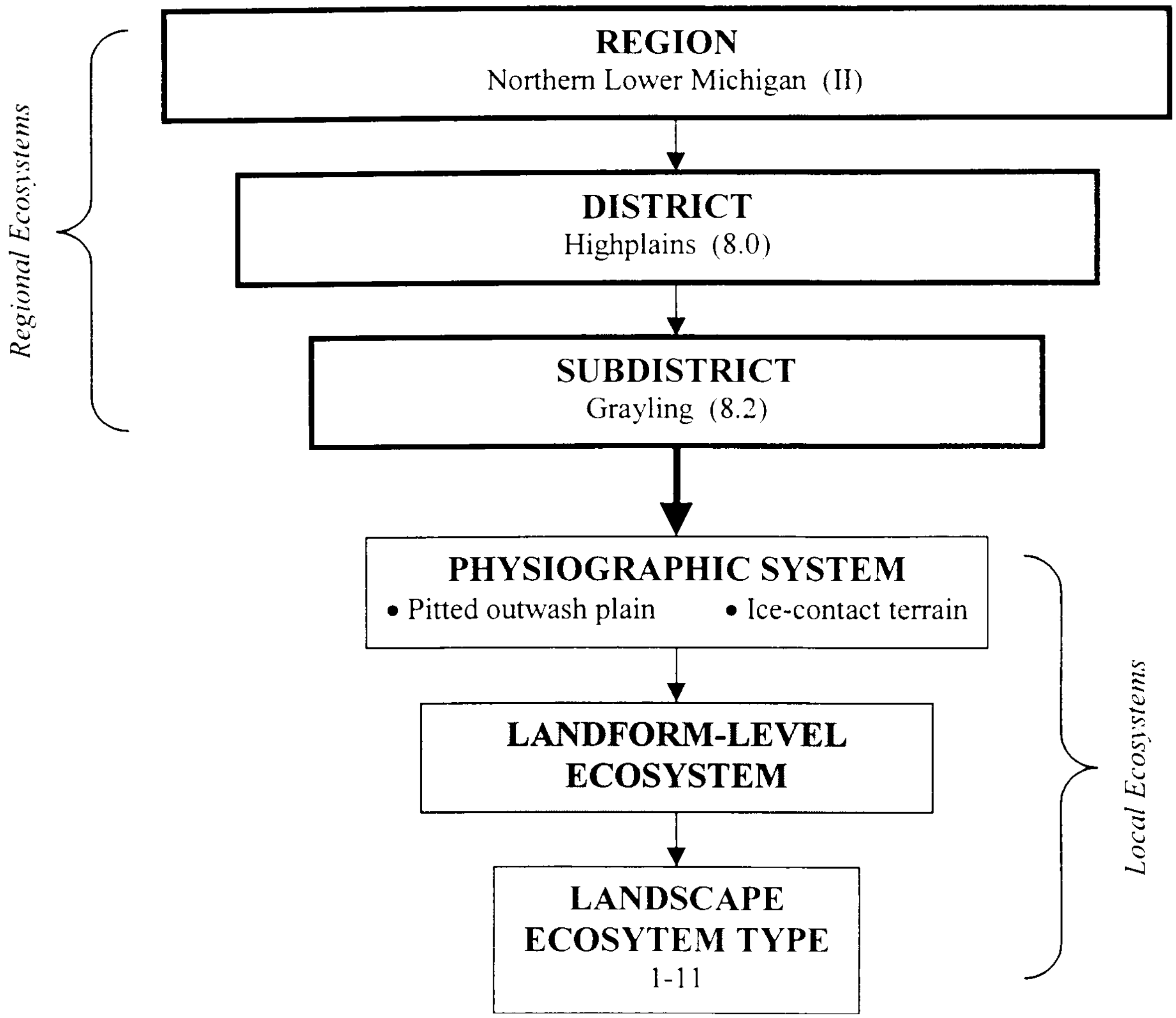

Figure 1.5. Landscape ecosystem hierarchy of the Mack Lake burn, Oscoda Co., northern Lower Michigan. (Modified from Albert et al. 1986, Barnes et al. 1998.)

(physiography, microclimate, soil, and vegetation) of landform-level landscape ecosystems in northern Lower Michigan (see Kashian 1998). Its overall goal was to provide wildlife biologists and land managers with a landscape ecosystem framework for monitoring Kirtland's warbler occurrence over time, and for determining *apriori* areas that are best suited for Kirtland's warbler management.

The general objective of my research was to develop an ecological framework of landform-level landscape ecosystems to examine the spatial and temporal pattern of colonization and occupancy of the Mack Lake burn by Kirtland's warbler. The specific objectives were to:

1) identify, describe, and map the physiographic systems and landform-level ecosystems of the Mack Lake burn using a multi-factor approach.

2) contrast the magnitude of variation in microclimate (temperature) among the high-elevation terrain, low-elevation terrain, and glacial meltwater drainage channels of the Mack Lake burn.

    - what is the average maximum and minimum growing season temperature difference between the high- and low-elevation terrain?

    - how do the glacial meltwater drainage channels compare in average maximum and minimum temperature with the high- and low-elevation terrain?

3) determine the spatial pattern of colonization and occupancy of the Mack Lake burn by the Kirtland's warbler from 1986-1997 in relation to

landform-level ecosystems and their physiographic, microclimatic, edaphic, and vegetative characteristics.

- among years, is the spatial distribution of singing-male warblers across the Mack Lake burn correlated with elevation?
- among years, is the spatial distribution of singing-male warblers across the Mack Lake burn correlated with geographic position?
- in each year, are singing-male warblers distributed across landform-level ecosystems in a nonrandom fashion?
- among years, are singing-male warblers distributed across landform-level ecosystems in a nonrandom fashion?

II. STUDY AREA

Location

Research was conducted on a ca 6,800-ha tract of jack pine-dominated ecosystems within the Mack Lake basin. The basin is located at 44° 38' N latitude and 84° 08' W longitude, approximately 10 km south of Mio, Michigan in southeastern Oscoda county. The basin lies within the Grayling Subdistrict (8.2) of the Highplains District (8) of Region II (northern Lower Michigan) as described in the Regional Landscape Ecosystems of Michigan (Albert et al. 1986; Figure 1.3). The Mack Lake basin is part of the Mio Ranger District of the Huron National Forest.

On May 5, 1980 a wildfire consumed ca 9,700-ha of public forests and private holdings within the Mack Lake basin (Simard 1983). The research was conducted on the site of this wildfire. A map of the study area, representing approximately 72% of the total area burned, is illustrated in Figure 2.1. The study was conducted in the western portion of the burn where conditions were most suitable for Kirtland's warbler occupancy. The study area is bounded by the 1980 burn line along its northern and southern borders. To the east and west, the study-area boundaries (as defined by warbler occupancy) were nearly consistent with those of the Mack Lake, Michigan 7.5-minute topographic quadrangle (United States Geological Survey 1972). The boundaries of the quadrangle were used in place of the proposed boundaries for convenience. The study area includes nearly all of Township 25 North, Range 3 East as well as the western-most edge of Township 25 North, Range 4 East of the Michigan Land-Economic Survey (Figure 2.1).

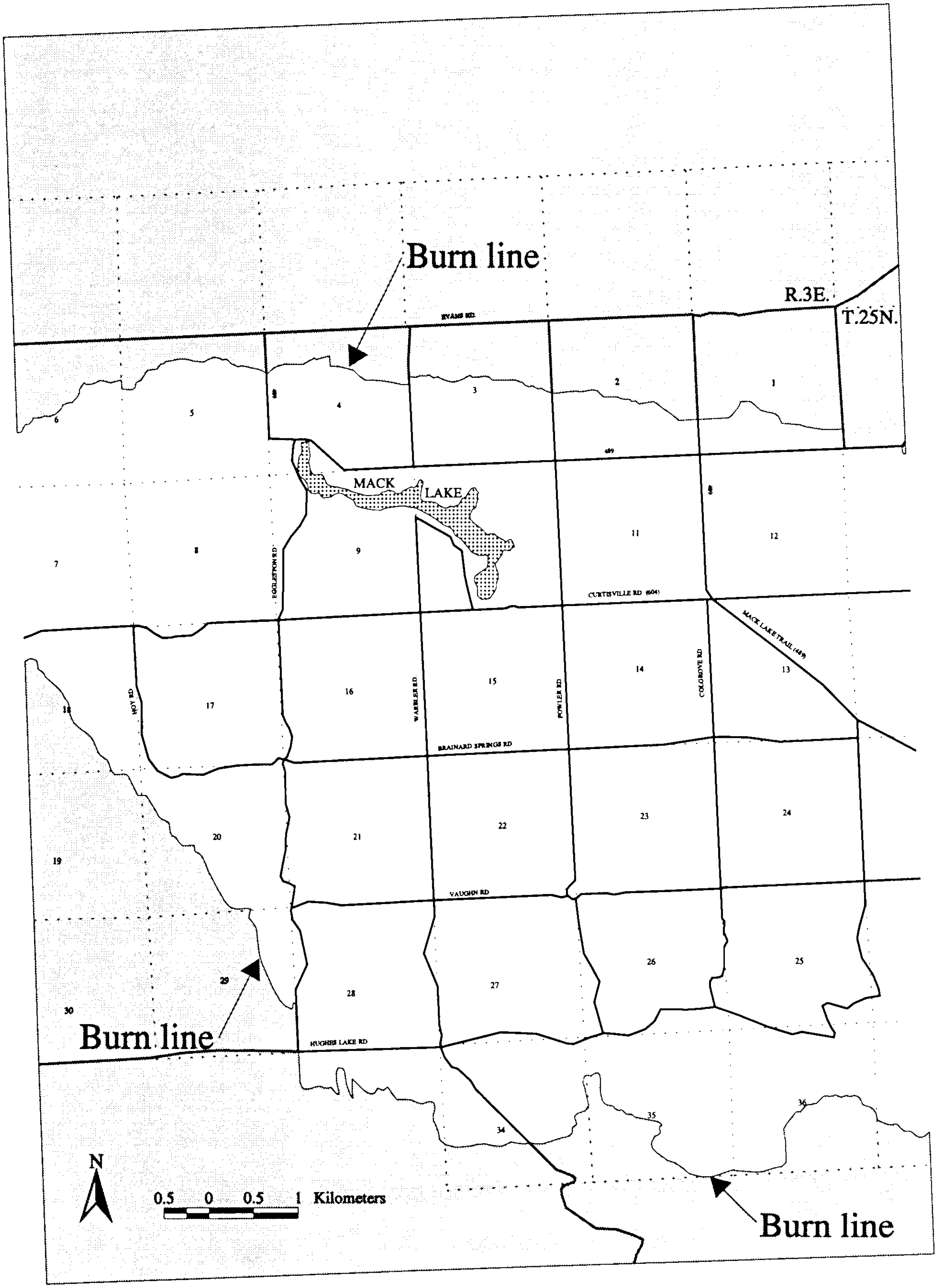

Figure 2.1. Map of the Mack Lake burn study area (white) bounded by the 1980 Mack Lake burn line to the north and the south. The study area encompasses 72% of the total area burned.

Macroclimate

The term macroclimate refers to climatic conditions that prevail over relatively large geographic areas (Bailey 1996, p. 51). At this macro-scale, climatic conditions are governed by three primary factors: latitude, continental position, and elevation. The macroclimate of the Mack Lake basin is largely a function of its regional location within the Highplains (District 8) of northern Lower Michigan (Albert et al. 1986; Figure 1.3). Because of its northern latitude, interior location, and high relative elevation, the Highplains District possesses the Lower Peninsula's most severe macroclimate.

The weather station nearest the Mack Lake basin is located at Mio, Michigan, approximately 10 km to the north. Mio has a continental type macroclimate that is characterized by larger temperature ranges than areas of similar latitude near the coasts where conditions are moderated by lakes Michigan and Huron (Michigan Dept. of Ag. 1989). According to Simard (1983), the average maximum temperature at Mio is 1° C warmer, the average minimum temperature is 2° C cooler, and the average annual precipitation is 150 mm less than stations just 50-60 km to the northwest. During the period 1888 (when record keeping began) to 1998, Mio has experienced temperatures ranging over a span of 98° C (159° F), a state record of long standing. Mio also holds the state record for the highest official temperature (44° C) recorded on July 13, 1936 (Michigan Weather Service 1974; Michigan Dept. of Ag. 1989; Keen 1993, p. 18).

Based on weather station data from the period 1951-1980, Mio has an annual daily mean temperature of 6.2° C, a July daily mean temperature of 19.6° C, and a January daily mean temperature of -8.1° C. Annual precipitation averages 690 mm (the lowest average of any station in the Lower Peninsula!), with 368 mm (53%) occurring during the growing season (May-September). Evaporation for May through October exceeds precipitation by 32% (Michigan Dept. of Ag. 1989).

The freeze-free period (i.e., growing season) for Mio averages 113 days, 2 days shorter than the average (115 days) for the Highplains district, which has the shortest and most variable growing season of any district in the Lower Peninsula (Albert et al. 1986, Michigan Dept. of Ag. 1989). The average date of the last freezing (0° C overnight minimum) temperature in the spring is May 29; the average date of the first freezing temperature in the fall is September 19. However, within the Mack Lake basin itself, Barnes et al. (1989) recorded below freezing minimum temperatures throughout the growing season i.e., during the months of June, July, and August. For additional data and discussion focusing on local climate variation (i.e., microclimate), see Chapter IV.

Pleistocene Glacial History

The glacial landforms of the Mack Lake basin formed late in the Port Bruce substage of the Wisconsinan glaciation, between 14,800 and 13,300 years before present (B.P.) (Burgis 1977). During this period, the retreating lobes of the Laurantide ice sheet moved across the Great Lakes region increasingly independent of one another, with large expanses opening up between them. One such "interlobate" area developed between the Lake Michigan and Saginaw glacier lobes between 14,800 and 13,800 years B.P. (Farrand and Eschman 1974). The Michigan-Saginaw interlobate rapidly increased in dimension as the lateral fronts of the Lake Michigan and Saginaw lobes withdrew across Michigan's northern Lower Peninsula to the north and southeast, respectively.

The map of Lower Michigan in Figure 2.2 illustrates the extent of the interlobate area

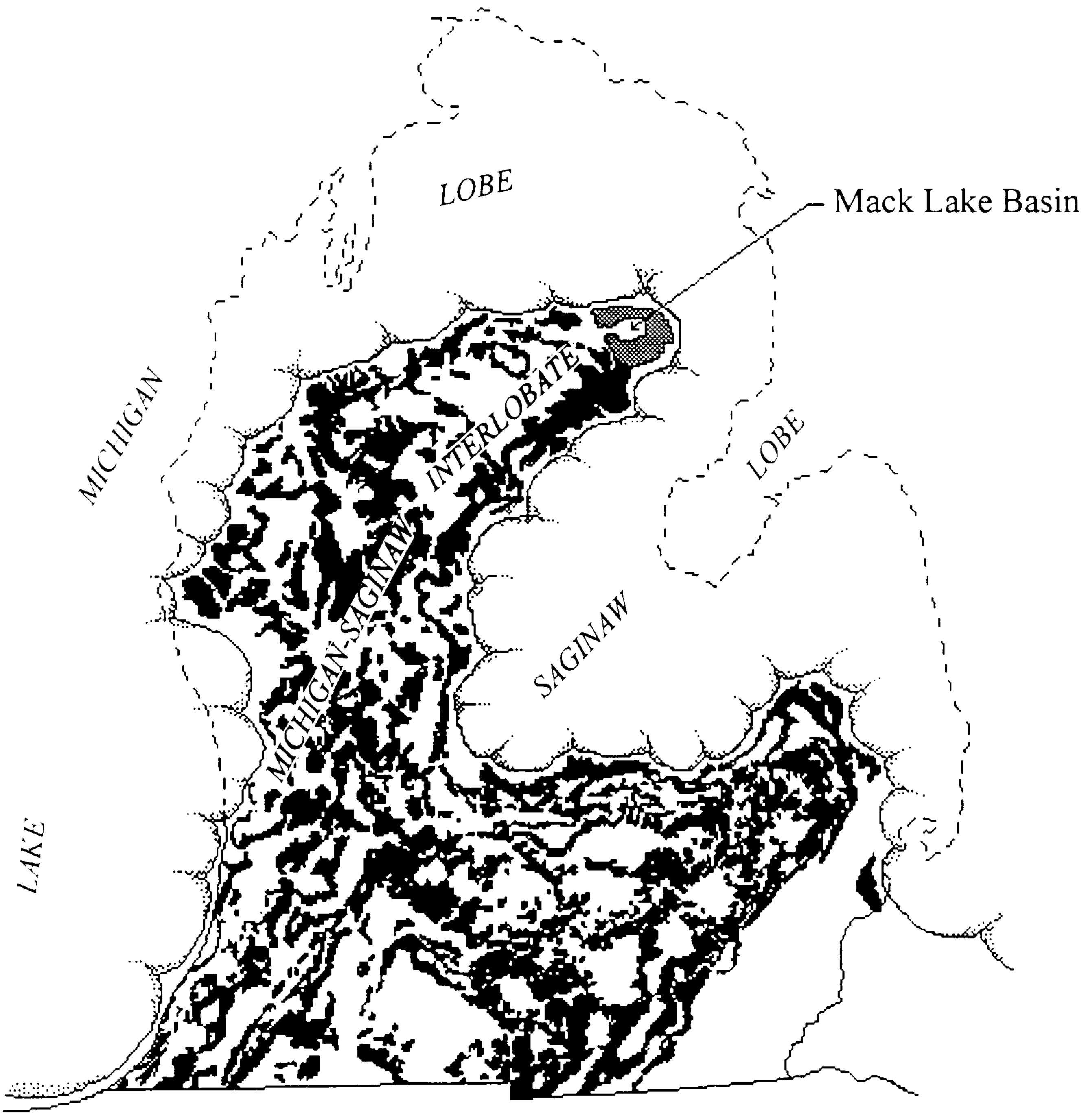

Figure 2.2. Map of ice cover in Lower Michigan approximately 13,800 years ago. Black regions within the Michigan-Saginaw interlobate area represent morainic systems deposited prior to this time. Stippling denotes the segment of theWest Branch morainic system that forms the Mack Lake basin. (Modified from Farrand and Eschman 1974.)

around 13,800 years B.P. By this time the apex or northeastern-most extension of the Michigan-Saginaw interlobate stood in what is now southeastern Oscoda county. Here the glacial landforms that are part of the Mack Lake basin were deposited in a series of events involving both the Lake Michigan and Saginaw glacier lobes. Figure 2.3 illustrates the shape, size, and relative position of these glacial features – characteristics that uniquely reflect the orientation of each ice front during their formation.

The U-shaped West Branch moraine (Figure 2.3) bordering the Mack Lake basin to the north and east was built as the rapidly retreating Lake Michigan front paused briefly, depositing its load of unsorted glacial till before continuing its northerly retreat. To the south, the Maltby kames were deposited when the slowly retreating Saginaw front temporarily stalled, causing the glacier ice to decay or "rot" in place (Burgis 1977). The slowly melting ice likely developed numerous fissures and hollows, allowing large ice blocks to calve off and separate completely from the main glacier (Embleton and King 1975). During the disintegration, meltwater streams deposited layers of sands and gravels on, against, and generally "in contact" with the stagnating ice. The form of these stratified water-laid deposits was later modified by slumping subsequent to the melting of remaining ice, creating semi-stratified ice-contact terrain, also termed kettle-and-kame topography (Thornbury 1969, p. 379). Kettles, or ice-block depressions, formed where buried ice blocks melted out from beneath overlying water-laid deposits. Kames, for which the area is named, formed where water-laid accumulations in fissures and hollows slumped down as the ice melted away leaving behind a complex of steep-sided mounds and ridges.

The central portion of the basin surrounding Mack Lake is occupied by a sequence of broad, terraced pitted-outwash plains. The plains formed as large volumes of meltwater,

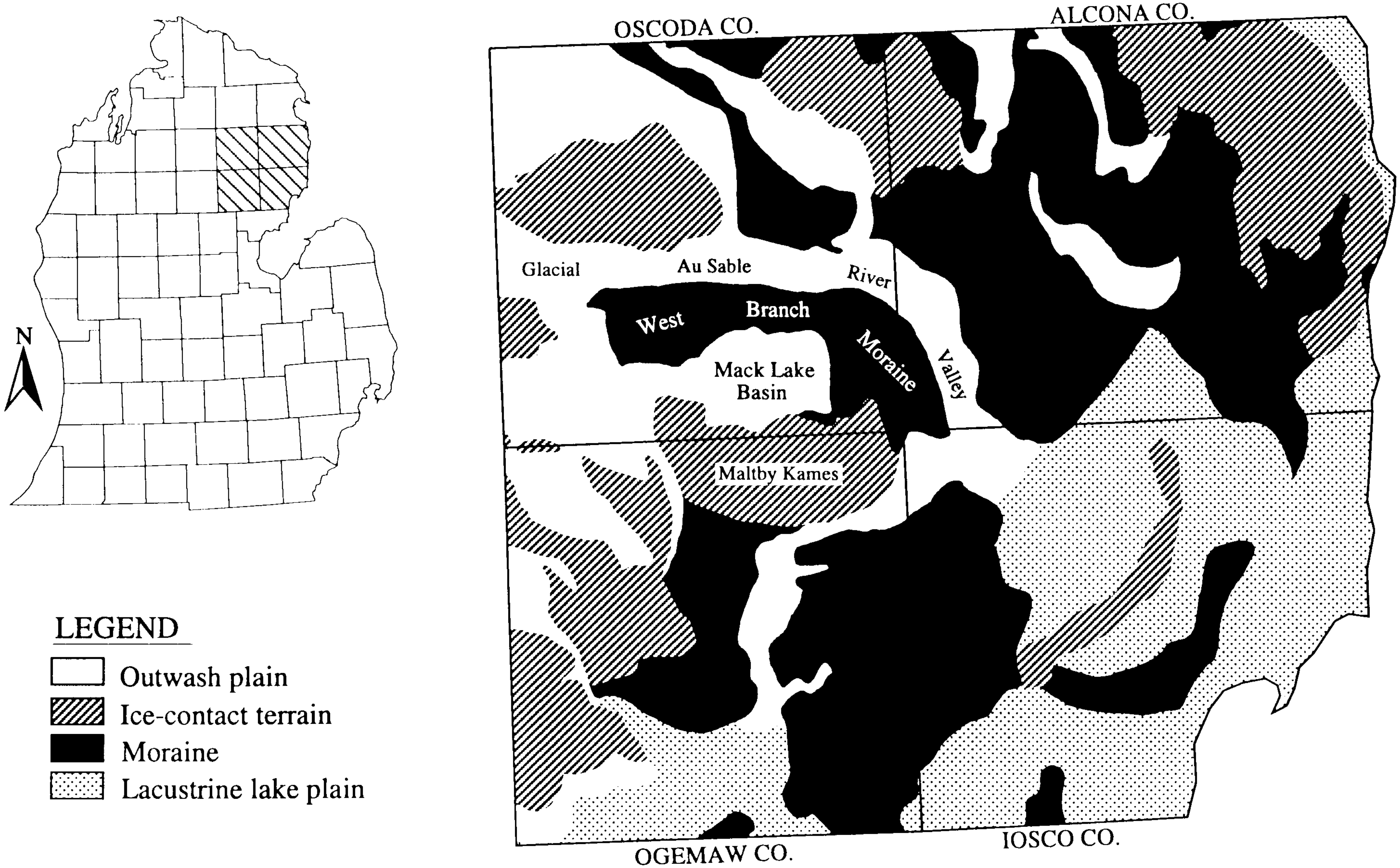

Figure 2.3. Map of glacial landforms occurring in the four-county region surrounding the Mack Lake basin. The basin itself, a broad pitted-outwash plain, is bordered by the West Branch Moraine to the north and east, and by the Maltby Kames (ice-contact terrain) to the south (Modified from Farrand 1982).

flowing westward off the receding Lake Michigan and Saginaw lobes, deposited multiple layers of well-sorted sands and gravels. The pitted character of the plains likely resulted from the burial of stagnant glacier ice, either as glacier remnants left behind during recession or as detached ice blocks swept beyond the glacier front by rushing meltstreams (Hambrey 1994, p. 165). Slow thawing of the buried ice caused subsidence of the overlying deposits leaving behind small depressions or pits (i.e., pitted-outwash plains) in the otherwise level outwash surface.

Debris-laden meltwaters probably continued to build up the surface of the outwash plain for nearly 200 years between 13,800 and 13,600 years B.P. (Burgis 1977). During this period, coalescing meltwater streams were responsible for eroding two prominent drainage channels in the outwash surface. The channels carried meltwaters westward away from the basin to tributaries feeding the Glacial AuSable River.

Physiography and Soil

Physiography

The Mack Lake basin is on the eastern edge of the Highplains (District 8) of northern Lower Michigan (Albert et al. 1986; Figure 1.3). As its name suggests, the Highplains is an elevated plateau characterized by broad glacial outwash plains and terraces. The continuity of the flat terrain is interrupted by numerous large kamic masses that rise above the outwash plains. Steep ridges deposited as end moraines are also common along the district's northern and southern borders. The Mack Lake basin is unique in that it has in common to it each of the major physiographic complexes or systems described above, i.e., the Mack Lake outwash plain, the West Branch moraine, and the Maltby kames (Burgis 1977; Figure 2.4). Although each physiographic system (outwash plain, moraine, ice-contact terrain) has, by definition, its own characteristic physiography (i.e., surficial form and geologic parent material), it is the spatial juxtaposition of these features that contributes to the basin-like physiography of the study area as a whole.

The elevation of the Highplains District averages 326 m, the most elevated of any district in the Lower Peninsula (Albert et al. 1986). By comparison, the average elevation of the Mack Lake basin is 381 m. Mack lake itself occupies the lowest elevation (357 m); the highest elevation (450 m) occurs in the ice-contact terrain to the southeast.

Overall, the physiography of the basin is two-leveled, i.e., stair-stepped, with high-elevation outwash terraces and ice-contact terrain to the south and low-elevation outwash plains and post-glacial meltwater channels to the north surrounding Mack Lake (Barnes et al. 1989, Barnes and Zou 1989, Zou et al. 1992; Figure 2.4). The boundary between the high- and low-elevation terrain features is arbitrarily distinguished along the 372 m contour line (Barnes et al. 1989; Figure 2.4a). The low-elevation terrain consists of a series of flat to very gently rolling pitted outwash plains. Pits or shallow depressions averaging 3.3 m deep occur scattered throughout the area (Figure 2.4b). The post-glacial meltwater drainage channels located west-southwest of Mack Lake average 425 m wide (Figure 2.4a); depth below the general land-level averages 10 m, ranging from 3 to 15 m.

In the southern part of the study area, the high-elevation terrain is characterized by both nearly-level terraces and very hilly ice-contact terrain (Figure 2.4a). The average elevation of the terraces is 375 m, and slopes rarely exceed 5%. This region ranges in elevation from 347 to 450 m; slopes vary from 3 to 30%. Kettle depressions are found throughout the high-level terrain but become larger, deeper, and more common further south.

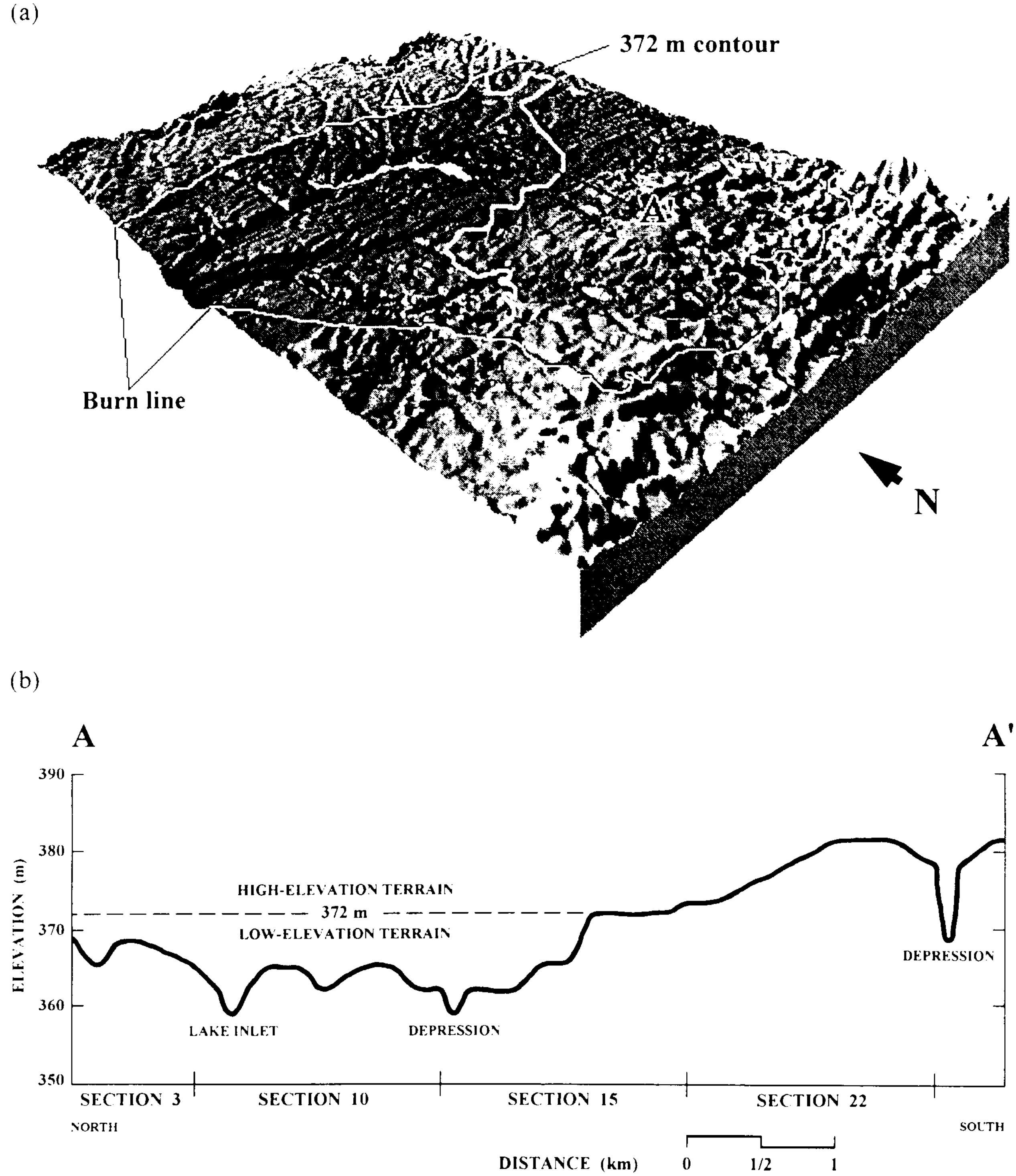

Figure 2.4. The Mack Lake basin: (a) digital elevation model illustrating topography and surficial features (area shown is approximately 13.6 x 9.6 km); (b) elevational profile along transect AA' demonstrating the topographic break (ca 372 m) dividing the high- and low-elevation terrain features. (After Barnes and Zou 1989.)

They average 9.5 m deep, and range from 1.6 to 17.6 m (Figure 2.4b).

Soil

The mineral soils of the Mack Lake basin developed in the relatively-unweathered sand and gravel parent material that remained following deglaciation just over 13,300 years ago. Sands (medium-fine to very coarse) and gravels predominate because finer-textured materials, notably silt- and clay-size particles, were more readily entrained by meltwater flow and transported out of the basin. However, in some parts of the basin, significant amounts of silt and clay occur in the form of narrow lenses or bands of fine-textured particles between adjoining layers of sand.

In the northern part of the study area, soils of the outwash plains surrounding Mack Lake are dominated by Entisols and Spodosols of the Grayling (Typic Udipsamments) and Rubicon (Entic Haplorthods) series, respectively (Veatch et al. 1931). Mineral soil texture is typically medium sand, ranging from medium-fine to very coarse sand; fine-textured banding is generally absent (Zou et al. 1992). Soils are excessively drained. In the outwash terraces and ice-contact terrain to the south, Entisols of the Graycalm series (Alfic Udipsamments) dominate with less frequent occurrences of Grayling and Rubicon sand; Alfisols of the Montcalm series (Eutric Glossoboralfs) are also present. Mineral soil texture of the Graycalm and Montcalm series ranges from fine to loamy sand. Fine-textured banding is a distinguishing characteristic of these series; bands range in texture from loamy sand to sandy clay loam. Soils are typically somewhat-excessively drained depending on the amount and depth of fine-textured bands (Zou et al. 1992).

Vegetation

Prior to the 1980 wildfire, 42% (4,040-ha) of the total area burned had an overstory of jack pine (Simard et al. 1983). Sixty-two percent of the jack pine was in the pole-size class with the remaining 38% in the seedling- and sapling-size classes (Simard et al. 1983). A portion of the area had regenerated naturally following periodic wildfires between 1910 and 1946, and the remainder had been planted. Jack pine stand densities ranged from less than 250 stems/ha in open stands to patches of regeneration in excess of 12,500 stems/ha (Simard et al. 1983). Tree heights varied from 6 to 18 m; diameter at breast height (dbh) ranged from 10 to 25 cm.

According to Simard et al. (1983), jack pine in the area was associated with scattered plantations of red pine (*Pinus resinosa* Ait.) (16%) and mixed stands of pine and oak (northern pin oak (*Quercus ellipsoidallis* E. J. Hill) and northern red oak (*Quercus rubra* L.)) (8%). Hardwood stands (26%) were concentrated primarily along the eastern and southeastern boundaries of the burn. Principal species included northern pin and northern red oaks, trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and scattered white (*Pinus strobus* L.) and red pine (Simard et al. 1983).

Ground-cover vegetation in jack pine and mixed pine-oak stands was typical for the area and included low sweet blueberry (*Vaccinium angustifolium* Ait.), trailing arbutus (*Epigea repens* L.), and sweetfern (*Comptonia peregrina* L.). Bracken fern (*Pteridium aquilinum* L.), common oak sedge (*Carex pensylvanica* Lam.), mosses (*Dicranum spp.*), and lichens (*Cladina spp.*) were also present.

One week after the wildfire, jack pine seed-count samples were taken in the burned-over area by Simard et al. (1983). Seed counts averaged 750,000 seeds/ha, and conditions were described as ideal for germination and survival of jack pine (Simard et al. 1983). At the end of the first growing season, the range of jack pine seedlings per hectare was 5,000 to 42,500 (Barnes et al. 1989). As a result, a dense, patchy mosaic of naturally regenerated jack pine dominates the current vegetation. The most common associate of jack pine is northern pin oak. Clonal, fire-dependent species including bigtooth and trembling aspens are present to a lesser extent, especially in moist depressions near Mack Lake and in the finer-textured soils of the ice-contact terrain. For a detailed account of post-fire vegetation occurrence and distribution as well as descriptions of individual landscape ecosystem types, see Chapter IV.

Fire History

Wildfire has been an integral part of jack pine ecosystems for millions of years (Simard and Blank 1982). Although the Mack Lake basin has only been a feature of the northern Michigan landscape since the Wisconsinan glaciation (13,800 years B.P.), post-glacial pollen records indicate that jack and red pines attained dominance in the northern Lower Peninsula as early as 10,000 years ago following a northward migration from glacial refugia centered on the Appalachian Highlands (Yeatman 1967, Bernabo and Webb III 1977, Delcourt and Delcourt 1991). Thus, there is little question that jack pine, and the periodic wildfires required for its regeneration, have been associated with the Mack Lake basin for thousands of years.

Because jack pine is easily killed by wildfire, it is difficult to obtain long-term dendrochronological records from jack pine stands. However, following the 1980 Mack Lake wildfire, Simard and Blank (1982) developed a 160-year fire history of the area using several scattered red pine trees that had established in the 1820s. Results from fire-scar counts indicated at least 37 individual fires had occurred in the 8,000-ha sample area during the 160-year period of record. Therefore, the mean fire frequency for the Mack Lake area is approximately 1 fire/4.2 years.

Of the 37 fires reported by Simard and Blank (1982), six large fires (4,000+ hectares) have occurred since 1815 (1815, 1862, 1874, 1886, 1946, and 1980). During presettlement time (1815-1849), the mean large-fire frequency for the Mack Lake area was 1 fire/35 years; since settlement (1850-1980) the large-fire frequency increased to 1 fire/26 years.

On May 5, 1980, the most recent large wildfire burned more than 3 times the total area that had burned on the Huron National Forest in the previous 34 years (Simard and Blank 1982). The fire began as the 84-ha Crane Lake prescribed burn and was ignited in jack pine slash at 10:30 a.m. by U.S. Forest Service personnel. The burn was being conducted for site-preparation prior to jack pine replanting for Kirtland's warbler habitat. At 12:06, the fire spotted into standing jack pine and by 12:15 the fire was out of control. In the first 3½ hours, the fire advanced 12 kilometers at an average rate of 3.4 km/h. The peak rate of spread (9.6 to 12.8 km/h) equaled the fastest recorded rate for which data are available. Just six hours after ignition, the fire had burned 8,000-ha (over 80% of the total area burned!). In all, the fire burned 9,700 ha, consumed 270,000 tons of fuel, and released 3,000 kJ's of energy – the equivalent of 90 thunderstorms. For a comprehensive account of the Mack Lake wildfire, including a detailed fire chronology, fire behavior, and site effects, see Simard et al. (1982).

III. METHODS

Landform-Level Ecosystem Classification and Mapping

Field Methods

A multifactor landscape ecosystem approach (see Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985, and Archambault et al. 1990) was used to develop a landform-level ecosystem classification and map of the Mack Lake burn study area. An iterative method was employed whereby successive approximations of putative landform units were determined. Each successive approximation served as a working hypothesis that was tested in the field and revised as necessary to yield a final classification and map. The procedure was accomplished using:

1) aerial photographs and topographic maps (1st and 2nd approximations),
2) field reconnaissance and transect sampling (1st and 2nd approximations),
3) permanent-plot sampling (3rd approximation), and
4) data compilation and statistical analyses (final classification and map).

1ST APPROXIMATION

Prior to the initiation of field work, a first approximation of putative landform-level ecosystems was developed for the study area. This approximation was based largely on the hierarchical landscape framework (i.e., spatial context) of physiographic systems (i.e., outwash plain and ice-contact terrain) and constituent ecosystem groups (i.e., high- and low-elevation terrain) originally provided by Barnes et al. (1989; Table 1.1).

With the aid of topographic maps and aerial photographs, the outwash plain physiographic system was subdivided into several hypothetical landform-level ecosystem units. Given the basin-like physiography of the study area, elevational differences provided the primary ecological basis for the initial assignment of putative landform boundaries. The highly dissected and heterogeneous ice-contact terrain physiographic system was treated as a single unit in the landform-level classification. This first approximation of putative landforms boundaries provided the basis for field testing conducted during the 1995 field season.

2ND APPROXIMATION

Field reconnaissance and transect sampling were used to test the initial landform boundaries. Reconnaissance was conducted along tentative landform boundaries and across core areas of putative landforms. Transect sampling was used to refine boundary delineation in areas where reconnaissance revealed boundaries to be indistinct.

Pairs of parallel transect lines were established such that each pair of lines straddled the boundary of a putative landform. The distance between the lines of each transect pair varied (100-200 m) depending on the width of the transition zone between landforms. A random spin of a compass dial was used to determine the azimuth and distance (number of chains) from a known point to the start of each transect line. The azimuth shared by each pair of lines was arbitrarily determined based on the prevailing bearing of the proposed landform boundary. Data was gathered along transect lines at 40-60 m intervals or at any significant change in microtopography or ground-cover vegetation. At each interval a 5 x 10 m sample plot was established with the long axis perpendicular to the line. Five to six plots were established per transect line.

Physiographic data recorded at each transect plot included specific landform, aspect, slope position, slope percent, Terrain Shape Index (McNab 1989), and a description of microtopography.

A soil auger boring was taken at a random point in each plot. Depth, texture, and field pH of major soil horizons and at 50 cm intervals below the surface were measured from the boring. Depth of organic matter; depth to the water table; soil profile drainage; and presence, depth, and thickness of fine-textured banding were also recorded. Along each transect, and adjacent to the plot closest to the halfway point, a soil pit was excavated to a depth of 2 m and the soil profile was described in detail according to Soil Conservation Service procedures (Soil Survey Staff 1975). In addition to measuring the variables listed above, horizon structure, horizon color, percent gravel (2-75 mm diameter) and cobble (75-250 mm diameter) content, depth of concentrated plant rooting, and depth to maximum plant rooting were estimated. A soil sample was collected from each of the profile's major horizons for laboratory analysis of horizon texture and pH. At the bottom of each pit, an auger boring was taken to a depth of approximately 5 meters. Texture and field pH at 50 cm intervals below the surface and depth to the water table were determined from the boring.

Species and diameter at breast height (dbh) to the nearest 0.1 cm were recorded for all live and standing dead overstory (at least 9.1 cm dbh) trees. Species and dbh of all live understory (1.5-9.0 cm dbh) stems were tallied by 2.5 cm diameter class. Height to the nearest 10 cm and dbh of three to five dominant jack pine stems (i.e., tallest trees) was recorded, and the density and patchiness of jack pine in each plot was estimated. Additionally, the height of three dominant northern pin oak stems was recorded and the number of northern pin oak seedlings and sprout clumps was tallied. Areal coverage of all ground-cover (< 1.5 cm dbh) species, bare ground, and woody debris on the forest floor was estimated in each 5 x 10 m plot using 12 coverage classes (Table 3.1). A sampling frame representing 0.1% (250 cm^2) of the plot area was used to standardize coverage estimates. Nomenclature follows Voss (1972, 1984, and 1997) for vascular plants.

Information gathered through reconnaissance and transect sampling was used to revise the hypothesized landform boundaries and generate a second approximation of putative landforms. This second approximation provided the basis for field testing conducted during the 1996 field season.

3RD APPROXIMATION

Plot sampling was conducted within proposed landform units to 1) characterize each unit based on physiographic, soil, and vegetative attributes, and 2) examine the degree of distinctness of each landform using univariate and multivariate statistical methods (Pregitzer and Barnes 1984, Spies and Barnes 1985). Plot sampling was limited to those landforms that had been occupied by the Kirtland's warbler during the period 1986-1995. The protocol employed to sample unoccupied landforms is described later in this section.

A total of 55 sample plots were measured during the 1996 field season. Plots were selected to provide a representative sample of landscape ecosystem types within each landform unit (Table 3.2). Of the 55 plots sampled, 37 plots were relocated permanent 200-m^2 (10 x 20 m) ecosystem-type plots established from 1986-1988 by Barnes et al. (1989, Zou et al. 1992; see Chapter I). The remaining 16 plots were established in 1996 to 1) replace selected permanent plots that could not be relocated, or 2) collect data in areas not previously sampled. A map of sample plot locations is provided in Appendix C.

Table 3.1 Coverage class scale used in estimating and recording the areal coverage of ground-cover species in sample plots.

Coverage Class	Range of Coverage (%)	Median of Class (%)	Number of Frames	Area in Plot (250 cm^2 frame)	Area in Plot (1,000 cm^2 frame)
0.25	Trace-0.005	0.0025	0-0.05	0-12.5 cm^2	0-50 cm^2
0.5	0.005-0.01	0.0075	0.05-0.1	12.5-25 cm^2	50-100 cm^2
1	0.01-0.1	0.055	0.1-1.0	25-250 cm^2	100-1000 cm^2
2	0.1-0.5	0.3	1-5	250-1250 cm^2	1000-5000 cm^2
3	0.5-1	0.75	5-10	1250-2500 cm^2	0.5-1.0 m^2
4	1-2	1.5	10-20	0.25-0.5 m^2	1-2 m^2
5	2-4	3.0	20-40	0.5-1.0 m^2	2-4 m^2
6	4-8	6.0	40-80	1-2 m^2	4-8 m^2
7	8-16	12.0	80-160	2-4 m^2	8-16 m^2
8	16-32	24.0	160-320	4-8 m^2	16-32 m^2
9	32-64	48.0	320-640	8-16 m^2	32-64 m^2
10	64-100	82.0	640-1000	16-25 m^2	64-100 m^2

Table 3.2 Distribution of plots sampled within the Mack Lake burn, Oscoda Co., northern Lower Michigan, by landscape ecosystem type (Barnes et al. 1989, Zou et al. 1992; Table 1.1).

	Number of Plots Sampled	
Landscape Ecosystem Type	Plots Est. 1986-1988	Plots Est. 1996
Low-elevation Terrain		
1	6	3
2	4	
3	1	
4	2	4
5	3	
**		4
High-elevation Terrain		
6	4	3
7	1	2
8	6	
9	5	
10	4	
11	3	
Total	39	16

** Previously unidentified landscape ecosystem type distinguished in 1996.

New plots were established using the stratified random sampling design developed in 1986 (Zou 1988, Barnes et al. 1989). Reconnaissance was used to identify representative areas (i.e., landscape ecosystem types) to be sampled within each putative landform. At each site, a random spin of a compass dial was used to determine the azimuth and distance (number of chains) to the northeast corner of the plot. Each plot (10 x 20 m) was subdivided into eight equal 5 x 5 m subplots (Zou 1988; Figure 3.1). The northeast corner of each plot was permanently marked with a 30-cm length of reinforcing rod.

Physiographic data collected at each sample plot included specific landform, elevation, aspect, topographic position (upper slope, midslope, footslope, channel, depression), slope percent, and Terrain Shape Index (McNab 1989). Additionally, the terrain surface was described (plane, convex, concave), microrelief was classified (flat, furrowed, undulating, other), and the degree of pitting was ranked (flat, slightly pitted, somewhat pitted, somewhat severely pitted, or severely pitted).

A soil pit was excavated (2 m deep) adjacent to each of the 16 sample plots established in 1996. A random compass spin was used to determine pit location with respect to the plot, and a complete soil profile description was made according to the method described above (Soil Survey Staff 1975). Soil pits were not excavated at the relocated sample plots because complete soil profile descriptions and results of soil laboratory analyses were already on record (Barnes et al. 1989, unpublished data).

Species and dbh to the nearest 0.1 cm were recorded for all live and standing dead overstory (at least 9.1 cm dbh) trees. Species and dbh of all live understory (1.5-9.0 cm dbh) stems in each 5 x 5 m subplot (Figure 3.1) were tallied by 2.5 cm diameter class. Height to the nearest 10 cm of three dominant (i.e., tallest trees) northern pin oak stems in each

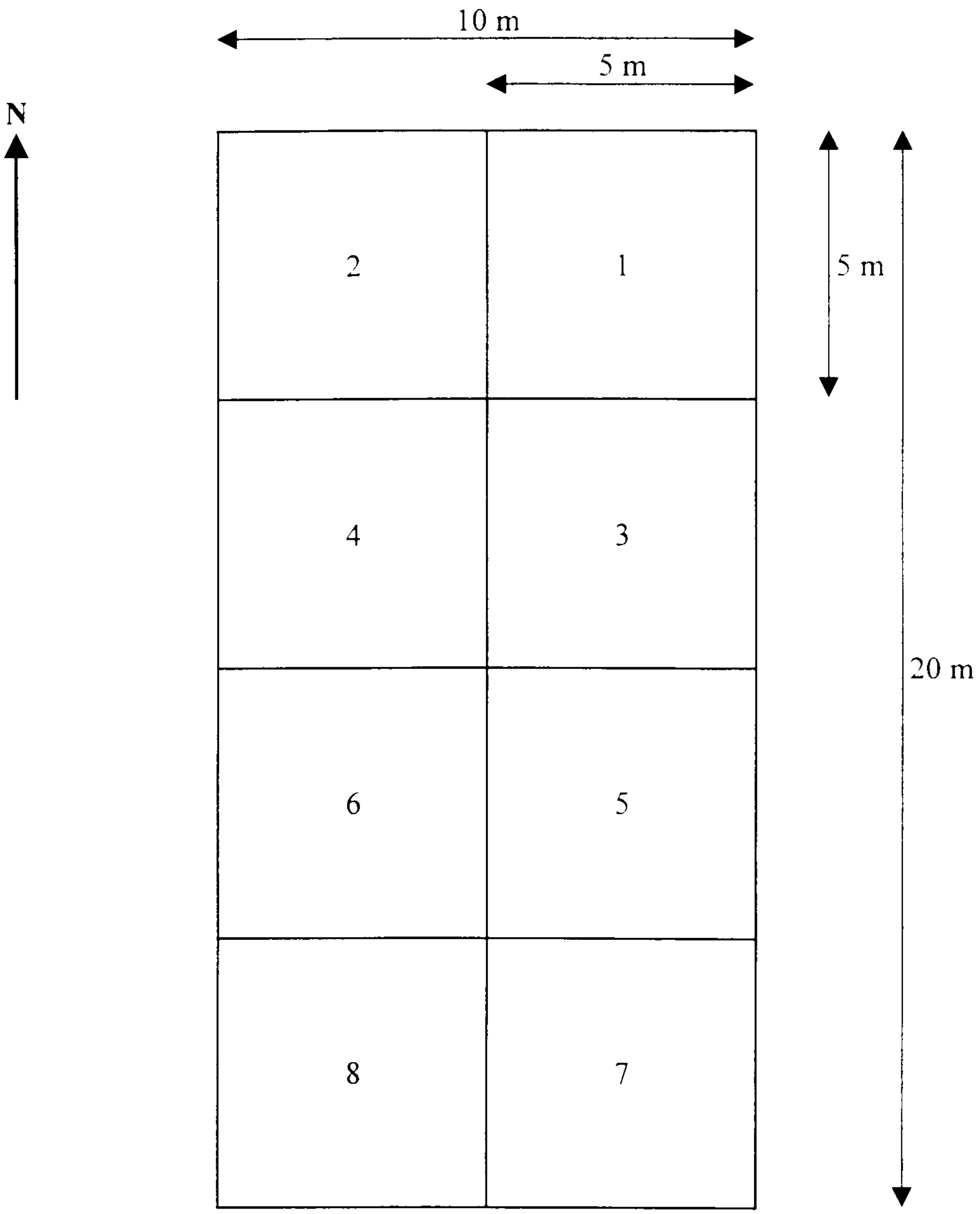

Figure 3.1. Diagram of 10 x 20 m sample plot and 5 x 5 m subplots (1-8).

plot was recorded and the number of northern pin oak seedlings, seedling clumps, and sprout clumps was tallied. The coverage of six vertical stand structural layers (moss-creeper, herbaceous, shrub-sapling, small tree) was recorded by class: (1) 0%, (2) 1-10%, (3) 11-40%, (4) 41-75%, (5) 76-100%. Additionally, the canopy coverage of jack pine and northern pin oak in each plot was estimated to the nearest 1.0 percent and stand density (i.e., crown closure) in both the plot and the general area was recorded by class: sparse (0-18%), medium (19-32%), dense (> 32%).

Two 5 x 5 m subplots (Figure 3.1), one at each end of the main plot, were randomly selected (i.e., subplot 1 or 2 and subplot 7 or 8) and 3 dominant (i.e., tallest) jack pine stems were identified in each. Height to the nearest 10 cm, dbh, height of the lowest live branch, and height of the lowest coincident pair of live branches was estimated for each stem. Dominant trees were also assigned an "openness" class. Each tree was divided radially into four quadrants and the number of open quadrants were recorded and classified as follows: 0 (closed grown), 1 (somewhat closed grown), 3 (somewhat open grown), 4 (open grown). Additionally, around the perimeter of both subplots (clockwise from the northeast corner), the height of the lowest live branch and lowest pair of live branches was recorded by class for the first five understory (1.5-9.0 cm dbh) jack pine trees encountered. The above-ground height classes are as follows: 1 (0-20 cm), 2 (21-40 cm), 3 (41-60 cm), 4 (61-80 cm), 5 (81-100 cm), 6 (101-120 cm), 7 (121-140 cm), 8 (> 140 cm).

The areal coverage of all ground-cover (< 1.5 cm dbh) species was estimated in a randomly determined 100-m^2 (5 x 20 m) subplot using 12 coverage classes (Table 3.1). A sampling frame representing 0.1% (1000 cm^2) of the sample area was used to standardize coverage estimates. Ground-cover species absent in the 5 x 20 m subplot but present within

5 meters of it were assigned the lowest coverage class. Additionally, the coverage of jack pine, northern pin oak, bare ground, and downed woody debris was recorded.

The sampling protocol outlined above was modified considerably to characterize the ecological attributes of the proposed landform never occupied by Kirtland's warbler. The modified protocol combined extensive reconnaissance with random-point sampling. Reconnaissance was used to identify, as far as possible, individual landscape ecosystem types, i.e., the range of ecological variation present within the landform unit. Reconnaissance was followed by point sampling of physiography, soil, and vegetation at several randomly established locations within each ecosystem type.

Between two and four random points were located in each ecosystem type. The total number of points in each type was based on the cumulative land area of the type. A random spin of a compass dial was used to determine the azimuth and distance (number of chains) to each point from the approximate center of the ecosystem.

Physiographic data collected at each point included specific landform, aspect, slope position, slope percent, Terrain Shape Index (McNab 1989), and a description of microtopography.

A soil auger boring was taken at each point, and a general description of the soil profile was made. The description included the depth, texture, and field pH of all major soil horizons as well as the field pH at the surface and at 40 cm. Notes on distinguishing soil profile characteristics were recorded where appropriate. Depth to the water table and notes on the presence of standing water were also recorded.

A species list was compiled of the dominant and associate tree and shrub species found to occur within a 10 m radius of the point in both the overstory and understory layers.

A similar list was compiled of all dominant shrub and herbaceous plant species found in the ground-cover layer. Additionally, the presence and absence of both jack pine and northern pin oak in each of the three structural layers was noted.

Laboratory Methods

Soil samples collected in the field were air dried, crushed, and passed through a 2 mm sieve. Soil texture analysis, as described by the American Society of Agronomy (1986), was used to determine the proportion of sand, silt, and clay in 100-g soil samples. The sand-sized fraction (0.05-2.0 mm in diameter) was oven-dried and dry-sieved to determine the proportion of very fine, fine, medium, coarse, and very coarse sand present.

The pH of 30-g soil samples was determined in a 1:1 soil to deionized water solution using a Fisher pH meter with a glass combination electrode. Solutions were stirred thoroughly and allowed to settle 3 times; measurements were taken after solutions were allowed to stand for at least 30 minutes.

Statistical Methods

DATA TRANFORMATIONS

Aspect, recorded in the field as azimuth, was transformed for statistical analyses using the following formula: Aspect' = cosine ($Aspect_{max}$ – Aspect) + 1, where Aspect' is the transformed aspect and $Aspect_{max}$ is the aspect (45°) considered optimal for plant growth (Beers et al. 1966).

Soil texture variables, collected and analyzed by horizon, were transformed to a weighted average (based on horizon thickness) for two depth intervals (10-30 cm and 10-150 cm) to standardize the data among characteristically different soil profiles (see Spies 1983). Soil pH (10-30 cm and 30-150 cm) and percent pebble and cobble content (0-150 cm) were similarly transformed.

Coverage classes assigned to ground-cover species in the field were transformed to the median percent-coverage value associated with each class (see Table 4.1). An abundance measure of each ecological species group (Barnes et al. 1989; see Chapter I) was obtained by summing the median-percent coverage values of all species in the group.

UNIVARIATE ANALYSES

One-way analysis of variance (ANOVA) was used to test for significant differences among landform-level ecosystems with respect to 75 physiographic (4), soil (35), and vegetative (36) variables. An alpha (α) of 0.05 was used for all hypothesis tests. The assumption of normality was evaluated using skewness and kurtosis coefficients, the Lilliefors test, a histogram of residuals, and a plot of residuals versus expected values. The assumption of homogeneity of variances was evaluated using the Modified Levene's test (Neter et al. 1996) and a plot of residuals versus estimates. Because variables of ground-cover coverage frequently contained zero values, moderate to serious departures from the assumptions were common. If one or more assumptions of the ANOVA model were violated, the Kruskal-Wallis nonparametric analysis of variance was used (Conover 1980).

Pairwise multiple comparisons of group means were evaluated for all variables using the Bonferroni method (Neter et al. 1996). All univariate and multivariate statistical procedures were performed using SYSTAT 6.0 (SPSS, Inc. 1996).

MULTIVARIATE ANALYSES

Principal components analysis (Jackson 1991) was used to summarize the multi-dimensional variation in the physiographic and soil data and to ordinate the landform-level ecosystems. Variables selected for inclusion in the principal components analysis were limited to those exhibiting significant differences among landforms at the 5% level. Additionally, in cases where two variables measured the same property but over different depth intervals (e.g., percent sand, 10-30 cm and percent sand, 10-150 cm), only the variable with the highest ANOVA F-statistic (or Kruskal-Wallis p-value) was included in the analysis. Using these selection criteria, the original set of 39 physiographic and soil variables was reduced to 16 variables.

Because several variables were measured on different scales, the principal components were extracted using the correlation matrix. The geometric relationship among 49 sample plots was examined in the ordination space of the first two principal components[1]. The contribution of each original variable to the first two components was interpreted by examining the absolute magnitude of the factor loadings (i.e., eigenvector coefficients) computed by SYSTAT.

Discriminant analysis (Williams 1981, 1983; see also Pregitzer and Barnes 1984, Spies and Barnes 1985, and Archambault et al. 1990) was used to evaluate the distinctness of the landform-level ecosystems distinguished in the field. Variables selected for inclusion in the discriminant analysis were limited to those exhibiting significant differences among landforms at the 5% level (Gauch 1983). Discriminant functions were computed using three different subsets of the original variables: a physiography-soil subset, a ground-cover

[1] Due to the considerable ecological variability associated with individual ice-block depressions, plots sampled in ecosystem types 5 and 11(n = 6; Table 4.2) were not included in the multivariate analyses.

vegetation subset, and a subset combining the previous two. Predictor variables in each set were selected for canonical variates analysis using interactive forward stepwise discriminant analysis (SPSS, Inc. 1996). An interactive stepping procedure was used instead of an automatic routine so that candidate variables could be selectively entered and/or removed from the model at each step. In this way, variable selection is guided, to a greater extent, by one's own knowledge of the subject and experience with the data (SPSS, Inc. 1996).

The relationship among landform units (based on discriminant scores of sample plots) was examined in the ordination space of the first two canonical variates. Pearson product-moment correlations of the original variables with the canonical variates were computed to aid in the interpretation of the canonical variates (see Spies 1983). Separate ordination diagrams were plotted to evaluate the discriminating ability of each variable subset. The probability of misclassification for each subset was estimated using the jackknife or leaving-one-out method of computing discriminant functions (SPSS, Inc. 1996).

Canonical variates analysis assumes multivariate normality and homogeneity of covariances. Although these assumptions were not formally tested, violations are suspected due to the relatively small sample size and the large number of variables relative to the number of observations (sample plots) per group (landform).

Microclimate Study

Field Methods

Local variation in the microclimate of the Mack Lake burn was first recognized and measured by Barnes et al. (1989; see also Zou et al. 1992) during the 1986 and 1987 field seasons. In 1995, a microclimate study was initiated to document the magnitude of temperature variation in selected areas of the burn. A total of 14 temperature recording stations were established in 3 physiographically distinct areas: high-elevation terrain (n = 6 stations), low-elevation terrain (n = 6 stations), and glacial meltwater drainage channels (n = 2 stations). A map showing the locations of temperature recording stations in 1995 is presented in Appendix D. Each station consisted of 2 maximum-minimum thermometers placed 30 cm above the ground and positioned 3 to 5 m apart; stations were located 20 to 40 m away from roads for convenience. Stations in each area were established, in so far as possible, at the same elevation (high-elevation terrain, 381 m (1250 ft); low-elevation terrain, 366 m (1200 ft); and glacial meltwater drainage channels, 354 m (1160 ft)).

All stations were established the first week of May, 1995 and were visited twice weekly each Wednesday and Thursday from May 17 to July 17 and again on August 23 and 24. Supplementary readings were taken on days when unusual temperature extremes were expected, i.e., following frosts or exceptionally hot weather. A total of 23 readings were taken at each station during the 1995 field season.

The protocol of the temperature study was modified in 1997 to focus in greater detail on the microclimate of the glacial meltwater drainage channels. Four additional recording stations were established in the channels to balance the number of stations across areas (i.e., n = 6 stations per area). During the 1997 field season, stations in the channels and the low-elevation terrain were visited once a week on the same day from mid-May to mid-August. Again, supplementary readings were taken on days when unusual temperature extremes were expected. A total of 12 readings were taken at each station in 1997.

Statistical Methods

One-way analysis of variance was used to test for significant differences in average weekly and daily maximum and minimum temperature (i.e., all readings pooled by level) among physiographic levels (high-elevation terrain, low-elevation terrain, and glacial meltwater drainage channels). The assumption of normality was evaluated using skewness and kurtosis coefficients, the Lilliefors test, a histogram of residuals, and a plot of residuals versus expected values. The assumption of homogeneity of variances was evaluated using Bartlett's test and a plot of residuals versus estimates. Pairwise multiple comparisons of average maximum and minimum temperature among physiographic levels were evaluated using the Bonferroni method (Neter et al. 1996). Additionally, a two-way repeated measures ANOVA was used to test for significant differences in the season-long patterns of weekly and daily maximum and minimum temperature change among physiographic levels. One grouping factor was used with three levels corresponding to the number of areas (physiographic levels) being compared; one trials factor was used with 11 (12) levels related to the number of weekly (daily) temperature readings taken at each station. As no serious departures from the assumption of compound symmetry were observed, the univariate (within-subjects) F-test proved valid for the analysis.

Kirtland's Warbler Occupancy of Landform-Level Ecosystems

Field Methods

Annually, cooperators from the Department of Natural Resources, the Department of Military Affairs, the U.S. Forest Service, the U.S. Fish and Wildlife Service, and volunteers (Weinrich 1996) conduct an official census of the Kirtland's warbler population. During the census, usually the second week of June, selected areas are systematically checked for the presence of singing-male warblers. Census personnel simultaneously traverse tracts of young jack pine along parallel transect lines placed at 0.4-km (¼ mile) intervals. Regularly spaced stops (ca 4 chains apart) are made along transects to listen for the loud, and usually persistent, song (most observers can hear the song for at least 0.3 km). Approximate locations of singing males are recorded in the field on sketch maps, and adjacent maps are compared to minimize double-counting (Weinrich 1996). For census purposes, it is assumed that each singing male is mated with one female. Therefore, the annual "breeding population" is estimated to be twice the number of singing males (Mayfield 1953, Ryel 1979b).

Office Methods

Annual census records for the Mack Lake Kirtland's Warbler Management Area (KWMA) were acquired from the U.S. Forest Service, Huron National Forest, Mio Ranger District, for the period 1986-1997. Records included maps showing the census locations of singing-male warblers in each year. Warbler locations in each year were transferred to Mack Lake, Michigan 7.5-minute topographic quadrangle sheets (United States Geological Survey 1972). Topographic quadrangles were used to assign an approximate elevation to the census location of each singing male.

Census records for the Mack Lake KWMA also were acquired in digital form. ArcView 3.0 GIS was used to overlay annual census data (i.e., ArcView point themes representing warbler locations) on a digitized map of landform boundaries. The number of singing males occurring within each landform in each year (1986-1997) was counted, and the surface area of each landform was determined. Additionally, an approximate coordinate position (i.e., UTM easting and northing) was computed for the census location of each singing male, and the mean coordinate position (Shaw and Wheeler 1985) occupied by singing males in each year was determined. Coordinate geometry was used to calculate the approximate straight-line distance (m) moved between mean coordinate positions in successive years.

Statistical Methods

Four hypotheses were identified for testing. To test hypothesis (1), that among years, the spatial distribution of singing male warblers across the Mack Lake burn is associated with elevation, simple linear regression was used to describe the relationship between the average elevation of the singing-male warbler population and year of occupancy (1986-1997). The assumption of normality was evaluated using skewness and kurtosis coefficients, the Lilliefors test, a histogram of residuals, and a normal probability plot of residuals. The assumption of homogeneity of variances was evaluated using a plot of residuals versus estimates. No serious departures from the assumptions were observed. To linearize the data, the independent variable (time) was transformed using the natural logarithm.

To test hypothesis (2), that among years, the spatial distribution of singing-male warblers across the Mack Lake burn is correlated with geographic position, a multivariate ANOVA was used to test for significant differences in the spatial mean (i.e., the mean coordinate position based on UTM eastings and northings) of the singing-male warbler population among years. The assumption of normality was evaluated using skewness and kurtosis coefficients, the Lilliefors test, a histogram of residuals, and a normal probability plot of residuals. The assumption of homogeneity of variances was evaluated using the Modified Levene's test (Neter et al. 1996) and a plot of residuals versus estimates. No serious departures from the assumptions were observed.

To test hypothesis (3), that in each year, singing-male warblers are distributed among landform-level ecosystems in a nonrandom (specific) fashion, a one-way Chi-square goodness-of-fit test was conducted for each year (1986-1997). The Chi-square test assumes that each observation (bird) has an equal probability of occurring in each category (landform). To meet this assumption, the observed frequencies (birds per landform) were weighted by the surficial area of each landform. Additionally, the test assumes that expected frequencies in a given category not be too small, e.g., no expected frequency should be less than one and not over 20% of expected frequencies should be less than five (Remington and Schork 1985). Due to low population numbers during the initial years of site colonization (1986-1989), expected frequencies were, in many cases, less than five and occasionally less than one. To meet the assumption, the number of observations (i.e., singing males) was doubled, thereby increasing the expected frequencies. Because it is commonly accepted that the number of singing males represents one half of the total warbler population (Mayfield 1953), the transformation not only satisfied the assumption (for 1988 and 1989), but also more closely approximated the true population size.

To test hypothesis (4), that among years, singing-male warblers are distributed across landform-level ecosystems in a nonrandom (specific) fashion, a two-way Chi-square test for independence was conducted for the 12-year period (1986-1997). Again, to meet the assumptions of the test the number of observations (i.e., singing males) was doubled.

IV. RESULTS AND DISCUSSION

Landform-Level Ecosystem Classification and Description of the Mack Lake Burn

Landform-Level Ecosystem Classification

Four low-elevation and two high-elevation landform-level ecosystems (i.e., landforms) were distinguished and mapped within the Mack Lake burn (Figure 4.1). In the landscape ecosystem classification developed for the study area (Table 4.1), landforms (I-VI) constitute the second hierarchical level below the two major high- and low-elevation terrain features identified by Barnes et al. (1989, Barnes and Zou 1989, Zou et al. 1992; Figure 1.5). Each landform is named according to physiography, soil drainage, soil texture, fertility, and, where applicable, the characteristic ecological species group. Nested within landforms, eleven individual landscape-ecosystem types (Barnes et al. 1989), representing the finest level of ecosystem delineation, complete the classification.

Several physiographic, soil, and vegetative variables examined in the univariate analysis were useful in differentiating individual landform-level ecosystems and in characterizing their ecological attributes. Among the many physiographic and soil variables distinguishing the landforms, elevation, silt and clay content, gravel and cobble content, total accumulated banding, depth to banding, and laboratory pH were most useful (Table 4.2). Vegetative variables most effective in distinguishing the landforms included both height and coverage of jack pine and northern pin oak, total number of northern pin oak clumps, number of tree and shrub species, coverage of shrub species, and coverage of the *Arctostaphylos uva-ursi*, *Ceonothus ovatus*, and *Rosa blanda* species groups (Table 4.3). Detailed descriptions of the six landform-level ecosystems, including their physiography, microclimate, soil, and

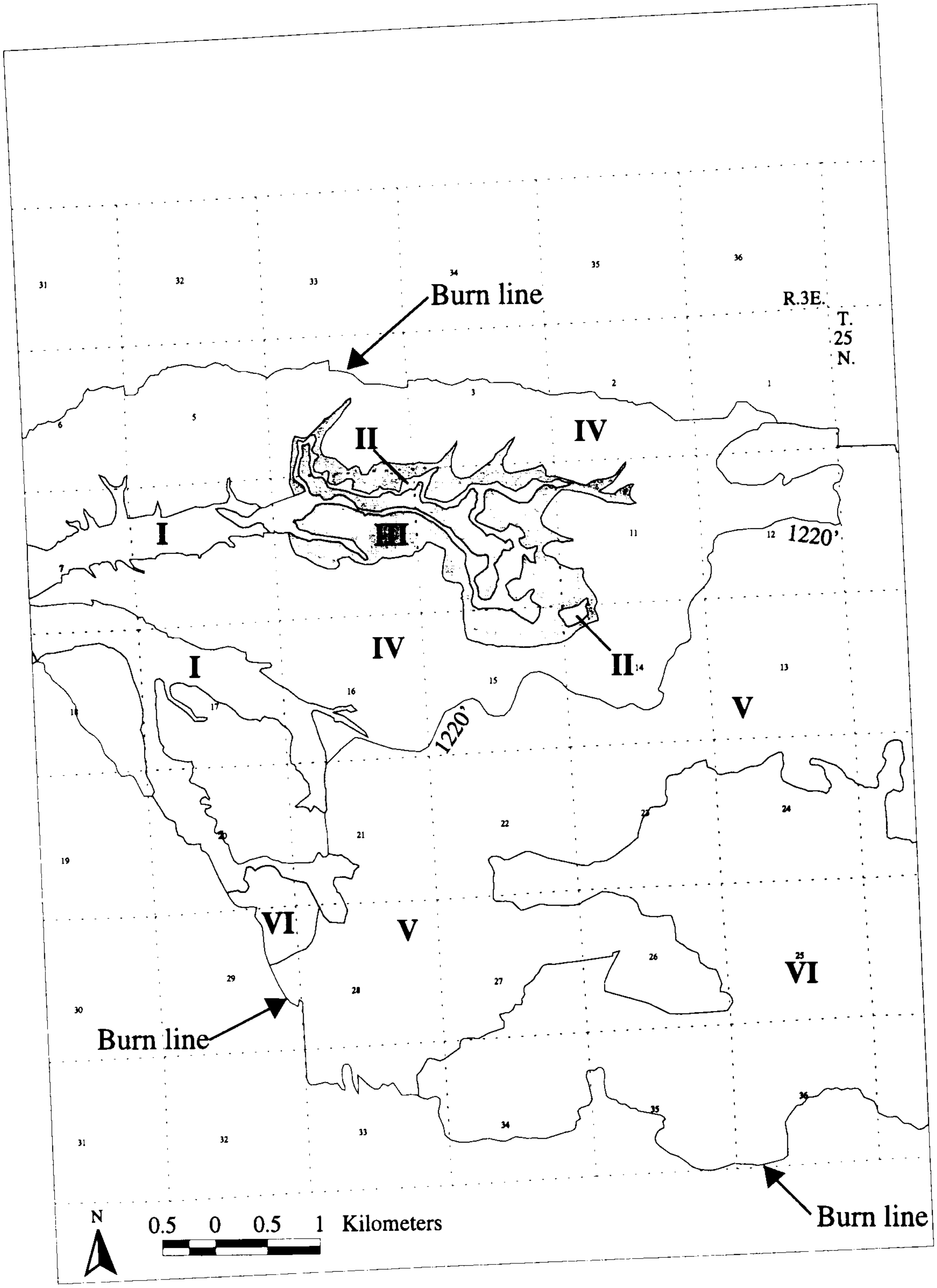

Figure 4.1. Landform-level ecosystems of the Mack Lake burn study area, Oscoda Co., northern Lower Michigan: (I) low-elevation outwash channels, (II) low-elevation lake-margin outwash plain, (III) low-elevation water-table influenced pitted-outwash plain, (IV) low-elevation excessively drained pitted-outwash plains, (V) high-elevation outwash plains, (VI) high-elevation ice-contact terrain. Note: The 1220 ft contour line marks the arbitrary boundary between the high- and low-elevation terrain features.

Table 4.1 Classification of landscape ecosystems of the Mack Lake burn, Oscoda Co., northern Lower Michigan.[1]

Low-elevation Outwash Channels and Plains (Elevation 350-372 m).

I. Outwash Channels

1. Glacial meltwater drainage channels (6-15 m deep); excessively to somewhat excessively drained, medium to medium-fine sand with a distinct pebble/cobble layer; infertile; *Vaccinium, Arctostaphylos*

II. Lake margin outwash plain; seasonally flooded, sapric muck (< 30 cm) over medium sand; variable fertility

III. Pitted outwash plain with water table influence (< 4 m); excessively to somewhat excessively drained, loamy sand to sand with gravel and cobbles; infertile; *Vaccinium, Rosa*

IV. Pitted outwash plains; excessively to somewhat excessively drained; *Prunus*

A. Level to gently sloping terrain (depressions < 1.5 m deep)

2. Outwash plain; medium to medium-fine sand; very infertile

3. Outwash plain; medium sand; infertile (areas of higher relative elevation between glacial meltwater drainage channels)

4. Outwash plain; sand to loamy sand over bands of fine texture; infertile

B. Depressions (1.5-6 m deep)

5. Depressions with extreme microclimate; soil as in ecosystems 2-4

High-elevation Outwash Plains and Ice-contact Terrain (Elevation 372-390 m)

V. Outwash plains; excessively to well drained; *Rosa*

C. Level to gently sloping terrain

6. Outwash plain; gently sloping topography, medium sand; very infertile

7. Outwash plain; level topography, >25% fine sand in upper 50-70 cm; infertile

8. Outwash plain; loamy sand to sand, 5-10 cm (cumulative) of fine-textured bands; slightly infertile

9. Outwash plain; loamy sand soil or a relatively thick band of fine texture (> 10 cm); slightly to moderately infertile

D. Depressions

10. Depressions (3-15 m deep) with extreme microclimate; soil as in ecosystems 6-9

VI. Ice-contact terrain

11. Ice-contact terrain; moderately steep slopes (3-30%), excessively to somewhat excessively drained, sandy kamic hills; infertile; *Ceonothus, Gaultheria*

[1] Landscape ecosystem type numbers (1-11) were modified from Barnes et al. (1989; Table 1.1) such that the current order reflects increasing elevation from the lowest (1) to the highest (11) ecosystem type.

Table 4.2 Summary of physiographic and soil variables for five landform-level ecosystems within the Mack Lake burn, Oscoda Co., northern Lower Michigan (values are means, s.d. in parentheses).[1]

	Landform-level Ecosystem									
	Low-elevation Terrain						High-elevation Terrain			
Site Variable	Landform I (n=6)		Landform III (n=4)		Landform IV (n=14)		Landform V (n=21)		Landform VI (n=4)	
Elevation (m)[a]	354.89	(4.62)	361.42	(1.98)	368.69	(2.04)	375.88	(4.38)	381.61	(7.29)
Transformed aspect	0.53	(0.58)	0.59	(0.75)	0.78	(0.75)	1.09	(0.69)	0.87	(0.80)
Slope (%)[a]	2.08	(2.33)	2.50	(2.20)	1.46	(0.93)	1.86	(1.52)	7.13	(8.13)
Maximum slope (%)[a]	2.33	(2.14)	3.25	(1.44)	1.82	(1.46)	2.21	(1.71)	7.38	(7.89)
Sand, 10-30 cm (%)[a]	88.37	(3.33)	87.59	(1.95)	91.34	(3.33)	87.08	(4.50)	91.28	(1.25)
Very coarse sand, 10-30 cm (%)	1.34	(1.17)	1.60	(0.79)	1.38	(1.66)	0.99	(0.47)	1.13	(1.06)
Coarse sand, 10-30 cm (%)[a]	6.15	(3.58)	10.84	(4.01)	4.43	(3.09)	3.73	(1.86)	4.00	(2.27)
Very coarse + coarse sand, 10-30 cm (%)[a]	7.49	(4.67)	12.44	(4.56)	5.69	(5.52)	4.72	(2.06)	5.13	(3.33)
Medium sand, 10-30 cm (%)	55.31	(4.24)	64.08	(3.42)	57.13	(8.31)	57.39	(11.62)	61.70	(2.74)
Fine sand, 10-30 cm (%)	29.02	(6.47)	21.28	(4.21)	26.71	(9.58)	24.80	(8.65)	22.55	(4.24)
Very fine sand, 10-30 cm (%)	3.85	(1.38)	2.20	(0.65)	2.57	(1.96)	3.64	(2.48)	1.95	(0.53)
Fine + very fine sand, 10-30 cm (%)	32.87	(7.32)	23.48	(4.54)	29.29	(10.57)	28.44	(10.64)	24.50	(4.59)
Silt, 10-30 cm (%)	8.49	(3.01)	9.84	(2.71)	5.71	(4.16)	9.16	(4.57)	5.40	(2.03)
Clay, 10-30 cm (%)	3.57	(1.23)	3.76	(0.29)	3.03	(2.43)	4.08	(1.31)	3.35	(0.93)
Silt + Clay, 10-30 cm (%)[a]	12.06	(3.44)	13.6	(2.82)	8.73	(3.44)	13.24	(4.50)	8.75	(1.28)
Sand, 10-150 cm (%)[a]	95.23	(1.35)	93.72	(1.41)	95.77	(1.95)	91.15	(6.03)	95.38	(1.58)
Very coarse sand, 10-150 cm (%)	1.15	(0.34)	2.30	(1.37)	1.46	(1.73)	1.30	(1.90)	1.60	(1.90)
Coarse sand, 10-150 cm (%)[a]	5.97	(1.78)	13.54	(4.47)	4.81	(4.59)	5.24	(6.63)	4.95	(4.49)

[1] Plot sampling was not conducted in Landform II due to its limited extent and wetland characteristics, which render it unsuitable for Kirtland's warbler occupancy.
[a] indicates significance at $\alpha = 0.05$

Table 4.2 (continued)

	Landform-level Ecosystem									
	Low-elevation Terrain						High-elevation Terrain			
Site Variable	Landform I (n=6)		Landform III (n=4)		Landform IV (n=14)		Landform V (n=21)		Landform VI (n=4)	
Very coarse + coarse sand, 10-150 cm (%)	7.11	(1.98)	15.83	(5.77)	6.30	(6.26)	6.55	(8.49)	6.55	(6.42)
Medium sand, 10-150 cm (%)	60.28	(8.79)	65.25	(3.72)	61.47	(9.60)	57.43	(9.10)	64.25	(10.72)
Fine sand, 10-150 cm (%)	28.11	(9.58)	17.46	(6.87)	25.97	(10.81)	25.24	(8.87)	22.63	(12.12)
Very fine sand, 10-150 cm (%)	2.59	(1.31)	1.45	(1.07)	2.38	(3.62)	3.31	(2.78)	1.93	(1.15)
Fine + very fine sand, 10-150 cm (%)	30.70	(10.83)	18.91	(7.91)	28.35	(12.82)	28.55	(10.65)	24.55	(13.26)
Silt, 10-150 cm (%) [a]	3.71	(1.21)	5.54	(1.68)	2.51	(1.81)	5.57	(3.46)	2.93	(1.74)
Clay, 10-150 cm (%)	1.64	(0.34)	2.14	(0.78)	1.81	(1.49)	3.69	(3.59)	1.73	(0.38)
Silt + Clay, 10-150 cm (%) [a]	5.36	(1.34)	7.69	(2.41)	4.32	(1.89)	9.27	(6.15)	4.66	(1.58)
Gravel + cobbles, 0-150 cm (%) [a]	8.70	(7.34)	8.20	(7.33)	3.38	(6.71)	2.04	(2.27)	0.78	(0.96)
Field pH, 0-10 cm	4.48	(0.35)	4.62	(0.48)	4.62	(0.37)	4.83	(0.40)	4.70	(0.37)
Depth to field pH 7.0 (cm)	141.33	(53.35)	120.25	(18.12)	235.43	(100.37)	209.14	(95.59)	250.25	(38.83)
Laboratory pH, 10-30 cm	5.14	(0.14)	5.29	(0.28)	5.04	(0.26)	5.19	(0.29)	5.20	(0.25)
Laboratory pH, 30-150 cm [a]	5.71	(0.37)	6.08	(0.53)	5.24	(0.47)	5.60	(0.44)	5.48	(0.11)
Accumulated banding, < 150 cm (cm) [a]	0.00	(0.00)	0.00	(0.00)	1.86	(6.40)	12.71	(19.10)	3.25	(4.72)
Accumulated banding, > 150 cm (cm) [a]	3.33	(5.16)	3.00	(3.56)	0.00	(0.00)	5.26	(8.02)	3.75	(4.79)
Total accumulated banding (cm) [a]	3.33	(5.16)	3.00	(3.56)	1.86	(6.40)	17.98	(23.77)	7.00	(6.78)
Depth to lamellae, < 2 cm thick (cm) [a]	500.00	(0.00)	500.00	(0.00)	443.71	(143.70)	264.67	(182.22)	307.50	(222.62)
Depth to band, > 2 cm thick (cm) [a]	400.00	(156.97)	407.50	(106.89)	472.79	(101.83)	157.67	(153.27)	268.25	(188.61)
Depth to band, > 10 cm thick (cm)	400.00	(156.97)	500.00	(0.00)	472.79	(101.83)	371.90	(194.20)	500.00	(0.00)
Depth to maximum rooting (cm) [a]	131.83	(43.15)	147.00	(17.93)	89.57	(25.25)	109.43	(36.13)	95.25	(28.86)
Depth to water table (cm) [a]	999.00	(0.00)	390.00	(94.78)	999.00	(0.00)	999.00	(0.00)	999.00	(0.00)

[a] indicates significance at $\alpha = 0.05$

Table 4.3 Summary of vegetation variables related to stand structure, growth of jack pine and northern pin oak, and the occurrence and coverage of tree, shrub, and ground-cover species for five landform-level ecosystems within the Mack Lake burn, Oscoda Co., northern Lower Michigan (values are means, s.d. in parentheses).[1]

	Landform-level Ecosystem									
	Low-elevation Terrain						High-elevation Terrain			
Variable	Landform I (n=6)		Landform III (n=4)		Landform IV (n=14)		Landform V (n=21)		Landform VI (n=4)	
Height of jack pine (cm) [a]	379.31	(32.68)	439.48	(14.99)	441.25	(55.91)	515.51	(69.24)	517.38	(27.56)
Number of jack pine stems [a]	137.33	(90.17)	65.75	(21.53)	155.43	(135.56)	225.62	(118.30)	200.00	(144.27)
Number of jack pine stems per 5x5 m subplot	17.16	(11.26)	8.22	(2.69)	19.43	(16.94)	28.20	(14.79)	25.00	(18.03)
Patchiness (covariance) of jack pine stems [a]	0.57	(0.21)	0.92	(0.33)	0.61	(0.23)	0.36	(0.13)	0.58	(0.49)
Height of lowest live jack pine branch (cm) [a]	62.08	(36.03)	59.67	(23.31)	101.00	(46.12)	145.48	(46.38)	134.07	(43.12)
Height of lowest pair of live pine branches (cm) [a]	81.33	(30.01)	74.71	(17.56)	117.24	(45.48)	162.69	(39.97)	154.28	(30.51)
Height of northern pin oak (cm) [a]	36.17	(42.61)	26.83	(19.00)	176.53	(172.23)	372.63	(210.08)	513.33	(178.33)
Number of n. pin oak stems (cm) [a]	0.17	(0.41)	0.00	(0.00)	5.71	(11.57)	9.38	(12.11)	25.75	(17.06)
Number of n. pin oak seedlings, < 1 m [a]	5.83	(5.49)	3.75	(3.30)	21.00	(23.71)	52.48	(22.38)	71.50	(56.84)
Number of n. pin oak seedling clumps, < 1 m [a]	2.83	(4.07)	2.25	(2.87)	9.64	(13.07)	30.33	(17.48)	46.5	(42.00)
Number of n. pin oak sprout clumps, < 1 m [a]	0.50	(1.22)	0.25	(0.50)	2.79	(4.44)	8.76	(5.28)	19.75	(6.40)
Total number of n. pin oak clumps, < 1 m [a]	3.33	(3.83)	2.50	(3.32)	12.43	(16.69)	39.43	(17.67)	66.25	(43.42)
Number of tree species [a]	2.17	(0.41)	1.75	(0.50)	2.21	(0.43)	2.90	(0.89)	3.00	(0.82)
Number of shrub species [a]	7.33	(1.51)	8.75	(1.71)	7.07	(1.44)	9.81	(3.09)	9.75	(3.50)
Number of tree + shrub species [a]	9.50	(1.64)	10.50	(2.08)	9.29	(1.64)	12.71	(3.48)	12.75	(3.59)
Number of grass species [a]	7.17	(2.14)	11.00	(0.00)	5.36	(1.08)	4.33	(2.13)	4.75	(3.77)
Number of herbaceous + grass species [a]	20.17	(4.22)	24.50	(3.79)	15.14	(3.82)	14.14	(5.74)	14.75	(8.50)

[1] Plot sampling was not conducted in Landform II due to its limited extent and wetland characteristics, which render it unsuitable for Kirtland's warbler occupancy.

[a] indicates significance at $\alpha=0.05$

Table 4.3 (continued)

Vegetation Variable	Landform I (n=6)		Landform III (n=4)		Landform IV (n=14)		Landform V (n=21)		Landform VI (n=4)	
	Landform-level Ecosystem									
	Low-elevation Terrain						High-elevation Terrain			
Coverage of tree species, > 1.5 cm dbh (%)[a]	57.17	(27.96)	41.75	(18.76)	51.32	(26.55)	72.17	(18.36)	65.50	(15.00)
Coverage of shrub species (%)[a]	4.50	(0.00)	34.88	(37.33)	4.04	(1.20)	9.50	(9.17)	20.25	(10.50)
Coverage of jack pine, > 1.5 cm dbh (%)[a]	41.67	(22.99)	22.50	(18.57)	44.43	(27.27)	61.90	(20.80)	50.50	(23.85)
Coverage of jack pine, < 1.5 cm dbh (%)	4.21	(9.70)	0.08	(0.15)	0.79	(1.59)	1.11	(1.40)	3.26	(5.83)
Coverage of northern pin oak, > 1.5 cm dbh (%)[a]	0.13	(0.31)	0.00	(0.00)	1.61	(3.45)	5.53	(9.54)	15.19	(11.16)
Coverage of northern pin oak, < 1.5 cm dbh (%)[a]	0.53	(0.75)	0.16	(0.16)	0.57	(0.81)	2.17	(2.61)	2.25	(0.87)
Cov. of *Arctostaphylos uva-ursi* species group (%)[a]	17.70	(33.41)	31.27	(34.57)	7.81	(10.60)	1.59	(0.91)	3.53	(2.90)
Cov. of *Ceonothus ovatus* species group (%)[a]	0.51	(1.25)	0.18	(0.28)	0.02	(0.08)	0.05	(0.11)	23.58	(39.34)
Cov. of *Gaultheria procumbens* species group (%)[a]	0.05	(0.05)	0.07	(0.03)	0.07	(0.13)	0.29	(0.32)	0.55	(0.90)
Cov of *Prunus pensylvanica* species group (%)[a]	0.95	(0.72)	0.50	(0.76)	1.13	(1.39)	0.35	(0.29)	0.05	(0.06)
Cov. of *Rosa blanda* species group (%)[a]	0.16	(0.15)	8.18	(10.85)	1.40	(4.36)	30.19	(37.29)	31.15	(21.45)
Cov. of *Vaccinium angustifolium* species group (%)	41.60	(31.06)	53.85	(22.23)	31.09	(28.56)	25.67	(25.64)	20.90	(22.49)
Coverage of *Cladina* spp. (%)[a]	0.25	(0.27)	0.15	(0.17)	0.23	(0.11)	0.09	(0.10)	0.10	(0.13)
Coverage of moss (%)	0.33	(0.23)	0.03	(0.03)	0.69	(1.54)	0.54	(0.68)	0.16	(0.16)
Coverage of lichen (%)	0.78	(0.63)	0.18	(0.14)	12.31	(24.23)	3.06	(7.08)	0.30	(0.00)
Coverage of woody debris (%)	4.75	(3.84)	1.76	(2.84)	7.20	(7.72)	13.16	(12.03)	3.19	(2.15)
Coverage of bare ground (%)	0.12	(0.14)	0.01	(0.03)	0.09	(0.12)	0.08	(0.11)	0.16	(0.16)

[a] indicates significance at $\alpha = 0.05$

vegetation, are presented in the following section.

Landform-Level Ecosystem Descriptions

LANDFORM I: Low-elevation outwash channels; excessively to somewhat excessively drained, medium to medium-fine sand with a distinct pebble/cobble layer in the upper 50 cm; infertile; *Vaccinium*, *Actostaphylos*.

PHYSIOGRAPHY: Broad (160-1125 m wide), low-elevation post-glacial meltwater drainage channels, located west and southwest of Mack Lake (Figure 4.1). Channel floors are level to very gently sloping (0-3% slope), typically occur 9-15 m below the general land level, and are topographically the lowest features (elev. 350-361 m) in the Mack Lake basin. Channel walls are abrupt and steeply sloping; slopes range from 30-70%.

MICROCLIMATE[2]: Cold air drains out of the high- and low-elevation landforms and collects in the channels (Figure 4.1). As a result, growing season temperatures are colder on average here than anywhere in the Mack Lake basin. Although damaging frosts and below freezing minimum temperatures persist late into the growing season, cold-air drainage to areas outside the study area combined with heat reradiation from the channel walls and air recirculation by prevailing wind currents probably result in somewhat higher minimum temperatures than are observed in closed depressions.

SOIL: The soil is classified as Grayling sand (Typic Udipsamments), and occurs commonly in its gravelly phase (Veatch 1931). Average sand content from 10-150 cm (95.2%) is the second highest observed (Table 4.2). The texture is medium sand, although fine plus very fine sand may make up a significant portion of horizons above 150 cm. Fine plus very fine sand content from 10-30 cm averages 32.9%, the highest of any landform. Gravel and cobbles typically occur in bands or layers of varying thickness. Gravel/cobble content above 150 cm averages 8.7%, the highest of any landform. A distinct gravel/cobble layer occurs in the upper 50 cm; coarse fragments constitute greater than 30% of the volume of the layer. The soil is excessively to somewhat excessively drained.

The pH from 30-150 cm averages 5.7 (Table 4.2). The depth to a field pH of 7.0 or greater (141.3 cm) is the second lowest observed.

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[2] Results of the microclimate study are presented later in this chapter.

VEGETATION: Jack pine height at 16 years averages 379.3 cm, the shortest of any landform (Table 4.3) and the average height of northern pin oak (36.2 cm) is among the shortest observed. The coverage of jack pine (> 1.5 cm dbh) (41.7%) is low; the coverage of northern pin oak (0.1%) is very low. The richness of tree and shrub species (9.5) is relatively low, while the richness of herbaceous and grass species (20.2) is the second highest observed.

Ground-cover vegetation is typically sparse; the coverage of shrub species (4.5%) is among the lowest observed (Table 4.3). Northern pin oak regeneration in the ground cover (< 1 m tall) is rare. The *Arctostaphylos* and *Vaccinium* species groups[3] attain relatively high coverage.

DISCUSSION: The landform constitutes 6.5% of the total area mapped (7,035 ha), and 14.2% of the low-elevation terrain (Figure 4.1). Site conditions are relatively homogenous across the unit, an observation supported by Barnes et al. (1989, Zou et al. 1992) who identified only one landscape ecosystem type (ecosystem type 1; Table 4.1) within the landform.

The landform is noted for extremely poor site conditions resulting from the very cold microclimate, frequent late-season frosts, and infertile soil. Low minimum growing season temperatures and nutrient poor soil are most clearly reflected in short, slow-growing jack pine (Table 4.3). Northern pin oak seedlings and sprouts also exhibit severely stunted growth; new oak shoots and emerging leaves almost always exhibit visible frost damage. Oaks that do persist are often found beneath the canopies of jack pine, which act to moderate the microclimate near the ground by trapping radiated heat (Barnes et al. 1989). The vigor of both jack pine and northern pin oak increases markedly with elevation along the channel walls. Here microclimate is somewhat less severe due to the higher elevation and the reradiation of heat. This observation is consistent with those of Barnes et al. (1989) who observed less vigorous jack pine and northern pin oak growth in ice-block depressions compared to that of adjacent non-depression areas. Kashian (1998) also reported differential growth in pine and oak between high- and low-elevation landforms at Bald Hill East.

The distinct gravel/cobble layer in the upper 50 cm of the soil profile largely distinguishes the channel soils from soils elsewhere within the burn. The layer typically

[3] A description of each ecological species group, including a list of member species, is presented in Appendix A.

consists of assorted gravel mixed with numerous medium and large cobbles 10-20 cm in diameter. The presence of the layer is significant in that it marks a relatively finite period of extremely rapid meltwater flow during which these coarse fragments were transported and subsequently deposited. Although it is difficult to speculate on the details or chronicle the specific events that preceded the formation of this layer, it seems clear that rather extraordinary geomorphic processes were involved.

SIMILAR LANDFORMS: Landform I is ecologically most similar to landform III (Table 4.1). The soil water regime is the same or slightly drier than that of landform III; less silt and clay in the soil profile of landform I is probably compensated for by significantly more fine plus very fine sand (Table 4.2). The water table, a potential source of soil water in landform III, occurs well below the zone of plant rooting in landform I. Landform I is distinguished from landform III by less fertile soil and a colder microclimate. The virtual absence of the *Rosa* species group, which occurs commonly in landform III, is evidence of the nutrient-poor soil (Table 4.3). Markedly shorter, slow-growing jack pines and northern pin oaks reflect both the infertility and the low minimum growing season temperatures.

LANDFORM II[4]: Low-elevation lake margin outwash plain; seasonal standing water; sapric muck over medium sand; variable fertility.

PHYSIOGRAPHY: Level to very gently sloping (< 1% slope), low-elevation (elev. 357-359 m), outwash plain wetland with associated shallow stream drainages and depressions adjacent to Mack Lake (Figure 4.1). The landform is largely limited to a distinct, narrow (< 350 m wide) band of outwash lowland ringing the Mack Lake shoreline. Lakeshore development, however, particularly along the southern shore, has left the unit almost indistinguishable in many locations. This unit is the only wetland landform-level ecosystem within the Mack Lake basin. Isolated upland areas that occur adjacent to Mack Lake (e.g., the Mack Lake campground and vicinity) were mapped as part of this unit.

MICROCLIMATE: Although growing season temperatures are likely colder on average here than in the landforms of the high-elevation terrain, the proximity of the unit to

[4] Plot sampling was not conducted in Landform II due to its limited extent and wetland characteristics, which render it unsuitable for Kirtland's warbler occupancy. The above description is based on reconnaissance and random point sampling of physiography, soil, and vegetation.

Mack Lake may have a local moderating affect, resulting in less extreme average temperatures, and less severe and less frequent frosts than might be otherwise expected.

SOIL: The soil is variable. Houghton muck, and to a lesser extent, Newton sand are the dominant soil series (Veatch 1931). Typical surface soils (upper 20-30 cm) consist of a layer of sapric muck derived from woody and herbaceous plant tissues. The subsurface layers are deep deposits of medium to medium-fine sand. The water table is within 50 cm of the surface throughout the year and is at or above the surface in the spring and during wet periods. The pH at the surface averages 4.5. The pH at 40 cm is circumneutral (pH 7.0).

VEGETATION: This is the only landform in which jack pine is not the dominant tree species. Indeed, jack pine and northern pin oak are conspicuously rare in all stand layers. Trees of overstory and understory size do occur commonly on the drier microsites, but they are largely absent from the wetter drainages and depressions. The dominant overstory tree of the drier microsites is white pine; paper birch is a common associate. Wet-site overstory codominants include black spruce, tamarack, red maple, and trembling aspen. The dominant understory tree species are speckled alder and willow. Understory associates include black spruce, tamarack, and nannyberry.

The diversity of species in the ground cover is high due to the abundance of available microsites (e.g., pits, mounds, pools, mudflats, etc.). Dominant ground-cover shrubs include *Alnus rugosa*, *Cornus foemina, Spiraea alba, Vaccinium myrtilloides, Chamaedaphne calyculata*, and *Ledum groenlandicum*. Common herbaceous dominants include *Carex stricta*, *Onoclea sensibilis*, *Trientalis borealis*, *Coptis trifolia*, *Scirpus cyperinus,* and *Sphagnum* spp.

DISCUSSION: The landform constitutes 1.7% of the total area mapped (7,035 ha), and a relatively minor portion (3.7%) of the low-elevation terrain (Figure 4.1). Although landscape ecosystem types have not been formally distinguished within the landform, site heterogeneity is particularly high due to 1) the variable microtopography, 2) the variable substrate (i.e., mineral vs. organic), and 2) the variable water-table depth.

Site quality is largely dependent on water-table depth and local hydrology. Site conditions range from very infertile stagnant pools and acid mounds supporting typical bog vegetation to slightly fertile wet mudflats dominated by a diverse assemblage of grasses and sedges.

SIMILAR LANDFORMS: Landform II is ecologically unique. Wetland conditions, including a high water table, seasonal standing water, and an organic (sapric muck) surface soil, distinguish the unit from all other landform-level ecosystems. The wet and often saturated conditions are clearly reflected in the virtual absence of jack pine and the presence of wetland trees and shrubs in all stand layers.

LANDFORM III: Low-elevation pitted-outwash plain with water table influence; somewhat excessively to excessively drained loamy sand to sand with gravel and cobbles; infertile; *Arctostaphylos*, *Rosa*.

PHYSIOGRAPHY: Level to gently sloping (0-5% slope), low-elevation (elev. 359-363 m), pitted-outwash plain surrounding and located within 350 m of Mack Lake. The unit forms a concentric band around the lake up to 550 m wide (Figure 4.1). The otherwise level outwash surface is sparsely pitted with shallow (< 2.0 m deep) remnant ice-block depressions. Additionally, along the northern and eastern borders of the landform, the surface was eroded in several locations by intermittent glacial meltwater streams, leaving behind a series of narrow abandoned drainages.

MICROCLIMATE: Growing season temperatures are colder on average here than in the landforms of the high-elevation terrain. Frosts occur throughout the growing season, but tend to be most frequent and severe in drainages and depressions where cold air is trapped.

SOIL: The soil is classified as Grayling sand, and occurs commonly in its gravelly phase (Veatch 1931). The texture ranges from medium to medium-coarse sand; medium (65.3%) and coarse (13.5%) sand content (10-150 cm) are the highest of all landforms (Table 4.2). The texture of the upper 30 cm may approach loamy sand due to the relatively high silt and clay content. Gravel and cobbles occur frequently in bands or layers of varying thickness; a distinct gravel/cobble layer exists between 120 and 140 cm. Gravel/cobble content above 150 cm (8.2%) is the second highest observed. The water table occurs at an average depth of 390 cm, significantly shallower than all other upland landforms (Table 4.2). The soil is excessively to somewhat excessively drained.

The pH from 30-150 cm averages 6.1, the most basic of any landform (Table 4.2). The depth to a field pH of 7.0 or greater (120.3 cm) is the shallowest observed.

VEGETATION: The average height of jack pine at 16 years (439.5 cm) is moderate compared to other landforms (Table 4.3). Northern pin oak height averages 26.8 cm, the shortest of any landform. Jack pine coverage (> 1.5 cm dbh) (22.5%) is low; northern pin oak coverage (0.0%) is nonexistent. Species richness across stand structural layers is relatively high. The number of tree and shrub species averages 10.5, and the number of herbaceous and grass species averages 24.5, the highest of any landform.

Ground-cover vegetation is abundant; the coverage of shrub species averages 34.9%, the highest of any landform (Table 4.3). Northern pin oak regeneration in the ground cover (< 1 m tall) is rare. The *Arctostaphylos* species group attains its highest coverage here. The *Rosa* species group is also characteristic of the landform.

DISCUSSION: The landform constitutes 4.4% of the total area mapped (7,035 ha), and 9.7% of the low-elevation terrain (Figure 4.1). Although landscape ecosystem types have not been formally distinguished within the unit, reconnaissance and plot sampling suggest that the diversity of site conditions across the landform is relatively low.

The soil has probably the greatest water and nutrient holding capacity of any upland landform in the low-elevation terrain. Although the soil is relatively infertile, the high silt and clay content, particularly above 30 cm, slows drainage and limits nutrient loss. Bands of gravel interspersed with numerous large cobbles (ca 15 cm) may also impede drainage temporarily. In addition, although there is some question as to whether or not jack pine roots are absorbing water from the water table, fluctuation of the water table during the spring may result in the upward transport of nutrients (e.g., Ca^{++}) from the calcarious parent material below. This fluctuation may explain, at least in part, why the depth to a pH of 7.0 or greater (120.3 cm) is the shallowest observed. The moister, more fertile conditions are reflected in the relatively high coverage of the *Rosa* species group, which is virtually absent elsewhere in the low-elevation terrain (Table 4.3). A deep rooting zone (147.0 cm; Table 4.2) and high ground-cover species richness are further evidence of water and nutrient availability.

Despite the availability of water and nutrients, the rarity and very slow growth of northern pin oak is largely due to the cold microclimate. Oak seedlings and sprouts, where present, are severely stunted and show signs of repeated frost damage; oak stems average just 26.8 cm tall as compared to landform IV where stems average 176.5 cm tall (Table 4.3). The growth of jack pine also may be curtailed, to some extent, by the cold microclimate. Despite moister, more fertile soil, average jack pine height (439.5 cm) does not differ significantly from that of landform IV (441.3 cm) which is warmer but yet has drier, less fertile soil.

SIMILAR LANDFORMS: Landform III is most similar to Landform IV (Table 4.1). It is distinguished from landform IV by moister, more fertile soil, and a slightly colder microclimate. The soil has a greater capacity to hold water and nutrients because of the higher silt and clay content. A deeper rooting zone is evidence of greater available soil water; a higher pH reflects greater available nutrients. The proximity of the water table to the surface may also augment soil water and nutrient availability. The presence of the *Rosa* species group in landform III is evidence of the moister, more fertile conditions than in landform IV.

LANDFORM IV: Low-elevation pitted-outwash plain; excessively to somewhat excessively drained, deep, acid medium to medium-fine sand; very infertile to infertile; *Prunus*.

PHYSIOGRAPHY: Broad, level to gently sloping (0-6% slope), low-elevation (elev. 366-372 m), pitted outwash plain occupying the central portion of the Mack Lake basin (Figure 4.1). In general, the outwash plain surface slopes gradually in all directions toward Mack lake; the highest elevations typically occur along its outer perimeter. Isolated areas of higher elevation also occur in the form of narrow outwash terraces located between the prominent glacial meltwater drainage channels (Figure 4.1). The majority of the outwash plain is pitted with remnant ice-block depressions of varying size; depressions range from 1.5 to 6.0 m deep.

MICROCLIMATE: Cold air drains out of the high-elevation terrain to the south, and settles in the low-elevation terrain surrounding Mack Lake (Figure 4.1). As a result, growing season temperatures are colder on average here than in the landforms of the high-elevation terrain. Frosts occur throughout the growing season, but tend to be most frequent and severe in closed depressions and valleys where cold air is trapped.

SOIL: The soil is classified as Grayling sand (Veatch 1931). Sand content from 10-150 cm averages 95.7%, the highest of any landform (Table 4.2). The texture is medium sand, although fine sand may make up a significant portion (ca. 25%) of horizons above 150 cm. Bands and lamellae of fine texture (loamy sand to sandy clay loam; Graycalm and

Montcalm soil series) are rare. Silt and clay content from 10-150 cm averages 4.3%, the lowest of any landform (Table 4.2). The soil is excessively to somewhat excessively drained.

The pH from 30-150 cm averages 5.2, the most acid of any landform (Table 4.2). The depth to a field pH of 7.0 or greater (235.4 cm) is among the deepest observed.

VEGETATION: The average height (at 16 years) and coverage (> 1.5 cm dbh) of jack pine (441.3 cm, 44.4%) and northern pin oak (176.5 cm, 1.6%) are moderate compared to other landforms (Table 4.3). Species richness across stand structural layers is low. The number of tree and shrub species averages 9.3, the lowest of any landform; the number of herbaceous and grass species (15.1) is among the lowest observed.

Ground-cover vegetation is typically sparse; the coverage of shrub species averages 4.0%, the lowest of any landform (Table 4.3). The coverage of lichen species (12.3%) is high, and in some areas the ground-cover vegetation is limited entirely to a thin mat of lichens and mosses. Northern pin oak regeneration in the ground cover (< 1 m tall) is rare to locally common. The *Prunus* species group attains its highest coverage here.

DISCUSSION: The landform constitutes 32.9% of the total area mapped (7,035 ha), and includes a major portion (72%) of the low-elevation terrain (Figure 4.1). Although four landscape ecosystem types are recognized within the unit (Barnes et al. 1989, Zou et al. 1992; Table 4.1), the diversity of site conditions is relatively low due to the dominance of ecosystem type 2.

The landform is noted for its dry, infertile to very infertile soil and relatively cold microclimate. Short, slow growing jack pine, low species richness, and sparse ground-cover vegetation all reflect the low water and nutrient holding capacity of the excessively drained, strongly acid, Grayling sand that dominates the unit (Figure 4.3). These findings are consistent with those of Shetron (1972) who described Grayling sand as the poorest soil for jack pine in northern Lower Michigan. Site productivity is further influenced by the cold microclimate. Northern pin oak is particularly susceptible to damage from freezing temperatures and late season frosts (Barnes et al. 1989). Young oak seedlings and sprouts, where present, tend to be stunted and new shoot growth commonly shows signs of frost damage. The slow growth of jack pine, particularly in ice-block depressions, is also attributable in part to the low minimum growing season temperatures (Barnes et al. 1989).

In addition to the influence of site factors, fire has played a major role in shaping the composition and abundance of the vegetation, particularly in the ground cover. For example, during the 1980 wildfire, some areas were burned so severely that the organic soil surface horizons were virtually destroyed. As a result, the ground-cover vegetation on these most infertile sites is often limited to a thin layer of lichen and moss. Pearsall et al. (1995) described a similar pattern of vegetation in the fire-prone ecosystems of the University of Michigan Biological Station in northern Lower Michigan.

The high coverage of the *Prunus* species group compared to other landforms is difficult to explain. Previous research by Barnes et al. (1989) identified this group as characteristic of the moister, more fertile uplands of the high-elevation terrain. This apparent inconsistency may reflect the very shade-intolerant character of most members of the group. Conditions in the high-elevation terrain have become increasingly unsuitable to shade-intolerant species as the crowns of faster-growing jack pines have rapidly closed in on each other. Thus, high coverage of the *Prunus* group here and elsewhere in the low-elevation terrain (Table 4.3) is perhaps more an indicator of current light availability rather than of soil water or nutrient regimes.

SIMILAR LANDFORMS: Landform IV is ecologically most similar to landform III (Table 4.1). The units occur adjacent to each other, occupy similar low-elevation topographic positions, and have similar microclimates. The primary difference is that the soil of landform IV has a lower water and nutrient holding capacity. The proportion of silt and clay in the soil (10-150 cm) is half that of landform III (4% vs. 8%), and the pH from 30-150 cm is significantly more acid (5.2 vs. 6.1) (Table 4.2). In addition, the water table occurs at a depth well below the zone of plant rooting, whereas in landform III the water table occurs within 4 m of the surface – well within the rooting zone of jack pine and oak. The drier, more infertile conditions are evidenced by the virtual absence of the *Rosa* species group, which does occur commonly in landform III (Table 4.3).

LANDFORM V: High-elevation terraced outwash plains; excessively drained medium and medium-fine sand to somewhat excessively drained loamy sand interspersed with bands of fine texture; variable fertility; *Rosa*.

PHYSIOGRAPHY: Broad, level to gently sloping (0-5% slope), high-elevation (elev. 369-384 m), terraced outwash plains occupying part of the southern and eastern portion of the Mack Lake basin (Figure 4.1). Terrace elevation increases with distance from Mack Lake; the highest elevations typically occur along the southwestern perimeter of the landform. Isolated areas of higher elevation (e.g., small outwash terraces) are common. The outwash plains are pitted with several large and scattered small remnant ice-block depressions; depressions range from 3 to 15 m deep.

MICROCLIMATE: Due to the elevated topographic position, growing season temperatures are significantly warmer on average here than in the landforms of the low-elevation terrain. Late season frosts are rare; however, below freezing minimum temperatures are not uncommon in ice-block depressions where cold air is trapped.

SOIL: The soil is highly variable. Graycalm sand (Alfic Udipsamments), and to a lesser extent, Montcalm loamy sand (Eutric Glossoboralfs) are the dominant soil series. Grayling and Rubicon (Entic Haplorthods) sands are also present. Sand content from 10-150 cm averages 91.2%, the lowest of any landform (Table 4.2). The texture ranges from medium to occasionally loamy sand; medium-fine sand is most common. Layers of sand are typically interspersed with bands and lamellae of fine-texture (Graycalm and Montcalm series). Total accumulated banding (loamy sand to sandy clay loam) above 400 cm averages 18.0 cm, significantly higher than all other landforms. Average silt and clay content from 10-150 cm (9.3%) is the highest observed[5]. The soil is excessively to well drained.

The pH from 30-150 cm averages 5.6 (Table 4.2). The pH of fine-textured bands is often significantly higher than that of the surrounding sands; band pH ranges from 6.5 to 8.0. The depth to a field pH of 7.0 or greater (bands not included) (209.1 cm) is among the deepest observed.

VEGETATION: The average height of both jack pine (515.5 cm) and northern pin oak (372.6 cm) at 16 years are among the tallest observed (Table 4.3). Coverage of jack pine

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[5] Average silt and clay content does not reflect the amount of silt and clay contained in bands or lamallae of fine-texture less than 2 cm thick. As a result, actual silt and clay content is higher than reported.

(> 1.5 cm dbh) averages 61.9%, the highest of any landform; northern pin oak coverage (5.5%) is the second highest observed. Species richness varies with stand structural layer. The richness of tree and shrub species (12.7) is high, while the richness of herbaceous and grass species (14.1) is among the lowest observed.

Ground-cover vegetation is variable in both composition and distribution. Northern pin oak regeneration in the ground cover (< 1 m tall) is abundant (Table 4.3). The *Rosa* species group attains its highest coverage here.

DISSCUSSION: The landform constitutes 30.9% of the total area mapped (7,035 ha), and includes a considerable portion (56.7%) of the high-elevation terrain (Figure 4.1). Five constituent landscape-ecosystem types are recognized (Barnes et al. 1989; Table 4.1). The diversity of site conditions is relatively high compared to other Mack Lake basin landforms due in part to the number of distinct ecosystem types present but also due to the fine-scale mosaic in which these ecosystem types occur.

The soil is typically moister and more fertile than that of other landforms due to 1) the high content of very-fine sand, silt, and clay (10-150 cm), and 2) the widespread occurrence of fine-textured-soil banding (Figure 4.2). Fine-textured banding, which contributes significantly to the water and nutrient holding capacity of the soil (White and Wood 1958, Hannah and Zahner 1970, Shetron 1972), is associated, to a varying degree, with three of the five landscape ecosystem types present (types 8, 9, 10; Table 4.1). As a result, the growth of jack pine and northern pin oak in these ecosystem types is noticeably faster (as evidenced by taller trees; Figure 4.3) than in those types where textural bands are rare or absent. This observation is consistent with the findings of Shetron (1972) who reported significantly increased jack pine growth on banded soils of the Graycalm and Montcalm series compared to unbanded soils of the Grayling series. High tree and shrub species richness and high coverage of the *Rosa* species group (Figure 4.3) provides further evidence of the availability of water and nutrients. The unexpectedly low species richness in the groundcover (i.e., herbaceous and grass species) in spite of the moister, more fertile conditions is very likely a product of insufficient light resulting from the dense jack pine-oak cover.

The site quality of the landform is further increased by the warm microclimate. Compared to landforms in the low-elevation terrain, significantly higher minimum growing season temperatures and less frequent, less severe frosts likely contribute, in part, to the observed vigor of both jack pine and northern pin oak. However, because soil water and nutrient status is confounded with elevation (the soils of high-elevation landforms tend to be moister and more fertile), the effect of temperature alone on the growth of pine and oak is difficult to quantify. Nevertheless, the abundance of well established oak seedlings and sprouts (outside of ice-block depressions) (Figure 4.3), and the virtual absence of visible frost damage on new shoots and leaves points toward the significance of the microclimatic influence.

SIMILAR LANDFORMS: Landform V is ecologically most similar to landform VI (Table 4.1). The landforms occur adjacent to each another, occupy similar high-elevation topographic positions, and have similar microclimates. The primary difference relates to the physical geomorphic processes that accompanied their formation. The parent material of landform V was deposited by glacial meltwater streams in the form of an outwash plain, whereas the parent material of landform VI was deposited following the slow-melting of buried ice blocks which produced the distinct kettle-kame topography of ice-contact terrain. As a result, landform V is much less rugged, lacking the extremely hilly, heterogeneous topography associated with landform VI. In addition, the soils of landform V are generally moister and slightly more fertile than the soils of landform VI due to the higher content of fine sand, silt, and clay, and the greater frequency of fine-textured-soil banding. The occurrence of ecological species groups on the two landforms is similar; the virtual absence of the *Ceonothus* species group in landform V reflects a soil moisture regime that is generally moister and spatially less variable than that of landform VI where the group is abundant (Figure 4.3).

LANDFORM VI: High-elevation ice-contact terrain; excessively to somewhat excessively drained, medium to fine sand; slightly infertile; *Ceonothus*, *Gaultheria*.

PHYSIOGRAPHY: Abruptly hilly, high elevation (elev. 373-390 m), ice-contact terrain. Moderately steep (3-30% slope) kamic hills and ridges dominate; kames are regularly interspersed with deep kettle (ice-block) depressions (3 to 15+ m deep).

MICROCLIMATE: The ice-contact uplands (i.e., kamic hills and ridges) are characterized by some of the most elevated topography in the Mack Lake basin. As a result, growing season temperatures are significantly warmer on average here than in the landforms of the low-elevation terrain. Although late-season frosts are rare, below freezing minimum temperatures are common in the bottoms of kettle depressions where cold air is trapped.

SOIL: The soil is variable. Rubicon sand, and to a lesser extent, Graycalm sand represent the dominant soil series. Sand content from 10-150 cm averages 95.4% (Table 4.2). The texture is medium sand, although fine plus very fine sand may make up a significant portion (ca. 25%) of horizons above 150 cm. Medium sand content from 10-150 cm (64.3%) is the second highest observed. Layers of sand may be interspersed with bands and lamellae of fine-texture (Graycalm series). Total accumulated banding (loamy sand to sandy clay loam) above 400 cm averages 7.0 cm. The soil is excessively to somewhat excessively drained.

The average pH from 30-150 cm (5.5) is among the lowest observed (Table 4.2). The depth to a field pH of 7.0 or greater averages 250.3 cm, the deepest of any landform.

VEGETATION: The average height of jack pine (517.4 cm) and northern pin oak (513.3 cm) at 16 years exceeds that of all other landforms (Table 4.3). The coverage of jack pine (> 1.5 cm dbh) (50.5%) is the second highest observed; northern pin oak coverage averages 15.2%, the highest of any landform. Species richness varies with stand structural layer. The richness of tree and shrub species averages 12.8, the highest of any landform, whereas the richness of herbaceous and grass species (14.8) is relatively low.

Ground-cover vegetation is typically abundant; the coverage of shrub species (20.3%) is the second highest observed (Table 4.3). Northern pin oak regeneration in the ground cover (< 1 m tall) is the most abundant of any landform (Table 4.3). The *Ceonothus* and *Gaultheria* species groups attain their highest coverage here.

DISCUSSION: The landform constitutes 23.0% of the total area mapped (7,035 ha), and 43.3% of the high-elevation terrain (Figure 4.1). Two very distinct landscape ecosystem types are recognized within the landform, i.e., kettle (ice-block) depressions (type 10) and kamic hills and ridges (type 11) (Barnes et al. 1989; Table 4.1). The diversity of site conditions, however, is much higher than the number of ecosystem types would suggest due to the variability in physiography (i.e., slope, aspect, parent material), microclimate, and soil associated with individual kettles and kames.

Soil water and nutrient availability are among the highest of any Mack Lake burn landform due largely to the occurrence of fine-textured-soil banding. The observed vigor of both jack pine and northern pin oak (as evidenced by tree height data; Table 4.3) reflects, in part, the marked influence of texture bands on soil water and nutrient regimes. However, because texture bands are somewhat less prevalent, often occur deep in the soil profile, and are interspersed in a soil matrix that is typically sandier than elsewhere in the high-elevation terrain, soil water status, particularly nearer the surface, is highly variable. High coverage of the both the *Rosa* (dry to moderately moist soils) and the *Ceonothus* (very dry to dry soils) species groups (Barnes et al. 1989; Appendix A) evidence the variability in available soil water at or near the surface (Table 4.3).

The warm microclimate almost certainly contributes to the overall site quality of the landform. The observed vigor of both jack pine and northern pin oak (outside of kettle depressions) reflects, in part, the higher minimum growing season temperatures and less frequent, less severe frosts which distinguish the microclimate of the ice-contact uplands from that of landforms in the low-elevation terrain. In particular, the prolific growth of oak stems in the understory, the abundance of well established oak seedlings and sprouts in the ground cover, and the virtual absence of visible frost damage on new oak shoots and leaves provides the most clear evidence of the microclimate influence on site quality (Table 4.3).

SIMILAR LANDFORMS: Landform VI is ecologically most similar to landform V (Table 4.1). Rugged, hilly kettle and kame topography distinguishes the ice-contact terrain of landform VI from the broad, level outwash plains of landform V. The soils of the ice-contact uplands are drier and somewhat less fertile than the soils of landform V due to the higher sand content (i.e., less silt and clay) and the less frequent occurrence of fine-textured-soil banding. The drier conditions associated with the sandier kamic hills and ridges are reflected in the high coverage of the *Ceonothus* species group which is virtually absent in landform V.

Multivariate Analyses of Landform-Level Ecosystems

Considerable variation was found among the five landform-level ecosystems based on a principal components analysis of 16 physiographic and soil variables (Table 4.4). The positions of the five landforms are reasonably well-separated in the plane of the first two principal components (Figure 4.2). Although, nearly all the landforms grade into one another, the principal component plot reveals that each unit has a more or less distinct region of concentration in the ordination space. Additionally, the relative positions of the landforms are supported by field observations. First, landforms that are most distinct in their physiographic and/or soil attributes (landforms 1, 3, and 4) exhibit the greatest degree of separation in the ordination space (Figure 4.2). Conversely, landforms most similar in their physiographic and/or soil characteristics generally occur clustered near to one another (landforms 4, 5, and 6). Second, landforms exhibiting the most homogenous site conditions (landforms 1 and 3), i.e., having the lowest within-landform ecological diversity and the fewest constituent landscape-ecosystem types (Table 4.1), exhibit the most tightly clustered data points. As the diversity of constituent ecosystem-types increases (landforms 4 and 5), so increases the degree of cluster dispersion (Figure 4.2).

The first 3 principal components were found to account for 32, 53, and 66% of the cumulative variance in the data set (Table 4.4). Variables loading heavily on the first principal component include accumulated banding (0-150 cm), total accumulated banding, depth to banding, and silt and clay (10-150 cm). Thus, the primary gradient extracted in the principal component analysis is related to soil water and nutrient availability. Landform-level ecosystems having relatively moist, fertile soils with considerable fine-textured-soil banding (landforms 5 and 6) are distributed along the positive portion of the first axis, while

Table 4.4 Comparison of relative variation among five landform-level ecosystems as determined by a principal components analysis of 16 physiographic and soil variables; Mack Lake burn, Oscoda Co., northern Lower Michigan.

Principal Component	1	2	3
Eigenvalue	5.1	3.4	2.1
Cumulative % variance	32	53	66
Variable		**Coefficient**	
Elevation	0.49	-0.39	-0.26
Slope, %	0.11	-0.05	-0.96
Maximum slope, %	0.06	-0.04	-0.96
Sand,10-30 cm	-0.53	-0.55	-0.11
Coarse sand, 10-30 cm	-0.43	0.70	-0.12
Very coarse + coarse sand, 10-30 cm	-0.45	0.67	-0.06
Silt, 10-150 cm	0.77	0.43	0.02
Silt + clay, 10-150 cm	0.78	0.43	0.01
Gravel and cobbles, 0-150 cm	-0.24	0.67	0.10
Accumulated banding, 0-150 cm	0.89	0.07	0.16
Total accumulated banding	0.87	0.15	0.11
Depth to lamellae, < 2 cm thick	-0.70	0.09	0.11
Depth to banding, > 2 cm thick	-0.87	0.06	0.05
Laboratory pH, 30-150 cm	0.12	0.68	0.03
Depth to maximum rooting	0.01	0.56	-0.33
Depth to water table	0.26	-0.62	0.13

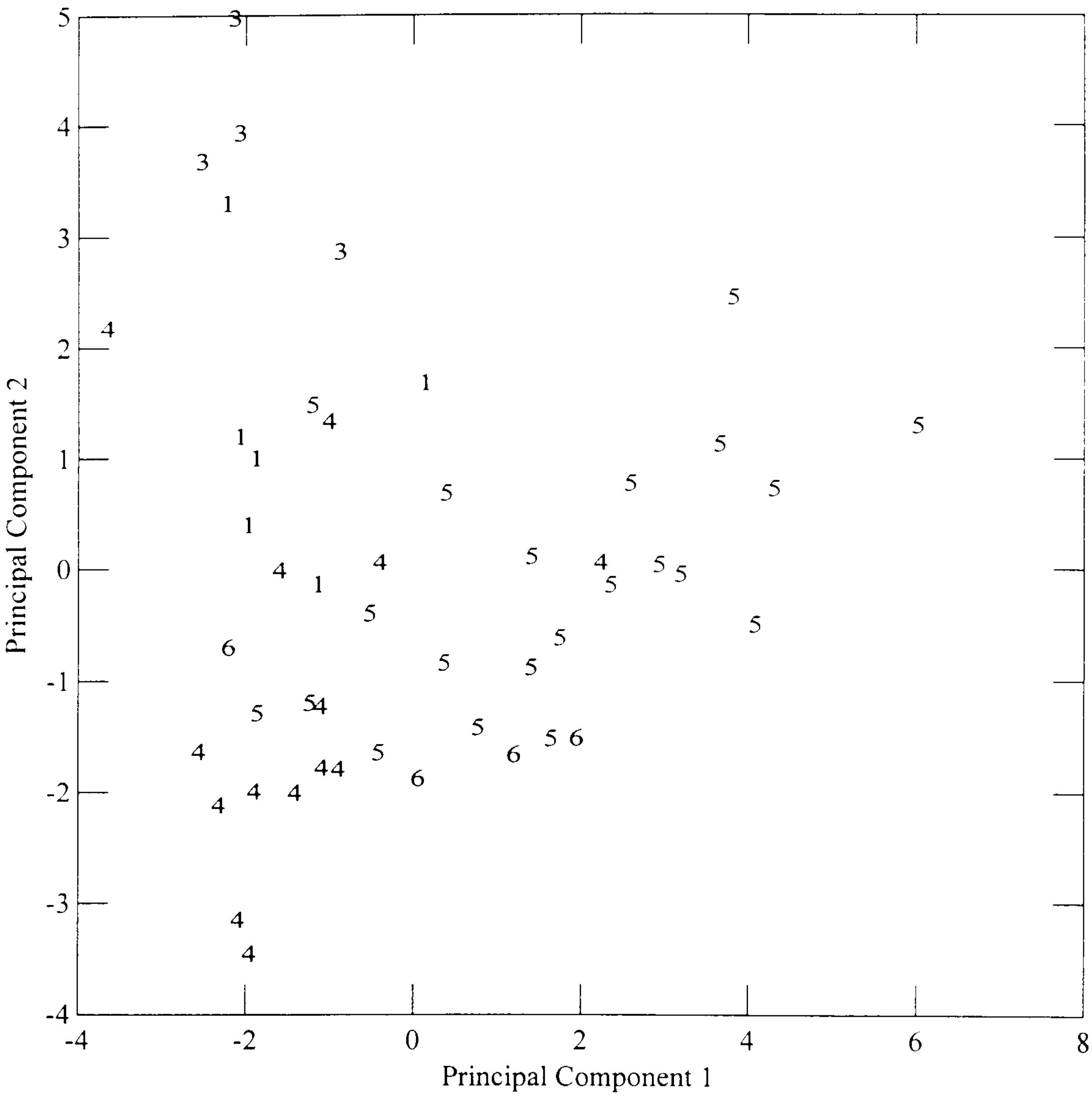


Figure 4.2. Ordination of 49 sample plots of 5 landform-level ecosystems along the first 2 principal components of an analysis of 16 physiographic and soil variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Numbers identify landform-level ecosystems.

those landforms with very dry, very infertile soils and little or no banding (landforms 1 and 4) are distributed along the negative portion (Figure 4.2). Variables loading heavily on the second principal component include the soil texture variables of coarse sand (10-30 cm), very coarse + coarse sand (10-30 cm), gravel and cobbles (0-150 cm) and depth to the water table, as well as the soil reaction variable of laboratory pH (30-150) (Table 4.4). Hence, the second gradient extracted in the analysis also may be interpreted as soil water- and nutrient-related. Landforms with soils dominated by coarse-textured sand, gravel, and cobbles, a slightly to moderately acid pH, and a relatively high water table (landforms 1 and 3) occur along the positive portion of the second axis (Figure 4.2). Conversely, those landforms with soils lacking significant coarse fragments and having a moderately to strongly acid pH (landforms 4 and 6) occur near the origin and along the negative portion of the second axis.

A discriminant analysis, based on 14 physiographic and soil variables (Table 4.5), revealed the marked distinctness of the 5 landform-level ecosystems attributable to site factors. In general, the positions of the five landforms are very well-separated in the plane of the first two canonical variates (Figure 4.3). The relationships among the landforms in Figure 4.3 are supported by field observations. Minor overlap is observed between low-elevation landforms I and III which occur near to one another in the landscape (Figure 4.1) and share very similar, coarse-textured parent materials. Landforms V and VI, which occupy similar high-elevation topographic positions and have similar soil attributes (i.e., finer-textured, banded soils), also exhibit minor overlap. Landform IV, characterized by deep medium sands, virtually no coarse fragments, and little or no fine-textured banding, is clearly separated from the others (Figure 4.3). The overall misclassification rate for the discriminant function based on the set of physiography and soil variables was 6%; the jackknifed

Table 4.5 Comparison of relative variation among five landform-level ecosystems as determined by a canonical variates analysis of 14 physiographic and soil variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Coefficients ≥ 0.43 are significant with $p < 0.05$.

Canonical Variate	1	2	3
Eigenvalue	9.7	1.9	1.0
Cumulative % variance	74	88	96
Variable		**Correlation Coefficient**	
Elevation	-0.90	0.30	0.15
Slope, %	-0.10	0.19	0.21
Transformed aspect	-0.30	-0.05	-0.01
Sand,10-30 cm	0.16	0.53	-0.17
Very fine sand, 10-30 cm	-0.08	-0.34	-0.21
Medium sand, 10-30 cm	0.01	0.08	0.34
Very fine sand, 10-150 cm	-0.16	-0.14	-0.14
Medium sand, 10-150 cm	0.19	0.21	0.19
Coarse sand, 10-150 cm	0.27	-0.17	0.49
Very coarse sand, 10-150 cm	0.06	0.06	0.22
Silt, 10-150 cm	-0.23	-0.46	0.29
Gravel and cobbles, 0-150 cm	0.48	-0.35	0.16
Depth to banding, > 2 cm thick	0.68	0.45	0.04
Total accumulated banding	-0.46	-0.36	0.11

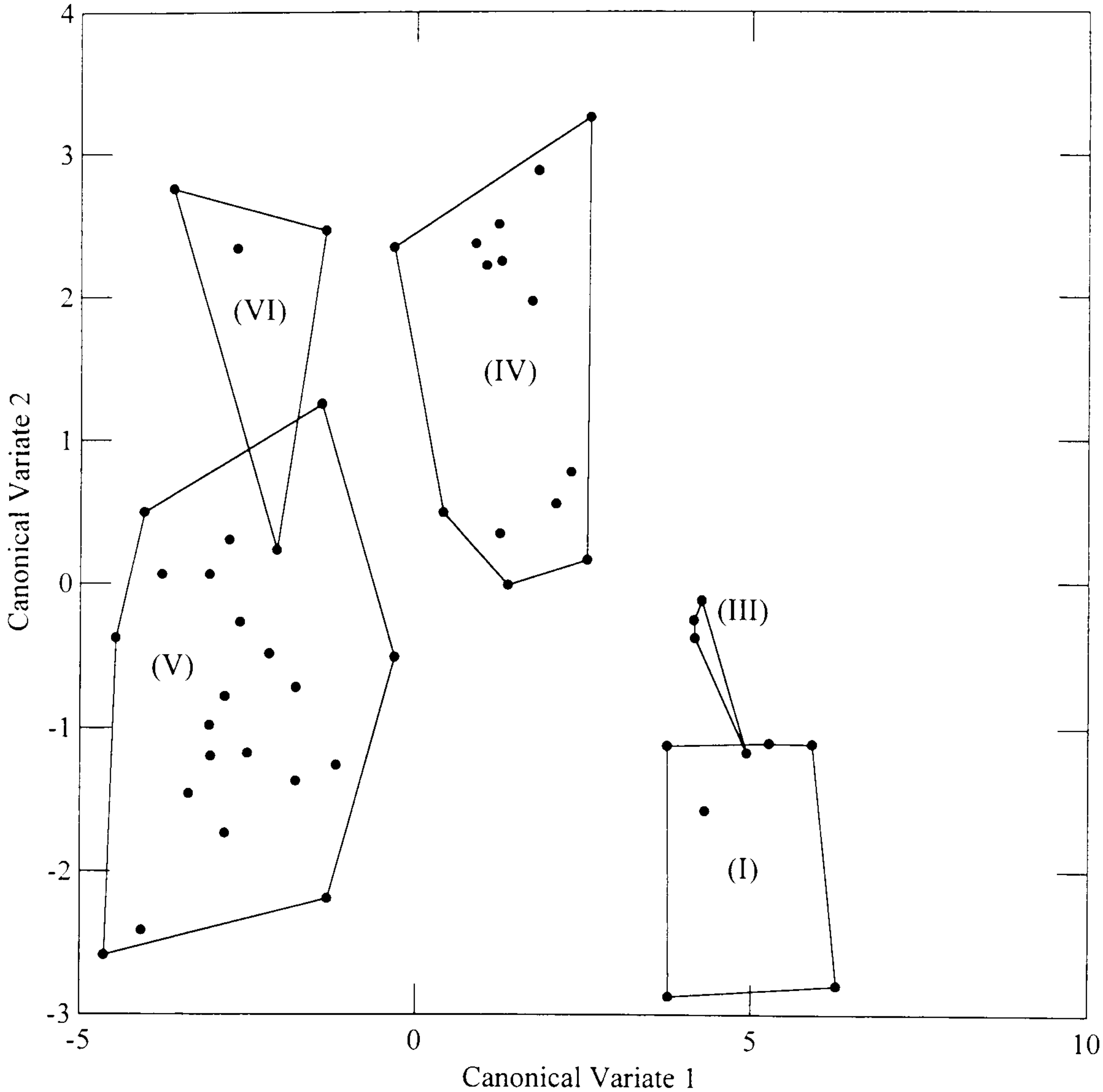


Figure 4.3. Ordination of 49 sample plots of 5 landform-level ecosystems along the first 2 canonical variates of an analysis of 14 physiographic and soil variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Roman numerals in parentheses identify landform-level ecosystems.

misclassification rate was 20%.

The first three canonical variates were found to account for 74, 88, and 96% of the cumulative variance in the physiography-soil variable set (Table 4.5). Average elevation exhibited a very high negative correlation with the first canonical variate (CV), whereas depth to banding exhibited a high positive correlation. Landforms I and III, distributed along the positive portion of the first CV axis, occupy low-elevation positions where fine-textured banding, when present, generally occurs deep in the soil profile. Conversely, landforms V and VI, distributed along the negative portion of the first CV axis, occupy high elevation positions where banding occurs throughout the soil profile. The second canonical variate had a high positive correlation with sand (10-30 cm) and a high negative correlation with silt (10-150). Landforms with the greatest ratio of sand to silt (landforms IV and VI) occur along the positive portion of the second CV axis, while landforms with the greatest ratio of silt to sand (landforms III and V) occur along the negative portion (Figure 4.3).

A second discriminant analysis, derived from a subset of nine ground-cover species variables (Table 4.6), revealed the distinctness of the five landform-level ecosystems attributable to biotic factors. Four of the five landforms (landforms I, III, V, and VI) appear as distinct ecological units when plotted in the plane of the first two canonical variates (Figure 4.4). The landforms are not as clearly separated in the ordination space based on ground-cover species as they were by physiography and soil. Landforms III and VI, well-separated from the remaining units and from one another, exhibit perhaps the greatest ground-cover diversity as measured by the range of ecological species groups present and the marked dominance of shrubby vegetation. Although landforms I and V also show clear separation from one another, both share a fair a amount of overlap with landform IV. The

Table 4.6 Comparison of relative variation among five landform-level ecosystems as determined by a canonical variates analysis of nine ground-cover vegetation variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Coefficients ≥ 0.43 are significant with $p < 0.05$.

Canonical Variate	1	2	3
Eigenvalue	3.1	1.1	0.1
Cumulative % variance	49	81	98
Variable	**Correlation Coefficient**		
Number of northern pin oak clumps, < 1 m	0.17	0.87	0.07
Number of shrub species	0.12	0.47	-0.32
Number of grass species	0.43	-0.66	-0.33
Coverage of jack pine, < 1.5 cm dbh	0.09	-0.01	0.25
Coverage of shrub species	0.59	-0.01	-0.43
Coverage of *Arctostaphylos* species group	0.29	-0.72	0.08
Coverage of *Rosa* species group	0.32	0.62	-0.39
Coverage of *Ceonothus* species group	0.46	0.29	0.40
Coverage of *Gaultheria* species group	0.19	0.50	-0.12

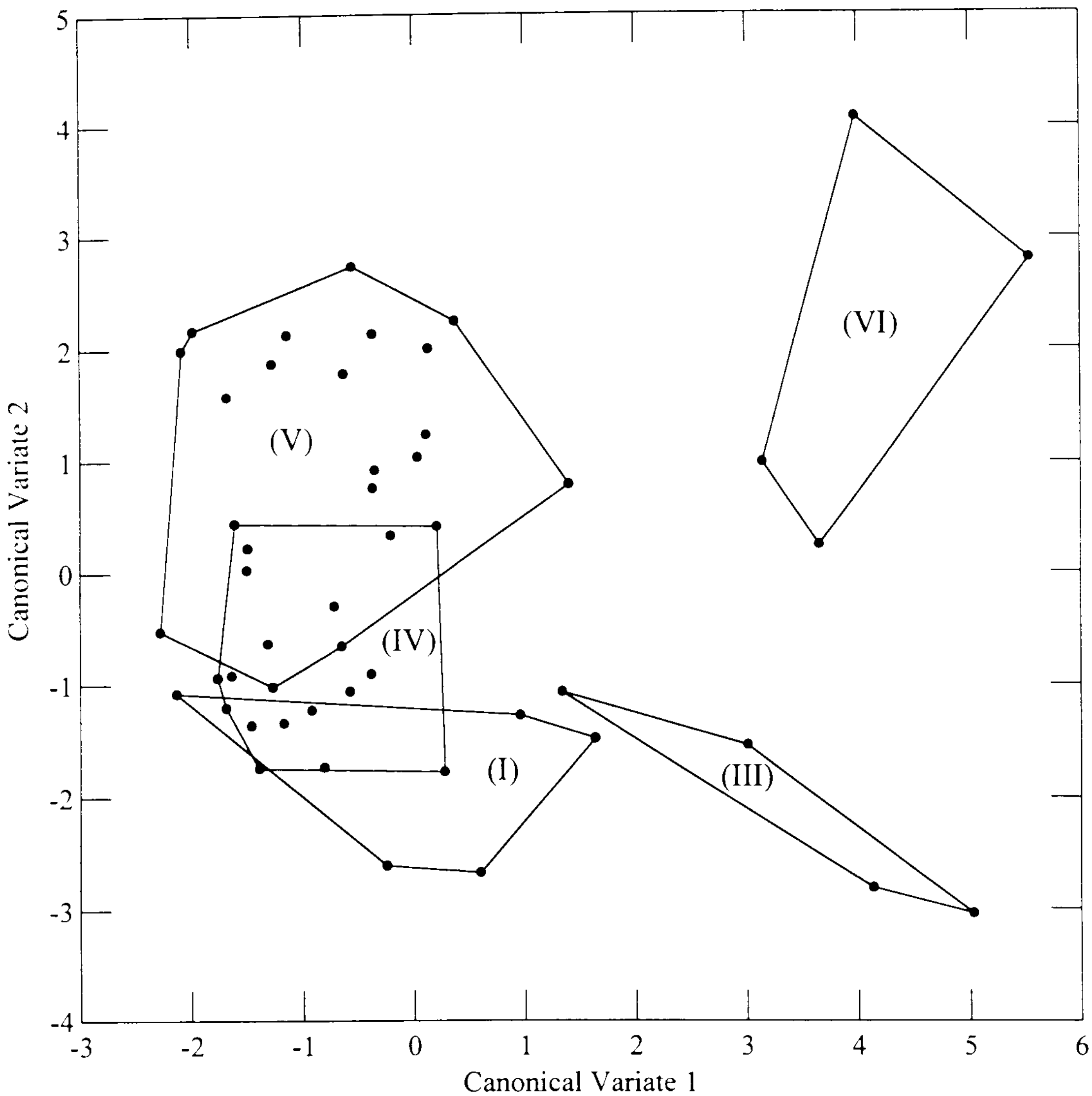


Figure 4.4. Ordination of 49 sample plots of 5 landform-level ecosystems along the first 2 canonical variates of an analysis of 9 ground-cover vegetation variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Roman numerals in parentheses identify landform-level ecosystems.

observed overlap is consistent with field observations as landforms IV and V both exhibit considerable within-landform ecological diversity. The overall misclassification rate for the discriminant function based on the set of ground-cover species variables was 12%; the jackknifed misclassification rate was 27%. Both error rate estimates are considerably higher than those obtained with the physiography-soil variable set.

The first three canonical variates were found to account for 49, 81, and 98% of the cumulative variance in the ground-cover species data set (Table 4.6). Variables highly correlated with the first canonical variate include the coverage of shrub species and the coverage of the *Ceonothus* species group. Landforms III and VI, both separated from all other units along the positive portion of the first CV axis, exhibit high shrub coverage. In addition, landform VI exhibits exceptionally high coverage of the Ceonothus species group. The second canonical variate had a strong positive correlation with the number of northern pin oak clumps, and strong negative correlations with the coverage of the *Arctostaphylos* species group and the number of grass species. As such, landforms are distributed along the second CV axis following a gradient, running from top to bottom, of decreasing ground-cover oak, increasing coverage of the *Arctostaphylos* species group, and an increasing number of grass species. This approximates a gradient of increasing light availability (i.e., decreasing stand density) from top to bottom.

A third discriminant analysis, derived from a combined variable set of four physiography, six soil, and five ground-cover vegetation variables (Table 4.7), revealed the marked ecological distinctness of the five landform-level ecosystems attributable to physical and biotic factors. Use of the combined variable set produced larger eigenvalues, tighter clustering, and a greater degree of spatial separation among landforms in the plane of the first

Table 4.7 Comparison of relative variation among five landform-level ecosystems as determined by a canonical variates analysis of ten physiographic and soil variables, and five ground-cover vegetation variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Coefficients ≥ 0.43 are significant with $p < 0.05$.

Canonical Variate	1	2	3
Eigenvalue	22.2	2.5	1.7
Cumulative % variance	82	91	97
Variable	**Correlation Coefficient**		
Elevation	0.90	0.07	-0.14
Slope, %	0.22	-0.48	-0.17
Maximum slope, %	0.21	-0.50	-0.15
Transformed aspect	0.27	0.15	0.09
Coarse sand, 10-150 cm	-0.21	-0.35	0.29
Silt + Clay, 10-150 cm	0.25	0.10	0.62
Gravel + cobbles, 0-150 cm	-0.45	-0.25	0.30
Depth to banding, > 2 cm thick	-0.59	-0.22	-0.47
Depth to maximum rooting	-0.21	-0.23	0.50
Laboratory pH, 30-150 cm	-0.11	-0.21	0.58
Number of n. pin oak sprout clumps, < 1 m	0.71	-0.23	-0.10
Number of grass species	-0.50	-0.50	0.23
Coverage of *Arctostaphylos* species group	-0.56	-0.36	-0.16
Coverage of *Vaccinium* species group	-0.28	-0.15	0.12
Coverage of *Rosa* species group	0.54	-0.28	-0.36

two canonical variates than attained using either of the variable subsets (Figure 4.5). Moderately fertile high elevation landforms (V and VI) are located along the right side of the ordination, whereas very infertile low-elevation landforms (I and IV) are found in the upper-left portion of the ordination. The rugged, dissected physiography of landform VI (ice-contact terrain) and the diverse ground-cover vegetation of landform III (water-table influenced outwash) result in the clear separation of these landforms from all others. The discriminant function derived from the combined variable set resulted in perfect (100%) classification of the 49 sample plots; the jackknifed misclassification rate was just 6%. Both error rate estimates represent considerable improvements over those obtained with either the physiography-soil or the ground-cover vegetation variable subsets.

The first three canonical variates were found to account for 82, 91, and 97% of the cumulative variance in the combined variable set (Table 4.7). Average elevation and the number of northern pin oak sprout clumps both exhibited high positive correlations with the first canonical variate, while depth to banding, coverage of the *Arctostaphylos* species group, and the number of grass species were all negatively correlated. Variables correlated with the second canonical variate included maximum slope, slope, and the number of grass species.

Microclimate Study

Microclimate differs considerably among three major physiographic levels (high-elevation terrain, low-elevation terrain, and glacial meltwater drainage channels) within the Mack Lake burn (Figure 4.6). Topographically mediated cold-air drainage among the levels is largely responsible for marked differences in average weekly and daily maximum and minimum temperature. During the period of record, weekly and daily maximum temperatures

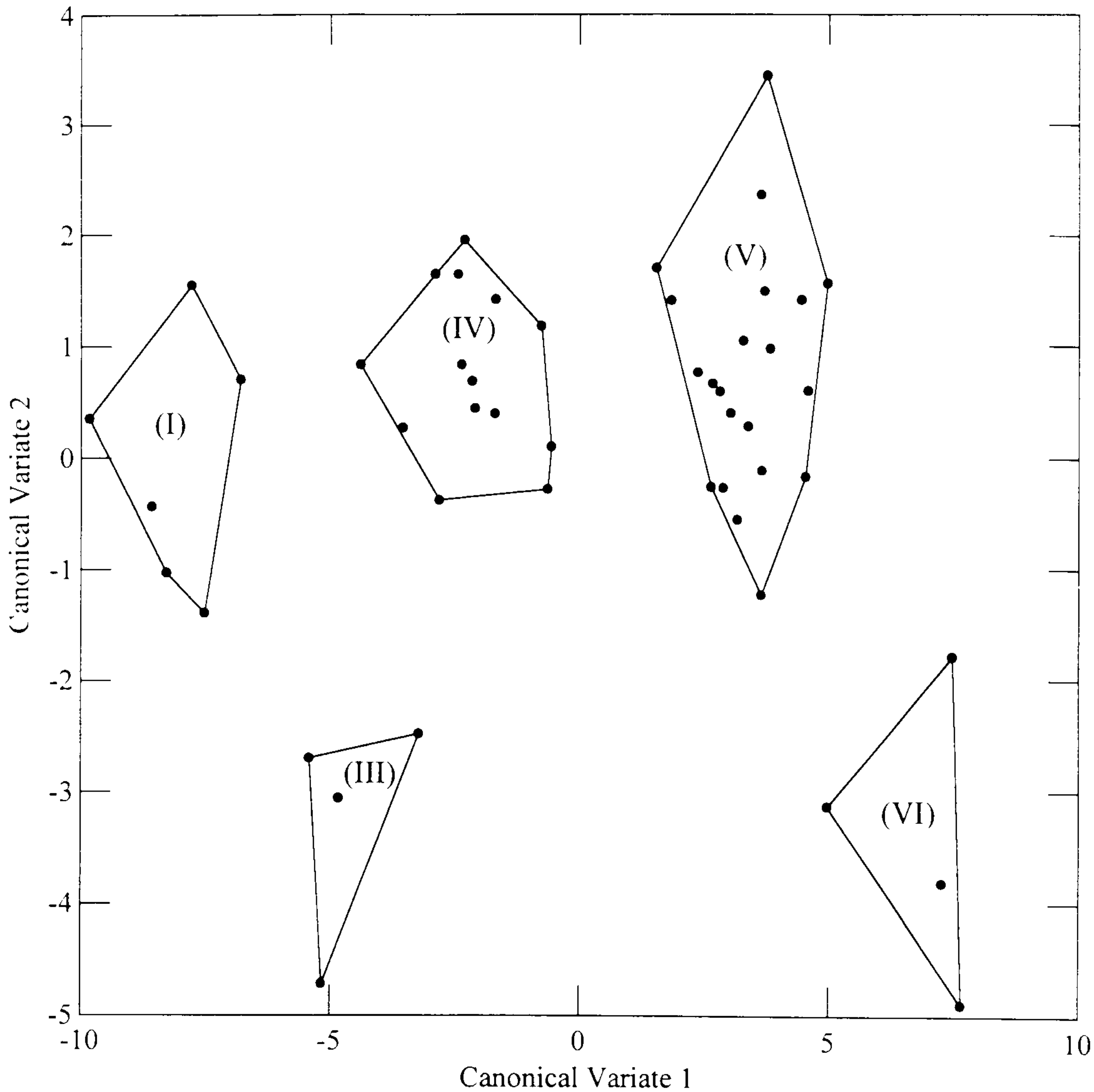


Figure 4.5. Ordination of 49 sample plots of 5 landform-level ecosystems along the first 2 canonical variates of an analysis of 10 physiographic and soil variables, and 5 ground-cover vegetation variables; Mack Lake burn, Oscoda Co., northern Lower Michigan. Roman numerals in parentheses identify landform-level ecosystems.

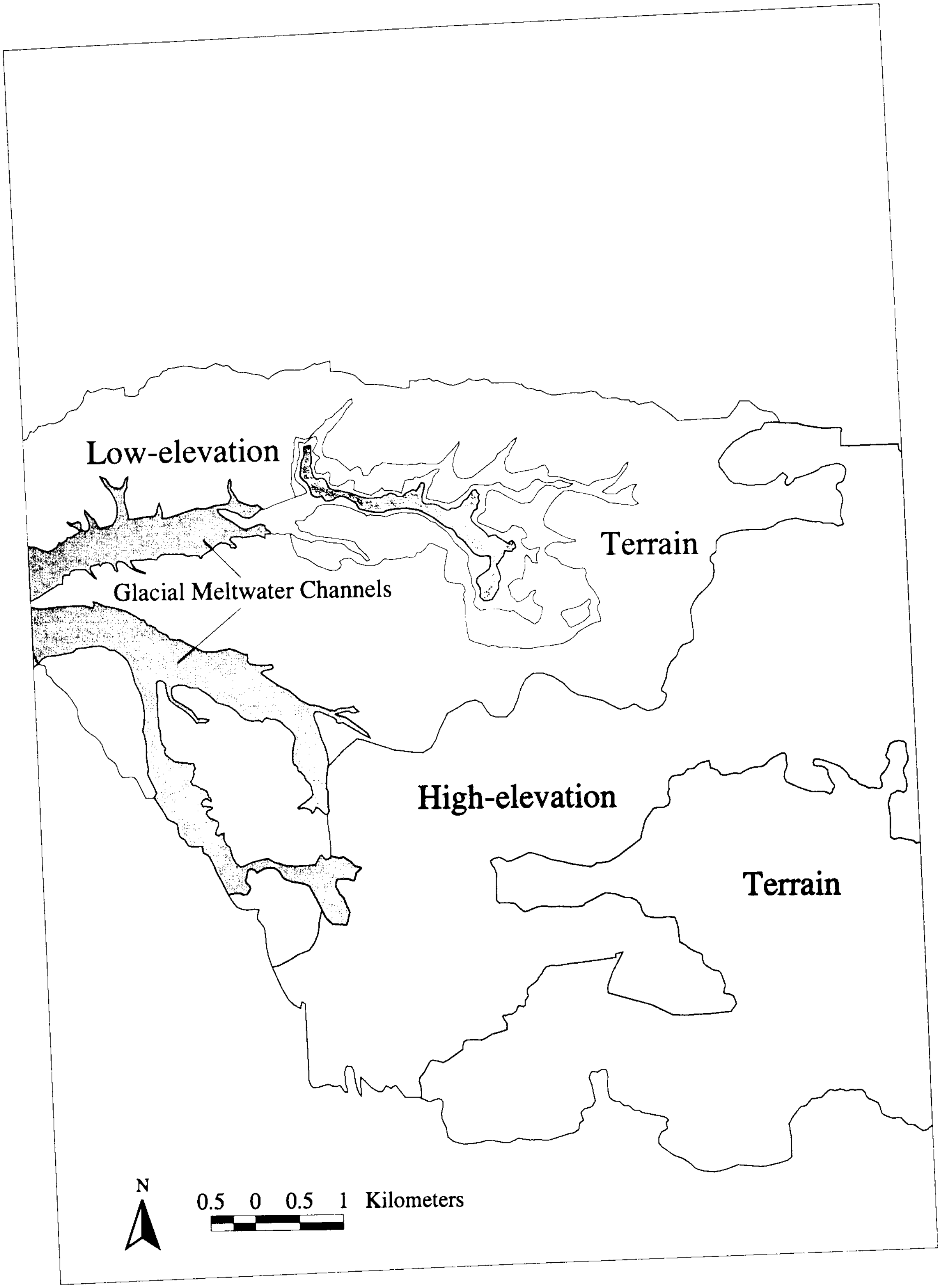


Figure 4.6. Major physiographic levels of the Mack Lake burn study area, Oscoda Co., northern Lower Michigan: (1) high-elevation terrain, (2) low-elevation terrain, and (3) glacial meltwater drainage channels.

in the low-elevation terrain were significantly lower than in the high-elevation terrain, averaging 2.7°C (4.8°F) lower in each case (Table 4.8). Similarly, weekly and daily minimum temperatures in the low-elevation terrain averaged 3.0°C (5.4°F) and 1.6°C (2.8°F) lower, respectively, than in the high-elevation terrain. The difference in weekly minimum temperature was statistically significant (Table 4.8).

Although weekly and daily maximum and minimum temperatures in the glacial meltwater channels were consistently lower than in the adjacent uplands of the low-elevation terrain, these differences were not statistically significant (Table 4.8). These results were corroborated by supplementary temperature data (not presented) collected in 1997. Sample-plot data and field observations from the glacial meltwater channels (e.g., the virtual absence of northern pin oak and the reduced vigor of jack pine), however, suggest that the microclimate difference between the two levels is undoubtedly significant from an ecological standpoint. Factors contributing to the unexpectedly high maximum and minimum channel temperatures may include heat reradiation from the channel walls, cold-air recirculation by prevailing wind currents, and cold-air drainage to areas outside of the study area.

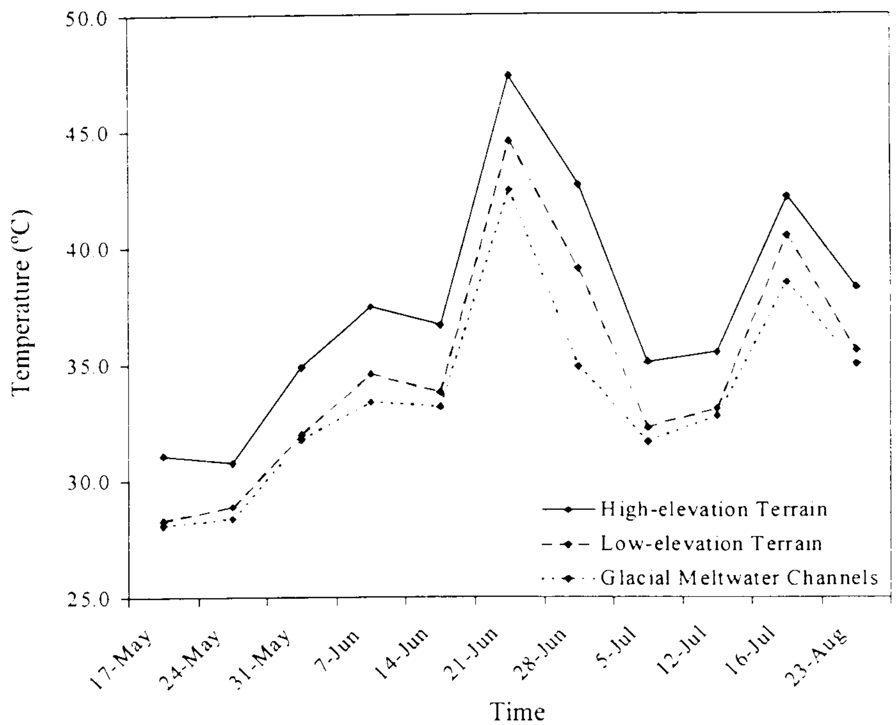
Using a repeated measures analysis of variance (within-subjects results), marked differences in the patterns of weekly (Figure 4.7) and daily (Figure 4.8) temperature change were found among physiographic levels. The significance of the interaction between weekly minimum temperature and site ($p = 0.00001$) indicated a highly significant difference in the season-long patterns of weekly minimum temperature among physiographic levels (Figure 4.7b). The interaction between weekly maximum temperature and site, however, was not significant ($p = 0.096$), indicating a similar pattern of change in weekly maximum temperature among physiographic levels (Figure 4.7a). Finally, season-long patterns of daily

Table 4.8 Comparison of weekly and daily maximum and minimum temperature among major physiographic levels of the Mack Lake burn, Oscoda Co., northern Lower Michigan and the weather station at Mio, Michigan (May 17-August 24, 1995) (values are means, s.d. in parentheses).

	Glacial Meltwater Channels	Low-elevation Terrain	High-elevation Terrain	Mio Weather Station
Weekly Temperature				
Maximum (°C)[a]	33.7 (4.3)	34.8 (4.9)	37.5 (5.0)	30.9 (5.1)
Maximum (°F)[a]	92.7 (7.7)	94.6 (8.9)	99.4 (9.0)	87.6 (9.1)
Minimum (°C)[a]	-1.0 (3.2)	-0.1 (3.2)	2.9 (3.4)	4.0 (5.0)
Minimum (°F)[a]	30.1 (5.7)	31.8 (5.7)	37.2 (6.2)	39.2 (9.0)
Daily Temperature				
Maximum (°C)[a]	28.6 (5.1)	28.7 (5.7)	31.4 (6.2)	26.8 (5.1)
Maximum (°F)[a]	83.5 (9.1)	83.7 (10.2)	88.5 (11.2)	80.3 (9.2)
Minimum (°C)	5.6 (9.6)	6.1 (9.1)	7.7 (8.1)	9.0 (8.5)
Minimum (°F)	42.1 (17.3)	43.0 (16.4)	45.8 (14.6)	48.1 (15.3)

[a] indicates significance at $\alpha = 0.05$ using one-way ANOVA

(a)



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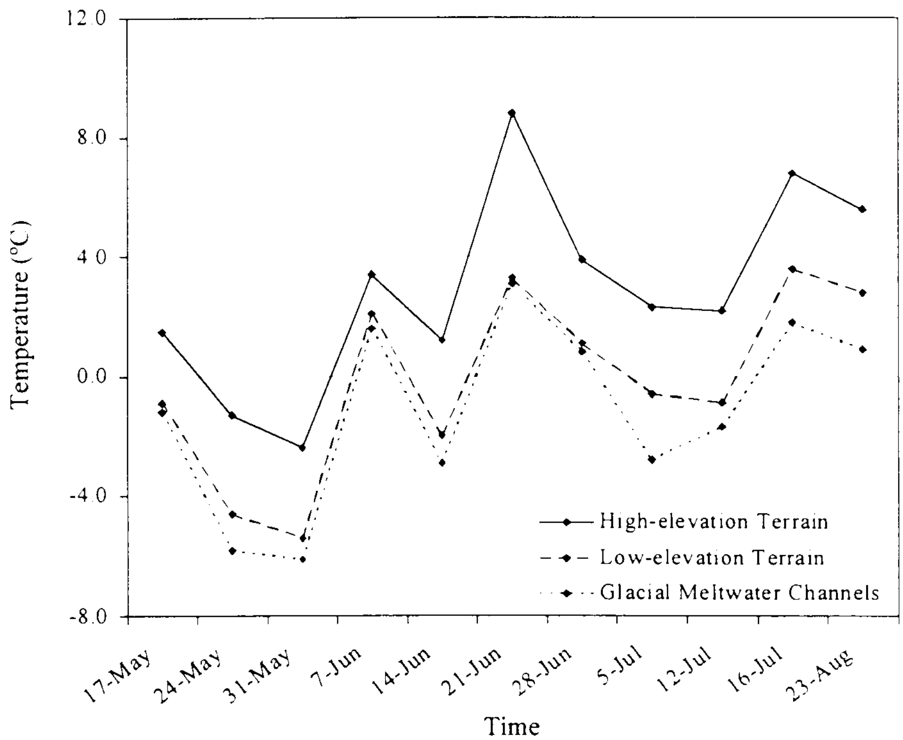

Figure 4.7. Comparison of week-to-week maximum (a) and minimum (b) temperature trends among the high-elevation terrain, low-elevation terrain, and glacial meltwater channels during the period May 17 to August 23, 1995; Mack Lake burn, Oscoda Co., northern Lower Michigan.

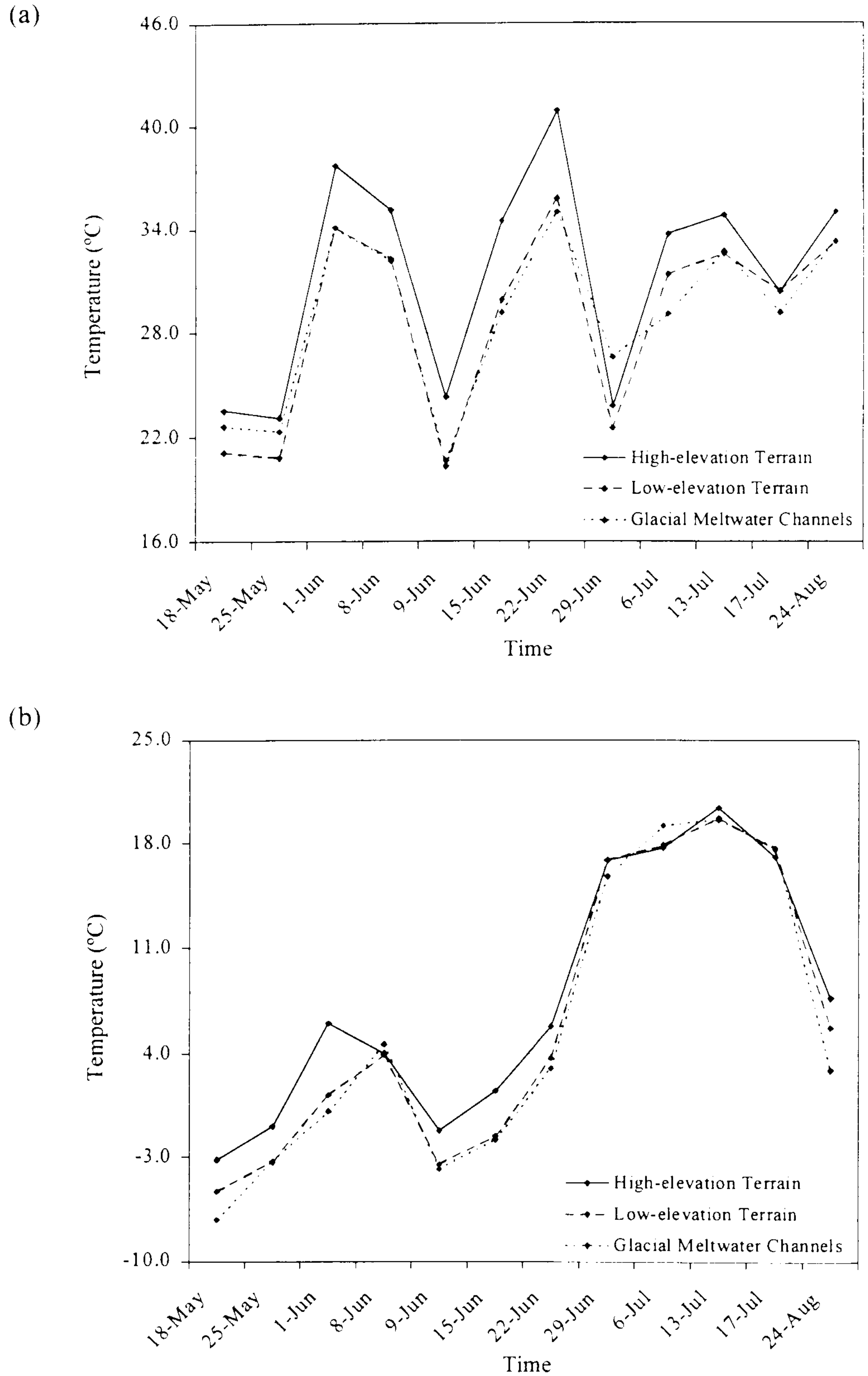

Figure 4.8. Comparison of day-to-day maximum (a) and minimum (b) temperature trends among the high-elelvation terrain, low-elevation terrain, and glacial meltwater channels during the period May 18 to August 24, 1995; Mack Lake burn, Oscoda Co., northern Lower Michigan.

maximum (Figure 4.8a) and minimum (Figure 4.8b) temperature were found to be significantly different among physiographic levels based on the significance of the respective interaction terms ($p < 0.0005$). These results are similar to those of Kashian (1998) who reported marked differences in the patterns of maximum and minimum temperature change between high- and low-elevation landforms at Bald Hill East in northern Lower Michigan.

The microclimate of the Mack Lake basin is characterized by marked temperature extremes. Throughout the growing season, weekly and daily maximum and minimum temperatures recorded across physiographic levels were consistently more extreme (i.e., characterized by higher maximum and lower minimum temperatures) than those recorded officially at the weather station in Mio, Michigan (Table 4.9). Thus, the study area is subject to fluctuations in temperature over a markedly wider range than that of areas outside of, and adjacent to, the basin. Averaged across physiographic levels, weekly and daily temperatures within the burn fluctuated over a range of 34.7°C (62.6°F) and 23.1°C (41.6°F), respectively (Table 4.9). At Mio, however, weekly and daily temperatures fluctuated over a far narrower range, averaging just 26.9°C (48.4°F) and 17.8°C (32.2°F), respectively.

Extremes in temperature further illustrate the microclimate differences among the physiographic levels themselves (Table 4.10). In both the glacial meltwater channels and the low-elevation terrain, below-freezing (0°C) minimum temperatures were recorded on 10 separate occasions in May (17, 18, 24, 25, 31), June (9, 14, 15), and July (5, 12), 1995. Among these dates, the glacial meltwater channels consistently exhibited the most extreme minimum temperatures as evidenced by the number of records below -1.1°C (30°F). In contrast, below-freezing temperatures were recorded in the high-elevation terrain just five times, and only during May (18, 24, 25, 31) and June (9). The weather station at Mio

Table 4.9 Microclimate variation in the range of weekly and daily temperatures among major physiographic levels of the Mack Lake burn, Oscoda Co., northern Lower Michigan and the weather station at Mio, Michigan (May 17-August 24, 1995).

	Glacial Meltwater Channels	Low-elevation Terrain	High-elevation Terrain	Mio Weather Station
Weekly Temp. Range (°C)	34.7	34.9	34.6	26.9
Weekly Temp. Range (°F)	62.6	62.9	62.2	48.4
Daily Temp. Range (°C)	23.0	22.6	23.7	17.8
Daily Temp. Range (°F)	41.4	40.7	42.7	32.2

Table 4.10 Microclimate variation in selected maximum and minimum temperatures among major physiographic levels of the Mack Lake burn, Oscoda Co., northern Lower Michigan and the weather station at Mio, Michigan (May 17-August 24, 1995).

	Glacial Meltwater Channels	Low-elevation Terrain	High-elevation Terrain	Mio Weather Station
Readings below -1.1°C (30 °F)	10	7	4	1
Readings below 0 °C (32 °F)	10	10	5	6
Readings above 32.2 °C (90 °F)	11	13	16	5
Readings above 37.8 °C (100 °F)	2	3	5	2
Readings above 46.1 °C (115 °F)	0	0	1	0

reported below-freezing temperatures on May 18, 24, 25, 31, and on June 9 and 14. Maximum temperatures of 32.2°C (90°F) or higher were recorded in the glacial meltwater channels on 11 occasions during June (1, 7, 14, 21, 22, 28), July (12, 13, 16), and August (23, 24) (Table 4.10). In addition to the above dates, temperatures in the low-elevation terrain exceeded 32.2°C on June 8 and July 5. In contrast, maximum temperatures in the high-elevation terrain rose above 32.2°C on 16 separate occasions spanning the entire period of record (May-August). Extreme maximum temperatures of 37.8°C (100°F) or higher were recorded just twice (June 21 and July 16) in the glacial meltwater channels, and three times (June 21, 28, and July 16) in the low-elevation terrain (Table 4.10). In the high-elevation terrain, maximum temperatures exceeded 37.8°C five times during June (21, 28, 22), July (16), and August (23). A season-high average maximum temperature of 47.2°C (117°F) was recorded in the high-elevation terrain on June 21. In Mio, temperatures rose above 32.2°C just five times (June 21, 28, and July 13, 16 and 23), and reached 37.8°C only twice (June 14 and July 16).

Kirtland's Warbler Occupancy of Landform-Level Ecosystems

Over the 12-year period 1986-1997, a spatially distinct pattern of Kirtland's warbler colonization and occupancy was observed among the high- and low-elevation terrain landform-level ecosystems (Figure 4.9). When census locations from the first three years of warbler occupation (1986-1988) are compared to census locations from 1995-1997, the pattern of initial warbler occurrence clearly favors the high-elevation terrain landforms, whereas in later years, the pattern visibly shifts in favor of the low-elevation terrain landforms (Figure 4.9). The extent of this high- to low-elevation shift in warbler occurrence

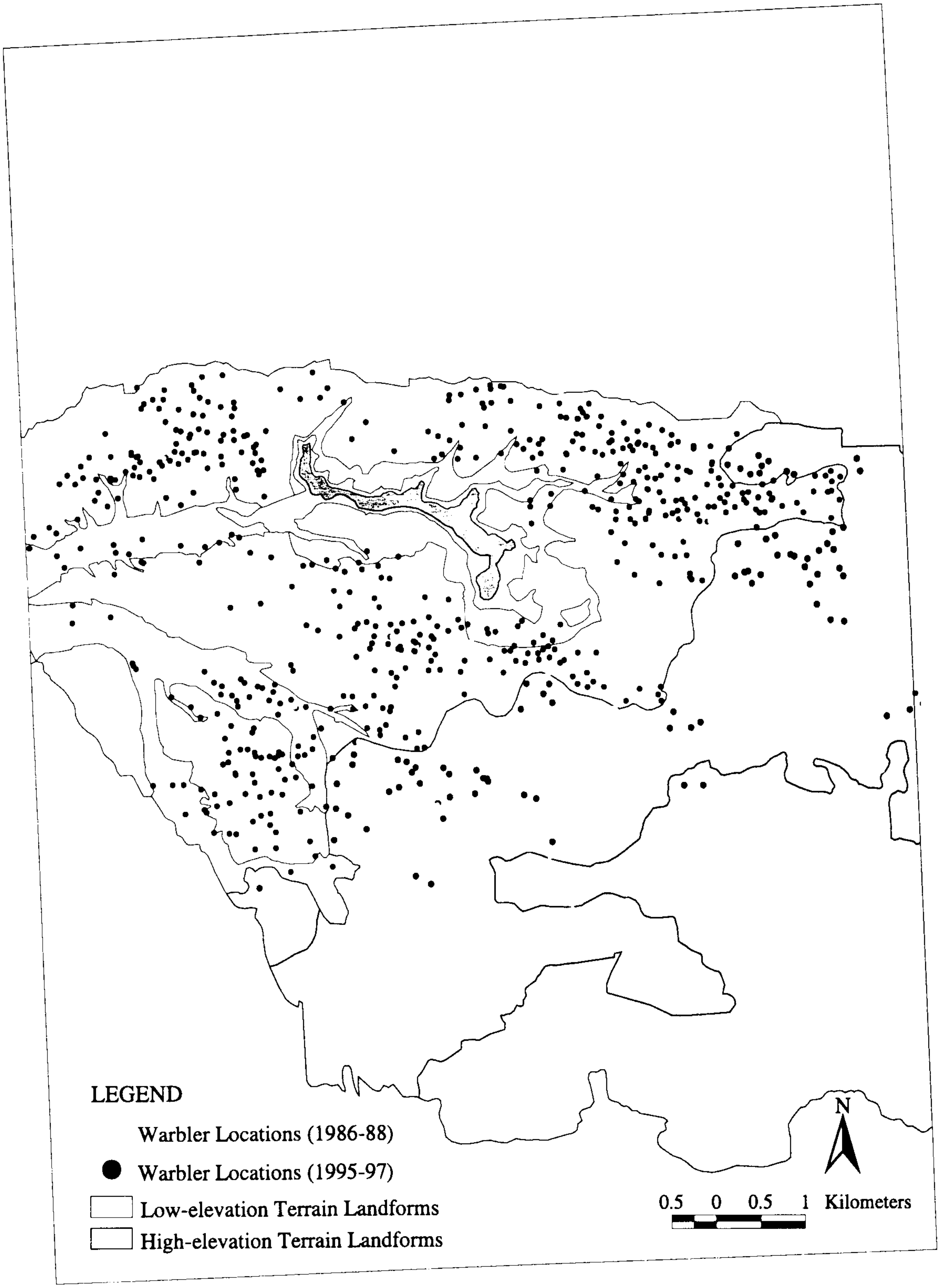

Figure 4.9. Landform-level ecosystem map of the Mack Lake burn, Oscoda Co., northern Lower Michigan showing the locations of singing-male Kirtland's warblers. During the first three years of warbler occupation (1986-1988), 62% of the warbler population occupied the high-elevation terrain landforms. From 1995-1997, 86% of the population occupied the low-elevation terrain landforms.

is illustrated most clearly when the position of the population spatial mean is plotted over time (Figure 4.10). Using a multivariate analysis of variance, significant differences in the population spatial mean ($p < 0.00001$) were found among years (1986-1997). A significant decreasing relationship ($r^2 = 0.90$; $p < 0.00001$) between the average elevation of the Kirtland's warbler population and the year of occupancy (1986-1997) further demonstrates the systematic progression of warbler occupation and its apparent link to landform-level ecosystems (Figure 4.11). These observations are consistent with those of Kashian (1998) who reported a similar spatial pattern of Kirtland's warbler colonization and occupancy between the high- and low-elevation landforms at Bald Hill East in northern Lower Michigan.

The results presented above provide very strong evidence in support of the connection between Kirtland's warbler occurrence and landform-level ecosystems. A two-way Chi-square test for independence confirmed the presence of a very significant dependent relationship ($p < 0.00001$) between the distribution of warblers among landform-level ecosystems and the year of occupancy (1986-1997). In addition, the results suggest the presence of a non-random (i.e., specific), spatially explicit pattern of Kirtland's warbler occupation among landform-level ecosystems over time. A one-way Chi-square goodness-of-fit test (corrected for landform area) confirmed that the distribution of warblers among landform-level ecosystems in each year (1986-1997) was indeed non-random (Table 4.11).

The observed shift in the spatial pattern of Kirtland's warbler occurrence described herein can be explained in terms of the physical (i.e., physiography, microclimate, and soil) and biotic (tree height growth, stand structure, and ground-cover composition) factors that characterize the high- and low-elevation terrain features and their constituent landform-level

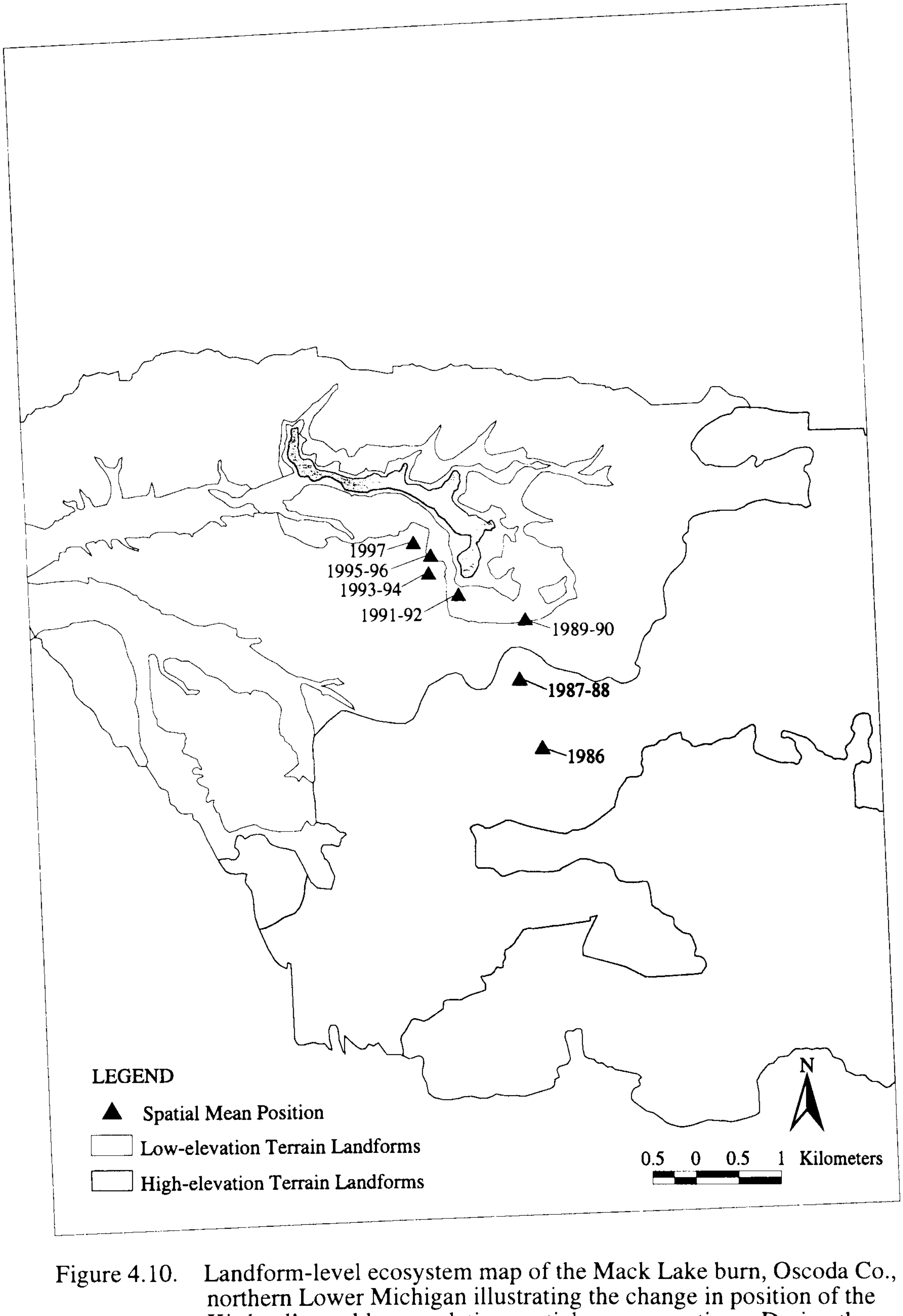

Figure 4.10. Landform-level ecosystem map of the Mack Lake burn, Oscoda Co., northern Lower Michigan illustrating the change in position of the Kirtland's warbler population spatial mean over time. During the 12-year period of record (1986-1997), the spatial mean migrated approximately 3.0 km.

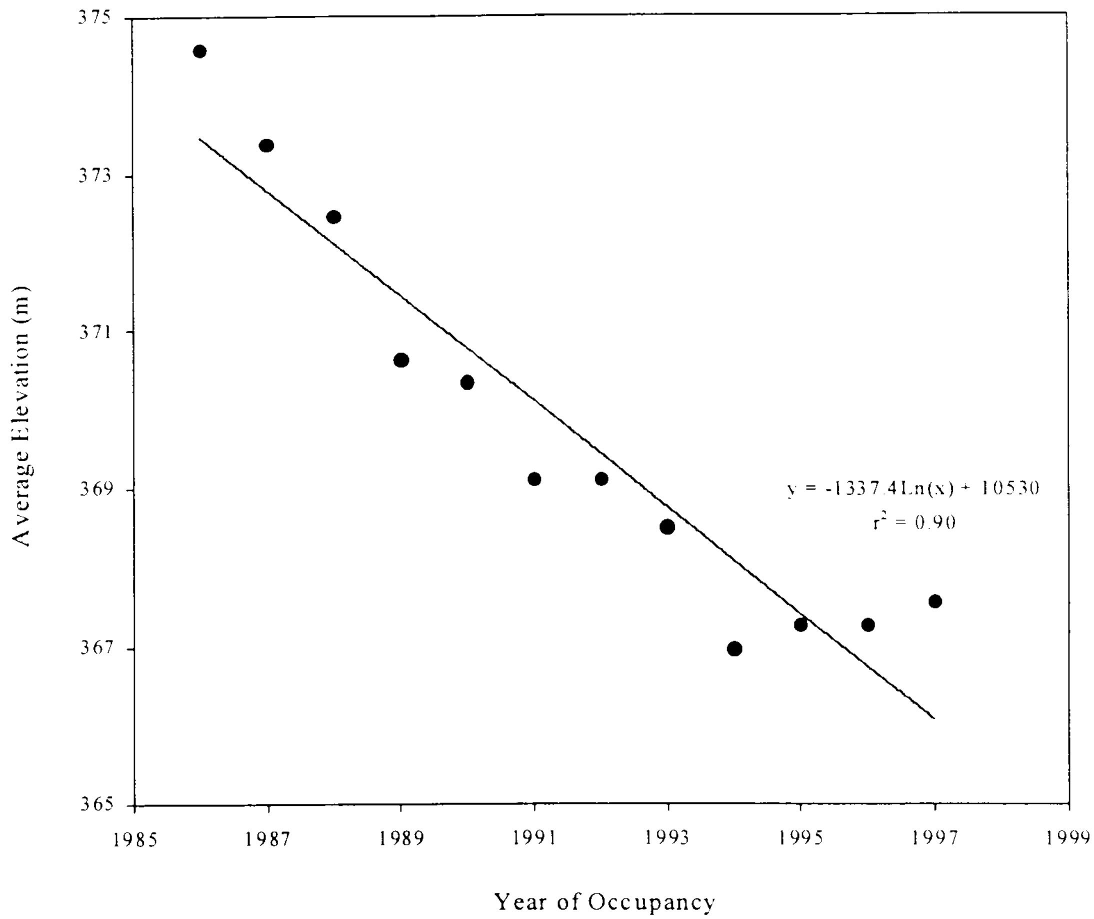

Figure 4.11. Temporal rate of change in the average elevation of the Kirtland's warbler population (1986-1997); Mack Lake burn, Oscoda Co., northern Lower Michigan.

Table 4.11 Randomness in the pattern of Kirtland's warbler occurrence among landform-level ecosystems based on a Chi-square goodness-of-fit test; Mack Lake burn, Oscoda Co., northern Lower Michigan. Significance (at $\alpha=0.05$) indicates a non-random (specific) pattern of warbler distribution among landforms in that year.

Year of Occupancy	Number of Singing-Male Warblers	p-value
1986*	14	0.00274
1987*	28	0.00341
1988	78	< 0.00001
1989	101	< 0.00001
1990	159	< 0.00001
1991	208	< 0.00001
1992	250	< 0.00001
1993	291	< 0.00001
1994	297	< 0.00001
1995	271	< 0.00001
1996	203	< 0.00001
1997	123	< 0.00001

* Warbler population numbers were too few in 1986 and 1987 to meet the assumptions of the Chi-square test.

ecosystems (Figure 4.12). In 1986, the bulk of the Mack Lake Kirtland's warbler population (71%) occupied landforms in the high-elevation terrain (landforms V and VI; Figure 4.12b). Moister, more nutrient rich soils, a warmer microclimate, and taller, faster-growing jack pines and northern pin oaks distinguished the high-elevation landforms from those in the low-elevation terrain. As a result, trees in landforms V and VI reached heights suitable for warbler colonization (ca 1.4 m) more rapidly than did trees in the other landforms. Although warblers remained concentrated in the high-elevation terrain during the first three years of colonization (1986-1988), occupancy of the area steadily decreased over time as rapidly-growing tree crowns closed in on one another and habitat suitability deteriorated (Figure 4.12a). During this same period, habitat in the low-elevation terrain became increasingly suitable as the slower-growing pines and oaks reached appropriate heights (ca 1.4 m) for colonization. In 1989, as warbler occupancy systematically progressed into the low-elevation landforms (landforms I, III, and IV), a marked shift occurred in the spatial pattern of warbler occurrence (Figure 4.12). By 1993, 73% of the Mack Lake population occupied landforms in the low-elevation terrain, a complete reversal in the spatial pattern of occurrence observed in 1986 (Figure 4.12a).

Although the Kirtland's warbler colonized all five jack pine-dominated landform-level ecosystems, the timing of initial colonization, and the duration of subsequent occupancy, differed considerably among units (Table 4.12). Typically, early colonization occurs on landforms that support fast-growing jack pines (Barnes et al. 1989). Accordingly, landforms V and VI, characterized by relatively high soil water and nutrient availability, a warm microclimate, and rapid jack pine growth, were the first to be intensively colonized (Table 4.12). Although landform IV was also among those occupied early (colonized in

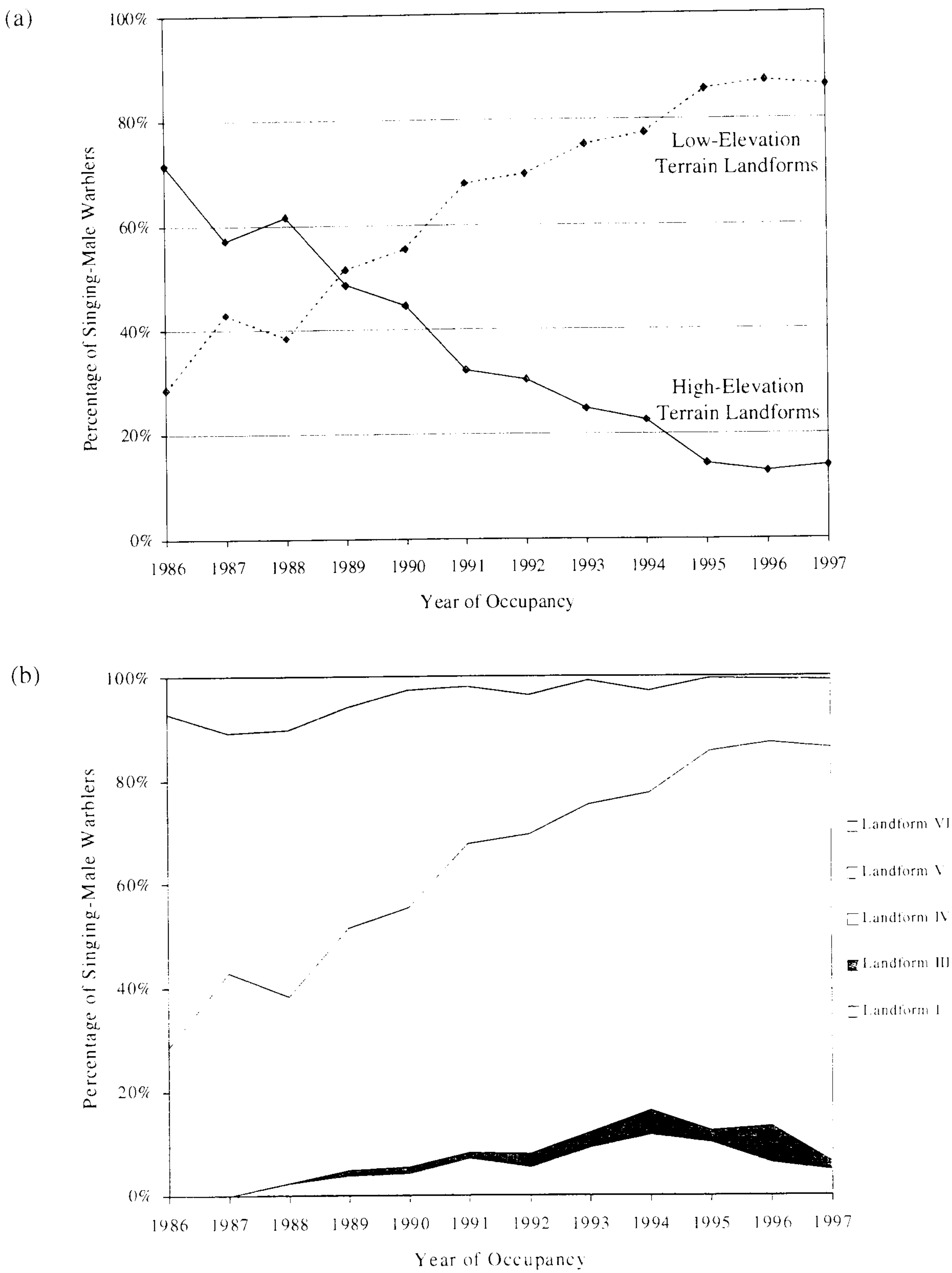

Figure 4.12. Percentage of singing-male Kirtland's warblers occupying (a) the high- and low-elevation terrain features and (b) individual landform-level ecosystems within each (1986-1997); Mack Lake burn, Oscoda Co., northern Lower Michigan.

Table 4.12 Occupancy of landform-level ecosystems by the singing-male Kirtland's warbler population (1986-1997); Mack Lake burn, Oscoda Co., northern Lower Michigan.

	First Year of Occupancy[1]	Year of Peak Occupancy	Last Year of Occupancy[2]	Occupancy Duration[3]
Low-elevation Terrain				
Landform I	1991	1994	1997	7
Landform III	1994	1996	1996	3
High-elevation Terrain				
Landform IV	1986	?	?	>12
Landform V	1986	1986	?	>12
Landform VI	1986	1987	1989	4

1 Defined as the first year of occupancy by greater than or equal to 5% of the warbler population.
2 Defined as the last year of occupancy by greater than or equal to 5% of the warbler population.
3 Defined as the number of years of occupancy by greater than or equal to 5% of the warbler population.

1986 by three singing males), initial colonization was very likely associated with only scattered patches of relatively tall jack pine in ecosystem types 3 and 4 (Table 4.1). Late colonization typically occurs on landforms that support slow-growing jack pines (Barnes et al. 1989). Thus, landform I, characterized by very dry, nutrient poor soils, a cold micro-climate, and slow jack pine growth, was not occupied until 1991 (Table 4.12). Landform III, which also supported relatively slow pine growth, was colonized even later (1994). In this particular case, however, the interpretation of landform characteristics in relation to warbler colonization is somewhat confounded by the small relative size (ca 310 ha) of the landform and the rather fragmented nature of the habitat (by private development, roads, fuel-breaks, wetlands, etc.) within it.

The duration of Kirtland's warbler occupancy also differs markedly among landform-level ecosystems (Table 4.12). As was the case with early colonization, short-duration warbler occupancy is associated with landforms that support fast-growing pines. Landform VI, characterized by moist, nutrient rich soils, a warm microclimate, and rapid jack pine growth, was occupied for just four years. In spite of relatively poor site conditions and relatively slow jack pine growth, Landform III was occupied for only three years. Again, the small relative size and fragmented habitat of the landform somewhat confounds the interpretation of landform characteristics in relation to occupancy duration.

Long-duration warbler occupancy is characteristic of landforms that 1) support slow-growing pines, or 2) are characterized by a diversity of landscape ecosystem types which results in differential within-landform jack pine growth. For example, landforms I and IV, both of which support slow-growing pines, are among the longest occupied units within the Mack Lake burn. Landform I was occupied for seven years, whereas landform IV will likely remain occupied through the year 2000 (Table 4.12). In spite of slightly more favorable site conditions and more rapid jack pine growth, landform IV was occupied considerably longer than landform I due to the greater diversity of landscape-ecosystem types (i.e., site heterogeneity) within it. Similarly, landform V, a unit that generally supports fast-growing pines, will likely remain occupied through 1999 because of the exceptionally high within-landform site heterogeneity. Overall, because of the remarkable diversity of landform-level ecosystems and constituent ecosystem types within the Mack Lake burn, occupancy of the entire area by Kirtland's warbler has been prolonged well beyond what would be expected if the burn were characterized by less heterogeneous (i.e., less diverse) site conditions.

V. GENERAL DISCUSSION

Ecological Relationships Affecting Kirtland's Warbler Occurrence

The landscape ecosystem approach, as applied to the 1980 Mack Lake burn, reveals that the spatial and temporal pattern of Kirtland's warbler occurrence is strongly governed by the physical (physiography, microclimate, and soil) and biotic (vegetation) components of landscape ecosystems (Figure 5.1). The complex interrelationships between the ecosystem components mediate the pattern of Kirtland's warbler colonization and occupancy both directly and indirectly. The high- and low-elevation physiography of the Mack Lake burn not only controls soil water and nutrient availability below the surface, but also acts to modify air temperature at and above the surface (Barnes et al. 1998, p 226; Figure 5.1). Variation in local air temperature results from the high-to-low pattern of cold-air drainage within the basin; soil water and nutrient availability is largely a function of soil texture and pH, properties that differ considerably among the specific parent materials of the major glacial landforms (e.g., ice-contact terrain, outwash plains, etc.). In turn, microclimate and soil have a strong and predictable influence on the development of vegetation, particularly on the distribution and growth of jack pine and northern pin oak (Figure 5.1).

Of the major ecosystem components, vegetation, as mediated by microclimate and soil, exerts the most direct influence on Kirtland's warbler occurrence (Figure 5.1). Warblers nest only on sites where jack pine is 5 to 23 years old and 1.4 - 5.0 m tall (Probst and Weinrich 1993), and jack pine height growth is strongly influenced by site quality. Therefore, the growth of jack pine markedly affects the timing of initial site colonization and the duration of site occupancy by Kirtland's warbler. Thus, understanding the degree to

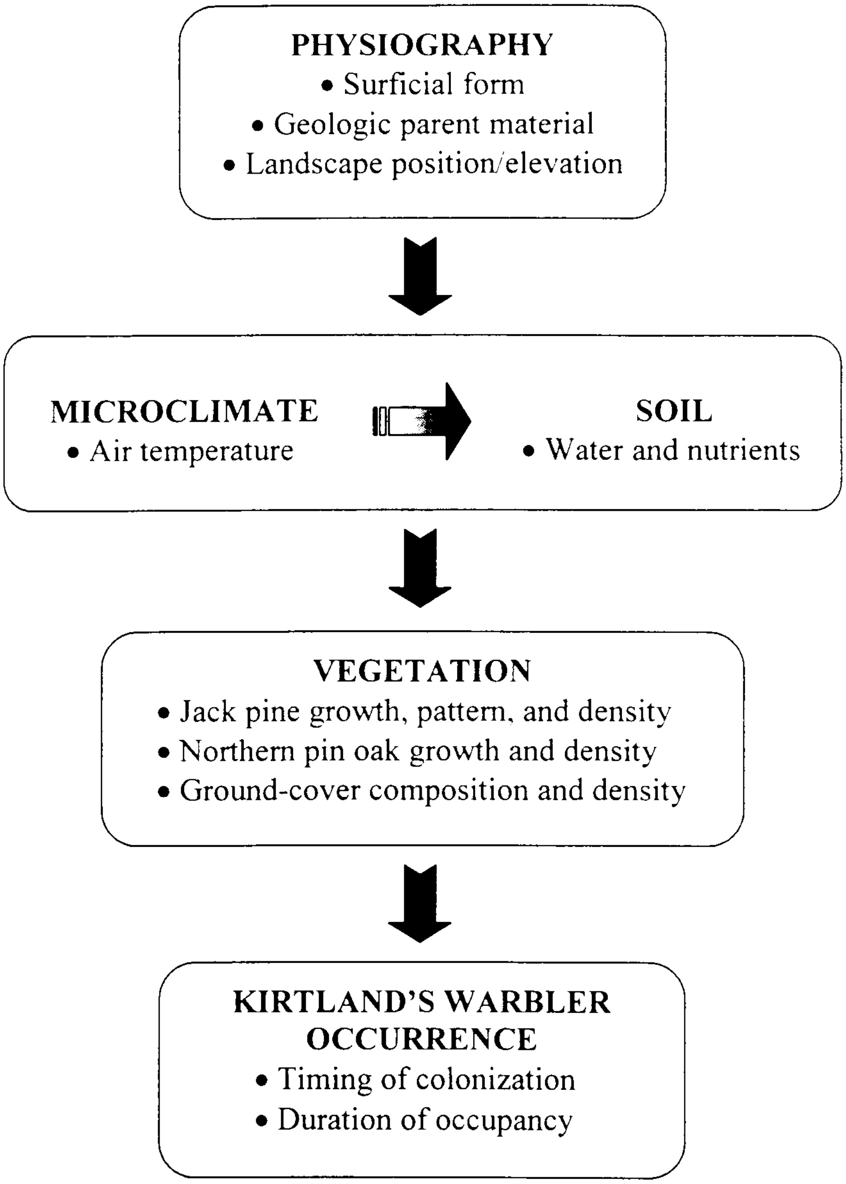

Figure 5.1. Schematic diagram illustrating the major ecological factors that influence Kirtland's warbler occurrence among the landscape ecosystems of the Mack Lake burn, Oscoda Co., northern Lower Michigan. (Modified from Barnes et al. 1998, p. 636.)

which various site factors influence Kirtland's warbler occurrence is key to interpreting and predicting spatial and temporal patterns of warbler colonization and occupancy within the Mack lake burn and across the breeding range. By employing a multifactor ecological approach, and simultaneously integrating physiographic, climatic, edaphic, and vegetative factors, the complex relationships between Kirtland's warbler and its supporting ecosystems can be well understood.

Among the landform-level ecosystems of the Mack Lake burn, significant differences in jack pine height (Table 4.3) largely reflect the combined influence of microclimate and soil related attributes. For example, the relatively tall, fast-growing pines of landforms in the high-elevation terrain are the result of warmer minimum temperatures and moister, more nutrient rich soils. Conversely, the relatively short, slow-growing pines of the low-elevation landforms are the product of colder minimum temperatures and drier, more nutrient poor soils.

Although the contributions of single factors to differences in jack pine growth were not quantified in this study, several investigators have reported their effects. Despland and Houle (1997) found that jack pine growth was limited by air temperature and length of the growing season on well-drained sandy terraces in the valley of the Great Whale river in subarctic Québec. Kashian (1998) reported significant differences in jack pine height growth due to topographic-mediated microclimate variation between otherwise similar high- and low-elevation landforms at Bald Hill East in north central Lower Michigan. Because of the sensitivity of jack pine growth to temperature conditions (Botkin et al. 1991), late-season frosts represent a potentially important growth-limiting factor. Barnes et al. (1989) observed new jack pine shoot growth to be killed by below-freezing minimum temperatures in June.

Additionally, the vigor of pines in frost-pocket depressions was found to be markedly less than that of pines in non-depression areas due to the lower minimum temperatures (Barnes et al. 1989). Similar responses to freezing temperatures in low-lying frost pockets have been observed in eastern hemlock (*Tsuga canadensis*) (Hough 1945) and in a number of deciduous tree species (Spurr 1957).

The effect of soil water and nutrient availability on the growth of jack pine also has been shown in a number of studies. Jameson (1971) concluded that soil water regime, soil nutrient regime, and soil texture probably exert a greater influence on jack pine height growth than most other site factors. Among the landforms of the Mack Lake burn, soil water and nutrient regimes are largely a function of soil texture as it relates to the presence and abundance of fine-textured soil banding. Fine-textured bands, resulting from both pedogenic (Wurman et al. 1959, Dijkerman et al. 1967, Berg 1984) and depositional (Hannah and Zahner 1970) processes, are distinctive features of both the Graycalm and Montcalm soil series (Hannah and Zahner 1970, Werlein 1998) which dominate the high-elevation terrain. Shetron (1972) found jack pine growth in northern Lower Michigan to be significantly greater on Graycalm and Montcalm soils than on unbanded Grayling soils due to the better soil water regime. Pawluk and Arneman (1961) reported highly significant correlations between jack pine growth in north central Minnesota and the content of fine sand, silt, and clay in the upper portions of the sola. Additionally, interbedded bands of fine-texture were observed to increase site quality for jack pine by restricting water percolation and by increasing the amount and electrolyte status of ground water (Pawluk and Arneman 1961). Other investigators have similarly reported increased site productivity and tree growth on sites with fine-textured soil banding (Van Eck and Whiteside 1958, White and Wood 1958, Hannah and Zahner 1970, Host et al. 1988, McFadden et al. 1994) and finer-textured soils in general (Zahner and Hendrich 1966, Shetron 1969).

Variation in both microclimate and soil are predictable given a knowledge of landform-level ecosystems and their distinguishing physiographic characteristics (Barnes et al. 1998, p. 227). Deviations in microclimate, specifically differences in maximum and minimum air temperature, are largely a function of local topography (Geiger 1965, Bailey 1996, Barnes et al. 1998). Within a given macroclimate, landforms that inherently occupy low-lying positions that are adjacent to high-lying landforms (e.g., glacial meltwater drainage channels) will be characterized for the most part by relatively cold microclimates. Alternatively, landforms that are associated with elevated topography (e.g., moraines and ice-contact terrain surrounding Mack Lake) typically will be distinguished by relatively warm microclimates. Variation in soil properties, particularly soil texture and the incidence of fine-textured soil banding, is similarly predictable with respect to specific landforms. For example, among the landforms of the Mack Lake burn, the incidence of fine-textured banding, and finer-textured soil in general, increases significantly with proximity to the ice-contact terrain. This observation is consistent with that of Kashian (1998), who found finer-textured materials in outwash physiographic systems to decrease in frequency with increasing distance from ice-contact physiographic systems.

Landscape Ecosystem Diversity and Kirtland's Warbler Occurrence

The Mack Lake burn is characterized by a remarkable diversity of landscape ecosystems occupied by Kirtland's warbler. In fact, the 5 landform-level ecosystems, and 11 landscape ecosystem types nested within them, are largely representative of the broad range of jack pine-dominated landscape ecosystems occupied by Kirtland's warbler across its 13-county range of occurrence in northern Lower Michigan. Historically, Kirtland's warbler habitat has often been considered (and indeed appears!) rather homogenous in terms of its general characteristics, i.e., large stands of young jack pine growing on Grayling sand. However, careful examination of the Mack Lake burn confirms that what is generically defined as Kirtland's warbler habitat, actually encompasses a great deal of ecological heterogeneity. The landform-level ecosystem map of the Mack Lake burn is, in part, a graphical expression of this heterogeneity (Figure 4.1). Thus, it appears that the Kirtland's warbler will occupy a wide range of landforms and constituent ecosystem types as long as jack pine of the appropriate height and spatial configuration are present. This observation is consistent with that of Kashian (1998), who associated Kirtland's warbler occurrence with 10 different kinds of jack pine-dominated landforms in north central Lower Michigan.

Ecosystem diversity, defined as the kinds and patterns of landscape ecosystems within a specified area (Lapin and Barnes 1995), is particularly important in that it exerts strong control over the potential duration that Kirtland's warbler will occupy a given area. In general, as ecosystem diversity increases, so increases site heterogeneity and the range of physiographic, climatic, and edaphic conditions present. Site heterogeneity in turn results in differential rates of jack pine growth and, consequently, differential patterns of Kirtland's warbler occupancy over time. All else being equal, sites supporting rapid jack pine growth will be colonized earlier and will be occupied for a relatively short duration whereas sites supporting slow jack pine growth will colonized later and will be occupied for a relatively long duration. Thus, areas characterized by several different kinds of landscape ecosystems (i.e., heterogeneous site conditions) will be colonized sooner and will remain occupied longer than areas characterized by only one or very few landscape ecosystems. Because site heterogeneity tends to increase with increasing land area, a large tract will potentially remain occupied by warblers for a longer period than a small tract assuming jack pine of the appropriate height and spatial configuration are present on both. This relationship may explain, in part, why warblers are thought to "prefer" large stands (Walkinshaw 1983, p. 35) and why the most successful warbler colonies have been associated with stands 200 acres and larger (Byelich 1976).

The lengthy occupancy of the Mack Lake burn by Kirtland's warbler (13 years through 1998) is largely attributable to the number of specific kinds of landscape ecosystems present and their spatial pattern of occurrence. The site heterogeneity is a product of glacial history, geomorphic processes, climate, soil properties, fire regime, and the combined influence of these factors on the composition and structure of the vegetation. The diversity of landscape ecosystems observed within the burn reflects site heterogeneity at multiple spatial scales. The spatially juxtaposed high- and low-elevation terrain features provide broad-scale physiographic and microclimatic heterogeneity. Nested within the high- and low-elevation terrain, landform-level ecosystems represent the meso-scale heterogeneity of physiography and related soil properties. Finally, landscape ecosystem types form a diverse mosaic within landforms. They are an expression of the heterogeneity of soil and vegetation, i.e., composition and community structure, at the finest spatial scale. Thus, the pronounced ecological diversity of the burn site is manifested in ecosystem units at all levels of the local ecosystem hierarchy (Figure 1.5). It follows that spatial and temporal patterns of Kirtland's warbler occurrence are more clearly understood and explained when considered in the context of a multiscale, multifactor landscape ecosystem framework.

The research presented herein provides a detailed record of the spatial and temporal pattern of Kirtland's warbler colonization and occupancy observed among the landform-level ecosystems of the Mack Lake burn (e.g., Figure 4.10; Table 4.12). However, several important caveats regarding the analysis and interpretation of the underlying data should be considered. First, census locations of singing-male warblers used in determining both the timing of landform colonization and the duration of landform occupancy (e.g., Table 4.12) do not represent actual Kirtland's warbler nest locations. Nest location data are virtually nonexistent because nests are well camouflaged and physically locating nests would likely disrupt breeding. However, because male warblers are fiercely territorial (Mayfield 1960, Walkinshaw 1983) and territory size is generally small (< 8.5 ha; Walkinshaw 1983), census locations are assumed to closely approximate nest locations.

Second, the accuracy of the census is based largely on the assumption that every male is counted and is counted only once. The census protocol itself is specifically designed to minimize double counting, and checks are made to ensure that birds counted on adjacent transect lines are not the same. Obviously, little can be done to make certain that every male warbler is counted because this requires not only that every potential nesting area is thoroughly checked, but also that every male sings such that it can be tallied. Because the Mack Lake burn has been such a large and successful nesting area, its annual census has probably been more thorough and more carefully conducted than that of other areas. Nevertheless, given the size of the census area and the density of the birds being counted, some measurement error is undoubtedly present. However, given that the analysis of spatial pattern is more heavily dependent on the relative number of birds distributed among landforms rather than on the absolute number, the affect of measurement error on the results is considered minimal.

Implications for the Management of Kirtland's Warbler

Under natural conditions the jack pine and jack pine-northern pin oak communities that form the breeding grounds of the Kirtland's warbler are produced only by wildfire (Mayfield 1960, p. 32). Due to the decrease in the number of large fires over the last half-century, increased reliance has been placed on jack pine plantations as the preferred method of providing suitable habitat for Kirtland's warbler populations. The first major effort to develop and maintain large tracts of jack pine specifically for use as warbler nesting habitat was made in 1957 (Mayfield 1963). Kirtland's warbler habitat management currently involves over 57,000 ha on 23 separate management areas on State and National Forest lands. In spite of these efforts, however, the majority of the habitat developed by planting on management areas has been generally less suitable than habitat produced naturally by wildfire (Kepler et al. 1996). The dramatic increase in the Kirtland's warbler population following wildfires at Bald Hill (1975) and Mack Lake (1980) has provided strong evidence in support of Probst (1986) and others who have suggested that a lack of suitable nesting habitat has been the primary factor limiting the species. Although a record 805 singing-male warblers were tallied in 1998 (Figure 1.2), the majority of these birds, 76% of which occupied plantation habitat, were probably the "overflow" that colonized new areas following the saturation of the Mack Lake burn (Barnes et al. 1998, p. 634). With the burn now nearing the end of its duration of occupancy (Figure 1.2), maintenance of current population levels will depend largely on the success of plantations, and more specifically on the ability of managers to successfully identify areas that can support large numbers of birds over the long term.

The landscape ecosystem approach, as applied to the 1980 Mack Lake burn, indicates that spatial and temporal patterns of Kirtland's warbler occurrence are grounded in the physical and biotic components of landscape ecosystems (Figure 5.1). The attributes of landscape ecosystems appear to provide a sound ecological explanation for why warblers differentially colonize and occupy specific landscapes across their breeding range. Thus, the landscape ecosystem approach has direct application to the management of the Kirtland's warbler. The approach provides managers with a useful tool for assessing the degree to which a potential management area will meet a given management objective. For example, if the goal of management is to provide plantation habitat that will support a warbler population relatively quickly (e.g., to rescue a crashing population), identifying a landform-level ecosystem that supports fast-growing jack pine (e.g., ice-contact terrain) would be appropriate. Alternatively, if the objective is to maximize the period of time that warblers will occupy a given area, identifying a landform-level ecosystem that is characterized by a diversity of constituent ecosystem types (i.e., heterogeneous site conditions) would be desirable. The study of the Mack Lake burn and its occupancy by Kirtland's warbler has been instrumental in encouraging managers to shift their focus from individual stands to entire landscapes. The findings at Mack Lake have also influenced, and have been incorporated into specific guidelines for locating warbler management areas in the context of a landscape ecosystem framework (Kashian 1998). In conclusion, there is little question that if the Kirtland's warbler population is to be sustained in the 21st century, habitat suitable in quality, quantity, and spatial orientation must be continuously produced (Kepler et al. 1998).

The landscape ecosystem approach represents a very practical means toward this most important end.

VI. SUMMARY AND CONCLUSIONS

Introduction

The Kirtland's warbler (*Dendroica kirtlandii* Baird) is a federally endangered songbird, and the rarest member of the wood warbler family (Parulidae) in North America. The breeding range of Kirtland's warbler is largely restricted to four counties in northern Lower Michigan where the bird nests only in ecosystems dominated by large tracts (> 32 ha) of young (5-23 year old), fire-prone jack pine, or jack pine mixed with northern pin oak. The warbler nests on the ground in stands characterized by dense jack pine canopy cover (20-60%) growing in a contagious pattern interspersed with numerous small openings. Historically, this characteristic pattern of vegetation was maintained by periodic wildfires. In the last half-century, however, fire suppression and forest fragmentation have greatly reduced the number of large fires and in turn the amount of available breeding habitat. The availability of breeding habitat is thought to be the single most important factor limiting the Kirtland's warbler population.

Kirtland's warbler is an inextricable part of the sand outwash plain, jack pine-oak forest landscape ecosystems in north central Lower Michigan. Landscape ecosystems are geographic, volumetric, layered segments of air and land (physiography and soil) plus organic contents (biota) extended areally over a particular part of the earth's surface. Ecosystems occur nested within one another in a hierarchy of spatial sizes at regional (regions, districts, and subdistricts; Albert et al. 1986) and local (physiographic systems, landform-level ecosystems, and landscape-ecosystem types; Barnes et al. 1998, p. 34-40) levels. Because Kirtland's warbler populations belong to and depend on complex ecological systems, a more complete understanding of warbler behavior can be gained when the bird is studied in the context of its supporting ecosystems.

Although considerable research has focused on the bird itself, comparatively little detailed information was available on the site-specific landscape ecosystems that form the habitat of Kirtland's warbler. The 1980 Mack Lake burn provided an opportunity to study Kirtland's warbler occurrence and behavior in relation to the landscape ecosystems of a highly diverse and productive area of its breeding grounds. Research was conducted on the site of the 9,700-ha burn from 1986-1988 (Barnes et al. 1989, Zou et al. 1992), and a framework of local landscape ecosystems was developed. Two prominent high- and low-elevation terrain features and 11 constituent landscape ecosystem types were distinguished and described. The results demonstrated that specific kinds of landscape ecosystems and their spatial pattern of occurrence markedly affect the timing of warbler colonization and the duration of warbler occupancy.

The three-year study of the Mack Lake burn, coupled with continued monitoring of the Kirtland's warbler population at Mack Lake from 1989-1994, provided baseline information to examine the long-term (1986-1997) spatial pattern of Kirtland's warbler occupancy. Benefits derived from such research include 1) a complete and detailed record of warbler occurrence in an area of highly productive warbler habitat beginning with initial site colonization and ending with site abandonment, and 2) an understanding of the interrelated physical and biotic factors (e.g., physiography, microclimate, soil, and vegetation) that drive observed changes in the spatial pattern of warbler occurrence over time.

My research was part of a larger project initiated in 1995 to study patterns of Kirtland's warbler colonization and occupancy in relation to the physical and biotic components of landform-level landscape ecosystems on the breeding grounds in northern Lower Michigan (Kashian 1998). Its overall goal was to provide wildlife biologists and land managers with a landscape ecosystem framework for monitoring Kirtland's warbler occurrence over time, and for determining *apriori* areas that are best suited for Kirtland's warbler management.

The general objectives of my research were to develop an ecological framework of landform-level ecosystems for the Mack Lake burn and to determine the spatial and temporal pattern of colonization and occupancy of these ecosystems by Kirtland's warbler. Specific objectives were to:

1) identify, describe, and map the physiographic systems and landform-level ecosystems of the Mack Lake burn using a multi-factor approach.
2) contrast the magnitude of variation in microclimate (temperature) among the high-elevation terrain, low-elevation terrain, and glacial meltwater drainage channels of the Mack Lake burn.
3) determine the spatial pattern of colonization and occupancy of the Mack Lake burn by the Kirtland's warbler from 1986-1997 in relation to landform-level ecosystems and their physical (physiography, microclimate, and soil) and biotic (tree growth, stand structure, and ground-cover composition) components.

Methods

A multifactor landscape ecosystem approach was used to develop a landform-level ecosystem classification and map of the Mack Lake burn study area. An iterative method was employed whereby successive approximations of putative landform units were determined. Each approximation served as a working hypothesis that was tested in the field and revised as necessary to yield a final classification and map.

Fieldwork was conducted during the summers of 1995, 1996, and 1997. Field reconnaissance and transect sampling were used to test and refine the delineation of tentative landform boundaries. Forty-nine 10 x 20-m permanent plots were sampled among 5 putative landform units in order to 1) characterize each unit based on physiographic, soil, and vegetative factors and 2) evaluate the degree of distinctness of each landform using univariate (analysis of variance) and multivariate (principal components and discriminant analyses) statistical methods.

A microclimate study was conducted to document the magnitude of temperature variation among major physiographic levels within the Mack Lake burn. Fourteen temperature recording stations were established among 3 levels: high-elevation terrain (n = 6), low-elevation terrain (n = 6), and glacial meltwater drainage channels (n = 2). Each station consisted of 2 maximum-minimum thermometers placed 30 cm above the ground. A total of 23 readings were taken per station (twice per week) during the 1995 field season; 12 additional readings were taken per station (once per week) during the 1997 field season. One-way analysis of variance was used to test for significant differences in average maximum and minimum temperature among physiographic levels. Repeated measures analysis of variance was used to test for significant differences in the season-long patterns of maximum and minimum temperature change among physiographic levels.

Annual census records were acquired for the Mack Lake Kirtland's Warbler Management Area for the period 1986-1997. The spatial and temporal pattern of Kirtland's warbler occurrence was examined and interpreted in relation to landform-level ecosystems and their physical and biotic characteristics. Univariate (simple linear regression) and multivariate (mutivariate analysis of variance) statistical methods were used to examine the relationship between spatial position and year of occupancy (1986-1997). In addition, Chi-square analyses were used to assess the significance of the pattern of warbler distribution among landform-level ecosystems over time.

Results and Conclusions

1. Two high-elevation and four low-elevation landform-level ecosystems were identified, described, and mapped within the Mack Lake burn study area. Landform units were distinguished in the field based on characteristic differences in physiography, microclimate, soil, and vegetation. An ecological classification integrating current and previous (Barnes et al. 1989, Zou et al. 1992) research was developed for the range of hierarchical ecosystem units recognized within the burn. Two major physiographic features (high- and low-elevation terrain) constitute the broadest level of the classification. Nested within and composing the high- and low-elevation terrain features were landform-level ecosystems. High-elevation landforms include abruptly hilly ice-contact terrain and level to gently sloping outwash plains; low-elevation landforms range from broad pitted-outwash plains to deep glacial meltwater drainage channels. Within landforms, 11 individual landscape-ecosystem types represent the finest level of ecosystem delineation and classification.

2. The Kirtland's warbler occupied five landform-level ecosystems within the Mack Lake burn. The 5 landforms, and 11 ecosystem types nested within them, represent a remarkable diversity of ecosystems dominated by jack pine and jack pine-northern pin oak communities. The diversity of warbler-occupied landscape ecosystems within the Mack Lake burn alone (e.g., ice-contact terrain, pitted-outwash plains, glacial meltwater drainage

channels, etc.) is largely representative of the broad range of ecosystems occupied by Kirtland's warbler across its 13-county range of occurrence in northern Lower Michigan.

3. The ecological distinctness of the five jack pine-dominated landform-level ecosystems was supported by the results of multivariate statistical analyses. Landforms were best distinguished when the sum total of physical (physiography and soil) and biotic (tree height, stand structure, and ground-cover composition) factors were combined in the analysis. Landforms were distinguished more clearly by the variable set based on physiographic and soil characteristics than by the set based on vegetative characteristics alone.

4. The examination of Kirtland's warbler occurrence from 1986-1997 in relation to the spatial framework of landform-level ecosystems confirmed and further revealed the extent of the high- to low-elevation pattern of warbler colonization and occupancy first recognized by Barnes et al. (1989). During the first three years of warbler occupation (1986-1988), 62% of the population occupied the high-elevation terrain landforms. However, in the last three years of record (1995-1997), 86% of the population occupied the low-elevation terrain landforms. Tracking the systematic progression of the population spatial mean over time showed that Kirtland's warbler favored landforms in the high-elevation terrain from 1986-1988 and landforms in the low elevation terrain from 1989-1997. A significant decreasing relationship ($r^2 = 0.90$; $p < 0.00001$) between the average elevation of the warbler population and the year of occupancy further demonstrated the extent of the high- to low-elevation shift. Finally, a highly significant dependent relationship ($p < 0.00001$) was observed between the distribution of warblers among landform-level ecosystems and the year of occupancy from 1986-1997.

5. The timing of initial Kirtland's warbler colonization and the duration of warbler occupancy among landform-level ecosystems can be explained in terms of the physical (microclimate and soil) and biotic (tree height) characteristics of the individual landform units. For example, landform VI (ice-contact terrain), characterized by relatively high soil water and nutrient availability, a warm microclimate, and fast-growing jack pine, was colonized in 1986 and remained occupied for only 4 years. Conversely, landform I (glacial meltwater drainage channels), characterized by relatively low soil water and nutrient availability, a cold microclimate, and slow-growing jack pine, was not colonized until 1991 but remained occupied for 7 years. In addition, landform V (high-elevation outwash plains), composed of diverse landscape ecosystem types, i.e., a mosaic of productive and unproductive sites, was initially colonized in 1986, and was still occupied after 12 years.

6. Marked microclimatic variation was observed among the three major physiographic levels (high-elevation terrain, low-elevation terrain, and glacial meltwater drainage channels) of the Mack Lake burn. Cold-air drainage, even in terrain with relatively low relief (< 50 m over 6.5 km), results in significant, season-long differences in average maximum and minimum temperature among levels. In the low-elevation terrain, weekly and daily maximum temperatures were significantly lower than in the high-elevation terrain, averaging 2.7°C (4.8°F) lower in each case. Weekly and daily minimum temperatures in the low-elevation terrain were also significantly lower than in the high-elevation terrain, averaging 3.0°C (5.4°F) and 1.6°C (2.8°F) lower, respectively. Although maximum and minimum temperatures in the glacial meltwater channels were consistently lower than in the adjacent uplands of the low-elevation terrain, these differences were not statistically significant. In general, the Mack Lake burn is subject to fluctuations in temperature over a

markedly wider range, i.e., characterized by higher maximum and lower minimum temperatures, than that of areas outside of, and adjacent to, the basin. Average weekly and daily temperatures within the burn fluctuated over a range of 34.7°C (62.6°F) and 23.1°C (41.6°F), respectively. At Mio, however, weekly and daily temperatures fluctuated over a far narrower range, averaging just 26.9°C (48.4°F) and 17.8°C (32.2°F), respectively. The exceedingly harsh, topographically-mediated microclimate of the Mack Lake burn is important in that it favors the early colonization and long-term occupancy of the area by Kirtland's warbler.

7. The 1980 Mack Lake wildfire consumed ca 9,700 ha of pine and pine-oak communities across a diversity of landform-level ecosystems and constituent landscape ecosystem types. The juxtaposition of high- and low-elevation landforms, and the fine-scale mosaic of ecosystem types within them, has prolonged the occupancy of the Mack Lake burn by Kirtland's warbler well beyond what would be expected if the area were characterized by less heterogeneous site conditions. My research demonstrates that ecosystem diversity, i.e., the number of specific kinds of landscape ecosystems, and their spatial pattern of occurrence, markedly affect the potential duration that warblers will occupy an area. Site heterogeneity as a function of local ecosystem diversity is, therefore, a key factor to consider when identifying areas that can be managed for long-duration (ca 12-15 years) Kirtland's warbler occupancy.

8. The research indicates that studies with a focus on landscape ecosystems, and their components of physiography, climate, soil, and vegetation, provide a sound ecological framework for understanding the spatial and temporal behavior and occurrence of Kirtland's warbler populations. The landscape ecosystem approach, therefore, can be usefully applied

throughout the breeding range of the Kirtland's warbler to assist managers in determining appropriate management areas for the continued recovery of this endangered species.

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APPENDICES

APPENDIX A: ECOLOGICAL SPECIES GROUPS OF THE MACK LAKE BURN, OSCODA CO., NORTHERN LOWER MICHIGAN[1]

SPECIES GROUP	ECOLOGICAL CHARACTER
1. *Arctostaphylos uva-ursi* group *Arctostaphylos uva-ursi* *Comptonia peregrina* *Epigaea repens* *Antennaria neglecta* *Polygala polygama* *Potentilla tridentata* *Andropogon gerardii* *Schizachyrium scoparium* *Carex pensylvanica* *Danthonia spicata* *Panicum linearifolium* *Oryzopsis pungens*	Very wide range of occurrence: from very dry and very infertile to moderately moist and moderately fertile; species do not exhibit greater coverage where better moisture and nutrient conditions exist.
2. *Vaccinium angustifolium* group *Vaccinium angustifolium* *Amelanchier sanguinea* *Prunus pumila* *Prunus virginiana* *Helianthus longifolia* *Solidago hispida* *Solidago spathulata*	Very wide range of occurrence: from very dry and very infertile to moderately moist and moderately fertile; species take advantage of slightly better moisture and nutrient conditions by having greater coverage on dry, infertile sites.
3. *Prunus pensylvanica* group *Prunus pensylvanica* *Melanpyrum lineare* *Physalis virginiana* *Deschampsia flexuosa*	Ranges from very dry to very slightly moist, and very infertile to slightly infertile; species exhibit the greatest coverage on dry and very infertile sites.
4. *Ceanothus ovatus* group *Ceanothus ovatus* *Gaylussacia baccata* *Hamamelis virginiana* *Anemone cylindrica* *Aster ptarmicoides* *Convolvulus spithamaeus* *Senecio pauperculus* Bromus kalmii	Ranges from very dry to dry and from infertile to slightly infertile; species exhibit the greatest coverage on very dry, slightly infertile sites.

[1] As determined by Barnes et al. (1989)

SPECIES GROUP	ECOLOGICAL CHARACTER
5. *Gaultheria procumbens* group *Gaultheria procumbens* *Amelanchier spicata* *Crataegus* spp. *Diervilla lonicera* *Lonicera dioca* *Frageria virginiana* *Pyrola elliptica* *Taenidia integerrima*	Ranges from very dry to moderately moist and from infertile to moderately fertile; not typically found on very infertile sites; species occur most often on very slightly moist, slightly fertile sites.
6. *Rosa blanda* group *Rosa blanda* *Populus grandidentata* *Populus tremuloides* *Prunus serotina* *Rubus flagellaris* *Salix humilis* *Maianthemum canadense* *Pteridium aquilinum* *Oryzopsis asperifolia* *Schizachne purpurascens*	Ranges from dry to moderately moist and from infertile to moderately fertile; species take advantage of the most fertile and moist sites by having the greatest coverage on the moderately fertile and moderately moist sites.

APPENDIX B: LANDSCAPE ECOSYSTEM TYPE DESCRIPTIONS OF THE MACK LAKE BURN, OSCODA CO., NORTHERN LOWER MICHIGAN[1]

ECOSYSTEM 1: Low-elevation outwash plain; deep, acid, medium and medium-fine sand.

Physiography

Flat to gently sloping outwash plain (0-6% slope); elevation 365-372 m – the lowest of all upland ecosystems.

Soils – Grayling series

Texture: Deep medium sand with 20-40% fine sand plus very fine sand. Horizons lack lamellae or bands of fine texture.

Drainage: Excessively drained – lacking bands of fine texture to slow drainage.

Development: A/E horizon generally 2.5-3.5 cm thick; C horizon occurs at an average depth of 101 cm.

Stone and gravel content: Lacking distinct pebble/cobble band in the upper 150 cm. Pebbles may be scattered throughout the B horizon; total content typically less than 2%. Gravel bands frequently found at depths of 200-400 cm.

pH: Weighted pH of upper 150 cm is typically the most acid of all ecosystems. From 10-30 cm the weighted pH averages 4.9. pH from 30-150 cm averages 5.0. Average depth to a field pH of 7.0 or greater occurs at 302 cm (ranging from 200-400 cm), one of the deepest of all ecosystem types.

Discussion and comparison with other ecosystems

This ecosystem covers a major portion of the low-elevation outwash plain and may be considered the standard, non-depression ecosystem type for the low-elevation terrain.

Distinguished from ecosystem 2 by a lower relative elevation, and more acid sands to greater depths. Distinguished from ecosystem 3 by the absence of significant fine-textured bands.

[1] As described by Barnes et al. (1989)

ECOSYSTEM 2: Higher, isolated outwash plateaus between major channels in low-elevation outwash plain: deep medium sand.

Physiography

Flat to gently sloping (0-6% slope). Relatively higher, isolated outwash plateaus between the major channels of the low-elevation outwash plain.

Soils

Texture: Deep medium sand. Fine sand plus very fine sand may compose up to 25% of the soil. Gravel layers may be found at depths of 120-400 cm.

Drainage: Excessively drained.

Development: A/E horizon is 3-4 cm thick. The C horizon occurs at an average depth of 94 cm.

Stone and gravel content: Pebbles may be scattered throughout the upper 150 cm. A distinct pebble/cobble layer may or may not be present.

pH: Weighted pH from 30-150 cm averages 5.6. Average depth to a field pH of 7.0 or greater occurs at 168 cm.

Discussion and comparison with other ecosystems

The isolated, relatively high topographic position within the low-elevation outwash plain indicates a slightly different history in the deposition and erosion of outwash parent material by glacial meltwater.

Distinguished from the low-elevation outwash of ecosystem 1 by a relatively higher and isolated position, a higher pH from 30-150 cm, a shallower depth to an average pH of 7.0 or greater, and a slightly thicker E horizon. Ecosystem 2 tends to have more coarse plus very coarse sand and less fine plus very fine sand than ecosystem 1.

ECOSYSTEM 3: Sand or loamy sand over bands of fine texture in low-elevation outwash plain.

Physiography

Flat to gently sloping (0-3% slope). Occurs at various elevations in the low-elevation outwash plain.

Soils

Texture: Medium and fine sand or loamy sand over bands (total thickness greater than 10 cm) of fine texture (loam, clay loam, and clay). Bands occur at depths up to 3 meters.

Drainage: Somewhat excessively drained to well drained. Drainage impeded by bands of fine texture at varying depths – usually below 50 cm.

Development: Oe/Oa horizon relatively thick (typically 2.5-4.5 cm thick); A/E horizon typically 3-4 cm thick; C horizon occurs at an average depth of 115 cm.

Stone and Gravel Content: Pebbles occur occasionally in the upper 150 cm.

pH: Weighted pH from 30-150 cm is relatively high, averaging 6.1. Average depth to field pH of 7.0 or greater occurs at 157 cm, and at least at the depth of fine-textured bands.

Discussion and comparison with other ecosystems

Distinct from all other low-elevation outwash ecosystems due to band(s) of finer texture, loamy sand horizons often present in the upper 150 cm, and higher pH at depths from 30-150 cm. The fine-textured bands significantly increase moisture and nutrient availability.

ECOSYSTEM 4: Outwash drainage channel; deep, somewhat excessively drained sands with distinct pebble/cobble layer in the upper 50 cm.

Physiography

Major outwash drainage channels eroded by glacial meltwater streams. Channels are typically 6-15 m below the general land level and act as cold air sinks (frost pockets), especially on days with little wind. The channel bottom is flat with slopes ranging from 0-2%. Channels range from 160-1125 m wide.

Soils

Texture: Deep medium sands with variable amounts of fine plus very fine sand. A distinct pebble/cobble layer occurs in the upper 50 cm. Some areas may have horizons with a higher percentage of fine plus very fine sand or bands of fine texture.

Drainage: Somewhat excessively drained; pebble/cobble band slows drainage somewhat.

Stone and gravel content: Mainly limited to a pebble/cobble band in the upper 50 cm. Pebbles and cobbles occupy greater than 30% of the volume of the band. Gravel is generally not scattered throughout the horizons.

pH: Weighted pH from 30-150 cm averages 5.9. Average depth to field pH of 7.0 or greater occurs at 170 cm.

Discussion and comparison with other ecosystems

Distinguished from other outwash ecosystems by lower relative elevation, lower minimum temperatures, and slightly better moisture conditions (due to the pebble/cobble band).

Distinguished from depressions in the low-elevation outwash plain by the inability to trap cold air as well, and by the distinct pebble/cobble band.

ECOSYSTEM 5: Depressions in the low-level outwash plain; sand to sandy loam soils.

Physiography

Closed depressions forming a pitted outwash plain, typically 1.5-6.0 m below the general land level.

Soils

Texture: Soils variable; medium sand (with 25-40% fine sand) to loamy medium sand. Bands of fine texture may be present.

Drainage: Somewhat excessively drained to excessively drained; drainage may be slowed by loamy sands and fine-textured bands.

Development: A/E horizon moderately to well developed (4 cm thick on average) likely due to denser grass roots. Upper B horizon typically less yellow or darker and grayer in color than those in low-elevation uplands. Depth to C horizon highly variable.

Stone and gravel content: Typically with 0-1% pebbles and cobbles in the upper 150 cm, though a pebble/ cobble band may be present.

pH: Weighted pH from 30-150 cm is relatively low, averaging 5.1. pH from 10-30 cm also averages 5.1. Depth to field pH of 7.0 or greater is relatively deep, averaging 248 cm.

Discussion and comparison with other ecosystems

Distinguished from low-elevation upland ecosystems by locally lower topographic position, resulting extreme microclimate, relatively thick A/E horizon, and less yellow or darker and grayer upper B horizon. Distinguished from the outwash channel by a lack of definite pebble/cobble layer, and a less yellow or darker and grayer darker upper B horizon.

The lower relative elevation of the closed depressions results in lower minimum temperatures due to the trapping of cold air. Minimum temperatures for depressions of all depths (from 1.5-6 m) varied similarly with respect to their associated uplands – depression minimum temperatures were 4-7°F lower than adjacent upland minimum temperatures. Differences in maximum temperature did not show such a clear trend.

ECOSYSTEM 6: High-elevation outwash; deep medium sand.

Physiography

Flat to gently sloping terrain (0-5% slope); elevation 369-381 m – typically 6-12 m higher than ecosystems in the low-elevation outwash plain.

Soils

Texture: Deep medium sand; up to 25% fine sand plus very fine sand.

Drainage: Excessively drained.

Development: A/E horizon moderately well-developed – 4 cm thick on average; C horizon occurs at an average depth of 95 cm.

Stone and gravel content: Pebbles/cobbles scattered in the upper 150 cm, distinct pebble/cobble bands sometimes present. Gravel bands found at depths of 150-350 cm.

pH: Weighted pH from 10-30 cm averages 5.1. pH from 30-150 cm averages 5.5. Average depth to field pH of 7.0 or greater extremely variable, ranging from 73-370 cm.

Discussion and comparison with other ecosystems

Distinct from high-elevation outwash ecosystems 8 and 9 by lack of fine-textured bands. Distinguished from ecosystem 7 by having less than 25% fine plus very fine sand from 10-30 cm, or by the lack of very thin bands of fine texture. Distinguished from ecosystem 10 by more level topography.

Distinguished from low-elevation outwash ecosystems by a higher absolute elevation, hence a warmer microclimate.

ECOSYSTEM 7: High-elevation outwash; relatively high proportion of fine sand and/or thin bands of fine texture totaling less than 5 cm in thickness.

Physiography

Flat with 0-2% slopes; elevation 369-381 m.

Soils

Texture: Deep sands with 25% or greater of fine sand plus very fine sand from 10-30 cm. May have lamellae of fine textured soil totaling less than 5 cm in thickness.

Drainage: Somewhat excessively drained to excessively drained. Drainage slowed somewhat by fine sand and/or bands of fine texture.

Development: The A/E horizon averages 3.7 cm. The depth of the C horizon is one of the shallowest of the 11 ecosystem types, occurring at a depth averaging 64 cm.

Stone and gravel content: Pebbles and/or cobbles may be present or absent.

pH: Weighted pH from 30-150 cm averages 5.2. Average depth to a field pH of 7.0 or greater is moderately deep at 223 cm.

Discussion and comparison with other ecosystems

Distinct from ecosystem 6 by having greater than 25% fine plus very fine sand from 10-30 cm, or by having very thin bands of fine texture. Distinct from ecosystems 8 and 9 by lacking bands of fine texture. Distinct from ecosystem 10 by more level topography, and usually by a slightly thinner E horizon. Ecosystem 7 also typically has a thin Oe/Oa horizon (averaging 1 cm thick), and a relatively shallow B horizon.

Distinguished from low-elevation outwash ecosystems by a higher absolute elevation, hence a warmer microclimate.

ECOSYSTEM 8: High-elevation outwash; loamy sand and medium to fine sand in upper B horizon over bands of loam totaling 5-10 cm in thickness.

Physiography

Nearly flat to gently sloping (1-5% slope); elevation 369-381 m.

Soils

Texture: Loamy sand from 10-30 cm. From 30-150 cm medium sand with 30-40% fine plus very fine sand and with bands of fine texture (usually sandy loam); total thickness of bands measures 5-10 cm typically at depths of 70-170 cm.

Drainage: Somewhat excessively drained. Drainage is slowed by loamy sands in the upper B horizon and by fine-textured bands.

Development: C horizon occurs at an average depth of 105 cm.

Stone and gravel content: Pebbles and cobbles occur either scattered throughout the B horizon or in a band confined to the upper 150 cm.

pH: Weighted pH from 30-150 cm is relatively high averaging 5.8, and typically greater than 5.4. Average depth to field pH of 7.0 or greater is moderately deep, occurring at 200 cm.

Discussion and comparison with other ecosystems

Distinct from other high-elevation outwash ecosystems by having loamy sand and sand over bands of loam totaling 5-10 cm in thickness. pH from 30-150 cm is greater than 5.4 while pH from 30-150 cm in ecosystems 7 and 10 is typically less than 5.4. Distinct from ecosystem 10 by having more level topography.

Distinguished from low-elevation outwash ecosystems by a higher absolute elevation, hence a warmer microclimate.

ECOSYSTEM 9: High-elevation outwash; loamy sand throughout upper 80 cm or sands and loamy sand over a layer of fine-textured soil (sandy loam to clay) greater than 10 cm thick.

Physiography

Flat to gently sloping (0-2% slope); elevation 370-381 m.

Soils

Texture: Loamy sand throughout upper 80 cm, or sands (medium or fine) and loamy sand in upper horizons underlain by a single layer of fine-textured soil (sandy loam, clay loam, or clay) greater than 10 cm thick at depths of 60-120 cm.

Drainage: Somewhat excessively drained. Drainage slowed by loamy sand horizons in the upper 150 cm or by a layer (greater than 10 cm thick) of fine textured soil.

Development: A/E horizon relatively thick, ranging from 3-5 cm. C horizon occurs at a moderate depth averaging 93 cm.

Stone and gravel content: Pebbles and cobbles occur scattered throughout horizons and in distinct bands. Pebbles/cobbles occupy 1-13% of the upper 150 cm.

pH: Weighted pH form 30-150 cm averages 5.6. Average depth to pH of 7.0 or greater occurs at a depth of 167 cm.

Discussion and comparison with other ecosystems

Distinguished from ecosystem 7 and 8 by loamy sand throughout upper 80 cm or a single band (greater than 10 cm thick) of fine textured soil, and resulting improved moisture and nutrient availability.

Distinguished from low-elevation outwash ecosystems by a higher absolute elevation, hence a warmer microclimate.

ECOSYSTEM 10: Ice-contact terrain.

Physiography

Very hilly with slopes varying from 3-30%; elevation 378-390 m.

Soils – Rubicon series

Texture: Deep medium sand with up to 40% fine plus very fine sand. Coarse sand and gravel often found at depths of 200-400 cm.

Drainage: Excessively drained.

Development: A/E horizon is moderately well-developed ranging from 4-6 cm, and averaging 4.5 cm. Depth to C horizon is moderate, averaging 95 cm.

Stone and gravel content: Pebbles and cobbles may be scattered throughout horizons in the upper 150 cm.

pH: Weighted pH from 30-150 cm averages 5.2. Depth to pH of 7.0 or greater is relatively deep, averaging 264 cm.

Discussion and comparison with other ecosystems

Very hilly topography distinguishes this ecosystem from all others. Distinct from depressions due to a higher relative elevation, and resulting warmer microclimate.

ECOSYSTEM 11: Depressions in high-elevation outwash terraces and ice-contact terrain.

Physiography

Closed depressions located at the general land level of 369-384 m. Depression depths vary from 3-15 m below the general land level.

Soils

Texture: Soils variable; often medium to medium-fine sand and loamy sand horizons, though upper horizons can vary from sand to sandy loam. Sandy loam bands may occur as deep as 300 cm.

Drainage: Varies from excessively to well drained.

Development: A/E horizon typically thickest of all ecosystem types, averaging 8.4 cm. The B horizon is typically darker and grayer than that of upland ecosystems (often with a Munsell color notation of 10 YR 3/4). Average depth to C horizon is relatively shallow – 76 cm.

Stone and gravel content: Variable; pebbles/cobbles absent to concentrated in some horizons.

pH: Weighted pH from 30-150 cm averages 5.2. Depth to pH of 7.0 or greater is moderately deep, ranging from 200-400 cm.

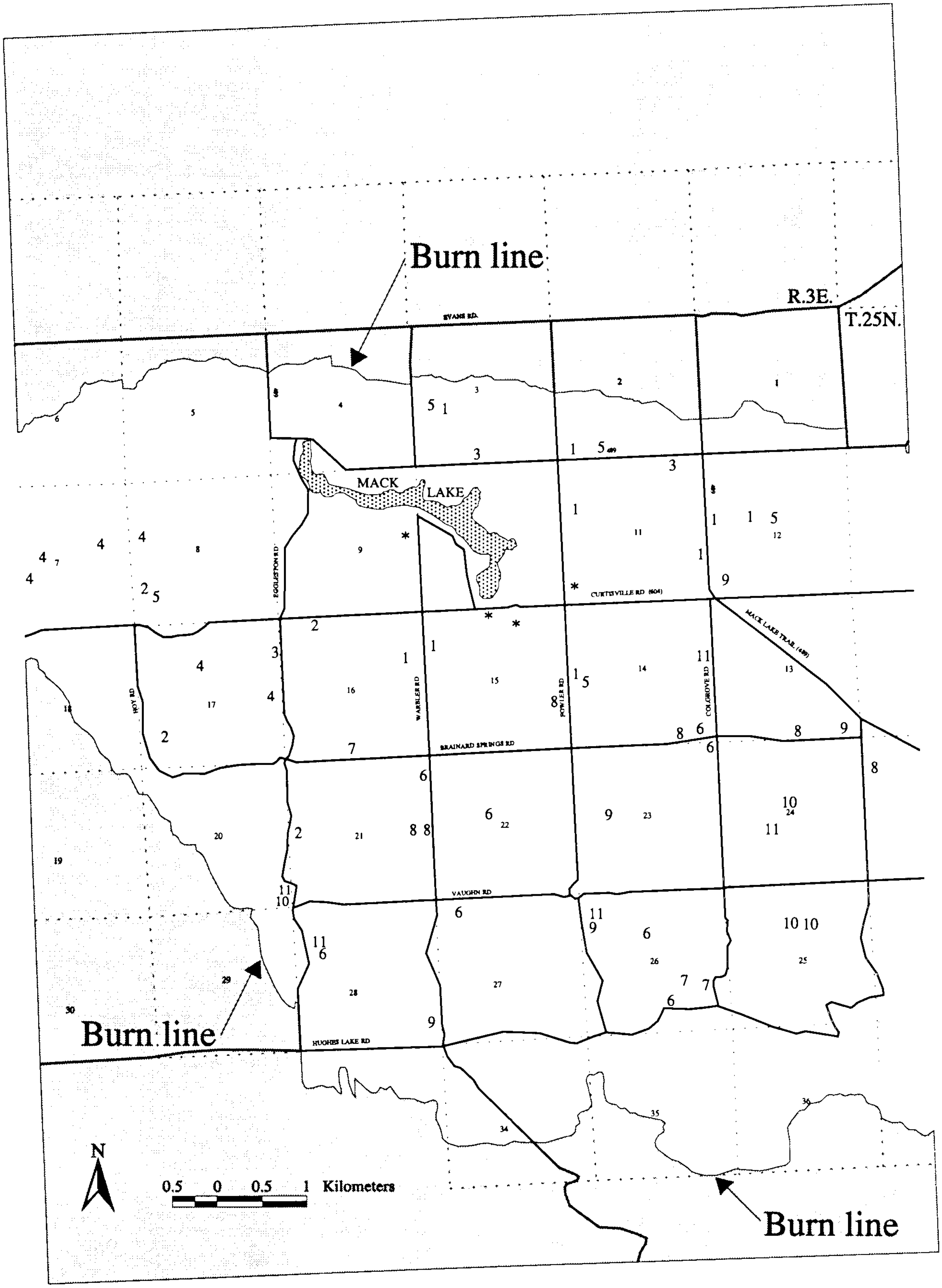
Discussion and comparison with other ecosystems

The lower relative elevation of depressions results in lower minimum temperatures due to the trapping of cold air. The difference in minimum temperature observed between depression bottoms and adjacent high-elevation uplands increases with increasing depression depth.

Deeper depressions (those greater than 20 ft) have slightly higher (2-4° F) maximum temperatures than their associated uplands, whereas shallower depressions have slightly lower (2-4° F) maximum temperatures than their associated uplands.

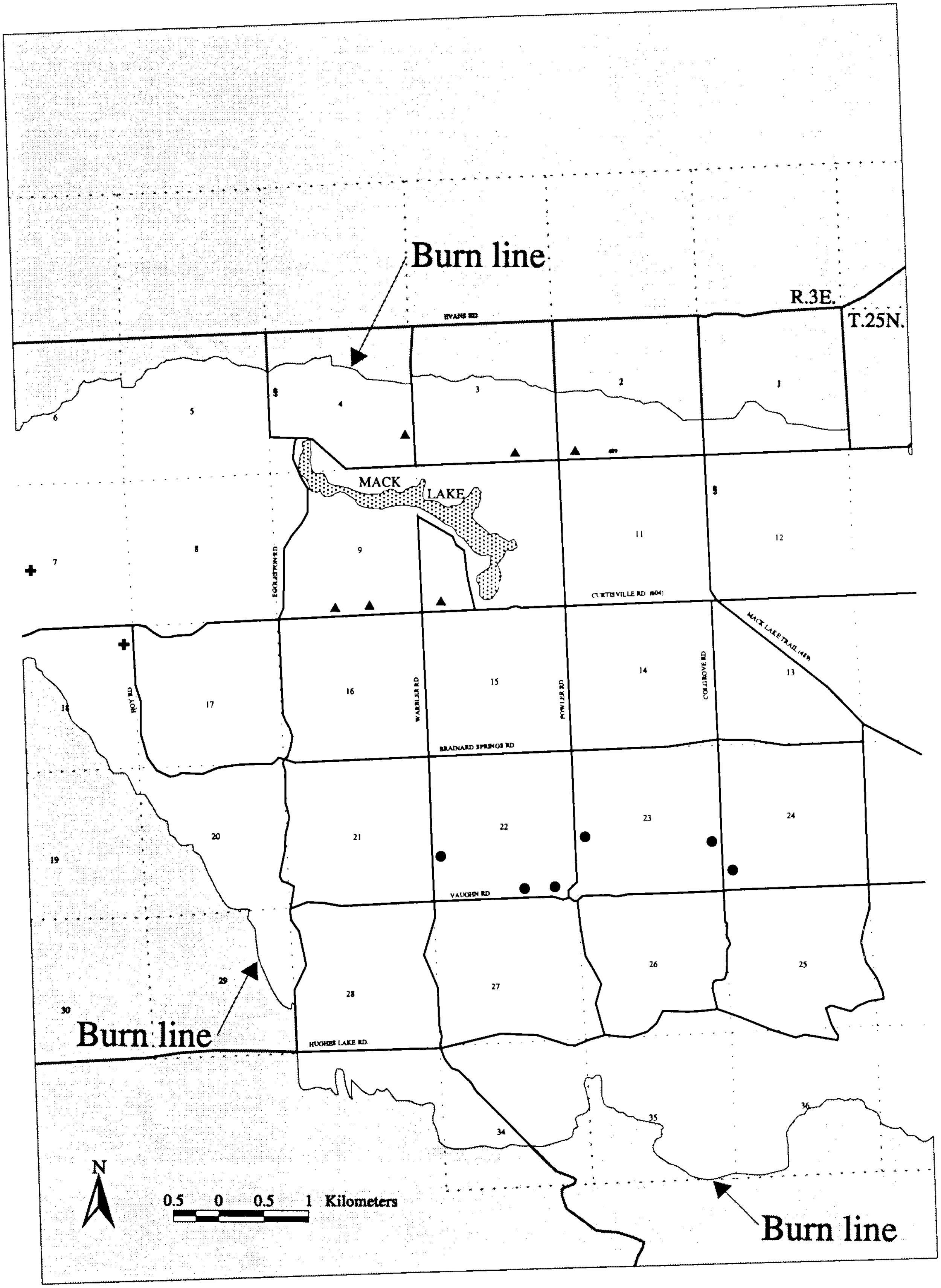
Distinguished from ice-contact terrain and all high-elevation outwash ecosystems by lower relative topographic position and more extreme microclimate. Distinguished from low-elevation outwash depressions by the higher absolute elevation of the general land level, the greater depression depths, and the greater occurrence of fine-textured soil horizons. Distinguished from all other ecosystems by a thicker A/E horizon and a darker colored upper B horizon.

APPENDIX C: SAMPLE PLOT LOCATIONS[1]



[1] Sample-plot locations are shown by large numbers whose value indicates the landscape-ecosystem type (Table 1.1). Public land survey sections are shown by small numbers. Asterisks (*) indicate sample-plot locations in a previously unidentified landscape-ecosystem type.

APPENDIX D: TEMPERATURE RECORDING STATION LOCATIONS[1]



[1] Locations of temperature recording stations visited in 1995 indicated by a "●" in the high-elevation terrain, a "▲" in the low-elevation terrain, and a "✚" in the glacial meltwater drainage channels.