

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

by

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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

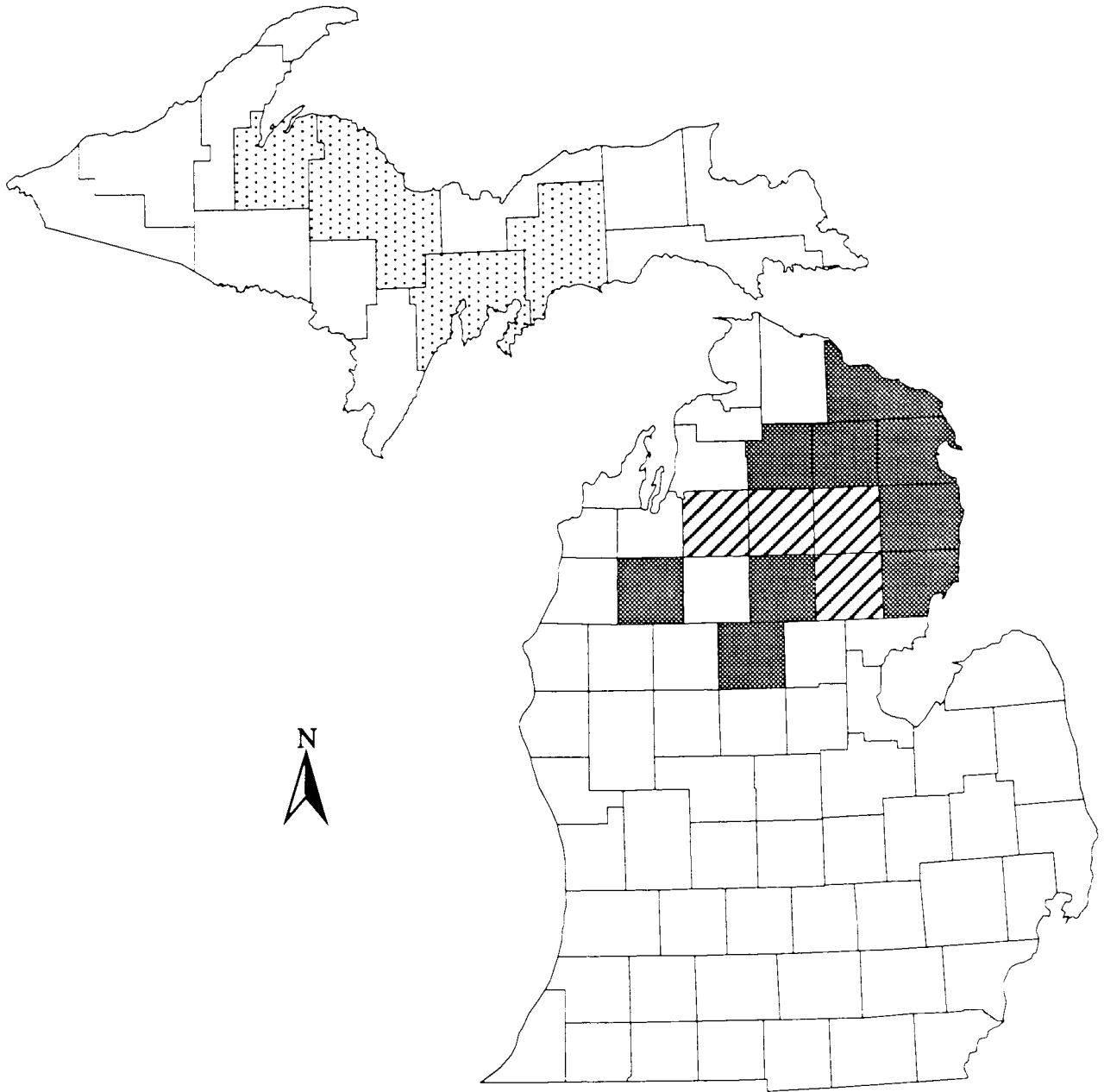


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Central states and parts of Canada (Tilghman 1979; Walkinshaw 1983, p. 17; Probst 1986). breeding has never been documented outside of northern Michigan (Probst 1986).

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 ellipsoidalis* 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

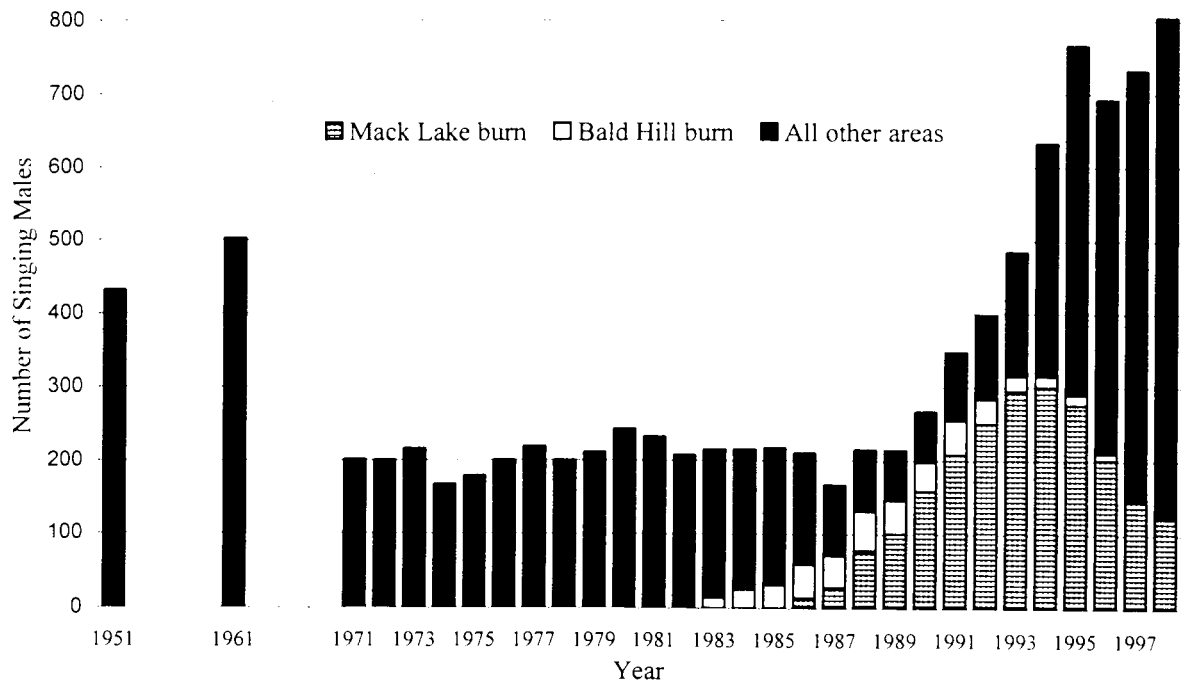


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in cowbird parasitism, the ensuing recovery effort became focused instead on the availability of suitable breeding habitat (Ryel 1981b; Probst 1986, 1988). The amount of suitable habitat, and thus the number of Kirtland's warblers, is thought to have 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 Württemberg (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.

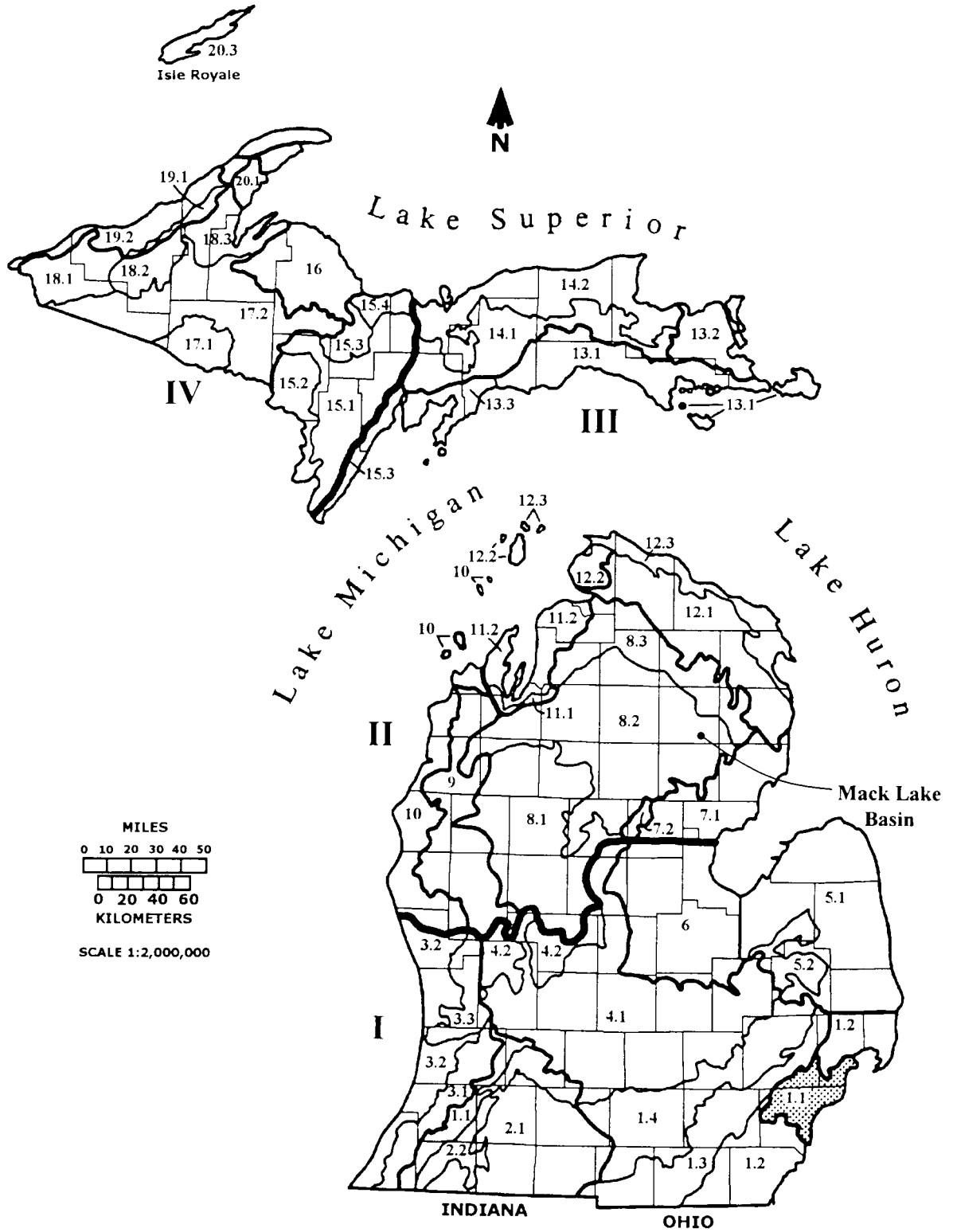


Figure 1.3. Map of regional landscape ecosystems of Michigan. Three hierarchical levels are mapped: Regions I-IV, Districts 1 to 20, and Subdistricts within many Districts. (After Albert et al. 1986.)

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*

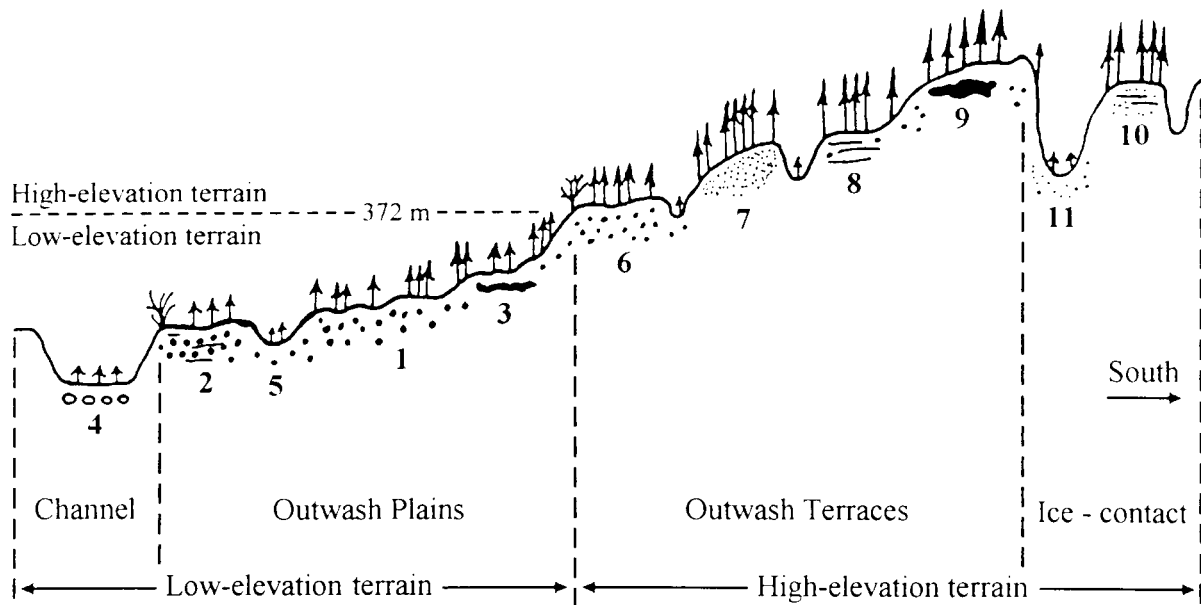


Figure 1.4. Physiographic diagram of part of the Mack Lake burn, Oscoda Co., northern Lower Michigan illustrating the spatial arrangement of high- and low-elevation terrain features and constituent landscape ecosystem types (1-11). The boundary between the high- and low-elevation terrain was arbitrarily 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

