Landscape Ecosystems of the Mack Lake Burn, Northern Lower Michigan, and the Occurrence of the Kirtland's Warbler

Wayne S. Walker, Burton V. Barnes, and Daniel M. Kashian

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 northern Michigan. Although considerable research has focused on the bird, comparatively little information is available on the specific landscape ecosystems occupied by the warbler. The 9,700 ha Mack Lake burn provided an opportunity to track the pattern of Kirtland's warbler occurrence in relation to the ecosystems of a highly diverse and productive area of its breeding range. Using a multifactor landscape ecosystem approach, two high-elevation and four low-elevation landform-level ecosystems were identified, described, and mapped. The spatial pattern of warbler occurrence over time was strongly mediated by the physical and biotic components of the ecosystems. During the first 3 yr of warbler occupation (1986–1988), the high-elevation landforms, characterized by relatively warm temperatures, moister, more fertile soils, and faster growing jack pines, supported 62% of the population. Thereafter, a major shift occurred to the low-elevation landforms. During the last 3 yr of record (1995–1997), the low-elevation landforms, characterized by colder temperatures, drier, less fertile soils, and slow-growing jack pines, supported 86% of the population. The juxtaposition of high- and low-elevation landforms, and the fine-scale ecosystem diversity within them, prolonged the duration of warbler occupancy beyond what would be expected in less heterogeneous conditions. As demonstrated here, the landscape ecosystem approach provides a sound, ecological framework for understanding patterns of Kirtland's warbler occurrence and for assisting managers in identifying appropriate management areas for the continued recovery of the species. For. Sci. 49(1):119–139.

Key Words: Landform, ecosystem diversity, jack pine, endangered species conservation.

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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. Since the discovery of the first nest in 1903 (Wood 1904), the known breeding range of the warbler has been limited to the dry, glacial outwash plain, jack pine–northern pin oak forest ecosystems of northern Michigan. 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 of Michigan, an area approximately 120 × 160 km (Mayfield 1960, p. 9, Probst 1986). Four counties in the central portion of the range—all within the drainage of the Au Sable River—have supported 85% or more of the total population for over 25 yr (Weinrich 1996).

Warblers nest only in areas where young (5 to 23 yr 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 generally limited to stands greater than 32 ha in size characterized by jack pine canopy cover of between 20% and 60% growing in a patchy pattern and 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, often at or near the edges of openings, sheltered beneath living pine branches and ground vegetation (Mayfield 1960, p. 73, Walkinshaw 1983, p. 77). An area is typically abandoned 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 and structural characteristics of jack pine, which in turn depends on physical site factors including physiography, climate, and soil (Walkinshaw 1983, p. 65).

The first attempt to estimate Kirtland's warbler numbers was made in 1951; 432 singing-males were counted, and the total population was estimated at ca. 1,000 individuals (Figure 1). Ten years later the census was repeated with similar results, suggesting the population was maintaining itself (Mayfield 1962). However, a 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). The principal reason for the decline appeared to be nest parasitism by the brown-headed cowbird (*Molothrus ater*) (Mayfield 1960, p. 144, Ryel 1981, Walkinshaw 1983, p. 145). In response to the perceived threat, the U.S. Fish and Wildlife Service implemented a program to trap and remove cowbirds from warbler breeding areas. Although nest parasitism was reduced to 3.4% during the first 10 yr of cowbird control (1972–1982) (Kelly and DeCapita 1982), annual warbler population numbers showed little change, remaining at about 400 individuals through 1989 (Figure 1).

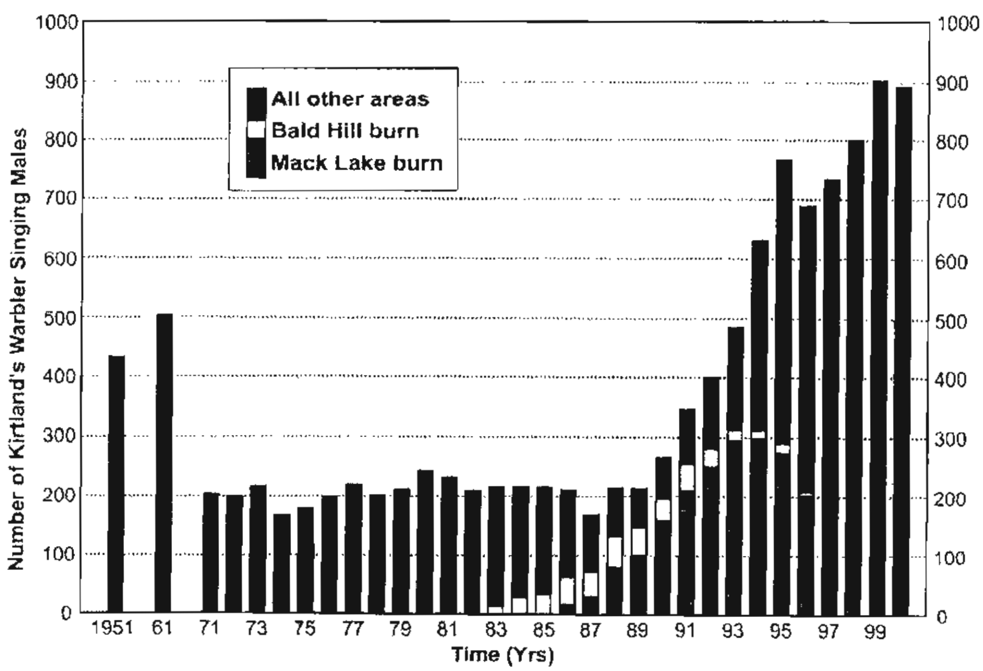

Figure 1. Abundance of Kirtland's warblers from 1951 (year of first census) to 2000 based on the annual census of singing males. The 1971 census revealed a 60% decline in the total population. The population remained at or near the 1971 level through 1989. The increase in population beginning in 1990 coincided with the major increase in suitable habitat (ca. 4,500 ha) observed following the Bald Hill (1975) and Mack Lake (1980) burns.

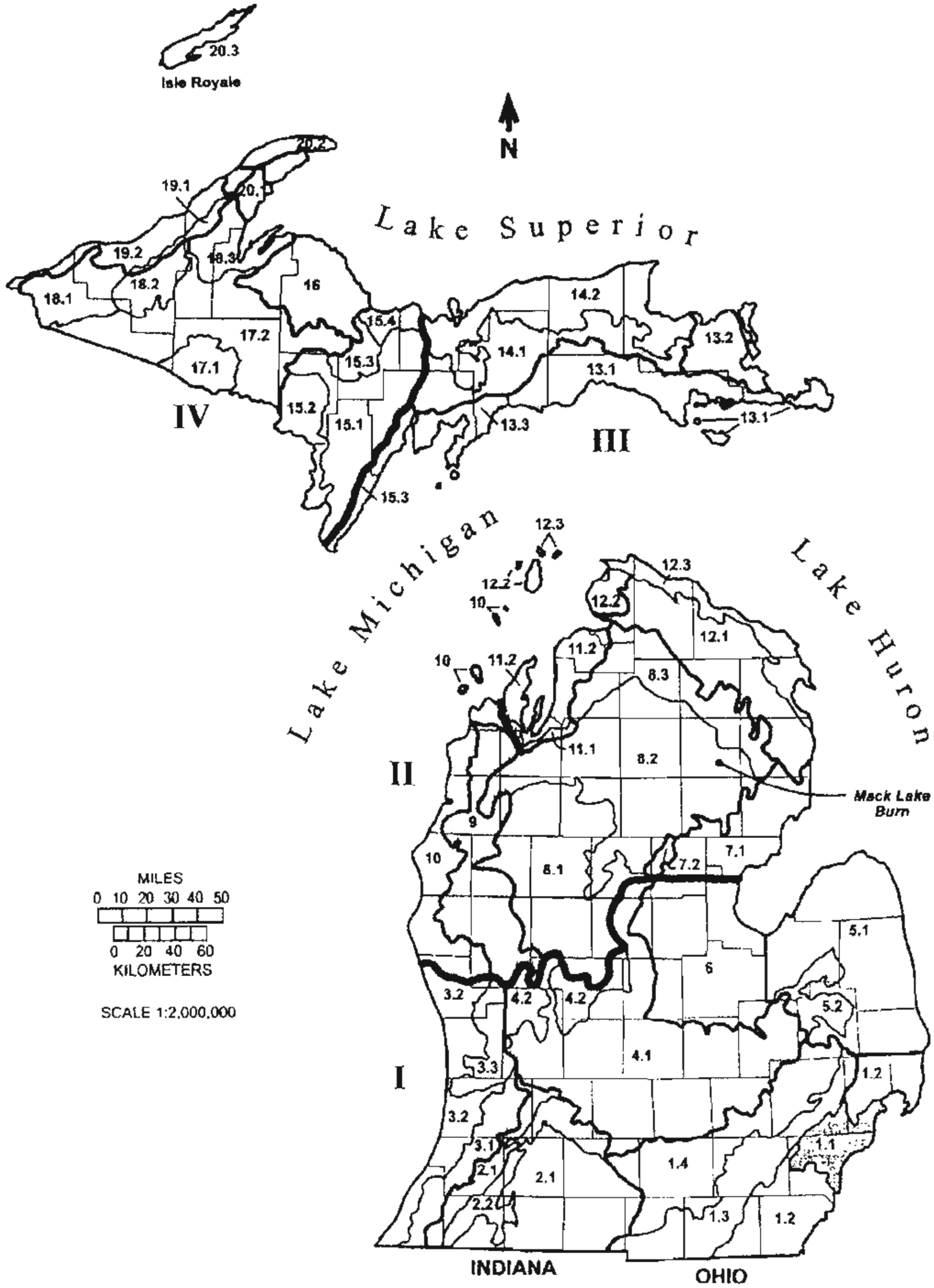

Figure 2. Map of regional landscape ecosystems of Michigan. Three hierarchical levels are mapped: Regions I-IV, Districts 1 to 20, and subdistricts within many districts. Boundaries were determined by integrating climatic, physiographic, soil, and vegetative variables. Names of all ecosystem units and their descriptions are found in Albert et al. (1986).

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 this effort was to develop a framework of landscape ecosystem units as the basis for understanding long-term patterns of Kirtland's warbler occurrence and behavior. Two physiographically distinct groups of ecosystems were distinguished and mapped, including a region of high-elevation terraced outwash plains and hilly ice-contact terrain in the southern part of the basin and a region of low-elevation pitted-outwash plains in the central part of the basin surrounding Mack Lake. Nested within the high- and low-elevation terrain features, 11 landscape-ecosystem types were distinguished based on fine-scale differences in physiography, microclimate, soil, and ground cover vegetation (Barnes et al. 1989). These units were defined in a typological sense but were not mapped (Zou et al. 1992).

During the first 3 yr of warbler occupancy (1986–1988), warblers preferentially colonized the high-elevation terrain over the low-elevation terrain (Barnes et al. 1989, Zou et al. 1992). Of the 14 singing-male warblers to colonize the Mack Lake burn in 1986, 71% occupied the high-elevation terrain; the remaining 29% occupied the low-elevation terrain. In 1987 and 1988, approximately 60% of the Mack Lake population occupied the high-elevation terrain. The apparent preference for the high-elevation terrain was attributed to the markedly different physiography which resulted in a warmer microclimate, moister, more nutrient-rich soils, and jack pine regeneration that was taller, faster growing, and somewhat denser than that in the low-elevation terrain (Barnes 1993). Warblers were also found to preferentially colonize specific landscape-ecosystem types within the high- and low-elevation terrain features (Zou et al. 1992).

The initial 3 yr (1986–1988) study of the Mack Lake burn provided an ecological baseline to monitor long-term (1986–1997) change in the occurrence of the Mack Lake Kirtland's warbler population and to identify the ecological factors affecting the change. This study was undertaken to determine the spatial and temporal pattern of warbler occupancy across the Mack Lake burn using a framework of landform-level ecosystems, broader-scale ecosystem units that could be more easily identified and mapped in the field than the fine-scale ecosystem types. Our primary objectives were to (1) distinguish and map individual landform-level ecosystem units (i.e., landforms) nested within the high- and low-elevation terrain features of the Mack Lake burn, and (2) characterize the spatial and temporal pattern of landform colonization and occupancy by the Kirtland's warbler in relation to elevation, geographic position, and physical site factors including microclimate and soil. The original landscape ecosystem classification of Barnes et al. (1989) provided the initial spatial framework. The relative position of the landform

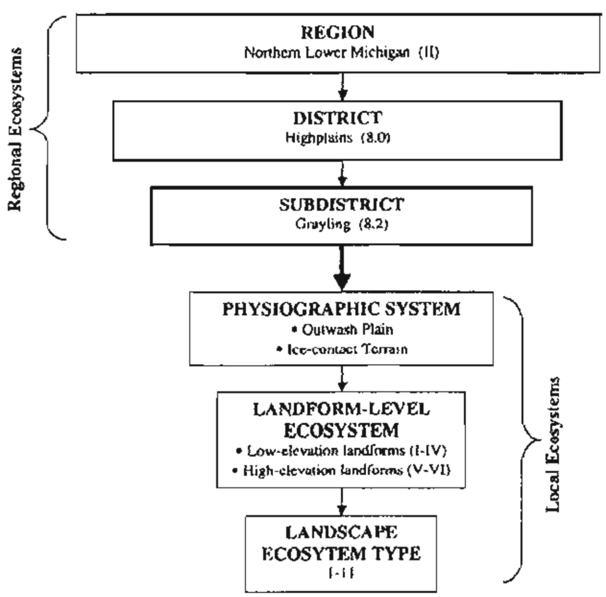

Figure 3. Landscape ecosystem hierarchy of the Mack Lake burn, northern Lower Michigan. (Modified from Albert et al. 1986, Barnes et al. 1998.)

unit within the ecosystem hierarchy of the Mack Lake burn is shown in Figure 3. The broad goal of this research, together with a companion study conducted on the site of the 1975 Bald Hill burn (Kashian and Barnes 2000), is to provide resource managers with a landscape ecosystem framework for understanding patterns of Kirtland's warbler occurrence in space and time. These insights can then be used for identifying *a priori* areas that will best meet specific Kirtland's warbler management objectives.

Study Site Description

Research was conducted on an approximately 6,800 ha tract of jack pine-dominated ecosystems within the Mack Lake basin. The basin is located 10 km south of Mio, MI (44°38'N, 84°08'W) on the Huron National Forest. The study was conducted in the western portion of the 1980 Mack Lake burn where postfire conditions were most suitable for the regeneration of jack pine and subsequent occupancy by the Kirtland's warbler.

The study area lies within the Grayling Subdistrict (8.2) of the Highplains District (8) of Region II (northern Lower Michigan) as described by Albert et al. (1986; Figure 2). Because of its northern latitude, interior location, and high relative elevation, the Highplains District possesses the most severe macroclimate in Michigan's Lower Peninsula (Albert et al. 1986). The weather station nearest the Mack Lake basin is located at Mio, MI. 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). The freeze-free period averages 113 days, 2 days shorter than the average (115 days) for the Highplains, which has the shortest and most variable growing season of any district in the Lower Peninsula (Albert et al. 1986, Michigan Department of Agriculture 1989).

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 yr ago (Burgis 1977). Physiographic systems, including outwash plain, moraine, and ice-contact terrain, are represented here. The physiography of the basin is two-leveled, with high-elevation outwash terraces and ice-contact terrain to the south and low elevation pitted-outwash plains and postglacial meltwater drainage channels to the north and surrounding Mack Lake (Barnes et al. 1989, Barnes and Zou 1989, Zou et al. 1992) (Figure 4). The boundary between high- and low-elevation terrain features is arbitrarily distinguished along the 372 m elevational contour. Elevation within the basin ranges from 357 to 450 m. Slopes rarely exceed 5% but can approach 30% in the ice-contact terrain.

Mineral soils of the low-elevation outwash plains are primarily 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, but ranges from medium fine to very coarse sand (Zou et al. 1992); soils are excessively

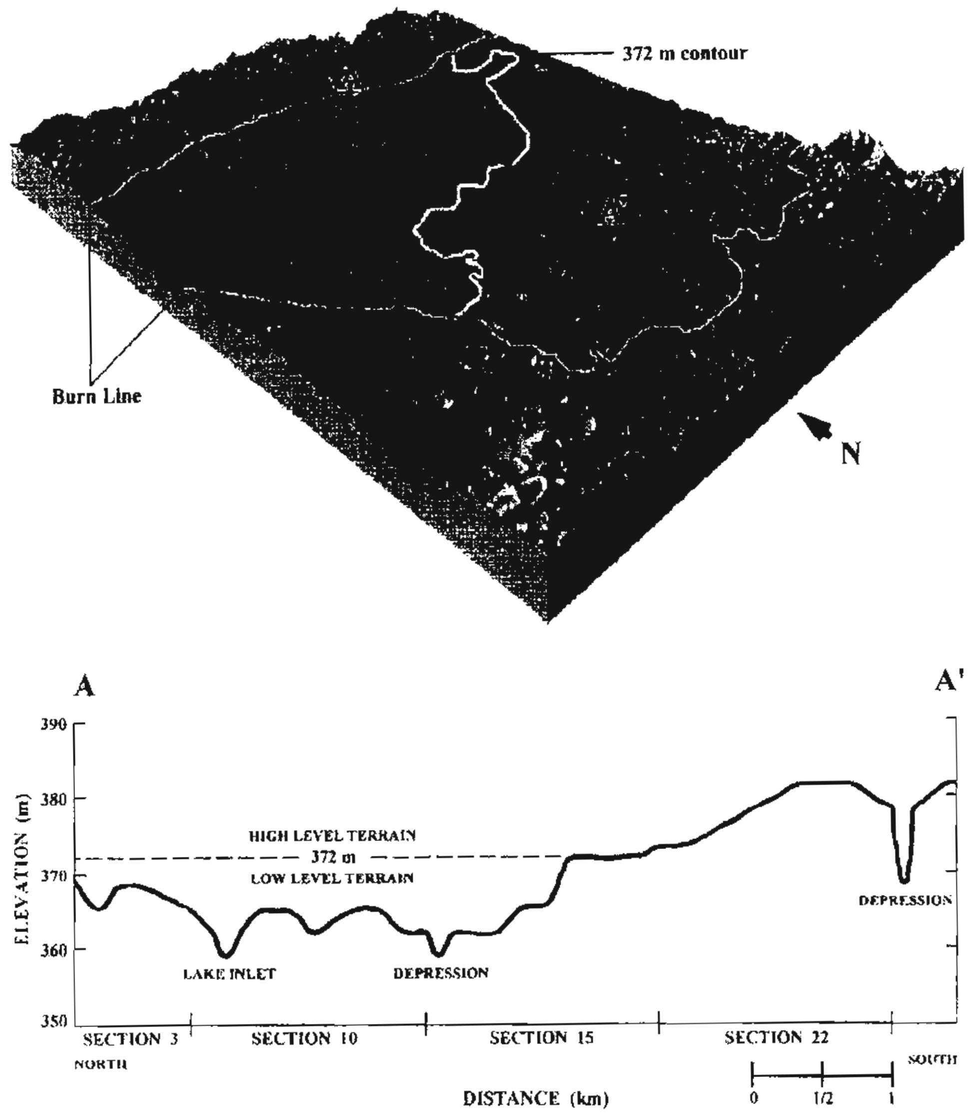

Figure 4. The Mack Lake basin: (top) digital elevation model illustrating topography and surficial features (area shown is approximately 13.6 × 9.6 km); (bottom) elevational profile along transect AA' demonstrating the topographic break (ca. 372 m) dividing the high- and low-elevation terrain features. (After Barnes and Zou 1989.)

drained. In the high-elevation outwash terraces and ice-contact terrain, Entisols of the Graycalm series (Alfic Udipsamments) dominate; 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; thin bands of fine texture are a distinguishing characteristic. Bands range in texture from loamy sand to sandy clay loam. Soils are typically somewhat excessively drained; however, drainage varies with the amount and depth of fine-textured banding (Zou et al. 1992).

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. 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. Jack pine stands were associated with scattered plantations of red pine (*Pinus resinosa* Ait.) (16%) and mixed stands of pine and northern pin oak (8%). One week after the wildfire, jack pine seed counts averaged 750,000 seeds/ha (Simard et al. 1983). At the end of the first growing season, jack pine seedling densities ranged from 5,000 to 42,500 seedlings/ha (Barnes et al. 1989). As a result, a dense, patchy mosaic of jack pine and jack pine mixed with northern pin oak dominates the current vegetation.

The mean fire frequency for the Mack Lake area (8,094 ha) based on a 160 yr fire history (1820–1980) is approximately 1 fire per 4.2 yr (Simard and Blank 1982). During presettlement time (1815–1849), the interval between large (4,000+ ha) fires was 35 yr; since settlement (1850–1980) the large fire interval decreased to 26 yr.

Methods

Landform-Level Ecosystem Classification and Mapping

Field Methods

A landform-level ecosystem classification and map of the Mack Lake burn study area was developed using a multifactor landscape ecosystem approach (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985). 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. The first approximation was based largely on the original hierarchical landscape framework of physiographic systems (outwash plain and ice-contact terrain) and constituent ecosystem groups (high-elevation and low-elevation terrain) provided by Barnes et al. (1989) (Figure 4). Based on study of aerial photographs and topographic maps, the outwash plain was subdivided into several hypothetical landforms. Given the basin-like physiographic character of the study area, elevational differences provided the primary basis for the assignment of provisional landform boundaries. The highly dissected and heterogeneous ice-contact terrain was treated as a single landform unit. The delineation of putative landform boundaries was refined during the course of field reconnaissance and transect sampling. Intensive plot sampling, data compilation, and statistical analyses provided the basis for further testing and revision of the landform-level ecosystem classification and map.

Forty-nine 200 m^2 (10 × 20 m) sample plots were measured within the landform units. Plot sampling was limited to those landforms that had been occupied by the Kirtland's warbler since 1986. Sampling was conducted to (1) characterize each landform 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). Of the 49 plots sampled, 33 plots were relocated permanent ecosystem-type plots established between 1986 and 1988 by Barnes et al. (1989). The remaining 16 plots were established in 1996 to replace selected permanent plots that could not be relocated or to collect data in areas not previously sampled. All plots were established using a stratified random sampling design (Zou 1988, Barnes et al. 1989).

In the field, the physiography of the plot and the adjacent area was recorded, including the elevation, aspect, and slope percent. A soil pit was excavated to a depth of 2 m, and a complete profile description was made according to Natural Resource Conservation Service procedures (Soil Survey Staff 1975). At the base of each pit, a 3 m auger boring was taken. The depth, texture, and field pH of each horizon and at 50 cm intervals below the surface were recorded for the entire profile. Depth to the water table, depth of maximum plant rooting, and the presence, depth, and thickness of fine-textured soil banding were also measured. A soil sample was collected from each horizon for laboratory analyses.

Vegetation in the plots was sampled as follows: the species and diameter at breast height (dbh) of all live and standing dead overstory trees > 9.1 cm dbh were recorded. Understory trees were tallied by species and diameter class (1.5–4.0, 4.1–6.6, and 6.7–9.0 cm dbh) in each of 8 nested 25 m^2 (5 × 5 m) subplots. The height of three dominant (i.e., tallest) northern pin oak stems in each plot was recorded, and the number of northern pin oak seedlings and sprout clumps was tallied. The coverage of four vertical stand structural layers (moss-creeper, herbaceous, shrub, and small tree) was recorded by class (0, 1–10, 11–40, 41–75, and 76–100%), and the canopy coverage of jack pine and northern pin oak in each plot was estimated to the nearest 1%. Two 5 × 5 m subplots, one at each end of the main plot, were randomly selected and the total height, dbh, and height of the lowest live branch of 3 dominant jack pine stems were recorded in each.

The areal coverage of all species < 1.5 cm dbh was estimated in a 100 m^2 (5 × 20 m) subplot using a 12-class system (1, trace–0.005; 2, 0.005–0.01; 3, 0.01–0.1; 4, 0.1–0.5; 5, 0.5–1.0; 6, 1.0–2.0; 7, 2.0–4.0; 8, 4.0–8.0; 9, 8.0–16.0; 10, 16.0–32.0; 11, 32.0–64.0; 12, 64.0–100.0%) (Zou 1988). A sampling frame representing 0.1% (1000 cm^2) of the sample area was used for ocular calibration in standardizing coverage estimates. All vascular plants were identified to species; nomenclature follows Voss (1972, 1984, 1997).

Laboratory Methods

Soil samples collected in the field were air-dried, crushed, and passed through a 2 mm sieve. The hydrometer method of soil texture analysis (Gee and Bauder 1986) was used to determine the proportion of sand, silt, and clay in 100 g 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. The pH of 30 g soil samples was determined in a 1:1 soil to deionized water solution using a Fischer pH meter with a glass combination electrode.

Statistical Analyses

Discriminant analysis (Williams 1981, 1983) was used to evaluate the distinctness of five landform-level ecosystems distinguished in the field. Forty-nine sample plots representing five landforms with at least four plots per unit were used in the analysis. One-way analysis of variance (ANOVA) with $\alpha = 0.05$ was used to screen 75 physiographic (4), soil (35), and vegetative (36) variables for inclusion in the discriminant analysis. If one or more assumptions of the ANOVA model were violated, the Kruskal-Wallis nonparametric analysis of variance was used (Conover 1980).

Discriminant functions were computed using three different subsets of the original variables: a physiography-soil subset, a ground-cover vegetation subset, and a set representing a combination of these subsets. Predictor variables in each subset were selected for canonical variates analysis using interactive forward stepwise discriminant analysis (SPSS, Inc. 1996). Pearson product-moment correlations of the original variables with the canonical variates were computed to aid in the interpretation of the canonical variates (Spies and Barnes 1985). Error rates in discriminant analysis were estimated using the jackknife or leaving-one-out method.

For the above analysis, the combined areal coverage of each ecological species group (i.e., a unique group of plant species repeatedly occurring together and exhibiting similar environmental tolerances; Barnes et al. 1989) was used as a variable. A single coverage value for each group was obtained by first transforming the coverage class assigned to ground cover species in the field to the median percent-coverage value of each class; median percent-coverage values were then summed for all species in the group.

Microclimate Study

A microclimate study was initiated in 1995 to document the magnitude of temperature variation in selected areas of the burn. A total of 14 temperature recording stations were established in three physiographically distinct areas: (1) high-elevation terrain (n = 6 stations), (2) low-elevation terrain (n = 6 stations), and (3) glacial meltwater drainage channels (n = 2 stations). In each area, stations were established, as far as possible, at the same elevation (high-elevation terrain = 381 m, low-elevation terrain = 366 m, and glacial meltwater drainage channels = 354 m). Stations consisted of two maximum-minimum thermometers placed 30 cm above the ground and positioned 3 to 5 m apart. All stations were established the first week of May and visited twice weekly through mid-August. A total of 23 readings were taken at each station.

Kirtland's Warbler Occupancy of Landform-Level Ecosystems

Field Methods

Annually, state and federal cooperators conduct an official census of the Kirtland's warbler population (Weinrich 1996). During the census, usually the second week of June, selected areas are systematically checked for the presence of singing-male warblers. Tracts of young jack pine are simultaneously traversed by census personnel along parallel transect lines spaced 400 m apart. Regularly spaced stops (ca. 80 m apart) are made along transects to listen for the loud, usually persistent song; approximate locations of singing males are then recorded on sketch maps (Weinrich 1996). Although the social system is known to be a mix of unmated (Probst and Hayes 1987) and polygynous (Radabaugh 1972, Bocetti 1994) males, for census purposes it is assumed that each singing male is mated with a single female. Therefore, the annual "breeding population" is estimated to be twice the number of singing males (Mayfield 1953, Ryel 1979).

Office Methods

Annual census records for the Mack Lake Kirtland's Warbler Management Area (KWMA) were acquired from the USDA Forest Service, Huron National Forest, for the period 1986 to 1997. Census locations of singing-male warblers were transferred to 7.5 minute topographic quadrangle sheets, and an approximate elevation was assigned to the location of each bird. Birds found within or on the boundaries of known fill-in plantations were removed from consideration. ArcView GIS 3.1 (ESRI 1997) was used to determine the number of singing males occurring within each landform in each year. The approximate coordinate position (i.e., UTM easting and northing) of each singing male was also calculated, and the mean coordinate position (i.e., population spatial mean) occupied by singing males in each year was determined (Shaw and Wheeler 1985).

Statistical Analyses

First, simple linear regression was used to describe the relationship between the average elevation of the Mack Lake Kirtland's warbler population and the year of occupancy (1986–1997). To linearize the data, the independent variable (time) was transformed using the natural logarithm. Second, multivariate analysis of variance (MANOVA) was used to test for significant differences in the geographic position of the warbler population spatial mean over time. Finally, a two-way Chi-square test for independence was conducted to determine if the population was distributed across landform units in a nonrandom (specific) fashion over the 12 yr period of record.

Results and Discussion

Classification and Description of Landform-Level Ecosystems

Four low-elevation and two high-elevation landform units were distinguished and mapped within the Mack Lake burn (Figure 5). In this ecosystem classification (Table 1), landforms (I-VI) constitute the second hierarchical level, one level below the two major high- and low-elevation terrain features identified by Barnes et al. (1989, Zou et al. 1992) (Figure 3). Landform units were characterized according to physiography, microclimate, soil texture, soil drainage, and site condition (Table 2). Nested within landforms, 11 individual landscape-ecosystem types (Barnes et al. 1989), representing the finest level of ecosystem delineation, complete the classification (Table 1).

Several physical and biotic factors were useful in differentiating the landform units 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 effective (Table 3). Vegetative variables most useful in characterizing landform differences 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*, *Ceanothus ovatus*, and *Rosa blanda* ecological species groups (Table 4).

Multifactor Comparison of Landform-Level Ecosystems

Among the three variable subsets used in the discriminant analysis, the combined set, including four physiographic, six soil, and five ground-cover vegetation variables (Table 5), was most useful in revealing the marked ecological distinctness of the five landform-level ecosystems. Use of the combined variable set produced larger eigenvalues, tighter clustering, and a greater degree of spatial separation among units than was attained using either the physiography-soil (14 variables) or ground-cover vegetation (9 variables) variable subsets alone (Figure 6). The relationships among the landforms in Figure 6

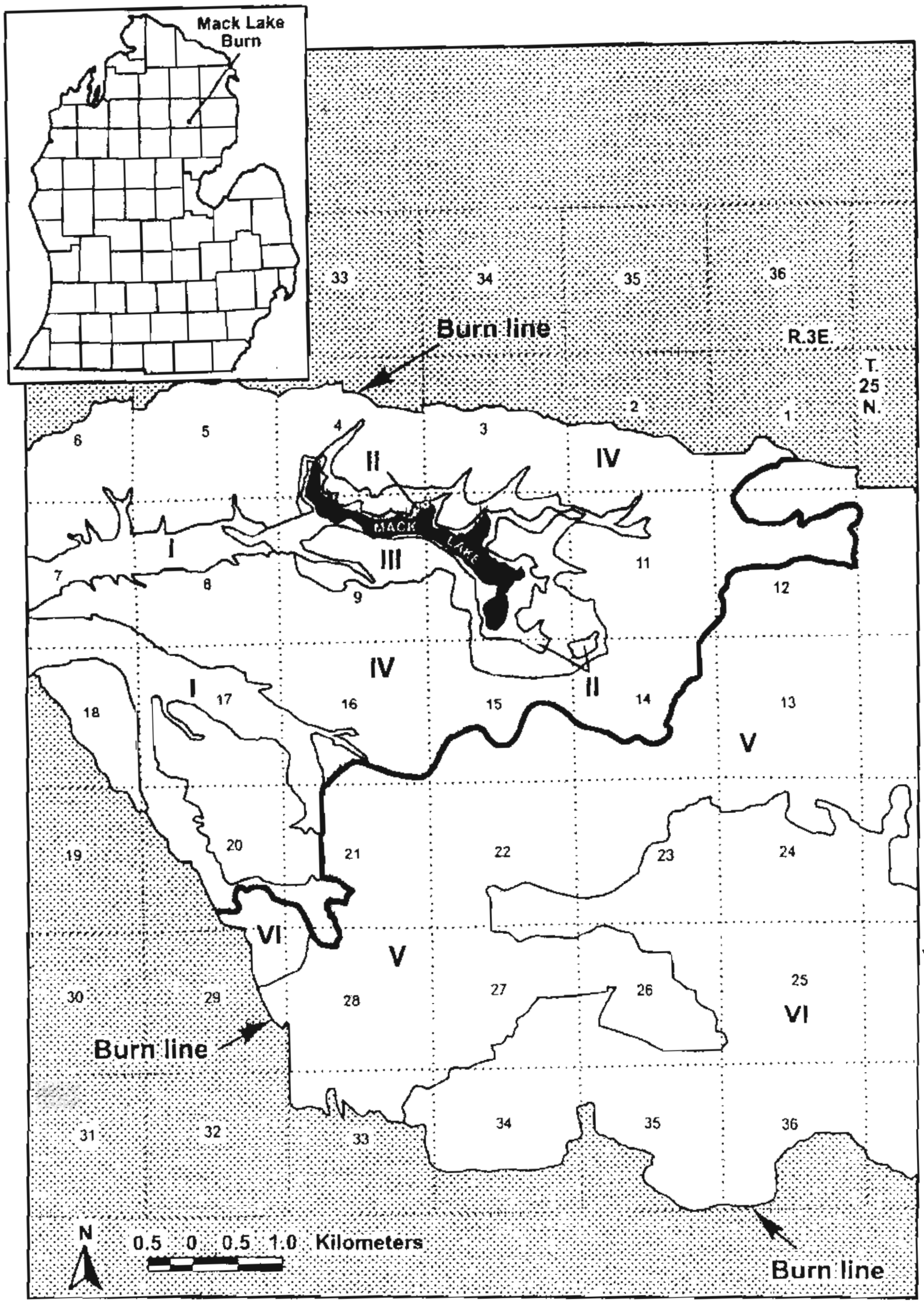

Figure 5. Landform-level ecosystems of the Mack Lake burn, northern Lower Michigan: (I) low-elevation outwash channels, (II) low-elevation lake-margin outwash plain, (III) low-elevation water table-influenced pitted-outwash plain, (IV) low-elevation excessively drained pitted-outwash plains, (V) high-elevation outwash plains, (VI) high-elevation ice-contact terrain. The boundary (heavy line) between the high- and low-elevation landforms is 372 m.

are supported by field observations. Moderately fertile, high-elevation landforms (V and VI) are located along the right side of the ordination, whereas the most infertile, low-elevation landforms (I and IV) are found in the upper-left portion. 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 units 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 (overall 6%; jackknife 20%) or the ground-cover vegetation (overall 12%; jackknife 27%) variable subsets. The discriminant analyses indicate that individual

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

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 in the upper 50 cm; 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 (0–6%); 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; loamy sand to 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 (0–5%)
    - 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 and ridges; infertile; *Ceonothus*, *Gaultheria*

ecosystem factors could not be used alone with high reliability to classify and map the landforms.

The first three canonical variates were found to account for 82, 91, and 97% of the cumulative variance in the combined variable set (Table 5). Average elevation and the number of northern pin oak sprout clumps both exhibit high positive correlations with the first canonical variate, while depth to banding, coverage of the *Arctostaphylos uva-ursi* ecological species group, and the number of grass species are all negatively correlated. Variables correlated with the second canonical variate include maximum slope, slope, and the number of grass species (Table 5).

Kirtland's Warbler Occupancy of Landform-Level Ecosystems

Over the 12 yr period 1986-1997, a spatially distinct pattern of Kirtland's warbler colonization and occupancy was observed among the high- and low-elevation landform-level ecosystems (Figure 7). When census locations from the first 3 yr of warbler occupation (1986–1989) are compared to census locations from 1995–1997, warbler colonization initially favors the high-elevation landforms, whereas in later years, colonization visibly shifts to the low-elevation landforms. The extent of this high- to low-elevation shift is illustrated most clearly when the position of the population spatial mean is plotted over time (Figure 8). Using MANOVA, the mean position of the warbler population was found to migrate significantly ($P < 0.00001$) over the 12 yr period of record. A significant decreasing relationship ($r^2 = 0.90$; $P < 0.00001$) between the average elevation of the warbler population and the year of occupancy (1986–1997) further demonstrates the systematic progression of Kirtland's warbler occupation (Figure 9). Overall, our results provide strong evidence in support of the linkage between Kirtland's warbler occurrence and individual landscape ecosystem units. A Chi-square test for independence confirmed the presence of a significant dependent relationship ($P < 0.00001$) between the distribution of warblers among the five landform-level ecosystems and the year of occupancy (1986–1997).

The observed shift in the spatial pattern of Kirtland's warbler occurrence 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 ecosystems (Figure 10). In 1986 and 1987, the bulk of the Mack Lake warbler population occupied the high-elevation landforms. Moister, more nutrient-rich soils, a warmer microclimate, and taller, faster-growing jack pines and northern pin oaks distinguish the high-elevation landforms from those in the low-elevation terrain. As a result, trees in landforms V and VI (Figure 5) 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, occupancy of the area steadily decreased over time as the tree crowns rapidly closed in on the openings and the vegetative cover deteriorated (Figure 10). During this same period, habitat in the low-elevation terrain became increasingly suitable as the slower-growing pines reached heights appropriate for colonization. In 1989, as warblers systematically colonized landforms I, III, and IV (Figure 5) in greater numbers, a marked shift occurred in the spatial pattern of warbler occupation (Figure 10). By 1993, 73% of the Mack

Table 2. Comparative summary of selected ecological attributes among landform-level ecosystems of the Mack Lake burn, Oscoda Co., northern Lower Michigan.

Landform	Surface area (ha)	Physiography	Microclimate	Soil texture/drainage	Site condition	Response of dominant vegetation
I	453.7	Broad (160–1125 m wide), low-elevation (350–361 m) glacial meltwater drainage channels.	Maximum/minimum growing-season temperatures are the lowest recorded, averaging 33.7°C and –1.0°C respectively; late-season frosts occur with the greatest frequency.	Medium to medium-fine sand with a distinct gravel/cobble layer above 50 cm; excessively to somewhat excessively drained.	Very dry, nutrient-poor; very cold.	Short, very slow-growing jack pine (PB) and northern pin oak (QE); oak seedlings and sprouts are rare; oaks exhibit visible frost damage where present.
II	119.9	Nearly level, low-elevation (357–359 m) outwash-plain wetlands and shallow drainages adjacent to Mack Lake.	Growing-season temperatures are typically lower than in the high-elevation landforms; proximity to Mack Lake may have a moderating influence.	Sapric muck (< 30 cm) over medium to medium-fine sand; water table remains above 50 cm year round.	Moist, nutrient-poor; cold.	PB and QE are virtually absent due to the seasonally flooded conditions; overstory dominants include black spruce, tamarack, red maple, and trembling aspen.
III	310.9	Gently sloping, low-elevation (359–363 m) pitted-outwash plain within 350m of Mack Lake.	Maximum/minimum growing-season temperatures are significantly lower than in the high-elevation landforms, averaging 34.8°C and –0.1°C, respectively.	Gravelly loamy to medium sand; water table averages 390 cm; excessively to somewhat excessively drained.	Slightly moist, variable nutrients; cold.	PB and QE height growth is limited by the cold microclimate; oak seedlings and sprouts are uncommon and appear severely stunted.
IV	2318.0	Broad, level to gently sloping, low-elevation (366–372 m) pitted-outwash plain.	Growing-season temperatures are not significantly different from those in Landform III; below-freezing (< 0°C) temperatures occur twice as often as in the high-elevation landforms.	Deep, acid, medium to medium-fine sand; excessively drained.	Very dry and nutrient poor; cold.	PB and QE height growth is curtailed by the low soil water and nutrient-holding capacity and the cold microclimate.
V	2174.7	Broad, level to gently sloping, high-elevation (369–384 m), terraced outwash plains.	Maximum/minimum growing-season temperatures are significantly higher than in the low-elevation landforms, averaging 37.5°C and 2.9°C, respectively; late season frosts are rare.	Excessively drained medium and medium-fine sand to well drained loamy sand heavily interbedded with bands of fine texture (loamy sand to sandy clay loam).	Variable moisture and nutrients; warm.	Noticeably taller, fast-growing PB and QE predominates; oak seedlings and sprouts are common.
VI	1658.2	Moderately steep kamic hills and ridges; kames regularly interspersed with deep (3 to 15+ m) kettle depressions.	Growing-season temperatures are not significantly different from those in Landform V; late-season frosts are rare outside of kettle depressions where cold air is trapped.	Medium to fine sand; soils may be interspersed with bands of fine texture; excessively to somewhat excessively drained.	Variable moisture and nutrients; warm.	PB and QE height growth (outside kettle depressions) exceeds that of all other landforms; oak stems are abundant and vigorous in all stand layers.

Lake warbler population occupied the low-elevation landforms, a reversal of the initial pattern of occupancy observed in 1986 and 1987.

Although Kirtland's warblers colonized all of the jack pine-dominated landforms within the Mack Lake burn, the timing of initial colonization and the duration of subsequent occupation differed considerably among the units (Table 6). In general, landforms that are colonized early by warblers are those that favor the rapid height growth of jack pine (Barnes et al. 1989, Kashian et al. *this issue*). Accordingly, landforms V and VI, characterized by relatively high soil water and nutrient availability, a warm microclimate, and fast-growing

Table 3. 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).*

	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)†	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 (%)†	2.08	(2.33)	2.50	(2.20)	1.46	(0.93)	1.86	(1.52)	7.13	(8.13)
Maximum slope (%)†	2.33	(2.14)	3.25	(1.44)	1.82	(1.46)	2.21	(1.71)	7.38	(7.89)
Sand, 10–30 cm (%)†	88.37	(3.33)	87.59	(1.95)	91.34	(3.33)	87.08	(4.50)	91.28	(1.25)
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)
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)
Silt + Clay, 10–30 cm (%)†	12.06	(3.44)	13.6	(2.82)	8.73	(3.44)	13.24	(4.50)	8.75	(1.28)
Sand, 10–150 cm (%)†	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 (%)†	5.97	(1.78)	13.54	(4.47)	4.81	(4.59)	5.24	(6.63)	4.95	(4.49)
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)
Silt, 10–150 cm (%)†	3.71	(1.21)	5.54	(1.68)	2.51	(1.81)	5.57	(3.46)	2.93	(1.74)
Silt + Clay, 10–150 cm (%)†	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 (%)†	8.70	(7.34)	8.20	(7.33)	3.38	(6.71)	2.04	(2.27)	0.78	(0.96)
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, 30–150 cm†	5.71	(0.37)	6.08	(0.53)	5.24	(0.47)	5.60	(0.44)	5.48	(0.11)
Total accumulated banding (cm)†	3.33	(5.16)	3.00	(3.56)	1.86	(6.40)	17.98	(23.77)	7.00	(6.78)
Depth to band, < 2 cm thick (cm)†	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)†	400.00	(156.97)	407.50	(106.89)	472.79	(101.83)	157.67	(153.27)	268.25	(188.61)
Depth to maximum rooting (cm)†	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)†	999.00	(0.00)	390.00	(94.78)	999.00	(0.00)	999.00	(0.00)	999.00	(0.00)

* 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.

† Indicates significance at $\alpha = 0.05$.

pines, were the first to be intensively colonized (Table 6). Although landform IV was also among those occupied early (colonized in 1986 by three singing males), colonization was likely associated with only scattered patches of relatively tall pines in ecosystem types 3 and 4 (Table 1). Conversely, late colonization is typically associated with landforms that favor slow jack pine height growth (Barnes et al. 1989, Kashian et al. *this issue*). As a result, landform I, characterized by very dry, nutrient poor soils, a cold microclimate, and slow-growing pines, was not occupied until 1991 (Table 6). Landform III, which also supports relatively slow-growing pines, was colonized even later (1994).

The duration of Kirtland's warbler occupancy also differs markedly among the landform units (Table 6). As in the case of early colonization, short-duration warbler occupancy is associated with landforms that favor rapid jack pine height growth (Kashian and Barnes 2000, Kashian et al. *this issue*). Landform VI, characterized by relatively moist, nutrient-rich soils, a warm microclimate, and fast-growing jack pines, was occupied for just 4 yr. In spite of relatively poor site conditions and relatively slow pine growth, landform III was occupied for only 3 yr. However, in this particular case the duration of warbler occupancy was necessarily short due to the fragmented nature of the habitat (by private development,

Table 4. 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).*

	Landform-level ecosystem									
	Low-elevation terrain						High-elevation terrain			
	Landform I		Landform III		Landform IV		Landform V		Landform VI	
Vegetarian variable	(n = 6)		(n = 4)		(n = 14)		(n = 21)		(n = 4)	
Height of jack pine (cm)[†]	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[†]	137.33	(90.17)	65.75	(21.53)	155.43	(135.56)	225.62	(118.30)	200.00	(144.27)
Height of lowest live jack pine branch (cm)[†]	62.08	(36.03)	59.67	(23.31)	101.00	(46.12)	145.48	(46.38)	134.07	(43.12)
Height of northern pin oak (cm)[†]	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[†]	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 seedling clumps, < 1 m[†]	2.83	(4.07)	2.25	(2.87)	9.64	(13.07)	30.33	(17.48)	46.50	(42.00)
Number of n. pin oak sprout clumps, < 1 m[†]	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[†]	3.33	(3.83)	2.50	(3.32)	12.43	(16.69)	39.43	(17.67)	66.25	(43.42)
Number of tree species[†]	2.17	(0.41)	1.75	(0.50)	2.21	(0.43)	2.90	(0.89)	3.00	(0.82)
Number of shrub species[†]	7.33	(1.51)	8.75	(1.71)	7.07	(1.44)	9.81	(3.09)	9.75	(3.50)
Number of grass species[†]	7.17	(2.14)	11.00	(0.00)	5.36	(1.08)	4.33	(2.13)	4.75	(3.77)
Coverage of shrub species (%)[†]	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 (%)	4.21	(9.70)	0.08	(0.15)	0.79	(1.59)	1.11	(1.40)	3.26	(5.83)
Coverage of n. pin oak, < 1.5 cm dbh (%)[†]	0.53	(0.75)	0.16	(0.16)	0.57	(0.81)	2.17	(2.61)	2.25	(0.87)
Coverage of *Arctostaphylos uva-ursi* species group (%)[†]	17.70	(33.41)	31.27	(34.57)	7.81	(10.60)	1.59	(0.91)	3.53	(2.90)
Coverage of *Ceonothus ovatus* species group (%)[†]	0.51	(1.25)	0.18	(0.28)	0.02	(0.08)	0.05	(0.11)	23.58	(39.34)
Coverage of *Gaultheria procumbens* species group (%)[†]	0.05	(0.05)	0.07	(0.03)	0.07	(0.13)	0.29	(0.32)	0.55	(0.90)
Coverage of *Prunus pensylvanica* species group (%)[†]	0.95	(0.72)	0.50	(0.76)	1.13	(1.39)	0.35	(0.29)	0.05	(0.06)
Coverage of *Rosa blanda* species group (%)[†]	0.16	(0.15)	8.18	(10.85)	1.40	(4.36)	30.19	(37.29)	31.15	(21.45)
Coverage 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. (%)[†]	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)

* 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.

[†] Indicates significance at $\alpha = 0.05$.

roads, fuel-breaks, wetlands, etc.) within the already limited extent (ca. 310 ha) of the unit.

Long-duration warbler occupancy is associated with landforms that (1) support slow-growing jack pines, or (2) are characterized by a diversity of constituent landscape ecosystem types which results in differential within-landform jack pine height growth (Kashian and Barnes 2000, Kashian et al. *this issue*). For example, landforms I and IV, both of which support slow-growing pines, are among the longest occupied units within the burn (Table 6). Landform I was occupied for 7 yr, whereas landform IV will likely remain occupied through the year 2000. In spite of more favorable site conditions and more rapid jack pine growth, landform IV has been occupied considerably longer than landform I due to the greater diversity of landscape ecosystem types within it (Table 1). Similarly, landform V, a unit that generally supports fast-growing pines, will likely remain occupied through 2000 because of the very high within-landform site heterogeneity. Overall, due to the remarkable diversity of landform-level ecosystems and constituent ecosystem types within the Mack Lake burn, occupancy of the entire area by the Kirtland's warbler has been prolonged beyond what would be expected if the site were characterized by ecologically less heterogeneous (i.e., less diverse) site conditions.

General Discussion and Conclusions

Ecological Relationships Affecting Kirtland's Warbler Occurrence

The landscape ecosystem approach, as applied to the 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 including growth, composition, and structure) components of landscape ecosystems (Figure 11). The complex interrelationships between the individual ecosystem components mediate the pattern of Kirtland's warbler colonization and occupancy both directly and indirectly. The physiography of the Mack Lake basin not only controls soil

Table 5. Comparison of relative variation among five landform-level ecosystems as determined by a canonical variates analysis of ten physiographic and soil variables, and five groundcover 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

water and nutrient availability below the surface, but also acts to modify air temperature at and above the surface (Figure 11). 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., outwash plain vs. ice-contact terrain). In turn, microclimate and soil have a strong and predictable influence on the development of vegetation, particularly on the growth and structural characteristics (i.e., density and spatial distribution) of jack pine and northern pin oak (Figure 11).

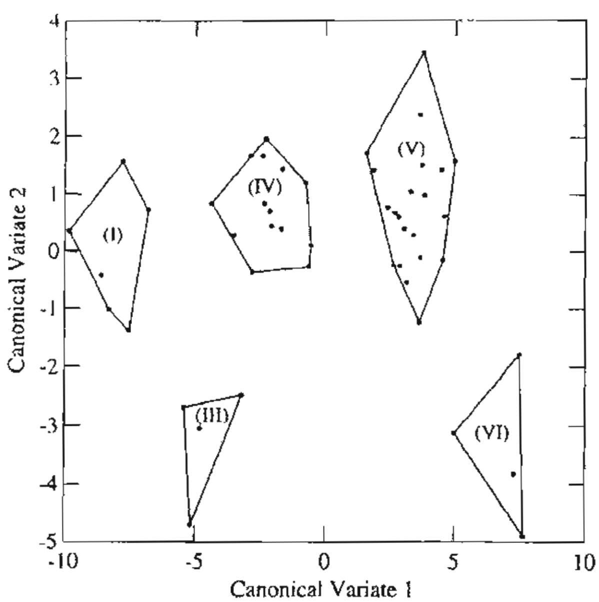

Figure 6. Ordination of 49 sample plots among 5 landform-level ecosystems along the first 2 canonical variates of an analysis of 10 physiographic and soil variables and 5 ground-cover vegetation variables; Mack Lake burn, northern Lower Michigan. Roman numerals in parentheses identify landform units.

Of the major ecosystem components, vegetation exerts the most direct influence on Kirtland's warbler occurrence (Figure 11). Warblers only colonize sites where jack pine is 5 to 23 yr old and 1.4–5.0 m tall (Probst and Weinrich 1993), and jack pine height growth is strongly influenced by site quality (Jameson 1965). As a result, the growth of jack pine, as mediated by site factors, markedly affects the timing of initial site colonization and the duration of site occupancy by the warbler. Thus, by simultaneously integrating physical and biotic factors, the complex relationships between Kirtland's warbler and its supporting ecosystems are revealed. Our research demonstrates that understanding the degree to which various physical and biotic factors influence Kirtland's warbler occurrence is fundamental to interpreting and predicting spatial and temporal patterns of warbler colonization and occupancy not only within the Mack Lake burn but across the entire breeding range as well.

Although the contributions of individual site factors to differences in the growth of jack pine 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 and Barnes (2000) reported significant differences in jack pine height growth due to topographic-mediated microclimate variation between otherwise similar high- and low-elevation landforms at the Bald Hill burn 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 that below-freezing minimum temperatures in June killed new jack pine shoot growth. In addition, the vigor of pines in frost-pocket depressions was found to be markedly less than that of pines in non-depression areas due to lower minimum temperatures (Barnes et al. 1989).

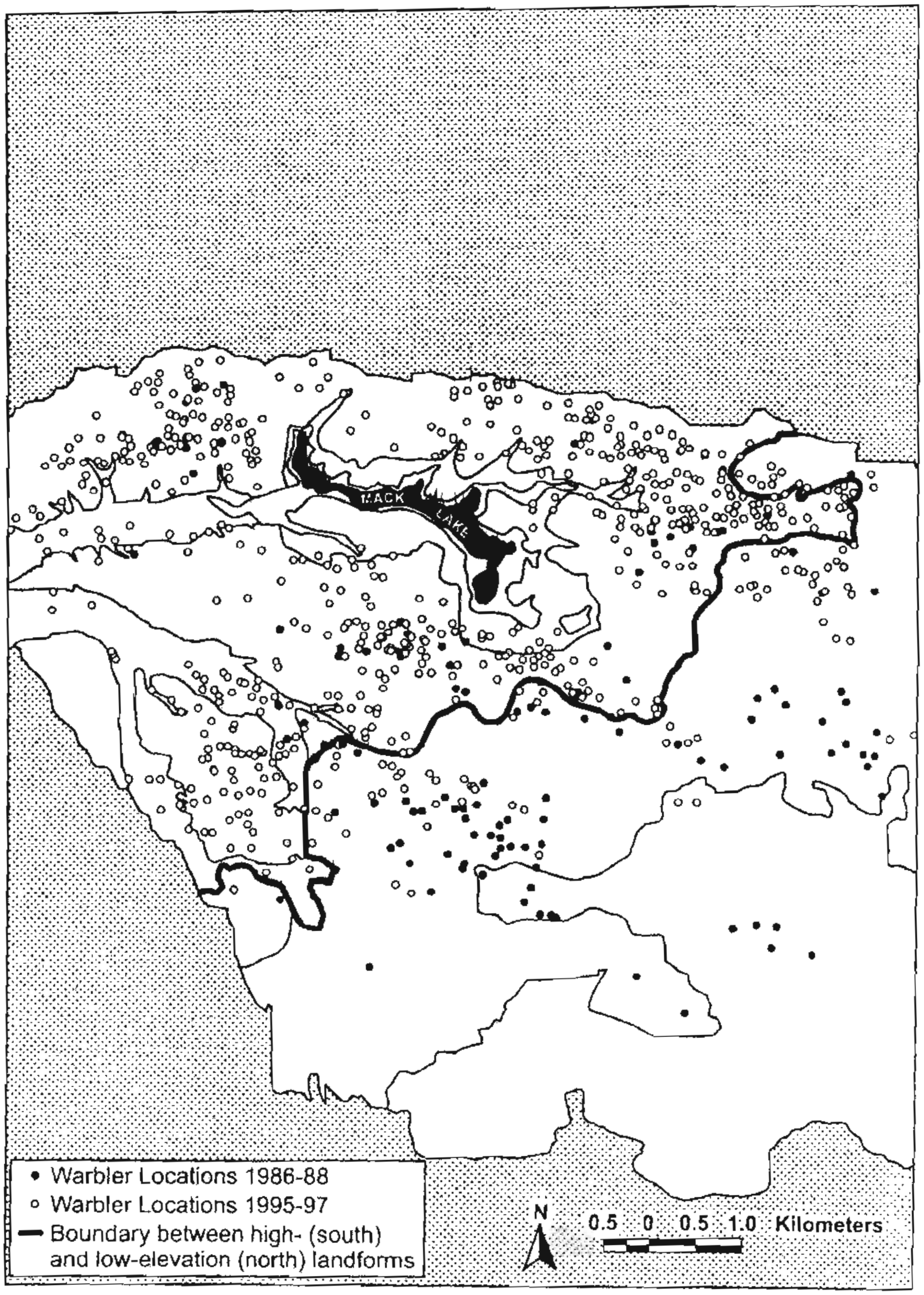

Figure 7. Landform-level ecosystem map of the Mack Lake burn, northern Lower Michigan, showing the census locations of singing-male Kirtland's warblers. During the first 3 yr of warbler occupation (1986–1988), 62% of the warbler population occupied the high-elevation landforms. From 1995–1997, 86% of the population occupied the low-elevation landforms.

The effect of soil water and nutrient availability on the growth of jack pine has also been demonstrated. Jameson (1965) 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 particularly 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 distinguishing features of both the Graycalm and Montcalm soil series (Hannah and Zahner 1970, Werlein 1998), which dominate the high-elevation landforms. Shetron (1972) found jack pine growth in northern Lower Michigan to be significantly greater on Graycalm and Montcalm soils than on unbanded soils of the Grayling series 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

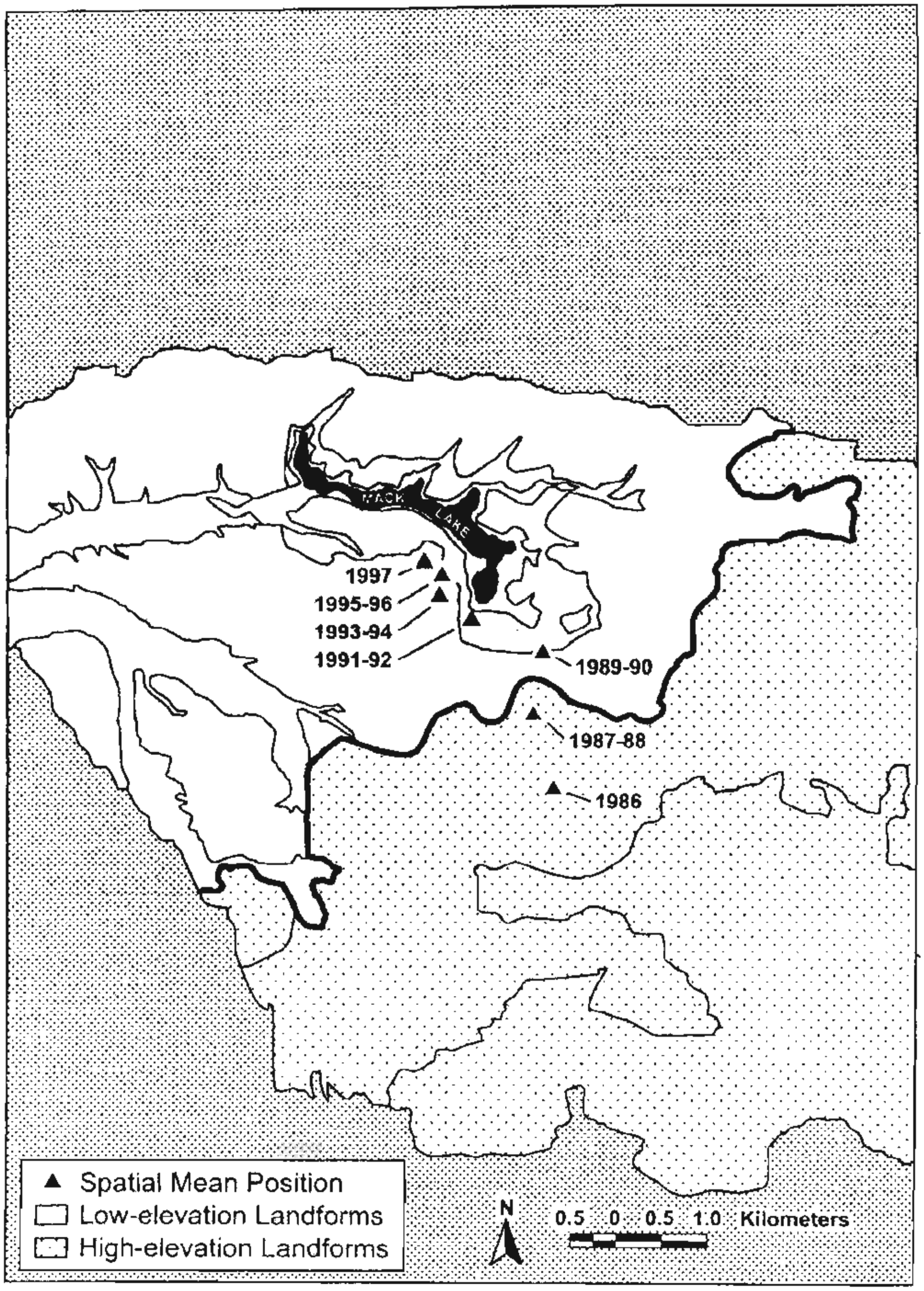

Figure 8. Landform-level ecosystem map of the Mack Lake burn, northern Lower Michigan, illustrating the change in position of the spatial mean of the Kirtland's warbler population over time. During the 12 yr period 1986–1997, the mean position of the population migrated approximately 3.0 km.

in the upper portions of the sola. In addition, 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).

Among the landform-level ecosystems of the Mack Lake burn, significant differences in jack pine height growth (Table 4) largely reflect the combined influence of microclimate- and soil-related attributes. For example, the relatively tall, fast-growing pines of the high-elevation landforms are the result of warmer growing-season temperatures and moister, more nutrient-rich soils. Conversely, the short, rather slow-growing pines of the low-elevation landforms are the product of colder growing-season temperatures and drier, more nutrient-poor soils.

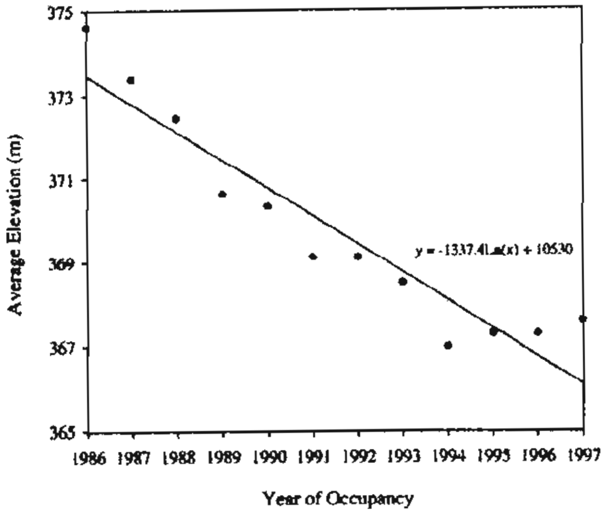

Figure 9. Change in the average elevation of the Kirtland's warbler population (1986–1997); Mack Lake burn, northern Lower Michigan.

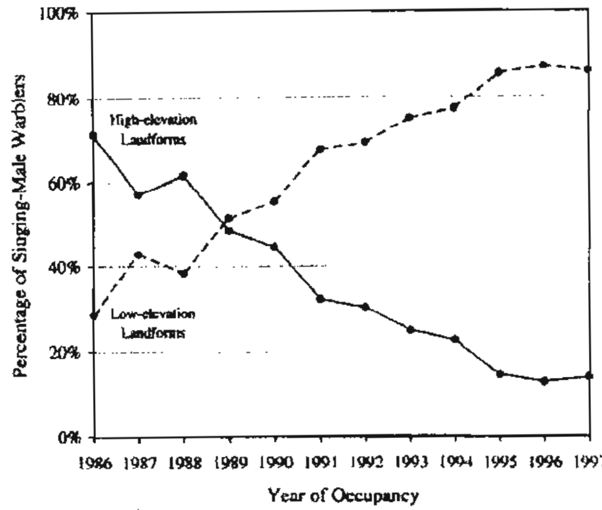

Figure 10. Percentage of singing-male Kirtland's warblers occupying the high- and low-elevation landforms (1986–1997); Mack Lake burn, northern Lower Michigan.

Landscape Ecosystem Diversity and Kirtland's Warbler Occurrence

The Mack Lake burn is characterized by a remarkable diversity of landscape ecosystems occupied by the Kirtland's warbler. In fact, the 5 landform-level ecosystems, and the 11 landscape ecosystem types nested within them, are very typical of the range of jack pine-dominated landscape ecosystems occupied by the warbler across its 13 county range of occurrence in northern Lower Michigan (Kashian et al. *this issue*). In the past, the breadth of this ecological diversity has remained largely understudied because wildlife biologists and land managers have focused primarily on the biotic component (i.e., jack pine and Kirtland's warbler) of these ecosystems. Our research emphasizes the considerable site heterogeneity that characterizes Kirtland's warbler habitat although it may be perceived as relatively homogeneous stands of jack pine. The landform-level ecosystem map of the Mack Lake burn provides a graphical representation of part of this heterogeneity—heterogeneity that is expressed in unique spatial and temporal patterns of warbler colonization and occupancy.

Ecosystem diversity, defined as the kinds and patterns of landscape ecosystems within a specified area (Lapin and Barnes 1995), is of particular importance in that it exerts strong control over the potential duration that warblers will occupy a given area. Within the Mack Lake burn, ecosystem diversity 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 vegetation. In general, as ecosystem diversity increases, so increases site heterogeneity and the range of physiographic, climatic, and edaphic conditions present. Site heterogeneity is typically reflected in differential rates of jack pine growth and, consequently, differential patterns of Kirtland's warbler occurrence over time (Kashian and Barnes 2000). 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 pine growth will be colonized later and will remain occupied for a relatively long duration. Therefore, 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 ecosystems. Based on the research at Mack Lake, a companion study to examine landscape ecosystem diversity and Kirtland's warbler occurrence across the range of sites currently and formerly occupied was conducted by Kashian et al. and is reported in the article that follows in this issue.

The lengthy occupancy of the Mack Lake burn by Kirtland's warbler (15 yr through 2000) is largely attributable to the diversity of landscape ecosystems present. Because ecosystem diversity typically increases with increasing land area, a

Table 6. Occupancy of landform-level ecosystems by the Kirtland's warbler (1986–1997); Mack Lake burn, Oscoda Co., northern Lower Michigan.

	First occupancy*	Peak occupancy	Last occupancy†	Occupancy duration
Low-elevation landforms				
Landform I	1991	1994	1997	7
Landform III	1994	1996	1996	3
Landform IV	1986	—	—	>12
High-elevation landforms				
Landform V	1986	1986	—	>12
Landform VI	1986	1987	1989	4

* Defined as the first year of landform occupation by ≥ 5% of the Mack Lake warbler population.

† Defined as the last year of landform occupation by ≥ 5% of the Mack Lake warbler population.

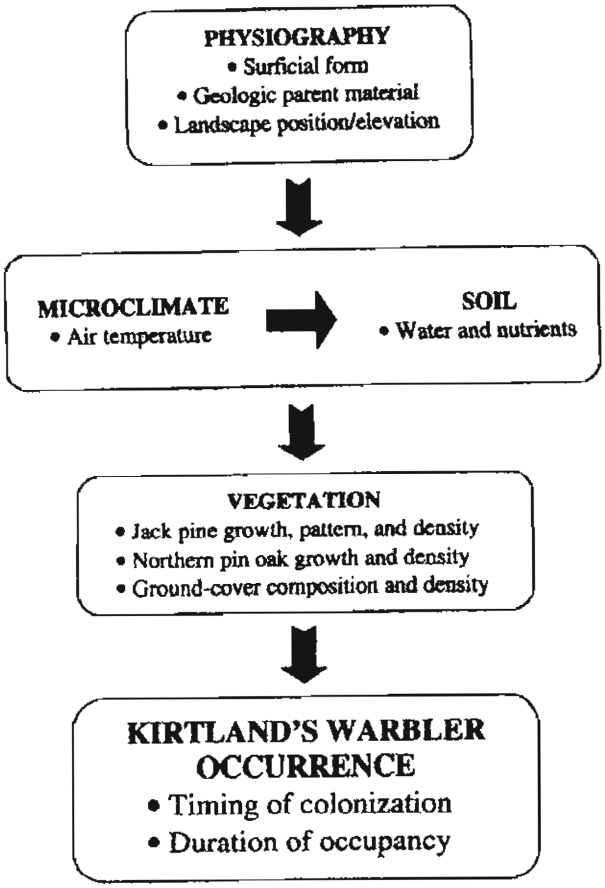

Figure 11. Schematic diagram illustrating the major ecological factors that influence Kirtland's warbler occurrence among the landscape ecosystems of the Mack Lake burn, northern Lower Michigan. (Modified from Barnes et al. 1998.)

large tract will potentially remain occupied by warblers for a longer period than will a small tract, assuming jack pine of the appropriate height and spatial configuration are present on both. This observation is consistent with the findings of Kashian and Barnes (2000), who found landform-level ecosystem diversity to be responsible for extending Kirtland's warbler occupation of the Bald Hill burn at least 4–6 additional years. This relationship may explain, in part, why warblers are thought to "prefer" large stands of jack pine (Walkinshaw 1983, p. 35) and why the most successful warbler colonies have been associated with stands 200 ac and larger (Byelich 1976).

This research presents the results of a long-term effort to track the spatial pattern of Kirtland's warbler colonization and occupancy within one of the largest and perhaps most successful tracts of contiguous warbler habitat known. The monitoring techniques and related analyses employed in this effort were based in large measure on data from the annual census of Kirtland's warbler singing males. Although the Kirtland's warbler census is conducted with the highest degree of care and consistency, certain important caveats regarding the analysis and interpretation of the census data should be considered. First, census locations of singing-male warblers do not represent actual warbler nest locations. However, because male warblers are fiercely territorial (Mayfield 1960, p. 45, Walkinshaw 1983, p. 47), and territory size is small (< 8.5 ha; Walkinshaw 1983, p. 74) compared to that of individual landforms, census locations are reasonably assumed to contain nest locations.

Second, the accuracy of the census is based largely on the assumption that every male warbler is counted and is counted only once. The census protocol itself is specifically designed to minimize double counting, and attempts are made to ensure that birds tallied on adjacent transect lines are not the same males with large or double territories. It is virtually impossible, however, to ensure that every male warbler is counted, since 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 successful nesting area, its annual census has probably been conducted more thoroughly and with greater care than that of other, less successful areas. Nevertheless, given the overall size of the area occupied and the density of the birds being counted, some measurement error is to be expected. Our analysis of the spatial pattern of Kirtland's warbler colonization and occupancy is based more heavily on the relative number of birds distributed among landforms over time rather than on the absolute number. Therefore, the effect of any measurement error on the results is considered negligible.

Implications for the Management of the 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. 23). Because of the decrease in the occurrence of large wildfires observed across the breeding range during the 20th century (Ryel 1981), jack pine plantations have become the preferred method of providing suitable habitat for warbler populations. The first directed effort to develop and maintain large tracts of jack pine specifically for use as Kirtland's warbler nesting habitat was made in 1957 when the Michigan Conservation Commission formally established three 1,000 ha management areas (Mayfield 1963, Radtke and Byelich 1963). Currently, habitat management for the warbler involves over 57,000 ha on 23 different state and federal management areas. In spite of these efforts, however, habitat developed by planting on management areas has been generally less suitable in terms of warbler reproductive success than habitat produced naturally by wildfire (Bocetti 1994). 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. With the Mack Lake burn very near the end of its duration of occupancy (Figure 1), maintenance of current population levels may depend entirely on the success of plantation habitat and on the continued ability of managers to administer the recovery program in a manner that is cost effective and efficient.

This research, an application of the landscape ecosystem approach to characterize Kirtland's warbler habitat occupancy, indicates that spatial and temporal patterns of warbler occurrence are grounded in the interrelated physical and biotic components of landscape ecosystems (Figure 11). Knowledge of these ecological relationships has advanced our understanding of why warblers differentially colonize, occupy, and abandon specific landscapes across their breeding range. Thus, we believe the landscape ecosystem approach has direct application to the management of the Kirtland's warbler, and potentially other endangered species as well. A landscape framework provides resource managers with a useful tool for evaluating *a priori* the extent to which a potential management area will accomplish specific management objectives. For example, if managers determine that a tract of plantation habitat is needed relatively quickly (e.g., to rescue a crashing population), identifying landforms that support fast-growing jack pine (e.g., ice-contact terrain) would be appropriate. Alternatively, if managers seek to maximize the duration that warblers will occupy a given area, identifying landforms that are characterized by (1) very poor site conditions, or (2) a diversity of constituent landscape ecosystem types (i.e., heterogeneous site conditions) would be desirable. This research has been instrumental in encouraging wildlife biologists and resource managers to shift their focus from organisms, i.e., jack pine and the Kirtland's warbler, to entire landscape ecosystems. This does not mean that organisms are unimportant—quite the contrary. However, it does mean in practical terms that we never deal just with organisms but always and necessarily with ecological systems of which organisms are notable and interacting parts (Rowe 1990). These results have also influenced, and have been incorporated into, specific guidelines for identifying potential Kirtland's warbler management areas in the context of a landscape ecosystem framework (Kashian 1998). In conclusion, it is clear that if Kirtland's warbler populations are to be sustained in the 21st century, habitat suitable in quality, quantity, and spatial orientation must be continuously produced (Kepler et al. 1996). The landscape ecosystem approach represents a very practical means toward this end.

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