Landscape Ecosystems of Northern Lower Michigan and the Occurrence and Management of the Kirtland's Warbler

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

ABSTRACT. The Kirtland's warbler (*Dendroica kirtlandii* Baird) is an endangered songbird that nests in northern Lower Michigan in ecosystems dominated by young jack pine (*Pinus banksiana* Lamb.). An ecological, multifactor approach was used to determine the range and characteristics of landform-level ecosystems supporting the warbler and to compare the spatial and temporal patterns of warbler occupation among these ecosystems. Using an ecosystem rather than a strictly biological approach, the landforms occupied by the warbler are very diverse. Twelve landforms were identified based on 61 sites currently or formerly occupied by the warbler. Average annual jack pine height growth, an indicator of stand structural features that influences initial warbler colonization and duration of occupancy, differed significantly among landforms, resulting in marked differences in warbler occurrence in time and space across the breeding range. Landforms with favorable growing conditions for jack pine were colonized earliest and were occupied for the shortest duration, whereas landforms with unfavorable growing conditions were colonized relatively late but were occupied longest. Different ecological factors, such as the spatial position of landforms, microclimate, soil texture, or a combination of these factors, may account for favorable or unfavorable growing conditions for jack pine, which in turn affects the timing and duration of warbler occupancy. The classification and description of ecosystems occupied by the warbler provides an ecological framework for warbler management, especially when plantations rather than wildfire are the primary source of warbler habitat. For. Sci. 49(1):140–159.

Key Words: Ecosystem classification, endangered species, jack pine, landforms, physiography.

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THE KIRTLAND'S WARBLER (*Dendroica kirtlandii* Baird) is an endangered songbird that nests only in ecosystems dominated by jack pine (*Pinus banksiana* Lamb.) primarily in six counties in northern Lower Michigan. The Kirtland's warbler was officially listed as a federally endangered species in 1967, and the availability of suitable breeding habitat was quickly recognized by the Kirtland's Warbler Recovery Team as a principal factor limiting warbler populations (Mayfield 1963, Byelich et al. 1976, Ryel 1981, Probst 1986, Probst and Weinrich 1993, Kepler et al. 1996). The warbler nests mainly in dry, sandy, glacial outwash ecosystems dominated by young jack pine 1.4 to 5.0 m tall in stands at least 32 ha in area and having at least 2,000 stems/ha (Mayfield 1960, Probst 1988, Probst and Weinrich 1993). In these ecosystems, jack pines are typically arranged in a patchy configuration interspersed with grassy openings (Mayfield 1960, Zou et al. 1992). Kirtland's warblers most often nest on the edges of these openings under nest-sheltering lower live branches; stands of trees taller than 5.0 m are quickly abandoned once lower live branches are shaded out and/or small openings become overgrown.

The success of warbler management hinges upon the cooperative work of both foresters and wildlife biologists for managing warbler habitat. Young stands in northern Lower Michigan were historically created by wildfires (Van Tyne 1951, Mayfield 1960, 1975, 1983, Whitney 1987, Comer et al. 1995a). The occurrence of wildfires in this region was steadily reduced during the 20th century by effective fire suppression (Ryel 1981) and increased fragmentation due to clearcutting, agriculture, and road construction. Accordingly, the Kirtland's Warbler Recovery Plan (Byelich et al. 1976) mandated the use of large jack pine plantations to ensure a continuous supply of suitable habitat for the warbler. These plantations, together with occasional large wildfires, have allowed the Kirtland's warbler population to increase from <200 singing males in the early 1970s to 1,085 in 2001 (Figure 1), representing one of the most successful recovery programs resulting from the Endangered Species Act (Solomon 1998). Assuming no large wildfires occur in the next few decades, jack pine plantations may become the only source of warbler habitat. Therefore, understanding the interactions of physical and biotic factors and how these factors influence warbler occupancy of plantations is a crucial research objective if management is to meet population objectives and be efficient and cost-effective.

Future Kirtland's warbler management will require a shift from a stand-level, biotic focus to one that considers broad-scale ecosystem units. Many authors have suggested a shift in focus from organisms to whole ecosystems in preserving endangered species (Scott et al. 1987, Scott 1990, Barnes 1993, Franklin 1993, LaRoe 1993, Taylor 1993, Rowe 1992, 1994, 1998). Likewise, many public and private forest managers have begun to employ an ecosystem perspective in their land management decisions, and such an approach has proven valuable in modern forestry (Barnes et al. 1982, Brooks and Grant 1992, Rowe 1992, 1994, Jones and Lloyd 1993, O'Hara et al. 1994, Salwasser 1994). In particular, because the Kirtland's warbler nests only in stands of jack pine of a narrow range of height and structure, understanding the timing of initial warbler colonization and

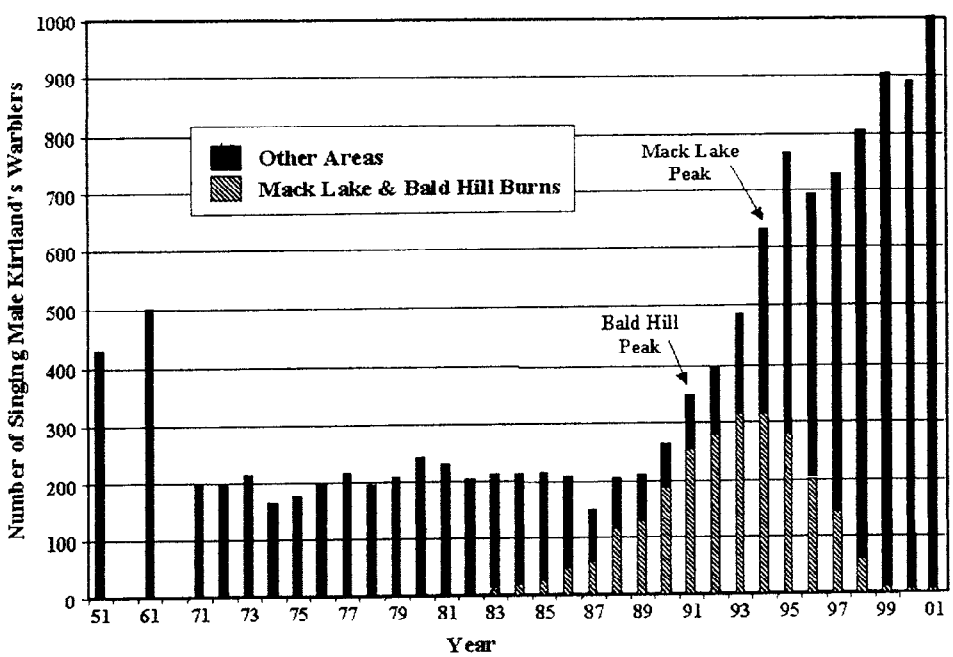

Figure 1. Change in population numbers of singing male Kirtland's warblers in northern Lower Michigan from 1951 to 2001. Data are based on the annual warbler census. The initial rise in the abundance of Kirtland's warblers corresponded with an increase in suitable habitat as created by two major wildfires (at Bald Hill in 1975 and at Mack Lake in 1980). However, the total warbler population continued to increase even after the local warbler populations at Bald Hill and Mack Lake peaked and began to decrease, suggesting the importance of plantations as the primary source of warbler habitat.

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the duration of occupancy of specific stands depends strongly on understanding the site factors that affect jack pine establishment, growth, and succession. Thus, warbler management depends as strongly on the management of land as it does on the management of the warbler itself.

In northern Lower Michigan, a landscape ecosystem approach provides a useful perspective for understanding Kirtland's warbler occupation of ecosystems dominated by jack pine. Landscape ecosystems are volumetric tracts of land consisting of interacting physical site factors of climate, physiography, soil, and water, as well as biota (Rowe 1988, Rowe and Barnes 1994, Barnes et al. 1998, p. 3–6), are spatially explicit, and are organized within a hierarchy (Albert et al. 1986, Albert 1995, Barnes et al. 1998, p. 3). In this approach (Figure 2), regions and districts are bounded at the broadest scale primarily by an integration of macroclimatic and gross physiographic factors (Figure 3). Macroclimate is more or less homogeneous at the subdistrict scale, and these units are distinguished by differences in physiography, soil, and vegetation. Subdistricts may be further subdivided into physiographic systems that correspond to glacial landforms, such as outwash plains, ice-contact terrain, and moraines that may extend over 100s of km. Physiographic systems contain landform-level ecosystems, which in turn contain landscape ecosystem types (Figure 2). Because warbler management requires large stands of jack pine, it most often takes place at the scale of landform-level ecosystems within a subdistrict. At all levels within the hierarchy, physiography, defined as physical geography and consisting of surface form and parent material, plays a key role in determining ecosystem units. Physiography mediates microclimate, hydrology, soil formation, nutrient status, and the type and frequency of natural disturbance (Barnes et al. 1982, Grimm 1984, Rowe 1988, Whitney 1986, Bailey 1987, Host et al. 1987, Swanson et al. 1988).

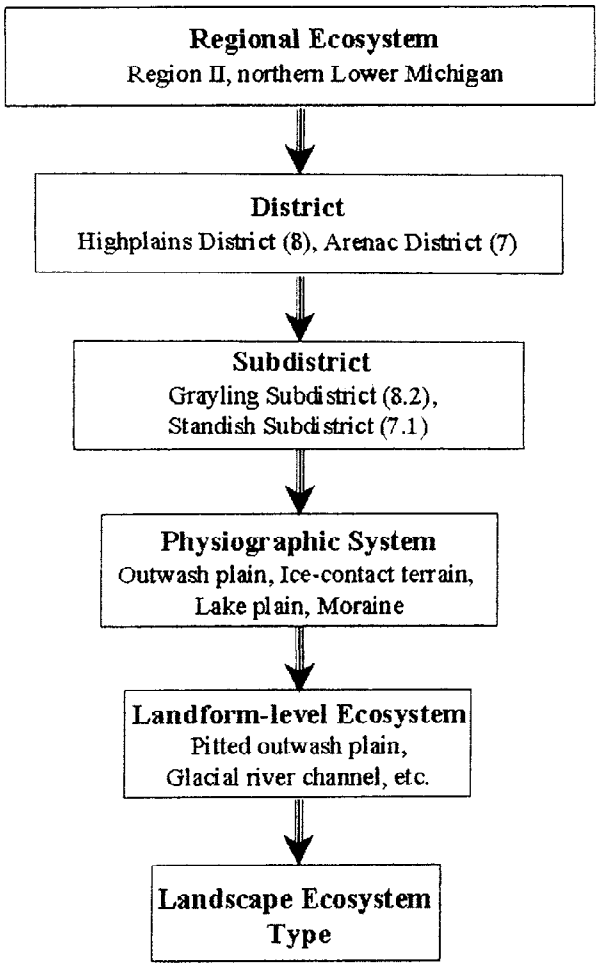

Figure 2. Diagram depicting the hierarchical, nested organization of landscape ecosystems occupied by the Kirtland's warbler at successively smaller spatial scales in northern Lower Michigan.

Applying this understanding of physiography, ecosystems may be defined at multiple scales and classified though simultaneous integration of climate, landform, soil, and vegetation within a regional landscape ecosystem framework. For example, broad-scale physiography at the landform scale was found to mediate microclimate, soil, nutrient status, vegetation composition and spatial pattern, and jack pine height growth at the 10,000 ha Mack Lake burn (Barnes et al. 1989, Zou et al. 1992, Walker et al. this issue) and at the 500 ha Bald Hill burn (Kashian and Barnes 2000) in northern Lower Michigan. The interrelationships of these factors also appeared to control spatial and temporal patterns of warbler occupancy across the burned areas (Barnes et al. 1989, Kashian and Barnes 2000, Walker et al. this issue). The linkage of warbler occupancy to landform-level ecosystems suggests that the patterns of Kirtland's warbler occurrence in space and time is strongly controlled by both physical and biotic factors (Barnes 1993). This landscape ecosystem approach is superior to single-factor classifications or classifications based on overlain layers of single factors, because these methods tend to ignore or overlook detailed ecological interrelationships among the factors (Spies and Barnes 1985a).

The nesting habitat of the Kirtland's warbler has been studied in detail, but the bulk of this research has focused on characteristics of vegetation (Smith 1979, Buech 1980, Probst and Hayes 1987, Probst 1988, Zou 1988, Nelson 1992, Probst and Weinrich 1993) rather than on whole ecosystems. The small fraction of these studies that describes site characteristics includes fine-scale studies scattered across the breeding range. These fine-scale studies do not reflect the diversity of landscape ecosystems present that may directly cause differing patterns of Kirtland's warbler occupancy. In addition to ecosystem classification studies (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985a, Albert et al. 1986, Hix 1988, Archambault et al. 1990, Simpson et al. 1990, Host and Pregitzer 1992, Albert 1995, Zogg and Barnes 1995, Hix and Pearcy 1997, Baker and Barnes 1998), a landscape ecosystem approach has been applied extensively in Michigan as the basis for protecting several rare or endangered plants and animals (Taylor 1993), as a predictive tool with which to organize an systematic inventory of rare or endangered species (Albert 1993), and to assess plant biodiversity (Lapin and Barnes 1995, Pearsall 1995).

Our general objectives were to identify and describe the landform-level landscape ecosystems (hereafter termed

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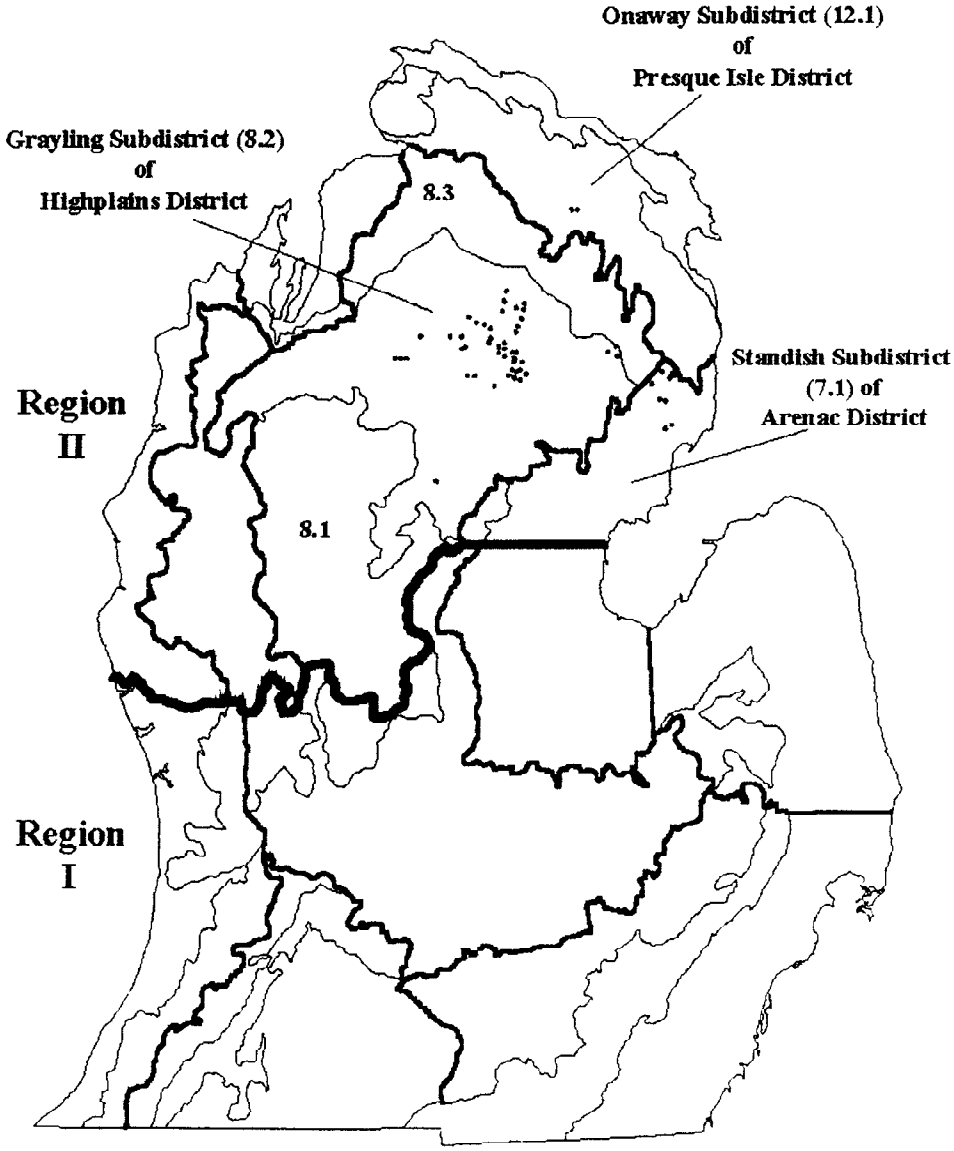

Figure 3. Regional landscape ecosystems of northern Lower Michigan (Albert et al. 1986) with locations of 61 study sites (denoted by markers) currently or formerly occupied by Kirtland's warblers. The majority of warblers are concentrated within the Grayling Subdistrict (8.2) of the Highplains District (8), while fewer warblers are also found in the Standish Subdistrict (7.1) of the Arenac District (7).

landforms) of areas currently or formerly occupied by the Kirtland's warbler in northern Lower Michigan and to relate the time of initial warbler colonization and duration of occupancy to the physiography, microclimate, soil, and vegetation of these landscape ecosystems. Our specific objectives were to: (1) determine and describe the range of ecological characteristics of areas currently or formerly occupied by the warbler in northern Lower Michigan in terms of physiography, microclimate, soil, and vegetation; (2) relate the time of initial colonization and duration of Kirtland's warbler occupancy for selected landforms to the physical and biotic factors of those landforms; and (3) provide management recommendations for agencies responsible for Kirtland's warbler recovery based on our research.

Study Area

Study sites were defined by the current or former locations of singing male warblers as determined by field maps compiled during official annual warbler censuses. Although census records do not represent actual nest locations, the territoriality and small territory size (8.5 ha; Walkinshaw 1983) of male warblers relative to stand size allow census locations to serve as a reasonable approximation of warbler occupation. Research was conducted at 61 sites of current or former warbler occupation in northern Lower Michigan (44°30′N, 84°30′W). Fifty sites were located in the Highplains District (8) of Region II (northern Lower Michigan) as described by Albert et al. (1986), and 11 study sites were located in the Arenac District (7) and the Presque Isle District (12) of Region II (Figure 3).

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The Highplains District has the most severe climate in Lower Michigan due to its inland location, northern latitude, and high elevation relative to the surrounding area (Albert et al. 1986). Temperature conditions are unpredictable during spring and fall; late-spring and even mid-summer freezes are common. The growing season is both the shortest and the most variable in Lower Michigan. The mean annual temperature is 6.7°C, and the average temperature during the growing season (May through September) is 16.9°C. Physiography tends to govern microclimate in the Highplains, and cooler air tends to collect in low-lying areas (Albert et al. 1986). In contrast, the Arenac District to the east exhibits a climate moderated by Lake Huron, resulting in a growing season that is considerably longer than in the Highplains District (133 vs. 115 days) and markedly fewer days before the last spring freeze (210 vs. 300; Albert et al. 1986). The Arenac District exhibits only a slightly higher average annual temperature (7.3°C) and mean growing-season temperature (17.8°C) than the Highplains.

The physical geography of the Highplains and Arenac Districts is the result of an extensive glacial meltwater drainage system, resulting in a broad, sandy outwash plain broken by high, flat-topped features of sand and gravel. Specific fluvioglacial features in the region include flat and pitted outwash plains, glacial river and meltwater channels, outwash deltas, ice-contact or ice-stagnation features, and sandy lake plains (Farrand 1982). The outwash plain that forms the Highplains is relatively flat and has 0–2% slopes. The majority of the relief in the region is on or near end moraines or ice-contact terrain, including ice-block depressions or kettle-kame topography, where slopes are typically 5–10% and less frequently 20–40 %. A major flat, glacial outwash delta in the Arenac District lies at a lower lake-plain elevation. The mineral soils of both districts are dominated by sands of the Grayling series (Typic Udipsamments), characterized by excessively drained, acid, relatively undeveloped medium sand, although medium-fine or fine sand is occasionally present (Werlein 1998). In the relatively homogeneous Grayling sands, subtle changes in texture and pH create important differences in soil water and nutrient availability for plants. Sands of the Graycalm series (Alfic Udipsamments), typified by the presence of thin, fine-textured bands of loamy sand to sandy clay loam in the lower horizons, are also particularly common on or near ice-stagnation features of the area (Werlein 1998).

The vegetation of the study area is dominated by jack pine and, to a lesser degree, northern pin oak (*Quercus ellipsoidalis* E.J. Hill). During the presettlement period, closed forests of jack pine surrounded small pine barrens on outwash plains in the region, and similar forests of jack pine intermixed with red pine (*P. resinosa* Aiton) and eastern white pine (*P. strobus* L.) or northern pin oak were found particularly on the ice-contact terrain in the region much as they are today. Vegetation on this terrain was variable, ranging from northern hardwood forests in areas of infrequent fire to jack pine-northern pin oak forests and barrens on the driest sites. In the Arenac District, jack pine-oak forests and barrens were also dominant (Comer et al. 1995a, 1995b).

Fire was the dominant force in the genesis and maintenance of jack pine forests that supported the Kirtland's warbler in presettlement times (Albert 1995, Comer et al. 1995a). The fire interval for jack pine forests in the Highplains District was approximately 27 yr during the presettlement period, and today is approximately 31 yr (Simard and Blank 1982). The dry, coarse-textured outwash soils common to the area favored jack pine, which in turn encouraged a fire regime that perpetuated flammable species (Whitney 1986). The juxtaposition of glacial landforms was also important in forming the mosaic of pine vegetation, as the prevalent westerly winds carried fires for long distances over flat areas without major topographic interruption (Comer et al. 1995a).

Methods

Field Methods

Official census records were obtained from the Michigan Department of Natural Resources and used to define the study sites. These data were plotted on 7.5 min topographic maps to create a composite map of Kirtland's warbler locations for each study site for each year of occupation. Sites were considered occupied if they contained at least one singing male Kirtland's warbler for at least 2 successive years. The physiographic system associated with each study site was identified based on aerial photographs and topographic maps, and sites were assigned to one of three independent levels of study intensity. A high-intensity study was conducted to understand the types of ecosystem characteristics that may affect jack pine growth and, ultimately, warbler occupancy. Transect sampling was used in a moderate-intensity study to sample additional landforms once important ecological interrelationships were identified with the high-intensity study, and a classification of landforms was built. Finally, a low-intensity study was conducted to examine the classification in as many other areas not sampled across northern Lower Michigan as possible.

For the high-intensity study, six sites were selected that had complete or nearly complete census records. Five of the six sites were located in the Highplains District and represent a gradient of different physiographic features and topographic conditions. Two of these sites, at the Bald Hill area, were described and studied in detail by Kashian and Barnes (2000). The sixth site, located in the Arenac District, provided the opportunity to study warbler occupation in a different regional landscape ecosystem. For the moderate-intensity study, 12 sites independent of those in the high-intensity study were chosen that contained small to moderately sized stands with complete or nearly complete census records. These sites were chosen both to investigate a greater range of landforms and to determine the repeatability across the landscape of the landforms identified in the high-intensity study. Given that our sampling design included only those landforms occupied by warblers, replication of samples was difficult, and some landforms were quantitatively sampled (in the high-intensity or moderate-intensity studies) only once. For the low-intensity study, 44 additional study sites were selected to investigate warbler occupation on diverse landforms. A working classification of landforms repre-

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sented by the study sites at each level was constructed and refined as sampling progressed.

For the high-intensity study, fifty 10 × 20 m plots (200 m^2) were established within occupied areas using a stratified random design (Spies and Barnes 1985a). At least eight plots were established per landform at each study site. Physiographic data were collected in each plot including elevation, aspect, slope percent, surface shape, and degree of outwash pitting in the general area (expressed as a categorical pitting index, where 1 = no pitting and 5 = very pitted). A soil pit about 2 m^2 was dug to a depth of 180 cm in a randomly selected quarter of the plot. The top 150 cm were described in detail according to Natural Resource Conservation Service procedures (Soil Survey Staff 1975), and soil samples were collected from each horizon. Soil texture and pH data were also collected at standardized 50 cm intervals from the top of the profile and from the bottom of the pit to a depth of 500 cm using a soil auger. Data on organic matter depth and pH were collected at a random location within each of the three remaining plot quarters, and the general drainage class of the plot area was estimated. When pH 7.0, pH 8.0, or the water table was not reached within the soil profile, it was assigned a maximum depth of 600 cm for analyses, a value slightly deeper than within reach of the soil auger. Depth to lamellae (bands <2 cm thick) and banding (>2 cm thick) were assigned a maximum depth of 999 cm for analyses, since banding was not likely present or ecologically important if it was not reached within 3 to 5 m.

All live and standing dead trees >1.5 cm in diameter at breast height (dbh) were recorded by species. The total height of five dominant jack pines and three dominant northern pin oaks was recorded to the nearest 0.1 m. The age of each of the five dominant pines was determined using the average of two cores extracted with an increment borer approximately 30 cm above the ground. Tree height was standardized between sites by dividing by tree age and expressing the result as an average annual height growth increment. Comparing annual jack pine height growth across stands of different densities and ages is feasible given the relatively negligible effect of stand density on the growth of young pines (Guilkey and Westing 1956). In addition, we sampled only stands of an age (<35 yr old) when jack pine height growth over time exhibits a fairly linear relationship (Carmean and Lenthall 1989).

The 5 × 20 m subplot (100 m^2) not containing the soil pit was used to estimate the percent aerial coverage of all ground cover species, including woody stems <1.5 cm dbh, by coverage class using a 12 class scale (0.25, <0.005%; 0.05, 0.005–0.01%; 1, 0.01–0.1%; 2, 0.1–0.5%; 3, 0.5–1%; 4, 1–2%; 5, 2–4%; 6, 4–8%; 7, 8–16%; 8, 16–32%; 9, 32–64%; 10, 64–100%). Standardized coverage estimates were made using a sampling frame that was 0.1% (1,000 cm^2) of the subplot. Nomenclature follows Voss (1972, 1984, 1997) for vascular plants; all nonvascular plants except *Cladina* were recorded as "mosses" or "lichens." Coverage of ground flora species was used to develop ecological species groups for use as indicators of site conditions (Spies and Barnes 1985b, Kashian 1998). Percent coverage of jack pine and northern pin oak in the ground cover layer was also estimated for both the subplot and the entire plot. The percent coverage of the dominant plant groups including trees, shrubs, forbs, grasses, mosses, and lichens was recorded for the entire 10 × 20 m plot.

Sampling of the 12 moderate-intensity study sites involved the establishment of 2 perpendicular transects at each site, each with a random start. Four 5 × 10 m (50 m^2) transect plots were established at random distances from predetermined points along each transect. Within each transect plot, the same physiographic data were collected as at the high-intensity study sites. Soil auger borings were taken adjacent to each plot, and soil texture, pH, and the presence and amount of fine-textured banding were determined at the surface and at 50 cm intervals to a depth of approximately 4 m. Additional data, including depth to alkaline pH (8.0) and drainage class were also collected. A shallow soil pit (ca. 50 cm deep) was dug adjacent to the auger point to examine and record thickness and pH of organic horizons and to collect a sample of subsurface horizons (20 to 40 cm). Vegetation data were collected using the same methods as at the high-intensity study sites. Aerial coverage of ground cover vegetation was estimated for the entire 5 × 10 m plot.

The low-intensity study included descriptive data that were not quantitatively analyzed. These study sites were selected to represent the range of landforms occupied by the warbler. Using field reconnaissance, the physiography, soil, and vegetation of each area were recorded. Soil was examined to a depth of 3 m with a soil auger, and qualitative data regarding general texture, the presence of fine-textured banding, depth to alkaline soil (pH 8.0), general soil pH, and depth to water table were collected. Qualitative vegetation data included an estimate of overstory tree density, the degree of patchiness and openness, the presence of overstory trees other than jack pine, and dominant ground cover species.

Laboratory Methods

The texture of soil samples collected in the field was confirmed in the laboratory using the hydrometer method, as modified by Grigal (1973), in order to determine the proportion of sand, silt, and clay in 100 g samples. The sand fractions were oven-dried and dry-sieved to determine the amount of very coarse, coarse, medium, fine, and very fine sand (Day 1965). The pH of 30 g samples was determined in a 1:1 soil-to-water solution (w/v) using a Fischer pH meter with a glass combination electrode.

Statistical Methods

Univariate one-way analysis of variance (ANOVA) with $\alpha = 0.05$ was used to compare mean values of 91 physiography, soil, and vegetation (tree growth, stand structure, and ground cover) variables among landforms identified in the high-intensity study. The Kruskal-Wallis test for nonparametric ANOVA (Conover 1980, p. 229–230) was used when appropriate transformations were not successful in meeting the assumptions of the ANOVA model. To examine the ecological distinctness of landforms identified in the field, variables from the six high-intensity landforms were entered into canonical variates analysis (Williams 1981). Variables found significant with ANOVA were entered into forward stepwise discriminant

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analysis (Jenrich 1977) using a stopping rule set at α to enter and remove = 0.15 in order to select subsets of variables to include in canonical variates analysis. Error rates were tested using the jackknife method of discriminant analysis (Hand 1981, p. 163–165). Interpretation of canonical variates was facilitated by correlating the canonical variates with the original variables (Spies and Barnes 1985a). Because the distributions of the selected variables showed no serious departures from normality or homogeneity, assumptions of discriminant analysis (multivariate normality and equal covariances) were not tested. Analysis of the 12 moderate-intensity study sites was identical to that of the high-intensity sites, comparing a modified set of 54 variables among landforms. The mean annual height growth increment of jack pine was compared across all landforms identified in the high-intensity and moderate-intensity studies with analysis of covariance (ANCOVA), using stand age as a covariate.

Results and Discussion

Classification and Description of Landforms

Twelve landforms occupied by the Kirtland's warbler were identified, described and classified (Table 1); 10 of these were quantitatively distinguished. At the highest hierarchical level of the classification, the majority of Kirtland's warblers occupy two regional landscape ecosystems in northern Lower Michigan (the Standish Subdistrict of the Arenac District and the Grayling Subdistrict of the Highplains District) that are characterized by markedly different physical and biotic factors, particularly macroclimate, the occurrence of northern pin oak, and jack pine height growth (Table 2). Only one landform, characterized by flat topography and coarse soil (Tables 3 and 4), was distinguished within the Arenac District (landform 1). Most importantly, the warmer macroclimate of this landform markedly distinguishes it from those in the Highplains District. Consequently, the timing of warbler colonization and the duration of occupancy are very different between the two regional ecosystems.

Within the Grayling Subdistrict of the Highplains District, Warblers occupied landforms in both outwash plain and ice contact physiographic systems, both common in the region. These two physiographic systems form the second level in the hierarchical classification (Table 1). Within these physiographic systems, 11 landforms were distinguished and characterized based on differences in physiography at broad and fine scales, microclimate, soil texture, and ground cover vegetation (Table 2). At the third level of the classification, landforms within outwash physiographic systems are typically either nonpitted (landforms 2–7), characterized by flat topography, or pitted (landforms 8–9), characterized by rolling, fine-scale topography and a mosaic of diverse site conditions. Nonpitted outwash plains in outwash physiographic systems are further distinguished based on their topographic position in the landscape and include those having poor, homogeneous site conditions (landforms 2 and

Table 1. Classification of landforms occupied by Kirtland's warblers in the Grayling (Highplains District) and Standish (Arenac District) Subdistricts in northern Lower Michigan. Species name in italics represents the dominant ecological species group for the landform.

Standish Subdistrict (7.1)
- Lake plain physiographic system
  - 1. Nonpitted outwash plains; coarse and medium-coarse sand with gravel; banding absent; excessively drained; warm and infertile; *Solidago*

Grayling Subdistrict (8.2)
- Outwash plain physiographic systems and outwash plains associated with ice-contact terrain
  - Nonpitted outwash plains
    - 2. Low-lying, extremely flat glacial river channel; coarse and medium-coarse sand with pebbles and cobbles; banding uncommon or absent; excessively drained; cold and very infertile; *Prunus*
    - 3. Flat topography; coarse to medium-coarse sand and gravel; banding uncommon or absent; excessively drained; very infertile; *Vaccinium*
    - 4. Low-elevation landform of flat two-level outwash plain[1]; medium sand; banding absent; excessively drained; cold and infertile; *Prunus, Arctostaphylos*
    - 5. High-elevation landform of flat two-level outwash plain[2]; medium sand; banding uncommon or absent; excessively drained; warm and infertile; *Comptonia*
    - 6. Flat topography; medium to fine sand; banding occasional or absent; water table within 2 m; somewhat poorly drained; infertile; *Rubus*
    - 7. Flat topography; medium-fine to fine sand; banding common; well drained; moderately infertile; *Rosa*
  - Pitted outwash plains
    - 8. Flat to moderately sloping[3]; medium-coarse to medium-fine sand; banding absent; excessively drained, *Solidago*
    - 9. Flat to moderately sloping; fine and medium-fine sand and banded soil to medium-coarse sand and no banding; moderate number of local ecosystem types; excessively drained to well drained; variable fertility; *Comptonia*
  - Outwash plains associated with ice-contact terrain
    - 10. Nonpitted outwash plains; flat topography; very fine to fine sand; banding common to frequent and moderate; well drained; moderately infertile; *Maianthenum*
    - 11. Pitted outwash plains; flat to moderately sloping; fine sand and banded soil to medium sand and no banding; many local ecosystem types; excessively to well drained; variable fertility; *Maianthemum, Gaultheria*
- Ice-contact physiographic system
  - 12. Kettle-kame topography[4]; steep to slight slopes; medium sand to sandy loam; banding variable; excessively to somewhat excessively drained; Gaultheria, *Rosa*

[1,2] Landforms sampled at the same study site (the Bald Hill burn; see Kashian and Barnes 2000).
[3] Landform sampled by reconnaissance only.
[4] Landform identified by Barnes et al. (1989) and not sampled in this study.

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Table 2. Summary of selected ecological characteristics among landforms occupied by the Kirtland's warbler in northern Lower Michigan.

Landform[1]	Physiography	Climate	Soil texture and drainage	Site conditions	Response of dominant vegetation	Time of initial colonization	Duration of occupancy
1	Broad, flat, nonpitted outwash plain on glacial outwash delta in Arenac District; outwash physiographic system	Lake Huron-moderated macroclimate; growing season averages 15 days longer than Highplains District; early- and late-season frosts are rare.	Coarse to medium-coarse sand with pebbles and cobbles throughout the profile; fine-textured banding is absent; excessively drained	Very dry, very nutrient poor; warm	Very fast growing jack pine (31.6 cm/yr) and northern pin oak; oak seedlings and sprouts are common and vigorous and exhibit little frost damage; *Solidago hispida* species group is representative	Very early, often at stand age 5 yr or younger	Very short, often for less than 6 yr
2	Broad, flat, nonpitted outwash plain in glacial river channel; lies low in landscape; very homogeneous site conditions; outwash physiographic system	Growing season is slightly colder than at higher landscape positions in the Highplains District; occasional midsummer frosts.	Coarse and medium-coarse sand with pebbles and cobbles throughout the profile; banding is uncommon or absent; excessively drained	Very dry, very nutrient poor; cold	Slow growing jack pine (23.1 cm/yr); occasional northern pin oak seedlings and sprouts with frost damage; *Prunus pumila*	Late, often at age 10 yr or later	Long, from 10–14 yr
3	Broad, flat, nonpitted outwash plain; very homogeneous site conditions; outwash physiographic system	Growing season temperatures similar to most landforms in the Highplains District.	Coarse to medium-coarse sand with pebbles and cobbles throughout the profile; banding is uncommon or absent; excessively drained	Very dry, very nutrient poor; cool	Slow growing jack pine (23.3 cm/yr); frequent northern pin oak seedlings and sprouts; *Vaccinium angustifolium*	Late, usually around age 10 yr	Long, from 10–14 yr
4	Low-elevation landform of broad, flat, nonpitted two-level outwash plain; outwash physiographic system	Minimum growing season temperatures are lower than most landforms in the Highplains District; midsummer frosts are common.	Medium sand; banding is absent; excessively drained	Very dry, nutrient poor; very cold	Very slow growing jack pine (21.6 cm/yr); northern pin oak is absent; *Prunus pumila* and *Arctostapylos uva-ursi*	Late, though in conjunction with warbler occupation of adjacent high-elevation landform	Long, though in conjunction with warbler occupation of adjacent high-elevation landform
5	High-elevation landform of broad, flat, nonpitted two-level outwash plain; outwash physiographic system	Growing season temperatures are similar or warmer than most landforms in the Highplains District.	Medium sand; banding is uncommon or absent; excessively drained	Very dry, nutrient poor; warm	Fast growing jack pine (26.5 cm/yr); oak seedlings and sprouts are common and exhibit slight frost damage; *Comptonia peregrina*	Early, usually at age 6–7 yr	Moderate, often for 7–9 yr

(Table 2 continued on p. 148)

3), an extreme microclimate (landforms 4 and 5), a high water table (landform 6), and fine-textured soil banding and fertile site conditions (landform 7; Tables 3 and 4). Pitted (landform 10) or nonpitted (landform 11) outwash plains, with characteristics similar to those of other outwash plains are also associated with broad ice-contact features mapped by Farrand (1982). Areas mapped by Farrand as "ice-contact" are described to occur as "kames, eskers, and in interlobate tracts," but also "include small areas of proglacial outwash as well as sandy till." Therefore, we have included such outwash-plain sites of flat or pitted topography as a landform group within the outwash plain physiographic system (Table 1) rather than the ice-contact physiographic system.

Multivariate Analyses of Landforms

Very good separation in ordinate space (Figure 4) was obtained among the six landforms in the high-intensity

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Table 2 continued

Landform[1]	Physiography	Climate	Soil texture and drainage	Site conditions	Response of dominant vegetation	Time of initial colonization	Duration of occupancy
6	Broad, flat, nonpitted outwash plain within two meters of water table; outwash physiographic system	Growing season temperatures are similar to most landforms in the Highplains District.	Medium to fine sand; banding is occasional or absent; somewhat poorly drained	Moist, nutrient poor; cool	Slow growing jack pine (23.2 cm/yr); northern pin oak is uncommon; *Rubus flagellaris*	Late, often at age 10 yr, though rarely occupied	Long, from 10–14 yr, though rarely occupied
7	Broad, flat, nonpitted outwash plain; outwash physiographic system	Growing season temperatures are similar to most landforms in the Highplains District.	Medium-fine to fine sand; banding is common; well drained	Dry to dry-mesic, moderately nutrient poor; cool	Moderate growing jack pine (24.4 cm/yr); frequent northern pin oak seedlings and sprouts; *Rosa blanda*	Moderate, often at age 8–9 yr	Moderate, from 7–9 yr
9	Pitted outwash plain; moderate slopes to flat; outwash physiographic system	Growing season temperatures are similar to most landforms in the Highplains District.	Variable; medium-coarse to fine sand; banding is common to absent; excessively to well drained	Variable soil moisture and nutrients; cool	Variable; fast growing to slow growing jack pine; frequent northern pin oak seedlings and sprouts; *Comptonia peregrina* species group is most representative	Early, as fertile sites with fast growing pines colonized within 5 yr	Long, as unfertile sites with slow growing pines are occupied for 10–14 yr.
10	Flat, nonpitted outwash plain; ice-stagnation feature physiographic system	Growing season temperatures are similar to most landforms in the Highplains District.	Fine to very fine sand; banding is common and moderate in size; well drained	Dry-mesic, moderately nutrient poor; cool	Moderate growing jack pine (25.2 cm/yr); northern pin oak seedlings and sprouts are common; *Maianthemum canadense*	Early, often within 5 yr	Moderate, from 7–9 yr
11	Pitted outwash plain; moderate slopes to flat; ice-stagnation feature physiographic system	Growing season temperatures are similar to most landforms in the Highplains District.	Variable; medium to fine sand; banding is common and heavy to absent; excessively to well drained	Variable soil moisture and nutrients; cool	Variable; fast growing to slow growing jack pine; frequent northern pin oak seedlings and sprouts; *Maianthemum canadense* and *Gaultheria procumbens*	Early, as fertile sites with fast growing pines colonized within 5 yr	Very long, as unfertile sites with slow growing pines are occupied for 15 yr or longer.

[1] Landforms 8 and 12 were not sampled as part of this study and are not described here. See Table 1 for brief descriptions.

study using 18 physiographic, soil, and ground cover variables. The multivariate analysis supports our ecological observations and interpretations of differences among the landforms. Each of the six study sites was located on a distinct landform within our classification. Pitted outwash landforms with poorly rinsed sand and moderately fertile soil (landforms 9 and 11) are found in the upper right of the ordination and are well separated from one another. Flat, homogeneous, infertile landforms with high coverage of ground cover oak (landforms 1, 2, and 4) are found at the left side of the ordination. Landform 5, a high-level outwash plain, is well separated from the three other outwash landforms due to its low coverage of ground cover oak (Table 3). Overlap occurs only between landforms 2 and 9, probably due to the high site heterogeneity associated with landform 9. The discriminant function developed with the 18 variables had a perfect (100%) classification rate, and the jackknife misclassification rate was only 12%.

The first three canonical variates accounted for 65, 83, and 91% of the cumulative variance. Pitting, very fine sand (50–150 cm), and coverage of moss were all positively correlated with the first canonical variate. Coverage of grass and ground cover oak were negatively correlated (Table 5). Accordingly, pitted landforms with reasonably high coverage of moss (landforms 9 and 11) are distributed at the positive portion of the first canonical axis, while landforms exhibiting high coverage of ground cover oak (landforms 1 and 5) are found on the negative portion of the axis (Figure 4, Table 5).

For the moderate-intensity study, a reasonably good separation (Figure 5) was obtained for 7 landforms using 14 physiography, soil, and ground cover vegetation variables.

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Table 3. Selected physiography, soil, and vegetation characteristics of landforms studied in the high-intensity study in northern Lower Michigan. All variables shown are significant at $\alpha = 0.05$.

Site variable		Landform-level ecosystem 1	2	4	5	9	11
Pitting Index[1]	Mean	1.13	1.00	1.00	1.00	2.88	2.30
	SD	0.35	0.00	0.00	0.00	0.83	0.68
% very fine sand (0–150 cm)	Mean	0.56	0.90	0.71	0.74	1.68	2.25
	SD	0.14	0.38	0.37	0.49	1.02	1.08
% fine sand (0–150 cm)	Mean	13.69	17.15	18.90	24.06	27.45	27.69
	SD	2.71	4.95	6.01	13.25	7.81	3.98
% coarse sand (50–150 cm)	Mean	12.92	11.98	9.17	5.24	3.76	5.12
	SD	4.78	4.42	3.93	5.02	2.24	1.82
% very coarse sand (0–150 cm)	Mean	1.50	1.14	0.68	0.51	0.64	0.76
	SD	1.04	0.94	0.41	0.61	0.70	0.28
% cobbles (0–150 cm)	Mean	0.17	0.07	0.19	0.08	0.12	0.50
	SD	0.22	0.13	0.17	0.15	0.11	0.27
Accum. banding, <150 cm (cm)[1]	Mean	0.00	0.38	0.00	0.00	2.75	13.30
	SD	0.00	0.74	0.00	0.00	4.71	21.69
Depth to lamellae (<2 cm; 999 max)[1]	Mean	999.00	777.88	999.00	729.38	574.88	374.40
	SD	0.00	409.55	0.00	378.63	455.96	432.24
Coverage of ground-cover oak[1]	Mean	4.13	1.88	0.63	3.91	1.91	1.25
	SD	0.64	0.99	0.68	1.56	1.28	0.86
Solidago species group coverge[1]	Mean	1.16	0.19	1.06	0.19	0.16	0.08
	SD	0.69	0.37	1.27	0.35	0.23	0.17
Prunus species group coverage	Mean	1.19	2.50	3.99	1.59	1.31	0.28
	SD	0.90	1.89	3.23	1.20	1.02	0.46
Comptonia species group coverage	Mean	4.66	8.12	6.88	9.28	4.84	4.28
	SD	1.39	3.17	3.02	2.88	1.67	1.35
Gaultheria species group coverage	Mean	0.28	0.97	0.44	2.00	0.59	4.18
	SD	0.45	1.12	0.73	2.01	0.89	3.19

[1] Indicates significance at $\alpha = 0.05$ using Kruskal-Wallis test.

Table 4. Selected physiography, soil, and vegetation characteristics of landforms studied in the moderate-intensity study in northern Lower Michigan. Due to methodological differences between study levels, landforms sampled at both the high-intensity and the moderate-intensity studies are summarized separately in Tables 2 and 3. All variables shown are significant at $\alpha = 0.05$ except where noted.

Site Variable		Landform-level ecosystem 1	3	6	7	9	10	11
Pitting Index[1]	Mean	1.00	1.00	1.00	1.00	1.88	1.00	2.00
	SD	0.00	0.00	0.00	0.00	0.35	0.00	0.92
% very fine sand, (20–40 cm)	Mean	2.14	1.07	2.91	3.25	2.07	3.24	1.85
	SD	1.34	0.28	1.20	2.08	0.40	0.71	0.82
% fine sand, (20–40 cm)	Mean	21.73	16.86	28.98	29.84	23.13	34.83	19.84
	SD	5.89	4.13	7.51	11.10	4.70	5.24	4.36
% coarse sand, (20–40 cm)	Mean	9.82	9.98	5.15	6.59	6.68	2.75	8.16
	SD	1.88	3.08	1.29	3.27	1.74	0.61	2.65
% very coarse sand (20–40 cm)	Mean	1.54	1.50	0.99	1.22	0.76	0.32	0.81
	SD	0.22	0.85	0.86	0.75	0.47	0.09	0.83
Total accum. banding (cm)[1]	Mean	0.88	0.25	4.03	10.46	10.75	7.61	14.78
	SD	2.02	0.46	13.31	3.26	7.45	4.28	13.08
Depth to lamellae[1]	Mean	887.25	808.63	778.00	379.54	113.13	167.22	364.44
	SD	206.93	353.08	473.68	284.84	59.34	75.21	374.81
Coverage of ground–cover oak	Mean	4.58	0.34	0.44	1.32	0.78	2.14	2.33
	SD	2.78	0.42	0.52	0.89	0.62	1.58	1.51
Coverage of grass	Mean	5.72	5.69	9.08	12.74	5.31	7.42	7.35
	SD	2.04	2.88	5.75	3.85	3.22	1.91	3.86
Solidago species group coverage[2]	Mean	1.38	0.03	0.03	0.16	0.00	0.81	0.16
	SD	0.53	0.09	0.11	0.31	0.00	0.95	0.30
Rubus species group coverage	Mean	0.00	0.00	4.28	0.17	0.00	0.00	0.13
	SD	0.00	0.00	3.02	0.47	0.00	0.00	0.36

[1] Indicates significance at $\alpha = 0.05$ using Kruskal-Wallis test.
[2] Indicates lack of significance at $\alpha = 0.05$.

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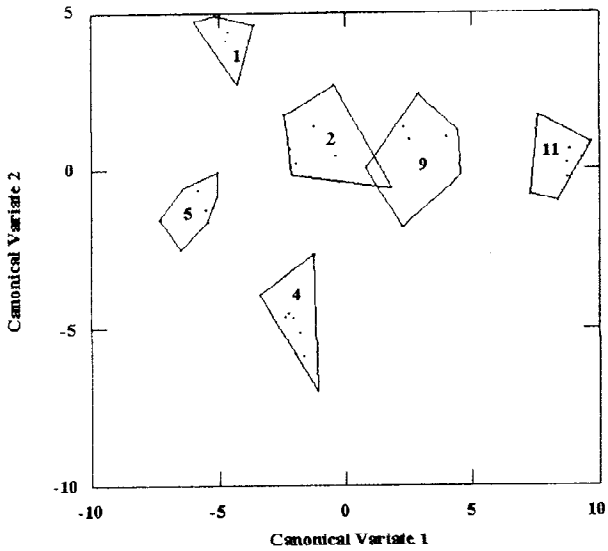

Figure 4. Ordination of 50 plots of 6 landforms in northern Lower Michigan along the first 2 canonical variates of an analysis of 18 physiography, soil, and ground cover vegetation variables.

Seven of the 12 moderate-intensity study sites were located on landforms not identified in the high-intensity study. Landform 6, which exhibits a high water table through much of the growing season, is well separated on the right side of the ordination. This landform overlaps slightly with landform 7 (banded outwash plain), perhaps due to the combination of similar physiography and the presence of moist species groups in both landforms (Table 4). Landform 9, a pitted landform in an outwash physiographic system, nearly completely overlaps with landform 11, showing their strong similarity. Landform 1 is well separated from all others near the top of the ordination. In particular, it is separated from landforms with fertile soils and high ecological diversity (landforms 9 and 11), as well as from landform 6, which is not as dry. Pitted landforms exhibit high within-landform variability in the ordination, reflecting the high diversity of ecosystem types within the landforms. Finally, landforms 3 (unbanded outwash plain) and 10 (nonpitted outwash plain in an ice-stagnation physiographic system) exhibit tight clusters, reflecting the presence of relatively few ecosystem types within these flat, homogeneous landforms. The overall misclassification rate for the discriminant function developed with these variables was 9%, and the jackknife misclassification rate was 24%.

The first three canonical variates accounted for 38, 56, and 72% of the cumulative variance. The first canonical variate was positively correlated with total sand (20–40 cm), coverage of grass, and coverage of the *Rubus hispida* species group, and negatively correlated with pitting (Table 6). Thus, landforms exhibiting high coverage of species occurring on moist sites (landforms 6 and 7; Table 4) are distributed on the positive portion of the first canonical axis. Pitted landforms (landforms 9 and 11) are found on the negative portion of the axis (Figure 5). The second canonical variate is positively correlated with total sand (20–40 cm) and depth to lamellae, and pitting is strongly negatively correlated (Table 6). Again, landforms with low proportions of silt and clay or banding (landform 1) are located on the positive portion of the second canonical axis, while pitted landforms (landforms 9 and 11) are distributed on the negative portion (Figure 5, Table 6).

Jack Pine Height Growth Patterns Among Landforms

Jack pine height growth, as mediated by physical site factors, is significantly different among all landforms ($P < 0.001$; Figure 6), and stand age was not significant as a covariate ($P = 0.10$). The rate of jack pine height growth in landform 1 is higher than any other landform sampled.

Table 5. Eigenvalues and correlation coefficients for 6 landforms in northern Lower Michigan as determined by 18 physiography, soil, and ground-cover vegetation variables for the first 3 canonical variates of an analysis based on 50 plots from the high-intensity study. Coefficients ≥ 0.28 are significant at α = 0.05.

Canonical variate	1	2	3
Eigenvalue	21.7	6.1	2.6
Cumulative % variance	65	83	91
Variable		Correlation coefficient	
Pitting index	0.59	0.15	0.06
Landform index	0.31	−0.23	0.14
Transformed aspect	0.07	−0.29	−0.09
Maximum slope	0.20	−0.09	0.32
Cobbles, 0–150 cm	0.44	−0.19	0.16
Fine sand, 0–150 cm	0.33	−0.06	0.21
Very fine sand, 50–150 cm	0.62	0.10	0.13
Depth to pH 8.0	0.01	−0.40	0.28
pH of lowest horizon (lab)	−0.01	0.29	−0.04
Coverage of ground-cover oak	−0.50	0.56	0.07
Coverage of grass	−0.52	−0.58	0.25
Coverage of moss	0.68	0.22	−0.01
Coverage of lichen	−0.32	−0.42	0.22
Coverage of *Cladina*	0.10	−0.49	−0.15
Coverage of *Solidago* species group	−0.23	−0.12	0.29
Coverage of *Arctostaphylos* species group	−0.01	0.34	−0.06
Coverage of *Comptonia* species group	−0.33	−0.22	−0.22
Coverage of *Gaultheria* species group	0.41	−0.01	0.01

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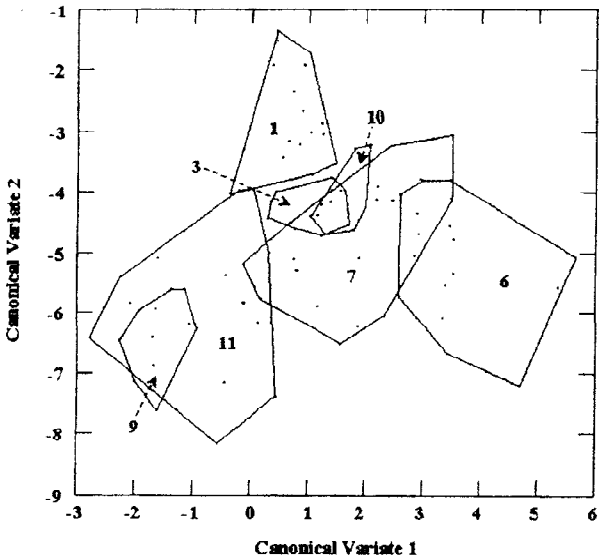

Figure 5. Ordination of 97 plots of 7 landforms in northern Lower Michigan along the first 2 canonical variates of an analysis of 14 physiography, soil, and ground cover vegetation variables.

although soil conditions are poor. The dry, infertile, sand soils are generally characteristic of landform 1 and other landforms as well. This suggests that the relatively warm regional climate of the Arenac District is probably the most important factor causing the rapid height growth of jack pine and the abundance of northern pin oak on this landform.

Significant ecological and statistical height growth differences in jack pine were also found among landforms of the Highplains District (Figure 6). Jack pine growth was found to be slowest on outwash plain landforms 2, 3, 4, and 6 where conditions such as poor soil or a cold microclimate make them unfavorable for plant growth. Jack pine height growth was found to be fastest on landforms with more favorable soil and microclimate such as landforms 5, 9, 10, and 11. Considerable within-landform variation in soil texture and soil banding was characteristic of landforms 9 and 11. Although growth was relatively fast in these landforms, the large standard error indicates the variability in growth rates of trees on different sites within these units. The most remarkable height growth differences among the outwash plains was recorded on adjacent high- and low-elevation landforms 4 and 5 of the Bald Hill burn area, where the warmer microclimate of landform 5 resulted in much faster height growth than in the colder microclimate of landform 4 (Kashian and Barnes 2000). Pines growing on outwash plains associated with ice-contact terrain (landforms 10 and 11) generally exhibit relatively rapid growth due to their finer textured soils. This relationship is observed repeatedly within the Highplains District, and specifically in landform 12 (at the Mack Lake burn; see Walker et al. this issue). Thus, individual site factors of local topography, climate, soil texture, and soil banding markedly affect jack pine height growth either singly or in combination and can be readily identified in the field.

Kirtland's Warbler Occupancy Among Landforms

Warbler occurrence—specifically the timing of initial colonization and the duration of occupancy of a particular stand of jack pine—varied markedly among landforms. Warbler colonization occurs at an earlier stand age on landforms that exhibit favorable conditions for height growth of jack pine (Table 2). For example, plantations in landform 1 are typically colonized within 5 to 6 yr, in part reflecting the very rapid growth of jack pine that occurs as a result of the relatively warm macroclimate of this lake-moderated subdistrict. Landform 5, characterized by a warm microclimate, and landform 10, characterized by relatively high soil water and nutrient availability, also exhibit rapid jack pine height growth and subsequent early warbler colonization (Table 2). Warbler colonization occurs at a later stand age on landforms that exhibit slow-growing jack pines as a result of unfavorable growing conditions. Warbler colonization may be late if soil is poor (landform 3), microclimate is cold (landform 4), a

Table 6. Eigenvalues and correlation coefficients for 7 landforms in northern Lower Michigan as determined by 14 physiography, soil, and ground-cover vegetation variables for the first 3 canonical variates of an analysis based on 97 plots from the moderate-intensity study. Coefficients ≥ 0.20 are significant at $\alpha = 0.05$.

Canonical variate	1	2	3
Eigenvalue	8.3	3.8	2.0
Cumulative % variance	38	56	72
Variable		Correlation coefficient	
Pitting index	–0.49	–0.46	0.02
Very coarse sand, 20–40 cm	–0.09	–0.08	0.26
Coarse sand, 20–40 cm	–0.46	–0.19	0.48
Very fine sand, 20–40 cm	0.20	–0.01	0.02
Total sand, 20–40 cm	0.72	0.56	0.23
Depth to pH 7.0	–0.10	0.12	0.28
Depth to lamellae	0.30	0.49	–0.04
Coverage of shrubs	0.25	–0.20	0.07
Coverage of grass	0.53	–0.33	–0.01
Coverage of moss	–0.23	–0.14	0.29
Coverage of lichen	–0.10	0.13	–0.01
Coverage of *Cladina*	0.23	–0.03	–0.48
Coverage of *Solidago* species group	–0.01	–0.19	–0.22
Coverage of *Rubus* species group	0.44	–0.03	0.20

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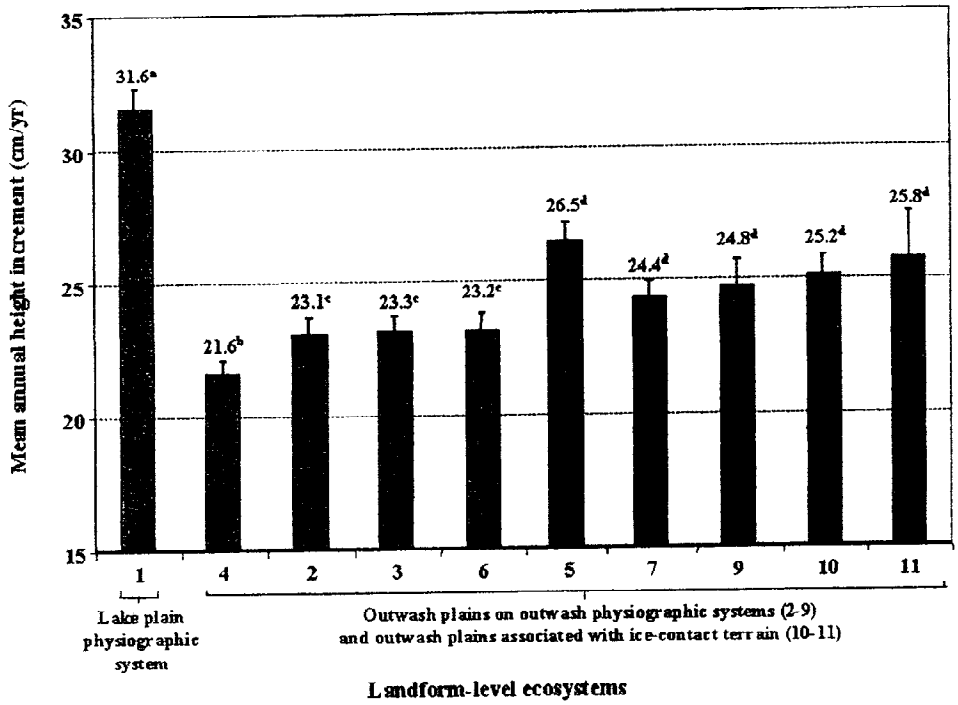

Figure 6. Comparison of height growth of jack pine based on mean annual height increment for the 10 landforms in northern Lower Michigan described in the detailed and moderate level studies. Landform 1 is found in a different regional ecosystem (Arenac District) than landforms 2–10 (Highplains District). Values sharing a similar superscript are not significantly different at $\alpha = 0.05$. Error bars represent ± one standard error.

root-restricting water table is present (landform 6), or due to a combination of these factors (landform 2).

The duration of warbler occupancy among landforms also differed markedly. Warblers occupy a given stand for a longer duration on landforms where jack pine growth is slow. Warblers remain for a long duration in landform 2, for example, due to poor soil conditions and a cold microclimate, both of which result in slow pine growth (Table 2). The duration of warbler occupancy is also long in other landforms that exhibit unfavorable conditions for jack pine growth (landforms 3, 4, and 6). In contrast, landforms where site factors favor rapid jack pine growth are occupied for only a short duration. For example, jack pine plantations in landform 1 are typically occupied for less than 5 yr (Table 2). In general, early warbler colonization is accompanied by a short duration of occupancy on landforms that favor rapid jack pine growth. Conversely, late warbler colonization is associated with a long duration of occupancy on landforms that exhibit unfavorable conditions for jack pine growth. Landforms intermediate in site quality (e.g., landform 7) tend to be colonized moderately early and occupied for a moderate duration (Table 2).

Warbler colonization may occur early and duration of occupancy may also be long on heterogeneous landforms that contain a mosaic of diverse site conditions. Landforms 9 and 11 are characterized by early colonization and long Kirtland's warbler occupancy, which may be attributed to the different rates of jack pine growth in different local ecosystem types within the study site (Table 5). In this situation, relatively fertile local ecosystems where pines grow faster are occupied relatively early in the life of the stand, and ecosystems with slow-growing trees are occupied late and for a long duration. The juxtaposition of groups of fast- and slow-growing trees in a single landform results in relatively early colonization and long occupancy of the landform as a whole (Table 2). Notably, warbler occupation may be long both on landforms with high within-landform heterogeneity and on strongly homogeneous landforms exhibiting poor growing conditions (landforms 2 and 3).

Broad-Scale Ecological Factors and Kirtland's Warbler Occurrence

Of the 44 study sites examined in the low-intensity study, 8 (18%) were located outside of the Grayling Subdistrict, and only 6 (14%) occurred outside the Highplains District. The relatively few study sites found outside the Highplains District (Figure 2) emphasizes the importance of regional ecosystem characteristics. The relatively harsh conditions for tree establishment and growth make the Highplains District the regional ecosystem with the highest concentration of jack pine in Lower Michigan and, consequently, the bulk of the warbler breeding range. Outside this district, conditions are generally more favorable for other tree species, large stands of jack pine rarely occur except in areas of frequent fire, and warblers are rare or absent.

Three of the 44 study sites (7%) were located on outwash plains associated with ice-contact terrain; 35 sites (80%) were found on outwash plain physiographic systems, and 6

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(13%) were found on lake plain physiographic systems in the Arenac District. The high proportion of occupied areas on outwash plain physiographic systems is probably representative of the breeding range, illustrating the affinity of jack pine and consequently Kirtland's warblers for broad, flat, dry outwash plains. Of the 35 study sites on outwash plains, 34 (74%) were flat and 9 (26%) exhibited rolling (pitted) topography. All three sites on outwash plains associated with ice-contact terrain were pitted. Approximately 44% of the study sites examined included fine-textured soil banding, known to increase the productivity of jack pine-dominated outwash plains (Hannah and Zahner 1970). All 3 study sites on outwash plains associated with ice-contact terrain were banded, as were 17 (49%) of those in outwash physiographic systems. On outwash plain physiographic systems, 5 of the 9 pitted study sites were also banded, and the remaining 13 banded sites were flat. The 44 low-intensity study sites generally corroborated the landform classification, as most were readily classified based on reconnaissance. Landform 7 was the most commonly encountered landform (11 sites), representing 25% of the low-intensity study. Landforms encountered with moderate frequency included landform 3 (16%), landform 1 (14%), landform 9 (11%), landform 6 (7%), and landform 2 (5%). Landforms 4, 5, 10, and 11 were each encountered once (2% each). Landform 12 (9%) was identified based on reconnaissance only (Table 6), and two other study sites were sampled in the Presque Isle District (Figure 2).

General Discussion and Conclusions

The spatial and temporal pattern of Kirtland's warbler occupancy of any given stand of jack pine can best be understood and predicted when warblers and trees are viewed as parts of an integrated ecological system (Figure 7). As illustrated in Figure 7, warbler occupancy is related to ecosystems that vary in vegetative characteristics of jack pine (though not directly measured in this study, these may include growth, branching, crown development, foliar density) and ground-vegetative cover. These are, in turn, strongly influenced by soil and climatic factors, which are mediated by physiographic features developed in glacial times. Suitable warbler habitat may therefore be identified by understanding glacial geology and dependent physiographic, soil, and climatic (both macro- and microclimatic) factors. In this manner, initial warbler colonization and duration of warbler occupancy for a given area can be predicted without the presence of vegetation (such as a recent clearcut) or in areas supporting jack pine of any age, assuming that the area will eventually have the minimum jack pine stocking for warbler occupancy through planting or natural regeneration. Therefore, this ecological approach is a powerful tool that is not necessarily dependent on the presence of jack pine or its current height.

The occurrence of Kirtland's warblers is affected by the interrelationships of ecosystem characteristics expressed at local and regional scales (Barnes et al. 1989; Barnes et al. 1998, p. 630–636). Most previous research has been

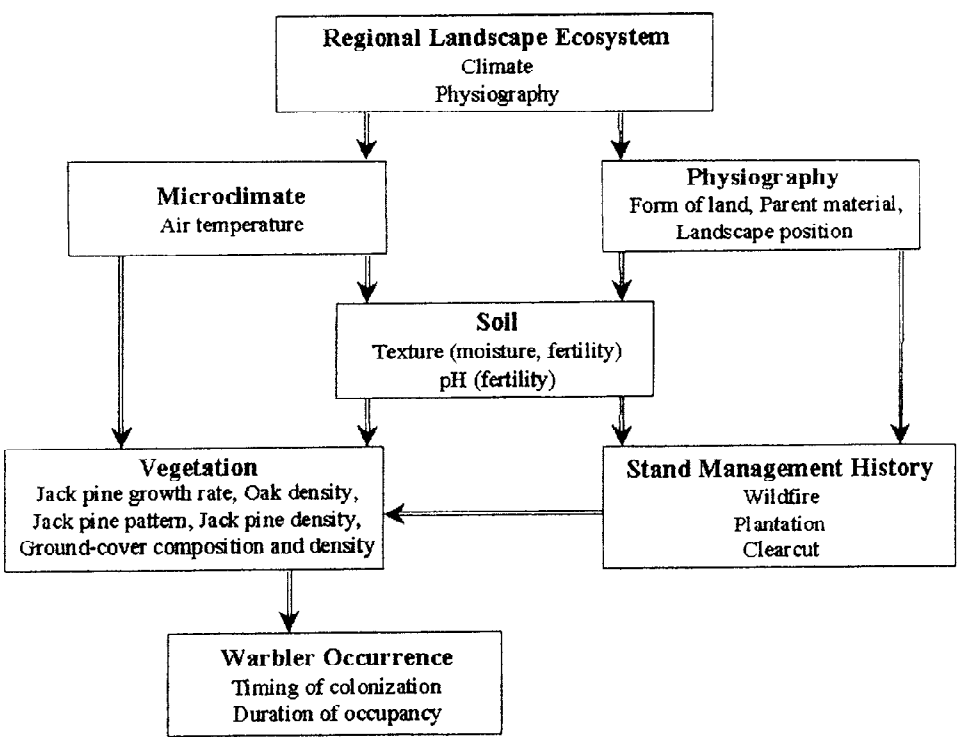

Figure 7. Schematic diagram depicting the interconnection of factors affecting the occurrence of Kirtland's warblers within landforms in northern Lower Michigan. Arrows represent direct interactions between ecological factors.

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focused at local scales (Smith 1979, Buech 1980, Probst and Hayes 1987, Nelson 1992), and suggests that the occurrence of warblers on a particular tract of land is controlled mainly by the pattern, composition, and growth of jack pine and associated vegetation within that tract or by the total population and its sorting across the breeding range (Probst 1988, Probst and Weinrich 1993). However, in the sense that vegetation is a response to the physical site characteristicsthat define each landform, warbler occurrence is perhaps best understood in the context of these factors. At the local scale, physiography influences local air temperature (microclimate) due to cold-air drainage between adjacent landforms (e.g., landforms 4 and 5). Physiography also determines soil characteristics such as moisture and fertility (Figure 7) because it directly influences soil texture and pH among major glacial features. For example, we observed that fine-textured soil banding often occurred on outwash plains associated with ice-contact terrain or in close proximity to ice-contact terrain and on pitted outwash landforms, results similar to those of Zou et al. (1992) and McFadden (1993). Differences in microclimate and soil between landforms influence both vegetation composition and growth, which differ significantly among landforms and ecosystem types (Walker et al. this issue). These findings are consistent with other studies that show jack pine growth is affected by microclimate (Barnes et al. 1989), soil water, nutrient regime, and soil texture (Pawluk and Arneman 1961, Jameson 1965, Shetron 1972), or the presence of fine-textured banding (Pawluk and Arneman 1961, Hannah and Zahner 1970, Host and Pregitzer 1992).

Assuming stands of trees of a density and spatial pattern appropriate for warbler habitat are present (such as those that may be provided by warbler plantations or wildfires that burn areas with suitable prefire jack pine stocking), warbler occurrence at a local scale over time is strongly influenced by the growth of jack pine and related structural features, thus reflecting the interrelationships of physical and biotic factors of ecosystems (Table 2). Stand density and pattern is influenced by stand history (wildfire, plantation, or natural regeneration after clearcutting), and stand history, at least in terms of wildfire, is in turn affected by physiography (Figure 7). Warbler colonization is late, and the duration of occupancy is long, on landforms that are unfavorable to jack pine growth, whereas colonization is early and the duration of occupancy is short where conditions are favorable. Vegetative characteristics other than jack pine growth, including the distribution of northern pin oak and the composition of ground cover vegetation, are also influenced by microclimate and soil (Kashian and Barnes 2000). The presence or absence of oaks or particular ground cover species may be important to warblers as potential food sources or as cover or habitat for competing species or predators. Furthermore, the presence of oak promotes early colonization of a stand due to rapid sprout-growth for a minimum foliage volume (Probst and Weinrich 1993).

It is important to note that jack pine growth is not a direct cause of the relative time of warbler colonization of a given area or the duration of its occupancy. Undoubtedly, a complex combination of stand, tree, and ground cover characteristics (e.g., the foliage volume identified by Probst and Weinrich 1993) are required to meet the vegetation criteria necessary for successful warbler breeding. However, jack pine height or height growth is an easily measured trait that is strongly related to the observed patterns of warbler occupancy and is used in this study to verify the influence of physical site factors on warbler occupancy. Because jack pine growth is markedly influenced by climate and soil factors, we can readily ascertain those landforms where short- or long-duration occupancy is likely based on their distinctive physiographic, climatic, and soil attributes.

At regional scales, macroclimate (annual precipitation, growing season length, etc.) and gross physiography (large glacial features such as the central glacial interlobate area of Lower Michigan) are important factors that influence warbler occurrence. Macroclimate strongly affects the distribution and growth of vegetation including jack pine (Botkin et al. 1991). Jack pine is common in the Highplains District in part because it is able to thrive in the variable, relatively harsh climate that characterizes the region. The gross physiography of regional ecosystems determines the characteristic landform-scale physiography occurring within them, which in turn influences vegetative characteristics. Jack pine is most common on dry, infertile, sandy sites found on outwash plains, which are much more abundant in the Highplains District than in other districts in northern Lower Michigan.

The natural distribution of jack pine, and consequently of Kirtland's warblers, is essentially a result of fire frequency superimposed on a combination of factors that affect site quality within a regional ecosystem context. Since jack pine has flammable foliage that tends to facilitate wildfire, fire is more frequent on sites that favor jack pine over other species. In contrast, productive sites are favorable to tree species that are more demanding of soil water and nutrients and less flammable than jack pine, and fire is less frequent. For example, ice-contact physiographic systems often contain landforms that have fire regimes and site conditions that favor black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.), red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx.), red pine, and eastern white pine. Jack pine is often only present where fire is most frequent, often resulting in a patchwork of oak and jack pine communities on these physiographic systems. Because of the interrelationships of physical and biotic factors and fire frequency, Kirtland's warblers are found less often on ice-contact terrain than on outwash plains. Similarly, warblers have never occupied moraine physiographic systems, which have soils too moist and nutrient-rich for jack pine. Fire is far less frequent on these more mesic, rolling systems so that nutrient and moisture-demanding tree species such as sugar maple (*A. saccharum* Marsh.), red maple, trembling aspen, and northern red oak (*Q. rubra* L.) are able to out-compete jack pine, and warblers are not present.

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Landform Heterogeneity and Kirtland's Warbler Occurrence

The Kirtland's warbler occupies a remarkable range of landforms in the Highplains District in northern Lower Michigan. However, because of the apparent homogeneity of jack pine stands following fire or planting and the sandy soils that support them, it is often assumed that Kirtland's warbler habitat is homogeneous across the breeding range. The landform heterogeneity observed in our study area illustrates the diverse conditions of warbler occupancy where jack pine is dominant. Clearly, there are additional landforms occupied by the warbler we have not described in this study, including four at the Mack Lake burn (Walker et al. this issue). Moreover, the diversity of landforms occupied by the Kirtland's warbler will probably increase with time, as warblers expand their breeding range into additional regional landscape ecosystems outside of northern Lower Michigan (Probst 1988, Probst and Weinrich 1993).

The site heterogeneity that exists among and within landforms is an important factor in understanding the duration of warbler occupancy. For example, the large tract of jack pine resulting from the ca. 10,000 ha Mack Lake burn extends across five different landforms (Walker et al. this issue). Similarly, jack pine cover supports warblers over two adjacent landforms (landforms 4 and 5) at the Bald Hill burn (Kashian and Barnes 2000). At both the Mack Lake and the Bald Hill burns, the significant difference in the growth of jack pine that occurs among landforms acts to lengthen the overall duration of warbler occupancy by creating differential patterns of warbler colonization and duration of occupancy. Thus, the diversity of landforms within an area may be at least as important as the size of the area as a whole (Kashian and Barnes 2000).

In addition to among-landform heterogeneity, heterogeneity also exists within landforms that contain a mosaic of ecosystem types (i.e., landforms 9 and 11). Within a single landform, sites where jack pines grow faster are occupied by warblers relatively early in the life of the stand, those with slow-growing trees are occupied late and for a long duration, and the landform as a whole exhibits relatively early colonization and long occupancy. Within-landform heterogeneity may increase the duration of warbler occupation as compared to a landform that is homogeneous. For example, landform 11, a pitted landform with many ecosystem types, includes the burn near Buck's Crossing in Crawford County, a small stand occupied nearly as long as any other since the warbler census was initiated in 1951. Although a complex disturbance history of many of these landforms confounds causal inferences for warbler occupancy, the Buck's Crossing area and similar landforms that contain a mosaic of ecosystem types may be important as efficient, long-lasting sources of warbler habitat within a relatively small area in the absence of intensive management that may mimic landform effects on warbler occupation.

Implications for Kirtland's Warbler Management

The large stands of young, dense jack pine required by the Kirtland's warbler for nesting habitat were historically provided only by wildfires (Mayfield 1960, Byelich et al. 1976). The effectiveness of fire suppression in northern Lower Michigan during the last century, however, has led to the use of plantations as an increasing source of warbler habitat. Although some scientists believe that plantations are less desirable than stands produced by wildfire in terms of warbler preference and breeding habitat quality (Mayfield 1962, Bocetti 1994, Kepler et al. 1996), the ability of plantations to provide an adequate stocking of jack pine for warbler occupation and thus to support and increase warbler populations has been demonstrated. For example, the dramatic increase in the warbler population in the late 1980s that was associated with the production of warbler habitat by two major wildfires at Bald Hill and Mack Lake continued even after the amount of available habitat at these areas began to decline (Figure 1). Furthermore, plantations provided 73% of all occupied warbler habitat in 1999 when the warbler population had reached its peak of 904 singing males, and 76% of all warblers were censused in plantations in the year 2000 (J. Weinrich and P. Huber, pers. comm.).

The highest density of warblers within the breeding range will be achieved by increasing the probability of early stand colonization and by maximizing the duration of occupancy of a stand (Probst 1988). Therefore, selecting appropriate sites for these plantations is of the utmost importance if current warbler population levels are to be maintained and further expanded. Currently, managers are skilled at locating sites that will provide suitable warbler habitat. However, the consequence of an unfamiliarity of the landform heterogeneity that exists across the warbler breeding range (as well as the effects of that heterogeneity on warbler occupation) is a philosophy of warbler management that relies on the timing and scheduling of plantations to provide continuous warbler habitat over the long term. While such a philosophy is necessary for successful warbler management, knowledge of landform effects on warbler occupancy of individual plantations is also important if management is to be efficient and cost-effective. For example, current strategies to extend warbler occupation on a single landform include such intensive techniques as pre-fire strip cutting, fill-in planting, and overstory removal/advanced regeneration (Probst 1988). However, given the ability to determine the interrelationships of warbler occurrence and physical and biotic factors of landform-level ecosystems as provided by our research (Figure 7), the timing and duration of Kirtland's warbler occupancy become predictable for each landform. Therefore, managers may determine in advance the patterns of warbler occupation of a given plantation established on a particular landform in the absence of more intensive management techniques.

Physical factors of the landscape itself can provide the initial basis for planning the location of warbler management areas, and different landforms may be targeted to meet a particular management objective. If the goal is to quickly produce warbler habitat (for example, in the event of an unexpected population drop), then managers may select landforms that lead to rapid tree growth and rapid warbler occupation (e.g., landforms 1 and 5). In contrast, if the goal is to both increase early colonization and the

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duration of occupancy as Probst (1988) suggests, then the manager may target heterogeneous landforms that includes a diversity of site conditions (landforms 9 and 11). Finally, if the management objective is to maximize the amount of time a particular plantation is occupied, then landforms characterized by unfavorable growing conditions (landforms 2, 3, and 4) should be selected for management areas.

Landforms exhibiting different combinations of ecological factors may result in similar patterns of warbler colonization and duration of occupancy. For example, warbler occupancy occurs late and for a long period in landforms 2, 3, and 6. However, the unfavorable conditions for jack pine growth in each may be either the result of poor soil conditions associated with coarse soil texture (landform 3), a root-restricting high water table (landform 6), or both poor soil conditions and a cold microclimate (landform 2). Similarly, jack pine growth is fairly rapid in landform 10 (Figure 6) as a direct result of high soil water and nutrient availability associated with finer soil texture and the presence of fine-textural soil banding. However, the warmer regional macroclimate of the Arenac District also results in stand conditions that favor early warbler occupancy in landform 1 despite the presence of unfavorable soil conditions. Even within the severe regional climate of the Highplains District, however, jack pine growth is rapid in landform 5 because of the warm microclimate created by its juxtaposition with a landform at a lower topographic position. Guidelines for site selection based on this research have been incorporated into Kirtland's warbler management (Kashian 1998) as managers have recognized the interconnection between physical and biotic factors and warbler occurrence.

An ecosystem approach, as demonstrated by our research, provides a useful framework for managers not only in selecting landforms for management areas, but in planning the size of plantations as well. Kirtland's warblers are thought to prefer stands of jack pine greater than 32 ha (80 ac) in area (Mayfield 1960, Byelich et al. 1976, Walkinshaw 1983). In particular, Mayfield (1983) suggested that large plantations better mimic the large wildfires that produced warbler habitat during presettlement time, a factor emphasized by Bocetti (1994) as necessary for successful warbler management. In response, managers have recently initiated the creation of jack pine plantations up to 800 ha (2,000 ac) in size to attract more warblers, promote early colonization, and increase the duration of warbler occupancy. From an ecosystem perspective, however, the duration of use of a stand by warblers may be a function of among-landform heterogeneity rather than of stand size per se. Since larger jack pine-dominated areas are more likely to encompass a diversity of landforms (e.g., Mack Lake and Bald Hill), such large areas are more likely to be occupied earlier and for a longer duration than smaller stands. Although implementing large plantations may appear to be the most appropriate management strategy, long warbler occupancy has occurred in several stands smaller than 120 ha on single landforms that exhibit a mosaic of diverse local site conditions (landforms 9 and 11). A small plantation placed in a landform containing high within-landform heterogeneity may therefore accomplish similar management objectives as a large plantation extending over several homogeneous landforms. Staggered planting in uniform landforms (Probst 1988) mimics the effects of high within-landform heterogeneity in lengthening the duration of warbler occupancy, and the success of this strategy in the past suggests that the ability of a manager to identify these landforms would be an important means to successful warbler management without the implementation of expensive management techniques.

The biology of the Kirtland's warbler on its breeding grounds has been intensively studied and is probably as well understood as any endangered species in North America. In the past, managers have created thousands of acres of jack pine plantations under the assumption that they will be occupied by warblers. Because plantations have been successful and now form the basis of warbler management, the characteristics of landscape ecosystems capable of attracting large numbers of warblers and maximizing the duration of time they will occupy them should be determined if management is to be efficient while remaining effective. Rather than following a strictly biological approach that considers mainly plant and animal demography and dispersal, this study provides the framework for understanding warbler occurrence in the context of the landscape ecosystems in northern Lower Michigan. Such an approach presents a perspective that stresses an ecological basis for the perpetuation and management of species populations.

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