

Landscape influence on the spatial and temporal distribution of the Kirtland's warbler at the Bald Hill burn, northern Lower Michigan, U.S.A.¹

Daniel M. Kashian and Burton V. Barnes

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.). We used the landscape ecosystem approach to identify two adjacent landform-level ecosystems located at different elevations within the area burned by the 1975 Bald Hill fire in Crawford County, Michigan. Eighty-five percent of the warblers occupied the high-elevation landform from 1982 to 1987 compared with only 25% from 1992 to 1997, indicating a shift in warbler occupancy of the burn from the high- to the low-elevation landform by 1991. Although similar in soil, the landforms have significantly different microclimates as mediated by physiography. Because of a warmer microclimate, jack pines in the high-elevation landform exhibited faster growth and were colonized first by the warbler; the trees in the cooler low-elevation landform grew more slowly and were colonized later. We suggest that the presence of two adjacent landform-level ecosystems within a single burned area prolonged the warbler occupancy of the burn. Thus, a broad-scale ecosystem approach that considers physical site factors as well as vegetative characteristics is useful for understanding the complex interactions that affect spatial and temporal species distributions across the landscape. Such an approach may benefit the management of particular endangered species, especially when the size of management areas is considered to be a crucial element of species preservation.

Résumé : La paruline de Kirtland (*Dendroica kirtlandii* Baird) est un oiseau chanteur menacé qui niche dans le nord du Bas-Michigan, dans des écosystèmes dominés par de jeunes pins gris (*Pinus banksiana* Lamb.). Nous avons utilisé une approche écosystémique à l'échelle du paysage afin d'identifier, sur la base des modelés, deux écosystèmes adjacents localisés à différentes altitudes à l'intérieur de la zone brûlée par le feu de 1975 à Bald Hill, dans le comté de Crawford, au Michigan. Quatre-vingt cinq pour cent des parulines utilisaient l'écosystème situé à haute altitude de 1982 à 1987, comparativement à 25% seulement de 1992 à 1997; ce qui indique un déplacement dans l'occupation des brûlis par les parulines, de l'écosystème situé à haute altitude vers l'écosystème situé à basse altitude, dès 1991. Malgré la similitude des sols, les écosystèmes ont des microclimats significativement différents qui s'expliquent par la physiographie. En raison d'un microclimat plus chaud, les pins gris de l'écosystème situé à haute altitude croissent plus rapidement et ont été colonisés en premier par les parulines, tandis que les arbres de l'écosystème situé à basse altitude, plus froid, croissent plus lentement et ont été colonisés plus tard. Nous suggérons que la présence de deux écosystèmes, qui diffèrent sur la base des modelés mais sont adjacents à l'intérieur d'un même brûlis, a permis d'allonger la période durant laquelle la paruline a utilisé ce brûlis. Par conséquent, une approche écosystémique à grande échelle qui tient compte des facteurs physiques et des caractéristiques de la végétation, aide à la compréhension des interactions complexes qui affectent la répartition spatiale et temporelle des espèces au niveau des paysages. Une telle approche peut contribuer à la gestion d'une espèce menacée, particulièrement lorsque la taille des aires aménagées est considérée essentielle au maintien de l'espèce.

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Introduction

During the last two decades, ecologists and silviculturalists have emphasized the importance of a broad-scale perspective to better understand and manage forest productivity and to conserve plant and animal species. Such an ap-

proach has proved valuable in determining appropriate silvicultural techniques for land management (Barnes et al. 1982; Brooks and Grant 1992; Rowe 1992; Jones and Lloyd 1993; Salwasser 1994), and its application represents the beginnings of a paradigm shift in modern forestry (O'Hara et al. 1994; Rowe 1994). For biological diversity, the concept of

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D.M. Kashian² and B.V. Barnes. School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109-1115, U.S.A.

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²Corresponding author. Present address: Departments of Zoology and Forest Ecology and Management, University of Wisconsin-Madison, Madison, WI 53706, U.S.A. e-mail: dm Kashian@students.wisc.edu

saving whole ecosystems to better understand and conserve the species within them has been advocated throughout the 1990s (e.g., Franklin 1993; Orians 1993). A synthesis of the goals of conservation of forests and preservation of biodiversity, however, has eluded managers and is usually not holistic, although the same ecological concepts are applicable and valuable to both fields (Kohm and Franklin 1997).

The Kirtland's warbler (*Dendroica kirtlandii* Baird) is an endangered songbird whose limited breeding range is centered in northern Lower Michigan. The nesting habitat requirements of the Kirtland's warbler are extremely narrow; Mayfield (1960) and Walkinshaw (1983) described Kirtland's warblers as nesting almost solely under young, 8- to 20-year-old jack pine (*Pinus banksiana* Lamb.) on dry, infertile sands of the Grayling series (Werlein 1998). Kirtland's warblers generally occupy dense (>2500 stems/ha) stands at least 32 ha in area (Mayfield 1960), historically of wildfire origin, and often exhibiting a patchy distribution of trees (Zou 1988; Barnes et al. 1989). Warblers nest on the ground most commonly under lower live branches that serve to shelter the nest and act as step-down perches, so that both jack pine height and density are important in providing an appropriate foliage volume for warblers to nest (Probst and Weinrich 1993). Warblers quickly abandon a stand once the trees grow taller than approximately 5 m (16 ft) (Mayfield 1960; Probst and Weinrich 1993).

In 1951, the first Kirtland's warbler census revealed a population of 432 singing males, or an estimated 864 individuals if an equal sex ratio is assumed (Mayfield 1953). The population decreased to 201 singing males by 1971, and the Kirtland's warbler was placed on the U.S. Fish and Wildlife Service Endangered Species List. The availability of suitable breeding habitat, which had decreased with fire suppression and forest fragmentation during the late 20th century, is considered to be the principal factor limiting the Kirtland's warbler population (Mayfield 1963; Ryel 1981; Probst 1986). Consequently, the provision of warbler breeding habitat became the central goal of warbler management beginning in the 1970s as an effort to aid in the recovery of the species. Coincident with two major wildfires in 1975 and 1980, large-scale jack pine plantations and the protection of known warbler breeding areas have led to an increase of the total warbler population to an estimated 891 singing males in the year 2000 (J. Weinrich, personal communication). Assuming a continuing trend of fire suppression and intensive warbler management in future decades, jack pine plantations will soon become the only source of warbler habitat. In the year 2000, 76% of all warblers were found on plantations (J. Weinrich, personal communication). With the growing emphasis on plantations for warbler management, it is essential to understand the characteristics of whole ecosystems that provide for the longest period of warbler occupation.

Warbler research is traditionally vegetation based. It has been dedicated to quantifying stand characteristics such as tree height, cover, and density (Smith 1979; Buech 1980; Probst and Hayes 1987; Probst 1988; Nelson 1992; Probst and Weinrich 1993) and patchiness (Zou 1988), primarily because a main objective of warbler management is to provide habitat that mimics as closely as possible jack pine stands created after wildfire. Similarly, the plethora of work on other endangered species that examines their conserva-

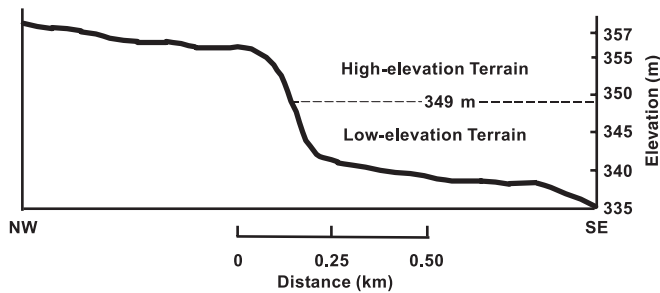
tion at the scale of landscapes (e.g., Pulliam et al. 1992; Breininger et al. 1995, 1999; King et al. 1997; Tucker et al. 1998) also centers on broad-scale vegetation patterns rather than entire ecosystems. In contrast, the landscape ecosystem approach (Bailey 1996; Barnes et al. 1998) first considers the physical site factors that provide the context for the organisms that live and reproduce within ecosystems at multiple scales. These relatively stable ecosystem components provide the basis for understanding vegetation components and dynamics, which in turn, influence animal populations. Landscape ecosystems are three-dimensional, spatially explicit, mappable tracts of land consisting of interacting physical site factors such as climate, physiography, soil, and water, as well as biota (Rowe 1961, 1984, 1988; Rowe and Barnes 1994; Barnes et al. 1998). Landscape ecosystems are organized hierarchically, proceeding from the highest level of regional landscape ecosystems to successively smaller units nested within each other (Bailey 1996), including districts, subdistricts, physiographic systems, landform-level ecosystems, and landscape ecosystem types (Albert et al. 1986; Albert 1995; Barnes et al. 1998). Warbler management most often takes place at the scale of landform-level ecosystems. For example, at the Mack Lake burn in northern Lower Michigan, Barnes et al. (1989) and Zou et al. (1992) used the landscape ecosystem approach to show that Kirtland's warbler occurrence was strongly related to the constraining effects of physiography, microclimate, and soil on jack pine height growth and patchiness and the presence of northern pin oak. Such a spatial and temporal shift in occupancy across the burned area directly related to these factors was described by Barnes (1993), Barnes et al. (1998, pp. 630–636), and Walker (1999).

Kirtland's warblers first occupied the 485-ha 1975 Bald Hill burn, Crawford County, northern Lower Michigan, in 1982, and a warbler population persisted there until 1997. Relative to other areas occupied by the warbler, the Bald Hill burn was occupied at a fairly typical stand age but supported warblers for a very long time (Kashian 1998). Here, we examine the landscape ecosystem characteristics of the Bald Hill burn for insight into the ecological reasons for the spatial occurrence and long duration of warbler occupation of the burned area. Specific objectives were to (i) describe the ecological characteristics of the landform-level ecosystems of the Bald Hill burn in terms of physiography, microclimate, soil, and vegetation; (ii) determine Kirtland's warbler occupancy of the landforms from 1982 to 1997; and (iii) relate warbler occupancy to the physical and biotic factors of the landforms.

Study area

The Bald Hill fire was started 10 May 1975 by artillery fire in an area of mixed jack pine and northern pin oak (*Quercus ellipsoidalis* E.J. Hill) on the Camp Grayling Military Reservation in east-central Crawford County, Michigan. The fire burned two distinct portions of the Bald Hill area, including a larger southeastern portion that is the focus of this study. The study area is located at 44°43'N, 84°27'W, approximately 22.5 km northeast of Grayling, Mich. The region has a harsh, continental climate because of its inland location, northern latitude, and high elevation relative to the surrounding landscape (average elevation 365 m vs. 210 m in the surrounding area). Temperatures are unpredictable during spring and

Fig. 1. Cross section of the topography of the Bald Hill burn, Crawford County, Michigan, showing change in elevation along a northwest–southeast transect through the centre of the burn.



fall; late-spring and even midsummer freezes are possible. The growing season is short and variable from year to year, but the region is considered to have the shortest growing season (82 days) and the second-lowest average annual temperature (6.3°C) in the Lower Peninsula of Michigan (Albert et al. 1986; Albert 1995). Microclimate is governed by physiography in the region, and cold air tends to collect in low-lying areas, which tend to exhibit cooler minimum temperatures throughout the year.

The study area consists of two flat glacial outwash plains juxtaposed in the landscape and separated by a slope that drops approximately 9 m over 0.10 km (Fig. 1). The elevation of the high-elevation landform averages 353 m and is separated by a 9% slope from the low-elevation landform, which averages 340 m in elevation. We arbitrarily chose the center of the slope (349-m contour) as the boundary between the two landforms. The upper and lower slopes were treated as part of the high- and low-elevation landforms, respectively, for the purposes of this study, since few warblers have been found on the steep slope. The landscape surrounding the study area is a complex mosaic of fluvio-glacial features, including flat outwash plains, pitted outwash plains, and ice-contact terrain. The mineral soils of the study area are dominated by the excessively drained, acid, undeveloped medium sands of the Grayling series (Werlein 1998). Medium-fine and fine sands are occasionally present. The extreme western portion of the high-elevation landform is mapped as the Graycalm series (Werlein 1998), which is characterized by medium sand with bands of fine-textured sand or sandy loam in the lower horizons.

The vegetation of the study area has been dominated by jack pine since presettlement time, maintained by large wildfires (Comer et al. 1995). The majority of the burned area regenerated to jack pine after the 1975 fire; northern pin oak is far less common in the low-elevation landform. The study area was first occupied by three male warblers in 1982, the eighth year after the burn. The number of warblers within the burned area increased annually, peaking in 1991 at 36 warblers and ending in 1997 with one. The western portion of the area was burned again by a wildfire on 11 May 1990, resulting in a sudden reduction of the warbler habitat created by the Bald Hill fire. Fewer singing males were subsequently censused in 1990, one year before the population at Bald Hill reached its maximum.

Methods

Sampling

Census maps and data obtained from the Michigan Department of Natural Resources in July 1995–1997 were used in determining initial warbler colonization and duration of occupancy; these data and field reconnaissance were used to define the area to be sampled. Initial sampling involved description and comparison of the landform-level ecosystems to determine ecological differences between them. Intensive sampling was conducted using sixteen 10 ×

20 m sampling plots, where eight plots were established in each landform using a stratified random design (Spies and Barnes 1985a). In the high-elevation landform, plots were not located in that portion of the area reburned in 1990. Physiography, microclimate, soil, and vegetation were used to examine the distinctness of the landform-level ecosystems (Barnes et al. 1982; Spies and Barnes 1985a).

Physiographic variables recorded for each plot included landform index (McNab 1993; modified for determination from topographic maps), elevation, aspect, slope percent, surface shape, terrain shape index (McNab 1989), and degree of outwash pitting in the adjacent area (expressed as a categorical pitting index, where 1 is no pitting and 5 is very pitted). A soil pit of about 2 m² was excavated to a depth of 180 cm in a quarter of the plot selected randomly with a compass spin. The top 150 cm of the soil profile were described in detail (Soil Survey Staff 1975), and soil samples were collected from each horizon. Soil texture and pH were also collected at standardized 50-cm intervals from the top of the profile. Additional data taken from the face of the soil pit included the presence, depth, and amount of pedogenetic or nonpedogenetic fine-textured bands (Hannah and Zahner 1970); maximum rooting depth; and depth to water table. A soil auger was used at the bottom of the pit to sample soil texture and pH at 50-cm intervals to a depth of 500 cm. Drainage class (e.g., Spies and Barnes 1985a) of the plot area was also estimated. Data on organic matter depth and pH were recorded at a random location within each of the three remaining undisturbed quarters of the plot.

The textures of soil samples collected in the field were confirmed in the laboratory with the hydrometer method as modified by Grigal (1973). The proportions of sand, silt, and clay were determined 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:water solution (w/v) using a Fischer pH meter with a glass combination electrode. Because jack pine growth is most closely related to physical soil properties (Pawluk and Arneman 1961), chemical properties other than soil pH were not examined.

Given the potential influence of physiographic features on microclimate (Geiger 1965; Rowe 1988; Swanson et al. 1988; Bailey 1996) and hence on plant growth and community composition, maximum and minimum temperature was measured in the high- and low-elevation landforms for 12 consecutive weeks at eight stations between 14 May and 13 August 1996. Because of the often remote location of sample plots, temperature readings were taken independent of the sample plots but included four stations in each landform. Each station was located 20–60 m from roads in a small opening and consisted of a pair of maximum–minimum thermometers mounted 30 cm above the ground on wooden stakes. Thermometers were read twice weekly on consecutive days and reset after each reading. The first reading of each week was treated as a record of the maximum and minimum temperatures of the previous week. Because thermometers were reset after this reading, the second reading of each week was treated as an average daily temperature representative of that week. Temperature data were analyzed for differences between the two landforms. Official weather data collected at the nearest weather station in Grayling, Mich., were used for comparison.

All live and dead standing trees >1.5 cm in diameter at breast height (DBH) were counted by species. The height of five dominant jack pines and three dominant northern pin oaks within the plot were recorded to the nearest 0.1 m. Tree height was determined using a range pole marked with 5-cm intervals. Tree age of each of the five dominant pines was determined using the average of two cores extracted with an increment borer approximately 0.3 m from the ground. Tree height growth between landforms was represented as an average annual height growth increment by di-

viding total tree height by tree age. The number of open sides of each dominant jack pine, defined as the number of vertical quarters of a tree enclosed by the surrounding canopy, was recorded. The percent aerial coverage of jack pine and northern pin oak over the entire plot was also visually estimated. For each plot, the number of oak clumps (living oak stump sprouts >1 m tall) and the number of oak seedlings were recorded. In addition, because the height of lowest live jack pine branches has been found to be essential for warbler occupation (Probst and Weinrich 1993), the height to the lowest live branch and lowest whorl were recorded for 10 randomly selected trees.

The 5 × 20 m subplot not containing the soil pit was used to estimate the percent aerial coverage of all groundcover species, including woody stems smaller than 1.5 cm DBH, by coverage class using a 12-class scale (0.25, <0.005%; 0.5, 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%). Standardized coverage estimates were made using a wooden sampling frame that was 0.1% of the subplot (1000 cm²). All coverage estimates were made during August of 1995 and 1996. Nomenclature follows Voss (1972, 1984, 1997) for vascular plants; all nonvascular plants except *Cladina* were recorded as “mosses” or “lichens.” The coverage of ground-flora species were used in part to develop ecological species groups for use as phytometric indicators of site conditions in jack pine dominated ecosystems (Spies and Barnes 1985b; Kashian 1998). In addition, coverage of jack pine and northern pin oak in the groundcover layer was estimated for both the subplot and the entire plot. The coverage of dominant plant groups in the subplot including trees, shrubs, forbs, grasses, mosses, and lichens was also estimated.

Analysis

Mean values of physiography, soil, vegetation, and growth variables from each landform-level ecosystem were compared using a two-sample Student's *t* test. The Fischer least-squares difference (LSD) method was used for pairwise multiple comparison of means. A level of significance of $\alpha = 0.05$ was used for landform comparisons and for all other statistical analysis. In most cases, the data did not exhibit serious departures from assumptions of normality and homogeneity. Where transformations were not successful in meeting these assumptions, the nonparametric Mann-Whitney *U* test was used (Conover 1980).

For the microclimate study, each pair of daily maximum, daily minimum, weekly maximum, and weekly minimum readings was averaged for each station. Univariate two-way repeated-measures analysis (Neter et al. 1990), using landform as a grouping factor and time (weeks or days) as a trial factor, was used to compare the microclimate of each landform. Comparisons of mean maximum and minimum temperatures between the high- and low-elevation landforms were made on both a daily and a weekly basis using the among-subjects *F* test. Week-to-week and day-to-day minimum and maximum temperature differences over the entire summer for each landform were compared using the interaction term in the within-subjects *F* test. No serious departures from the assumption of compound symmetry were found in repeated-measures analyses.

To determine the change in distribution of warblers across the landforms over time, the elevation of each censused singing male was determined from its plotted location on 7.5' topographic maps for each year of occupancy. The relationship of warbler elevation over time was examined with simple linear regression. The locations of singing male warblers for each year between 1982 and 1997 were digitized into a geographical information system (GIS) and the ground coordinates of each warbler calculated to determine the mean location (or centroid) of the warbler population for each year of occupation. Finally, the initial warbler colonization and duration of occupancy of each landform was examined using one-way, single classification chi-square analysis for independence to

examine the randomness of the distribution of singing males across the study area over time.

Results

Comparison of physical site factors between landforms

Although both landforms were flat with no pitting (pitting index = 1) and had negligible slopes, physiography of high- and low-elevation landforms was markedly different by the juxtaposition of landforms and the 9-m elevational difference between them that allows cold-air drainage into the valley (Table 1, Fig. 1). In contrast, soils were very similar (Table 1) and, hence, provide a “common garden” basis for examining jack pine growth and associated features, including warbler occupancy. Soils of both landforms were of the same parent material, and the >95% sand content and similarity in sand fractions indicates the extremely dry and infertile growing conditions. Soils of the high-elevation landform were only slightly finer and exhibited only trace amounts of fine-textured banding (Table 1), which is important in improving site quality of very dry sites (Hannah and Zahner 1972).

Over the entire 1996 growing season, the microclimate of the low-elevation landform was significantly colder than that of the high-elevation landform (Table 2). The daily and weekly minimum temperatures averaged 1.25°C ($p = 0.001$) and 3.04°C ($p < 0.001$) lower, respectively, in the low-elevation than in the high-elevation landform; the mean daily (0.9°C; $p = 0.16$) and mean weekly maximum (1.8°C; $p = 0.06$) temperatures in the low-elevation landform were also lower but not significantly different from the high-elevation landform. The weekly and daily ranges of temperature in each landform throughout the 1996 growing season illustrate the extreme microclimate conditions that occur because of the topographic position of the landforms and subsequent downward cold-air flow.

The interaction of landform and temperature was highly significant for weekly minimum temperatures ($p < 0.001$), indicating that the pattern of weekly minimum temperatures throughout the summer of 1996 was different between landforms (Fig. 2a). The high- and low-elevation landforms exhibited similar patterns of week-to-week maximum temperatures, as the interaction term for weekly maximum temperatures was not statistically significant ($p = 0.45$). However, the low-elevation landform displayed significantly different day-to-day minimum ($p < 0.001$) and maximum ($p < 0.001$) temperature patterns from the high-level landform (Fig. 2b), indicated by a significant interaction term for both comparisons. Notably, the difference in microclimate between the landforms occurred throughout the growing season. Remarkably, below-freezing temperatures were recorded in the low-elevation landform during all 4 months of the field season; in contrast, freezing temperatures were recorded in the high-elevation landform only in May and in early June. Conversely, average maximum temperatures in the high-elevation landform generally reached higher temperatures more often than those in the low-elevation landform (Table 3). A comparison of microclimate data to the official weather data collected at Grayling suggests the presence of more extreme temperatures in the study area. If the Grayling weather data are considered average for the region,

Table 1. Comparison of high- and low-elevation landforms of the Bald Hill burn, Crawford County, Michigan, using selected physiographic and soil variables.

Variable	High (<i>n</i> = 8)	Low (<i>n</i> = 8)	<i>p</i>
Physiography			
Plot elevation (m)	353.57 (1.34)	342.98 (1.63)	<0.001
Slope (%)	0.32 (0.56)	-0.02 (0.68)	0.291
Aspect	0.82 (0.54)	1.02 (0.74)	0.548
Soil texture			
Coarse fraction, 0–150 cm (%)	5.70 (5.16)	9.20 (3.75)	0.121
Coarse sand, 0–150 cm (%)	5.19 (4.58)	8.52 (3.36)	0.119
Medium sand, 0–150 cm (%) ^a	65.22 (10.14)	67.41 (3.53)	0.513
Fine sand, 0–150 cm (%)	24.06 (13.25)	18.90 (6.01)	0.333
Fine fraction, 0–150 cm (%)	24.80 (13.52)	19.61 (6.25)	0.342
Clay, 0–150 cm (%)	2.16 (0.65)	2.00 (0.46)	0.526
Accumulated banding >150 cm (cm) ^a	1.94 (3.82)	0.00 (0.00)	0.174
Depth to lamellae (999 max) (cm) ^a	729.38 (378.63)	999.00 (0.00)	0.064
Soil pH			
pH, soil surface	4.13 (0.12)	4.37 (0.32)	0.059
pH, 150 cm	6.95 (0.46)	6.74 (0.44)	0.365
Depth to pH 7.0 (600 max) (cm)	208.13 (110.65)	192.50 (96.62)	0.304
Depth to pH 8.0 (600 max) (cm)	500.00 (166.90)	437.50 (138.23)	0.338

Note: Values are means with SD given in parentheses.

^aA nonparametric Mann–Whitney *U* test was used for the comparisons.

Table 2. Comparison of microclimate for high- and low-elevation landforms of the Bald Hill burn in terms of weekly and daily maximum and minimum temperatures, 14 May to 13 August 1996.

	Weekly temperatures (°C)		Daily temperatures (°C)	
	Low	High	Low	High
Minimum	-1.63 (4.26)	1.41 (4.04)	5.41 (4.93)	6.66 (4.52)
Maximum	31.33 (2.77)	33.1 (2.92)	28.13 (4.29)	28.99 (4.96)

Note: Values are means with SD given in parentheses.

then the study area is characterized by a warmer-than-average microclimate in the high-elevation landform and a colder-than-average microclimate in the low-elevation landform (Table 3).

Comparison of vegetation between landforms

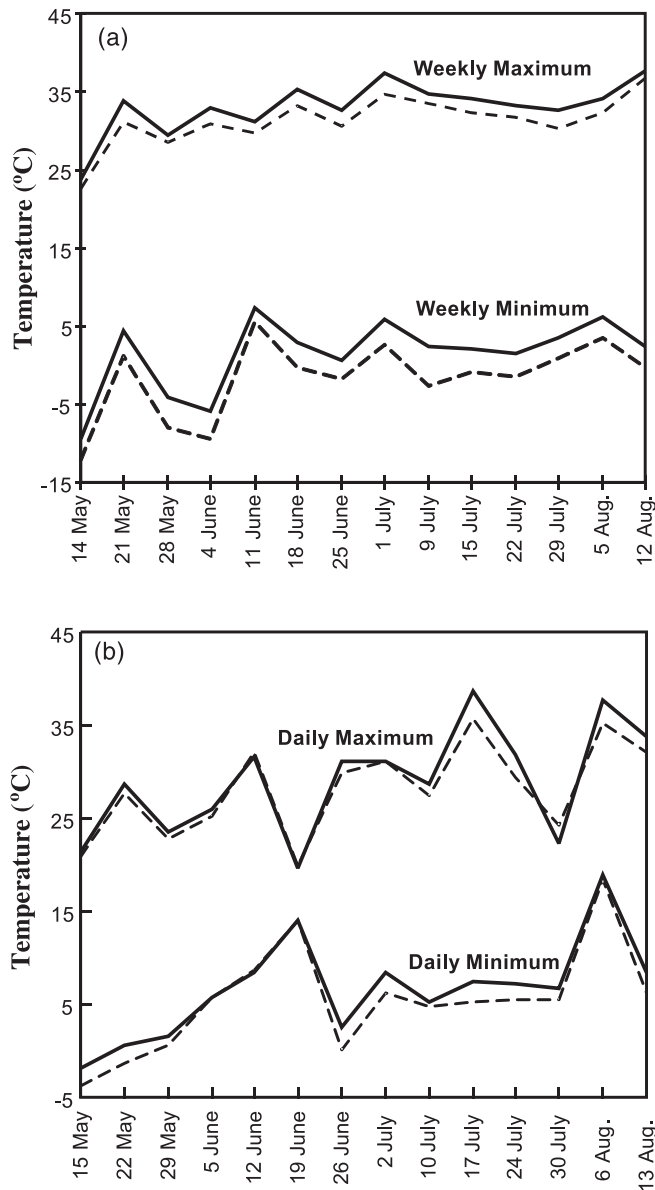
Jack pine and northern pin oak growth and density showed striking differences between the two landforms (Table 4), perhaps reflecting differences in microclimate. In the high-elevation landform, jack pines grew significantly faster (26.5 vs. 21.6 cm/year), were denser (7938 vs. 3825 stems/ha), and were more prevalent in the groundcover layer. Maximum rooting depth of jack pine was significantly deeper in the high-elevation (111.5 cm vs. 85.4 cm in the low-elevation landform) because trees were taller and more vigorous, resulting in more extensive root systems. Likewise, the coverage of northern pin oak in the canopy and the understory (trees 1.5–4.5 cm DBH) was high in the high-elevation landform and absent in the low-elevation landform. Northern pin oak height was also clearly different (5.45 vs. 0.19 m); oaks found in the low-elevation landform were mainly small seedlings in the ground cover or stunted sprouts from trees killed during the wildfire or by frost, in contrast to the common overstory or understory oaks found in the high-elevation landform. Groundcover vegetation composition found in the two landforms was very similar

(Table 4). Differences in vegetation (particularly jack pine height growth and the abundance of northern pin oak) appear to be controlled by microclimate, given that each landform is otherwise very similar in site quality.

Spatial and temporal distribution of Kirtland's warblers

The duration of occupancy by Kirtland's warblers at the Bald Hill burn is long relative to most other areas within the warbler breeding range (Kashian 1998). Warblers first colonized the high-elevation terrain and systematically progressed into the low-elevation terrain; 85% of singing male warblers in the first 6 years of occupancy were found in the high-elevation terrain, compared to only 25% in the final 6 years; this shift to the low-elevation terrain occurred by 1991 (Fig. 3a). Considering that only the high-elevation terrain was initially occupied and only the low-elevation terrain was occupied in later years, differential occupation of the two landforms extended the occupation of the entire burned area as a whole by 4–6 years (Fig. 3b). Spatially, the warbler population exhibited a differential and unidirectional pattern of warbler occupation across the study area between 1982 and 1997 (Fig. 4). Chi-square analyses indicate that this steady movement was nonrandom ($p < 0.05$) in the early (1984–1987) and late (1994) years of warbler occupation with the majority of warblers found in the high-elevation ter-

Fig. 2. Comparison of the weekly (a) and daily (b) maximum and minimum air temperatures for high- and low-elevation landforms of the Bald Hill burn. The solid and broken lines represents the high and low-elevation landform, respectively.



rain and low-elevation terrain, respectively. Warblers were too few in 1982, 1983, 1995, 1996, and 1997 to meet the assumptions of the chi-square analysis. The average elevation of warbler occupation each year decreased linearly with time as the warbler population shifted from high elevations to low ($y = 2359.18 - 0.32x$, $r^2 = 0.93$, $p = 0.0001$).

Discussion

Examination of the 16-year warbler movement across the two landforms burned by the Bald Hill fire shows that initial warbler colonization and duration of occupation are strongly correlated with differences in the landform-level characteristics of microclimate and jack pine height growth and density. The majority of warblers initially colonized the warmer

Table 3. Comparison of high- and low-elevation landforms at the Bald Hill burn and the Grayling, Mich., weather station in terms of number of temperature readings below 0°C, above 32.2°C, and above 37.8°C for 14 May to 13 August 1996.

	High	Low	Grayling
No. of readings below freezing (0°C)	4	10	3
No. of readings above 32.2°C	14	9	2
No. of readings above 37.8°C	1	0	0

high-elevation landform, where taller and denser jack pines first provided an appropriate foliage volume for warblers to nest (Mayfield 1960; Walkinshaw 1983; Probst and Weinrich 1993). More warblers colonized the low-elevation landform as trees there grew taller with time. By 1991, a distinct shift had occurred in warbler occupation to the low-elevation terrain. This shift from high-elevation to low-elevation terrain may be partially attributed to the loss of warbler habitat in the high-elevation landform as a result of the second fire in 1990. Rather than causing the shift, however, which was already underway, the second fire may have simply expedited it.

The slow growth of jack pine in the low-elevation landform is attributed primarily to the cold microclimate because soil factors are very similar in both low- and high-elevation landforms. Rarely in glacial terrain do two distinct, adjacent landforms exhibit highly similar soil characteristics. Since soil factors affecting moisture regime in sandy soils are typically the major source of variation in jack pine growth, the Bald Hill area provides an excellent example of the influence of microclimate on jack pine growth. Jack pine growth is strongly affected by air temperature, especially at the southern extent of its distribution in northern Lower Michigan (Botkin et al. 1991). In fact, the growth and regeneration of jack pine is most strongly affected by climate at the limits of its distribution, where extremes of temperature tend to overwhelm other factors affecting its growth (Botkin et al. 1991; Despland and Houle 1997). Similar to this study, Barnes et al. (1989) recorded visible effects of freezing temperatures on new shoot growth of jack pine in May and a reduction in vigor of pines in depressions at Mack Lake. Alternatively, determining causal factors of tree height differences may be confounded by stand density differences between the landforms. Stand density, although highly variable, is lower in the low- than in the high-elevation landform (Table 4). However, we observed shorter jack pines (less height growth) in the low-elevation landform even in patches where density was similar to that in the high-elevation landform.

Microclimatic variation at the Bald Hill burn may explain more than jack pine height growth and warbler occupation differences between landforms. Jack pine regeneration may also be influenced by the marked difference in microclimate between the two landforms, since seedlings are negatively affected by freezing temperatures during early stages of their development (Kozłowski and Pallardy 1997). In addition to an effect of cold temperatures on existing trees, frost-pocket effects on the germination and early development of jack pine seedlings immediately following wildfire may in part be a factor controlling the density of open jack pine stands

Table 4. Comparison of high- and low-elevation landforms of the Bald Hill burn using selected variables of woody and herbaceous plants.

Variable	High (<i>n</i> = 8)	Low (<i>n</i> = 8)	<i>p</i>
Jack pine			
Jack pine height growth rate (cm/year)	26.51 (3.26)	21.64 (1.35)	0.002
Stand density (stems/ha)	7938.0 (5144.5)	3025.0 (1794.0)	0.041
Jack pine canopy coverage (%)	66.13 (20.91)	45.13 (11.17)	0.025
Coverage of groundcover jack pine ^a	2.88 (1.64)	0.78 (1.15)	0.010
Height to lowest live pine branch (cm)	148.45 (41.25)	67.53 (31.42)	0.001
Maximum rooting depth (cm)	111.50 (20.63)	85.38 (21.61)	0.027
Northern pin oak			
Northern pin oak height (m)	5.45 (1.79)	0.19 (0.12)	0.001
No. of understory oak	23.63 (17.83)	0.00 (0.00)	<0.001
Northern pin oak canopy coverage (%) ^b	21.75 (15.74)	0.00 (0.00)	0.002
Coverage of groundcover oak ^a	3.91 (1.56)	0.63 (0.68)	<0.001
Groundcover vegetation			
No. of herbaceous species	12.63 (4.17)	15.75 (4.71)	0.182
No. of grass species ^b	5.38 (1.30)	6.63 (0.92)	0.043
Coverage of shrubs (%)	15.88 (4.25)	15.34 (4.64)	0.815
Coverage of forbs (%)	6.47 (3.71)	5.97 (3.40)	0.783
Coverage of grasses (%)	12.66 (4.75)	14.53 (4.56)	0.434
Coverage of lichens (%)	4.88 (3.18)	6.38 (2.72)	0.328

Note: Values are means with SD given in parentheses.

^aCoverage is expressed as the average coverage class value. See text for explanation.

^bA nonparametric Mann–Whitney *U* test was used for the comparisons.

(Sorensen 1983). Low-density stands may then perpetuate themselves based on seed-source availability following the next fire, and a systematic effect of cold microclimate exists over time for low stand density in low-lying areas. Thus, the relative openness of low-lying areas such as depressions and glacial outwash channels at Mack Lake (Barnes et al. 1989) and the low-elevation landform in this study may occur because of frost effects. In this sense, microclimate may also indirectly influence groundcover vegetation, in that greater plant diversity and significantly higher coverage of grasses in the low-elevation landform may be attributed to the increased amount of light or moisture reaching the forest floor because of low stand density. The low stand density found on the low-elevation landform of the study area may reflect prefire stand conditions such as low prefire pine density in addition to the site conditions found there.

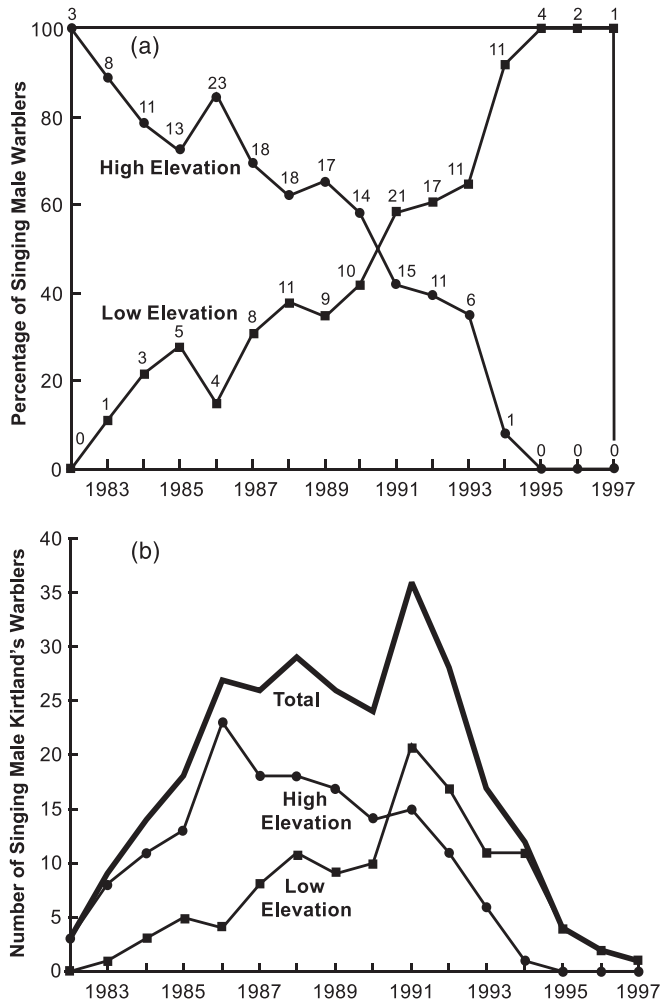
Microclimatic variation as mediated by physiography may also explain many of the differences in northern pin oak growth and coverage observed between landforms. Oak was virtually absent from the low-elevation landform, which is probably not caused by soil fertility and is unlikely to be due to disturbance, since both landforms are equally susceptible to fire. However, the low-elevation landform is characterized by severe, repetitive freezing that persists late into the spring, compared with the high-elevation landform. Although it is more frost hardy than other oak species, northern pin oak is susceptible to damage by freezing temperatures (Barnes et al. 1989; Burns and Honkala 1990). Oaks in the low-elevation landform, if present, tended to be stunted, flushed later in the spring than oaks in the high-elevation landform, and showed signs of heavy frost damage such as wilted leaves and dead shoots and branches. Although oaks in the high-elevation landform also displayed signs of frost damage, the oaks were not stunted, flushed earlier, and frost

damage was lighter than oaks in the low-elevation landform. Because of frost damage, oaks in the low-elevation landform were found only in the groundcover layer (Table 4). Ground-cover oaks were typically small (<1 m) plants sprouting from a single root system following fire and frost damage. In addition, groundcover oaks in the low-elevation landform were most often found under the canopies of jack pines, which may act to moderate the severe microclimate (Spurr 1957; Barnes et al. 1989; Chen et al. 1993; Chen and Franklin 1997). Microclimate, therefore, appears to be the primary site factor that is responsible for the differences in the coverage of northern pin oak between the two landforms.

The differential height growth rate of jack pine between the two landforms lengthened the duration of warbler occupancy at the Bald Hill burn as a whole. The warmer, more favorable growing conditions for jack pine in the high-elevation landform caused it to be solely occupied during the first year of occupancy (1982), and the delay in jack pine growth in the low-elevation landform caused it to be solely occupied in 1995–1997. In addition, during 2 years only one warbler was found on either the low-elevation landform (1983) or the high-elevation landform (1994). These single warblers are likely either instances of warblers occupying marginal habitat near occupied suitable habitat (e.g., Probst and Weinrich 1993) or are the result of site heterogeneity within the landform-scale units that would provide small “pockets” of suitable habitat within the larger area of marginal habitat. With these considerations, at least six additional years of warbler occupation at the Bald Hill burn may be due to the diversity of landforms found within it.

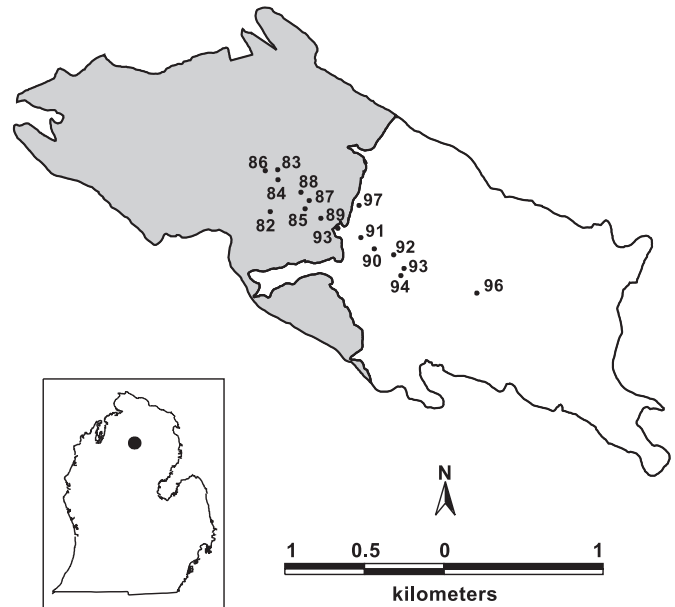
The influence of landform diversity on warbler occupation has important implications for warbler management. For example, in the original *Kirtland's Warbler Recovery Plan*, Byelich et al. (1976) suggested that only jack pine stands of

Fig. 3. Comparison of the number of singing male warblers occupying high- and low-elevation landforms of the Bald Hill burn from 1982 to 1997. (a) Percentage of singing male Kirtland's warblers occupying each landform; numbers above points represent the actual number of singing male warblers found on that landform that year. (b) Offset of peak occupancy between landforms, which resulted in a longer occupation of the entire burn as a whole.



a large size would support warblers for an extended time. Although large stands support more warblers each year than small stands, stand size per se may be less responsible for a long duration of warbler occupancy than the increased site variation (represented here as multiple landforms) that occurs within a large land area. Therefore, large stands may be most useful within areas of nonuniform physiography. Similarly, small stands, originally thought to hold warblers for only short durations, may be successfully occupied for longer durations if they are located upon diverse physiography. Furthermore, staggered planting in areas of uniform physiography, as suggested by Probst (1988), may be analogous to even-aged planting in areas where physiography is diverse in terms of lengthening warbler occupancy. The success of such a planting strategy in the past suggests that the ability to identify large-scale site variability that may cause differential jack pine growth (analogous to staggering ages) would be very beneficial to Kirtland's warbler management.

Fig. 4. Annual locations of the centroid of the warbler population across the Bald Hill burn from 1982–1997. Shaded area represents the high-elevation landform; unshaded area represents the low-elevation landform. The mark in the inset shows the location of the burn in the Lower Peninsula of Michigan.



Few studies (except Spurr 1957) have attempted to link the interactions of physiography, microclimate, and soil to plant or animal growth and distribution. We conclude that a broad-scale ecosystem approach is needed to understand the complex interactions that affect spatial and temporal species distributions across the landscape and that such an approach may benefit the management of particular endangered species. Knowledge of stand-structural characteristics are useful in explaining the presence or absence of Kirtland's warblers, but a landscape ecosystem approach that integrates physiography, microclimate, soil, and vegetation provides the framework for understanding the timing of initial colonization, duration of occupancy, and spatial pattern of warbler occupation across landform-level ecosystems over time. By shifting focus from bird species and stands of trees to volumetric ecosystems, we can provide an ecological framework with which to further understand warbler behavior for use in warbler management. In other words, understanding the Kirtland's warbler as an endangered species may best be accomplished by better understanding the spaces to which it belongs (Barnes 1993).

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