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## DISTINCTIVENESS, USE, AND VALUE OF MIDWESTERN OAK SAVANNAS AND WOODLANDS AS AVIAN HABITATS

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**ABSTRACT.**—Oak savannas and woodlands historically covered millions of hectares in the midwestern United States but are rare today. We evaluated the ecological distinctiveness and conservation value of savannas and woodlands by examining bird distributions across a fire-maintained woody-vegetation gradient in north-west Indiana encompassing five habitats—open habitats with low canopy cover, savannas, woodlands, scrublands, and forests—during migration, breeding, and overwintering. Savannas and woodlands were significantly different in overall bird species composition from open and forest habitats but were often intermediate between open and forest in guild densities. Few bird species were consistently and highly concentrated in savannas or woodlands, and the Red-headed Woodpecker (*Melanerpes erythrocephalus*) was the only species significantly more abundant in savannas and woodlands than in open, scrub, and forest habitats. Fire frequency over a 15-year interval was a significant predictor of bird community composition and was positively related to species diversity, spring transient migrant density, and density of the most threatened species. Each habitat type had characteristics potentially important for avian conservation. Scrub had the highest density of transient migrants, which suggests it plays an important role as migration stopover habitat. More species were significantly concentrated in open or forest habitats than in the other habitats. Lack of species concentration and intermediate community composition suggested that birds experienced savannas and woodlands more as ecotones than as habitats distinct from forests or grasslands. However, this intermediate character can benefit conservation, as evidenced by savannas and woodlands having the highest density of the most threatened species along this woody-vegetation gradient. *Received 20 October 2005, accepted 27 August 2006.*

**Key words:** ecotones, fire frequency, indicator species, oak savanna, oak woodland, seasonal effects, stopover habitat.

### Características Únicas, Uso y Valor de las Sabanas y Bosques Abiertos de Roble del Oeste Central como Hábitats para las Aves

**RESUMEN.**—Las sabanas y los bosques abiertos de roble cubrían históricamente millones de hectáreas en el oeste central de Estados Unidos, pero hoy son muy raros. Evaluamos las características ecológicas únicas y el valor de conservación de las sabanas y los bosques abiertos mediante el estudio de la distribución de especies de aves a través de un gradiente de vegetación leñosa mantenido por el fuego en el noroeste de Indiana. Este gradiente comprendió cinco tipos de hábitats (ambientes abiertos con baja cobertura de dosel, sabanas, bosques abiertos, matorral y bosques cerrados) y el estudio fue realizado durante la migración, la reproducción y el periodo de invernada. Las sabanas y los bosques abiertos fueron significativamente diferentes al ambiente abierto y al bosque cerrado en cuanto a la composición de especies, pero en muchos casos presentaron una densidad de gremios intermedia

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entre la densidad observada en ambientes abiertos y de bosque cerrado. Pocas especies se concentraron en grandes cantidades y de manera regular en las sabanas o los bosques abiertos, y el carpintero *Melanerpes erythrocephalus* fue la única especie significativamente más abundante en las sabanas y los bosques abiertos que en los ambientes abiertos, el matorral y el bosque cerrado. La frecuencia del fuego a través de un intervalo de 15 años predijo de manera significativa la composición de la comunidad de aves y se relacionó positivamente con la diversidad de especies, con la densidad de aves en tránsito de primavera y con la densidad de las especies más amenazadas. Cada tipo de hábitat tuvo características potencialmente importantes para la conservación de las aves. El matorral tuvo la densidad más alta de aves en tránsito, lo que sugiere que este hábitat tiene un papel importante como parada para las aves migratorias. La concentración de especies fue significativamente mayor en el ambiente abierto o de bosque cerrado que en los demás hábitats. La falta de concentración de especies y una composición comunitaria intermedia sugieren que las aves perciben los ambientes de sabana y de bosque abierto como un ecotono más que un hábitat diferenciado de los bosques cerrados o los pastizales. Sin embargo, esta característica intermedia puede beneficiar la conservación de las aves, ya que las sabanas y los bosques abiertos tuvieron las mayores densidades de especies amenazadas a través de esta gradiente de vegetación leñosa.

SAVANNAS, GRASSY LANDSCAPES interrupted by scattered trees, are the native biome across 1.6 billion hectares of the earth, including >50 million hectares of North America and nearly half of Africa, Australia, and South America (Scholes and Archer 1997). Temperate savannas and grasslands have the highest ratio of conversion to human uses versus protection for conservation of any of the world's major terrestrial biomes and are, therefore, considered endangered in many locations (Hoekstra et al. 2005). Today, actual global savanna coverage is determined by a dynamic that includes loss of savanna to agriculture and other human use, gain of savanna from conversion of forests to anthropogenic savannas, and fire suppression that converts grasslands and savannas to scrublands, woodlands, and forests with higher canopy cover. The balance of this interaction has caused most savanna to be lost from the midwestern United States, where >10 million hectares of savanna once occurred (Auclair 1976, Nuzzo 1986). Of the historical savanna sites in the Midwest that persist in conservation preserves, many have undergone structural changes, especially increases in woody vegetation density associated with decreased fire frequency (Abrams 1992, Bowles and McBride 1998). Many disturbance-dependent savanna birds, such as the Baltimore Oriole (*Icterus galbula*) and the Red-headed Woodpecker (*Melanerpes erythrocephalus*), have declined in

post-1966 Breeding Bird Survey data; this is likely related, in part, to decreased fire frequency (Brawn et al. 2001, Hunter et al. 2001).

Recognition of these landscape changes motivates efforts to restore oak savannas and woodlands in the Midwest (Leach and Ross 1995). However, few studies in the Midwest, or worldwide, have looked across the grassland-forest continuum to compare how woody plant cover affects ecosystem properties (Breshears 2006). Although management goals along the continuum are often defined by density of woody vegetation, the effects of restoration on animal populations must be understood if the desirability and quality of restoration are to be evaluated (Morrison 1995). Here, we examine how restoration of a midwestern landscape that historically contained oak savannas and woodlands might affect bird communities and how desirable such potential restorations might be for avian conservation.

Temple (1998) posited a central question for evaluating the desirability of savanna restoration for birds. Is midwestern oak savanna a biome, a habitat type distinct from grasslands and forests with its own collection of specialist species, or an ecotone, containing an amalgam of generalists and species that are more concentrated in grasslands or forests (Leach and Givnish 1999)? Knowing the extent to which savannas or woodlands are distinct from grasslands and forests—and how they are especially

valuable to avian conservation—could help determine whether to manage habitat for specific vegetation characteristics that differentiate savannas and woodlands from forests and grasslands. Although comparisons of bird communities across the larger grassland–forest continuum are uncommon, comparisons of bird communities over parts of the gradient have been made, examining, for example, the effects on bird communities of conversion of closed-canopy forests to savannas in the Midwest (Davis et al. 2000, Brawn 2006).

We examined the effects of habitat structure on bird populations across an open-forest gradient in northwest Indiana. The landscape included prairies, black oak (*Quercus velutina*) savannas and woodlands, and forests at the time of initial Euro-American settlement (Cowles 1899, Rohr and Potzger 1951, Bacone et al. 1980). The savanna landscape was maintained by a combination of soil, climate, and fire (Henderson and Long 1984, Taylor 1990, Cole and Taylor 1995) with low organic content of sandy soils and frequent fires limiting tree density. Between 1830 and 1981, average tree density in much of the study area increased two- to four-fold, mainly because of fire suppression (Henderson and Long 1984). During that interval, fire suppression at many sites, frequent fire at other sites, and soil disturbance (Wilcox et al. 2005) produced a variety of habitat types that can be arrayed in a gradient centered on savannas and ranging from open habitats with little woody vegetation to forests. Today, land managers in this region typically use fire to restore and maintain areas of low canopy cover. Relating fire frequency to composition of bird communities is, therefore, important for predicting outcomes of fire-based landscape management of savannas in the Midwest (Davis et al. 2000, Brawn et al. 2001, Brawn 2006) and worldwide (Mills 2004, Pons and Wendenburg 2005).

We looked at bird use of habitats along the open-forest gradient to address questions important to the definition, management, and value of oak savannas and woodlands in the Midwest. Are savannas and woodlands distinct avian habitat types compared to other habitat types along the woody-vegetation gradient? How does fire frequency affect avian community composition? How do the relationships between bird habitat use and vegetation density vary with season? The few studies that

have examined relationships between woody-vegetation structure and bird use of savanna landscapes in the Midwest have emphasized habitat-use patterns during the breeding season (Callahan 1996, Temple 1998, Davis et al. 2000, Brawn 2006). In North America, areas adjacent to large bodies of water are considered to be of high priority for conservation as migration stopover sites (Petit 2000). Our study sites are near Lake Michigan, a 500-km-long stretch of water with a north–south orientation, the fourth largest freshwater lake in the world. Spring migrants arriving in northwest Indiana, at the lake's southern terminus, must decide either to migrate over the large expanse of water or select the east or west shores of the more than 100-km-wide lake for migration. Fall migrants following the lake's shore can be funneled into northwest Indiana (Brock 1997). Given this region's strategic location with regard to migration, we asked how different habitats along the gradient are used as stopovers for migrating birds and how the use and value of savannas might therefore vary seasonally.

#### METHODS

*Survey locations.*—We examined relationships between bird habitat use and habitat structure at 102 points, from April 1998 to October 2002, at Indiana Dunes National Lakeshore (41°38'N, 87°09'W; 6,000 ha;  $n = 75$  points), Tefft Savanna Nature Preserve and Jasper-Pulaski Fish and Wildlife Area (41°10'N, 86°58'W; 3,250 ha;  $n = 24$  points) (Dancey 1991), and Hoosier Prairie Nature Preserve (41°31'N, 87°27'W; 225 ha;  $n = 3$  points).

Midwestern oak savanna is characterized by widely spaced oak trees, a robust herbaceous ground layer, and limited subcanopy woody vegetation. Survey points represented a gradient of five habitat types that arose from changes to savannas since initial Euro-American settlement and a gradient of woody vegetation cover that historically existed across the prairie–forest transition zone of the Midwest (Anderson 1998). The five habitat types were (1) open habitats, with little woody vegetation to form an overhead canopy or subcanopy, including prairie remnants maintained by frequent fires and anthropogenically disturbed sites with low canopy cover because of past soil disturbances, such as farming and sand mining

(Wilcox et al. 2005); (2) savannas with moderate oak-dominated canopy cover and little woody understory vegetation; (3) woodlands similar to savannas but with greater canopy cover; (4) scrub habitats with high density of black oak sprouts <5 m in height that often arise following intense fires; and (5) forests with high canopy cover from larger trees and with several woody vegetation layers containing multiple tree species. We used a densiometer (Nuttall 1997) to measure canopy cover around the survey points and defined "open" as <20% canopy cover ( $n = 15$  points), savanna 20–50% ( $n = 19$ ), and woodlands 50–90% ( $n = 30$ ). Forests ( $n = 24$ ) had >90% cover and >300 woody stems >10 cm diameter at breast height (DBH)  $\text{ha}^{-1}$ . Regardless of canopy cover, scrub ( $n = 14$ ) had >1,000 woody stems 2.5–10 cm DBH  $\text{ha}^{-1}$ . With the exception of one woodland point, all non-forest points had <300 stems >10 cm DBH  $\text{ha}^{-1}$ . Although consensus in defining canopy-cover cut points among these habitats is lacking, these cutoffs are similar to those found in several schemes used to classify plant communities in this region (Leach and Ross 1995).

*Habitat assessment.*—Sites for counting birds were delineated so that density of smaller (<10 cm DBH) or larger (>10 cm DBH) woody vegetation around each point was relatively uniform and representative of one of the five habitat types. Birds were counted and vegetation cover assessed only within the delimited area. Around each bird survey point, vegetation cover was measured in six 0.05-ha (25.2 m diameter) circular plots. Average vegetation cover across a 100-m-radius circle surrounding the survey point was then estimated by inverse distance weighting interpolation of cover values from these six plots (ARCGIS 9, ESRI, Redlands, California).

Vegetation cover was measured within several strata in each plot. Densiometer readings were taken at the plot center (Canopy Cover). We also measured (1) cover of vegetation within 1 m of the ground (Low Ground Vegetation); we used a point-intercept method to measure percentage of cover <0.3 m in height and a 1- $\text{m}^2$  frame, divided into 100 sections, to measure percentage of vertical cover 0.3–1 m in height, and then averaged the two results; Elzinga et al. 1998); (2) percentage of vertical cover of vegetation 1–2 m in height (measured with the divided frame; High Ground Vegetation); (3) number of

living woody shrubs, sprouts, saplings, or small trees 2.5–10 cm DBH (Shrub Density); (4) number of living trees >10 cm DBH (Tree Density); and (5) number of dead woody stems >2.5 cm DBH (Dead Tree Density) (measurements 3–5 were determined by total counts). We calculated (6) fire frequency over the past 15 years, within 100 m of a bird survey point (Fire Frequency), based on maps of fires from 1983 to 2002:

$$\text{Fire Frequency} = \sum_{i=1}^{15} \text{Area}_i$$

where  $\text{Area}_i$  is the proportion of the 100-m radius circle burned in year  $i$ . Prescribed burning for management in this area began ~15 years before the start of the present study. Most fires were low- to moderate-intensity, non-growing-season ground fires with occasional more intense fires that reached the tree canopy, including some during summer.

*Bird counts.*—At each survey point, birds were counted over an unlimited distance, within the established site perimeter, for 5 min. Counts were conducted from approximately one hour after sunrise through midmorning when wind speed was <20  $\text{km h}^{-1}$  and, for winter counts, under conditions of minimal snow cover and temperature greater than  $-5^\circ\text{C}$ . One observer (R.G.) made most of the observations (93%). Observers were trained in distance estimation. Birds observed while flying were included in analyses only if the species was primarily an aerial forager.

We counted birds during spring migration (15 April–20 May), breeding season (1 June–15 July), fall migration (1 September–15 October), and winter (15 November–15 March). Each point was visited 48 times. From April 1998 to April 2001, each point was visited three times during each season, except two visits during winter 2001. During the final two years, April 2001–October 2002, winter visits were discontinued and the numbers of spring, breeding, and fall visits were 3, 2, and 3 in the fourth year and 2, 1, and 2 during the fifth year. Within a season, repeat visits to a point were separated by approximately two weeks, with longer intervals to span the winter.

We categorized a species' guild membership into nine categories based on foraging substrate and food type: (1) ground granivore; (2) canopy,

understory, or bark insectivore; (3) ground omnivore; (4) canopy or understory omnivore; (5) aerial insectivore; (6) canopy or understory granivore; (7) frugivore; (8) vermivore; and (9) ground insectivore (DeGraaf et al. 1985). We classified each species as a Neotropical shorter-distance or temperate migrant or as a resident (Brock 1997, Gough et al. 1998). Migrants that did not breed or overwinter in northwest Indiana were termed "transient migrants."

*Density and conservation value calculations.*—To reduce bias related to differences in detectability among species (Rosenstock et al. 2002, Bart et al. 2004), we used distance sampling to convert raw counts to an estimate of species density (Buckland et al. 2001). Six conventional distance-sampling models (uniform-cosine, uniform-simple polynomial, half normal-cosine, half normal-Hermite polynomial, hazard rate-cosine, and hazard-rate-simple polynomial) were fitted for each species with  $\geq 100$  observations. One model was selected on the basis of Akaike's Information Criterion (AIC) and on the fit of the model at short observation distances (Thomas et al. 2004). For less frequently observed species, the detection function used in the density-estimation calculation was estimated by pooling distance observations over species similar to this rarer species (Buckland et al. 2001). Similar species had approximately the same size, habitat-use patterns, and vocal characteristics and were usually within the same genus or family.

Densities were calculated by season and habitat type. To obtain an index of species abundance across seasons, the fall and spring migration densities were averaged into a migration-season mean, and then densities from migration, summer, and winter seasons were averaged. This overall mean gave relatively more weight to species present throughout the year and emphasized three major temporal uses of habitat—for breeding, for overwintering, and as a migratory stopover site.

A conservation concern score has been proposed for U.S. and Canadian landbirds, based on data from the Partners in Flight (PIF) program (Rich et al. 2004). Species were assigned a PIF combined score from 4 (lowest conservation concern) to 20 (highest concern). Species scores in the present study ranged from 5 to 17. We calculated the total density of birds in each of three approximately equal score ranges, 5–8, 9–12, 13–17, to examine how habitat characteristics

were related to density of lower-, intermediate-, and higher-concern species.

*Statistical analysis.*—We used principal curve analysis to ordinate avian community data from the 102 sample points (De'ath 1999, Walsh 2005). Principal curve ordination assumes that the 102 samples occur along a smooth curve in a high-dimensional space whose axes represent abundance of the sampled species. Points are assumed to occur along this principal curve in the same order as they occur along an underlying, often complex, ecological gradient that affects community composition. By regressing measured habitat variables on the points' locations along the principal curve, we examined whether these habitat variables were likely components of the ecological gradient underlying the principal curve. The curve was standardized to a length of 1. Because habitat predictors were z-score-transformed, coefficients of the regression of habitat predictors on principal curve scores indicated how much the principal curve score changed with a change in a predictor of  $\pm 1$  SD, controlling for the effects of the remaining predictors.

We used indicator-species analysis to evaluate the degree to which a species was regularly and exclusively observed in only one habitat type (Dufrene and Legendre 1997). Indicator values (IV) ranged from 0 (no indication) to 100 (perfect indication). Perfect indication of a species for a habitat occurred if that species was observed in every sample of that habitat and if the species was never observed in another habitat type (McCune and Mefford 1999). Each species had an IV for each of the five habitats, but the species had the best indication for the habitat with the highest IV, and only that score was considered in analysis. Significance of that highest IV was evaluated by a Monte Carlo test comparing IVs calculated from the observed density data with IVs calculated from the same density data randomly assigned to habitat types. In searching for species characteristic of a habitat, we considered species whose highest IV score was significant in the Monte Carlo test and was  $> 25$ , a threshold IV used by Dufrene and Legendre (1997).

Habitats were mainly defined by canopy cover ranges. We used multivariate regression tree (MRT) analysis to determine how well canopy cover split the 102 points into groups that were homogeneous in bird species composition



(De'ath 2002). The MRT analysis started by determining the canopy cover that divided the 102 points into the two groups that were most homogeneous in species composition and then continued splitting the resulting groups, on the basis of canopy cover, into ever smaller, ever more homogeneous groups, forming a regression tree. Homogeneity was measured as Bray-Curtis similarity of composition among points within a group. Cross-validation was used to select the tree that minimized the total error (lack of similarity of species composition among points within a group) summed across all groups.

We calculated the coefficient  $B_{\text{Fire}}$  from the regression of Fire Frequency (not z-score-transformed) on overall density of each guild standardized by division by the guild mean.  $B_{\text{Fire}}$  represented the estimated percentage of change in a guild's density, relative to that guild's mean, for each additional fire occurring over the 15-year interval in which Fire Frequency was calculated.

For multiple comparisons following significant ( $P < 0.05$ ) one-way analyses of variance

(ANOVA), we used Tukey's test if the data did not violate the homogeneity-of-variance assumption, and the Games-Howell multiple-comparisons test if that assumption was not met (SPSS, Chicago, Illinois). Significance of differences in community composition among habitat types was determined by analysis of similarity (ANOSIM; PRIMER, Clarke and Gorley 2001).

RESULTS

*Ability of open-forest vegetation gradient to predict bird community composition.*—Canopy Cover, Fire Frequency, and each of the five vegetation layers differed significantly across the five habitats (one-way ANOVA,  $P < 0.05$ ; Fig. 1). We made 25,028 observations of 129 bird species ( $n_{\text{Spring}} = 115$  species,  $n_{\text{Breeding}} = 87$ ,  $n_{\text{Fall}} = 102$ ,  $n_{\text{Winter}} = 33$ ) (Table 1). Overall, 372 observations (1.5%) were not identified to species and were not included in analyses. For the 129 species, rank order correlation (Spearman's  $r$ ) between raw counts of observations of a species and species density as estimated by distance sampling

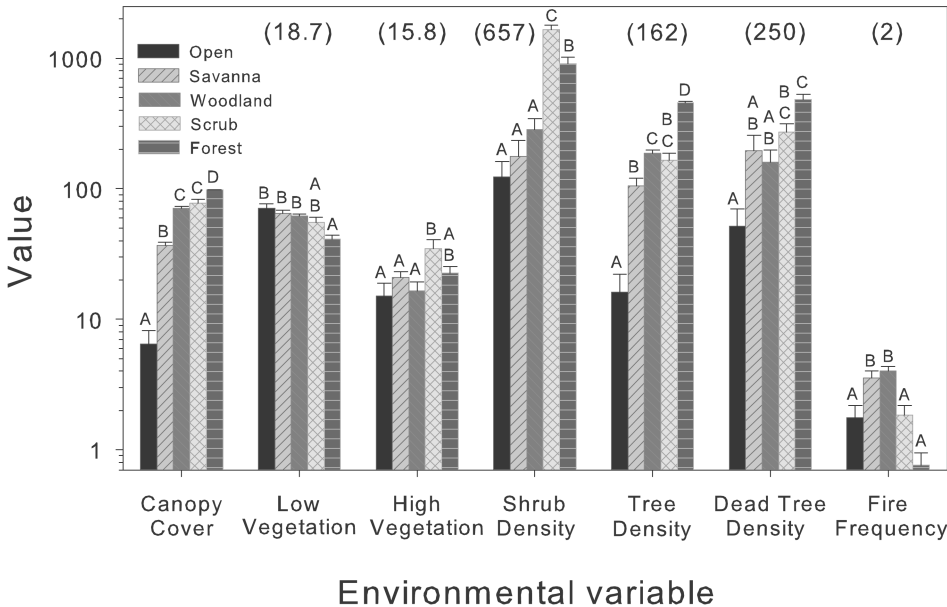


FIG. 1. Differences in habitat characteristics along an open-forest gradient in northwest Indiana. Within a variable, habitats sharing the same superscript letter do not differ significantly (one-way ANOVA,  $P > 0.05$ ). Canopy Cover, Low Ground Vegetation (Low Vegetation), and High Ground Vegetation (High Vegetation) are percentages. Shrub Density, Tree Density, and Dead Tree Density are stems  $\text{ha}^{-1}$ . Fire Frequency is the equivalent number of times a 100-m radius area around a point completely burned over 15 years. Standard deviations of variables across all 102 points are shown in parentheses above each set of bars as a reference for z-score-based analyses.

TABLE 1. Mean overall density ( $\pm$  SE) (birds ha<sup>-1</sup>) of the five most abundant species per habitat and nine most abundant guilds along open-forest gradient in northwest Indiana. Species density rank within each habitat is shown in parentheses.

Species	Open	Savanna	Woodland	Scrub	Forest	
Red-headed Woodpecker ( <i>Melanerpes erythrocephalus</i> ) <sup>3</sup>	0.09 $\pm$ 0.03 <sup>AB</sup> (31)	0.44 $\pm$ 0.08 <sup>C</sup> (4)	0.74 $\pm$ 0.12 <sup>C</sup> (4)	0 <sup>A</sup> (92)	0.15 $\pm$ 0.03 <sup>B</sup> (21)	
Eastern Wood-Pewee ( <i>Contopus virens</i> ) <sup>2</sup>	0.02 $\pm$ 0.01 <sup>A</sup> (56)	0.21 $\pm$ 0.03 <sup>B</sup> (21)	0.13 $\pm$ 0.02 <sup>B</sup> (24)	0.13 $\pm$ 0.02 <sup>B</sup> (30)	0.44 $\pm$ 0.04 <sup>C</sup> (3)	
Red-eyed Vireo ( <i>Vireo olivaceus</i> ) <sup>2</sup>	0.01 $\pm$ 0.004 <sup>A</sup> (74)	0.10 $\pm$ 0.02 <sup>B</sup> (30)	0.08 $\pm$ 0.01 <sup>B</sup> (37)	0.47 $\pm$ 0.07 <sup>C</sup> (3)	0.71 $\pm$ 0.08 <sup>C</sup> (2)	
Tufted Titmouse ( <i>Baeolophus bicolor</i> ) <sup>1</sup>	0.12 $\pm$ 0.03 <sup>A</sup> (22)	0.32 $\pm$ 0.05 <sup>B</sup> (10)	0.31 $\pm$ 0.04 <sup>B</sup> (13)	0.49 $\pm$ 0.07 <sup>BC</sup> (2)	0.76 $\pm$ 0.08 <sup>C</sup> (1)	
Golden-crowned Kinglet ( <i>Regulus satrapa</i> ) <sup>3</sup>	0.12 $\pm$ 0.06 <sup>A</sup> (21)	0.25 $\pm$ 0.07 <sup>AB</sup> (14)	0.52 $\pm$ 0.11 <sup>B</sup> (7)	0.74 $\pm$ 0.21 <sup>B</sup> (1)	0.31 $\pm$ 0.08 <sup>AB</sup> (6)	
American Robin ( <i>Turdus migratorius</i> ) <sup>1</sup>	0.31 $\pm$ 0.05 <sup>A</sup> (8)	0.36 $\pm$ 0.04 <sup>A</sup> (8)	0.90 $\pm$ 0.06 <sup>B</sup> (2)	0.42 $\pm$ 0.08 <sup>A</sup> (5)	0.31 $\pm$ 0.03 <sup>A</sup> (5)	
American Tree Sparrow ( <i>Spizella arborea</i> ) <sup>4</sup>	0.58 $\pm$ 0.20 <sup>B</sup> (4)	0.04 $\pm$ 0.02 <sup>AB</sup> (47)	0.10 $\pm$ 0.08 <sup>AB</sup> (32)	0 <sup>A</sup> (92)	0 <sup>A</sup> (95)	
Field Sparrow ( <i>S. pusilla</i> ) <sup>2</sup>	4.69 $\pm$ 0.29 <sup>C</sup> (1)	1.86 $\pm$ 0.15 <sup>C</sup> (1)	0.77 $\pm$ 0.08 <sup>B</sup> (3)	0.14 $\pm$ 0.04 <sup>A</sup> (28)	0.15 $\pm$ 0.03 <sup>A</sup> (20)	
White-throated Sparrow ( <i>Zonotrichia albicollis</i> ) <sup>3</sup>	0.11 $\pm$ 0.04 <sup>A</sup> (25)	0.22 $\pm$ 0.08 <sup>AB</sup> (17)	0.55 $\pm$ 0.14 <sup>B</sup> (6)	0.44 $\pm$ 0.29 <sup>AB</sup> (4)	0.17 $\pm$ 0.08 <sup>AB</sup> (17)	
Dark-eyed Junco ( <i>Junco hyemalis</i> ) <sup>4</sup>	1.05 $\pm$ 0.45 <sup>A</sup> (2)	1.19 $\pm$ 0.70 <sup>A</sup> (2)	0.65 $\pm$ 0.27 <sup>A</sup> (5)	0.22 $\pm$ 0.14 <sup>A</sup> (20)	0.08 $\pm$ 0.03 <sup>A</sup> (36)	
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> ) <sup>2</sup>	0.16 $\pm$ 0.07 <sup>AB</sup> (17)	0.21 $\pm$ 0.07 <sup>B</sup> (20)	1.39 $\pm$ 0.22 <sup>C</sup> (1)	0.33 $\pm$ 0.09 <sup>B</sup> (9)	0.02 $\pm$ 0.01 <sup>A</sup> (54)	
Brown-headed Cowbird ( <i>Molothrus ater</i> ) <sup>1</sup>	0.55 $\pm$ 0.07 <sup>D</sup> (5)	0.46 $\pm$ 0.06 <sup>CD</sup> (3)	0.31 $\pm$ 0.04 <sup>AC</sup> (12)	0.17 $\pm$ 0.03 <sup>B</sup> (24)	0.20 $\pm$ 0.02 <sup>AB</sup> (14)	
American Goldfinch ( <i>Carduelis tristis</i> ) <sup>1</sup>	1.03 $\pm$ 0.13 <sup>C</sup> (3)	0.42 $\pm$ 0.06 <sup>B</sup> (5)	0.32 $\pm$ 0.04 <sup>B</sup> (11)	0.39 $\pm$ 0.05 <sup>B</sup> (7)	0.18 $\pm$ 0.02 <sup>A</sup> (16)	
Guilds	$B_{Fire}$	Open	Savanna	Woodland	Scrub	Forest
Ground granivore	11.2*	7.55 $\pm$ 0.55 <sup>D</sup>	4.33 $\pm$ 1.06 <sup>BCD</sup>	4.13 $\pm$ 0.59 <sup>C</sup>	1.44 $\pm$ 0.27 <sup>AB</sup>	0.76 $\pm$ 0.10 <sup>A</sup>
Canopy, understory, and bark insectivore	-7.1**	1.46 $\pm$ 0.19 <sup>A</sup>	2.34 $\pm$ 0.22 <sup>B</sup>	2.65 $\pm$ 0.18 <sup>B</sup>	3.83 $\pm$ 0.56 <sup>BC</sup>	3.95 $\pm$ 0.24 <sup>C</sup>
Ground omnivore	4.6	2.42 $\pm$ 0.38 <sup>B</sup>	1.96 $\pm$ 0.19 <sup>B</sup>	1.86 $\pm$ 0.30 <sup>B</sup>	1.86 $\pm$ 0.22 <sup>B</sup>	0.85 $\pm$ 0.06 <sup>A</sup>
Canopy and understory omnivore	8.3***	0.87 $\pm$ 0.08 <sup>A</sup>	1.33 $\pm$ 0.10 <sup>B</sup>	1.41 $\pm$ 0.08 <sup>B</sup>	1.55 $\pm$ 0.26 <sup>AB</sup>	0.98 $\pm$ 0.07 <sup>A</sup>
Aerial insectivore	2.1	0.56 $\pm$ 0.12	0.71 $\pm$ 0.12	0.72 $\pm$ 0.06	0.63 $\pm$ 0.06	0.75 $\pm$ 0.06
Canopy and understory granivore	-4.5	0.69 $\pm$ 0.11 <sup>B</sup>	0.31 $\pm$ 0.05 <sup>A</sup>	0.24 $\pm$ 0.02 <sup>A</sup>	0.28 $\pm$ 0.03 <sup>A</sup>	0.29 $\pm$ 0.02 <sup>A</sup>
Frugivore	9.8*	0.21 $\pm$ 0.06	0.36 $\pm$ 0.09	0.35 $\pm$ 0.05	0.24 $\pm$ 0.05	0.28 $\pm$ 0.04
Vermivore	22.7***	0.15 $\pm$ 0.02 <sup>A</sup>	0.18 $\pm$ 0.03 <sup>A</sup>	0.44 $\pm$ 0.05 <sup>B</sup>	0.23 $\pm$ 0.06 <sup>AB</sup>	0.16 $\pm$ 0.02 <sup>A</sup>
Ground insectivore	-15.7**	0.16 $\pm$ 0.05 <sup>AB</sup>	0.07 $\pm$ 0.02 <sup>A</sup>	0.08 $\pm$ 0.01 <sup>A</sup>	0.09 $\pm$ 0.02 <sup>A</sup>	0.29 $\pm$ 0.05 <sup>B</sup>

Notes: Superscript 1-4 refer to season of species' highest mean density: 1 = spring, 2 = breeding, 3 = fall, and 4 = winter. Superscript A-D: for each species, habitats with same superscript letter do not differ significantly (one-way ANOVA,  $P > 0.05$ ).  $B_{Fire}$  is estimated percentage change in a guild's mean-standardized density with increased Fire Frequency (e.g.,  $B_{Fire} = 11.2$  for ground granivores, which signifies an increase of 11.2% of mean ground granivore density for a 1-fire-per-15-years increase in Fire Frequency;  $B_{Fire}$  significance: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

was 0.95. Pearson  $r$  between overall raw counts and distance-based overall density was 0.80.

Regression of habitat variables on principal-curve-ordination scores of sampled points demonstrated that the density of large and small woody vegetation had the largest absolute standardized regression coefficients, 0.18 for Tree Density and 0.16 for Shrub Density (Table 2). Thus, a change of 1 SD (Fig. 1) in Tree Density or Shrub Density between sample points resulted in average changes in principal curve scores equal to 18% and 16% of the total curve length, respectively, while controlling for effects of the remaining habitat predictors. Coefficients for Tree Density were not significant in fall and winter, and the six habitat variables explained more compositional variation ( $R^2 = 0.60$ ; Table 2) among sampling points during the breeding season than in the remaining seasons. Fire Frequency was a significant predictor of community composition in each season. Low Ground Vegetation was a significant predictor in winter.

A multivariate regression tree was calculated that split the 102 sampling points into groups homogeneous in bird composition, as a function of canopy cover. Four groups were defined by the regression tree: <32%, 32–50%, 50–92%, and >92% canopy cover. These four canopy-cover classes explained 25% of the variation in bird community composition among points and were similar to the actual canopy-cover ranges used to define nonscrub habitats (<20%, 20–50%, 50–90%, >90%).

Savannas and woodlands were significantly different in species composition from open and forest habitats in all seasons except winter (Table 3). Nine guilds accounted for >98% of total density within each habitat type. However, only one guild—omnivores feeding on canopy, understory, or bark substrates—was significantly more abundant in intermediate habitats (savanna, woodland, or scrub) than in open habitat or forest (Table 1).  $B_{\text{Fire}}$  ranged from –15.7% for ground insectivores (if Fire Frequency increased by 1 fire per 15 years, it is estimated that ground-insectivore density would decrease by 15.7% of mean ground-insectivore density) to 22.7% increase for vermivores (Table 1). Judging from guilds, savannas and woodlands had higher Bray–Curtis similarity (McCune and Mefford 1999) to open habitats (open–savanna guild similarity = 0.78, open–woodland = 0.74)

than to forests (savanna–forest = 0.65 and woodland–forest = 0.67).

*Concentration of species in habitats.*—Shannon–Wiener species diversity ( $H'$ ) per point increased with increased Shrub Density and Tree Density and with increased Fire Frequency (Table 2) and was highest in forests and lowest in open habitats (Table 3). Total species richness was greatest in woodlands and savannas (Table 3). Seasonally, richness was greatest in woodlands during spring, breeding, and fall seasons and was second greatest in savannas during breeding, fall, and winter (not shown). However, differences among habitats in mean number of species per point were not significant.

Among the 129 species, the number of species that significantly increased (one-way ANOVA,  $P < 0.05$ ) in overall density compared with the number of species that significantly decreased was 10:7 from open to savanna habitats, 19:7 from open to woodland, 8:5 from scrub to savanna, 11:7 from scrub to woodland, 14:11 from forest to savanna, and 16:14 from forest to woodland. Only the Red-headed Woodpecker increased significantly from open, scrub, and forest habitats to savanna (Table 1). Four species—Red-headed Woodpecker, American Robin, Baltimore Oriole (not shown), and Red-winged Blackbird—increased significantly from open, scrub, and forest habitats to woodlands.

Among species with significant indicator values (IV) >25, the fewest species reached their highest IV in savannas and woodlands (Fig. 2). Savannas had the fewest significant indicators in each season (not shown).

*Seasonal variation in habitat use.*—The arrangement of bird communities along the principal curve generally followed the order open, savanna, woodland, scrub, forest in all seasons except winter (Table 3). For the 111 species observed in more than one season, 43 species (39%) differed by two, or more, habitats in this order (e.g., open to woodland) in the habitats in which they reached their highest mean density in different seasons.

Density of shrubs, sprouts, saplings, and small trees (Shrub Density), which was highest in scrub habitats, was the only significant predictor of density of both spring and fall transient migrants (Table 2). Transient-migrant density was significantly higher in scrub habitats than in all other habitats except woodlands during the fall migration (Fig. 3A). Densities



TABLE 2. Coefficients from multiple regression of six z-score-transformed predictors on principal-curve ordination scores and Shannon-Wiener overall diversity (*H'*), total density of transient migrants and breeding birds, and overall density of species with PIF combined score = 9–12 or 13–17, based on 102 bird survey points in northwest Indiana.

	Intercept	Low ground vegetation		High ground vegetation	Shrub density	Tree density	Dead tree density	Fire frequency	<i>R</i> <sup>2</sup> (adjusted)
		vegetation	vegetation	vegetation					
Regression on ordination scores:									
Overall	0.42***	0.001	-0.02	-0.16***	-0.18***	-0.05*	-0.09***	0.49	
Spring	0.45***	-0.02	-0.03	-0.13***	-0.14***	-0.05	-0.06*	0.38	
Breeding	0.52***	0.01	-0.03	-0.16***	-0.15***	-0.03	-0.05*	0.60	
Fall	0.29***	0.04	0.02	-0.13***	0.01	-0.07**	-0.09***	0.30	
Winter	0.54***	0.05*	0.01	0.09***	0.04	0.03	-0.05*	0.31	
Response:									
<i>H'</i>	3.01***	0.03	-0.02	0.11**	0.14***	0.06	0.10**	0.35	
Spring migrants (ln)	1.50***	-0.13	0.11	0.22*	0.02	0.16	0.25**	0.18	
Fall migrants (ln)	1.66***	0.21	-0.20*	0.38***	0.05	-0.14	0.09	0.10	
Breeding birds	12.36***	1.49**	-1.38**	-0.57	-0.27	-0.59	-0.26	0.28	
PIF combined score 9–12	4.61***	0.20	0.01	-0.56*	-0.87***	-0.21	-0.63**	0.35	
PIF combined score 13–17	0.47***	-0.03	-0.10	-0.14*	-0.08	0.04	0.26***	0.31	

Significance of coefficients based on *t*-test. \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001. All regressions, except fall migrants, were significant at *P* < 0.001 (*F* ratio). Regression for fall migrants was significant at *P* < 0.05. *R*<sup>2</sup> for regression on ordination scores represents the percentage of species variation explained by the habitat variables.

TABLE 3. Ordination scores (mean principal-curve ordination scores [ $\pm$  SE]) by habitat type and season for 102 bird survey points in northwest Indiana, and diversity (total and per-point species richness and diversity [ $H'$ ]) by habitat type.

	Open	Savanna	Woodland	Scrub	Forest
<b>Ordination scores</b>					
Overall <sup>a</sup>	0.91 $\pm$ 0.01 <sup>E</sup>	0.58 $\pm$ 0.07 <sup>D</sup>	0.43 $\pm$ 0.04 <sup>C</sup>	0.22 $\pm$ 0.04 <sup>B</sup>	0.08 $\pm$ 0.01 <sup>A</sup>
Spring <sup>a</sup>	0.89 $\pm$ 0.02 <sup>E</sup>	0.57 $\pm$ 0.07 <sup>D</sup>	0.45 $\pm$ 0.05 <sup>C</sup>	0.28 $\pm$ 0.04 <sup>B</sup>	0.17 $\pm$ 0.02 <sup>A</sup>
Breeding <sup>a</sup>	0.90 $\pm$ 0.03 <sup>E</sup>	0.73 $\pm$ 0.05 <sup>D</sup>	0.55 $\pm$ 0.04 <sup>C</sup>	0.31 $\pm$ 0.05 <sup>B</sup>	0.20 $\pm$ 0.03 <sup>A</sup>
Fall <sup>a</sup>	0.59 $\pm$ 0.05 <sup>D</sup>	0.36 $\pm$ 0.07 <sup>C</sup>	0.25 $\pm$ 0.03 <sup>BC</sup>	0.19 $\pm$ 0.04 <sup>B</sup>	0.21 $\pm$ 0.04 <sup>A</sup>
Winter <sup>a</sup>	0.57 $\pm$ 0.06 <sup>B</sup>	0.50 $\pm$ 0.05 <sup>B</sup>	0.53 $\pm$ 0.04 <sup>B</sup>	0.33 $\pm$ 0.04 <sup>AB</sup>	0.34 $\pm$ 0.02 <sup>A</sup>
<b>Diversity</b>					
Total richness	96	99	109	91	94
Per-point richness <sup>b</sup>	38.9 $\pm$ 1.5	41.6 $\pm$ 1.3	42.2 $\pm$ 1.1	40.7 $\pm$ 1.5	40.3 $\pm$ 0.7
$H'$ <sup>b</sup>	2.53 $\pm$ 0.05 <sup>A</sup>	2.96 $\pm$ 0.08 <sup>B</sup>	3.01 $\pm$ 0.06 <sup>B</sup>	3.20 $\pm$ 0.05 <sup>BC</sup>	3.23 $\pm$ 0.02 <sup>C</sup>

<sup>a</sup>Within a season, habitats with the same superscript uppercase letter do not differ significantly in species composition, based on analysis of similarity (ANOSIM [Clarke and Gorley 2001],  $P > 0.05$  with Holm's adjustment for multiple comparisons [Legendre and Legendre 1998]).

<sup>b</sup>Habitats with same superscript letter do not differ significantly ( $P > 0.05$ ) on the basis of one-way ANOVA. No significant differences for per-point richness.

of year-round residents and of all species during the breeding season were highest in open habitats and lowest in scrub and forest habitats. Despite this, density of transient migrants was low in open habitats in both spring and fall.

*Predictors of risk of species extirpation.*—Density of species at the greatest risk of extirpation in this study (PIF combined score 13–17) was significantly higher in woodland and savanna habitats than in remaining habitats (Fig. 3B). Density of species at moderate risk of extirpation (PIF combined score 9–12) was highest in open habitats and second highest in savanna habitats. Fire Frequency was the strongest predictor (highest absolute standardized regression coefficient) of PIF combined score 13–17 density (Table 2). Total density of these highest-risk species increased as Fire Frequency increased. Shrub Density, Tree Density, and Fire Frequency were all significantly, negatively related to density of PIF combined score 9–12 species.

## DISCUSSION

*Distinctiveness of savannas and woodlands as avian habitats.*—Among communities arrayed along an environmental or ecological gradient, ecotonal communities are often species-rich, inhabited by few specialists, and intermediate in composition compared with communities at the gradient extremes (Temple 1998). Along a gradient of woody vegetation density, we asked

whether savanna and woodland bird communities might best be described as ecotonal or as distinctive in composition. As would be expected for an ecotone, total species richness was higher in savannas and woodlands than in open or forest habitats. Several species had consistent concentration in savannas or woodlands, as summarized by indicator values, but, as we would expect if savannas and woodlands were ecotonal, more species had significant, and generally higher, indicator values for open or forest habitats. Only one guild, omnivores feeding in trees and shrubs, was significantly more abundant in savannas and woodlands than in open and forest habitats. Otherwise, on the basis of guild densities, savannas and woodlands were generally intermediate in composition between open habitats and forests or were not significantly different. On the basis of a biogeographic analysis, Temple (1998) concluded that midwestern oak savannas were likely ecotonal habitats rather than distinct biomes for most vertebrate species. Although savanna and woodland bird communities were generally significantly different in total species composition from open and forest bird communities, (1) high species richness, (2) intermediate composition, (3) intermediate location along the ecological gradient that explains much of the variation in community composition, (4) scarcity of avian specialists, and (5) few species or guilds having significantly highest density in savannas or

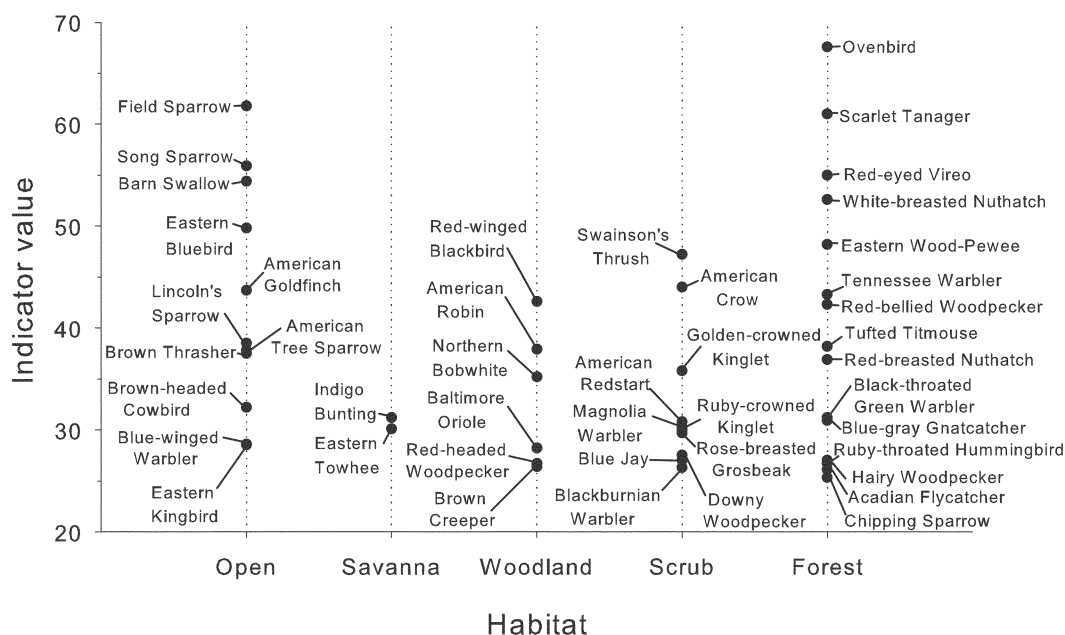


FIG. 2. Significant highest indicator values > 25 by habitat type for bird species at 102 survey points along an open-forest gradient in northwest Indiana. Scientific names of species not given in the text or in Table 2: Song Sparrow (*Melospiza melodia*), Barn Swallow (*Hirundo rustica*), Eastern Bluebird (*Sialia sialis*), Lincoln's Sparrow (*M. lincolni*), Brown Thrasher (*Toxostoma rufum*), Blue-winged Warbler (*Vermivora pinus*), Eastern Kingbird (*Tyrannus tyrannus*), Swainson's Thrush (*Catharus ustulatus*), American Crow (*Corvus brachyrhynchos*), American Redstart (*Setophaga ruticilla*), Magnolia Warbler (*Dendroica magnolia*), Ruby-crowned Kinglet (*Regulus calendula*), Downy Woodpecker (*Picoides pubescens*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Blackburnian Warbler (*D. fusca*), Blue Jay (*Cyanocitta cristata*), Scarlet Tanager (*Piranga olivacea*), White-breasted Nuthatch (*Sitta carolinensis*), Tennessee Warbler (*V. peregrina*), Red-bellied Woodpecker (*Melanerpes carolinus*), Red-breasted Nuthatch (*S. canadensis*), Black-throated Green Warbler (*D. virens*), Blue-gray Gnatcatcher (*Poliptila caerulea*), Ruby-throated Hummingbird (*Archilochus colubris*), Hairy Woodpecker (*Picoides villosus*), Acadian Flycatcher (*Empidonax vireescens*), Chipping Sparrow (*Spizella passerina*).

woodlands all suggest that savannas and woodlands, as they exist today, can reasonably be called ecotonal in northwest Indiana.

The relative lack of savanna or woodland specialists implies that even bird species abundant in savannas and woodlands often have other significant habitat associations. It has been suggested that the Red-headed Woodpecker may be one species sufficiently associated with savannas today to be considered a savanna specialist (Brawn 2006). In northwest Indiana, it was the only species significantly more abundant in savannas than in open, scrub, and forest habitats and one of only four species significantly more abundant in woodlands than in open habitat, scrub, and forest. Nonetheless, it was only a weak indicator

of savannas or woodlands, meaning that none of the five habitat definitions matched Red-headed Woodpecker habitat-use patterns closely. Indigo Buntings (*Passerina cyanea*) and Eastern Towhees (*Pipilo erythrophthalmus*), the only two significant savanna-indicators, are omnivorous ground- and shrub-foragers and nest in the shrub layer, which is not always present in savannas (Payne 1992, Greenlaw 1996). Thus, these two savanna indicators will likely be less abundant in savannas that lack the shrub layer, which suggests an important role for the shrub layer in enhancing avian diversity in savannas (Brawn 2006). The significant woodland-indicator species were divided between tree-foragers (Baltimore Oriole, Red-headed Woodpecker, and Brown

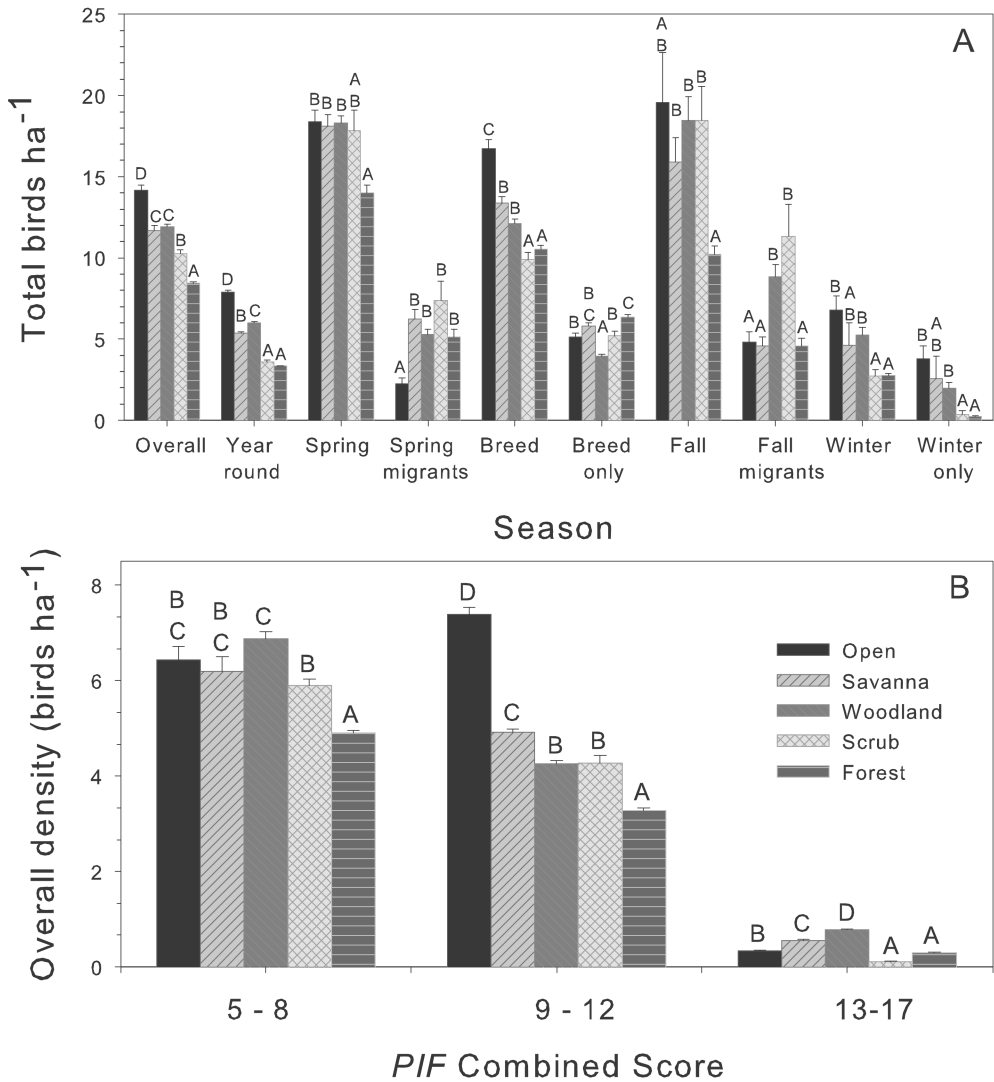


FIG. 3. (A) Mean ( $\pm$ SE) total density of birds by habitat, season, and migration status for 102 bird survey points along open-forest gradient in northwest Indiana. Spring and fall migrants are transient migrants. (B) Overall density of birds ( $\pm$ SE) as a function of species' risk of extirpation (PIF combined score) and habitat type. For both graphs, within a category, habitats with same superscript letter do not differ significantly (one-way ANOVA,  $P > 0.05$ ).

Creepers [*Certhia americana*] and ground-foragers (Red-winged Blackbird, American Robin, and Northern Bobwhite [*Colinus virginianus*]). Savannas and woodlands are often characterized as combining vegetation elements of grasslands and forests, and the significant woodland indicators represented both of these components. Overall, however, the avian guild composition of savannas and woodlands was more similar to

that found in open habitat, which suggests that birds used savannas and woodlands more as grasslands with occasional trees than as forests with frequent canopy gaps. Studies that compare bird assemblages in midwestern savannas to assemblages in nearby forests (Davis et al. 2000, Brawn 2006) may, therefore, be more likely to find significant differences in substrates and food types used by birds than if savannas were

compared to grasslands. Plant community succession with fire suppression often proceeds from very open habitats to forests, so we would expect the greatest changes in bird-community guild structure to occur during the latter stages of this successional process as savannas are converted to forests.

Whether to divide species assemblages occurring along ecological gradients into communities is a primary ecological question that is more often considered for plant communities (Clements 1936, Gleason 1939) than for animal communities (Temple 1998). The five habitats defined by vegetation in the present study—open habitats with low canopy cover, savannas, woodlands, scrublands, and forests—are commonly recognized in studies of plant communities (Anderson 1998) and in setting goals for plant community restoration (Packard 1997) along the open-forest gradient. The canopy cover ranges often used to define these plant communities were similar to ranges that maximized differences in bird community composition. Therefore, managing open, savanna, woodland, and forest habitats as distinct plant communities based on canopy cover will also tend to maximize differences in resulting bird communities. Increased distinctiveness is a community-level characteristic that can improve the efficiency of conservation efforts by decreasing overlap among communities. The MRT analysis suggested that this minimization of overlap could be achieved by managing the landscape to include sites within each of four canopy-cover ranges: 0–32%, 32–50%, 50–92%, and >92%.

Although density of large woody vegetation, the chief determinant of canopy cover, was a significant predictor of overall avian community composition, that relationship varied by season. Habitat suitability is often determined from bird–habitat relationships during the breeding season, when large woody vegetation was a significant predictor of community composition. However, by late fall and winter, after trees lost their foliage, Tree Density was no longer a significant predictor of community composition; cover of low ground vegetation, which includes seed-bearing herbaceous vegetation, an important winter food source, became a significant predictor of avian community composition; and distinctiveness of avian composition among the five habitats decreased. Therefore, the extent to which savanna and woodland bird

communities are distinctive within the open-forest gradient varied by season, and habitat characteristics other than canopy cover or tree density must be considered in differentiating avian communities in different seasons.

*Conservation value of habitats along the open-forest gradient for birds.*—Conservation value of habitats along the open-forest gradient can be assessed by avian community characteristics including species diversity, bird abundance, and status of threatened species. Prescribed burning is used to maintain and restore non-forest habitats, including savannas, along this gradient (Peterson and Reich 2001) and is, therefore, a primary tool for manipulating conservation value. Frequency of fires was a significant predictor of avian community composition in each season and was a significant predictor of overall density of six of nine guilds. The largest percentage of increase in guild density associated with increased fire frequency was in the density of vermivores, a guild whose density was dominated by American Robins, one of the most common North American species (Rich et al. 2004). The largest decrease associated with fire was in density of ground insectivores, a guild whose members (e.g., Ovenbird [*Seiurus aurocapilla*]) generally forage in the litter and, therefore, would be negatively affected by frequent fires. However, fire could have differential effects on avian density within a substrate. While ground-insectivore density decreased, ground-granivore density increased with increased fire frequency, likely because fire can stimulate growth of herbaceous vegetation, leading to increased availability of food for ground granivores.

Given the diverse ways in which fire affected community composition, it is to be expected that fire will have positive and negative effects on conservation value of habitats. Fire frequency, which was highest in savannas and woodlands, was positively related to potential goals of avian conservation management, including increased species diversity, increased spring-transient migrant density, and increased density of the most threatened species. However, fire frequency was not significantly related to total density of birds during the breeding season and was negatively related to density of moderately threatened species. Therefore, a tradeoff exists, in that frequent fires will tend to promote more threatened species at the expense of more



abundant but somewhat less threatened species. In comparison, conversions of forests to savannas in other parts of the Midwest through increased fire frequency have also resulted in increased species richness and increased abundance of some declining species (Davis et al. 2000, Brawn 2006), whereas, in Madagascar, species richness and conservation value were lower in savannas than in unburned forests (Pons and Wendenburg 2005).

Avian demography can be as greatly affected by events occurring during migration as by those during the breeding season (Silllett and Holmes 2002). Because of its position at the southern end of Lake Michigan, northwest Indiana is a migration stopover for many species (Brock 1997, Brawn and Stotz 2001, Cochran et al. 2004). Density of small woody vegetation, which was highest in scrub habitat, was a positive predictor of transient-migrant density, and during both migrations, transient-migrant density was highest in scrub habitat. In the fall, transient-migrant density was significantly higher in scrublands and woodlands than in the remaining habitats. Thus, along the gradient, scrublands may be especially important habitat for migrants. These scrublands often arise when oaks resprout from rootstocks of mature oaks following intense tree-killing fires and are often considered restoration way-stations, which possibly undervalues the importance of such disturbance-dependent habitats for migrating birds (Brawn et al. 2001, Rodewald and Brittingham 2004).

Cross-season habitat-use patterns of birds are varied. Some species use significantly different habitats for breeding, for migratory stopovers, and for overwintering, whereas other species use similar habitats in all seasons (Petit 2000). In northwest Indiana, ~39% of species changed habitat use among seasons by two or more habitats along the open-forest gradient—for example, reaching their highest density in open habitats in one season and in woodlands in another season. This emphasizes the potential usefulness of habitat diversity in meeting the year-round needs of birds in areas such as northwest Indiana, where combinations of soil, fire, topography, and climate historically produced a range of successional habitats in a small area (Cowles 1899). Indeed, each habitat in this study had characteristics that might be beneficial for conservation. Open habitats had

high bird densities in all seasons, especially of moderately threatened species, year-round residents, and breeding and overwintering species, and had relatively many specialist species. Savannas and woodlands were ecotonal and, by virtue of combining characteristics of other habitats, were visited by more species and had the highest total density of the most threatened species. In every comparison between species' densities in savannas or woodlands and species' densities in open, scrub, or forest habitats, more species had significantly higher density in savannas or woodlands than in the other habitats. Scrublands had the highest total density of transient migrants. Forests had the highest overall species diversity and the most species with significant high indicator values, which suggests that more species along the woody-vegetation gradient might be considered forest specialists. Given these significant benefits associated with each habitat type, a strong argument can be made for the desirability of combining these five habitat types in local landscapes. Nonetheless, the benefits of such local habitat diversity must be balanced against the knowledge that grasslands and savannas in the Midwest have sustained losses greater than nearly any other terrestrial ecosystem in the United States, which increases the relative value of these habitats in restorations of midwestern landscapes (Nuzzo 1986, Reinking 2005).

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