RESEARCH ARTICLE

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Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient

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ABSTRACT: There is limited understanding of the influence of fire and vegetation structure on bird communities in dry oak (*Quercus* spp.) savannas of the Upper Midwest and whether bird communities in restored savanna habitats are similar to those in remnant savannas. During the 2001 and 2002 breeding seasons, we examined the relationship between bird communities and environmental variables, including vegetation characteristics and site prescribed-burn frequencies, across a habitat gradient in dry oak savannas in central Minnesota. The habitat gradient we studied went from: (1) prairie to (2) remnant oak savanna to (3) oak woodland undergoing savanna restoration via fire or mechanical removal of woody vegetation to (4) oak woodland. We conducted fixed-radius point counts (n = 120) within habitats with either prairie groundcover or predominately oak canopy. We described canopy and groundcover characteristics at a sub-sample (n = 28) of non-prairie points, and collected canopy and woody species richness data and prescribed-burn frequencies over the past 20 years for all points. Observed bird communities were most strongly correlated with canopy cover and burn frequency and, to a lesser extent, attributes of the shrub component. Most savanna points had bird communities that were distinct from those found at oak woodland or oak woodland points undergoing restoration via burning. Savanna points similar to oak woodland points were in areas managed by periodic cutting rather than burning. Remnant savanna bird communities were more strongly associated with prescribed burning than those in other habitat types, but it appeared that most oak woodlands that had undergone ≥ 20 years of prescribed burning remained ecologically distinct from remnant savannas. This suggests that some savannas that have converted to oak woodlands may exist in an alternative, or stable, ecological state even following extended restoration efforts.

Index terms: alternative stable states, bird communities, fire, habitat restoration, oak savanna

INTRODUCTION

Oak (*Quercus* spp.) savanna was once common and widespread in the Upper Midwest, but is now one of the rarest vegetative communities (Curtis 1959; Packard 1993; Anderson 1998), extending over approximately 0.02% of its pre-Euro-American-settlement distribution (Nuzzo 1986). Savannas began to disappear after settlement in the mid- to late-1800s, and fire suppression in prairies and savannas resulted in some areas becoming overgrown by woody species such as American hazel (*Corylus americana* Walt.), smooth sumac (*Rhus glabra* L.), American elm (*Ulmus americana* L.), and choke cherry (*Prunus virginiana* L.) (White 1986; Davis et al. 1997; Bowles and McBride 1998), which in turn shaded out herbaceous groundcover. Oak savannas have been further fragmented by conversion for agriculture and grazing and by residential and commercial development (Bronny 1989; Bowles and McBride 1998).

In Minnesota, oak savanna is generally characterized by an open canopy with primarily bur oak (*Quercus macrocarpa* Michx.), pin oak (*Q. ellipsoidalis* Hill), or red oak (*Q. rubra* L.) overstory and grass or forb-dominated understory (McAndrews 1966; Davis et al. 1997; Peterson 1998; Leach and Givnish 1999; Will-Wolf and Stearns 1999). In dry oak savannas, unlike the more widespread mesic savannas, shrubby vegetation is often interspersed with prairie species in the understory (Will-Wolf and Stearns 1998).

The loss of oak savannas and other disturbance-mediated habitats (e.g., prairie) has had important implications for birds and other wildlife. Changes in habitat structure and foraging opportunities influence survival and reproduction through impacts on habitat selection and niche segregation (Cody 1985). In a study of North American Breeding Bird Survey (BBS) trends from 1966-1998, Brawn et al. (2001) found that a greater proportion of bird species found in open habitats (grassland, shrub-scrub, and savanna) experienced significant decreases in abundance than those associated with forested habitats. Forty percent of species associated with disturbance-mediated habitats declined significantly, while only 17% increased. Many of the species more closely associated with open habitats (lower percentages of canopy cover) and moderate-to-high burn frequencies have been declining throughout the Upper Midwest, including red-headed woodpeckers (*Melanerpus erythrocephalus* L.), field sparrows (*Spizella pusilla* Wilson), eastern kingbirds (*Tyrannus tyrannus* L.), eastern towhees (*Pipilo erythrophthalmus* L.), and golden-winged warblers (*Vermivora* *chrysoptera* L.) (Sauer et al. 2003). Davis et al. (2000) found that as oak woodlands were restored to savanna under various burn regimes, there was a shift in bird species composition and feeding guilds found along the restoration gradient. In that study, nine of the 20 species that were associated with frequently burned restoration sites declined in abundance in the Upper Midwest over the previous 35 years. More recently, Brawn (2006) found that 11 of 13 bird species breeding in both oak savanna and oak forest habitats experienced higher nesting success in oak savannas. Woodland habitats undergoing savanna restoration, therefore, may provide important new habitat for some declining species (Davis et al. 2000).

Restoration approaches in oak savannas in the Upper Midwest include mechanical or chemical intervention, reintroduction of natural disturbance processes, or some combination of these approaches. Many restoration efforts, such as some conducted at our study sites, focus primarily on using prescribed fire as a means of restoring oak savannas. This approach assumes that the return of disturbance and successional processes will lead to a return to historical (i.e., oak savanna) conditions (Suding et al. 2004). Whether these restoration approaches result in habitat conditions that approximate historical oak savannas remains unknown.

To assess the influence of restoration on bird communities and the relationships between bird community structure and habitat condition in Upper Midwest oak savannas, we expanded on the work of Davis et al. (2000) and examined the influence of vegetative characteristics and prescribed burn regimes on bird communities along a gradient from prairie to oak woodland. We studied three aspects of bird communities across this gradient: (1) presence of individual species, (2) abundance of species present, and (3) foraging strategies employed by bird species using different habitats (hereafter, feeding guilds). We included analysis of species presence, independent of abundance, to dampen the effects of common or highly detectable species, and analyzed feeding guilds to assess the impact of vegetation structure and burn frequency on niche segregation.

Because scale of study is important in understanding ecological relationships (Pearman 2002), we examined how these three aspects of bird community structure were related to environmental variables at both the local level (i.e., within approximately 100 m or less from where birds were detected) and patch level (i.e., within the larger habitat block where birds were detected). We examined: (1) how bird community structure was related to local vegetation characteristics (i.e., percent canopy cover, tree density, snag density, groundcover characteristics, and tree and shrub species richness); (2) how bird community structure was related to patch-level vegetation characteristics (i.e., percent canopy cover, canopy species richness, and shrub species richness); and (3) the influence of prescribed-burn frequency on bird community structure.

STUDY AREA

We conducted our study in east-central Minnesota on the Anoka Sandplain, a series of sand dunes laid down over glacial till approximately 5000 to 8000 years before present (Wovcha et al. 1995). At the time of Euro-American settlement, this region was dominated by scrubby oak woodlands with scattered oak barrens and openings and interspersed with marshes and swamps, prairies, and forests (Wovcha et al. 1995). Since then, logging, agriculture, and urbanization have altered the original landscape, resulting in a landscape that by the mid-1980s was dominated by cleared farmland (e.g., pastures) and land in agricultural production interspersed with remnant patches of native habitats. We conducted bird surveys and vegetation assessment on four study sites in Sherburne, Isanti, and Anoka Counties: Sherburne National Wildlife Refuge ('SNWR' – 12,424 ha), Sand Dunes States Forest (including Uncas Dunes Scientific and Natural Area; 'SDSF' – 4330 ha), Cedar Creek Natural History Area ('CCNHA' – 2200 ha), and Helen Allison Savanna (35 ha) (Figure 1). All four study sites were located on the Anoka Sandplain, and were embedded in the same landscape matrix.

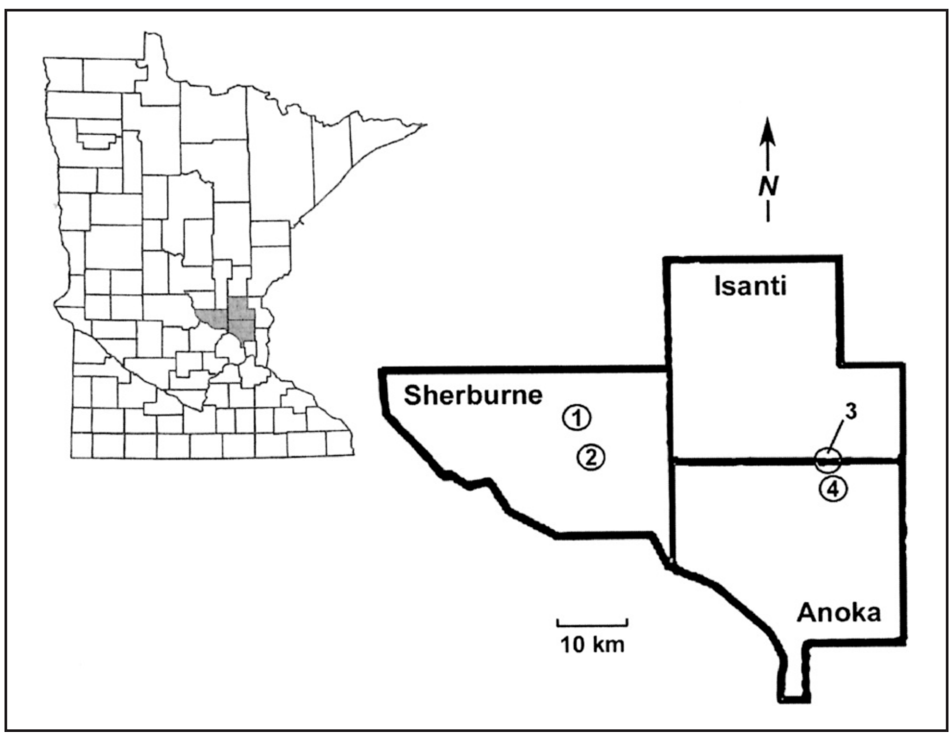

Figure 1. Location of the study sites in east-central Minnesota. Anoka, Isanti, and Sherburne Counties are located north of the Minneapolis-St. Paul metropolitan area. The numbered circles indicate study sites: (1) Sherburne National Wildlife Refuge; (2) Sand Dunes State Forest; (3) Cedar Creek Natural History Area; (4) Helen Allison Savanna.

Sherburne National Wildlife Refuge and SDSF are comprised largely of prairie, marsh, willow (*Salix* spp.) swamp, and wet meadow interspersed with oak woodland and dry oak savanna (Wovcha et al. 1995; Sundseth 1996) and both include areas of pine (*Pinus* spp.) plantation. Cedar Creek Natural History Area encompassed a large variety of plant communities including prairie, maple-basswood (*Acer* spp.-*Tilia americana)* forest, oak woodland, pine plantation, marsh, and bogs (Haarstad and Delaney 1998). Helen Allison Savanna primarily was comprised of dry oak savanna, with some areas of marsh and wet meadow (Faber-Langendoen and Davis 1995). Most remnant savannas and savanna restoration areas on the study sites were managed with prescribed burns alone or in combination with mechanical or chemical treatments. Up to and including the study period, the savannas and restoration sites at Sand Dunes State Forest were managed exclusively through cutting.

METHODS

We digitized aerial photographs of the four study sites into Geographic Information System (GIS) files to select survey plots. Based on aerial photographs, we identified upland habitats with either prairie groundcover or predominately oak canopy within each study site. We further stratified these upland habitats into four habitat types as follows: (1) prairie (< 5% canopy cover and prairie groundcover); (2) remnant oak savanna [(hereafter savanna), 5-65% canopy cover with no known record of succession to oak woodland]; (3) intact oak woodland [(hereafter oak woodland), > 65% canopy cover and ≤ 1 prescribed burn during 1982-2001]; and (4) burned oak woodland [(hereafter burned woodland), areas that had succeeded to oak woodland and were currently undergoing restoration to savanna via prescribed burns] (U.S. Fish and Wildlife Service, unpubl. data). On the SDSF, savanna management efforts excluded fire and consisted solely of mechanical removal of woody vegetation – we categorized these habitats as savannas, based on vegetation structure, but identified them separately in interpreting our results. We created polygons of each patch of these habitat types buffered to 100 m and randomly selected survey points from grids laid over polygons with core radii > 100 m in every direction. Survey points were ≥ 200 m apart.

Bird Communities

We conducted 100-m fixed-radius point counts largely following the protocol used by the U.S. Fish and Wildlife Service (USFWS) in Region 3 (Upper Midwest), which was adapted from the field method handbook of Ralph et al. (1993). The protocol also considered the recommendations of Drapeau et al. (1999) regarding length and temporal spacing of repeated counts. Observers recorded species detections by sight and call for 10 minutes during each count. We assumed that multiple calls from the same species were from one individual unless calls were simultaneous, near simultaneous, and opposing, or if otherwise confirmed visually. We conducted surveys between 0400 and 1000 CST from 23 May to 1 July. In hot weather (generally ≥ 29˚C), we completed surveys by 0900 CST and we repeated surveys at each point ≥ 5 days apart.

We conducted point counts within prairies, oak savannas, and burned and intact oak woodlands. In 2001, we conducted counts at 100 points within SNWR and Sand Dunes State Forest. In 2002, we discarded one oak woodland and one burned woodland point surveyed in 2001 because of inaccessibility and one prairie point because of conversion to pine plantation. We added 16 points at CCNHA and three at Helen Allison Savanna, for a total of 116 points in 2002. We visited each point twice per year and visited 97 points a total of four times over two years, and visited 22 points twice (Table 1).

We collected data on bird species presence and abundance, and assigned species to feeding guilds following DeGraaf et al. (1985). We defined abundance as the average maximum number of detections of each species at each point over the two years of the study. We based guilds on three components: (1) seasonal foraging techniques, (2) substrate, and (3) food types. We assigned species that fell into > 1 category of ≥ 1 guild components (e.g., food type – insectivore and frugivore) to a combined guild representing all feeding habits used during the breeding season (Davis et al. 2000; Table 2). The number and identity of foraging guilds is likely related to both vegetation structure and food availability, and we included analysis of the distribution of guilds across this habitat gradient to indirectly assess the potential influence of food availability and distribution on bird community structure.

Vegetation Characteristics and Burn Data

To assess relationships between vegetative structure and composition, we collected detailed vegetation data at 28 randomly selected non-prairie point count locations. We adapted data collection techniques from the Breeding Biology Research and Monitoring Database (BBIRD) protocol (Martin et al. 1997) and collected vegeta-

Table 1. Number of points and mean, SE, and 95% CI of reciprocal averaging axis-1 scores for bird abundances in prairie, savanna, burned woodland, and oak woodland on the Anoka Sandplain in east-central Minnesota. Bird community data at 116 survey points were collected during May-July 2002.

				Bounds of 95% CI	
Habitat type	*n*	$\bar{x}$	SE	Lower	Upper
Prairie	32	266.80	18.58	228.90	304.70
Savanna	30	-31.70	7.05	-46.10	-17.30
Burned woodland	28	-81.21	5.59	-92.70	-69.70
Oak woodland	26	-95.97	3.44	-103.00	-88.90

Table 2. Feeding guilds[a] detected at 86 survey points in remnant savannas, burned woodlands, and oak woodlands on 4 study sites on the Anoka Sandplain in east-central Minnesota. All birds were assigned to guilds following DeGraaf et al. (1985). The first column includes only 1 species that falls into the guild represented by each row; most guilds include multiple species. When > 1 types of ≥1 components of feeding guilds applied to a given species, the components were combined similar to Davis et al. (2000). Surveys were conducted May-July 2001 and 2002.

	Guild component		
Representative species	Food type	Substrate	Technique
Eastern towhee	O[a]	G	F
Brown thrasher	O	LCG	F
American redstart	I	LCA	GS
American robin	VO	GLC	GF
Baltimore oriole	O	UC	F
Blue jay	O	UCG	F
Downy woodpecker	I	B	G
House wren	I	LC	G
Blue-gray gnatcatcher	I	UC	G
Cedar waxwing	IF	UCA	GS
Downy woodpecker	IF	LCB	G
Eastern bluebird	IF	LCG	G
Eastern kingbird	I	A	S
Indigo bunting	O	LC	F
Mourning dove	G	G	G
Mourning warbler	I	G	G
Ovenbird	MI	G	G
Pileated woodpecker	I	B	E
Red-headed woodpecker	I	BA	GS
Red-shouldered hawk	C	G	H

[a] Key to abbreviations of guild components—*Food type:* O–omnivore; I–insectivore; V–vermivore; F–frugivore; G–granivore; C–carnivore; *Substrate:* LC–lower canopy; G–ground; A–air; UC–upper canopy; B–bark; *Technique:* F–forager; G–gleaner; S–sallier; E–excavator; H–hawker.

tion data at two 11.3-m radius plots at each location – one centered at the point count location, and the second centered 40 m east of that point. Within the 11.3-m radius plots, we recorded all species and diameter at breast height (dbh) of trees > 8 cm dbh, number of snags, and average canopy cover. Within a 5-m radius plot centered inside each 11.3-m radius plot, we recorded average percent cover of shrubs, brush (standing dead shrubs and brambles), grass/herbs, bare ground, fallen logs and woody debris, moss and ferns, and average shrub and brush heights. We also recorded woody species richness and percent canopy cover at all 119 point count locations. We measured percent cover, vegetation size and structure, and woody species richness because they may be directly related to the diversity of foraging and sheltering niches available to birds. We excluded prairie points from vegetation assessment because the values for most measured vegetation characteristics at prairie sites would be low or zero based upon the methodology used for identifying study areas and stratifying habitat types.

To derive patch-level environmental variables, we used data from multiple points within GIS habitat polygons created during the process of selecting survey locations. We derived estimates of patch-level variables opportunistically when multiple bird survey points were selected within a polygon. We averaged percent canopy cover and pooled tree and shrub species richness data from multiple points (≥ 2) within a habitat polygon to derive a composite measure of these variables for each patch.

From records kept by land managers, we determined the timing and locations of prescribed burns at each of our study sites since 1982. Through the time of the study, savannas in Sand Dunes State Forest were managed using periodic cutting rather than fire, so we assigned these points 0 burns since 1982. We calculated burn frequencies (number burns/yr) for each point and each patch over the period 1982-2001.

Data Analysis

We present descriptive statistics [e.g., means and standard error (SE)] to summarize habitat variables and compare characteristics of vegetation across habitat types using 1-way analysis of variance (ANOVA) and 95% confidence intervals (CI). To assess relationships between habitat variables, we used Pearson product-moment correlation. All parametric statistics were derived using JMP IN 4.0.4 (SAS Institute, Inc., Cary, North Carolina: use of trade names does not imply endorsement by either the U.S. Geological Survey or the University of Minnesota).

We used gradient analysis to relate species assemblages to various environmental factors (e.g., Blair 1996; De'ath 1999; Badgley and Fox 2000) and to elucidate relationships between individual bird species and habitat variables (e.g., James 1971). We screened all bird abundance data for obvious inconsistencies and unexplainable outliers and discarded highly improbable observations (e.g., recorded sighting of a lazuli bunting [*Passerina amoena* Say] was likely a misidentification of an indigo bunting [*Passerina cyanea* L.]). We excluded species detected at < 4 points from ordinations and statistical analysis because of small sample sizes.

We used canonical correspondence analysis (CCA), reciprocal averaging (RA), and simple linear regression to identify the environmental variables that best explained bird community structure. We conducted gradient analysis using environmental characteristics within the point-count radius and as pooled or averaged within the larger habitat patch. We performed RA on 2002 point count data from 23 savanna, burned woodland, and oak woodland points for which we also collected point-specific vegetation data. We included axis-1 RA scores for those points in simple linear regressions against environmental variables to determine which variables were associated ($P \leq 0.10$) with observed bird community patterns. We excluded environmental variables with low (≤ 5%) average cover values. When environmental variables were highly correlated ($|r| \geq 0.7$), we included the variable with the smaller *P*-value in regression analyses. We used results of simple linear regressions as a basis for CCAs at these two scales incorporating both environmental and bird community variables.

At the point level, we used CCA to relate percent canopy cover and bare ground, canopy and shrub species richness, tree density, shrub height, and burn frequency at 28 points where we measured these characteristics to presence and abundance of each bird species and feeding guilds detected at those points. At the patch level, we assessed the relationships between species presence, bird abundance, and feeding guilds from 86 points within 31 patches (9 savanna, 11 burned woodland, and 11 oak woodland) and burn frequency, average percent canopy cover, and total canopy and shrub species richness for those patches. We subjected all CCAs to 100 randomized runs of Monte Carlo tests of no linear relationship between matrices of bird communities and environmental variables (McCune and Grace 2002). We used time of day as the random number seed.

We used PC-Ord, Version 4.25 (McCune and Mefford 1999) for all gradient analyses. In the CCAs, we standardized row and column scores by centering and normalizing, in which site scores were rescaled to a mean of 0 and variance 1. We scaled ordination scores to optimize columns, which were bird species in the main matrix. In this approach, distances between species (or guild) scores approximate chi-square distances and, when environmental variables are included, allow direct spatial interpretation of relationships between the two (McCune and Mefford 1999).

RESULTS

Bird Communities

We detected 78 species within 100 m of survey locations during point counts – 69 species in 2001 and 77 species in 2002. We detected 54 species and 20 feeding guilds at > 4 points (Table 2). When we combined data from 2001 and 2002, the most commonly detected species in prairies were grasshopper sparrows (*Ammodramus savannarum* Gmelin), eastern meadowlarks (*Sturnella magna* L.), and field sparrows. In savannas, eastern towhees, field sparrows, and blue jays (*Cyanocitta cristata* L.) were the most frequently detected species, and in burned woodlands, red-eyed vireos (*Vireo olivaceous* L.), eastern wood-pewees (*Contopus virens* L.), and chestnut-sided warblers (*Dendroica pensylvanica* L.) were detected most frequently. In oak woodland, the species we detected most frequently were red-eyed vireos, ovenbirds (*Seiurus aurocapillus* L.), and eastern wood-pewees.

We detected the fewest bird species in prairies (*n* = 45) and the most in savannas (*n* = 64). Nine species, including four sparrow species, were found exclusively in prairies; we detected only three species exclusively in savannas.

Vegetation Characteristics and Burn Data

At the 28 non-prairie locations where we measured vegetation, average canopy cover ranged from 34.8 ± 7.2% ($\bar{x}$ ± SE) in savannas to 53.2 ± 11.0% in burned woodlands and 86.4 ± 1.8% in oak woodlands. Average shrub cover was more similar across habitat types at 33.5 ± 7.8%, 42.1 ± 6.5%, and 45.3 ± 7.9% for savannas, burned woodland, and oak woodlands, respectively. We found no significant differences in shrub ($F_{2,25} = 0.70$, $P = 0.507$) or brush cover ($F_{2,25} = 1.43$, $P = 0.259$) among habitat types. Percent grass cover and percent leaf litter were strongly correlated with canopy cover ($r_{grass} = -0.706$, $r_{leaf} = 0.881$, $P_{both} \leq 0.001$).

Vegetation characteristics in savannas, burned woodland, and oak woodlands were highly variable between plots at the same survey point and among pairs of plots within habitat types. Mean differences among plots within habitat types in percent canopy and percent brush cover were higher in savannas and burned woodlands than in oak woodlands, but differences in percent shrub cover were comparable among habitat types [95% CIs (9.5, 35.3), (7.6, 34.2), and (9.7, 37.5) in savannas, burned woodlands, and oak woodlands respectively]. The range of percent shrub cover extended > 50 percentage points in all three habitat types and appeared unrelated to canopy cover (unpubl. data). Differences in average shrub height were similar among habitat types, but average brush height was less variable in burned woodlands (95% CI of height differences [cm] between plots: 7.3, 20.7) than in savannas (12.1, 40.7) or oak woodlands (12.1, 39.1).

At the patch level, oak woodlands had both the highest mean woody species richness (4.9 canopy species, 11.7 shrub species/patch) and highest mean percent canopy cover (81%); savannas had the lowest mean woody species richness (3.2 canopy species/patch, 8.7 shrub species/patch) and percent canopy cover (33%).

Burn frequencies varied widely in savannas and burned woodlands. In savannas, prescribed-burn frequencies during 1982-2001 ranged from 0.0 burns/yr in Sand Dunes State Forest to 0.9 burns/yr at 1 point in CCNHA. Burn frequencies in burned woodlands ranged from 0.1 burn/yr at 5 points in SNWR to 0.9 burns/yr at 1 point in CCNHA. At the point level, burn frequencies were weakly negatively correlated with canopy cover (r = –0.394, $P = 0.038$) and tree density (r = –0.324, $P = 0.093$).

Relationships of Bird Communities to Environmental Variables

Bird communities at prairie points were highly distinct from bird communities in all other habitat types. Reciprocal averaging axis-1 values for prairie survey points from 2002 exhibited no overlap with points in other habitat types. Additionally, the range of RA axis-1 scores for prairie points was comparable to that of RA axis-1 scores for all other points combined (Table 1). Consequently, to improve our ability to distinguish bird communities in other habitat types, we excluded data from prairie points from further analyses.

At the local, or point level, burn frequency, percent canopy cover, percent bare ground, average shrub height, tree density, and canopy and shrub species richness were significantly related to bird communities and included in the CCAs with point count data from the same 28 points at which we collected local vegetation data (Table 3). We excluded moss and fern data because values at most points were small (< 5%) or zero. Percentages of grass and leaf litter were strongly correlated with percent canopy cover and, therefore, we excluded them from CCAs. At the patch level, we included burn frequency, percent canopy cover, and canopy and shrub species richness in CCAs as environmental variables.

Table 3. Parameter estimates of simple linear regressions of environmental variables on reciprocal averaging axis-1 scores of bird point-count data. Counts were conducted in 2002 at 23 points in savannas, burned woodlands, and oak woodlands on the Anoka Sandplain in east-central Minnesota.

Environmental variables	Parameter estimate	SE	*t* -ratio	*P*
Burn frequency	188.39	68.88	2.74	0.012
% canopy	– 1.94	0.33	– 5.89	< 0.001
% shrub	– 0.14	0.78	– 0.18	0.856
% brush	0.62	0.99	0.63	0.538
% grass	2.03	0.48	4.20	< 0.001
% leaf	– 1.96	0.45	– 4.37	< 0.001
% debris	– 0.57	2.06	– 0.28	0.784
% bare	8.87	3.23	2.74	0.012
Av. shrub ht	– 1.00	0.57	– 1.74	0.097
Average brush ht	– 0.35	0.57	– 0.61	0.550
Tree density	– 8.27	1.57	–5.26	< 0.001
No. snag	– 4.71	4.74	– 0.99	0.332
Average. DBH	0.65	2.82	0.23	0.820
No. canopy spp.	– 40.87	11.24	– 3.63	0.002
No. shrub spp.	– 8.99	4.74	– 1.90	0.071

Relationship of bird communities to local environmental variables

We conducted CCAs on data from 28 points, with 50 bird species and 20 feeding guilds. Sample scores for observed bird communities and those derived from environmental variables were highly correlated (|r| = 0.891 to 0.955, Monte-Carlo randomizations: $\bar{x} = 0.774$ to 0.826, $P =$ 0.01 to 0.03) (Table 4).

Based on CCA, bird species presence was strongly associated with percent bare ground, and shrub species richness had a weaker relationship with bird community structure than did burn frequency or canopy cover (Table 4). The presences of red-headed woodpeckers and brown thrashers (*Toxostoma rufum* L.) were strongly associated with high burn frequencies, the presences of golden-winged warblers and black-and-white warblers (*Mniotilta varia* L.) were strongly associated with shrub

Table 4. Summary statistics from canonical correspondence analyses of point-count data from 28 points in savannas, burned woodlands, and oak woodlands on the Anoka Sandplain in east-central Minnesota. Bird and vegetation data were collected May-July 2001 and 2002. Environmental variables were correlated with axis-1 ordination scores for each of the response variables.

	Axis-1 summary		Correlation with axis 1						
Response variable	Eigen-value	% variance explained	Burn frequency	% canopy cover	% bare ground	Average shrub height	Tree density	No. canopy species	No. shrub species
Abundances	0.253	14.0	– 0.811	0.720	– 0.371	0.517	0.708	0.627	0.472
Presence	0.159	10.5	– 0.709	0.794	– 0.397	0.454	0.759	0.645	0.425
Feeding guilds	0.101	15.8	– 0.741	0.750	– 0.375	0.511	0.751	0.597	0.451

height, and the presence of eastern phoebes (*Sayornis phoebe* Latham) was most strongly associated with greater canopy cover (Figure 2c).

Abundance of individual bird species was most strongly related to burn frequency and percent canopy cover. Although included in the CCA, percent bare ground had a relatively weak relationship to bird abundance. The differentiation of bird communities at savanna points from those at burned woodland and oak woodland points appeared more strongly related to burn frequency and shrub height than to percent canopy cover or canopy species richness (Figure 2a). Red-headed woodpeckers, brown thrashers, and field sparrows were strongly associated with high burn frequency, while eastern phoebes and black-throated green warblers (Alpha-code 'BTNW' in Figure 2; *Dendroica virens* Gmelin) were associated most strongly with high levels of canopy cover and tree density (Figure 2b).

Dominant feeding guilds shifted with changes in canopy cover and burn frequency (Figure 2d). Insectivory and air sallying were associated with high levels of canopy cover, and omnivory was strongly related to prescribed burning. Low-to-moderate burn frequencies were associated with omnivore lower canopy foragers and upper canopy gleaner/foragers, while omnivore lower canopy gleaner/foragers and ground foragers and insectivore/frugivores were associated with moderate-to-high burn frequencies (Figure 2d).

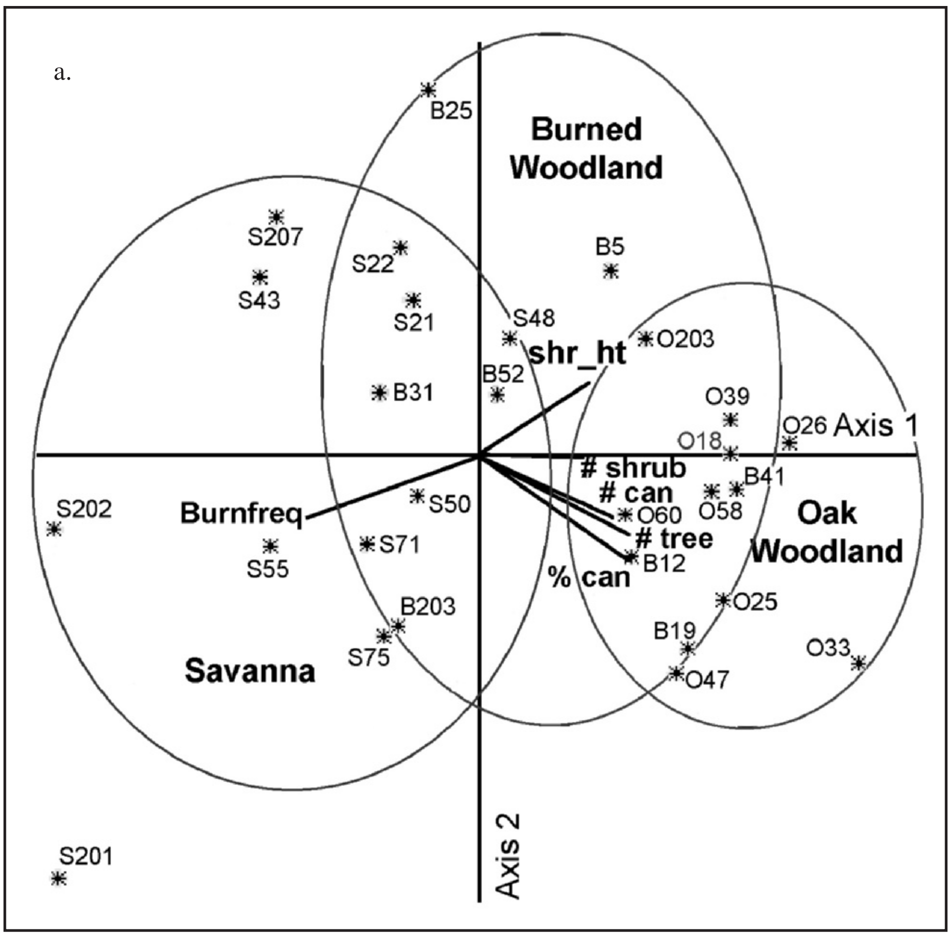

Figure 2. Biplots of canonical correspondence analysis for bird abundances (a and b), presence (c), and feeding guilds (d) from 28 survey points on the Anoka Sandplain in east-central Minnesota. Points are marked by an asterisk, and species or feeding guilds are marked with a diamond. Point labels with 'S' indicate savanna points, 'B' indicate burned woodland points, and 'O' indicate oak woodland points. Some labels were removed or shortened to improve clarity. Environmental variables include: *Burnfreq* – prescribed burn frequency over the period 1982-2001; *% can* – % canopy cover; *% bare* – % bare ground; *# tree* – average density of trees; *shr_ht* – average shrub height; *# can* – tree species richness; *# shrub* – shrub species richness. Bird and vegetation data were collected May-July 2001 and 2002.

Bird community structure at burned woodland points overlapped with that found in oak woodland and savanna points. Lark sparrows (*Chondestes grammacus* Say), Baltimore orioles (*Icterus galbula* L.), brown thrashers, and field sparrows were more strongly associated with savannas than with burned woodlands (Figures 2b and 2c), and we detected these species more frequently in savannas than in burned woodlands. All of these species were omnivorous, and most (with the exception of Baltimore orioles) fed on lower canopy or ground substrates. Many species, including black-capped chickadees (*Poecile atricapillus* L.), red-eyed vireos, and American redstarts (*Setophaga ruticilla* L.) were strongly associated with both burned woodland and oak woodlands.

Relationship of bird communities to patch environmental variables

Results of our patch-level analyses were similar to those at the point level. Bird species presence, abundance, and feeding guilds were strongly associated with canopy species richness and less strongly associated with shrub species richness. Bird community CCA scores were significantly correlated with linear combination scores of environmental variables ($|r|$ = 0.820 to 0.918, Monte-Carlo randomizations: $\bar{x}$ = 0.456 to 0.559, P = 0.01). Associations between species presence and feeding guilds and environmental variables were similar to those found for bird species abundances, although the strengths of these associations varied. The strengths of the associations of burn frequency and percent canopy with bird abundance were similar, whereas species presence and feeding guilds had slightly stronger associations with percent canopy cover (Table 5). CCA scores for bird communities in burned woodlands overlapped heavily with those both in oak woodlands and in savannas (Figure 3a). Insectivory, upper canopy gleaning, and air sallying were predominant in areas of moderate-to-high percent canopy cover whereas omnivory and lower canopy or ground foraging were predominant in areas undergoing prescribed burns (Figure 3b).

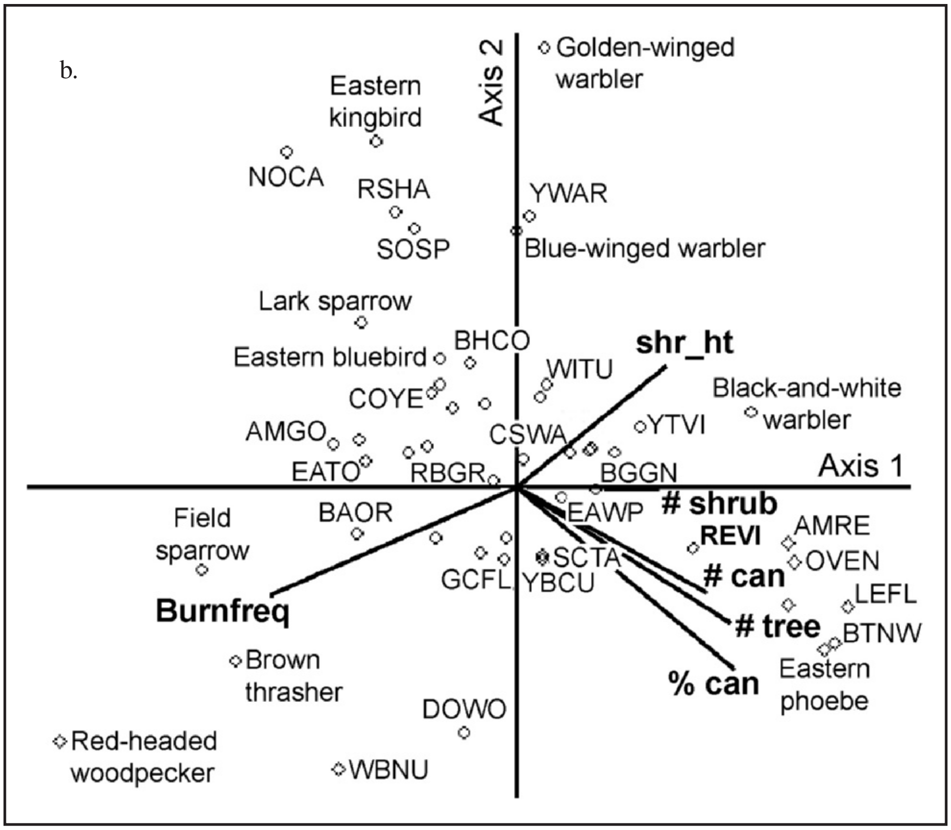

Figure 2 (b).

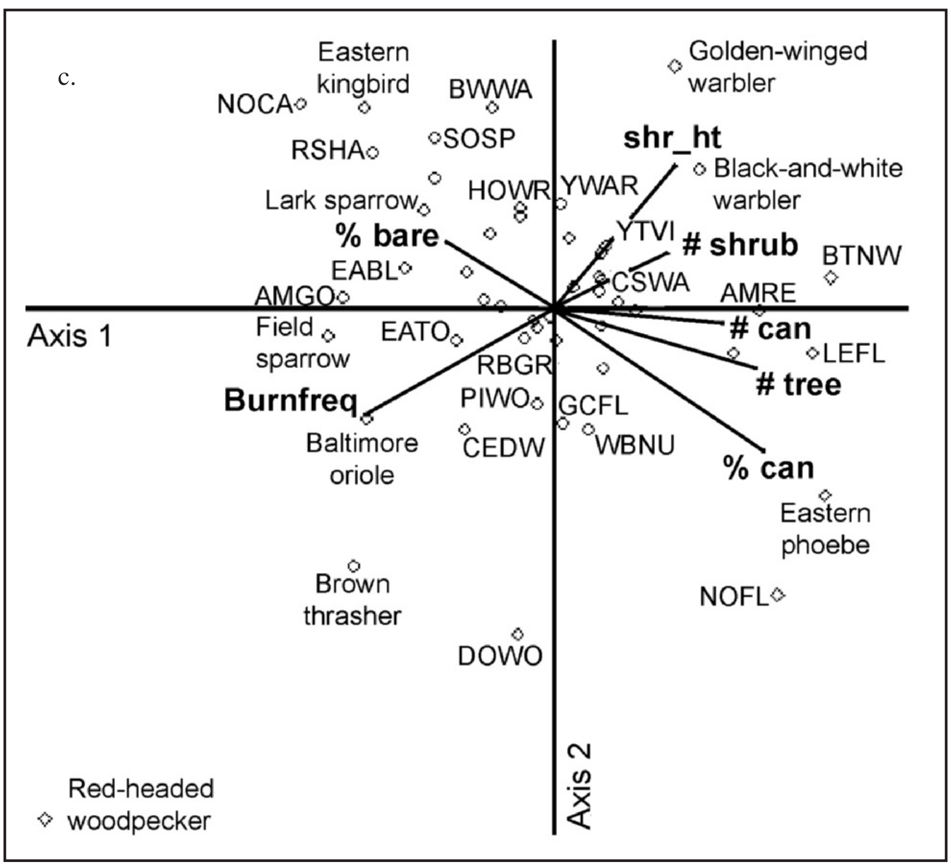

Figure 2 (c).

Bird communities at most savanna points were more strongly associated with varying frequencies of prescribed burning than with canopy cover or woody species richness. At savanna points, bird communities were generally more consistently associated with prescribed burns than bird communities in either burned woodland or oak woodland. The few exceptions were bird communities at points S5, S15, and S32 (Figure 3a), which were located in Sand Dunes State Forest. The axis-1 ordination values for those savanna points were more similar to oak woodland and burned woodland points than to other savanna points at sites outside of SDSF (Figure 3a). This is notable because savanna conditions at SDSF were maintained through mechanical management techniques and not fire.

DISCUSSION

Remnant and restored dry oak savannas support many bird species that recently have been declining in the Upper Midwest. Of ≥ 14 species detected more frequently in savannas than in other habitat types, BBS data from 1980-2002 indicated that ≥ 6 of these species experienced significant declines in the region (USFWS Region 3), and ≥ 4 species experienced significant increases (Sauer et al. 2003). Several species of special concern within USFWS Region 3 (U.S. Fish and Wildlife Service 2002), including blue-winged warblers (*Vermivora pinus* L.), golden-winged warblers, and red-headed woodpeckers, were most abundant in savannas. In our study, dry oak savannas in central Minnesota supported high bird species richness (including several species of special concern) compared to prairie and woodland habitats, and bird community structure across a habitat gradient that included dry oak savannas was most strongly associated with burn frequency, canopy cover, and attributes of the shrub component. Our results further suggest that management of these habitats through cutting rather than fire may not result in restored oak savannas that support bird communities similar to those in remnant savanna habitats.

We detected the lowest bird species richness in prairie habitats, and the highest in

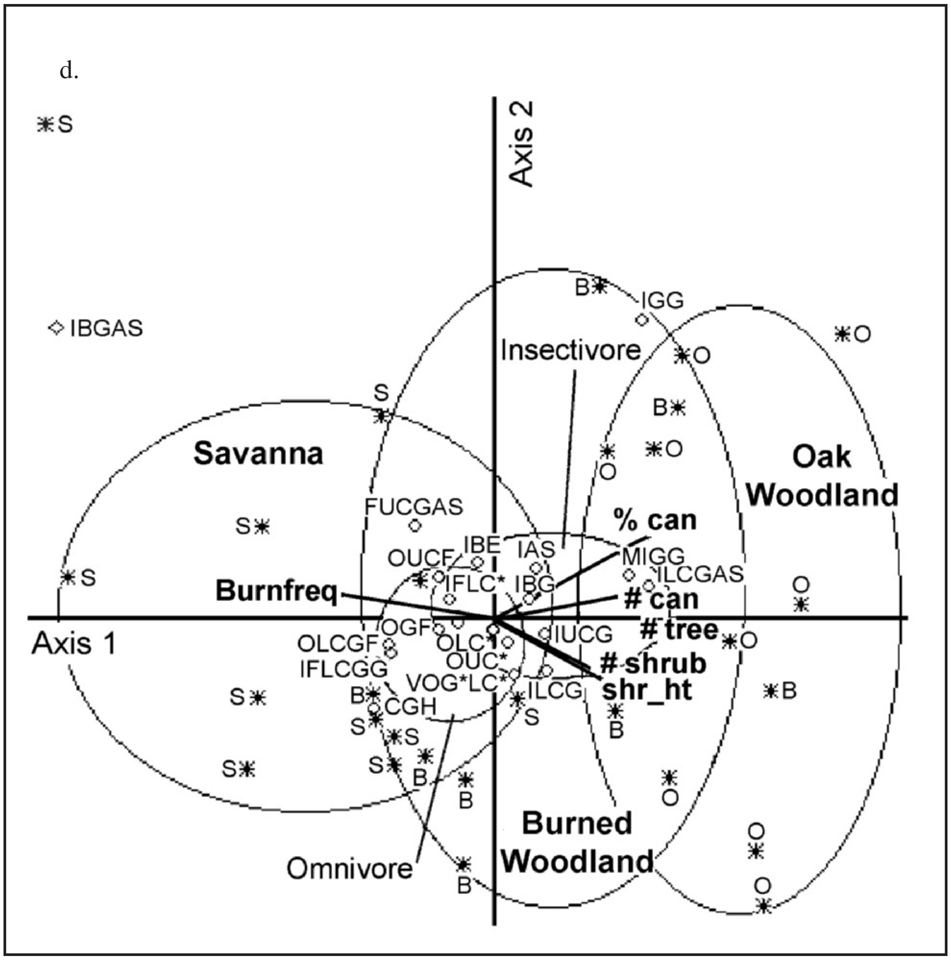

Figure 2 (d).

savannas, consistent with the expectation that α-diversity, or the number of species in a given habitat, is directly related to structural diversity (Cody 1985). Savannas are more structurally diverse than either prairies or oak woodlands because they include features of both habitat types, and may represent an ecotone, rather than a biome (Temple 1998). Grundel and Pavlovic (2007) studied bird communities across a habitat gradient that included oak savannas in Indiana, and concluded that birds experience savannas and woodlands more as ecotones than as habitats distinct from forests or grasslands. Our results based on bird species presence and abundance during the breeding season were also consistent with the notion that oak savannas function as an ecotone with respect to birds, except that restoration through mechanical means rather than burning did not result in bird communities similar to those in oak savannas. The reasons for these differences are not clear.

Unlike patterns in species presence and abundance, the diversity of bird foraging guilds was not highest in savannas compared to oak woodlands and burned oak woodlands. Numbers of feeding guilds among the three habitat types were similar, although there was a notable shift in feeding guilds represented along the gradient from oak woodland to savanna. In areas with heavier canopy cover that lacked prescribed fire, guilds comprised of insectivores were predominant. In areas with lower canopy cover and moderate-to-high frequencies of prescribed burning, most species were omnivorous feeders. There also appeared to be a slight shift from upper canopy and air foraging guilds in oak woodlands to lower canopy and ground foraging guilds in savannas. These results are consistent with findings by Davis et al. (2000), who reported that generalist and lower canopy foraging increased as oak woodlands were restored to savanna using prescribed burns.

At both point- and patch-level spatial scales, percent canopy cover and burn frequencies appeared to be the most important variables related to bird community structure. Tree and shrub species richness and shrub height also were related significantly to bird communities (Table 3), although shrub cover was not related to observed bird communities, perhaps because shrub cover was generally high in all habitat types except prairie. Overall, our axis-1 CCA vegetation models explained from 8.8-15.8% of variation (Tables 4 and 5)

Table 5. Summary statistics from canonical correspondence analyses of point-count data from 86 points located in 31 patches of savanna, burned woodland, and oak woodland on the Anoka Sandplain in east-central Minnesota. Point counts were conducted May-July 2001 and 2002; vegetation data were collected May-July 2001 and 2002. Environmental variables were correlated with axis-1 ordination scores for each of the response variables.

	Axis-1 summary		Correlation with axis 1			
Response	Eigenvalue	% variance	Burn frequency	% canopy	No. canopy species	No. shrub species
Abundances	0.242	10.9	0.847	– 0.849	– 0.747	– 0.428
Presence	0.154	8.8	0.775	– 0.871	– 0.780	– 0.386
Feeding guilds	0.073	11.4	0.759	– 0.903	– 0.685	– 0.354

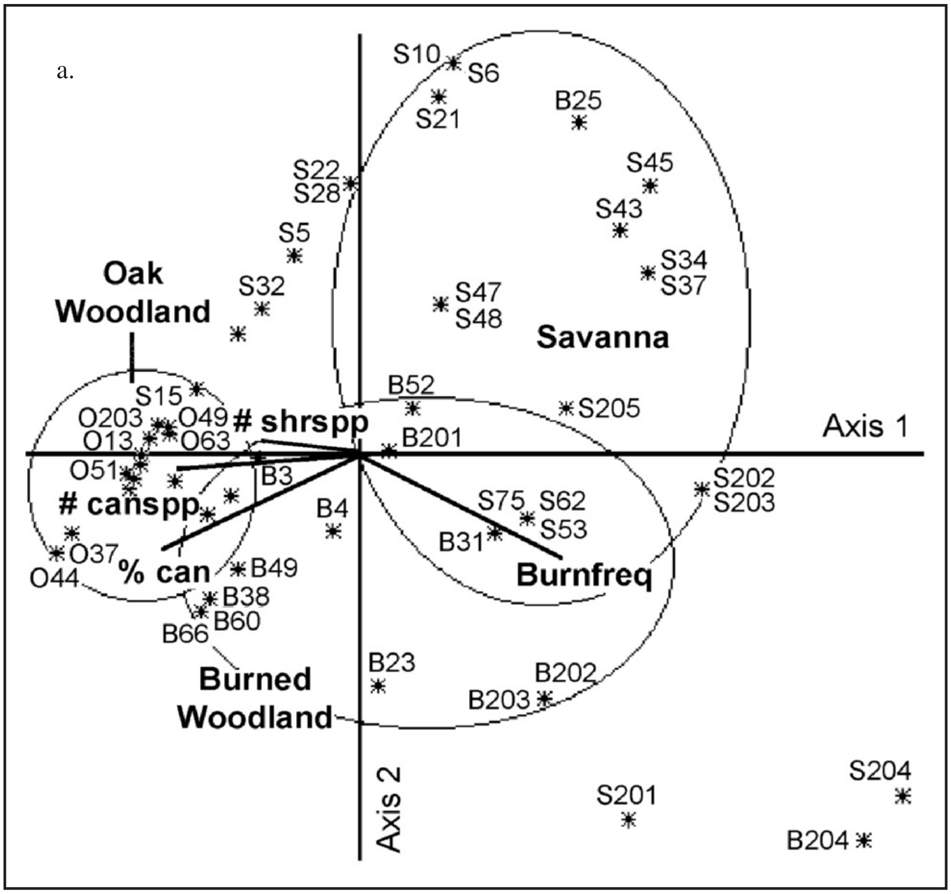

Figure 3. Biplots of canonical correspondence analysis for bird abundances (a) and feeding guilds (b) from 86 survey points within 31 habitat patches on the Anoka Sandplain in east-central Minnesota. Points are marked by an asterisk, and feeding guilds are marked with a diamond. Point labels with 'S' indicate savanna, 'B' indicate burned woodland, and 'O' indicate oak woodland. Some labels were removed to improve clarity. Environmental variables include: *Burnfreq* – prescribed burn frequency over period 1982-2001; *% can* – % canopy cover; *# canspp* – tree species richness; *# shrspp* – shrub species richness. Bird community data were collected May-July 2001 and 2002. Vegetation data were collected May-July 2000-2002.

in bird community structure, suggesting that bird communities were quite variable across the habitat gradient we studied, and that other factors we did not measure (e.g., food availability and distribution) likely influenced community structure.

Bird community structure in remnant savannas appeared to be most strongly related to burn frequency and less strongly related to shrub height and woody species richness. However, at savanna points managed with periodic cutting but not fire, bird communities appeared more similar to bird communities in oak woodlands than to those at other savanna points. We could not directly relate these results to any specific differences in vegetation, which suggests that although canopy and groundcover characteristics may be structurally similar between savannas managed with cutting and those managed with fire, the introduction of fire into an area may influence habitat enough to significantly change bird community structure. The bird community could be responding to differences in plant species composition (which we did not assess) or other biotic or abiotic factors influenced by management.

At only a few burned woodland points (e.g., B25, B31, CCB3) was bird community structure similar to bird community structure at most remnant savanna points (Figure 2a), suggesting that despite ≥ 20 years of prescribed burning, most burned woodlands remained ecologically distinct from remnant savannas. It is unclear whether savanna restoration in these woodlands is producing what could be described as continuous or linear change in structure from oak woodland to savanna (Eiswerth and Haney 2001; Muradian 2001) or whether burned woodlands, like oak woodlands and savannas, are a stable ecological state (Muradian 2001). Because many oak woodlands undergoing restoration have different species composition, structural characteristics, and ecosystem processes than remnant savannas, introduction of prescribed burns may create feedbacks that make woodlands resistant to savanna restoration (Suding et al. 2004).

To successfully transform burned woodlands out of a self-reinforcing ecological state, savanna restoration efforts may have to reach or exceed some unknown ecological threshold. Muradian (2001) defined an ecological threshold as that critical value of an independent variable in an ecological system that triggers a sudden change of that system from one stable state to another. The relative paucity of omnivores and ground-foragers in burned woodlands compared to savannas suggests that this change may involve a shift in groundcover characteristics that would accommodate species that feed at lower structural levels and on a wide variety of food types.

Management Implications

In our study, bird communities along a prairie to oak woodland gradient were most strongly related to a combination of prescribed burning regime and percent canopy cover. Woody species richness and shrub and groundcover characteristics also influenced these communities. Remnant savanna sites that had been managed with cutting alone appeared to support bird communities more similar to those found in woodland habitats than did other savanna points. However, restoration of oak savanna from oak woodland conducted using only prescribed burns over a ≥ 20 year period did not necessarily result in habitats that supported bird communities similar to those in remnant savannas. The prospect that ecological thresholds or some other nonlinear processes exist in these habitats (Eiswerth and Haney 2001) suggests that it may not always be possible to switch from oak woodland to savanna by merely rein-

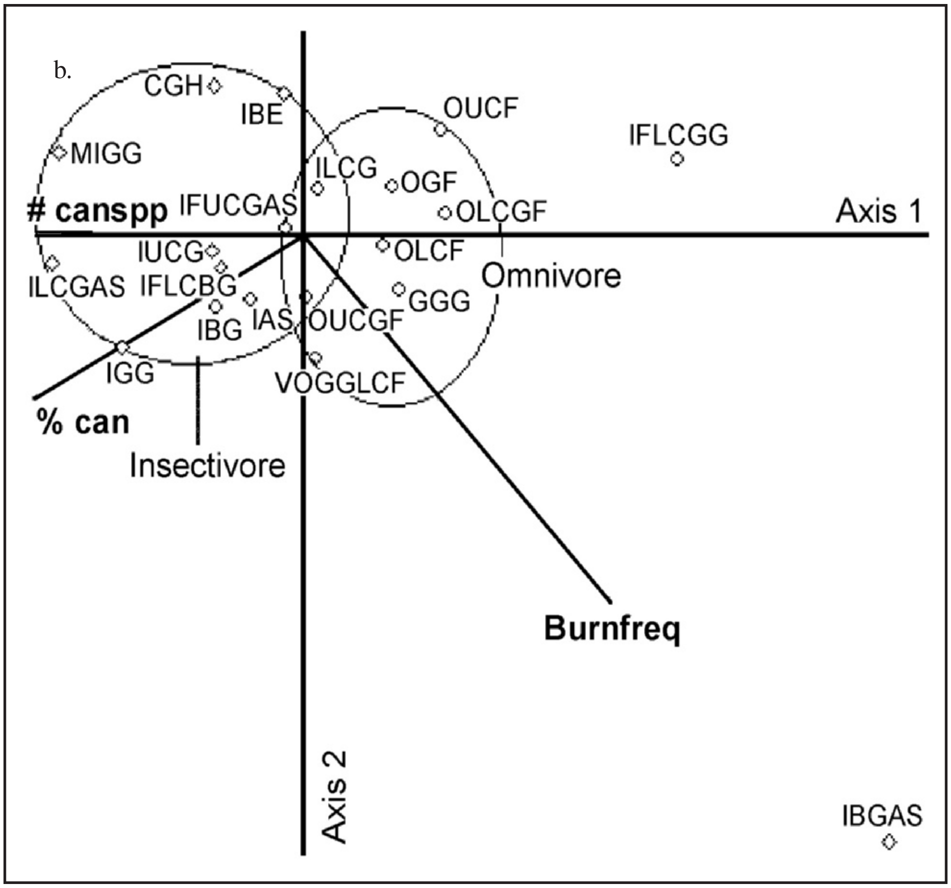

Figure 3 (b).

troducing fire, but as observed in western grasslands (Muradian 2001), some savanna restorations may also require chemical or mechanical interventions. Factors operating at a broader spatial context (e.g., proximity to habitats that could serve as a source of immigrants) may also influence bird community structure and the range of potential future conditions.

Our results also suggest how management for individual species could be enhanced by understanding how closely associated target species are with specific environmental conditions. For instance, red-headed woodpeckers were very strongly associated with high burn frequencies and were only weakly associated with other assessed environmental variables. Red-headed woodpeckers were most weakly associated with shrub height. In contrast, golden-winged warblers were most strongly associated with shrub height. Managers may manipulate habitat characteristics to enhance conditions for target species, and depending on the bird species of interest, concurrent management for multiple species may be possible.

Finally, our results highlight the complexity of restoration and assessing ecological condition of dry oak savannas in the Upper Midwest. We used bird community structure to assess ecological condition of oak savannas and whether restoration produced savannas that supported bird communities similar to those in remnant oak savannas, which provided insight that looking at vegetation structure alone did not (e.g., differences in bird communities between habitats managed with fire versus those managed with mechanical manipulation). However, other factors likely influence bird community structure in remnant and restored oak savannas (e.g., food availability and the landscape context of individual sites), and these need to be better understood to effectively manage these rare habitats.

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