

The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities

Catherine M. Mabry*, Lars A. Brudvig¹, Ryan C. Atwell²

Department of Natural Resource Ecology and Management, 339 Science II Hall, Iowa State University, Ames, IA 50011-3221, United States

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ABSTRACT

Species distributions are determined by complex interplays between multi-scale factors. Conservation management, however, often occurs at a single scale of the site level. This is true for bird communities of restored savannas and mixed woodlands in the central U.S. In this region, many historic open-canopy oak savanna habitats have become closed canopy mixed woodlands due to loss of landscape-scale disturbance from fire and grazing. Site-level management efforts return some mixed woodland habitats back to savanna through fire and mechanical thinning. Savanna and woodland historically formed complex mosaic landscapes at the ecotone between prairies and Eastern deciduous forests and now exist within landscapes that vary in amount of open (e.g., perennial grassland and row crop agriculture) and woodland habitat. To understand the interplay between site and landscape level factors in savanna restoration, we sampled the breeding bird community in four combinations of site and landscape: restored savanna in open landscapes, restored savanna in woodland landscapes, and closed canopy woodland in both landscapes. We found that the outcome of site-level savanna restoration depended on the surrounding landscape. Compared to other treatment types, restored savannas in open landscapes supported a distinctive bird community characterized by high species richness, bird abundance, and percent of ground feeders, shrub nesters, and edge species. Both savanna and woodland sites in the open landscape had a higher percent of species of conservation concern, while at both site and landscape levels, woodland was associated with a higher percent of area sensitive species and habitat specialists. Our results suggest savanna restoration efforts should focus on sites that exist either in open country or on edges where closed canopy forest meets open country. This strategy would combine site and landscape level benefits of savanna restoration for avian diversity, while also preserving the conservation benefits of large tracts of intact forest.

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1. Introduction

The importance of site- and landscape-level factors for determining patterns of animal populations has increasingly been recognized by ecologists (Sisk et al., 1997; Estades and Temple, 1999; Graham and Blake, 2001; Lee et al., 2002; Bennett et al., 2006). Despite calls to consider landscape context during land management (Bell et al., 1997; Marzluff and Ewing, 2001; Ruth et al., 2003), relatively small patches of remnant native habitat have often been the focus of conservation and management efforts in fragmented landscapes (Fahrig, 2003) and few studies have evaluated how

landscape level factors influence the outcome of site-level management (Bell et al., 1997; Huxel and Hastings, 1999; Scott et al., 2001). The consequences of a site-level focus in conservation and restoration are largely unknown, but may include unmet conservation goals or failed integration of working (i.e., agricultural) and conservation lands, especially in fragmented landscapes (Hobbs and Norton, 1996). An important step toward better matching management outcomes to management goals and for generalizing across restoration efforts is to disentangle site- and landscape-level factors during restoration and management.

Savannas and woodlands of the central U.S., and their attendant bird communities, provide an ideal system in which to test the interplay between site- and landscape-level factors. Both factors are likely to be important in this region because the savannas and woodlands: (1) were historically components of a shifting (i.e., spatially and temporally variable) landscape mosaic; (2) are of high conservation priority; (3) possess high variation in site-level composition and structure based on management history; and (4) are situated within a fragmented landscape mosaic composed of

* Corresponding author. Tel.: +1 515 294 1604; fax: +1 515 194 1995.
E-mail addresses: mabry@iastate.edu (C.M. Mabry), brudvig@msu.edu (L.A. Brudvig), ryancardiffatwell@gmail.com (R.C. Atwell).

¹ Present address: Michigan State University, Department of Plant Biology, East Lansing, MI 48824, United States. Tel.: +1 517 355 8262; fax: +1 517 353 1926.

² Present address: Office of Ecosystem Services and Markets, U.S. Department of Agriculture, 1800 M Street NW Suite 2143, Washington DC 20036.

either agriculture and grasslands or deciduous woodlands. Birds represent an excellent focal taxon because of their high level of conservation concern and the importance of both local and landscape factors to their conservation (e.g., Sisk et al., 1997; Graham and Blake, 2001; Tewksbury et al., 2006). In fact, landscape effects are a pivotal component of avian conservation strategies (Sisk et al., 1997; Estades and Temple, 1999; Graham and Blake, 2001; Lee et al., 2002; Bennett et al., 2006).

Current savanna management seeks to reinstate historical dynamics and distributions, which differ from present conditions. Historically, interactions between fire, climate, topography, soils, and large mammal grazing maintained a shifting landscape of woodland, savanna, and grassland communities within an extensive grassland/forest transition zone ranging from Texas to Minnesota (Gleason, 1922). Savannas were distinguished from woodland by scattered canopy trees, a diverse grass and forb dominated understory, often with a shrub component (Gleason, 1922; Cottam, 1949). After Euro-American settlement most historic savannas converted to closed canopy woodland, with a shift in overstory composition toward shade tolerant, fire intolerant species (Cottam, 1949; Anderson and Schwegman, 1991). To restore these sites to savanna, an open stand structure can be reinstated by reintroducing fire or by using mechanical thinning as a surrogate for fire (Anderson and Schwegman, 1991; Peterson and Reich, 2001; Brudvig and Asbjornsen, 2007).

Throughout the central U.S., land managers must decide whether to maintain these sites as woodland or restore them to the regionally rarer savanna state. These decisions are frequently based on historical information about vegetation structure and dynamics; however, recent work has demonstrated the value of explicitly incorporating avian conservation goals (Grundel and Pavlovic, 2008). Bird communities undergo site-specific changes following conversion of woodland to savanna, which are based on changes to vegetation structure and composition (Temple, 1998; Davis et al., 2000; Brawn, 2006; Grundel and Pavlovic, 2007). Because savannas were historically part of a shifting mosaic of habitats, the bird community composition at the site-level may also be influenced by species that are dominant in the surrounding landscape (Whitcomb, 1987; Temple, 1998). In short, maintaining ecotonal animal species in the central U.S. may depend on management efforts that consider both site conditions and the proximity of sites to source populations in the surrounding landscape (Temple, 1998; Brawn et al., 2001).

Moreover, the structural changes associated with both the shift from savanna to woodland and the subsequent restoration of woodland back to savanna present a conundrum for land managers. Forest succession and agricultural intensification have led to reductions in avian species associated with early successional habitats, edges, and shrublands, and many of these species are now a conservation concern (Whitcomb, 1987; Askins, 1993; Brawn et al., 2001). If sufficient shrub and ground habitat remains, restored savanna can increase these species (Davis et al., 2000; Blake, 2005; Brawn, 2006). However, restored savannas may also have lower densities of forest interior and specialist species of conservation concern (Wilcove, 1985; Whitcomb, 1987; Robinson et al., 1995). Maintaining and developing larger tracts of forest has been identified as a conservation priority for these species, particularly in landscapes dominated by small forest fragments (Norris et al., 2003; Whitcomb, 1987; Brawn and Robinson, 1996). These management outcomes suggest that there is a tradeoff between conserving early successional/shrub/edge species and forest interior species (Aquilani et al., 2000; King et al., 2001; Yahner, 2003).

In this research, we assessed the influence of both site-level management and landscape-level context on the breeding bird community. We used a series of sites maintained as closed canopy woodland or restored to savanna. Further, each of these sites exists

within one of the two regionally common landscape contexts: (1) wooded patches that are largely surrounded by agricultural land (row crop agriculture and perennial grassland), or (2) relatively intact and continuous woodland. We predicted that the outcome of site-level management would depend on the composition of this surrounding landscape. If landscape effects are important, we expected to observe bird communities that differed in wooded vs. open landscapes on sites with similar management regimes (e.g., for savanna or for woodland). Conversely, if site-level management is of primary importance, we expected to observe similar bird communities in sites managed the same way, regardless of surrounding landscape. By considering how site- and landscape-level factors interact to influence bird community composition, our study may provide insight into the dilemma of when and where to maintain or restore woodlands that previously existed in a savanna state.

2. Methods

2.1. Site description

Iowa is part of the North American tallgrass prairie/Eastern deciduous forest transition zone and is one of the three states in the U.S. that rank lowest in the amount of remaining natural vegetation (Klopatek et al., 1979), where much of the remaining habitat is fragmented and increasingly urbanized (Potts et al., 2004). Substantial efforts in the region have been directed towards understanding the consequences of savanna restoration on vegetation structure and function (e.g., Brudvig and Asbjornsen, 2007; Dettman and Mabry, 2008; Dettman et al., 2009; Brudvig, 2010). Our study was located in central Iowa, USA, and included 16 sites. Eight were located in landscapes dominated by perennial grassland and row crop agricultural fields (hereafter “open landscape”) and eight were located in landscapes dominated by deciduous upland forests (hereafter “woodland landscape”; Table 1). These represent two of the most common landscapes for breeding birds in the state of Iowa (Best et al., 1996). Within both landscape types we located four sites managed as oak savannas and four sites managed as upland woods. Savanna and woodland sites were identified in pairs (within 1 km. of each other) to ensure that surrounding landscapes possessed similar attributes, though we did not use a blocking factor in our analyses. All sites were underlain by deep, well-drained Alfisol and Mollic Alfisol soils.

The eight sites in the woodland landscape were located along Saylorville Lake, a U.S. Army Corps of Engineers reservoir north of Des Moines, IA (41°76'N, 93°82'W; hereafter, “Saylorville”), an area that historically supported oak savanna, grassland and forest (Asbjornsen et al., 2005). All non-oak and/or non-hickory species trees were mechanically removed from four 2–5 ha sites during the winters of 2002–2004 as part of an ongoing savanna restoration experiment. Each site was paired with a nearby woodland site similar in vegetative composition and structure to the savanna sites prior to restoration (Brudvig and Asbjornsen, 2007; Table 1). Both the savanna and woodland sites were immediately surrounded by larger expanses of forest on all sides. Predominant underlying soil series at Saylorville included the Lester (Mollic Hapludalf) and Hayden (Glossic Hapludalf) (Brudvig and Asbjornsen, 2007).

The eight open landscape sites were located approximately 50–100 km east of Saylorville. Four were at Neal Smith National Wildlife Refuge (NSNWR), near Prairie city, IA (41°33'N, 93°17'W), and four were at Grinnell College's Conard Environmental Research Area (CERA), near Kellogg, IA (41°43'N, 92°55'W). NSNWR is a ~2000 ha reserve dominated by agricultural land and tallgrass prairie, but includes patches of oak savanna and woodland. At NSNWR, two 1–3 ha savannas were restored from larger woodland patches and were paired with an adjacent site that remained

Table 1
 Characteristics of savanna and woodland sites and surrounding landscapes in a study of breeding bird communities in central Iowa, USA. Land cover types do not add up to 100% because urban, non-terrestrial, and minor land uses were not included in this tabulation.

Landscape	Site type	Location	Surrounding land cover			Plot-level description		
			Row crop agriculture ^a	Grassland ^b	Forest ^c	% Canopy cover \pm 1 SE	Trees/snags shrubs (/ha)	Prominent tree species (% individuals)
Woodland	Savanna	Saylorville1	0.0	6.8	37.8	59.5 \pm 3.5	440/45/1376	<i>Carya ovata</i> (46%), <i>Quercus alba</i> (26%)
Woodland	Savanna	Saylorville2	0.0	7.4	40.7	10.6 \pm 3.4	242/29/2064	<i>Q. rubra</i> (71%), <i>Q. alba</i> (8%)
Woodland	Savanna	Saylorville3	1.6	4.5	39.7	51.1 \pm 2.6	280/25/127	<i>Q. alba</i> (50%), <i>Ostrya virginiana</i> (32%)
Woodland	Savanna	Saylorville4	17.9	0.4	29.3	33.1 \pm 8.0	255/29/2140	<i>Q. alba</i> (40%), <i>Q. macrocarpa</i> (28%)
Woodland	Woodland	Saylorville1	0.0	6.5	42.4	74.2 \pm 6.6	815/76/1427	<i>O. virginiana</i> (34%), <i>C. ovata</i> (13%)
Woodland	Woodland	Saylorville2	0.0	6.3	39.5	77.4 \pm 4.8	1166/134/2064	<i>O. virginiana</i> (63%), <i>C. ovata</i> (13%)
Woodland	Woodland	Saylorville3	3.2	4.2	37.6	86.2 \pm 0.9	554/70/2726	<i>Q. alba</i> (53%), <i>C. ovata</i> (23%)
Woodland	Woodland	Saylorville4	24.7	2.0	17.4	74.3 \pm 5.2	834/229/1733	<i>Acer nigrum</i> (31%), <i>C. ovata</i> (18%)
Open	Savanna	NSNWR1	14.2	65.2	12.7	39.0 \pm 7.0	242/13/1580	<i>Q. macrocarpa</i> (50%), <i>Gleditsia triachanthos</i> (21%)
Open	Savanna	NSNWR2	66.8	18.4	6.7	31.9 \pm 3.1	134/0/2140	<i>Q. macrocarpa</i> (38%), <i>Ulmus americana</i> (29%)
Open	Savanna	CERA1	41.9	32.0	22.5	37.3 \pm 5.4	153/6/331	<i>Q. macrocarpa</i> (92%), <i>U. americana</i> (8%)
Open	Savanna	CERA2	35.9	36.5	20.5	34.9 \pm 3.0	280/0/790	<i>Q. macrocarpa</i> (88%), <i>C. ovata</i> (7%)
Open	Woodland	NSNWR1	24.2	60.7	13.5	48.7 \pm 4.3	1191/45/1962	<i>Celtis occidentalis</i> (39%), <i>U. americana</i> (23%)
Open	Woodland	NSNWR2	65.4	21.4	7.7	51.7 \pm 2.0	885/96/1197	<i>U. americana</i> (30%), <i>U. rubra</i> (30%)
Open	Woodland	CERA1	38.5	30.0	24.2	57.6 \pm 1.9	1083/76/637	<i>Tilia americana</i> (42%), <i>O. virginiana</i> (31%)
Open	Woodland	CERA2	35.7	31.4	27.7	59.8 \pm 5.1	650/70/815	<i>T. americana</i> (39%), <i>U. americana</i> (19%)

^a Cover classes: corn, soybeans, other row crop agriculture.

^b Cover classes: ungrazed grasslands, grazed grasslands, CRP.

^c Cover classes: deciduous forest, conifer forest, wet forest.

in woodland. One savanna had been used for cattle grazing until purchased by the US Fish and Wildlife Service in the early 1990s. Non-oak trees were removed from the savanna and understory prescribed fire carried out every 2–3 years (Table 1). The other savanna was used as a game preserve until purchased by the US Fish and Wildlife Service. Restoration was initiated in January 2004 with mechanical removal of all non-oak trees. A patchy, low intensity surface fire was conducted during February 2005 (Table 1). Predominant underlying soils series at NSNWR included the Gara (Mollic Hapludalf) and Ladoga (Vertic Hapludalf) (Asbjornsen et al., 2007).

CERA is a ~150 ha mosaic of tallgrass prairie, oak savanna, and mixed woodland. The landscape surrounding CERA is predominantly row crop agriculture and pasture. Restored savanna encompasses approximately 10-ha. Fire treatments began in 1992, with spring burns conducted in 1996–1998, and 2002–2005. Some mechanical thinning was also carried out from 1989 to 2000. The entire area was grazed until the 1940s (Larissa Mottl, Grinnell College, personal communication). A 19-ha closed canopy forest was located about 0.5 km from the restored savanna area. A portion of the forest has been managed with prescribed cool surface fire every 2–3 years since 1993. Predominant underlying soils series at CERA included the Downs (Mollic Hapludalf) and Lindley (Typic Hapludalf) (L. Mottl, personal communication).

2.2. Data collection

2.2.1. Birds

We conducted point-count surveys during the 2006 and 2007 breeding seasons. At Saylorville and NSNWR, points were placed in the center of 1–5 ha restoration sites and paired woodlands. At CERA, two points were placed in the 10-ha savanna restoration area and two points in the nearby 19-ha woodland. All points were a minimum of 200 m apart. Surveys began just before sunrise and concluded no more than 4 h after sunrise. Each point was visited three times/year during the breeding season, between late April and late June, with sampling limited to mornings without rain and with winds less than 15 kph. Study locations were rotated so that each was surveyed at different times. We surveyed each point for 10 min following a 10 min adjustment period, which is both standard and adequate for characterizing bird communities in our region (Blake, 2005). We recorded all singing, calling, and visible birds within 50 m of the point. Birds flying over the area above the tree tops were

not counted. We counted multiple birds per species only if birds were seen or heard simultaneously. Only species known to breed in Iowa were included in the analysis, although all birds were recorded during surveys.

To evaluate treatment effects on guilds, we classified each species into groups that included feeding and nesting guilds, and whether species were of benefit to agriculture by consuming weed seeds and insects (Appendix A). We also assessed conservation status using Partners in Flight (PIF) and Breeding Bird Survey (BBS) status (Appendix A). Guild data were obtained from Best et al. (1996). To determine species in our study that are undergoing long-term regional population decline, we used BBS trend data from 1966 to 2007 for Fish and Wildlife Service region 3, which includes our study area (www.mbr-pwrc.usgs.gov/bbs/). We also assessed conservation status using PIF region 22 (Eastern Tallgrass Prairie) combined scores and by determining whether PIF classified each species as focal for conservation (i.e., PIF listed the species as a continental or regional species of concern or stewardship; www.rmbo.org/pif/pifdb.html).

2.2.2. Vegetation

We sampled woody vegetation and canopy cover at each bird count point. Vegetation was surveyed in five subsamples located at the point center and at 30 m from the center in each of the four cardinal directions ($n = 5$ vegetation subsamples/bird survey point). We surveyed all trees (woody stems >5 cm diameter at breast height [1.3 m]) in a 10 m radius circle and all saplings (woody stems >150 cm height and <5 cm diameter at breast height) falling in a 5 m radius circle nested within the 10 m circle. We identified each individual to species, measured the height of saplings and the diameter at breast height of all trees. To quantify canopy cover, we collected one hemispherical photograph 1.5 m above each vegetation subsample location during cloudless early morning hours in September. We used a Coolpix 900 camera and a 270° fisheye lens, leveled and oriented so that the plane of the film faced north. We calculated the percentage of visible sky (inverse of canopy cover) with HemiView Canopy Analysis Software Version 2.1 (Delta-T Devices Ltd., 1999) and converted these values to percent canopy cover.

2.2.3. Landscape characterization

We characterized the landscape within 1 km surrounding each bird point using land cover data from the Iowa Department of

Natural Resources (<http://www.igsb.uiowa.edu/Browse/landcvt/landcvt.htm>), which we corrected where necessary with a digitized high resolution (<2 m) 2007 aerial photo (<http://ortho.gis.iastate.edu>). Percent land cover in three major cover types – row crop agriculture, grassland, and forest – were then calculated.

2.3. Data analysis

To understand how savanna and woodland differed in overall breeding bird species composition, we used multi-response permutation procedure (MRPP; McCune and Mefford, 1999). MRPP is a nonparametric test of the null hypothesis that no difference exists between groups (McCune and Grace, 2002). We defined groups three different ways – by sites (savanna vs. woodland), by landscape (open vs. wooded), and by sites-by-landscape. We then made pair-wise comparisons among the resultant six combinations of the site-by-landscape matrix. We used Sørensen distances as the similarity index and considered treatment effects significant at $p < 0.05$.

We used nonmetric multidimensional scaling (NMS) to ordinate sites by bird community composition and a second matrix of site- and landscape variables to examine associations between these environmental variables and the ordination axes (McCune and Mefford, 1999). We used Bray-Curtis as our distance measure for the ordination, as it is considered appropriate for ecological data (McCune and Grace, 2002). The second landscape matrix included the following variables: canopy cover, number of trees, snags, and sapling/ha, percent rowcrop agriculture, grassland, and forest (within 1 km). We used Pearson correlation coefficients to relate NMS axes to the environmental variables, and NMS axes to bird species axis scores. Specifications for the final NMS run included three axes, a random starting configuration on 30 runs with real data, and a final stability criterion of 0.0046 based on 20 iterations of randomized data (McCune and Grace, 2002).

To evaluate differences in bird species richness, abundance, and guild composition, we used two-way analysis of variance (ANOVA), with site types (woodland versus savanna) and landscape (wooded versus open) as independent variables treated as fixed factors. This resulted in four treatment levels, with four replicates per level: woodlands in a woodland landscape (woodland/woodland landscape), savannas in a woodland landscape (savanna/woodland landscape), woodlands in an open landscape (woodland/open), and savanna in an open landscape (savanna/open). Dependent variables were species richness, total abundance, combined PIF score, and the percent of species which were insectivores, cavity nesters, area sensitive species, edge species, short distance migrants, and species with BBS declining or PIF conservation status. To control for differences in bird abundance among the four treatments, guild and conservation status data were converted to proportions of species/site prior to analyses. We also used the same model to test estimated species richness using rarefaction, using Chao 1 as the richness estimator (Chao, 1987; Colwell, 2005), in order to ensure that any differences in richness were not driven by differences in the ability to detect species between woodland and savanna sites.

We tabulated the maximum number of individuals for each species counted at each point at any one time across all three sampling periods during a given year. We then averaged these values across the 2 years of sampling and used this figure in all analyses (hereafter referred to as average maximum counts). To reduce the importance of outliers in the ordinations, we eliminated species with only one occurrence from the multivariate analyses (McCune and Grace, 2002).

3. Results

MRPP analysis showed that, overall, breeding bird community composition differed at the site level between woodlands

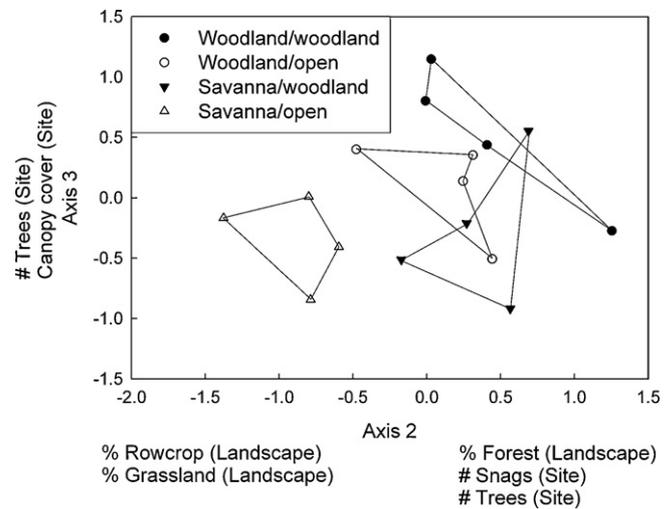


Fig. 1. Nonmetric multidimensional scaling (NMS) ordination of Midwestern savanna and woodland breeding bird communities located within open and woodland landscapes. Axes 2 and 3 are orthogonal and account for 42% and 30% of the variation in community data, respectively. Site- and landscape-level variables associated with both axes are presented in the figure margin.

and savannas (A [the chance-corrected within-group agreement statistic] = 0.028, $p = 0.02$), and at the landscape level between open and woodland landscapes ($A = 0.030$, $p = 0.02$). The magnitude of these differences was elevated for the interaction between site and landscape factors ($A = 0.081$, $p = 0.0006$). Savanna in open landscapes was distinct from each of the other three treatment types: savanna/woodland landscape ($A = 0.11$, $p = 0.007$); woodland/woodland landscape ($A = 0.14$, $p = 0.005$), and woodland/open landscape ($A = 0.10$, $p = 0.02$). Woodland/open landscape sites were distinct in composition from the woodland/woodland landscape sites ($A = 0.05$, $p = 0.05$).

The NMS ordination showed that savanna/open landscape sites were distinct from the woodland/woodland sites, with the other two site types of intermediate community composition (Fig. 1). Final stress for the ordination was 11.96 (stress values <20 are considered acceptable solutions, particularly those close to 10; McCune and Grace, 2002), with substantial contribution to stress reduction from the first three axes only. Axes 2 and 3 together accounted for 72% of the variation in bird species composition, while axis 1 accounted for only four percent of the variation. We, therefore, only further considered axes 2 and 3. Axis 2 accounted for 42% of the variation, with woodland/woodland sites clustered together on the positive end of the axis and savanna/open sites clustered together on the negative portion. The positive portion of the axis was associated with percent of forest in the landscape ($r = 0.37$) and with the number of snags ($r = 0.66$) and trees/ha ($r = 0.51$) at the site, and the negative portion associated with the amount of row crop agriculture ($r = -0.47$) and grassland ($r = -0.37$) in the surrounding landscape (Fig. 1). Axis 3 was associated with 30% of the variation, again separating woodland/woodland and savanna/open sites, although less clearly than Axis 2. The positive portion of the axis, where the woodland sites tended to cluster, was associated with canopy cover ($r = 0.71$) and the number of trees/ha ($r = 0.49$) at the site (Fig. 1).

We examined bird species underlying the patterns observed in the NMS analysis. We used Pearson correlation values between the axis scores and species scores, and considered birds significantly correlated with $r > 0.43$ or $r < -0.43$ ($p < 0.1$ for d.f. = 14). Birds associated with the negative or savanna/open portion of axis 2 require habitats with a mixture of grass, shrubs and other scattered woody vegetation (i.e., successional habitat) and included Brown Thrasher,

Table 2

Mean frequency of occurrence (maximum count) averaged over two years for species occurring in restored savannas and untreated closed canopy forests in the Midwest, U.S.A. S/O = savanna/open landscape; S/W = savanna/woodland landscape; W/O = woodland/open landscape; W/W = woodland/woodland landscape.

Species	S/O	S/W	W/O	W/W
Acadian Flycatcher	0.3	0.0	0.0	0.0
American Crow	0.3	0.0	0.1	0.0
American Goldfinch	1.4	2.5	1.6	1.1
American Redstart	0.4	0.9	0.3	0.5
American Robin	1.1	0.5	0.4	0.1
Baltimore Oriole	1.4	1.1	1.4	0.5
Barn Swallow	0.3	0.0	0.0	0.0
Barred Owl	0.0	0.0	0.3	0.0
Black-capped Chickadee	0.0	0.8	0.4	0.9
Blue-gray Gnatcatcher	0.9	1.6	0.9	1.1
Blue Jay	1.0	0.8	1.0	1.0
Brown Creeper	0.0	0.0	0.0	0.3
Brown-headed Cowbird	2.0	0.8	0.5	0.3
Brown Thrasher	0.5	0.1	0.0	0.0
Cedar Waxwing	0.4	0.0	0.0	0.0
Chimney Swift	0.0	0.3	0.0	0.0
Chipping Sparrow	1.1	0.0	0.0	0.0
Common Grackle	0.3	0.0	0.0	0.0
Common Yellowthroat	1.3	0.0	0.1	0.0
Cooper's Hawk	0.0	0.3	0.0	0.0
Dickcissel	0.3	0.0	0.0	0.0
Downy Woodpecker	0.4	0.6	0.5	0.6
Eastern Bluebird	0.1	0.1	0.0	0.1
Eastern Kingbird	0.3	0.0	0.0	0.0
Eastern phoebe	0.0	0.0	0.3	0.0
Eastern Towhee	0.4	0.4	0.4	0.0
Eastern Wood Peewee	1.3	1.5	1.6	0.8
European starling	0.8	0.0	0.0	0.4
Field Sparrow	1.1	0.0	0.0	0.0
Great Crested Flycatcher	0.5	1.1	1.3	1.0
Grey Catbird	1.5	1.8	0.5	1.3
Hairy Woodpecker	0.4	0.3	0.1	0.4
House Wren	2.3	1.9	2.4	1.9
Indigo Bunting	2.1	1.0	0.4	0.1
Least Flycatcher	0.0	0.3	0.1	0.0
Mourning Dove	0.4	0.1	0.1	0.0
Northern Cardinal	1.3	1.1	1.6	1.1
Northern Flicker	0.8	0.8	0.5	0.4
Northern Parula Warbler	0.3	0.0	0.0	0.0
Ovenbird	0.0	0.4	0.0	0.3
Red-bellied Woodpecker	1.0	0.6	1.1	0.5
Red-eyed Vireo	0.3	1.9	1.1	0.8
Red-headed Woodpecker	0.9	0.0	0.8	0.0
Red-tailed Hawk	0.4	0.0	0.0	0.0
Red-winged Blackbird	0.8	0.0	0.0	0.0
Rose-breasted Grosbeak	1.1	1.1	0.5	0.8
Ruby-throated Hummingbird	0.1	0.0	0.0	0.1
Scarlet Tanager	0.3	0.3	0.0	0.3
Song Sparrow	0.3	0.3	0.0	0.0
Tree Swallow	0.0	0.0	0.1	0.3
Tufted Titmouse	0.1	0.5	0.0	0.6
Turkey	0.0	0.3	0.0	0.0
White Breasted Nuthatch	1.3	0.9	1.4	0.9
Wood Duck	0.0	0.3	0.0	0.0
Wood Thrush	0.0	0.0	0.0	0.3
Yellow-bellied Sapsucker	0.0	0.0	0.0	0.3
Yellow-billed Cuckoo	0.0	0.1	0.3	0.0
Yellow-throated Vireo	0.4	0.8	0.8	0.5
Yellow Warbler	0.0	0.0	0.3	0.0

Brown-headed cowbird, Chipping Sparrow, Common Yellowthroat, Field Sparrow, Indigo Bunting, Red-headed Woodpecker, Rose-breasted Grosbeak. Birds associated with the positive portion of this axis were typical forest birds, including American Redstart, Blue-gray Gnatcatcher, Great crested flycatcher, Ovenbird, and Red-eyed and Yellow-throated vireos. Birds associated with the positive portion of axis 3 included Black-capped Chickadee, Downy Woodpecker, Northern Cardinal, Ovenbird, Tufted Titmouse, and Wood thrush (Fig. 1).

Table 3

Comparison of bird communities from oak savannas and woodlands (sites), located within woodland or open landscape. Numbers are mean percent of species with each trait, with the exception of richness and detections and composite PIF score. S/O = savanna/open landscape; S/W = savanna/woodland landscape; W/O = woodland/open landscape; W/W = woodland/woodland landscape. See Table 4 for statistical comparison of site types.

	S/O	S/W	W/O	W/W
Species richness	28.0	23.8	21.5	20.0
Number of detections	32.3	27.5	22.9	19.3
Estimated total richness (Chao 1)	33.8	30.8	26.5	24.1
<i>Primary food type</i>				
Insectivores	58.9	41.4	36.9	38.3
Omnivores	41.1	58.6	63.2	61.8
<i>Food substrate</i>				
Air	10.7	12.1	17.7	9.9
Bark	9.5	9.5	14.7	14.5
Ground	42.3	25.8	22.5	27.1
Shrub	24.2	28.3	24.7	27.9
Tree	13.2	24.4	20.4	20.5
<i>Nest substrate</i>				
Cavity	28.4	30.2	39.8	42.7
Shrub	42.9	36.1	25.9	29.7
Tree	28.7	33.6	34.2	27.6
<i>Migratory status</i>				
Neotropical migrant	48.0	57.7	51.6	53.4
Resident year round	23.5	24.6	31.4	35.5
Short distance migrant	28.5	17.7	17.0	11.1
<i>Conservation status</i>				
Parasitized by cowbirds	35.1	34.2	27.7	30.9
Edge species	69.9	44.9	47.7	38.8
Area sensitive	36.3	54.4	52.2	52.4
Habitat specialist	27.7	42.6	38.9	42.3
BBS declining	32.2	25.7	29.2	17.5
Combined PIF score	12.1	11.8	12.0	11.7
PIF conservation status	17.4	12.6	18.4	10.9
<i>Other</i>				
Benefit to agriculture	73.3	53.5	58.4	48.7

The frequency distribution of individual species showed that a number of species were restricted to savanna sites in the open landscape, including Acadian Flycatcher, Chipping Sparrow, Dickcissel, Eastern Kingbird, Eastern Bluebird, Field Sparrow and Red-tailed Hawk. Others were restricted to just savanna sites, including Brown Thrasher and Song Sparrow (Table 2). Red-headed Woodpecker, a species of particular conservation concern, was found in both savanna and woodland sites, but only within the open landscape. Conversely, Barred Owl, Brown Creeper, Eastern Phoebe, Tree Swallow, Wood Thrush and Yellow-bellied Sapsucker were confined to woodland sites in the woodland landscape (Table 2). Ovenbird was only found in the woodland landscape (Table 2).

Site and landscape scales were both important explanatory variables in the analysis of species richness, number of detections, estimated richness, guilds, and conservation status (Tables 3 and 4). These variables showed that savannas and woodlands support different groups of birds. Savanna sites had the greatest number of detections (i.e., recorded individuals) and the highest species richness. Richness estimated by rarefaction suggested that we recorded 77–83% of species inhabiting our sites (Table 3), with marginally significant greater estimated richness at savanna sites (Table 4). There was a trend for savannas in the open landscape to have the highest number of detections (Tables 3 and 4), but no evidence for an effect of detection bias on richness: we detected 77–83% of species in savannas and 81–83% of species in woodlands. Savannas in the open landscape had the highest percent of ground feeders as reflected in the significant interaction term from the ANOVA (Tables 3 and 4). Savannas, irrespective of landscape, had the highest proportion of insectivores and shrub nesters and lowest of

Table 4

Two-way Analysis of variance for bird communities from oak savannas and woodlands (sites), located within woodland or open landscape. *p*-Values in bold are significant at *p* < 0.05.

	MS landscape	MS site	MS interaction	MS error	<i>p</i> -Value Landscape	<i>p</i> -Value Site	<i>p</i> -Value Interaction
Species richness	33.1	105.1	7.6	9.7	0.09	0.006	0.40
Number of bird occurrences	70.1	310.6	1.3	17.0	0.06	0.001	0.80
Estimated richness (Chao 1)	28.9	193.9	0.4	54.5	0.50	0.08	0.94
<i>Primary food type</i>							
Insectivores (omnivores the same)	258.7	632.7	356.2	70.7	0.08	0.01	0.04
<i>Food substrate</i>							
Air	40.9	23.0	85.2	14.8	0.12	0.24	0.03
Bark	0.1	105.8	0.02	16.9	0.95	0.03	0.97
Ground	142.6	340.7	447.4	51.1	0.12	0.02	0.01
Shrub	54.2	0.02	0.6	41.4	0.27	0.98	0.91
Tree	126.3	10.5	121.4	49.7	0.14	0.65	0.14
<i>Nest substrate</i>							
Cavity	23.6	562.3	1.0	75.9	0.59	0.02	0.91
Shrub	9.4	544.8	112.6	55.3	0.69	0.009	0.18
Tree	3.2	0.1	134.5	45.0	0.79	0.96	0.11
<i>Migratory status</i>							
Neotropical migrant	130.9	0.6	63.5	57.1	0.1557	0.92	0.31
Resident	26.5	356.3	9.6	67.8	0.5435	0.04	0.71
Short distance migrant	275.3	327.9	23.7	58.6	0.05	0.04	0.54
<i>Conservation status</i>							
Parasitized by cowbirds	5.7	113.3	17.2	71.7	0.78	0.23	0.63
Edge species	1148.9	792.1	258.4	83.6	0.003	0.01	0.10
Area sensitive	335.9	192.6	318.2	104.0	0.09	0.20	0.11
Habitat specialist	335.4	118.2	132.8	103.7	0.09	0.31	0.28
BBS declining	0.15	0.03	0.007	0.01	0.002	0.11	0.40
Combined PIF score	0.45	0.04	0.003	0.07	0.02	0.46	0.84
PIF conservation status	150.6	0.47	7.0	29.9	0.04	0.90	0.64
<i>Other</i>							
Benefit to agriculture	867.7	392.1	102.5	98.5	0.01	0.07	0.33

omnivores. Wooded sites in both landscapes had a higher percentage of bark gleaners, cavity nesters, and year-round residents when compared to savannas (Tables 3 and 4).

The highest percent of edge species were found in the savanna sites in the open landscape, while the wooded sites in the open landscape had a higher percent of these species compared to the wooded sites in the wooded landscape. Sites in the open landscape, irrespective of whether they were savannas or woodlands, supported the highest percent of BBS declining species, and highest percent of species with PIF conservation status. The species in these sites also averaged the highest PIF combined score. However, the three combinations that included woodland supported a much higher percent of area sensitive and habitat specialist species (i.e., savanna in the open landscape supported a relatively low percent of these species; Tables 3 and 4).

4. Discussion

In this study, the outcome of site-level management for breeding bird communities depended on the composition of the surrounding landscape. Restored savannas were associated with a different breeding bird community than woodland sites, but only when surrounded by an open landscape. By considering individual species, guilds, and conservation status, we found that multiple arrays of sites and landscapes provided needed habitat for breeding birds. For example, restored savannas had the highest species richness and number of detections, and those in the open landscape had the highest percent of ground feeders, shrub nesters, and edge species. Savanna and woodland sites in the open landscape had the highest percent of species of conservation concern using BBS and PIF data. At both the site and landscape level, woodland was associated with a higher percent of area sensitive and habitat specialist species.

By evaluating site-level management and landscape context, our results demonstrate the potential for Midwestern savanna and woodland management to support two groups of declining birds – species that use successional, edge, and shrubland habitats and forest interior species. We believe that the intensive investment required to restore savanna in this region would yield the best return when focused on sites located on the margins of intact forest situated in open country. In this way, large patches of woodland would be left intact to promote area sensitive and forest interior bird species. This approach would combine the benefits of site-level savanna restoration with the benefits of open country landscape to support birds of conservation concern that use successional habitats. At the same time, this approach has the least potential to disrupt habitat for forest birds, particularly area sensitive species. The need to manage for both groups of species has been identified as a key forest bird management issue for eastern North America (Hunter et al., 2001).

Restoring savannas in the open country landscape may also be highly beneficial for breeding birds, although this approach may need to be taken with some caution: if restored savannas are embedded in a landscape of intensive cropland, restoration sites could become sink habitats. However, the outcome might differ if restored savannas have sufficient remnant vegetation in the surrounding landscape; this component of landscape context needs further study. It would also be fruitful to study similar combinations of site and landscape level variables in other regions to see if these patterns can be generalized.

Forest interior birds found in lower frequencies in restored savannas in this and other studies, including Ovenbird, Red-eyed Vireo, Scarlet Tanager and Wood Thrush (Davis et al., 2000; Brawn, 2006), could be supported by maintaining intact forest. At the same time, if restored savannas retained sufficient shrub and other woody vegetation (Davis et al., 2000; Brawn, 2006), we could

meet the habitat requirements of species of conservation concern that use early successional habitat, edges, and shrublands, including Brown Thrasher, Eastern Bluebird, Field Sparrow and Indigo Bunting (Robinson et al., 1995; Davis et al., 2000; Blake, 2005; Brawn, 2006).

Landscape factors have been shown to influence site-level processes for other habitat types and bird communities, indicating that our findings may apply to other systems and species. In California, habitat patches embedded within a landscape of the same habitat were more similar in avian community composition than patches embedded in a different landscape type, because habitat specialists co-occurred in patches and the surrounding landscape (Sisk et al., 1997). In Idaho, brood parasitism rates in riparian areas increased with presence of adjacent forested buffers but decreased with amount of surrounding agricultural land use (Tewksbury et al., 2006). In our study, forest interior birds were promoted in forested landscapes, supporting past findings of buffer effects (Sisk et al., 1997; Tewksbury et al., 2006). However, we also found that open country landscapes promoted savanna bird species, demonstrating the importance of dissimilar patch and surrounding landscapes for supporting ecotonal animal assemblages.

Other studies have also found landscape effects to be species or guild specific. In New Brunswick, landscape features were only an important explanatory variable for the occurrence of woodpeckers with larger home ranges (Warren et al., 2005). The frequency of open-nesting species in pine plantations in Chile depended mostly on a patch character (understory), while abundance of cavity nesting species in plantations increased with landscape characters (proximity to native forests and creeks) (Estades and Temple, 1999). An Ontario study showed the abundance of ovenbirds depended on amount of surrounding forest cover but this was not the case for two other forest specialist species (Lee et al., 2002). In Los Tuxtlas, Mexico, bird species that were restricted to forest habitat were more influenced by patch level factors than by landscape, but species without this restriction were more strongly influenced by the amount of arboreal vegetation than by characteristics of patches themselves (Graham and Blake, 2001). We also note that strong landscape effects are not a universal finding for birds (Lichstein et al., 2002), butterflies (Collinge et al., 2003), or other invertebrate

taxa (Mazerolle and Villard, 1999). Thus, even though landscape level effects are well-established in general, there is a need to determine if there are consistent situations where landscape effects do and do not apply.

We assumed that bird community composition provided a meaningful estimate of habitat quality. Confirmation of our conclusions requires verification that the bird frequencies we analyzed translate into actual nesting success (productivity and survival). The little data on nest success from restored savannas in this region provide mixed conclusions (Aquilani et al., 2000; Brawn, 2006). It would also be a fruitful line of future research to quantify the nesting success in restored savannas and to relate this variation to both landscape composition and to site-level variation in factors such as shrub cover and patch shape.

5. Conclusion

Our results provide a guide for ongoing savanna restoration work that has a high potential to benefit declining open country bird species while preserving habitat for forest interior species. Our hope is that these restoration efforts will increasingly involve teams of both researchers and land managers working within an adaptive management framework. This type of collaboration promises to help answer both fundamental research questions, and to provide information to benefit on the ground conservation work by land managers (Dettman and Mabry, 2008).

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Appendix A.

See Table A1.

Table A1

Bird species occurring at savanna and woodland survey points in a study of breeding bird communities in central Iowa, USA. to interpret guild and conservation status codes. See Appendix B.

Species	Food type	Food substrate	Nest substrate	Migratory status	Edge species	Area sensitive	Habitat specialist	BBS negative	Combined PIF value	PIF conservation species
Acadian Flycatcher (<i>Empidonax vireescens</i>)	I	A	T	NT	N	Y	Y	Y	16	Y
American Crow (<i>Corvus brachyrhynchos</i>)	O	G	T	R	Y	N	N	N	10	N
American Goldfinch (<i>Carduelis tristis</i>)	O	S	S	SD	Y	N	N	N	13	N
American Redstart (<i>Setophaga ruticilla</i>)	I	S	S	NT	N	Y	Y	N	13	N
American Robin (<i>Turdus migratorius</i>)	O	G	T	SD	Y	N	N	N	9	N
Baltimore Oriole (<i>Icterus galbula</i>)	O	T	T	NT	Y	Y	Y	N	18	Y
Barn Swallow (<i>Hirundo rustica</i>)	I	A	T	NT	Y	N	N	N	11	N
Barred Owl (<i>Strix varia</i>)	C	G	C	R	N	N	Y	N	13	N
Black-capped Chickadee (<i>Poecile atricapilla</i>)	I	S	C	R	N	N	N	N	11	N
Blue Jay (<i>Cyanocitta cristata</i>)	O	G	T	R	N	N	Y	Y	12	N
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	I	T	T	NT	N	Y	N	N	11	N
Brown Creeper (<i>Certhia americana</i>)	I	B	T	SD	N	Y	Y	N	10	N
Brown Thrasher (<i>Toxostoma rufum</i>)	O	G	S	SD	Y	N	N	Y	16	Y
Brown-headed Cowbird (<i>Molothrus ater</i>)	O	G	T	SD	Y	N	N	N	10	N
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	O	A	T	SD	Y	N	Y	N	9	N
Chimney Swift (<i>Chaetura pelagica</i>)	I	A	T	NT	Y	N	Y	N	15	Y
Chipping Sparrow (<i>Spizella passerine</i>)	O	G	S	NT	Y	N	Y	N	8	N
Common Grackle (<i>Quiscalus quiscula</i>)	O	G	T	SD	Y	N	N	N	11	N
Common Yellowthroat (<i>Geothlypis trichas</i>)	I	S	S	NT	Y	N	N	N	13	N
Cooper's Hawk (<i>Accipiter cooperii</i>)	O	A	T	SD	N	Y	Y	N	11	N
Dickcissel (<i>Spiza americana</i>)	O	G	S	NT	Y	Y	N	Y	18	N
Downy Woodpecker (<i>Picoides pubescens</i>)	I	B	C	R	N	Y	N	N	11	N
Eastern Bluebird (<i>Sialia sialis</i>)	I	G	C	SD	Y	Y	N	N	11	N
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	I	A	T	NT	Y	Y	N	Y	15	Y
Eastern Phoebe (<i>Sayornis phoebe</i>)	I	A	T	SD	N	Y	N	N	11	N
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	O	G	S	SD	Y	N	N	Y	12	N
Eastern Wood Peewee (<i>Contopus virens</i>)	I	A	T	NT	N	Y	Y	Y	13	N
European Starling (<i>Sturnus vulgaris</i>)	O	G	C	R	Y	N	N	N	10	N
Field Sparrow (<i>Spizella pusilla</i>)	O	G	S	SD	Y	Y	N	Y	17	Y
Gray Catbird (<i>Dumetella carolinensis</i>)	O	G	S	NT	Y	N	Y	N	12	N
Great crested Flycatcher (<i>Myiarchus crinitus</i>)	I	A	C	NT	N	Y	N	Y	14	Y
Hairy Woodpecker (<i>Picoides villosus</i>)	I	B	C	R	N	N	Y	N	11	N
House Wren (<i>Troglodytes aedon</i>)	I	S	C	NT	Y	N	N	N	10	N
Indigo Bunting (<i>Passerina cyanea</i>)	O	S	S	NT	Y	N	N	Y	11	N
Least Flycatcher (<i>Empidonax minimus</i>)	I	A	T	NT	N	Y	Y	Y	9	N
Mourning Dove (<i>Empidonax minimus</i>)	O	G	T	SD	Y	N	N	N	10	N
Northern Cardinal (<i>Cardinalis cardinalis</i>)	O	G	S	R	Y	N	N	N	9	N
Northern Flicker (<i>Colaptes auratus</i>)	I	G	C	SD	Y	Y	N	Y	16	Y
Northern Parula (<i>Parula americana</i>)	I	T	T	NT	N	Y	Y	N	12	N
Ovenbird (<i>Seiurus aurocapilla</i>)	I	G	G	NT	N	Y	Y	N	12	N
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	I	B	C	R	N	Y	Y	N	10	N
Red-eyed Vireo (<i>Vireo olivaceus</i>)	I	T	T	NT	N	Y	Y	N	10	N
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	I	A	C	SD	Y	N	N	Y	19	Y
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	C	G	T	SD	Y	N	Y	N	10	N
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	O	G	S	SD	Y	N	N	Y	13	N
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	O	T	S	NT	N	Y	N	N	13	N
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	O	S	T	NT	N	N	N	N	11	N
Scarlet Tanager (<i>Piranga olivacea</i>)	I	T	T	NT	N	Y	Y	N	13	N
Song Sparrow (<i>Melospiza melodia</i>)	O	S	S	SD	Y	N	N	N	10	N
Tree Swallow (<i>Tachycineta bicolor</i>)	I	A	C	SD	Y	N	N	N	8	N
Tufted Titmouse (<i>Baeolophus bicolor</i>)	I	S	C	R	N	Y	Y	N	12	N
White Breasted Nuthatch (<i>Sitta carolinensis</i>)	I	B	C	R	N	Y	N	N	9	N
Wild Turkey (<i>Meleagris gallopavo</i>)	O	G	S	R	N	Y	Y	N	12	N
Wood Duck (<i>Aix sponsa</i>)	O	G	C	SD	N	N	Y	N	NA	N
Wood Thrush (<i>Hylocichla mustelina</i>)	O	G	S	NT	N	Y	Y	N	14	Y
Yellow Warbler (<i>Dendroica petechia</i>)	I	S	S	NT	Y	N	N	N	9	N
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	O	B	C	SD	N	Y	Y	N	10	N
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	I	S	S	NT	N	Y	Y	Y	15	Y
Yellow-throated Vireo (<i>Dendroica dominica</i>)	I	T	T	NT	N	Y	Y	N	12	N

Appendix B.

See Table B1.

Table B1

Explanation of guild codes used to analyze response of breeding birds to savanna restoration.

<i>Food type</i>
I = insectivore
O = omnivore
*G = granivore
*C = carnivore
<i>Food substrate</i>
A = air
B = bark
F = flower (grouped with shrub)
G = ground
S = shrubs or lower tree canopy
T = upper tree canopy
<i>Nest substrate</i>
C = tree cavities
S = shrubs or saplings
T = tree branches
Bu = human structures (four species, not included in analysis)
G = ground/herbaceous vegetation (one species, lumped with shrub)
<i>Migratory status</i>
nt = neotropical migrant
r = regular
sd = short distance migrant
<i>Edge species</i>
Y = yes
N = no
<i>Area sensitive</i>
Y = yes
N = no
<i>Habitat specialist</i>
Y = yes
N = no
<i>BBS negative</i>
Y = yes
N = no
<i>PIF = Partners in Flight combined score</i>
<i>PIF species of conservation concern</i> (continental or regional species of concern/stewardship)
Y = yes
N = no

References

- Anderson, R.C., Schwegman, J.E., 1991. Twenty years of vegetational change on a Southern Illinois barren. *Natural Areas Journal* 11, 100–107.
- Aquilani, S.M., LeBlanc, D.C., Morrell, T.E., 2000. The effects of prescribed surface fires on ground- and shrub-nesting neotropical migratory birds in a mature Indiana oak forest, USA. *Natural Areas Journal* 20, 317–324.
- Asbjornsen, H., Brudvig, L.A., Mabry, C.M., Evans, C.W., Karnitz, H.M., 2005. Defining reference information for restoring ecologically rare tallgrass oak savannas in the Midwest. *Journal of Forestry* 103, 345–350.
- Asbjornsen, H., Tomer, M.D., Gomez-Cardenas, M., Brudvig, L.A., Greenan, C.M., Schilling, K., 2007. Tree and stand transpiration in a Midwestern bur oak savanna after elm encroachment and restoration thinning. *Forest Ecology and Management* 247, 209–219.
- Askins, R.A., 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology* 11, 1–34.
- Bell, S.S., Fonseca, M.S., Motten, L.B., 1997. Linking restoration and landscape ecology. *Restoration Ecology* 5, 318–323.
- Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation* 133, 250–264.
- Best, L.B., Freemark, K.E., Steiner, B.S., Bergin, T.M., 1996. Life history and status classifications of birds breeding in Iowa. *Journal of the Iowa Academy of Sciences* 103, 34–54.
- Blake, J.G., 2005. Effects of prescribed burning on distribution and abundance of birds in closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation* 121, 519–531.
- Brawn, J.D., 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20, 460–469.
- Brawn, J.D., Robinson, S.K., 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* 77, 3–12.
- Brawn, J.D., Robinson, S.K., Thompson III, F.R., 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32, 251–276.
- Brudvig, L.A., 2010. Woody encroachment removal from Midwestern oak savannas alters understory diversity across space and time. *Restoration Ecology* 18, 74–84.
- Brudvig, L.A., Asbjornsen, H., 2007. Stand structure, composition and regeneration dynamics following removal of encroaching woody vegetation from Midwestern oak savannas. *Forest Ecology and Management* 244, 112–121.
- Chao, A., 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43, 783–791.
- Collinge, S.K., Prudic, K.L., Oliver, J.C., 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology* 17, 178–187.
- Colwell, R.K., 2005. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 7.5. User's Guide and Application. Published at: <http://purl.oclc.org/estimates>.
- Cottam, G., 1949. The phytosociology of an oak woods in southwestern Wisconsin. *Ecology* 30, 271–287.
- Davis, M.A., Peterson, D.W., Reich, P.B., Crozier, M., Query, T., Mitchell, E., Huntington, J., Bazakas, P., 2000. Restoring savanna using fire: impact on the breeding bird community. *Restoration Ecology* 8, 30–40.
- Dettman, C.L., Mabry, C.M., 2008. Lessons learned about research and management: a case study from a Midwest lowland savanna, USA. *Restoration Ecology* 16, 1–10.
- Dettman, C.L., Mabry, C.M., Shulte, L.A., 2009. Restoration of Midwestern U.S. Savannas: one size does not fit all. *Restoration Ecology* 17, 772–783.
- Estates, C.F., Temple, S.A., 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecological Applications* 9, 573–585.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34, 487–515.
- Gleason, H.A., 1922. The vegetational history of the middlewest. *Annals of the Association of American Geographers* 12, 39–85.
- Graham, C.H., Blake, J.G., 2001. Influence of patch- and landscape-level factors on birds assemblages in a fragmented tropical landscape. *Ecological Applications* 11, 1709–1721.
- Grundel, R., Pavlovic, N.B., 2007. Distinctiveness, use, and value of Midwestern oak savannas and woodlands as avian habitats. *The Auk* 124, 969–985.
- Grundel, R., Pavlovic, N.B., 2008. Using conservation value to assess land restoration and management alternatives across a degraded oak savanna landscape. *Journal of Applied Ecology* 45, 315–324.
- Hobbs, R.J., Norton, D.A., 1996. Toward a conceptual framework for restoration ecology. *Restoration Ecology* 4, 93–110.
- Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29, 440–455.
- Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation, and restoration. *Restoration Ecology* 7, 309–315.
- King, D.I., DeGraaf, R.M., Griffin, C.R., 2001. Productivity of early successional shrubland birds in clearcuts and groupcuts in an eastern deciduous forest. *Journal of Wildlife Management* 65, 345–350.
- Klopatek, J.M., Olson, R.J., Emerson, C.J., Jones, J.L., 1979. Land-use conflicts with natural vegetation in the United States. *Environmental Conservation* 6, 191–199.
- Lee, M., Fahrig, L., Freemark, K., Currie, D.L., 2002. Importance of patch vs. landscape scale on selected forest birds. *Oikos* 96, 110–118.
- Lichstein, J.W., Simons, T.R., Franzreb, K.E., 2002. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications* 12, 836–857.
- Marzluff, J.M., Ewing, K., 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* 9, 280–292.
- Mazerolle, M.J., Villard, M., 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. *EcoScience* 6, 117–124.
- McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 4.34. MjM Software, Gleneden Beach, OR.
- Norris, W.R., Hemesath, L.M., Debinski, D.M., Farrar, D.R., 2003. Does bird community composition vary along a disturbance gradient in Northeast Iowa, USA forests? *Natural Areas Journal* 23, 262–273.
- Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11, 914–927.
- Potts, R., Gustafson, E., Stewart, S.I., Thompson, F.R., Bergen, K., Brown, D.G., Hammer, R., Radeloff, V., Bengston, D., Sauer, J., Sturtevant, B., 2004. The Changing Midwest Assessment: Land Cover, Natural Resources and People. GTR-NC-250, USDA Forest Service, North Central Research Station, St. Paul, MN.
- Robinson, S.K., Thompson III, F.K., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267, 1987–1990.
- Ruth, J.M., Petit, D.R., Sauer, J.R., Samuel, M.D., Johnson, F.A., Fornwall, M.D., Korschgen, C.E., Bennett, J.P., 2003. Science for avian conservation: priorities for the new millennium. *The Auk* 120, 204–211.

- Scott, T.A., Wehtje, W., Wehtje, M., 2001. The need for strategic planning in passive restoration of wildlife populations. *Restoration Ecology* 9, 262–271.
- Sisk, T.D., Haddad, N.M., Ehrlich, P.R., 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecological Applications* 7, 1170–1180.
- Temple, S.A., 1998. Surviving where ecosystems meet: ecotonal animal communities of Midwestern oak savannas and woodlands. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 86, 207–222.
- Tewksbury, J.J., Garner, L., Garner, S., Lloyd, J.D., Saab, V., Martin, T.E., 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. *Ecology* 87, 759–768.
- Warren, T.L., Betts, M.G., Diamond, A.W., Forbes, G.J., 2005. The influence of local habitat and landscape composition on cavity-nesting birds in a forested mosaic. *Forest Ecology and Management* 214, 331–343.
- Whitcomb, R.F., 1987. North American forests and grasslands: biotic conservation. In: Saunders, D.A., Arnold, G.W., Burbidge, A.A., Hopkins, A.J.M. (Eds.), *Nature Conservation: the Role of Remnants of Native Vegetation*. Surry Beatty & Sons Pty Limited, Australia, pp. 163–176.
- Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66, 1211–1214.
- Yahner, R.H., 2003. Responses of bird communities to early successional habitat in a managed landscape. *Wilson Bulletin* 115, 292–298.