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ECOSPHERE

Another tool in the toolbox? Using fire and grazing to promote bird diversity in highly fragmented landscapes

FINN C. PILLSBURY,[1,5],† JAMES R. MILLER,[2] DIANE M. DEBINSKI,[3] AND DAVID M. ENGLE[4]

[1]*Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa USA*
[2]*Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, Illinois USA*
[3]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa USA*
[4]*Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, Oklahoma USA*

Abstract. The grasslands of central North America have experienced drastic reductions in extent, removal of historic disturbance patterns, and homogenization of remaining fragments. This has resulted in steep declines for a broad swath of grassland biodiversity. Recent work in relatively extensive grasslands has demonstrated that mimicking historic disturbance patterns using a fire-grazing interaction can increase the abundance and diversity of grassland birds through increased habitat heterogeneity. We examined the efficacy of this management strategy for promoting avian diversity in highly fragmented landscapes, which represent the bulk of remaining grassland bird habitats in the tallgrass prairie region. We quantified the population density of obligate and facultative grassland bird species along transects in 13 experimental research pastures in the Grand River Grasslands of Iowa and Missouri (USA), divided among three treatments: 1) spatially discrete fires and free access by cattle ("patch-burn grazed"), 2) free access by cattle and a single complete burn ("grazed-and-burned"), and 3) a single complete burn with no cattle ("burned-only"). We expected that patch-burn grazing would produce a bird community that overlapped that of the grazed-and-burned and burned-only treatments, because it would provide habitat for species associated with both. However, an analysis of similarity (ANOSIM) showed that community structure on pastures managed using patch-burn grazing instead diverged significantly from both of the other treatments. Differences in community structure were most highly correlated with visual obstruction and wooded edge density in the landscape, suggesting bird communities are differentiated not only by their structural habitat requirements, but also by the varying degrees of sensitivity to landscape fragmentation of their component species. The future success of this management scheme for fragmented grasslands hinges on if, after an optimal stocking rate is identified, adequate habitat can be maintained for a diverse bird community, or whether fragmentation will perpetually limit the efficacy of this method in these landscapes.

Key words: analysis of similarity; community structure; fire; fragmentation; grassland birds; grazing; heterogeneity; Iowa; Missouri; nonmetric multidimensional scaling.

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[5] Present address: USDA-ARS, Jornada Experimental Range, Las Cruces, New Mexico 88005 USA.

† **E-mail:** fcp@nmsu.edu

INTRODUCTION

In landscapes that evolved with frequent and variable disturbances, fragmentation and homogenization can have especially pronounced impacts on biodiversity (Cousins et al. 2003, Parr and Andersen 2006). Central North American grasslands developed under a regime of fre-

quent, patchy fires and spatiotemporally variable grazing by ungulates, which created a shifting mosaic of vegetation patches of varying composition and structure (Fuhlendorf and Engle 2001, Collins and Smith 2006, Fuhlendorf et al. 2008). Since settlement, these landscapes have become increasingly fragmented, fire has been largely eliminated, and grazing patterns have become more uniform, resulting in the homogenization of remaining grassland fragments (Fuhlendorf and Engle 2001).

This widespread degradation of grassland habitats has spurred increased use of fire and grazing as management tools by agencies, nongovernmental organizations, and private landowners. Where grazing or fire have been reintroduced, however, they are most often used independently, not as the interdependent ecological processes that occurred historically (Collins 2000, Fuhlendorf and Engle 2001, Harrison et al. 2003, Fuhlendorf et al. 2008). The result is continued structural homogeneity, which tends to benefit generalists but is detrimental to species requiring either very recently disturbed or relatively undisturbed grassland habitats (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2008).

The tendency of existing management strategies tools to promote homogeneity has motivated the development of an interactive fire-grazing model that aims to foster habitat heterogeneity both spatially and temporally (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2008). Because grazing animals preferentially forage in the flush of new growth following a fire, applying spatially discrete fires to the landscape over time causes grazers to shift their activities to newly burned areas, allowing less recently burned vegetation to recover. The result is a grassland mosaic in structure and compostion that more closely approximates historical conditions (Fuhlendorf and Engle 2004, Kerby et al. 2007). This management framework has the potential to be a valuable tool in efforts to reverse losses of biodiversity by providing for species with diverse habitat requirements.

Recent work has demonstrated that managing grasslands with a fire-grazing interaction can indeed accommodate a broader diversity of grassland bird species by increasing habitat heterogeneity in time and space (Fuhlendorf et al. 2006, Coppedge et al. 2008). In pastures managed with a fire-grazing interaction, Fuhlendorf et al. (2006) observed much higher diversity in the grassland bird community compared to traditionally managed pastures, as a result of both disturbance-intolerant and disturbance-reliant species being present. Whereas that work was conducted on relatively large pastures (range: 400–900 ha; Fuhlendorf et al. 2006) embedded in extensive grasslands, avian responses to a fire-grazing interaction have not been studied in highly fragmented landscapes, which represent the bulk of remaining grassland bird habitats in the tallgrass region of central North America (Samson and Knopf 1994, With et al. 2008).

In assessing the efficacy of a fire-grazing interaction to promote grassland bird diversity, it is important to understand how landscape structure and spatial scale mediate the response of grassland birds in small, fragmented grasslands. The decrease in patch size and increase in edges that accompany fragmentation have been shown to decrease abundance, nest success, and nest density for many grassland bird species (Herkert 1994*a*, Stephens et al. 2003, Fletcher 2005, Ribic et al. 2009), and mediate the population responses of individual species to grassland habitat structure (Cunningham and Johnson 2006, Renfrew and Ribic 2008). These patterns suggest there are likely many proximate factors, operating at multiple scales, that influence habitat selection and use by grassland birds (Johnson and Igl 2001, Renfrew et al. 2005, Winter et al. 2005, 2006).

We examined patterns of habitat use by grassland birds on experimental pastures embedded in highly fragmented landscapes in southern Iowa and northern Missouri. Employing a combination of univariate and multivariate methods, we compared avian communities in pastures under patch-burn grazing to those in pastures managed using just grazing, and to those in pastures managed only with fire. Our purpose in doing so was to assess not only differences in individual metrics of diversity, but also to understand differences in species composition. Additionally, we examined the role of habitat and landscape characteristics in structuring bird communities, to better understand the specific factors associated with differences among treatments.

METHODS

Study area

In spring 2006, we delineated 13 experimental pastures in the Grand River Grasslands of Ringgold County, Iowa, and Harrison County, Missouri (USA). We selected both state-owned grassland reserves and private grazing lands as study pastures. The pastures ranged in size from 15 to 31 ha and were allocated to one of three treatments: 1) annual burning of spatially distinct patches with free access by cattle (patch-burn grazing, the specific management tool to implement the fire-grazing interaction, $N = 5$; mean area = 30.3 ha), 2) free access by cattle and a single complete burn (grazed-and-burned treatment, representative of practices on private lands, $N = 4$; mean area = 29.4 ha), and 3) no grazing and a single complete burn (burned-only treatment, representative of management practices on reserved lands in the region, $N = 4$; mean area = 20.9 ha). All treatments comprised pastures with and without a recent history of grazing, as well as both remnant and previously tilled acreage. Sites were therefore distributed among treatments nonrandomly, so that each treatment contained a range of land use histories. Land use histories are discussed in detail in McGranahan (2008). Although burning was rare on private land in the study area, grazed-and-burned pastures were subject to a single burn during the final study year to suppress invasive woody species and to maintain a three-year fire-return interval across treatments.

Grazed-and-burned and patch-burn grazing pastures were fenced, and were stocked at the rate of 1.25 animal unit months (AUM) per acre from May 1 to October 1, which is considered moderate for the region (Engle, *pers. obs.*). Each pasture was divided into three patches of approximately equal area. Patches in patch-burn grazing pastures were burned sequentially, one per year beginning in spring 2007, so that by the end of the study all three patches had been burned. All grazed-and-burned and all but one burned-only pastures were burned in spring 2009 (one burned-only pasture was inadvertently burned in spring 2008).

Grassland bird surveys

We counted all birds within 50 m of line transects from May–August of 2006–2009 (2006: n = 7 surveys/transect; 2007: n = 9; 2008: n = 8; 2009: n = 8). Between 1–3 transects ($\bar{x} = 1.92$) were established in each patch in 2006, oriented perpendicular to the patch's long axis. Transects were at least 150 m apart to minimize double counting and at least 50 m from patch edges to avoid counting birds outside the patch boundary. Line transects are preferred to point counts in open habitats, because sampling efficiency is higher and cryptic species are more likely to be observed (Buckland et al. 2001). We recorded the universal transverse mercator coordinates of each transect's start and end points, and used a global positioning system to relocate those points when conducting surveys. Groups of more than two conspecifics were excluded from analyses to reduce bias of late-season flocks. Birds seen flying overhead but not perching within 50 m of a transect were not counted. Surveys were conducted by a single observer between sunrise and approximately 1000 h, when grassland birds are most active (Ralph et al. 1993). Observers rotated visits to each transect to minimize bias. Surveys were not conducted on days of high winds or rain.

Habitat and landscape structure

To examine the relationship between grassland bird communities and habitat features, vegetation composition and structure were measured in 90, 0.5-m^2 quadrats placed at equal intervals along transects within each pasture each year. Habitat use by grassland bird species is consistently attributed to the varied structural requirements among species, so we were especially interested in those habitat features that we expected to differentiate bird communities. Thus, within each quadrat we measured visual obstruction by recording the highest line on a Robel pole that was 50% obscured (Robel et al. 1970). At approximately 1m above ground, one reading was taken in each cardinal direction at a distance of approximately 4 m. We also measured the percent cover of warm-season grasses, cool-season grasses, forbs, legumes, and litter, as these habitat elements each have specific structural attributes. In addition to these functional groups, we also measured the percent cover of *Festuca arundinacea*, a non-native cool-season forage grass with adverse effects on grassland

birds (Warner 1992, Barnes et al. 1995). These measurements used the following cover classes: 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100% (Daubenmire 1959). Because vegetation layers often overlap, total canopy cover could exceed 100% within a given quadrat. In addition to these structural measurements, we also calculated a metric of the extent of within-pasture wooded edges, as wooded edges have been observed to be detrimental to several grassland bird species, e.g., Sedge Wren (*Cistothorus platensis*; Henningsen and Best 2005, Cunningham and Johnson 2006), Grasshopper Sparrow (*Ammodramus savannarum*; Ribic and Sample 2001, Fletcher and Koford 2002), and Bobolink (*Dolichonyx orizivorus*; Fletcher and Koford 2003, Cunningham and Johnson 2006). Within-pasture wooded edge density was defined specifically as:

$$\frac{[\text{Wooded perimeter}] + [\text{Length of linear features}]}{\text{Pasture area}}$$

where linear features are defined as those narrower than 10 m. For wooded features wider than 10 m, we measured the entire perimeter of each feature.

Because landscape context is recognized as an important factor affecting grassland bird population density (e.g., Cunningham and Johnson 2006, Renfrew and Ribic 2008), we calculated several metrics of habitat extent and fragmentation in the landscape surrounding each study pasture. Using ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA), we delineated grass and tree cover around study pastures using 2-m resolution true color digital orthophotos taken during August 2005 (U.S. Department of Agriculture 2005). We specifically looked at two landscape variables that have been identified as correlates of abundance of different species: the amount of grass cover and the density of wooded edges (e.g., Ribic and Sample 2001, Fletcher and Koford 2003, Cunningham and Johnson 2006, Murray et al. 2006) We measured these variables at two different spatial scales: 0–300 m and 300–1000 m from pasture edges. The first scale was chosen to examine the effect of landscape composition and configuration immediately surrounding a pasture. We chose the second scale to examine the importance of landscape characteristics removed from the pastures themselves. We chose a maximum distance of 1000 m because regressions of variance in grass cover and wooded edge density against distance from pasture edges showed an asymptote at 1000 m, beyond which there was no additional uncaptured variance among pastures. Percent cover and edge density metrics (except within-pasture wooded edge density) were calculated using the V-LATE extension of ArcGIS 9.1 (Lang and Tiede 2003).

Data analysis

We calculated an index of observed density of all obligate and facultative bird species to use in our analyses. Observed density was defined as the maximum number of individuals per hectare detected in a pasture during the course of the breeding season. Repeated pasture visits therefore allowed for better estimates of species abundance, given the phenological differences among species.

As a starting point for an investigation of avian response to a fire-grazing interaction, we compared the diversity of obligate and facultative grassland bird species (sensu Vickery et al. 1999) among treatments using a mixed model, with treatment and year as fixed effects, and pasture(year) as a random effect. Species diversity was quantified by species richness (S) and the Shannon diversity index (H).

Because univariate analytical methods can obscure differences in fundamentally multivariate data, we assessed variation in community structure among treatments with an analysis of similarity (ANOSIM), which tests for differences in within-treatment versus among-treatment community dissimilarity and generates a p-value based on 10,000 Monte Carlo simulations (Clarke 1993). We used Bray-Curtis distance as an ecological dissimilarity measure because it is most sensitive to differences in the most abundant species and less sensitive to infrequently observed species. Specifically, the Bray-Curtis dissimilarity metric converts a matrix of species abundances to percent relative abundances of each species in each pasture. This approach therefore makes sense for grassland bird communities which comprise a small number of species, differing only in their relative dominance in the bird community. In the context of this study, percent relative abundance is defined as the observed density of a species in a given

pasture, divided by the sum of observed densities of all species at that pasture. Data from each year were analyzed separately to examine annual differences among treatments. This analysis was conducted using the "anosim" function of the vegan package for R (Oksanen et al. 2010, R Development Core Team 2010).

We used nonmetric multidimensional scaling (NMDS; Kruskal 1964*a*, 1964*b*) to examine community dissimilarity among pastures and among years, using the "metaMDS" function in the vegan package for R (Oksanen et al. 2010). NMDS is an unconstrained, distance-based ordination technique in which the linear distance between pastures in ordination space corresponds to their rank-order dissimilarity as defined by a specified distance metric. We chose this ordination method for two reasons, one ecological and one methodological. First, we were interested in community differences among treatments, and a method that differentiates pastures graphically based on their ecological dissimilarity is conceptually congruous with our study framework. Second, NMDS has fewer restrictive assumptions and is less prone to spurious results than are other methods, and is especially robust to data that are not distributed normally (Fasham 1977, Minchin 1987). An iterative procedure, NMDS uses an algorithm to calculate the arrangement of pastures that best approximates community dissimilarity, maximizing the rank-order correlation between Euclidean distance in ordination space and the values in a dissimilarity matrix. Axes are therefore arbitrary and do not in themselves convey any meaningful information; the key element on which to focus is the relative inter-point distances in ordination space. Goodness-of-fit is measured by stress, which is inversely proportional to this rank order correlation. As in the ANOSIM procedure, we used the Bray-Curtis measure of dissimilarity, but we combined all pasture-year combinations into a single data matrix, thereby measuring ecological dissimilarity in both space and time.

To examine the distribution of individual species in ordination space, we fitted values of the percent relative abundance of a given species for each pasture-year (i.e., observed density divided by the sum of observed densities of all species) using the "ordisurf" function, which fits a smooth surface using thinplate splines with a Gaussian error distribution (Wood 2000, Oksanen et al. 2010). In doing this, we were able to illustrate variation in the relative proportions of individual species across ordination space as a way of visualizing the community differences underlying the resulting ordination diagram. This is a meaningful measure of species distributions in this context because our chosen dissimilarity metric for the analysis (Bray-Curtis) also measures differences among species in percent relative abundance. We used the vector-fitting procedure "envfit" in the vegan package for R (Oksanen et al. 2010) to examine the association of measures of habitat structure and landscape context with patterns of community structure. Fitted vectors are derived from a linear function where the response variable is the value of a given environmental measure at each pasture-year combination. There are k explanatory variables, where k is the number of axes in the ordination. The direction of the vector in k-dimensional ordination space indicates the direction of most rapid change in the variable, and vector length is proportional to the fit of the linear function, r^2. We used 10,000 Monte Carlo simulations to estimate a p-value for each fitted vector.

Results

Contrary to our expectations, patch-burn grazing did not lead to increased structural heterogeneity, as measured by the standard deviation of vegetation height across each pasture (Fig. 1A). Mean vegetation height also did not change greatly during the course of the study, but as expected, burned-only pastures had the highest mean during years 2–4 (Fig. 1B).

We observed 10,404 individual birds representing 63 species during the study, including 11 facultative grassland species and 9 grassland obligate species. A mean of 10.54 grassland bird species occurred at each study pasture, including a mean of 5.41 grassland obligate species. The most frequently observed species were Grasshopper Sparrow (20.0% of all observations), Red-winged Blackbird (*Agelaius phoeniceus*; 13.6%), and Bobolink (12.8%). Grassland obligate birds showed varied responses to the three main management treatments (Table 1). Species richness (S) did not differ significantly among

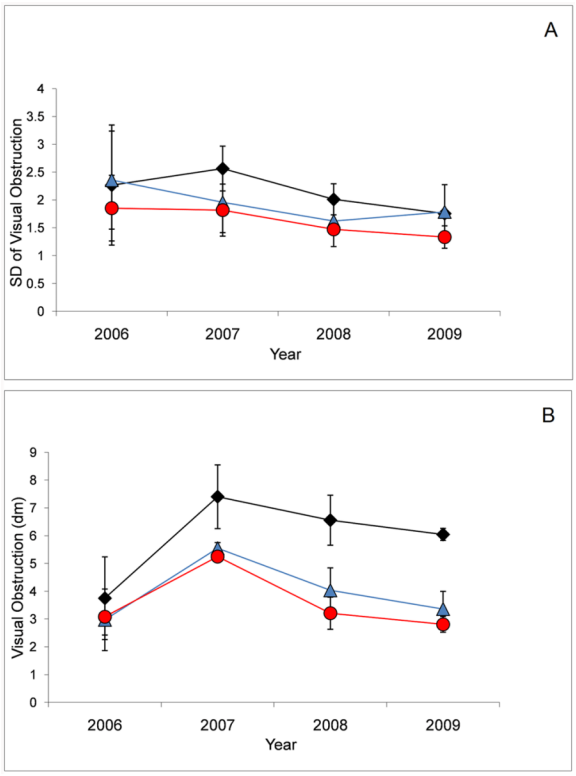


Fig. 1. Mean and standard deviation of visual obstruction on 13 pastures in the Grand River Grasslands, Iowa and Missouri, 2006–2009. Error bars correspond to confidence bounds at $\alpha = 0.05$. Shown are lines for three experimental treatments: patch-burn grazing (circles), grazed-and-burned (triangles), and burned-only (diamonds).

treatments ($F_{2,39} = 0.656$, $p = 0.525$), and no year effect was observed ($F_{3,39} = 1.926$, $p = 0.141$). Grassland obligate species richness (S_{obl}) likewise did not exhibit any differences among treatments ($F_{2,39} = 0.326$, $p = 0.725$) or study years ($F_{3,39} = 0.614$, $p = 0.610$). Species diversity, measured using the Shannon-Wiener Index (H), also exhibited no difference among treatments ($F_{2,39} = 0.408$, $p = 0.668$) or years ($F_{3,39} = 0.833$, $p = 0.484$).

Grassland bird community structure

During the pre-treatment year of 2006, bird community structure was not significantly different among treatments ($R = 0.141$; $p = 0.124$), but differences among treatments were significant in 2007 ($R = 0.359$; $p = 0.010$), 2008 ($R = 0.507$; $p = 0.002$), and 2009 ($R = 0.288$; $p = 0.036$). A fourth "treatment" was added in 2009, when an errant fire caused about 80% of two pastures to be burned. For the purpose of this analysis, those two pastures were considered separately. Pairwise comparisons between treatments showed no significant differences after applying a Bonferroni correction, perhaps due to the small sample size involved in the comparisons and the conservative nature of the correction.

NMDS attained a convergent two-dimensional solution with a stress of 12.9%, which Kruskal (1964*a*) considers a "fair" representation of the underlying data, on a scale where 5–10% is considered "good", 10–20% is "fair", and >20% is "poor". Although a three-dimensional solution would have resulted in lower stress, additional axes providing better fit by definition, we used a two-dimensional solution to ease interpretation of the resulting ordination diagrams. In ordination-space, the burned-only pastures remained grouped apart from the other two treatments during all four study years (Fig. 2). Patch-burn grazing and grazed-and-burned pastures overlapped considerably in 2006 and 2007 (Fig. 2A–B), but differentiated in the two subsequent study years (Fig. 2C–D). In addition to this divergence of the bird community by treatment over time, community structure within each treatment converged, as indicated by the decrease in distance between pastures within a given treatment in ordination space. An exception to this pattern is a single burned-only pasture that became increasingly atypical of that treatment over time, indicating that it had an unusual grassland bird community that differed greatly from other study pastures, although it began the study with community structure much more similar to other pastures.

Fitted response surfaces for the most abundant facultative and obligate grassland species gave some insight into the patterns in bird community structure underlying the ordination (Fig. 3). The arrangement of the ordination was driven to a large degree by the variability in the abundance of Grasshopper Sparrows across pastures and years (Fig. 3A), as this species had the greatest range of percent relative abundance, from less than 5% of the community to over 35%. Henslow's Sparrows (*Ammodramus henslowii*) were also a main source of community differen-

Table 1. Observed population density of obligate and facultative grassland birds on 13 pastures in the Grand River Grasslands, 2006–2009; observed density is defined as the maximum number of individuals per hectare observed on a pasture during a single round of bird transect surveys.

Species	Mean observed density			
	All Treatments	Burned-only	Grazed-and-burned	Patch-burn grazing
Obligate grassland species				
Grasshopper Sparrow	0.988	0.517	1.085	1.304
Bobolink	0.866	1.336	0.714	0.598
Eastern Meadowlark	0.606	0.415	0.732	0.661
Dickcissel	0.341	0.484	0.371	0.194
Henslow's Sparrow	0.328	0.589	0.109	0.292
Sedge Wren	0.261	0.619	0.094	0.100
Upland Sandpiper	0.002	0.004	—	0.003
Northern Harrier	0.002	0.005	—	—
Facultative grassland species				
Red-winged Blackbird	0.847	1.093	0.862	0.628
Brown-headed Cowbird	0.583	0.704	0.699	0.383
Common Yellowthroat	0.312	0.542	0.263	0.161
Eastern Kingbird	0.353	0.403	0.399	0.273
Mourning Dove	0.078	0.085	0.090	0.062
Eastern Bluebird	0.042	—	0.063	0.059
Northern Bobwhite	0.035	0.013	0.084	0.012
Loggerhead Shrike	0.029	0.017	0.029	0.040
Ring-necked Pheasant	0.017	0.009	0.005	0.033
Killdeer	0.006	0.011	—	0.008
Vesper Sparrow	0.011	0.007	0.015	0.011
Lark Sparrow	0.001	—	—	0.003

tiation, ranging from less than 5% to over 25% of the total observed density of facultative and obligate grassland birds (Fig. 3B).

Visual obstruction was the habitat variable most strongly correlated with the arrangement of pastures in ordination space ($r^2 = 0.315$, $p < 0.001$), followed by the percent cover of legumes ($r^2 = 0.306$, $p < 0.001$) and the percent cover of *F. arundinacea* ($r^2 = 0.284$, $p < 0.001$; Fig. 4). The landscape characteristics most strongly associated with the ordination were tree edge density at 0–300 m ($r^2 = 0.419$, $p < 0.001$) and 300–1000 m ($r^2 = 0.626$, $p < 0.001$). Within-pasture wooded edge density had a surprisingly weak correlation with the arrangement of pastures in the ordination ($r^2 = 0.103$, $p = 0.076$), as did the percent cover of grass at 0–300m ($r^2 = 0.013$, $p = 0.733$), although grass cover at 300–1000 m was more strongly correlated ($r^2 = 0.219$, $p = 0.002$; Table 2).

Discussion

We found that the grassland bird community did respond to the application of the fire-grazing interaction, but not necessarily in the ways we had initially expected. While there were no significant differences in simple measures of grassland bird diversity among management treatments, community structure diverged significantly during the course of the study. Study pastures grouped together in ordination-space by treatment (Fig. 2), and were arrayed along an axis of visual obstruction (Fig. 4). Visual obstruction is roughly analogous to vegetation biomass (Robel et al. 1970, Limb et al. 2007) and is redundant with other measures of structure (Harrell and Fuhlendorf 2002, Toledo et al. 2010), so this axis can be interpreted as a habitat structure gradient.

Pastures in the patch-burn grazing treatment had bird communities indicative of short, sparse vegetation structure with little litter accumulation, exemplified by the positive responses of Grasshopper Sparrow and Eastern Meadowlark (*Sturnella magna*) to this treatment (Fig. 3A, 3C). Community structure on burned-only pastures, in contrast, was indicative of relatively tall, dense vegetation with abundant litter that increased the percent relative abundance of Sedge Wren (Fig. 3D), Common Yellowthroat (*Geothlypis trichas*; Fig. 3E), Dickcissel (*Spiza americana*; Fig. 3F), and

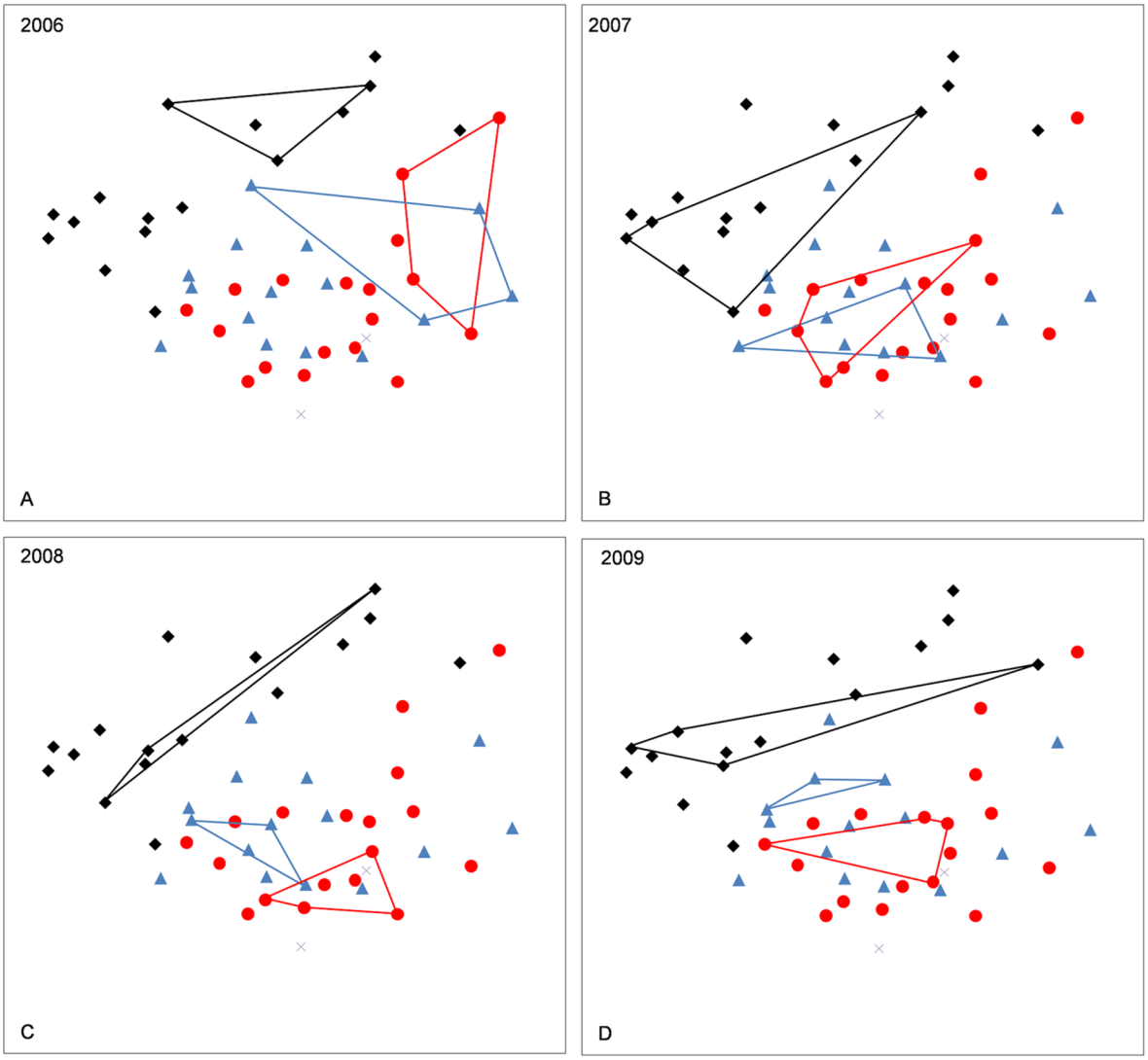


Fig. 2. Nonmetric multidimensional scaling of obligate and facultative grassland bird community structure in 13 pastures in the Grand River Grasslands, Iowa and Missouri, 2006–2009. Minimum convex polygons are presented for pastures in each of three experimental treatments: patch-burn grazing (circles), grazed-and-burned (triangles), and burned-only (diamonds). Points marked "X" denote two pastures that were accidentally 80% burned prior to the 2009 breeding season. Note that points are given for all years in each panel, but that only the points from a given year are included in polygons.

Bobolink (Fig. 3G) in that treatment. The most abundant facultative grassland species in this study, Red-winged Blackbird, also followed this pattern (Fig. 3H), which we had expected based on its association with dense vegetation in low, wet areas, much like the preferred habitats of the aforementioned Sedge Wren and Common Yellowthroat.

Interestingly, the percent relative abundance of Henslow's Sparrow followed a somewhat different pattern, the response surface being perpendicular to the habitat structure gradient. This species is normally associated strongly with abundant standing vegetation and is generally absent from grasslands grazed or burned too frequently or too intensely (Zimmerman 1988,

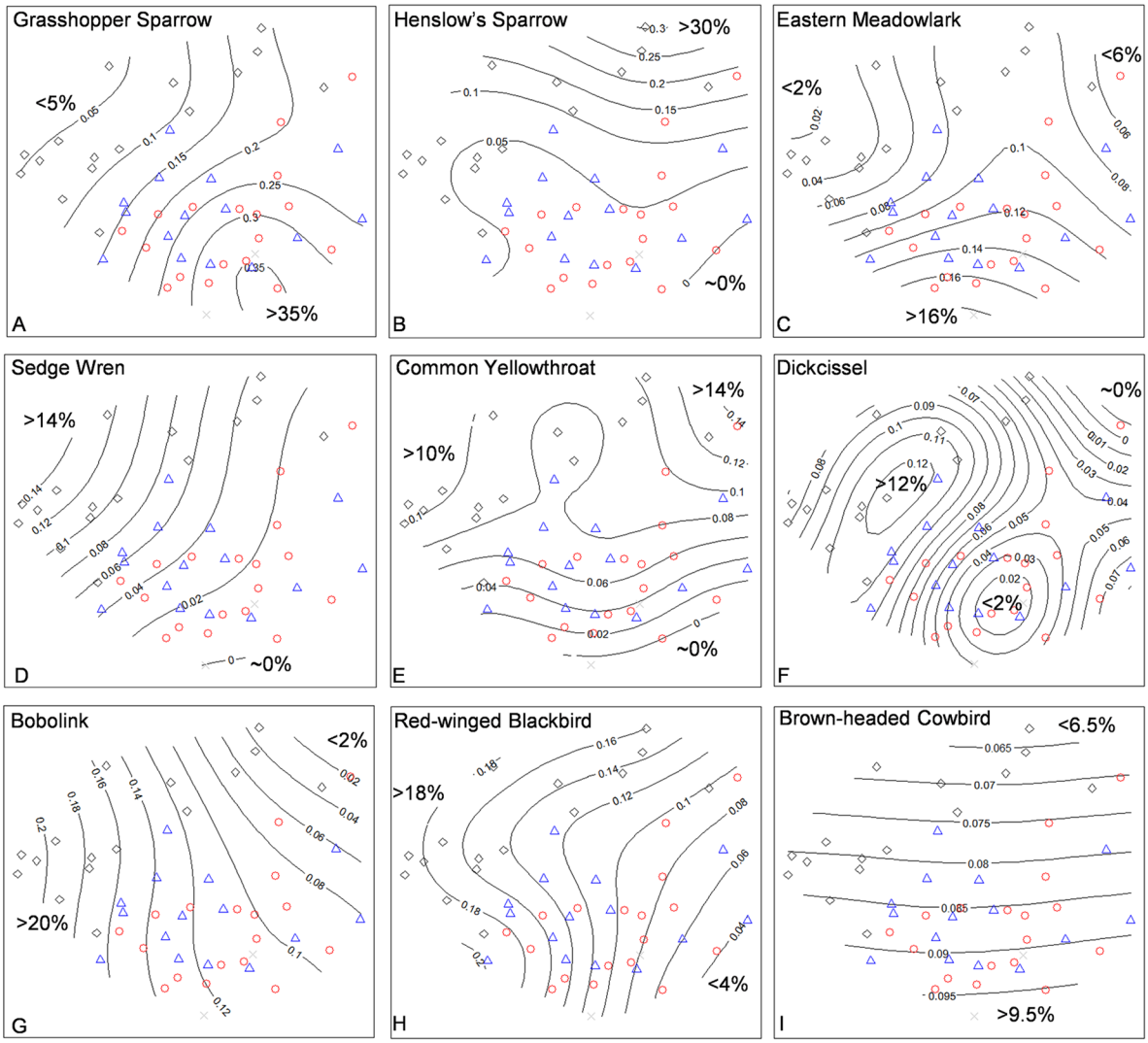


Fig. 3. Fitted response surfaces of the percent relative abundance of grassland obligate bird species in ordination space, based on a nonmetric multidimensional scaling of obligate and facultative grassland bird community structure in 13 pastures in the Grand River Grasslands, Iowa and Missouri, 2006–2009. Percentages refer to the minimum and maximum fitted contours of each response surface. Points are divided among three experimental treatments: patch-burn grazing (circles), grazed-and-burned (triangles), and burned-only (diamonds). Points marked "X" denote two pastures that were accidentally 80% burned prior to the 2009 breeding season.

Herkert 1994*b*, Herkert et al. 2002, Powell 2006), so we had expected it to follow the same pattern in our study. Instead, the shape of the response surface in ordination space was the result of its being strongly associated with a single burned-only pasture during the first three study years before the pasture was burned, so the bird community on that pasture differentiated from the others in the ordination based on the high percent relative abundance of Henslow's Sparrow.

Brown-headed Cowbird (*Molothrus ater*), also one of the species with highest observed density in this study, did not exhibit large differences across the ordination, meaning that it did not contribute greatly to differentiation in bird

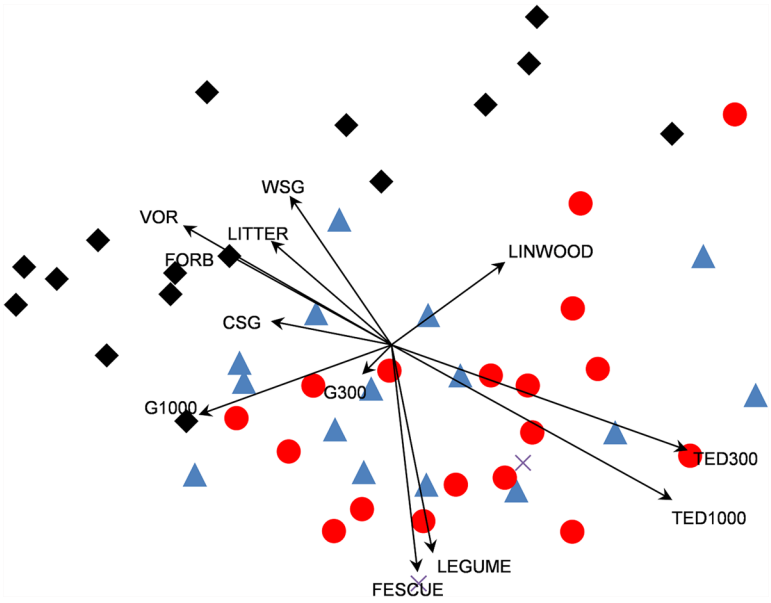


Fig. 4. Nonmetric multidimensional scaling of obligate and facultative grassland bird community structure in 13 pastures in the Grand River Grasslands, Iowa and Missouri, 2006–2009. Vectors indicate the direction of greatest correlation of a given variable with the ordination, and vector length is proportional to r^2. Points are divided among three experimental treatments: patch-burn grazing (circles), grazed-and-burned (triangles), and burned-only (diamonds). Points marked "X" denote two pastures that were accidentally 80% burned prior to the 2009 breeding season. See Table 2 for explanation of variable codes.

Table 2. Habitat and landscape variables used as correlates of grassland bird community structure, Grand River Grasslands, 2006–2009; see *Methods: Habitat and landscape structure* for variable descriptions.

Variable	Variable code	Mean	Range	r^2	p
Habitat structure					
Visual obstruction (cm)	VOR	44.6	18.8–90.8	0.315	<0.001
Percent cover tall fescue	FESCUE	29.8	0–60.1	0.284	<0.001
Percent cover warm season grass	WSG	16.4	0–64.1	0.166	0.012
Percent cover cool season grass	CSG	19.0	4.4–51	0.099	0.082
Percent cover forbs	FORB	24.8	7.9–60.4	0.148	0.020
Percent cover legumes	LEGUME	13.5	0–38.2	0.306	<0.001
Percent cover litter	LITTER	31.0	1.6–75.3	0.140	0.027
Landscape context					
Within-pasture edge density (m/ha)	LINWOOD	66.5	15.6–114.6	0.103	0.077
Percent cover grass (300 m)	G300	69.0	44.6–96.5	0.013	0.733
Tree edge density (300 m) (m/ha)	TED300	125.6	5.0–219.3	0.419	<0.001
Percent cover grass (1000 m)	G1000	63.0	49.0–87.3	0.219	0.003
Tree edge density (1000 m) (m/ha)	TED1000	89.0	45.2–117.8	0.626	<0.001

communities among pastures (Fig. 3I). This was expected, given that the species is an edge-associated species able to successfully exploit a range of fragmented grassland habitats like those in this study (Lowther 1993).

Grassland bird community structure did not exhibit the expected pattern in the patch-burn grazing and grazed-and-burned treatments. We had expected grazed-and-burned pastures to occupy the opposite end of a structural gradient from the burned-only pastures, with patch-burn grazing pastures overlapping the two, because they presumably would contain structural components from both other treatments. Instead, the

bird community at patch-burn grazing pastures was associated with species inhabiting the lower end of the structural gradient and grazed-and-burned pastures were instead intermediate. Neither the mean nor the standard deviation of visual obstruction differed between the two grazed treatments during any of the study years, indicating that patch-burn grazing did not result in the expected degree of structural heterogeneity compared to grazed-and-burned pastures. This was likely a consequence of having too high a stocking rate, which illustrates the importance of maintaining enough residual biomass every year to create the structural heterogeneity required by a diverse bird community.

Although visual obstruction was the habitat characteristic most highly correlated with differences in community structure among pasture-years, wooded edge density in the landscape was the variable most highly correlated with community structure differences overall, at both the 0–300 m and 300–1000 m scales ($r^2 = 0.419$ and 0.626, respectively). However, the vectors of visual obstruction and tree edge density (at both spatial scales) were in nearly perfect opposition, indicating that their effects on the bird community are highly correlated. This is notable, given that we found visual obstruction to be weakly correlated with tree edge density at both the 0–300 m and 300–1000 m scales ($r^2 = 0.11$ and 0.14, respectively). In other words, there was conflation in the responses of the bird community to habitat and landscape characteristics not because pastures with short vegetation structure were also more fragmented, but because species associated with taller vegetation structure were also associated with lower levels of landscape fragmentation. Our data suggest that Grasshopper Sparrow and Eastern Meadowlark may be less sensitive to fragmentation than other species, but the degree to which communities are structured by landscape versus habitat factors remains unclear. Both of these species have been observed to be negatively associated with habitat fragmentation (e.g., Herkert 1994*a*, Johnson and Igl 2001), which is not necessarily inconsistent with our findings because a lower degree of fragmentation sensitivity is not evidence of a lack of sensitivity. Despite the conflation of responses to vegetation structure and landscape fragmentation, we maintain that the observed differentiation in the grassland bird community by treatment is the result of structural differences among treatments. Because landscape context was constant during the course of the study, it follows that the treatments themselves are likely the cause of this differentiation.

The lack of structural heterogeneity in patch-burn grazed pastures, however, suggests that substantial reductions in the heavy stocking rates common to this study region still render patch-burn grazing ineffective at promoting avian diversity through an increase in heterogeneity. This stands in contrast to the work of Fuhlendorf et al. (2006), who observed grassland obligate species in a patch-burn grazing treatment that were not present in a traditionally-grazed treatment, as well as that of Coppedge et al. (2008), who found significantly higher grassland obligate species richness under patch-burn grazing in the Flint Hills. Worth noting, however, is that in those studies the grazed-and-burned treatment was subject to fire annually, rather than on a three-year fire-return interval, as was the case in the present study.

Because habitat use by grassland birds is generally mediated by landscape context (e.g., Cunningham and Johnson 2006, Renfrew and Ribic 2008), efforts to promote avian diversity in fragmented landscapes are, by their very nature, a daunting challenge. As such, it is that much more critical to manage those remaining grassland fragments effectively, especially when fragmented grasslands comprise such a large proportion of remaining grasslands in the tallgrass prairie region. Using a fire-grazing interaction to create a heterogeneous shifting mosaic has been successful elsewhere (Fuhlendorf and Engle 2001, 2004, Fuhlendorf et al. 2008), so future efforts in our study area will reevaluate the efficacy of patch-burn grazing with a reduced stocking rate to increase structural heterogeneity for the benefit of grassland birds. Even if an optimal stocking rate can be achieved, however, it is possible that fragmentation will remain a perpetually limiting factor on the efficacy of this method for promoting avian diversity in highly fragmented grassland landscapes. Additionally, it is important to note that this study did not address the effect of this type of management on reproductive success or other demographic parameters, which are not necessarily correlated

with population density (Bock and Jones 2004; Skagen and Adams, *in press*).

Therefore, although management practices using a fire-grazing interaction may have the potential to promote avian diversity in highly fragmented landscapes, a number of obstacles remain before these approaches can be adopted widely by private landowners or management agencies. Given the stark reductions in stocking rate that conceivably must take place relative to traditional pasture management, in the end these methods may be employed best on public land and recreational private lands, where revenues from cattle production are of secondary importance to other ecosystem services.

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