

THE EFFECT OF SEASON OF PRESCRIBED FIRE ON RICHNESS
AND ABUNDANCE OF BREEDING BIRD SPECIES AND
VEGETATION STRUCTURE IN MINNESOTA LOWLAND BRUSH
ECOSYSTEMS

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Rebecca A. Montgomery

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Dedication

For Tanner and Celia.

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PREFACE

The following chapters of this thesis represent manuscripts intended for publication, and formatting within each chapter reflects journal requirements of the intended scientific journal. As senior author I will be responsible for chapter contents but because these publications will have more than one coauthor, I will use plural pronouns. Expected coauthors include Rebecca Montgomery, Charlotte Roy, Lindsey Shartell, Lee Frelich, and David Andersen. I intend to submit Chapter 1, “Richness and Abundance of Breeding Birds as Related to Vegetation Structure in Lowland Brush Ecosystems” to the Journal of Wildlife Management in 2019. I intend to submit Chapter 2, “Season of Fire Effect on Breeding Birds and Vegetation Structure in Lowland Brush Ecosystems” to the Journal of Wildlife Management in 2019.

ABSTRACT

Lowland brush ecosystems provide critical habitat for diverse breeding bird communities in the western Great Lakes region of the United States. These ecosystems are disturbance-dependent and historically experienced fires occurring throughout plant growing and dormant seasons. Disturbance in brushland landscapes influences woody vegetation structure, which can increase in extent, density, and height without frequent or effective disturbance events. Woody vegetation structure has been shown to be important for breeding bird communities in upland and forest systems, but this has not been studied in lowland brush ecosystems. Additionally, there are few studies on how bird communities and lowland brush vegetation structure respond to fire.

Currently, lowland brush ecosystems in the Upper Midwest are predominately burned during spring months when plants are dormant. This may not mimic historical fire effects because before fire-suppression and control, fires occurred throughout snow free seasons, including summer and fall. In forests and grasslands, plant and bird species have been shown to respond distinctly to different seasons of fire, with the response of bird species being related to changes in vegetation structure and its role in nesting and foraging. No studies on season of fire have been done in lowland brush ecosystems.

We assessed baseline models relating bird species richness, bird total abundance, and abundance of frequently detected bird species to woody vegetation structure in lowland brush ecosystems. Frequently detected bird species included golden-winged warbler (*Vermivora chrysoptera*), sedge wren (*Cistothorus platensis*), and veery (*Catharus fuscescens*) which are Minnesota Species in Greatest Conservation Need. We then used a Before-After-Control-Impact experimental design to evaluate the magnitude

in change in response to spring, summer, and fall fire treatments of the same bird and vegetation variables. This allowed us to determine vegetation characteristics that are important to breeding birds and how the responses of birds and plants relate to season of fire.

Stem height and stem height diversity, which was a measure of vertical structural diversity, were related to the most frequently detected bird species and bird species richness. Although these vegetation variables did not respond significantly to spring, summer, and fall fire treatments compared to controls, they exhibited decreasing trends after fires. Additionally, changes in stem height were nearly statistically significant. Veery and yellow warbler (*Setophaga petechia*) decreased in abundance after summer (veery) and spring and fall (yellow warbler) season treatments and were related to stem height in baseline explanatory models. We posit that these species decreased in abundance due to decreases in stem height. In contrast, chestnut-sided warblers (*Setophaga pensylvanica*) increased in abundance after spring and fall fires. This species was also related to stem height and the number of woody plant species. Therefore, chestnut-sided warblers may have been responded to additional changes in vegetation from fire and notably, chestnut-sided and yellow warblers exhibited opposite responses to the same fire seasons even though these species exhibit similar life history traits.

Bird total abundance increased after summer and fall fires, the 2 seasons when prescribed fires are not typically conducted in the Upper Midwest. In our explanatory baseline models, the null model best explained bird total abundance and so although we were unable to relate this response to vegetation measurements, we suggest this response be considered in future management. Based on our results and the mix of responses to

spring, summer, and fall fire seasons, conducting prescribed fires during different seasons may support different breeding bird species. The overall breeding bird community may also benefit, especially if prescribed fire is implemented during the summer when plants are growing. Adding summer burns to disturbance management-regimes that are often restricted to the spring in lowland brush ecosystems may also provide managers with larger burn-windows.

Chapter 1

Richness and Abundance of Breeding Birds as Related to Vegetation Structure in Lowland Brush Ecosystems

Overview:

In many systems with woody plants, such as shrubs and trees, vegetation structure is strongly associated with bird species at community and individual levels. In the western Great Lakes region of the United States, lowland brush ecosystems provide critical habitat to a diverse suite of bird species and without effective management, changes in woody vegetation structure may decrease the value of these systems to bird communities. To assess the relationship between vegetation structure and bird species, we surveyed lowland brush ecosystems at 4 study sites in Minnesota, USA. We used mixed-effects models to assess the relationship between 6 structural vegetation characteristics of woody plants and woody plant species count, and richness and abundance of breeding bird species. Although the null model best explained bird total abundance, stem height diversity (a measure of vertical vegetation structural diversity) was positively and strongly related to bird species richness, based on confidence intervals not overlapping 0. Furthermore, average woody stem height was strongly related to abundance of 5 of the 10 most frequently detected avian species. Alder flycatcher (*Empidonax alnorum*), chestnut-sided warbler (*Setophaga pensylvanica*), veery (*Catharus fuscescens*), and yellow warbler (*Setophaga petechia*) abundances were all positively related to stem height and sedge wren (*Cistothorus platensis*) abundance was negatively related. A few species were strongly related to stem density or woody plant species count. These results suggest that

to support the highest number of breeding birds, promoting diverse structure in the woody plant community, may benefit species more than homogenously reducing brush. This may be accomplished by allowing for patches of tall shrubs to coexist within areas in which brush is reduced.

Key Words: Bird abundance, woody vegetation, shrub, lowland brush, brushlands, Minnesota, stem height diversity, stem density, stem height

INTRODUCTION

For >80 years, studies in ecosystems with woody plants have shown that vegetation structure affects the presence, density, and distribution of bird species (Lack 1933, Dunlavy 1935). Across spatial scales and ecosystems, studies on birds find that diverse vegetation structure supports diverse bird communities due to the partitioning of resources (MacArthur and MacArthur 1961, Tomoff 1974, Erdelen 1984, Tews et al. 2004). In their classic work, MacArthur and MacArthur (1961) found that forest bird species diversity and the vertical diversity of vegetation, referred to as foliage height diversity, were strongly, positively correlated. The relationship between vegetation structure and bird species diversity has been studied most in forests, followed by prairie, steppe or grassland ecosystems, and least studied in brush/scrub/shrublands (Tews et al. 2004).

Shrub- and brushlands are characterized by a variable mix of woody and herbaceous vegetation, and despite plant and bird communities being less studied compared to forests and prairies, bird species have been shown to be related to vegetation

structure in these systems (Curtis 1959, Tomoff 1974, Roth 1976, Mills et al. 1991, Tews et al. 2004, Austin and Buhl 2013). In desert scrub, Tomoff (1974) found breeding bird diversity to be positively correlated to the physiognomic cover diversity of 5 types of woody plants, due to an associated increase in food resources and nest sites. In arid shrubland, breeding bird density increased with increased woody vegetation density and volume, likely due to an increase in resources (Mills et al. 1991). In upland brushlands, bird species diversity was found to be strongly correlated with a measure of the horizontal diversity of woody vegetation structure (Roth 1976).

The mosaic of woody and herbaceous vegetation in brushlands is a result of frequent disturbance events such as fire and wind (Curtis 1959). Characteristics of brushland vegetation change more rapidly than the vegetation of woody plants in other systems, such as forests, because disturbance occurs more frequently in brushlands and woody-plant responses to disturbance occur on a shorter time-scale (Curtis 1959, Linde 1969, Lorimer and White 2003). For birds, the rapidly changing suitability of vegetation in brushlands may be less stable than in other systems (Switzer 1993, Schlossberg 2009). When disturbance does not occur frequently in brushlands, woody vegetation increases in height and density, and eventually results in homogenous cover (Curtis 1959). Similar cover occurs in brushlands when invasive woody plant species, such as common buckthorn (*Rhamnus cathartica*) and autumn olive (*Elaeagnus umbellata*), out-compete native species and remain dominant despite disturbance regimes that were historically effective at maintaining a mix of cover types (Robinson 1965, Van Auken 2000, Potts and Stephens 2009, Schlossberg and King 2010). In brushlands, breeding birds have been found to use both invasive and native shrubs for nesting (Schlossberg and King 2010).

Brushland managers use prescribed fire, mowing, shearing, mechanical removal, and herbicide application to manage woody vegetation, with some methods costing up to \$37,000/ha to apply. (Shafroth et al. 2009). Reducing overall woody vegetation is necessary when woody plants, including invasive plants, increase in extent, density, and height; however, simply reducing woody vegetation may not be sufficient if long-term management is focused on creating habitat for birds that rely exclusively on brushlands to breed. To best manage for bird species that require brushlands for breeding, more information is needed on the associations between bird species during the breeding season and structural vegetation characteristics (Fulbright et al. 2018).

In the Midwest, USA, most brushland ecosystems occur on state-owned land that are managed for wildlife (Askins 2001, MNDNR 2003). The lowland brush ecosystems within this region, specifically the states surround the Great Lakes, have been poorly studied in terms of breeding bird communities and management. Lowland brush ecosystems in this region consist of lowland brush/wetland interfaces and exhibit a variable mix of woody and herbaceous wetland plant cover and a high, persistent water-table (MNDNR 2003). Few published reports describe bird and plant communities in lowland brush ecosystems, but existing studies suggest high levels of diversity. Hanowksi et al. (1999) found that in the region surrounding the Great Lakes, bird species richness was higher in lowland brush ecosystems than in open grass/sedge meadows and some forest systems, and reported that >85% of species detected were considered to occur primarily in wetlands and lowland brush ecosystems. Hanowski et al. (1999) also suggested that high avian diversity may be related to vegetation structure and a mix of

woody and herbaceous cover, but that bird species requirements related to plants are generally unknown in lowland brush ecosystems.

We addressed the lack of information on Minnesota lowland brush ecosystem vegetation structure and bird species in east-central Minnesota, where lowland brush managers use prescribed fire, mowing, and shearing to reduce woody vegetation and maintain and create habitat for species of conservation concern (Curtis 1959, MNDNR 2003). In Minnesota, wildlife management of lowland brush ecosystems includes species of conservation concern; lowland brushlands make up approximately 20% (3.5 million hectares) of the landscape (USGS 2011) and provide critical habitat for >250 wildlife species including >80 Minnesota Species in Greatest Conservation Need, 38 of which are birds (MNDNR 2015).

Our objective was to evaluate associations between breeding bird species and vegetation structure in 4 east-central Minnesota lowland brush ecosystem study sites over a 3-year period. We modeled breeding bird species at the community and individual species levels in relation to vegetation characteristics. At the community level, we (1) developed models of bird species richness and total bird abundance, and at the species level we (2) developed models of abundance of the most frequently detected species. We hypothesized that bird species richness and total bird abundance would increase with stem height diversity and would not be related to measures of vegetation height and density because different species likely have different requirements for woody plant height and density (Tomoff 1974, Roth 1976, Mills et al. 1991, Tews et al. 2004). The identification of important vegetation structures for bird species is crucial for effective management (Fisher and Davis 2010) and we proposed to determine which, if any,

woody vegetation characteristics are associated with breeding birds to inform brushland management.

STUDY AREA

We evaluated lowland brush ecosystem bird communities and vegetation characteristics in east-central Minnesota (N46.9725790 W092.9853520) from 2016 to 2018. Several bird species of conservation concern in Minnesota have been documented in lowland brush ecosystems during their breeding seasons, including Species in Greatest Conservation Need such as Le Conte's sparrows (*Ammodramus leconteii*), golden-winged warblers (*Vermivora chrysoptera*), northern harriers (*Circus cyaneus*), sedge wrens (*Cistothorus platensis*), and veeries (*Catharus fuscescens*). Le Conte's sparrow populations are declining due to habitat loss attributed to fire-suppression (MNDNR 2015) and at least 40% of the global population of golden-winged warblers utilize habitat within Minnesota during the non-wintering season (Streby et al. 2017).

We conducted our study within 4 study sites that were identified by Minnesota Department of Natural Resources (MNDNR) wildlife managers as an area of lowland brush ≥ 162 ha. Study sites were on public land (Fig. 1). Within study sites, vegetative composition was similar and included the Minnesota native plant communities northern alder swamp, northern poor fen, northern wet meadow/carr, and willow dogwood swamp (MNDNR 2003). Woody plants included predominantly speckled alder (*Alnus rugosa*), willow species (*Salix* spp.), dogwood species (*Cornus* spp.), bog birch (*Betula pumila*), and low woody species associated with bogs, such as leatherleaf (*Chamaedaphne calyculata*) and Labrador tea (*Rhododendron groenlandicum*). Herbaceous plant species

varied more than woody plants among sites and included sedges (*Carex* spp.) typical of wet meadows, moss and bryophytes typical of boreal bogs, and grasses and forbs tolerant of wet conditions. Study sites were dominated by diverse herbaceous cover, interspersed with patches of woody shrubs. The majority of the land in study sites exhibited a persistent water-table, which rose with the occurrence of frequent or heavy rain.

METHODS

Bird Surveys

Using ArcGIS (ESRI 2015), we placed 32 avian point-count locations in each study site using systematic random placement and restricting points to be ≥ 100 m from the study site boundary and ≥ 225 m from other point-count locations. This allowed for non-overlapping, 100-m radii around each location. We conducted early-morning single-observer avian point-count surveys from late May to early June in 2016, 2017, and 2018 when male breeding birds were vocalizing. We did not conduct surveys on days with initial wind speeds > 19 km/h and canceled surveys if wind speeds increased to > 28 km/h during a survey period. We did not conduct surveys when precipitation was more than a drizzle or when electrical storm warnings were in effect (Hutto et al. 1986, Ralph et al. 1995).

We trained observers to identify bird species that have been documented in Minnesota lowland brush ecosystems both aurally and visually prior to conducting point-count surveys. Our protocol consisted of counting birds within a 100-m radius around point-count locations (Birds and Burns Network 2003, Hurteau et al. 2008). Observers

initiated surveys 30 min prior to sunrise and completed surveys before 0900 CDT (Hutto et al. 1986, Ralph et al. 1995). After arriving at the survey point and waiting quietly for 2 min, observers recorded all individual birds detected within 100 m for a 6-min period. During the surveys, observers recorded detection of individual birds for 3 2-min periods (Buckland et al. 2009). For each individual bird, observers recorded species and distance detected. Our protocol consisted of counting birds within a 100-m radius around point-count locations, and we trained observers to estimate detection distances ≤ 100 m by marking distances 5, 10, 25, 50, and 100 m from 4 point-count locations in each study site. Observers used these additional distances within 100 m during surveys to better distinguish between individuals of the same species that were detected at different distances. We provided observers with an image of a survey point with distance radii to serve as a visual aid to map estimated locations of birds throughout surveys to minimize the potential for counting individuals more than once.

We surveyed all point-count locations within a single study site in ≤ 2 mornings, with each observer surveying 8 locations. In 2016 we surveyed all 32 point-count locations within 4 study sites. In 2017 and 2018 we re-visited the same sites but surveyed less point-count locations (Table 1). Some study site sections had been treated for a study on brushland management and we only surveyed point-count locations within un-treated sections (see Hawkinson Chapter 2).

We surveyed all point-count locations 4 times each year. Each visit to a study site, we assigned a new section and therefore 8 new point-count locations to observers. In 2016 and 2017 we had 4 observers and point-count locations were surveyed by a unique

observer each time we conducted surveys; 4 unique observers independently conducted the 4 surveys at each point-count location during each June. In 2018 we had 2 observers and therefore had 2 unique observers for the 4 surveys conducted at each point-count location. In 2016 and 2017, during instances when an observer could not conduct surveys, some point-count locations were surveyed more than once by the same observer. This occurred infrequently and overall $\geq 75\%$ of point-count locations were not visited by the same observer more than once.

Bird behavior can change with time of day and surveying point-count locations at the same time each survey would potentially result in non-random variation in detection probability across survey locations based on how active or inactive birds were during surveys (Hutto et al. 1986). To survey all locations during a range of times, we conducted the 4 surveys at each point-count location at different times. Observers documented start times and avoided surveying at the same time as previous surveys (within 15 min). We also surveyed point-count locations in a different order each time we surveyed a study site. This consisted of making the first location different for at least half of surveys and re-assigning, including reversing, the order we surveyed point-count locations.

Vegetation Surveys

We quantified woody vegetation characteristics near avian point-count locations. During July-September 2016, 2017, and 2018, we sampled vegetation at 2 3-m fixed-radius vegetation plots placed 10 m north and east of each avian point-count location. We sampled woody plant species < 10 cm dbh and woody stems ≥ 10 cm dbh separately. We counted woody stems ≥ 10 cm dbh in 2 categories, live and dead (snag). We determined

early in our vegetation assessment that dead stems <10 cm dbh were not abundant and difficult to distinguish from live stems; therefore, we counted woody stems <10 cm dbh in a single category. We divided plots into 4 quadrants for ease of sampling. In each quadrant, we counted the number of stems <10 cm dbh for each species in 5 height classes (0-50, 51-100, 101-200, 201-300 and >300 cm; Salk et al. 2011, Fisichelli et al. 2012) We used a pole pre-marked at 50, 100, 150, 200, 250, and 300 cm to measure height. We divided counts of stems into 4 abundance categories (0-25, 26-50, 51-100, >100 stems). For snags, we did not identify species.

Vegetation covariates

We derived woody structural vegetation metrics from the paired vegetation plots at point-count locations. We considered paired plots as a single sample unit and calculated a single value from paired plots to associate with each point-count location. We used 3 measures of woody vegetation structure because bird species in brushlands have been shown to be related to a variety of structural vegetation characteristics (Curtis 1959, Lorimer and White 2003), such as diversity of physiognomy (Tomoff 1974), volume of vegetation (Mills et al. 1991), and horizontal diversity of vegetation structure (Roth 1976). We used a diversity index of woody stems to quantify the complexity of vegetation structure, referred to as stem height diversity (MacArthur and MacArthur 1961). We also calculated stem density (per ha) and average stem height (cm). We used 2 other measures that compared vegetation structure between the 2 paired plots and gave an estimate of horizontal structural diversity: difference in stem height and difference in stem density. We also included density of woody plant species (species per point)

because in addition to structure, different woody plant species can support distinct wildlife species (Erdelen 1984).

To calculate vegetation variables, we assigned the median value of the category intervals to categories of stem counts <10 cm dbh (i.e., 0–25 = 12.5, 26–50 = 37.5, 51–100 = 75 and >100 = 150 stems). We used stem height diversity to quantify vertical vegetation structure diversity, similar to the metric implemented for foliage cover by MacArthur and MacArthur (1961). Tomoff (1974) modified MacArthur and MacArthur’s foliage height diversity height profiles in models of breeding bird species in desert scrub communities, and we used a comparable approach, as shrub height categories in that study were similar to ours. We used our 5 height categories and the number of woody plant stems.

We used our 5 height categories and the number of woody plant stems and the package *vegan* (Oksanen et al. 2018) to calculate stem height diversity using Shannon’s True Diversity Index (Jost 2006), in the statistical program R (version 3.4.2, R Core Team 2017).

$$\exp\left(-\sum_{i=1}^S p_i \log_e p_i\right)$$

In the above equation, p_i is the proportional abundance of stems in i^{th} height profile, S is the number of stems in each height profile, and b is the natural logarithm. We calculated stem density (stems/ha) and average stem height using vegetation measurements from the paired vegetation plots at point-count locations. We also calculated the difference (absolute value) between paired plots in stem density and average stem height. We used these differences as measures of how variable vegetation

structure was adjacent to avian point-count locations. We calculated woody plant species count as the number of woody plant species in the 2 3-m radius (56.55 m²) paired plots (Gotelli and Colwell 2001).

Data Analysis

We assessed models relating breeding bird species at the community and individual species levels to vegetation characteristics in lowland brush ecosystems using mixed-effects models. We assigned vegetation covariates as fixed effects. We assigned year and study site as random effects and the 4 avian point-count surveys conducted at each avian point-count location as a nested random effect (within study site) to account for repeated measures at the same site and point-count location.

To determine which set of vegetation covariates best explained the data of each bird response variable we evaluated models in an information-theoretic framework (Burnham and Anderson 2002). For each bird response variable, we fit models of all possible combinations of the same set of fixed covariates, without interactions. Each model also included all random effects and the null model only included random effects. We calculated Akaike's Information Criterion (AIC_c) values adjusted for sample size for each model to make model comparisons (Akaike 1973, Burnham and Anderson 2002). We also used AIC_c model weights and deviance to facilitate relative rather than absolute model comparisons (Wagenmakers and Farrell 2004).

We constructed models with the package *lme4* (Bates et al. 2015) and the package *glmmTMB* (Brooks et al. 2017) in R (version 3.4.2, R Core Team 2017). We fitted models and calculated AIC_c and model weights using the package *MuMIn* (Bartoń 2018)

in R (version 3.4.2, R Core Team 2017). We considered the best-supported model for each response variable the model with the lowest AIC_c and competing models those with $\Delta AIC_c \leq 2$ compared to the best-supported model. For vegetation covariates of the best-supported models, we calculated confidence intervals around parameter estimates to determine the strength of the relationship between covariates and response variables. We determined a relationship to be strong if confidence intervals did not overlap 0.

To assess breeding birds at the community level, we constructed linear mixed-effects models of bird species richness and bird total abundance. To calculate bird species richness, we totaled the number of bird species detected during each point-count survey. To calculate bird total abundance, we totaled the number of birds detected during each point-count survey. Observed values of bird species richness and bird total abundance were normally distributed.

To assess breeding birds at the individual species level, we constructed generalized linear mixed-effects models of abundance of the most frequently detected bird species. We considered a species to be frequently detected if it was detected >200 times during the first year of surveys, 1-28 June 2016 ($n = 128$ point-count locations and 512 counts). For each frequently detected species, we totaled the number of individuals detected during each point-count survey.

Before developing models of frequently detected bird species abundance, we first examined detection functions for each species (Nichols et al. 2009). Using the statistical program JAGS, we summarized the probability of detecting a species using detected/not-detected (1 or 0) binary data recorded in 3 periods for each bird per species during point-count surveys (Plummer 2017). Across the 3 2-min periods in which observers recorded

detection of individual birds, cumulative detection probability was extremely high (>0.95) for all frequently detected species and we therefore concluded that incorporating species' detection functions into analyses would not influence models and did not incorporate distance estimates into models. These detection function results and our multi-species survey design indicate that our abundance indices accurately represented birds on the landscape (Johnson 2008).

Additionally, observed values of abundance of frequently detected bird species were not normally distributed. Before developing models of frequently detected bird species, we also determined the distribution that best fit data. We checked for overdispersion of the data for each species by comparing the mean and variance. We compared the AIC_c values of 3 full models (containing all covariates and random effects) fit with Poisson, negative binomial, and zero-inflated Poisson distributions (Akaike 1973). We determined the distribution that best fit data as the model with the lowest AIC_c (Akaike 1973).

RESULTS

From 1–28 June 2016, 29 May–21 June 2017, and 5–29 June 2018 we conducted 1,052 avian point-count surveys at 128 avian point-count locations on 4 study sites (Table 1). We detected 105 bird species, of which 23 were Minnesota Species in Greatest Conservation Need, and 21 were Fire-Dependent Species based on criteria developed by the Lakes States Fire Science Consortium that includes a total of 43 bird species (Table 2; LSFSC 2018). During July-September 2016, 2017, and 2018, we sampled 256 vegetation plots.

Bird Species Richness and Bird Total Abundance Models

The best-supported model of bird species richness included stem height diversity and stem density (Table 3). Bird species richness was positively and strongly related to stem height diversity (Table 4). Seven competing models existed for bird species richness ($\Delta\text{AIC} \leq 2$), 6 of which included stem height diversity. The best-supported model for bird total abundance was the null model (Table 5). There were 5 competing models ($\Delta\text{AIC} \leq 2$), each with a unique vegetation covariate, suggesting that no covariate explained variation in the data better than any other (Table 5) and that none of the models with a single vegetation covariate was better-supported than the null model.

Individual Bird Species Abundance Models

We considered frequently detected species to be (in order of detections during 2016, n) common yellowthroat (*Geothlypis trichas*, $n=1193$), sedge wren ($n=976$), alder flycatcher (*Empidonax alnorum*, $n=809$), swamp sparrow (*Melospiza georgiana*, $n=804$), Nashville warbler (*Leiothlypis ruficapilla*, $n=345$), chestnut-sided warbler (*Setophaga pensylvanica*, $n=345$), yellow warbler (*Setophaga petechia*, $n=324$), veery ($n=292$), clay-colored sparrow (*Spizella pallida*, $n=278$), and golden-winged warbler ($n=219$). These species were also the most frequently detected in 2017 and 2018.

For all species, except chestnut-sided warblers, the model with a Poisson distribution fit better than zero-inflated Poisson or negative binomial distribution models (Table 6). For chestnut-sided warbler abundance, the model with a zero-inflated Poisson distribution provided better fit than the Poisson distribution ($\Delta\text{AIC}_c = 12.67$) and negative binomial distribution models ($\Delta\text{AIC}_c = 2.98$).

The best-supported combinations of covariates varied among the 10 frequently detected species. Stem density and stem height each appeared in the best-supported models for 6 of the 10 species; stem density was strongly related to 2 species (clay-colored sparrow and sedge wren) and stem height was strongly related to 5 species (alder flycatcher, chestnut-sided warbler, yellow warbler, veery, and sedge wren; Table 4). The best-supported models of alder flycatcher and yellow warbler abundance contained only stem height (Table 6). Both species were positively and strongly related to stem height. The best-supported model of veery abundance included 3 covariates, but the only strong relationship was with stem height, and it was also positive (Table 4). The best-supported model of chestnut-sided warbler abundance included 3 covariates, one of which was stem height (Table 6). Chestnut-sided warbler abundance was strongly and positively related to stem height and woody species count (Table 4).

Of the 5 species strongly related to stem height, sedge wren was the only species that had a negative relationship (Table 4). In addition to being negatively and strongly related to stem height, sedge wren abundance was negatively and strongly related to stem density and woody species count (Table 4). Sedge wren abundance was positively and strongly related to only 1 covariate: difference in stem density (Table 4).

The best-supported model of sedge wren abundance exhibited the most negative and strong relationships with covariates. The only other species that was negatively related to a covariate in the best-supported model of its abundance was common yellowthroat; common yellowthroat abundance was negatively and strongly related to stem height diversity (Table 4).

Swamp sparrow was the only species with the null model as the best-supported model (Table 6). The second best-supported model of swamp sparrow abundance included only stem height and received a model weight similar to that of the null model ($\Delta AIC_c = 0.30$, $\omega = 0.05$, compared to null model $\omega = 0.06$; Table 6). The best-supported models of golden-winged warbler abundance and Nashville warbler abundance contained covariates but none were strongly related to abundance (Table 4).

DISCUSSION

Wildlife management in lowland brush ecosystems focuses on altering woody vegetation structure. We evaluated associations between vegetation structure and bird species in these ecosystems and our results suggest that a variety of structural vegetation characteristics are related to breeding birds at the community and individual species levels in lowland brush ecosystems. Stem height diversity was positively related to bird species richness, which is consistent with a large body of literature indicating that diverse vegetation structure is positively related to bird species diversity (MacArthur and MacArthur 1961, Tomoff 1974, Erdelen 1984, Tews et al. 2004, Müller et al. 2010).

For alder flycatchers, chestnut-sided warblers, veeries, and yellow warblers, higher abundances were positively related to higher stem height and shrubs did not exceed approximately 4 m in our study sites. Tall woody plant species such as *Salix* spp. and *Alnus rugosa* may have supported or attracted more individuals of these species during the breeding season for a variety of reasons. The height of shrubs in brushlands has not been previously shown to be related to breeding birds but in forests, the height of trees has been shown to affect birds far more than any other plant feature and was

correlated with bird density and the nesting, singing, and feeding behavior of certain species (Lack 1933). In our study, tall shrubs may have allowed breeding individuals to gain a vantage point for maintaining territories among competitors, allowed for more effective broadcasting of songs, and provided forage and nesting material associated with larger and older shrubs (Vale et al. 1982, Erdelen 1984). Sedge wren was the only species that was negatively related to multiple characteristics of vegetation structure, including stem height. Sedge wrens have already been well described in other ecosystems and prefer open herbaceous cover (Burns 1982).

In addition to stem height, stem height diversity was strongly related to lowland brush ecosystem bird communities. The positive association between bird species richness and structural vegetation diversity may be related to the partitioning of nesting and food resources, which has been well documented in other ecosystems with woody vegetation, especially forested systems (MacArthur and MacArthur 1961, Tomoff 1974, Erdelen 1984, Tews et al. 2004, Müller et al. 2010). In lowland brush ecosystems, as the proportion of number of woody plant stems in different height profiles increase in variability, it is likely that substrates for nests, predator-avoidance habitat, and foraging opportunities also increase. This variety would support more species with different habitat and breeding requirements.

Individual species differed in whether they were positively or negatively related to characteristics of vegetation structure and we did not find any characteristics to be related to overall abundance of breeding birds. This is a key consideration for management, which may be focused on creating habitat for bird species with opposing relationships and preferences to structural vegetation characteristics. For example,

allowing woody vegetation to increase in height may support several breeding bird species but it may also decrease suitable nesting and foraging cover for sedge wrens, which are a species of conservation concern. Lowland brush ecosystem bird communities are highly diverse, not only in the number of species on the landscape but in terms of the many cover-type and plant community preferences they exhibit (Table 2). The needs of frequently detected species in brushlands may contradict one another and management for entire lowland brush ecosystem bird communities will likely need to consider these differences to meet the objective of providing habitat for the entire suite of bird species that use these ecosystems.

Management Implications

Management regimes that promote a mix of short and tall woody plants are most likely to benefit a suite of breeding bird species in lowland brush ecosystems.

Additionally, bird species may not relate to woody stem height and stem density similarly in lowland brush ecosystems, further complicating management, although we found that height of woody plants is related to fewer bird species than the density of woody plants. Some brush management techniques may not impact height and density of woody vegetation in the same ways and monitoring of woody plant responses to treatments may not consider local-scale characteristics. If feasible, implementing management strategies that affect vegetation height and density distinctly may create vegetation structure that supports bird species.

Our results indicate that monitoring vegetation height and planning for long-term management would be useful strategies for managing lowland brush ecosystems.

Additionally, although woody vegetation overgrowth has been documented to degrade brushlands, our results suggest that tall woody vegetation is important to some breeding bird species. Our results also suggest that management that results in homogenously reducing the height of woody plants across a landscape is likely to support lower bird diversity. Although species that prefer shorter woody vegetation, such as sedge wren, may benefit from the homogenous reduction of woody vegetation, our results indicate that a large suite of species prefers tall woody vegetation. The homogenous reduction of woody plant height may reduce the value of lowland brush ecosystems to some breeding bird species in the way that homogenous tall and dense woody plant cover does when disturbance is absent. Creating vegetation structure between these extremes may best support the breeding bird diversity exhibited in lowland brush ecosystems.

Our results also indicate that increasing structural diversity may support more bird species on the landscape. Stem height diversity can be obtained with a mix of stem heights and densities, via woody plants at varying growth stages, and such structure can be promoted through spatially and temporally variable disturbance regimes and brush-reduction treatments. By managing for a mix of woody plant structural characteristics, many bird species may benefit in lowland brush ecosystems. For example, sedge wren and veery, both Minnesota Species in Greatest Conservation Need, have contradictory preferences for vegetation structure and can co-inhabit an area with both short and tall woody vegetation. Additionally, structurally diverse woody vegetation structure, with both short and tall stems may provide these and other species with more nesting and foraging surfaces and opportunities than vegetation that lacks structural variability.

Table 1. Summary of number of avian point-count locations surveyed in 4 east-central Minnesota, USA lowland brush ecosystem study sites, during June 2016, 2017, and 2018. We analyzed data from 128 avian point-count locations, some of which were visited again in 2017 (all were re-visited at Gerzin and Deer Run) and 2018. Fewer surveys in 2017 and 2018 were due to inability to survey point-count locations that underwent treatments for a collaborative study. The total number of point-count locations visited each year is indicated on the bottom row. Each point-count location was surveyed 4 times each year totaling 1,052 surveys.

Study site	Surveyed locations		
	2016	2017	2018
Gerzin	32	32	8
Deer Run	32	32	7
Hasty Brook	32	16	8
Highway 29	32	24	8
Total	128	104	31

Table 2. Summary of birds detected during 1,052 point-counts at 128 survey locations from 1–28 June 2016, 29 May–21 June 2017, and 5–29 June 2018 in east-central Minnesota, USA. Stars indicate species that are listed as a Minnesota Species in Greatest Conservation Need (MNDNR 2015). Underline indicate species that are listed as fire-dependent according to the Lake States Fire Science Consortium (LSFSC 2018). Six cover type and plant community preferences are exhibited (Rodewald 2015).

Species name	Scientific name	Number of detections	Cover-type/ Plant community
<u>Sedge wren*</u>	<i>Cistothorus platensis</i>	2,856	Grasslands
Common yellowthroat	<i>Geothlypis trichas</i>	2,748	Scrub
Alder flycatcher	<i>Empidonax alnorum</i>	2,154	Scrub
Swamp sparrow	<i>Melospiza georgiana</i>	1,997	Marshes
Veery*	<i>Catharus fuscescens</i>	1,037	Forests
Yellow warbler	<i>Setophaga petechia</i>	1,003	Open Woodlands
Nashville warbler	<i>Oreothlypis ruficapilla</i>	828	Forests
<u>Clay-colored sparrow</u>	<i>Spizella pallida</i>	715	Scrub
Chestnut-sided warbler	<i>Setophaga pensylvanica</i>	584	Open Woodlands
White-throated sparrow	<i>Zonotrichia albicollis</i>	495	Forests
Song sparrow	<i>Melospiza melodia</i>	464	Open Woodlands
<u>Golden-winged warbler*</u>	<i>Vermivora chrysoptera</i>	441	Open Woodlands
Gray catbird	<i>Dumetella carolinensis</i>	322	Open Woodlands
Wilson's snipe	<i>Gallinago delicata</i>	240	Marshes
Red-eyed vireo	<i>Vireo olivaceus</i>	232	Forests
American robin	<i>Turdus migratorius</i>	230	Open Woodlands
<u>Lincoln's sparrow</u>	<i>Melospiza lincolnii</i>	218	Scrub
Red-winged blackbird	<i>Agelaius phoeniceus</i>	206	Marshes
<u>LeConte's sparrow*</u>	<i>Ammospiza leconteii</i>	140	Grasslands
American goldfinch	<i>Spinus tristis</i>	125	Open Woodlands
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	124	Forests
American crow	<i>Corvus brachyrhynchos</i>	104	Open Woodlands
Blue jay	<i>Cyanocitta cristata</i>	95	Forests
Black-and-white warbler	<i>Mniotilta varia</i>	90	Forests
Black-billed cuckoo*	<i>Coccyzus erythrophthalmus</i>	89	Forests

Ovenbird	<i>Seiurus aurocapilla</i>	75	Forests
Cedar waxwing	<i>Bombycilla cedrorum</i>	69	Open Woodlands
Black-capped chickadee	<i>Poecile atricapillus</i>	52	Forests
Hermit thrush	<i>Catharus guttatus</i>	50	Open Woodlands
Mallard	<i>Anas platyrhynchos</i>	50	Lakes and Ponds
Mourning dove	<i>Zenaida macroura</i>	45	Open Woodlands
<u>American bittern*</u>	<i>Botaurus lentiginosus</i>	44	Marshes
American redstart	<i>Setophaga ruticilla</i>	44	Forests
Common raven	<i>Corvus corax</i>	42	Forests
Northern flicker	<i>Colaptes auratus</i>	37	Open Woodlands
Brown-headed cowbird	<i>Molothrus ater</i>	36	Grasslands
Chipping sparrow	<i>Spizella passerina</i>	36	Open Woodlands
Savannah sparrow	<i>Passerculus sandwichensis</i>	36	Grasslands
Least flycatcher	<i>Empidonax minimus</i>	33	Forests
<u>Sandhill crane</u>	<i>Antigone canadensis</i>	32	Marshes
Great-crested flycatcher	<i>Myiarchus crinitus</i>	31	Open Woodlands
<u>Northern harrier*</u>	<i>Circus hudsonius</i>	25	Grasslands
Blue-headed vireo	<i>Vireo solitarius</i>	22	Forests
Canada goose	<i>Branta canadensis</i>	21	Marshes
Tree swallow	<i>Tachycineta bicolor</i>	20	Lakes and Ponds
Ruffed grouse	<i>Bonasa umbellus</i>	18	Forests
Yellow-billed cuckoo*	<i>Coccyzus americanus</i>	18	Open Woodlands
Mourning warbler	<i>Geothlypis philadelphia</i>	15	Forests
Blackburnian warbler	<i>Setophaga fusca</i>	14	Forests
Cliff swallow	<i>Petrochelidon pyrrhonota</i>	11	Lakes and Ponds
<u>Field sparrow*</u>	<i>Spizella pusilla</i>	11	Scrub
Grasshopper sparrow*	<i>Ammodramus savannarum</i>	11	Grasslands
Red-breasted nuthatch	<i>Sitta canadensis</i>	10	Forests
Pileated woodpecker	<i>Dryocopus pileatus</i>	9	Forests
Wild turkey	<i>Meleagris gallopavo</i>	8	Open Woodlands
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	7	Towns
Ruby-throated hummingbird	<i>Archilochus colubris</i>	7	Open Woodlands
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	7	Forests
Yellow-throated vireo	<i>Vireo flavifrons</i>	7	Open Woodlands
American tree sparrow	<i>Spizelloides arborea</i>	6	Open Woodlands

<u>Brown thrasher*</u>	<i>Toxostoma rufum</i>	6	Scrub
Hairy woodpecker	<i>Dryobates villosus</i>	6	Forests
American woodcock*	<i>Scolopax minor</i>	5	Forests
Common grackle	<i>Quiscalus quiscula</i>	5	Open Woodlands
Downy woodpecker	<i>Dryobates pubescens</i>	5	Forests
American kestrel*	<i>Falco sparverius</i>	4	Grasslands
Eastern phoebe	<i>Sayornis phoebe</i>	4	Open Woodlands
Purple finch*	<i>Haemorhous purpureus</i>	4	Forests
<u>Sharp-tailed grouse*</u>	<i>Tympanuchus phasianellus</i>	4	Grasslands
Bald eagle	<i>Haliaeetus leucocephalus</i>	3	Forests
Black-throated green warbler	<i>Setophaga virens</i>	3	Forests
<u>Bobolink*</u>	<i>Dolichonyx oryzivorus</i>	3	Grasslands
Eastern wood-pewee	<i>Contopus virens</i>	3	Forests
<u>Ruby-crowned kinglet</u>	<i>Regulus calendula</i>	3	Forests
Wood thrush*	<i>Hylocichla mustelina</i>	3	Forests
<u>Yellow-bellied flycatcher</u>	<i>Empidonax flaviventris</i>	3	Forests
Belted kingfisher*	<i>Megaceryle alcyon</i>	2	Lakes and Ponds
<u>Eastern bluebird</u>	<i>Sialia sialis</i>	2	Grasslands
Eastern kingbird	<i>Tyrannus tyrannus</i>	2	Grasslands
Magnolia warbler	<i>Setophaga magnolia</i>	2	Forests
Nelson's sparrow*	<i>Ammospiza nelsoni</i>	2	Marshes
Northern goshawk*	<i>Accipiter gentilis</i>	2	Forests
Northern shoveler	<i>Spatula clypeata</i>	2	Marshes
<u>Sora</u>	<i>Porzana carolina</i>	2	Marshes
Swainson's thrush	<i>Catharus ustulatus</i>	2	Forests
White-breasted nuthatch	<i>Sitta carolinensis</i>	2	Forests
Winter wren*	<i>Troglodytes hiemalis</i>	2	Forests
<u>Three-toed woodpecker</u>	<i>Picoides dorsalis</i>	1	Forests
Blackpoll warbler	<i>Setophaga striata</i>	1	Forests
Blue-winged teal	<i>Spatula discors</i>	1	Marshes
Broad-winged hawk	<i>Buteo platypterus</i>	1	Forests
Great blue heron	<i>Ardea herodias</i>	1	Marshes
<u>Great gray owl</u>	<i>Strix nebulosa</i>	1	Forests
Killdeer	<i>Charadrius vociferus</i>	1	Grasslands
<u>Marsh wren</u>	<i>Cistothorus palustris</i>	1	Marshes

Northern waterthrush	<i>Parkesia noveboracensis</i>	1	Forests
<u>Olive-sided flycatcher*</u>	<i>Contopus cooperi</i>	1	Open Woodlands
<u>Pine warbler</u>	<i>Setophaga pinus</i>	1	Forests
Rock pigeon	<i>Columba livia</i>	1	Towns
Tennessee warbler	<i>Oreothlypis peregrina</i>	1	Forests
Trumpeter swan*	<i>Cygnus buccinator</i>	1	Lakes and Ponds
Turkey vulture	<i>Cathartes aura</i>	1	Open Woodlands
Warbling vireo	<i>Vireo gilvus</i>	1	Open Woodlands
Wood duck	<i>Aix sponsa</i>	1	Lakes and Ponds
Yellow-rumped warbler	<i>Setophaga coronata</i>	1	Forests

Table 3. Competing models, defined as models with an Akaike’s Information Criterion (adjusted for sample size) of <2 between the best-supported model and the model under consideration ($<2 \Delta AIC_c$) of bird species richness recorded during 1,052 point-count surveys in 4 east-central Minnesota, USA lowland brush ecosystem study sites, 1-28 June 2016, 29 May-21 June 2017, and 5-29 June 2018. Competing models presented are a subset of models fitted with all possible combinations of vegetation covariates. We report number of parameters (K), differences between AIC_c values (ΔAIC_c), weights for competing models (ω), and deviance. Vegetation covariates in models were derived from live woody plant species and included stem density (per ha), stem height (average height in cm), stem height diversity, difference in stem density (between paired plots), difference in stem height (between paired plots), and woody plant species count (the number of species in 56.55 m² paired plots). All models included year and study site as random effects and 4 avian point-count surveys conducted at each avian point-count location as a nested random effect (within study site). The null model was included for reference.

Model	K	ΔAIC_c^a	ω	Deviance
Stem height diversity + Stem density	3	0.00	0.10	4497.52
Stem height diversity	2	0.07	0.10	4496.51
Stem height diversity + Woody species count	3	1.34	0.06	4498.78
Stem height diversity + Difference in stem density	3	1.76	0.04	4499.43
Stem density + Stem height	3	1.84	0.04	4499.21
Stem height diversity + Stem density + Difference in stem density	4	1.86	0.04	4500.60
Stem height diversity + Difference in stem height	3	1.88	0.04	4499.37
Stem height diversity + Stem density + Stem height	4	1.96	0.04	4499.29

NULL	1	6.36	0	4501.644
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a. AICc value for the best supported model = 4529.95

Table 4. Covariate coefficient estimates and confidence intervals (CIs 95%) for covariates included in the best-supported models of bird species richness, bird total abundance, and frequently detected species recorded during 1,052 point-count surveys in 4 east-central Minnesota, USA lowland brush ecosystem study sites, 1–28 June 2016, 29 May–21 June 2017, and 5–29 June 2018. Vegetation covariates in models were derived from live woody plant species and included stem density (per ha), stem height (average height in cm), stem height diversity, difference in stem density (between paired plots), difference in stem height (between paired plots), and woody plant species count (the number of species in 56.55 m² paired plots). Estimates are based on the best-supported model, selected based on lowest AIC_c of models fitted with all possible combinations of vegetation covariates. Bold estimates indicate the covariate had strong support based on CIs not overlapping 0. Dashes indicate the covariate was not included in the best-supported model.

Response variable	Stem density	Stem height	Stem height diversity	Difference in stem density	Difference in stem height	Woody species count
Bird species richness	0.12 (-0.04,0.29)	-	0.25 (0.08, 0.41)	-	-	-
Bird total abundance	-	-	-	-	-	-
Alder flycatcher	-	0.10 (0.05, 0.15)	-	-	-	-
Chestnut-sided warbler	-	0.20 (0.09, 0.31)	-	-	-0.09 (-0.21, 0.02)	0.16 (0.06, 0.26)
Clay-colored sparrow	0.23 (0.10, 0.36)	-	-0.14 (-0.28, 0.00)	-	-	-

Common yellowthroat	-	-	-0.07 (-0.12, -0.03)	-	-	-
Golden-winged warbler	0.10 (-0.02, 0.22)	-	-	-	-	-
Nashville warbler	0.09 (-0.01, 0.20)	-0.18 (-0.38, 0.01)	0.22 (0.03, 0.42)	-	-	0.08 (-0.02, 0.18)
Sedge wren	-0.17 (-0.26, -0.08)	-0.11 (-0.18, -0.03)	-	0.07 (0.01, 0.14)	-	-0.11 (-0.20, -0.02)
Swamp sparrow	-	-	-	-	-	-
Veery	-0.10 (-0.20, 0.00)	0.17 (0.08, 0.25)	-	-0.07 (-0.15, 0.02)	-	-
Yellow warbler	-	0.18 (0.09, 0.27)	-	-	-	-

Table 5. Competing models, defined as models with an Akaike’s Information Criterion (adjusted for sample size) of <2 between the best-supported model and the model under consideration ($<2 \Delta AIC_c$) of bird total abundance recorded during 1,052 point-count surveys in 4 east-central Minnesota, USA lowland brush ecosystem study sites, 1–28 June 2016, 29 May–21 June 2017, and 5–29 June 2018. Competing models presented are a subset of models fitted with all possible combinations of vegetation covariates. We report number of parameters (K), differences between AIC_c values (ΔAIC_c), weights for competing models (ω), and deviance. Vegetation covariates in models were derived from live woody plant species and included stem density (per ha), stem height (average height in cm), stem height diversity, difference in stem density (between paired plots), difference in stem height (between paired plots), and woody plant species count (the number of species in 56.55 m² paired plots). All models included year and study site as random effects and 4 avian point-count surveys conducted at each avian point-count location as a nested random effect (within study site).

Model	K	ΔAIC_c^a	ω	Deviance
NULL	1	0.00	0.10	5150.07
Stem height	2	0.81	0.07	5151.66
Stem height diversity	2	1.41	0.05	5152.31
Woody species count	2	1.62	0.04	5152.51
Difference in stem density	2	1.74	0.04	5152.67
Stem density	2	1.78	0.04	5152.65

a. AIC_c score for the best supported model = 5183.53

Table 6. Competing models, defined as models with an Akaike’s Information Criterion (adjusted for sample size) of <2 between the best-supported model and the model under consideration ($<2 \Delta AIC_c$) of frequently detected bird species recorded during 1,052 point-count surveys in 4 east-central Minnesota, USA lowland brush ecosystem study sites, 1–28 June 2016, 29 May–21 June 2017, and 5–29 June 2018. Competing models presented are a subset of models fitted with all possible combinations of vegetation covariates. We report number of parameters (K), differences between AIC_c values (ΔAIC_c), weights for competing models (ω), and deviance. Vegetation covariates in models were derived from live woody plant species and included stem density (per ha), stem height (average height in cm), stem height diversity, difference in stem density (between paired plots), difference in stem height (between paired plots), and woody plant species count (the number of species in 56.55 m² paired plots). All models included year and study site as random effects and 4 avian point-count surveys conducted at each avian point-count location as a nested random effect (within study site). The null model, which only included random effects and an intercept term, was included for reference if it did not have a $\Delta AIC_c < 2$.

Species	Model	K	ΔAIC_c^a	ω	Deviance
Alder flycatcher ^b	Stem height	2	0	0.12	3068.01
	Stem height diversity	2	1.16	0.07	3069.17
	Stem height + Stem height diversity	3	1.41	0.06	3067.39
	Stem height + Difference in stem height	3	1.67	0.05	3067.65
	Stem height + Woody species count	3	1.8	0.05	3067.78

	Stem height + Stem density	3	1.83	0.05	3067.81
	NULL	1	11.96	0	3081.99
Chestnut-sided warbler ^c	Woody species count + Stem height + Difference in stem height	4	0.00	0.11	1713.77
	Woody species count + Stem height	3	0.49	0.09	1716.29
	Woody species count + Difference in stem height + Stem height diversity	4	1.06	0.07	1714.83
	Woody species count + Stem height + Difference in stem height + Stem height diversity	5	1.55	0.05	1713.28
	Woody species count + Stem height + Difference in stem height + Stem density	5	1.56	0.05	1713.29
	Woody species count + Stem height + Difference in stem height + Difference in stem density	5	1.58	0.05	1713.32
	Woody species count + Stem height + Stem density	4	1.67	0.05	1715.45
	Woody species count + Stem height + Difference in stem density	4	1.79	0.05	1715.56
	NULL	1	13.94	0	1733.80
Clay-colored sparrow ^b	Stem density + Stem height diversity	3	0.00	0.10	1828.34
	Stem density + Stem height diversity + Woody species count	4	0.71	0.07	1827.02
	Stem density + Stem height	3	0.95	0.06	1829.29
	Stem density + Woody species count	3	1.06	0.06	1829.40
	Stem density + Stem height diversity + Difference in stem height	4	1.07	0.06	1827.39
	Stem density + Woody species count + Stem height	4	1.09	0.06	1827.41
	Stem density	2	1.48	0.05	1831.84
	Stem density + Stem height diversity + Stem height	4	1.73	0.04	1828.04

Common yellowthroat ^b	NULL	1	10.15	0	1842.53
	Stem height diversity	2	0.00	0.12	3135.56
	Stem height	2	0.83	0.08	3136.39
	Stem height diversity + Difference in stem height	3	1.18	0.07	3134.72
	Stem height diversity + Stem height	3	1.63	0.05	3135.17
	Stem height diversity + Stem density	3	1.98	0.04	3135.52
Golden-winged warbler ^b	NULL	1	7.39	0	3144.97
	Stem density	2	0.00	0.11	852.17
	Difference in stem height	2	0.00	0.05	1538.63
	NULL	1	0.15	0.05	1538.78
	Stem density + Difference in stem height	3	0.41	0.04	1541.06
	Woody species count	2	0.56	0.04	1537.17
	Difference in stem height + Stem height diversity	3	0.74	0.04	1539.37
	Stem density + Difference in stem height + Stem height	4	0.77	0.04	1537.38
	Difference in stem height + Stem height	3	0.79	0.04	1535.37
	Stem density + Stem height diversity + Difference in stem height	4	0.88	0.04	1537.49
	Stem density + Stem height	3	1.03	0.03	1535.61
	Difference in stem height + Woody species count	3	1.05	0.03	1537.66
	Stem density + Stem height diversity	3	1.06	0.03	1537.67
	Stem density + Woody species count	3	1.42	0.03	1538.03
	Stem density + Difference in stem density	3	1.66	0.02	1538.27
Nashville warbler ^b	Stem density + Stem height + Stem height diversity + Woody species count	5	0.00	0.08	2173.39
	Stem density + Stem height + Stem height diversity	4	0.21	0.07	2175.64
	Stem density + Woody species count + Difference in	4	0.71	0.06	2176.13

	stem height				
	Stem density + Stem height + Stem height diversity + Woody species count + Difference in stem height	6	0.95	0.05	2172.31
	Stem density + Woody species count	3	1.00	0.05	2178.45
	Stem height + Stem height diversity + Woody species count	4	1.06	0.05	2176.48
	Stem density + Stem height diversity + Woody species count	4	1.43	0.04	2176.86
	Stem density + Stem height + Stem height diversity + Difference in stem height	6	1.64	0.04	2175.03
	Woody species count	2	1.76	0.03	2181.24
	Stem density + Stem height + Stem height diversity + Woody species count + Difference in stem density	6	1.84	0.03	2173.20
	NULL	1	8.67	0.001	2190.17
Sedge wren ^b	Stem density + Difference in stem density + Woody species count + Stem height	5	0.00	0.19	3337.10
	Stem density + Difference in stem density + Woody species count + Stem height diversity	5	0.21	0.17	3337.31
	Stem density + Difference in stem density + Woody species count + Stem height + Stem height diversity	6	1.20	0.11	3336.27
	Stem density + Difference in stem density + Woody species count + Stem height + Difference in stem height	6	1.66	0.08	3336.72
	Stem density + Difference in stem density + Woody species count + Stem height diversity + Difference in stem height	6	1.92	0.07	3336.99
	NULL	1	32.95	0	3378.15
Swamp sparrow ^b	NULL	1	0.00	0.06	2956.25

	Stem height	2	0.30	0.05	2954.54
	Difference in stem density	2	0.85	0.04	2955.08
	Stem height + Difference in stem density	3	0.89	0.04	2953.10
	Difference in stem height	2	0.95	0.04	2955.19
	Woody species count	2	1.03	0.04	2955.26
	Stem height diversity	2	1.07	0.04	2955.30
	Stem height + Woody species count	3	1.07	0.04	2953.28
	Stem height + Difference in stem density + Woody species count	4	1.33	0.03	2951.51
	Difference in stem density + Woody species count	3	1.65	0.03	2953.86
	Woody species count + Stem height diversity	3	1.66	0.03	2953.87
	Stem height + Difference in stem height	3	1.90	0.02	2954.11
	Difference in stem density + Stem height diversity	3	1.96	0.02	2954.17
	Stem density	2	1.99	0.02	2956.23
Veery ^b	Stem height + Stem density + Difference in stem density	4	0.00	0.12	2146.19
	Stem height + Stem density	3	0.30	0.10	2148.52
	Stem height + Stem density + Difference in stem density + Woody species count	5	0.73	0.08	2144.89
	Stem height + Stem density + Woody species count	4	1.21	0.07	2147.40
	Stem height + Stem density + Difference in stem density + Stem height diversity	5	1.87	0.05	2146.03
	Stem height + Difference in stem density	3	1.87	0.05	2150.09
	NULL	1	16.66	0	2168.93
Yellow warbler ^b	Stem height	2	0.00	0.18	2350.67
	Stem height + Stem height diversity	3	1.88	0.07	2350.53
	Stem height + Stem density	3	1.91	0.07	2350.56

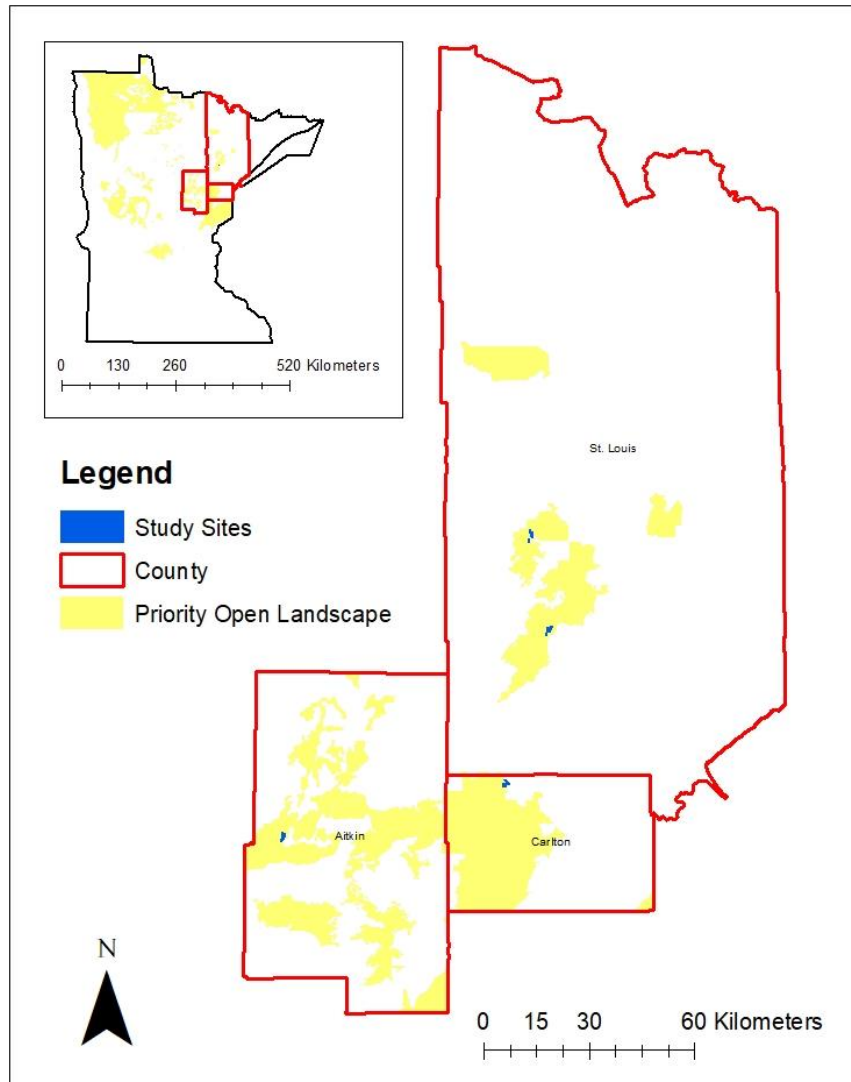
Stem height + Difference in stem density	3	1.94	0.07	2350.59
Stem height + Woody species count	3	1.98	0.07	2350.63
NULL	1	11.03	0.001	2363.72

a. AICc score for the best supported models: Alder flycatcher = 3085.88, chestnut-sided warbler = 1734.20, clay-colored sparrow = 1845.91, common yellowthroat = 3154.13, golden-winged warbler = 1555.22, Nashville warbler = 2191.91, sedge wren = 3356.03, swamp sparrow = 2971.06, veery = 2164.82, and yellow warbler = 2370.07.

b. Poisson was the best-fitting distribution, determined by lowest AICc.

c. Zero-inflated Poisson was the best-fitting distribution, determined by lowest AICc.

Figure 1. Locations of 4 lowland brush ecosystem study sites in east-central Minnesota, USA during a study of the effects of season of fire on birds and vegetation during 2016-2018. Study sites are within Priority Open Landscapes, determined by the Minnesota Department of Natural Resources. Study sites were on public land and managed by the Department of Natural Resources for wildlife habitat.



Chapter 2

Season of Fire Effect on Breeding Birds and Vegetation Structure in Lowland Brush Ecosystems

Overview:

In the western Great Lakes region of the United States, lowland brush ecosystems provide habitat to a diverse suite of bird species and without effective management, changes in woody vegetation structure may decrease the value of these systems to bird communities. Lowland brushland ecosystems are fire-dependent predominately burned as part of management prescriptions in the spring when plants are dormant and weather conditions are mild and conducive to prescribed fire. Historically, fires occurred throughout the plant growing season in lowland brush ecosystems whenever lightning occurred. Changes in fire patterns may result in vegetation structure and composition that doesn't provide habitat for bird communities associated with these ecosystems, and perhaps result in poorer quality habitat. We used a Before-After-Control-Impact experimental design to compare the effect of spring, summer, and fall fire treatments on bird and plant communities in 2 Minnesota lowland brush ecosystem study sites. Measures of woody vegetation structure (stem height diversity, stem height, stem density, and woody plant species count) did not change significantly after fires. For summer and fall fires, lack of vegetation response was due to patchiness of fire that burned few survey locations. Although spring fires burned most of the designated spring treatment areas, vegetation recovered quickly. However, bird total abundance increased significantly compared to controls after summer and fall fires. We measured changes in the number of

singing males detected and out of 10 frequently detected species, swamp sparrow (*Melospiza georgiana*), chestnut-sided warbler (*Setophaga pensylvanica*), yellow warbler (*Setophaga petechia*), and veery (*Catharus fuscescens*) responded significantly to 1 or more fire season treatments compared to controls. Swamp sparrow abundance decreased after spring fires, chestnut-sided warbler abundance increased after spring and fall fires, yellow warbler abundance decreased after spring and fall fires, and veery abundance decreased after summer fires. Except for both swamp sparrow and yellow warbler decreasing in abundance after spring fires, no 2 species responded to the same fire-season treatments in the same way. Based on our results, bird community diversity in lowland brush ecosystems would increase when summer and fall fires are incorporated into management regimes. Burning during these seasons may create conditions more similar to those present prior to fire suppression or resulting from fires applied only during spring. This may also allow managers of lowland brush ecosystems to utilize larger burn-windows.

Key Words: Prescribed fire, season of fire, bird abundance, disturbance, woody vegetation, shrub, lowland brush, brushlands, Minnesota, Before-After-Control-Impact

INTRODUCTION

The season in which fire occurs is an important factor in fire intensity, severity, behavior and the response of plant communities (Buckman 1964, Platt et al. 1988, Howe 1994, Sparks et al. 1999, Knapp et al. 2009, Glitzenstein et al. 2012, Weyenberg and Pavlovic 2014). Season of fire impacts plants based on phenological patterns of plant

carbon storage and resources (Platt et al. 1988, Howe 1994). For example, plant communities in brushlands, forests, and grasslands exhibit higher survival and more vigorous re-sprouting after being burned in dormant states compared to when actively growing (Buckman 1964, Austin and Buhl 2013, Brose et al. 2013). In contrast, fires in summer and early fall may promote patchiness in cover types, which has been shown to support greater wildlife species diversity in many systems (Fuhlendorf et al. 2006, Coppedge et al. 2008).

Season of fire also impacts wildlife communities, including bird communities (Sparks et al. 1999, Brennan et al. 2000, Reinking 2005, Fuhlendorf et al. 2006, Knapp et al. 2009). Indirect effects on heterogeneity of cover types and vegetation structure can impact substrates for nests, predator-avoidance cover, and foraging opportunities for birds (Westemeier 1973, Higgins 1986, Sparks et al. 1999, Brennan et al. 2000, Reinking 2005, Knapp et al. 2009). Additionally, in some seasons fire may move at speeds that create refugia, or unburned patches, which can be critical for birds that persist on the land as burns occur (Knapp et al. 2009). Birds may be susceptible to direct mortality from fire, depending on behavior and mobility, during different times of the year. For example, spring burns can cause direct mortality of early-season nesting birds and waterfowl (Horton 1930, Higgins 1986, Pilliod et al. 2006).

Even though plants and wildlife respond differently to fires that occur during different seasons, the timing of prescribed fire is often restricted by logistics and weather conditions to a single season and applied at different seasons compared to historical season of burn (Knapp et al. 2009). In fire-dependent ecosystems, including forests, brushlands, and grasslands, historical fires occurred across seasons, unlike current

prescribed fire regimes in which fires are often predominantly conducted during spring or cool seasons when plants are dormant (Knapp et al. 2009). In many managed systems, conditions influencing fire behavior, such as high temperatures, contribute to more unpredictable fires during growing than dormant seasons. Logistical challenges, including the control of smoke and maintaining safe temperatures for burn crews, make prescribed fires difficult to implement during the growing season (Knapp et al. 2009, Austin and Buhl 2013). However, for ecosystems that historically experienced fire during different seasons, lack of variability in season of fire may result in ecological changes, including shifts in plant and wildlife species community composition (Abrahamson and Hartnett 1990, Schwartz and Heim 1996, Knapp et al. 2009). This is especially true when fire is repeatedly applied at the same time of year (Knapp et al. 2009).

Shrub- and brushlands are fire-dependent ecosystems characterized by a variable mix of woody and herbaceous vegetation that evolved with fire and support diverse bird communities (Curtis 1959, Hanowski et al. 1999). Prior to widespread fire suppression, records of lightning strike occurrences suggest that fires occurred at moderate intervals during spring and fall plant dormant seasons, and summer growing seasons in brushland ecosystems (Zajac and Rutledge 2001, Lorimer and White 2003, MNDNR 2003, Curtis 1959). Without frequent or effective disturbance, woody vegetation eventually increases in density and extent, resulting in large areas of homogenous cover (Curtis 1959). Currently, brushland managers rely heavily on prescribed fire to reduce density, height, and extent of woody vegetation and promote diversity that includes both herbaceous and woody cover-types.

Although fire is the preferred method for maintaining vegetation conditions and supporting wildlife (Curtis 1959), brushland managers are often constrained to burn in the spring because fires are easier to control and more resources are available (Austin and Buhl 2013). Burning during different seasons may more accurately simulate the historical influence of fire in brushland communities; however, a strong focus on the season of fire or the effects of seasonably variable fire is absent in previous research or current management practices. In some instances brushland managers remove woody vegetation mechanically during different seasons, but this lacks the benefits and complex effects of fire, including making nutrients available and promoting heterogeneity of cover types (Hanowski et al. 1999, Austin and Buhl 2013).

Our objective was to assess the effect of season of prescribed fire on breeding birds and vegetation structure in lowland brush ecosystems, which historically exhibited fires with natural ignition sources that were seasonably variable. We asked, do birds and vegetation structure respond differently to spring, summer, and fall fires and compared to areas not burned? And, if birds responded differently to season of fire, where these responses related to changes in vegetation structure?

Based on earlier studies (Hanowski et al. 1999, Knapp et al. 2009), we hypothesized that 1) breeding bird communities and vegetation characteristics would change in response to spring, summer, and fall fire compared with areas not burned, 2) individual breeding bird species responses would differ among spring, summer, and fall fire treatments, and 3) breeding bird species and vegetation structure related to birds would respond to season of fire in the same directions. We did not specify the directions of bird responses, because there is little or no information about bird response to season

of fire in brushlands. Based on earlier studies of brushland plant responses to fire in different seasons (Linde 1969, Kost and De Steven 2000, Middleton 2002, Briggs et al. 2005, Brisson et al. 2006, Austin and Buhl 2013), we hypothesized lastly that 4) summer fires would reduce stem density and height more than spring and fall fires. In a companion study, stem height was positively related to the abundance of several frequently detected breeding bird species (Hawkinson Chapter 1). Changes to this characteristic of vegetation structure may result in changes in abundance of certain species.

STUDY AREA

We evaluated season of fire effects on lowland brush ecosystem bird communities and vegetation in east-central Minnesota (N46.9725790 W092.9853520) from 2016 to 2018. Lowland brush ecosystems make up approximately 20% (3.5 million hectares) of the landscape in Minnesota (USGS 2011) and provide critical habitat for >250 wildlife species including >80 Minnesota Species in Greatest Conservation Need, 38 of which are birds (MNDNR 2015). Several bird species of conservation concern in Minnesota have been documented in lowland brush ecosystems during their breeding seasons, including Species in Greatest Conservation Need such as Le Conte's sparrows (*Ammodramus leconteii*), golden-winged warblers (*Vermivora chrysoptera*), northern harriers (*Circus cyaneus*), sedge wrens (*Cistothorus platensis*), and veeries (*Catharus fuscescens*). Le Conte's sparrow populations are declining due to habitat loss attributed to fire-suppression (MNDNR 2015) and at least 40% of the global population of golden-winged

warblers utilize habitat within Minnesota during the non-wintering season (Streby et al. 2017).

We evaluated bird and vegetation response to season of fire within 2 study sites that were identified by MNDNR wildlife managers as being comprised of areas of lowland brush of ≥ 162 ha that could be subdivided into 4 sections of approximately similar size and vegetative composition through the use of firebreaks. Study sites were on public land and within Minnesota Department of Natural Resources Priority Open Landscapes, which are designated through a state-wide natural resource management plan and use natural boundaries from state-wide ecological classifications (Fig.1; Wendt and Coffin 1988). Study sites were subdivided into 4 sections for 3 prescribed fire season treatments (spring, summer, and fall) and 1 unburned section that served as a control. Each treatment was applied to ~ 41 ha and separated by fire breaks, which included breaks created by land managers and pre-existing drainage ditches and roads.

Within study sites, vegetative composition was similar and included the Minnesota native plant communities northern alder swamp, northern poor fen, northern wet meadow/carr, and willow dogwood swamp (MNDNR 2003). Predominant woody plants included speckled alder (*Alnus rugosa*), willow species (*Salix* spp.), dogwood species (*Cornus* spp.), bog birch (*Betula pumila*), and low woody species associated with bogs, such as leatherleaf (*Chamaedaphne calyculata*) and Labrador tea (*Rhododendron groenlandicum*). Herbaceous plant species varied more than woody plants between sites and included sedges (*Carex* spp.) typical of wet meadows, moss and bryophytes typical of boreal bogs, and grasses and forbs tolerant of wet conditions. Study sites were dominated by diverse herbaceous cover, interspersed with patches of woody shrubs. The

majority of area in study sites exhibited a persistent water-table, which rose with the occurrence of frequent or heavy rain. Study sites had not been managed with prescribed fire ≥ 5 years.

METHODS

Prescribed Fire Treatments

We defined prescribed fire seasons (spring, summer, and fall) based on weather events and plant phenological stages. Spring fires were executed after snowmelt and before leaf-out. Summer fires were executed during the plant growing season until plants began to show signs of senescence. Fall fires were executed after plants began to show signs of senescence until the ground was snow-covered. From November 2016 –May 2017, MNDNR burn crews executed spring, summer, and fall fire treatments across both study sites, totaling 2 spring, 2 summer, and 2 fall fire treatments (Table 1).

Bird Surveys

Using ArcGIS (ESRI 2015), we placed 32 avian point-count locations (8 per section) in each study site using systematic random placement and restricting points to be ≥ 100 m from the study site boundary and ≥ 225 m from other point-count locations, which allowed for non-overlapping 100-m radii around each location (for an example see Fig. S1). In the springs before and after prescribed fire treatments, we conducted early-morning, single-observer avian point-count surveys from late May to early June in 2016, 2017, and 2018 when male breeding birds were vocalizing. We did not conduct surveys on days with initial wind speeds > 19 km/h and canceled surveys if wind speeds increased

to >28 km/h during a survey. We did not conduct surveys when precipitation was more than a drizzle or when electrical storm warnings were in effect (Hutto et al. 1986, Ralph et al. 1995).

We trained observers to identify bird species that have been documented in Minnesota lowland brush ecosystems both aurally and visually prior to conducting point-count surveys. Our protocol consisted of counting birds within a 100-m radius around point-count locations (Birds and Burns Network 2003, Hurteau et al. 2008). Observers initiated surveys 30 min prior to sunrise and completed surveys before 0900 CDT (Hutto et al. 1986, Ralph et al. 1995). After arriving at the survey point and waiting quietly for 2 min, observers recorded all individual birds detected within 100 m for a 6-min period. During the surveys, observers recorded detection for individual birds for 3 2-min intervals (Buckland et al. 2009). For each individual bird, observers recorded species and distance from the point-count location to the estimated location of the bird. We counted birds within a 100-m radius around point-count locations, and we trained observers to estimate detection distances ≤ 100 m by marking distances 5, 10, 25, 50, and 100 m from 4 point-count locations in each study site. Observers used these marked distances during surveys to aid in distinguishing among individuals of the same species that were detected at different distances. We provided observers with an image of a survey point with distance radii to serve as a visual aid to map estimated locations of birds throughout surveys to minimize the potential for double counting.

We surveyed all point-count locations 4 times each year. We surveyed all 32 point-count locations within a single study site in ≤ 2 mornings, with each observer surveying 8 locations. At each visit to a study site, we assigned a new section and

therefore 8 new point-count locations to observers. In 2016 and 2017 we had 4 observers and surveyed point-count locations with a unique observer each time we conducted surveys; 4 unique observers independently conducted the 4 surveys at each point-count location during each June. In 2018 we had 2 observers and therefore had 2 unique observers for the 4 surveys conducted at each point-count location. In 2016 and 2017, during instances when an observer could not conduct surveys, some point-count locations were surveyed more than once by the same observer. This occurred infrequently and overall $\geq 75\%$ of point-count locations were not visited by the same observer more than once.

Bird behavior can change with time of day and surveying point-count locations at the same time each survey would potentially result in non-random variation in detection probability across survey locations based on how active or inactive birds were during surveys (Hutto et al. 1986). To survey all locations during a range of times, we conducted the 4 surveys at each point-count location at different times during the survey period. Observers documented start times and avoided surveying at the same time as previous surveys (within 15 min). We also surveyed point-count locations in a different order each time we surveyed a study site. This consisted of making the first location different for at least half of surveys and re-assigning, including reversing, the order that observers surveyed point-count locations.

Vegetation Surveys

We measured woody vegetation structure before and after fire treatments to assess changes related to season of fire because the effects of fire on bird communities are in

large part through effects on vegetation (Bock and Block 2005, Knapp et al. 2009). Before and after prescribed fire treatments, we quantified woody vegetation characteristics near avian point-count locations. During July-September 2016, 2017, and 2018, we sampled vegetation at 2 3-m fixed-radius vegetation plots placed 10 m north and east of each avian point-count location. We sampled woody plant species <10 cm dbh and woody stems \geq 10 cm dbh separately. We counted woody stems \geq 10 cm dbh in 2 categories, live and dead (snag). We determined early during vegetation sampling that dead stems <10 cm dbh were not abundant and difficult to distinguish from live stems; therefore, we counted woody stems <10 cm dbh in a single category. We divided plots into 4 quadrants for ease of sampling. In each quadrant, we counted the number of stems <10 cm dbh for each species in 5 height classes (0-50, 51-100, 101-200, 201-300 and >300 cm; Salk et al. 2011, Fisichelli et al. 2012) We used a pole pre-marked at 50, 100, 150, 200, 250, and 300 cm to measure height. We divided counts of stems into 4 abundance categories (0-25, 26-50, 51-100, >100 stems). For snags, we did not identify species.

We derived woody structural vegetation metrics from the paired vegetation plots at point-count locations related to bird abundance (Hawkinson Chapter 1) and that would likely change as a result of fire. We considered paired plots as a single sample unit and calculated a single value from paired plots to associate with each point-count location. We used 3 measures of woody vegetation structure because bird species in brushlands have been shown to be related to a variety of structural vegetation characteristics (Curtis 1959, Lorimer and White 2003), such as diversity of physiognomy (Tomoff 1974), volume of vegetation (Mills et al. 1991), and horizontal diversity of vegetation structure

(Roth 1976). We used a diversity index of woody stems to quantify the complexity of vegetation structure (stem height diversity), stem density (per ha), and average stem height (cm). These characteristics are likely shaped by fire because without fire or other forms of disturbance in brushlands, woody vegetation increases in height and density, and eventually results in homogenous cover (Curtis 1959). We also included counts of woody plant species because the season of fire can favor the regeneration and growth of specific plant species (Platt et al. 1988, Howe 1994), which can support distinct insect and wildlife species (Bulan and Barret 1971, Hansen 1986, Swengel 2001, Pilliod et al. 2006, Knapp et al. 2009).

We derived vegetation variables by assigning the median value of the category intervals to categories of stem counts <10 cm dbh (i.e., 0-25 = 12.5, 26-50 = 37.5, 51-100 = 75 and >100 = 150 stems). We used stem height diversity to quantify vertical vegetation structure diversity, similar to the metric implemented for foliage cover by MacArthur and MacArthur (1961). Tomoff (1974) modified MacArthur and MacArthur's foliage height diversity height profiles in models of breeding bird species in desert scrub communities, and we used a comparable approach, as shrub height categories in that study were similar to ours. We used our 5 height categories and the number of woody plant stems and the package *vegan* (Oksanen et al. 2018) to calculate stem height diversity using Shannon's True Diversity Index (Jost 2006), in the statistical program R (version 3.4.2, R Core Team 2017).

$$\exp\left(-\sum_{i=1}^s p_i \log_e p_i\right)$$

In the above equation, p_i is the proportional abundance of stems in i^{th} height profile, S is the number of stems in each height profile, and b is the natural logarithm. We calculated stem density (stems/ha) and average stem height using vegetation measurements from the paired vegetation plots at point-count locations. We calculated woody plant species count as the number of woody plant species in the 2.3-m radius (56.55 m²) paired plots (Gotelli and Colwell 2001).

Data Analysis

To assess the effect of season of fire on the bird community and woody vegetation structure we used a Before-After-Control-Impact study design (e.g., Green 1979, Stewart-Oaten et al. 1986, 1992). We compared bird and vegetation data collected before fire treatments to data collected at the same locations after fire treatments, within study site sections that were burned in spring, summer, and fall seasons. We also compared bird and vegetation measurements from unburned, control sections of each study site to those from fire season treatment sections within the same study site (Table 1). We used data from avian point-count surveys conducted during 1–25 June 2016, 29 May–21 June 2017, and 5–28 June 2018 and vegetation sampling conducted July–September 2016, 2017, and 2018. Across the 2 spring, 2 summer, and 2 fall fire treatments executed, we calculated changes in bird and vegetation metrics from 63 avian point-count locations and paired vegetation plots: 16 spring, 15 summer, 16 fall fire treatment, and 16 control survey locations (Table 1). One survey location in a summer fire treatment section was removed from the study due to change in land-owner participation.

Not all point-count locations and vegetation plots were burned within treated

sections due to the fire not carrying across all points, but evidence of fire was present within 100-m of all but 2 point-count locations (Table 1). Because we recorded birds detected within a 100-m radius and wanted to assess the effectiveness and patchiness of fires, we included all survey locations and plots in our analyses, even those that were unburned but within treated sections of study sites.

Because we surveyed bird and plant communities at the same times each year, the amount of time elapsed since fire season treatments differed among treatments (Table 1). We used data from the point-count surveys conducted the year after fire treatments to quantify changes in the bird community and vegetation structure (Table 1). Because our measurements varied in time elapsed since fire treatments, vegetation and bird responses were at different stages post fire when measured; therefore, we only compared fire season treatments to controls and not to one another.

To assess differences in the bird community between fire season treatments and controls, we compared bird species richness and bird total abundance. To assess differences in vegetation structure between fire season treatments and controls, we compared stem height diversity, total stem density, average stem height, and woody species count. For bird species richness we totaled the number of species detected across the 4 surveys at each point-count location during a single spring. For bird total abundance we averaged the total number of birds detected per point-count survey at each point-count location.

We also assessed the effect of fire season treatments on the abundance of

individual bird species for which we had >200 observations during surveys conducted in 2016. Before analyzing responses to fire treatments, we first examined detection functions for frequently detected species, to assess potential bias in detection probability for birds in burned areas vs. unburned areas (Smucker et al. 2005, Nichols et al. 2009, Zlonis et al. 2019). Using the statistical program JAGS (Plummer 2017), we estimated the probability of detecting a species using detected/not-detected (1 or 0) binary data recorded in 3 intervals for each bird during point-count surveys. Across the 3 2-min time intervals in which observers recorded detection of individual birds during point-count surveys, cumulative detection probability was extremely high (>0.95) for all frequently observed species. We therefore concluded that incorporating species' detection functions into analyses would not influence abundance estimates and was not necessary to include in assessments of changes in abundance in response to prescribed fire season treatments and thus did not incorporate distance estimates into models.

We compared pre- and post-fire measures of bird abundance and vegetation structure in linear, mixed-effects models to assess change from pre-fire to post-fire. We subtracted the mean pre-fire value from the mean post-fire value for each avian point-count location or co-located vegetation plots (i.e., response = post-pre, so negative values indicate decreases after fires). Because fires were executed throughout 2016-2018 and different fire season treatments were completed at the same study sites during different years, we included year and study site as random effects. This allowed us to look for general patterns across years and study sites. We included fire season treatment as the only fixed effect. This model, with season of fire as a fixed effect and study site and year

as random effects, is represented by the following equation:

$$Y_{ijk} = \alpha_0 + \alpha_1 x_{1,ijk} + \alpha_2 x_{2,ijk} + \alpha_3 x_{3,ijk} + b_i + b_j + \varepsilon_{ijk}$$

where Y_{ijk} represents bird and vegetation response variables obtained at the i th study site, $i = 1, 2$ and j th year, $j = 1, \dots, 3$ and k th avian point-count location, $k = 1, \dots, q$. Ideally the study design included $q = 32$ avian point-count locations per study site; however, 1 point-count location was removed from the study (described above). The parameter α_0 is the model intercept, and $\alpha_1, \alpha_2, \alpha_3$ are dummy variables identifying effects of the 3 fire season treatments at the i th study site, j th year, and k th avian point-count location. If $\alpha_1=1$, the fire season treatment is spring, if $\alpha_2= 1$, the fire season treatment is summer, and if $\alpha_3=1$, the fire season treatment is fall. All dummy variables ($\alpha_1, \alpha_2, \alpha_3$) equaling zero represent data collected from controls. Within a single level of year and a single level of study site, we collected 32 data points, 8 under each fire season treatment. Thus, our data consisted of 8 replicates of each unique year, study site, and treatment combination. Study site and year random effects are represented by b_i and b_j and account for differences among study sites and years unrelated to treatments. Year included 3 levels and compared pre- and post-fire data from 2016 to 2018, 2016 to 2017, and 2017 to 2018 (Table 1). Random effects are assumed to be independent and normally distributed with a mean of 0. The effect of study site is assumed to have a variance of σ^2_i . The effect of year is assumed to have a variance of σ^2_j . Residual variation is represented by ε_{ijk} and is assumed to have a mean of 0 and variance of σ^2_{ijk} .

We estimated parameters using the maximum likelihood method and included intercept (α_0), fixed effects ($\alpha_1, \alpha_2, \alpha_3$), and variance components ($\sigma^2_i, \sigma^2_j, \sigma^2_{ijk}$). We

used linear mixed-effects models with study site and year as random effects and fire season treatment as a fixed effect with the package *lme4* (Bates et al. 2015) in the statistical program R (version 3.4.2, R Core Team 2017). We tested for differences in the amount of change in bird and plant response variables between spring, summer, and fall fire season treatments and controls using a type II Wald chi-square test. If the amount of change in the response variable differed significantly among fire season treatments at $\alpha = 0.05$ we further examined which fire-season treatments were significantly different from controls using the package *lmerTest* (Kuznetsova et al. 2017). We summarized differences using least-square means and standard errors.

RESULTS

Bird Response

From 1–25 June 2016, 29 May–19 June 2017, and 5–28 June 2018 we conducted 568 avian point-count surveys at 63 avian point-count locations on 2 study sites (Table 1). We detected 85 bird species, of which 18 were Minnesota Species in Greatest Conservation Need, and 17 were Fire-Dependent Species based on criteria developed by the Lakes States Fire Science Consortium (Table 2; LSFSC 2018). During July–September 2016, 2017, and 2018, we also sampled 126 vegetation plots.

Models of bird total abundance, and abundance of swamp sparrow, chestnut-sided warbler, yellow warbler, and veery indicated a significant difference in response variables between ≥ 1 fire-season treatment and controls (Table 3). The change in bird total abundance differed significantly between summer fires and controls, and fall fires and controls ($P=0.012$). Following both summer and fall fire-season treatments, there was

an increase in bird total abundance. The increase in bird total abundance following fall fires was greater than the increase observed following summer fires (Fig. 2A). The estimated change in bird total abundance in controls was negative, suggesting that trends related to year and study site and unrelated to fire-season treatments caused a decrease in bird total abundance (Table 3).

To assess the effect of season of fire on frequently detected bird species, we considered (in order of detections during 2016, *n*) common yellowthroat (*Geothlypis trichas*, *n*=1193), sedge wren (*n*=976), alder flycatcher (*Empidonax alnorum*, *n*=809), swamp sparrow (*Melospiza georgiana*, *n*=804), Nashville warbler (*Leiothlypis ruficapilla*, *n*=345), chestnut-sided warbler (*Setophaga pensylvanica*, *n*=345), yellow warbler (*Setophaga petechia*, *n*=324), veery (*n*=292), clay-colored sparrow (*Spizella pallida*, *n*=278), and golden-winged warbler (*n*=219). These species were also the most frequently detected in 2017 and 2018.

Of 10 frequently detected species, a significant difference in swamp sparrow, chestnut-sided warbler, yellow warbler, and veery abundance occurred between ≥ 1 fire-season treatment and controls for (Table 3). For swamp sparrow, abundance decreased after spring fire season treatments (Table 3). In contrast, estimated abundance of this species increased not only in controls, but also in summer and fall fire treatments (Fig. 2B). Similarly, veery abundance decreased after summer fire but increased in all other categories: controls, and spring and fall fire treatments (Fig. 2E).

The change in both chestnut-sided warbler and yellow warbler abundance was significantly different between spring fires and controls, and fall fires and controls (Table 3). Compared to one another, these 2 species exhibited opposite responses to spring and

fall fire-season treatments. The average count of chestnut-sided warbler increased after spring and fall fire treatments and decreased in controls (Fig. 2C). In contrast, the average count of yellow warbler decreased after spring and fall fire treatments and increased in controls (Fig 2D). For both species, the changes in abundance that occurred following summer fire treatments was similar to the changes observed after spring and fall fires but not great enough to be statistically, significantly different from controls (Table 3).

Of bird species richness, bird total abundance, and the abundance of 10 frequently detected species, none of these response variables responded to fire season treatments in the same direction or to the same seasons, compared to one another. Compared to controls, swamp sparrow and veery abundance responded to a single fire season treatment (swamp sparrow decreased after spring and veery decreased after summer fires) and bird total abundance, chestnut sided warbler and yellow warbler abundance responded to 2 fire-season treatments (bird total abundance increased after summer and fall, chestnut sided warbler increased after spring and fall, and yellow warbler decreased after spring and fall fires). None changed significantly in response to all 3 fire season treatment types.

Vegetation Response

Prescribed fires differed in their spatial extent. Spring burns affected nearly all vegetation plots. Fall burns were more variable with one of the fall burns burning all vegetation plots but the other only burning 3 plots. At both sites, summer burned the least amount of vegetation plots (Table 1). A companion study is examining the patchiness of season of fire and the plant response to fire only in plots that were burned.

None of the 4 vegetation variables we measured (stem height diversity, stem density, stem height, and woody species count) were different (at $\alpha = 0.05$) between fire season treatments and controls (Table 4). However, following summer and fall fires, there were indications that stem height ($P=0.053$, Table 4) and height diversity ($P=0.087$ for model, Table 4) decreased.

DISCUSSION

Spring, summer, and fall prescribed fire treatments resulted in increases in total bird abundance and changes in abundance of breeding bird species in some frequently detected species in the lowland brush ecosystems we studied in the western Great Lakes region. Bird species exhibit varying responses to season of fire in other systems (Sparks et al. 1999, Brennan et al. 2000, Reinking 2005, Fuhlendorf et al. 2006, Knapp et al. 2009) and our results suggest that there are comparable changes in bird communities that differ by season of fire in lowland brush ecosystems. Contrary to our predictions, however, we did not observe change in vegetation structure following fire that might explain changes in bird communities.

The most mechanism for the patterns we observed likely was related to how birds selected territories based on indirect fire effects (Reinking 2005). Breeding bird species in shrublands exhibit high site-fidelity, and may return to territories occupied previously, even after intervening disturbance, such as fire (Schlossberg 2009). The birds that we detected after we implemented fire treatments likely selected territories based on how fires changed nesting, foraging and food availability, and neighboring competitors in vegetation that was burned the previous year (Knapp et al. 2009). Thus, significant

increases in abundance in certain treatment sections compared to controls may have been a result of birds preferring the effects of fire within the section or avoiding the effects of fire in nearby sections.

Stem height was the structural vegetation characteristic related to abundance of most of the frequently detected bird species in the lowland brush ecosystems we studied (Hawkinson Chapter I). In addition, stem height diversity was strongly related to the abundance of some bird species and bird species richness (Hawkinson Chapter I). Despite there being no statistically significant difference between vegetation responses to fire-season treatments and controls, there was an indication of trends toward decreased stem height and stem height diversity after all fire treatments (Table 4). Yellow warbler and veery abundance was strongly and positively related to stem height based on models of abundance we developed previously (Hawkinson Chapter 1, Fig. 2) and decreased in abundance after spring and fall (yellow warbler) and summer (veery) fires. This suggests that yellow warbler and veery may have avoided burned sections where stem height or ecological factors related to stem height, such as foraging and nesting cover, were disrupted.

Yellow warblers may have been indirectly and negatively affected by effects of fire and resulting decrease in vegetation height for several reasons, as their behaviors related to nesting, foraging, and defending breeding territories involve tall shrubs. First, yellow warblers nest approximately 3 m off the ground in the intersecting stems of shrubs such as *Salix* spp. and *Cornus* spp (Lowther et al. 1999). Nests have been documented to be as high as 12 m (Lowther et al. 1999), although shrub height in our study sites did not exceed 4 m. This preference for nesting in tall shrubs might have caused yellow warblers

to avoid areas where burns decreased shrub stem height. Second, yellow warblers prey on insects from shrubs while hovering, and shorter shrubs may make foraging less efficient. Third, males perch at the tops of shrubs to sing when defending territories (Ficken and Ficken 1965). All of these behaviors may have been influenced by decreases in stem height following fires (Morse 1966).

Veery, a species strongly related to stem height (Hawkinson Chapter 1) in the lowland brush ecosystems we studied, decreased in abundance following summer fires. Unlike yellow warbler, veeries nest on the ground, below shrubs and young trees (Heckscher et al. 2017). They exhibit a diverse diet that includes different types of insects, fruits, and amphibians (Heckscher et al. 2017). Although a decrease in stem height would not have affected where veeries placed nests, summer fires may have reduced the availability of food sources. In rangelands, summer fires reduced insect biomass (Bulan and Barret 1971, Hansen 1986, Swengel 2001). However, this has not been documented in brushland ecosystems and our summer fires were patchy, making it unlikely that veeries established territories away from areas treated by summer fires because of a reduction in resources.

Chestnut-sided warbler abundance was also strongly and positively related to stem height (Hawkinson Chapter 1) and yet this species increased in abundance following spring and fall fires. Chestnut-sided warbler abundance was also strongly and positively related to the number of woody plant species, which didn't change following fire. Taken together, these results suggest chestnut-sided warbler may have responded to factors other than stem height that were changed following fire. For example, even though the number of woody plant species did not change after fire treatments, plant species may

have responded differently to season of fire. For some structurally similar woody plants, responses to fire differ due to differences in plant growth rates and where plants store resources (Buckman 1964, Platt et al. 1988, Howe 1994, Austin and Buhl 2013, Brose et al. 2013) Many *Salix* spp., for example, are structurally similar but produce catkins and senesce at different times, which may have affected how they re-generated after fire treatments (Smith 2008) and in turn, influenced how chestnut-sided warblers selected breeding territories.

After fire-season treatments, chestnut-sided and yellow warbler abundances exhibited change in opposite directions (Fig 2C, D). These warbler species are similar in several ways and their interactions and competition during the breeding season may have shifted post-spring and -fall fires. Both chestnut-sided and yellow warblers nest in shrubs and feed on insects by hovering and hopping between woody stems (Ficken and Ficken 1965, Lowther et al. 1999, Byers et al. 2013). Compared to yellow warblers, chestnut-sided warblers nest lower in shrubs, at approximately 2 m above the ground (Byers et al. 2013). Even though these species nest at different heights within shrubs, a decrease in yellow warbler abundance may have allowed chestnut-sided warblers to occupy post-fire areas in higher densities than in the presence of higher abundances of chestnut-sided warblers that existed in pre-fire conditions.

Bird total abundance and swamp sparrow abundance, the only 2 bird response variables that were not associated with any vegetation structure variables in previous models (Hawkinson Chapter 1), responded significantly to fire treatments. As previously suggested for veeries, changes in bird total abundance may have been a result of changes in food abundance or availability. All of the frequently detected bird species we studied

exhibit a diet that includes insects (Rodewald 2015). Insect biomass can be influenced by season of fire in forests and grasslands, and several studies (Bulan and Barret 1971, Chamrad and Dodd 1973, Hansen 1986, Swengel 2001) have indicated that post-burn characteristics of plants are preferred by recolonizing insects. Insects may also respond to vigorous re-sprouting of shrub leaves on young stems, which has been documented in arid brushland ecosystems (Malanson and Leary 1982). However, not all insect responses to fire include increases in insect abundance and in rangelands, insect biomass and diversity decrease after summer fires (Bulan and Barret 1971, Hansen 1986, Swengel 2001). Further research on insect communities in brushlands and their response to fire may provide further insight into the mechanisms that result in changes in bird abundance.

We were unable to make strong conclusions about bird responses to fire being related to vegetation structure, because our measurements of vegetation structure did not change significantly after fire treatments compared to controls. However, stem height was marginally significant with a *P*-value of 0.053 (Table 4). A lack of consistent and strong responses from vegetation to fire treatments may have been for several reasons including: variation in the number of plots burned among seasons, rapid regrowth of post-fire woody plants, small sample size, and choice of vegetation measurements (i.e., we may not have measured vegetation in a way that accurately accounted for fire effects).

Many plots, especially those within summer fire treatments, were not directly burned and at plots where fire did consume woody vegetation, stem regeneration may have replaced dead, burned stems with new stems that reached similar heights and densities to those recorded prior to fire treatments (Table 1). In a companion study, plots were analyzed separately based on burned or unburned status and both stem height and

stem density changed significantly after fire season treatments, compared to controls. Additionally, that study distinguished between old and new plant growth and showed that re-generation occurred similarly among spring, summer, and fall fires (Knosalla, pers. comm.).

The plant communities were highly variable in our study sites and more vegetation plots may have produced more detailed measurements of fire-effects than our sample size ($n = 8$) allowed. Additionally, we measured all vegetation beginning in July when plants had already experienced significant growth. Measuring plants throughout the first weeks of growth, following the last consistent days of frost, may have also allowed us to assess responses to fire. An additional limitation related to the vegetation surveys we conducted includes a limited analysis of variables to indicate woody plant responses to fire. A collaborative study examines top-kill, burn patchiness, and burn severity, which will allow us to assess specific fire behavior and effects on vegetation (Knosalla, pers. comm.).

To improve understanding of the mechanism behind changes in lowland brush ecosystem bird communities to spring, summer, and fall fires, we have completed a preliminary analysis of how breeding bird and vegetation structure response variables change over time after spring fire season treatments (Appendix A). These results show that it may only take bird and woody plant species 2 years to return to pre-fire states. An additional year of data collection will be added to these analyses.

Management Implications

Lowland brush ecosystems in the western Great Lakes region of North America are often managed with prescribed fire in the spring to create and improve quality of habitat for wildlife and support diverse bird communities (Curtis 1959, Hanowski et al. 1999). However, little is known about how lowland brush ecosystem bird communities respond to fire and season of fire. The range of responses by bird species to spring, summer, and fall fires in our study suggests that limiting prescribed fire application to a single season may result in a narrow range of responses from the bird community, in lowland brush ecosystems. Our results suggest that bird community diversity in lowland brush ecosystems would increase when summer and fall fires are incorporated into management regimes, and likely provide conditions more similar to those present prior to fire suppression or resulting from fires applied only during spring.

Burning in seasons other than spring may allow managers to more frequently apply fire in these systems. This may become critical in the future, as conditions to safely apply prescribed fire are expected to become increasingly difficult to meet based on climate change projections of wetter weather through spring, summer, and fall seasons (Wuebbles and Hayhoe 2004) in the western Great Lakes region. If frequent burning is necessary to impact vegetation in lowland brush ecosystems, using a large burn window that is not limited to spring, may allow managers to maintain woody vegetation characteristics that support diverse breeding bird communities.

Table 1. Summary of data used for linear regression analysis of prescribed season of fire effects on lowland brush ecosystem bird communities east-central Minnesota, USA from 2016 to 2018. Dates of prescribed fires and the number of days that passed between fires and the start of avian point-count surveys is indicated for each fire treatment. Study sites were ≥ 162 ha and subdivided into 4 sections for 3 prescribed fire season treatments (spring, summer, and fall) and 1 unburned section that served as a control. Each treatment was applied to approximately 41 ha that contained 8 avian point-count locations. Vegetation and bird communities were surveyed before and after fires. Plant-growth days were determined by examining post-fire days that occurred between first and last frosts recorded at the weather station nearest to each site (AMS 2012). The number of avian point-count locations within a treated section is indicated by the point-count locations column and the number of vegetation plots and number burned is indicated by the vegetation plots (burned/total) column. From the fire treatments executed, we analyzed data from 16 spring, 15 summer, and 16 fall fire-treatment avian point-count locations and 16 unburned, control avian point-count locations across 3 years. Because data from unburned sections were used more than once to serve as a comparison to fire treatments that were implemented during different years within the same study site, we used 40 unburned, control data points.

Study site	Section	Point-count locations	Vegetation plots (burned/total)	Pre- and post-fire survey years	Treatment date	Total days elapsed between fire and first survey	Growing season days elapsed between fire and first survey
Hasty Brook	Spring	8	16/16	2016/2018	10 May	394	169

Hasty Brook	Unburned	8	-	2016/2018	2017	-	-
Highway 29	Spring	8	12/16	2016/2018	12 May	390	156
Highway 29	Unburned	8	-	2016/2018	2017	-	-
Hasty Brook	Summer	8	4/16	2017/2018	12	271	48
Hasty Brook	Unburned	8	-	2017/2018	September	-	-
Highway 29	Summer	7	4/14	2017/2018	2017	-	-
Highway 29	Unburned	8	-	2017/2018	11 August	300	73
Hasty Brook	Fall	8	13/16	2016/2017	2017	-	-
Hasty Brook	Unburned	8	-	2016/2017	16	195	18
Highway 29	Fall	8	3/16	2017/2018	November	-	-
Hasty Brook	Unburned	8	-	2016/2017	2016	-	-
Highway 29	Fall	8	3/16	2017/2018	19 October	231	17
Highway 29	Unburned	8	-	2017/2018	2017	-	-

Table 2. Summary of birds detected during 568 point-counts at 63 survey locations from 1–25 June 2016, 29 May–19 June 2017, and 5–28 June 2018 in east-central Minnesota, USA. Stars indicate species that are listed as a Minnesota Species in Greatest Conservation Need (MNDNR 2015). Underline indicates species that are listed as fire-dependent according to the Lake States Fire Science Consortium (LSFSC 2018). Six cover type and plant community preferences are exhibited (Rodewald 2015).

Species name	Scientific name	Number of detections	Cover-type/ Plant community
<u>Sedge wren*</u>	<i>Cistothorus platensis</i>	1,136	Grasslands
Common yellowthroat	<i>Geothlypis trichas</i>	1,084	Scrub
Alder flycatcher	<i>Empidonax alnorum</i>	888	Scrub
Swamp sparrow	<i>Melospiza georgiana</i>	723	Marshes
Veery*	<i>Catharus fuscescens</i>	534	Forests
Nashville warbler	<i>Oreothlypis ruficapilla</i>	356	Forests
Chestnut-sided warbler	<i>Setophaga pensylvanica</i>	319	Open Woodlands
Yellow warbler	<i>Setophaga petechia</i>	319	Open Woodlands
<u>Clay-colored sparrow</u>	<i>Spizella pallida</i>	241	Scrub
<u>Golden-winged warbler*</u>	<i>Vermivora chrysoptera</i>	206	Open Woodlands
Song sparrow	<i>Melospiza melodia</i>	204	Open Woodlands
White-throated sparrow	<i>Zonotrichia albicollis</i>	168	Forests
Gray catbird	<i>Dumetella carolinensis</i>	141	Open Woodlands
Red-winged blackbird	<i>Agelaius phoeniceus</i>	112	Marshes
American robin	<i>Turdus migratorius</i>	110	Open Woodlands
Red-eyed vireo	<i>Vireo olivaceus</i>	100	Forests
Wilson's snipe	<i>Gallinago delicata</i>	89	Marshes
American goldfinch	<i>Spinus tristis</i>	54	Open Woodlands
American crow	<i>Corvus brachyrhynchos</i>	48	Open Woodlands
Blue jay	<i>Cyanocitta cristata</i>	45	Forests
Ovenbird	<i>Seiurus aurocapilla</i>	42	Forests
<u>Lincoln's sparrow</u>	<i>Melospiza lincolni</i>	40	Scrub
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	39	Forests
Black-and-white warbler	<i>Mniotilta varia</i>	38	Forests

<u>American bittern*</u>	<i>Botaurus lentiginosus</i>	28	Marshes
Black-billed cuckoo*	<i>Coccyzus erythrophthalmus</i>	27	Forests
Savannah sparrow	<i>Passerculus sandwichensis</i>	24	Grasslands
Black-capped chickadee	<i>Poecile atricapillus</i>	21	Forests
Chipping sparrow	<i>Spizella passerina</i>	21	Open Woodlands
Mourning dove	<i>Zenaida macroura</i>	21	Open Woodlands
American redstart	<i>Setophaga ruticilla</i>	20	Forests
Mallard	<i>Anas platyrhynchos</i>	17	Lakes and Ponds
Cedar waxwing	<i>Bombycilla cedrorum</i>	16	Open Woodlands
<u>LeConte's sparrow*</u>	<i>Ammospiza leconteii</i>	16	Grasslands
Northern flicker	<i>Colaptes auratus</i>	15	Open Woodlands
Blue-headed vireo	<i>Vireo solitarius</i>	11	Forests
Hermit thrush	<i>Catharus guttatus</i>	11	Open Woodlands
Ruffed grouse	<i>Bonasa umbellus</i>	10	Forests
Canada goose	<i>Branta canadensis</i>	9	Marshes
Common raven	<i>Corvus corax</i>	9	Forests
Great-crested flycatcher	<i>Myiarchus crinitus</i>	9	Open Woodlands
Blackburnian warbler	<i>Setophaga fusca</i>	8	Forests
Least flycatcher	<i>Empidonax minimus</i>	8	Forests
Brown-headed cowbird	<i>Molothrus ater</i>	6	Grasslands
Pileated woodpecker	<i>Dryocopus pileatus</i>	6	Forests
Red-breasted nuthatch	<i>Sitta canadensis</i>	6	Forests
Yellow-billed cuckoo*	<i>Coccyzus americanus</i>	6	Open Woodlands
Yellow-throated vireo	<i>Vireo flavifrons</i>	6	Open Woodlands
<u>Brown thrasher*</u>	<i>Toxostoma rufum</i>	5	Scrub
Grasshopper sparrow*	<i>Ammodramus savannarum</i>	5	Grasslands
Hairy woodpecker	<i>Dryobates villosus</i>	5	Forests
Mourning warbler	<i>Geothlypis philadelphia</i>	4	Forests
Bald eagle	<i>Haliaeetus leucocephalus</i>	3	Forests
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	3	Towns
<u>Sandhill crane</u>	<i>Antigone canadensis</i>	3	Marshes
<u>Sharp-tailed grouse*</u>	<i>Tympanuchus phasianellus</i>	3	Grasslands

<u>Yellow-bellied flycatcher</u>	<i>Empidonax flaviventris</i>	3	Forests
American woodcock*	<i>Scolopax minor</i>	2	Forests
Black-throated green warbler	<i>Setophaga virens</i>	2	Forests
Eastern wood-pewee	<i>Contopus virens</i>	2	Forests
Northern goshawk*	<i>Accipiter gentilis</i>	2	Forests
<u>Northern harrier*</u>	<i>Circus hudsonius</i>	2	Grasslands
Purple finch*	<i>Haemorhous purpureus</i>	2	Forests
Ruby-throated hummingbird	<i>Archilochus colubris</i>	2	Open Woodlands
White-breasted nuthatch	<i>Sitta carolinensis</i>	2	Forests
Wild turkey	<i>Meleagris gallopavo</i>	2	Open Woodlands
Winter wren*	<i>Troglodytes hiemalis</i>	2	Forests
Belted kingfisher*	<i>Megaceryle alcyon</i>	1	Lakes and Ponds
Broad-winged hawk	<i>Buteo platypterus</i>	1	Forests
Blue-winged teal	<i>Spatula discors</i>	1	Marshes
Common grackle	<i>Quiscalus quiscula</i>	1	Open Woodlands
<u>Eastern bluebird</u>	<i>Sialia sialis</i>	1	Grasslands
Eastern kingbird	<i>Tyrannus tyrannus</i>	1	Grasslands
<u>Great gray owl</u>	<i>Strix nebulosa</i>	1	Forests
Northern waterthrush	<i>Parkesia noveboracensis</i>	1	Forests
Northern shoveler	<i>Spatula clypeata</i>	1	Marshes
<u>Olive-sided flycatcher*</u>	<i>Contopus cooperi</i>	1	Open Woodlands
<u>Ruby-crowned kinglet</u>	<i>Regulus calendula</i>	1	Forests
<u>Sora</u>	<i>Porzana carolina</i>	1	Marshes
Swainson's thrush	<i>Catharus ustulatus</i>	1	Forests
Tree swallow	<i>Tachycineta bicolor</i>	1	Lakes and Ponds
Warbling vireo	<i>Vireo gilvus</i>	1	Open Woodlands
Wood thrush*	<i>Hylocichla mustelina</i>	1	Forests
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	1	Forests
Yellow-rumped warbler	<i>Setophaga coronata</i>	1	Forests

Table 3. Least square means \pm SE of the magnitude of change in number of bird species, total abundance, and abundance of frequently detected species (those detected >200 times in the first year of surveys) within 100 m per point at unburned points and at points that burned in spring, summer, or fall in east-central Minnesota during 2016-2018. Stars indicate species that are listed as a Minnesota Species in Greatest Conservation Need (MNDNR 2015). Underline indicates species that are listed as fire-dependent by the Lake States Fire Science Consortium (LSFSC 2018). All species (including those not reported as frequently detected) were used to calculate bird species richness and total abundance. We used data from surveys conducted before and after burns during 1–25 June 2016, 29 May–21 June 2017, and 5–28 June 2018. The number of avian point-count locations is indicated by *n*. χ^2 values and degrees of freedom (df) come from Type II Wald Chi-square test. *P*-values come from linear mixed-effects models and test whether there was a significant difference between fire season treatments and unburned, controls at $\alpha = 0.05$. Bolded rows indicate an overall significant *P*-value associated with the model. We further assessed pairwise differences between each treatment and controls for significant models. Stars indicate level of significant difference between each fire season treatment and unburned controls.

Bird response variable	Unburned (<i>n</i> =16)	Spring (<i>n</i> =16)	Summer (<i>n</i> =15)	Fall (<i>n</i> =16)	χ^2	df	<i>P</i> -value
Bird species richness	-0.49 \pm 2.35	0.32 \pm 1.08	0.97 \pm 1.07	2.69 \pm 1.02	7.02	3	0.071
Bird total abundance	-0.81 \pm 1.97	0.47 \pm 0.54	1.26 \pm 0.53*	1.41 \pm 0.51 **	11.21	3	0.012
Common yellowthroat, <i>Geothlypis trichas</i>	-0.35 \pm 0.26	0.14 \pm 0.20	0.24 \pm 0.21	0.42 \pm 0.20	5.10	3	0.165
<u>Sedge wren*</u> , <i>Cistothorus</i>	0.29 \pm 0.26	0.45 \pm 0.32	-0.05 \pm 0.32	-0.36 \pm 0.30	3.74	3	0.292

<i>platensis</i>								
<i>Alder flycatcher, Empidonax alnorum</i>	-0.26 ± 0.11	0.11 ± 0.20	-0.21 ± 0.20	0.21 ± 0.20	3.31	3	0.347	
Swamp sparrow, Melospiza georgiana	0.21 ± 0.40	-0.60 ± 0.24*	0.21 ± 0.24	0.30 ± 0.23	8.19	3	0.042	
Nashville warbler, <i>Oreothlypis ruficapilla</i>	-0.34 ± 0.10	-0.14 ± 0.14	0.02 ± 0.14	0.15 ± 0.14	3.19	3	0.363	
Chestnut-sided warbler, Setophaga pensylvanica	-0.73 ± 0.41	0.40 ± 0.17*	0.06 ± 0.17	0.55 ± 0.16***	17.89	3	0.0005	
Yellow warbler, Setophaga petechia	0.13 ± 0.46	-0.48 ± 0.18*	-0.22 ± 0.18	-0.37 ± 0.17*	11.79	3	0.008	
Veery*, Catharus fuscescens	0.41 ± 0.24	0.03 ± 0.22	-0.70 ± 0.23**	0.12 ± 0.22	11.77	3	0.008	
<i>Clay-colored sparrow, Spizella pallida</i>	-0.07 ± 0.12	-0.13 ± 0.13	-0.34 ± 0.13	-0.12 ± 0.13	6.59	3	0.086	
Golden-winged warbler*, <i>Vermivora chrysoptera</i>	-0.29 ± 0.16	0.06 ± 0.15	0.34 ± 0.15	-0.07 ± 0.14	7.10	3	0.069	

P-value significance codes: * < 0.05, ** < 0.01, *** < 0.001

Table 4. Least square means \pm SE of the magnitude of change in vegetation surrounding avian point-count locations within 4 study sites in lowland brush ecosystems in east-central Minnesota, USA, during 2016-2018, divided into unburned sections or fire treatment sections burned in spring, summer, or fall. Two vegetation plots were located 10 m from point-count locations and vegetation was sampled before and after burns during July–September 2016, 2017, 2018. The number of avian point-count locations is indicated by *n*. χ^2 values and degrees of freedom (df) come from Type II Wald Chi-square test. *P*-values come from linear mixed-effects models and test whether a significant difference occurred between means of treatments and unburned sections at $\alpha = 0.05$.

Vegetation response variable	Unburned (<i>n</i> =16)	Spring (<i>n</i> =16)	Summer (<i>n</i> =15)	Fall (<i>n</i> =16)	χ^2	df	<i>P</i> -value
Average stem height (cm)	-1.85 \pm 11.00	-5.34 \pm 8.93	-22.03 \pm 9.10	-17.37 \pm 8.79	7.69	3	0.053
Stem height diversity	0.16 \pm 0.27	-0.18 \pm 0.26	-0.56 \pm 0.26	-0.50 \pm 0.26	6.57	3	0.087
Stem density (ha)	12204.0 \pm 10679.0	11031.0 \pm 15401.0	6566.0 \pm 15749.0	-6677.0 \pm 15401.0	1.10	3	0.776
Woody species count	0.1 \pm 0.3	-0.4 \pm 0.4	-0.1 \pm 0.4	-0.5 \pm 0.4	0.10	3	0.552

Figure 1. Locations of 2 lowland brush ecosystem study sites in east-central Minnesota, USA during a study of the effects of season of fire on birds and vegetation during 2016-2018. Study sites are within Priority Open Landscapes, determined by the Minnesota Department of Natural Resources. Study sites were on public land and managed by the Department of Natural Resources for wildlife habitat.

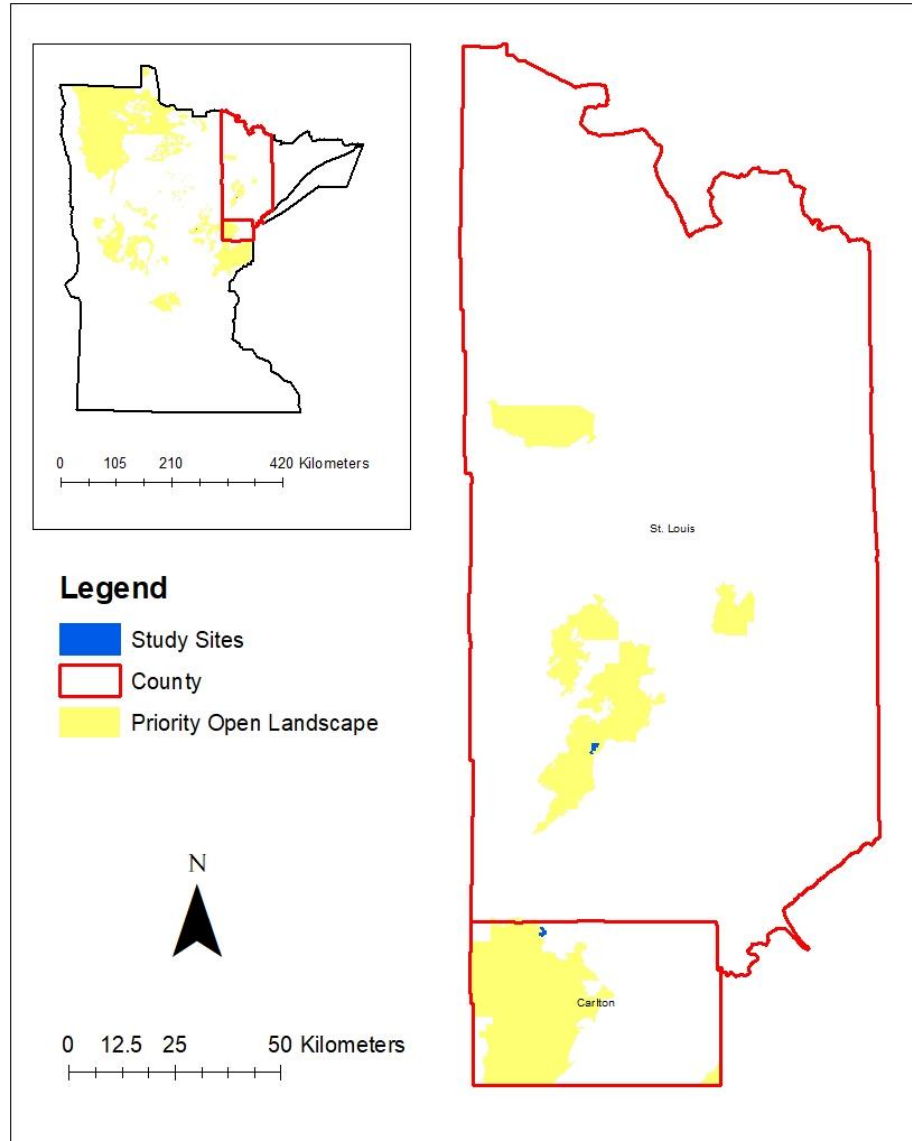


Figure 2. Bird response variables (panels A–E) that changed after fire during 2016–2018 in east-central Minnesota. Dots and lines represent least square means of response variable data (post-fire – pre-fire means) \pm SE. Dotted lines are placed at the unburned value, rather than 0, to better observe differences from unburned sections that changed due to yearly and study site patterns unrelated to treatment. Red indicates a significant difference between fire season treatment and unburned, controls at $\alpha = 0.05$. Graphs show data from bird total abundance (A), and abundances of swamp sparrow (B), chestnut-sided warbler (C), yellow warbler (D), and veery (E) per point-count location.

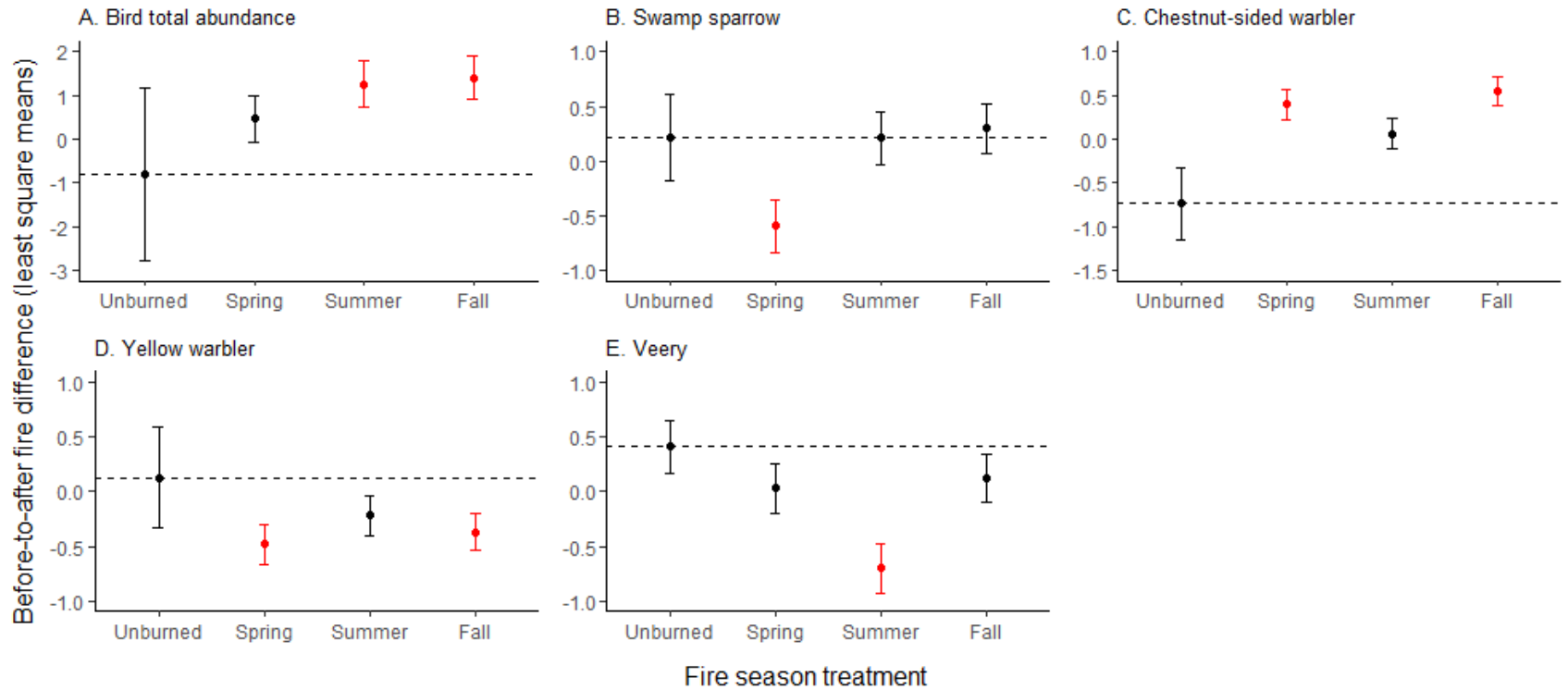
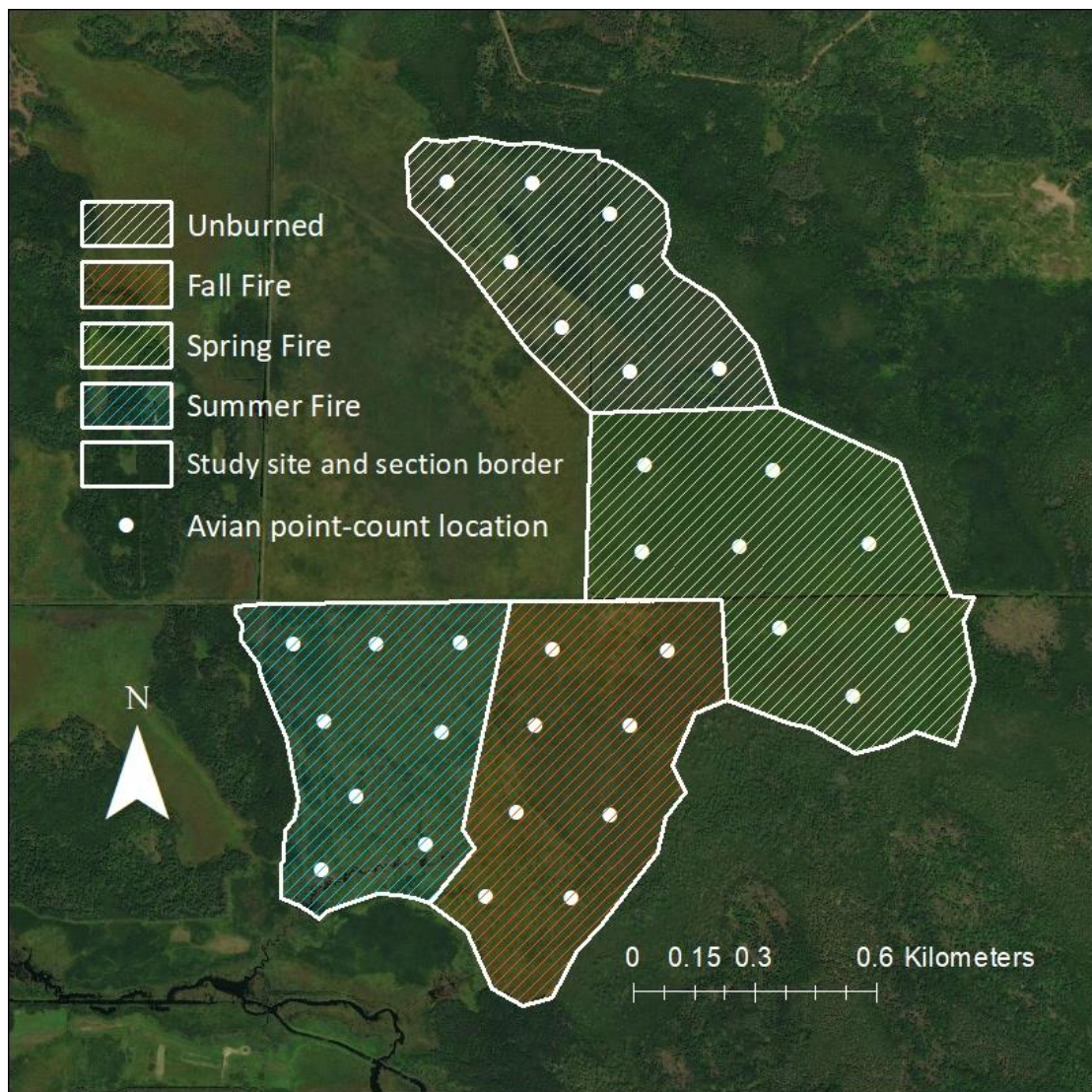


Figure S1. Example of a lowland brush ecosystem study site during 2016–2018 in east-central Minnesota. Study sites were approximately 162 ha in area and subdivided into 4 sections for 3 prescribed fire season treatments (spring, summer, and fall) and 1 unburned control. Each section was approximately 41 ha. Within each section we placed 8 avian point-count survey locations.



Appendix A. Responses of lowland brush bird and plant communities to fire over time.

We implemented spring fire treatments at 2 study sites on 10 May and 12 May 2017. Data were collected immediately after treatments and 1 year post-fire treatments. To compare the bird community between our categories of spring fire vs control over time, we used average bird species richness and bird total abundance per avian point-count location over 4 surveys each year. We also assessed the change in abundance of individual bird species for which we had >200 observations during surveys conducted in 2016 (n = 64 point-count locations and 256 counts). To assess changes in the vegetation structure and plant community, we assessed stem height diversity, stem density (per ha), and average stem height (cm), and woody species count. These metrics were determined by combining data collected at 2 vegetation plots located adjacent to point-count locations.

Bird and vegetation response variables characterize change from pre-fire to post-fire over a 2-year period. We subtracted the mean pre-fire value from the mean post-fire value for each avian point-count location or co-located vegetation plots (i.e., response = post-pre, so negative values indicate decreases after the burn). We compared pre- and post-fire data of study site sections treated with spring prescribed fires and controls across 2 year to year comparisons: Control 2016-2017, spring fire 2016-2017, control 2016-2018, and spring fire 2016-2018. This allowed us to compare the magnitude in change in response variables between spring fires occurring approximately 2 weeks before avian surveys and 1 month before vegetation surveys, and 1 year post-fire. Incorporating initial values allowed us to account for different baseline conditions among

sites. We used linear, mixed-effects models and included study site as a random effect and the 4 categories of control/fire/year comparison as the only fixed effect. This model is represented by the following equation:

$$Y_{ik} = \alpha_0 + \alpha_1 x_{1,ik} + \alpha_2 x_{2,ik} + \alpha_3 x_{3,ik} + \alpha_4 x_{4,ik} + b_i + \varepsilon_{ik}$$

where Y_{ik} represents bird and vegetation response variables obtained at the i th study site, $i = 1, \dots, 2$ and k th avian point-count location, $k = 1, \dots, 16$. Study site only included 2 levels and compared pre- and post-fire data from 2 study sites. The parameter α_0 is the model intercept, and $\alpha_1, \alpha_2, \alpha_3, \alpha_4$ are dummy variables identifying effects of the 4 control/fire/year comparisons at the i th study site and k th avian point-count location. If $\alpha_1=1$, the category is control 2016-2018, if $\alpha_2= 1$, the category is spring fire 2016-2018, and if $\alpha_3=1$, the category is control 2016-2017. All dummy variables ($\alpha_1, \alpha_2, \alpha_3, \alpha_4$) equaling zero represent the category of spring fire 2016-2017. Within a single level of study site, 16 data points were collected, 8 under spring fire season treatment and 8 control points. Thus, our data consists of 16 replicates of each unique study site and treatment combination. Study site random effect is represented by b_i and accounts for differences among study sites unrelated to treatments. The random effect is assumed to be independent and normally distributed with a mean of 0. The effect of study site is assumed to have a variance of σ^2_i . Residual variation is represented by ε_{ik} and is assumed to have a mean of 0 and variance of σ^2_{ik} .

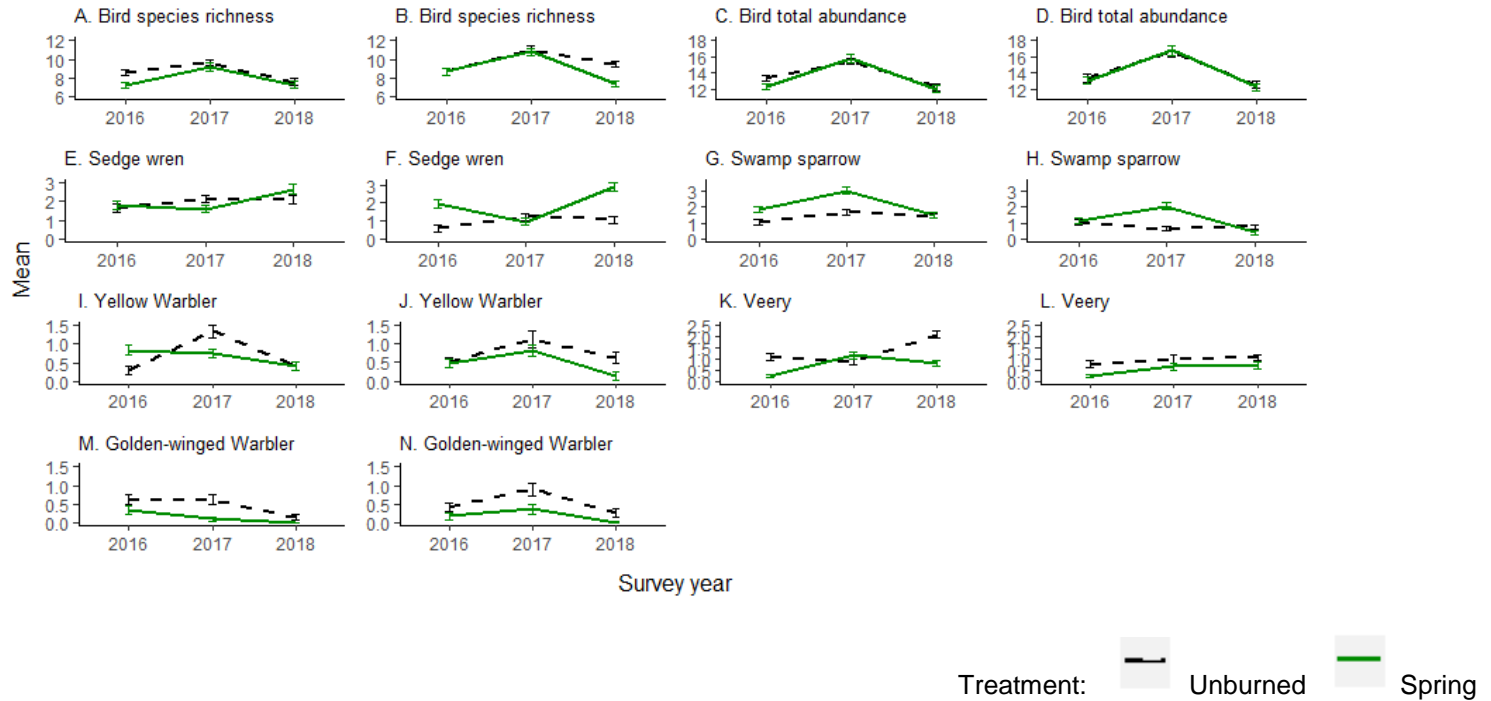
We estimated parameters using the maximum likelihood method and included intercept (α_0), fixed effects ($\alpha_1, \alpha_2, \alpha_3, \alpha_4$) and variance components ($\sigma^2_i, \sigma^2_k, \sigma^2_l, \sigma^2_m$)

We used linear mixed-effects models with study site as a random effect and the

control/fire/year comparison as a fixed effect with the package *lme4* (Kuznetsova et al. 2018) in the statistical program R (version 3.4.2, R Core Team 2017). We tested for differences in the amount of change in bird and plant response variables between spring, summer, and fall fire season treatments and controls using a type II Wald chi-square test at $\alpha = 0.05$.

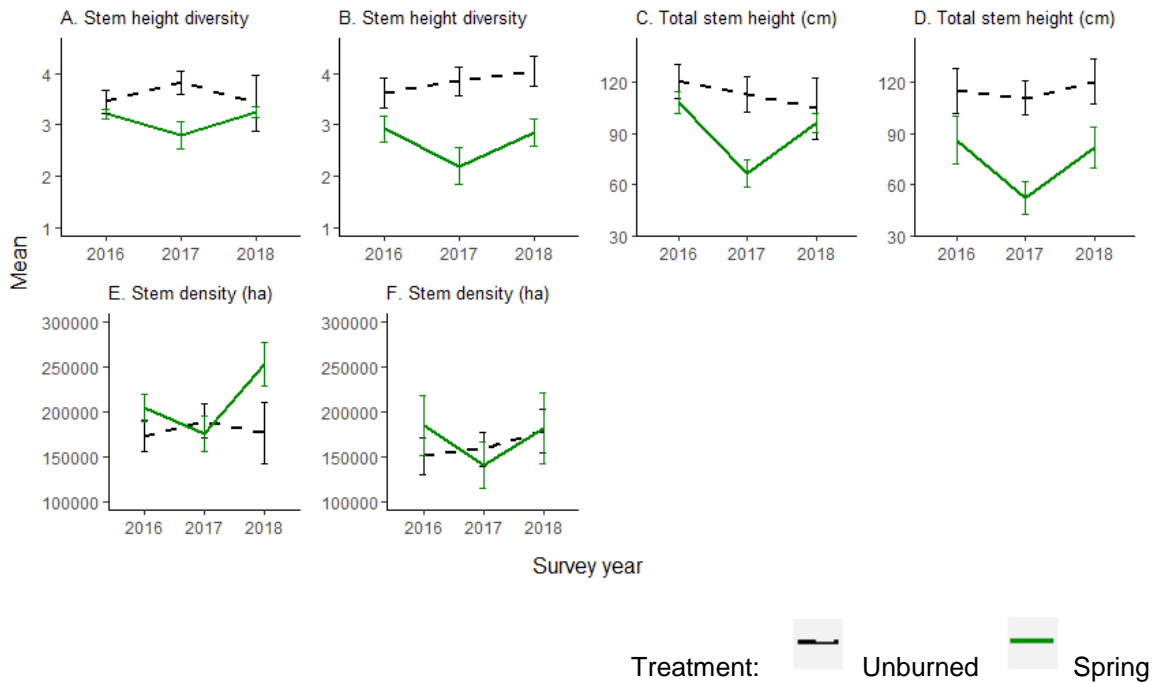
Time-series graphs indicate the variables with models that showed a significant difference among 4 control/fire/year comparisons (Appendix B and C). For all variables but 3 (yellow warbler, veery, and golden-winged warbler abundance) trends indicated that values shifted back towards a pre-fire state in 2018 when time-elapsed since fire was approximately 1 year. For each variable, trends were similar between the 2 sites. For bird variables, some changes that occurred from year to year were greater in controls than for fire treatments. This suggests that annual variation was present in bird populations, and changes in values occurred regardless of fire treatments. For vegetation variables, values changed from year to year in controls but much more drastically after fire treatments, in both sites. These data suggest that ecological characteristics of brushlands can recover to pre-fire conditions as little as 1-year after spring fires. We recommend surveys are conducted in 2019 to allow for additional comparisons. For example, collecting data 3-years post-spring fire would strengthen our knowledge of brushland recovery-time after fires. Additional surveys would also allow us to examine fire treatments executed at 2 additional study sites (Deer Run WMA in Aitkin county, and Gerzin in St. Louis county) and produce time-lines of bird and plant variables for summer and fall fires.

Appendix B. Time-series of bird response variables during 2016-2018 at 2 lowland brush ecosystem study sites in east-central Minnesota that were treated with spring prescribed fires. Bird response variables presented are those that changed significantly among survey years (x-axis) and control vs. fire treatment at $\alpha = 0.05$. Values associated with each year are means per avian point-count location and error bars represent 95% CIs. The first panel for each variable (A, C, E, G, I, K, M) is from study site Hasty Brook and the second panel for each variable (B, D, F, H, J, L, N) is from study site Highway 29. Hasty Brook was burned on 10 May 2017 and Highway 29 was burned on 12 May 2017.



Appendix C. Time-series of woody vegetation response variables during 2016-2018 at 2 study sites in east-central Minnesota that were treated with spring prescribed fires.

Woody vegetation response variables presented are those that changed significantly among survey years (x-axis) and control vs. fire treatment at $\alpha = 0.05$. Values associated with each year are means per 2 vegetation plots placed at avian point-count locations and error bars represent 95% CIs. The first panel for each variable (A, C, E) is from study site Hasty Brook and the 2nd panel for each variable (B, D, F) is from study site Highway 29. Hasty Brook was burned on 10 May 2017 and Highway 29 was burned on 12 May 2017.



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