RESTORING OAK SAVANNAS WITH MULTIPLE DISTURBANCES: THINNING, BURNING, AND TARGETED CATTLE GRAZING

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Dissertation Abstract

Temperate savannas are one of the rarest and most imperiled ecosystems in the world. In the Upper Midwest (USA), over 99% of pre-colonial oak savanna area has been lost due to extensive habitat conversion and altered disturbance regimes. In this region, savannas were characterized by a grass-sedge-forb ground layer and widely-spaced oaks (e.g., *Quercus macrocarpa*). This open structure was maintained historically by frequent disturbances including fires (primarily Indigenous burning) and grazing by megaherbivores (e.g., *Bison bison*). Due to fire suppression and the near extinction of native grazers, savannas often persist today in a degraded, woody-encroached state. Restoring savanna remnants is challenging because we don't know how to best apply contemporary restoration tools to mimic historic disturbances. To that end, my dissertation evaluated the response of oak savanna vegetation and wildlife to a gradient of restoration actions: 1) no management, 2) tree thinning, 3) thinning + burning, and 4) thinning + burning + cattle grazing.

I found that thinning and burning successfully increased canopy openness, herbaceous cover and diversity, and savanna-associated plant species such as *Ceanothus americanus*, *Andropogon gerardii*, *Galium boreale*, and *Agastache scrophulariifolia*. Bird abundance and species richness also responded positively to thinning and burning, while butterfly abundance/richness and the activity of most bat species did not differ across the restoration treatments. Thinning and fire had the unwanted effect of increasing shrub density, particularly *Corylus americana*. I then evaluated if shrub density could be reduced using short-duration targeted cattle grazing under high stocking density. The results suggest that targeted grazing with Angus/Angus cross cattle can be an effective tool to reduce shrub density in the short-term, but repeated management is needed to prevent resprout. I documented no negative impact of cattle grazing on birds, butterflies, or bats throughout the duration of this study. Overall, the results of my dissertation suggest that combining multiple restoration strategies partially achieves vegetation goals and improves bird habitat without negatively affecting butterfly and bat communities. A key takeaway from this work is that restoration outcomes are not dictated by how many management approaches are applied, but rather, the nuances of how they are applied.

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Prologue

The history of savannas in North America is deeply intertwined with a history of complex and ever-changing disturbance forces. North American savannas evolved under top-down pressure from megaherbivores that would have been comparable to present-day African savannas (Bakker et al., 2016; Flores, 2016; Sherow, 2007). Browsing and trampling by megaherbivores would have suppressed slow-growing woody species and promoted open habitats dominated by palatable herbaceous vegetation (Bakker et al., 2016). Humans arrived in North America at least 15,000 years ago (based on current knowledge e.g., Braje et al., 2017; Raghavan et al., 2015), and immediately began influencing savannas through the extensive hunting of megaherbivores (Abrams et al., 2021). Over-hunting, coupled with climatic/ecological upheaval during the glacial-interglacial transition, eventually led to the extinction of Pleistocene megafauna around 11,000 years ago (Martin, 1973; Meltzer, 2020).

After this mass extinction event, people became the dominant disturbance force on the landscape, as well as grazing by remaining herbivores like bison, elk, and deer (Abrams et al., 2021; O'Connor et al., 2020). Indigenous peoples shaped the structure and composition of vegetation through land clearing for settlements and agriculture, as well as burning (Nowacki et al., 2012). Historical documents, charcoal records, and dendrochronology indicate that Indigenous land uses increased rates of surface fires, with anthropogenic ignitions far outnumbering natural ignitions (i.e., lightning) in many locations (Delcourt & Delcourt, 1997; Gleason, 1913; Kipfmueller et al., 2021). In the Upper Midwest, the Ojibwe and Dakota people traditionally used fire for hunting bison and deer, clearing understory vegetation, promoting medicinal plants, pest control, and blueberry production (NPS, 2022; Deschenes & Bydlon, 2021). Similar to grazing, fire is a strong regulator of vegetation that maintains open, grass-dominated communities like oak savannas. Thus, the park-like ecosystems first encountered by early European settlers to North America were a product of 10,000 years of Indigenous land management (Cordova et al., 2011; Fuhlendorf et al., 2018).

During European colonization and settlement, Indigenous populations suffered from sweeping epidemics and forced relocation to reservations (Richter, 2001). This profoundly altered the historic fire regime that once maintained oak savannas. As Euro-Americans expanded westward, savannas were logged and cleared for agriculture, and bison, elk, and deer were over-hunted and nearly extirpated from their historic grassland ranges (Sherow, 2007; Flores, 2016). Starting in the 1920-30s, strict fire suppression policies initiated a new era of ecosystem dynamics. The lack of fire and grazing disturbances facilitated the succession of savannas to closed-canopy woodlands (Nowacki & Abrams, 2008). Fire-tolerant oaks were replaced by shade-tolerant, later-successional species such as red maple that were historically suppressed by fire (Nowacki & Abrams, 2008; Stambaugh et al., 2014). The resulting woodlands were shadier, cooler, and moister, which decreased the flammability of the fuel beds and made fires progressively more unlikely. This led to a positive feedback loop termed “mesophication” that promoted shade-tolerant species and suppressed fire-adapted species (Nowacki & Abrams, 2008).

The long, complex disturbance history of oak savannas helps us understand the current state of these ecosystems in the Midwest. The few persisting patches of savannas are often degraded, having filled in with woody vegetation in the absence of human fire and grazing disturbances (Nowacki & Abrams, 2008). In fact, it is estimated that less than 0.02% of original oak savanna acres persist today, making them one of the most imperiled ecosystems in North America (Nuzzo, 1986). Now on the brink of extinction, restoring oak savannas is becoming an increasingly common management priority in the United States (Dey et al., 2017). Restoration requires frequent prescribed disturbances; oak savannas cannot exist on the modern landscape without active management by people. Therefore, choosing to revive and maintain oak savannas is as much a cultural decision as it is an ecological one.

A challenge for restoration practitioners is determining how to recreate the dynamic fire and grazing patterns that occurred historically within the context of today’s highly-altered savanna remnants. For example, mesophied woodlands often do not have adequate fine fuels to carry prescribed fire (Nowacki & Abrams, 2008), so tree thinning must be used as a proxy for fire . Moreover, native herbivores have been replaced across North America by domestic livestock, primarily cattle (O’Connor et al., 2020). Many decades of Western science have been devoted to exploring these issues and determining the best combination of methods to restore degraded oak savannas (e.g., Bassett et al., 2020; Harrington & Kathol, 2009; White, 1983). Such widespread and ongoing attention underscores the complexity of restoring an ecosystem that was historically dependent on multiple, interacting disturbances.

Taking into consideration the long history and current status of savannas, this dissertation aims to advance the science and practice of oak savanna restoration through the application of multiple disturbances. I assessed how layering restoration strategies, namely thinning, burning, and cattle grazing, impacted oak savanna restoration outcomes. My study site was Sherburne National Wildlife Refuge (SNWR) in central Minnesota, where past management had created a prime opportunity to study the response of oak savanna communities to varied restoration histories. In Chapter 1, I characterize oak savanna vegetation across a gradient of restoration effort: 1) no management, 2) thinning only, 3) thinning + burning, and 4) thinning + burning + low-intensity grazing. Chapter 2 then evaluates the effectiveness of targeted cattle grazing for shrub control, and its impacts on the herbaceous layer. Lastly, Chapter 3 assesses how wildlife responds to efforts to restore oak savanna vegetation, specifically looking at butterflies, birds, and bats.

As a whole, this dissertation enhances our understanding of how oak savanna communities (plants and animals) respond to multiple restoration approaches. My work explores the nuances and challenges of reintroducing historic disturbances on contemporary landscapes, particularly the resilience of woody-encroached, mesophied savanna remnants to burning and grazing. It also sheds light on the efficacy and practicality of targeted grazing as a strategy to combat shrub encroachment. The results of this research have immediate relevance to restoration practitioners and provide valuable information to cattle managers interested in implementing targeted grazing. Ultimately, my dissertation is a small contribution to the larger, ongoing story of the development, destruction, and revitalization of North American savanna ecosystems.

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CHAPTER 1

Oak Savanna Vegetation Response to Layered Restoration Approaches: Thinning, Burning, and Grazing

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Chapter 1 Abstract

Temperate savannas are unique, biodiverse ecosystems that have undergone extensive habitat conversion globally. In the midwestern United States, 99% of historic oak savanna area has been lost. Most remaining patches of savanna are degraded due to woody encroachment following the removal of both fire and large herbivore disturbances from the landscape. Restoring degraded savanna remnants is challenging because we lack an understanding of how to best apply contemporary restoration tools to mimic historic disturbance dynamics. To that end, we evaluated the outcomes of ongoing oak savanna restorations that have received a gradient of restoration actions: 1) no management, 2) tree thinning, 3) thinning + burning, and 4) thinning + burning + cattle grazing. We assessed several metrics of restoration success including canopy, shrub, herbaceous, and non-native cover, herbaceous diversity, and plant community composition. We found that layering restoration approaches achieved certain, but not all, structural vegetation goals. Compared to no management, thinning and fire successfully increased canopy openness, herbaceous cover, and herbaceous diversity, but had the unwanted effect of increased shrub cover. The addition of low-intensity cattle grazing did not improve structural outcomes. We also found that each restoration treatment left a unique signature on understory plant community composition. Unmanaged and thin-only treatments were characterized by tree saplings and woodland herbs, while burned and grazed treatments were defined by shrubs and savanna-associate species. We conclude that reintroducing multiple disturbances does not guarantee the successful restoration of disturbance-dependent ecosystems such as oak savannas. Restoration outcomes are not dictated by how many management approaches are applied, but rather, the nuances of how they are applied such as burn season and livestock density.

1.1 Introduction

Temperate savannas are one of the most threatened biomes in the world due to extensive habitat conversion and minimal habitat protection (Hoekstra et al., 2005). This global trend is evident in the midwestern United States, where agricultural and urban expansion following widespread European settlement destroyed all but 0.02% of the original 13 million hectares of oak savanna (Nuzzo, 1986). In this region, savannas were characterized by scattered, open-grown oak trees, an undeveloped midstory, and an herbaceous understory dominated by grasses, forbs, and sedges (Curtis, 1959). This open, park-like structure was historically maintained by indigenous fire management, drought, and grazing by large herbivores such as bison and elk (Anderson et al., 1999). Interacting disturbances in savannas create habitat heterogeneity that supports a highly diverse herbaceous community and provides unique structural features for wildlife species, including several that are rare or in decline (Leach & Givnish, 1999). Species-rich, drought-tolerant, disturbance-adapted ecosystems like oak savannas are predicted to be resilient to future climate changes (Brandt et al., 2014). However, remnant savannas often exist in a degraded, woody-encroached state due to the removal of fire and large herbivores from the landscape after European settlement (Nowacki & Abrams, 2008). For these reasons, restoring the structure and function of oak savannas is becoming an increasingly common management priority in the United States (Dey et al., 2017).

Efforts to restore remnant oak savannas focus on reintroducing historic fire and grazing disturbances that reopen the canopy and promote a diverse herbaceous understory. Most early and long-term studies on oak savanna restoration focus on prescribed fire as a stand-alone disturbance and the effects of varying fire frequencies on vegetation dynamics (e.g., Faber-Langendoen & Davis, 1995; Peterson et al., 2007; White, 1983). From these studies, it is well-established that prescribed fire can be used in remnant oak savannas to reduce canopy cover, increase light availability, and promote the herbaceous understory. However, prescribed fire is not practical or effective in all situations. For example, reducing canopy cover with fire alone can take several decades, which may not fit the desired restoration timeline (Peterson & Reich, 2001 & 2008). Moreover, the fuel conditions in remnant savannas are often not adequate to carry prescribed fire due to mesophication (Nowacki & Abrams, 2008). Mesophication occurs when fire exclusion promotes the encroachment of mesophytic tree species into savannas, resulting in woodland that are more shady, cool, and moist with decreased fuel bed flammability (Nowacki & Abrams, 2008). In these situations, mechanical tree thinning can be used to supplement the effects of prescribed burning.

Tree thinning rapidly decreases stand density by selectively removing mesophytic species and trees with diameters larger than the fire-sensitive threshold (Peterson & Reich, 2001). Some studies have found that pairing mechanical thinning with prescribed fire leads to advantages over fire alone, namely greater canopy openness, species richness, and forb abundance (Bassett et al., 2020; Lettow et al., 2014). However, mechanically reducing canopy cover is not a substitute for prescribed fire because it does not control midstory saplings and shrubs (Peterson et al., 2007). Thinning may even favor woody species, as the rapid increase in light and nitrogen availability can initiate vigorous woody resprouting (Brudvig & Asbjornsen, 2007, Peterson et al., 2007). Once resprouting woody species are established in the midstory, fire is typically ineffective at removing them (Briggs et al., 2005; Miller et al., 2017). Thus, there remains a need to identify additional tools to supplement fire and thinning to achieve restoration goals.

Reintroducing large grazers to remnant savannas has been proposed as a complementary management approach to restore vegetation communities, with cattle serving as a modern analog for bison (Dey & Kabrick, 2015). While there are some behavioral differences between bison and cattle, they can have highly similar impacts on vegetation communities (Allred et al., 2011, Towne et al., 2005). Currently, cattle also provide a more practical and relevant option for achieving restoration objectives than bison, as they are a dominant pressure on grasslands worldwide (Allred et al., 2011). Cattle can control the woody midstory by browsing and trampling shrubs and saplings, and increase forb richness by preferentially grazing on dominant grass species (Hedtcke et al., 2009; Howe, 1999). Woody encroachment might be best combated by applying cattle grazing in tandem with fire, as some shrub species are best suppressed by grazing and others by fire (Harrington & Kathol, 2009). Despite these potential benefits, cattle grazing is rarely implemented in temperate oak savanna restorations, and data on its efficacy are scarce.

Since oak savannas were maintained throughout history by frequent fires and grazing, it follows that successful restoration depends on our ability to create modern-day proxies for these multiple, layered disturbances. Recent research shows that tree thinning, prescribed burning, and cattle grazing can individually accomplish certain, but not all, vegetation objectives (e.g., Brudvig & Asbjornsen, 2007; Peterson & Reich, 2001; Harrington & Kathol, 2009). Evidence is also beginning to accumulate that combining restoration strategies, i.e., thinning+burning or burning+grazing, has advantages over using each tool on its own (Bassett et al., 2020; Harrington & Kathol, 2009). Yet it remains unknown if all three disturbances – thinning, burning, and grazing – can be used as a layered approach to restore degraded oak savanna remnants. Therefore, we need to explore how savanna plant communities respond to a gradient of management activities in order to deepen our understanding of multiple disturbances applied in a restoration context.

The objective of this study was to characterize the impacts of different restoration strategies on oak savanna vegetation structure and community composition. We monitored oak savanna sites that received a gradient of restoration effort over the past four decades, including no management, thinning only, thinning and burning, and thinning, burning, and cattle grazing. We expected increasing restoration effort to correspond with shifts in vegetation metrics towards characteristics that define oak savannas, specifically, decreasing shrub stem density and cover and increasing herbaceous diversity and cover. We predicted tree canopy cover and basal area to decrease with thinning and fire, but not change with the addition of grazing. The results of this study will improve our understanding of how oak savanna communities respond to multiple disturbances and will be of immediate relevance to restoration practitioners interested in using a layered restoration approach.

1.2 Methods

1.2.1 Study Area

We conducted our study at the 12,400-hectare Sherburne National Wildlife Refuge (SNWR) in Sherburne County, Minnesota (45°29'45"N 93°41'28"W) (Figure 1-1). SNWR is located 80 kilometers northwest of Minneapolis/St. Paul within the Anoka Sand Plain, a flat and sandy outwash formed by the retreat of the Superior glacial lobe. Upland soils on the refuge are deep, excessively drained fine sands of the Zimmerman series (USDA NRCS). SNWR occupies the traditional homeland of the Dakota people, and later the Ojibwe people, who have stewarded the land for generations. Indigenous fire management, droughty soils, and grazing by bison and elk maintained oak savanna as the predominant vegetation type in the uplands, which were characterized by bur oak (*Quercus macrocarpa*) and northern pin oak (*Q. ellipsoidalis*) (Kratz and Jensen, 1983). In the mid-1800s, European settlers cut down many of the oaks and attempted to farm the area. Unlogged remnant savannas transformed into closed-canopy woodlands over the ensuing decades due to the alteration of the historic fire and grazing regimes. The federal wildlife refuge was established in 1965 through the acquisition of over 300 individual land holdings by eminent domain and is managed by the U.S. Fish & Wildlife Service. The current woody-dominated state of oak savannas at SNWR is similar to other remnant savannas across the Midwest (e.g., Abella et al., 2020; Tester, 1989), and is representative of a global trend of woody encroachment into grasslands (Stevens et al., 2017).

1.2.2 Restoration History & Site Selection

SNWR managers have designated oak savannas as a priority resource of concern and are working to restore woody-encroached remnants to their mid-1800s condition. The specific savanna restoration outcomes set in the *SNWR Habitat Management Plan* are as follows: 10-50% tree canopy cover consisting mostly of bur oak, 1-11 m^2 tree basal area per hectare, 2-15 standing dead trees per hectare, 5-35% shrub cover, ≥50% native herbaceous cover, and <50% invasive species cover (US Fish & Wildlife Service, 2019). These goals are aligned with the Minnesota native plant community classification for dry savannas (Aaseng et al., 2011), historic reference conditions for the upper Midwest (Curtis, 1959), and oak savanna guidelines from other U.S. regions (Burger et al., 2016).

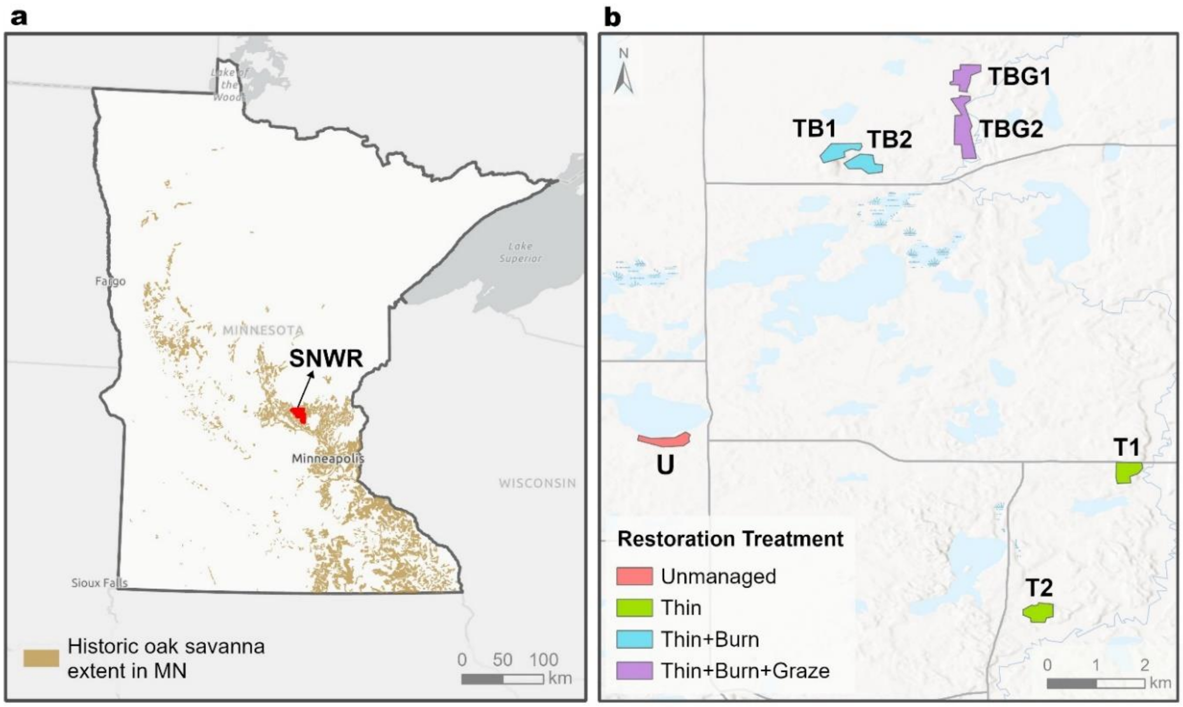

Figure 1-1. *Map of a) the location of Sherburne National Wildlife Refuge (SNWR) within Minnesota's historic oak savanna extent (MN DNR shapefile), and b) survey sites at SNWR labeled with treatment type: TBG (Thin+Burn+Graze), TB (Thin+Burn), T (Thin), or U (Unmanaged reference).*

To accomplish their restoration goals, refuge staff began conducting prescribed burns in the 1980s. Fires occurred every 2-8 years, with an average frequency of 5.2 years. All burns took place in the spring during the dormant season, apart from one summer burn in 2010. Typical burns included backing, flanking, and head fires with flame lengths of 0.5 to 3 meters depending on fuel loads and weather conditions. Refuge staff also implemented tree thinning between 2008-2016 to open the canopy of woody-encroached savanna remnants. Thinned sites had 50% of the basal area of standing trees removed, targeting non-oaks and red oaks (i.e., *Q. ellipsoidalis*, *Q. rubra*) while leaving bur oaks in place. Herbicide was applied directly to cut stumps to prevent resprouting. More recently, SNWR introduced cattle as a way to restore the historic grazing regime of oak savannas. In the summers of 2015 and 2019, a herd of cattle was rotated through two fenced grazing paddocks that averaged 60 ha in size. In 2015, 175 cow-calf pairs spent two weeks in each paddock, while in 2019 there were 100 pairs for six weeks each. The paddocks encompassed areas of both prairie and woody-encroached savanna, and the cattle spent the majority of their grazing time in the prairie, using the savanna for shade and water access. We therefore estimate that the impact of grazing in the savanna areas was low intensity.

The varied restoration history at SNWR has created a prime opportunity to study the response of oak savanna vegetation to a gradient of restoration efforts. In 2019, we met with Refuge managers and identified four restoration levels already in place on the SNWR landscape: 1) unmanaged, 2) thin only, 3) thin+burn, and 4) thin+burn+graze. We selected one unmanaged reference site that has received no restoration actions since the establishment of the refuge and two sites to represent each additional restoration treatment (Figure 1-1). The reference is a shady woodland area of predominantly *Acer rubrum* and *Quercus* species, which we believe to be an oak savanna remnant. Our seven total survey sites average 15 hectares in size, and a detailed restoration history of each site is summarized in Table 1-1. Pre-treatment data on starting conditions were not available for these sites.

Table 1-1. *Restoration histories of SNWR survey sites from 1980-2019 with the years each site received tree thinning, prescribed burning, or cattle grazing.*

Restoration Treatment	Survey Site	Thinned	Burned	Grazed
Unmanaged	U	-	-	-
Thin	T1	2016	-	-
	T2	2016	-	-
Thin+Burn	TB1	2013	1990, 1998, 2005, 2009, 2015, 2018	-
	TB2	2013	1990, 1998, 2005, 2009, 2015, 2018	-
Thin+Burn+Graze	TBG1	2008	1981, 1989, 1998, 2001, 2005, 2010[a], 2014	2015, 2019
	TBG2	2013	1980, 1984[b], 1991, 1995, 1998, 2005, 2012, 2016, 2018[c]	2015, 2019

a) This prescribed fire occurred in August and was the only growing season burn. b) In 1984, only the northern ~70% of this site burned according to map records. c) In 2018, a wildfire burned the southern ~50% of this site.

1.2.3 Field Methods

Within each survey site we established 30-35 permanent vegetation plots (232 plots total) that we surveyed annually in August from 2019-2021. Our sample size was selected based on a 95% confidence interval and a 5% error rate, using shrub data from previous oak savanna restoration research in the Anoka Sand Plain region (Reich, 2018). Fixed survey markers served as the center points for all vegetation surveys, though the size of the plots varied by vegetation layer. At all plots, we assessed the shrubs, saplings, and herbaceous layer. We used a 1-meter fixed radius plot to survey the shrubs and saplings. For shrubs, we recorded species, the number of living and dead stems, and the height class (1= <0.5m, 2= 0.5-1.5m, 3= >1.5m). For saplings, we recorded species, DBH, and height class (A= 1.6-2m, B= 2.1-3m, C= 3.1-4m, D= 4.1-5m, E= 5.1-6m, F= 6.1-8m, G= 8.1-10m). Saplings were defined as any woody species >1.5m tall, with a DBH <5cm. *Corylus americana* was always recorded as a shrub regardless of height, and *Q. rubra* and *Q. ellipsoidalis* were combined into a single species as they are often indistinguishable as seedlings. For the herbaceous layer, we used a 1m x 0.5m quadrat to record all species and their estimated cover classes. Cover classes were based on a modified Domin scale (1= 1%, 2= 2-5%, 3= 6-10%, 4= 11-25%, 5= 26-50%, 6= 51-75%, and 7= 76-100%). We also noted the percent cover of shrubs in the quadrat using the same scale. At a subset of 20 plots per site (140 plots total), we measured canopy closure using a spherical densiometer by taking an average of four readings (one in each of the cardinal directions). We also recorded the species and DBH of all trees >5cm within an 8-meter fixed radius plot.

Prior to analyses, we classified all saplings, shrubs, and herbaceous species as native or non-native. We also grouped herbaceous species by habitat type, using species lists from Curtis (1959), the MN Department of Natural Resources (DNR) (2003), and Pruka (1995) to identify species associated with oak savannas. Curtis (1959) and MN DNR (2003) report species with the highest relative frequency in statewide oak savanna survey plots and therefore represent “prevalent” savanna species. Pruka’s list uses expert knowledge to categorize savanna “indicators”, light-dependent understory species that tend to be limited to partial canopy conditions, and savanna “associates”, species found in a broader range of upland habitats. Though the Curtis and Pruka lists were developed for southern Wisconsin, they align well with the MN DNR’s list of common species in southern dry savannas of Minnesota (MN DNR, 2003). We define woodland herbs as those species that prefer shadier, moister habitat conditions than savanna associates.

1.2.4 Statistical Analysis

We conducted all analyses on vegetation structure and community composition in R version 4.2.0 (R Core Team, 2022). We checked assumptions of normality and homoscedasticity using the *simulateResiduals* function in the *DHARMa* package (Hartig, 2022). When these assumptions were not met, we used a Box-Cox transformation. We compared canopy cover and basal area across restoration treatments with linear mixed effects models using the *lmer* function in the *lme4* package (Bates et al., 2015). We constructed a model with treatment was a fixed effect and site as a random effect. We also used linear mixed effect models to assess herbaceous cover, richness, and diversity (Shannon index), and shrub stem density across restoration treatments with treatment as a fixed effect and year and plot nested within site as random effects. We were not interested in testing for differences in vegetation metrics among years, so we accounted for interannual variation by including year as a random effect. We included plot nested within site as a random effect to account for repeated measures at the same location. This blocked design with only two sites per treatment reduced our power and ability to detect significant differences among treatments, so we use $\alpha = 0.1$ as our significance threshold.

For vegetation metrics that did not meet the normality and homoscedasticity assumptions even after transformation (non-native herbaceous cover, non-native shrub density, young oak density), we used generalized linear mixed models in the *glmmTMB* package (Brooks et al., 2017). Again, the only fixed effect was treatment, and random effects included year and plot nested within site. We specified a negative binomial error distribution with a log link for young oak density and non-native shrub density, and a Tweedie distribution for non-native herbaceous cover. Due to the ordinal nature of the shrub cover class data, we evaluated shrub cover across treatments with cumulative link mixed models with the same fixed and random effects using the *clmm* function in the *ordinal* package (Christensen, 2019). For all above analyses, we conducted pairwise comparisons with the Tukey adjustment using the *emmeans* package when models were significant (Lenth, 2022).

Prior to multivariate analyses, we removed species that occurred in less than 3% of our plots and averaged herbaceous cover and shrub stem density by plot across the three years of data collection. We explored the herbaceous and woody species composition of each restoration treatment using non-metric multidimensional scaling (NMDS) with Bray-Curtis distances produced with the *metaMDS* function in the *vegan* package (Oksanen et al., 2022). For both the herbaceous and woody communities, we chose a three-dimensional solution to reduce stress and rotated the axes to maximally differentiate groups in two dimensions. We visualized the impact of treatment on community composition by drawing ellipses encompassing data within one standard deviation of the centroid. To assess whether there were statistical differences in community composition between treatments, we conducted permutational multivariate analysis of variance (PERMANOVA) with Bray-Curtis distances and 999 permutations using the *adonis* function from the *vegan* package. We also checked the assumption of homogeneity of group dispersions using the *betadisper* function. We then carried out pairwise comparisons using the *pairwise.perm.manova* function from the *RVAideMemoire* package (Hervé, 2022). To see which specific herbaceous and woody species were associated with each restoration treatment, we performed an indicator species analysis using the *multipatt* function from the *indicspecies* package (De Caceres & Legendre, 2009). Species were considered indicators at a significance level of $\alpha = 0.05$.

1.3 Results

Vegetation structure, richness, and diversity did not change incrementally with each added restoration action; instead, the greatest differences were between burned (i.e., thin+burn, thin+burn+graze) and unburned (i.e., thin, unmanaged) treatments. Each restoration treatment did generate a unique species community, with higher restoration effort corresponding with more savanna-associate species. Our analyses were designed to look for differences among treatments while controlling for interannual variation due to differences in climate and observers; therefore, we have chosen to focus our results and discussion on vegetation values averaged over the three years of data collection.

Average canopy cover differed among restoration treatments ($F_{3,3}$=8.1; p=0.06) and was significantly lower in the two burned treatments. Compared to the unmanaged reference, canopy cover was only 20% lower in the thin treatment, but over 50% lower in the thin+burn (t_3=3.9; p=0.09) and thin+burn+graze treatments (t_3=3.8; p=0.09) (Figure 1-2). As expected, cattle grazing did not influence canopy cover. Tree basal area followed a similar pattern to canopy cover with burning producing far more dramatic decreases than thinning (Table 1-2). While there were no significant differences in total sapling density, young oak density (seedlings + saplings) did differ among restoration treatments and was greatest in the unmanaged reference (Table 1-2). Compared to the reference, there were 130% fewer young oaks in the thin+burn treatment (t_3=6.2; p=0.02) and 95% fewer in the thin+burn+graze treatment (t_3=4.0; p=0.08).

Table 1-2. *Comparison of select vegetation metrics across oak savanna restoration treatments. Data represent 3-year averages over 2019-2021 (basal area was only measured in 2020) and are presented as raw mean ± SE. Young oaks include seedlings and saplings. Different letters indicate pairwise differences between restoration treatments at p=0.1. Note that canopy, shrub, and herbaceous cover values are presented in Figure 1-2.*

	Basal Area *(m^2 ha^{-1})*	**Shrub Density** *(stems m^{-2})*	**Young Oaks** *(stems m^{-2})*	**Herb Richness** *(species $plot^{-1}$)*	**Herb Diversity** *(H)*
Unmanaged	23.1 ± 3.1^a	7.4 ± 0.5	1.4 ± 0.2^a	3.5 ± 0.2	0.96 ± 0.06
Thin	20.1 ± 2.5^a	14.1 ± 0.5	0.9 ± 0.1^b	4.1 ± 0.1	1.07 ± 0.04
Thin+Burn	6.5 ± 1.6^b	15.7 ± 0.6	0.3 ± 0.1^c	5.5 ± 0.2	1.39 ± 0.03
Thin+Burn+ Graze	8.8 ± 1.6^b	15.2 ± 0.6	0.5 ± 0.1^b	5.4 ± 0.2	1.33 ± 0.03
Treatment	$F_{3,3}$ = 13.5, p = 0.03	$F_{3,3}$ = 2.8, p = 0.21	X^2 = 43.1, df = 3, p < 0.001	$F_{3,3}$ = 6.6, p = 0.08	$F_{3,3}$ = 5.2, p = 0.11

Shrub cover varied among restoration treatments (χ^2=57.8, df=3, p<0.001) and increased with increased restoration effort; average shrub cover was over 30% higher in thin+burn+graze treatment than in the reference site (t_3=6.9; p=0.02) (Figure 1-2). Total shrub stem density increased nearly twofold with thinning, but minimally increased with cattle grazing and burning (Table 1-2). Non-native shrub density also differed among restoration treatments (χ^2=58.4, df=3, p<0.001), but was low overall. Non-native shrubs were most common in the thin-only treatment (0.8 stems m^{-2}) and the reference (0.4 stems m^{-2}) and were negligible in the burned treatments (thin+burn = 0.01 stems m^{-2}; thin+burn+graze = 0.03 stems m^{-2}).

Herbaceous cover did not differ significantly across restoration treatments ($F_{3,3}$=3.8, p=0.15) but was 20-30% higher in the thin+burn treatment compared to all others (Figure 1-2). Non-native herbaceous cover varied across restoration treatments (χ^2=10.8, df=3, p=0.01) but was low overall, ranging from 2.2% in the reference and thin treatment, to 3.5% in the thin+burn+graze treatment, to 6.9% in the thin+burn treatment. There were also significant differences among restoration treatments in herbaceous richness and Shannon diversity (Table 1-2). Both richness and diversity increased incrementally with the additions of thinning and burning, but not grazing (Table 1-2).

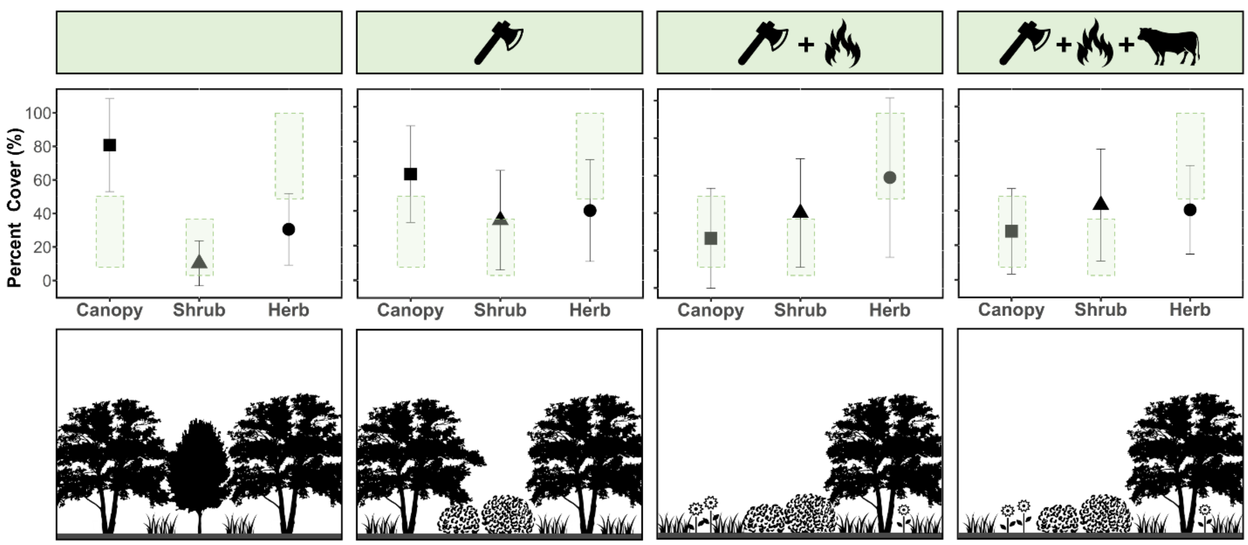

Figure 1-2. *Shifts in oak savanna vegetation structure as restoration efforts increase. Top row: restoration treatment. Middle row: average vegetation percent cover values compared to SNWR's oak savanna restoration goals (dashed green boxes are the target cover range). Canopy cover was measured only in 2020, while shrub and herbaceous cover values represent 3-year averages (2019-2021). Error bars are ±1 SD. Bottom row: illustration of structural differences across the treatments.*

PERMANOVA revealed significant differences in the centroids of the restoration treatments for both shrubs (p<0.001) and herbaceous plants (p<0.001). All pairwise comparisons were significant (p<0.01), meaning that each added restoration action produced a distinct vegetation community. For shrubs, the group dispersions were heterogeneous (p<0.001), so our PERMANOVA results must be interpreted with this caveat in mind; however, one can visually see clear differences in the locations of the group centroids (Figure 1-3). There were 13 woody and 36 herbaceous species associated with the different restoration treatments (see Appendix), and the top indicators are shown in Figure 1-3. For woody species, *A. rubrum* (red maple) was an indicator of the unmanaged reference only, while all three *Quercus* species, *Prunus serotina* (black cherry), and *Rhamnus cathartica* (common buckthorn) were common in both the reference and thin sites. *Rhus glabra* (smooth sumac) was an indicator solely of the thin+burn treatment, and *Ribes sp.* (gooseberry) was unique to thin+burn+graze. Both burned treatments were characterized by *Corylus americana* (American hazelnut) and *Ceanothus americanus* (New Jersey tea). For herbaceous species, the thin treatment was defined by *Maianthemum canadense* (Canada mayflower), *Parthenocissus quinquefolia* (Virginia creeper), and *Phryma leptostachya* (American lopseed). Indicators of the thin+burn treatment included *Amphicarpaea bracteata* (American hog peanut), *Desmodium glutinosum* (pointed-leaf tick trefoil), *Helianthus pauciflorus* (stiff sunflower), and *Agastache scrophulariifolia* (purple giant hyssop), while the thin+burn+graze treatment was associated with species such as *Galium boreale* (northern bedstraw), *Helianthus hirsutus* (hairy sunflower), and *Apocynum cannabinum* (dogbane).

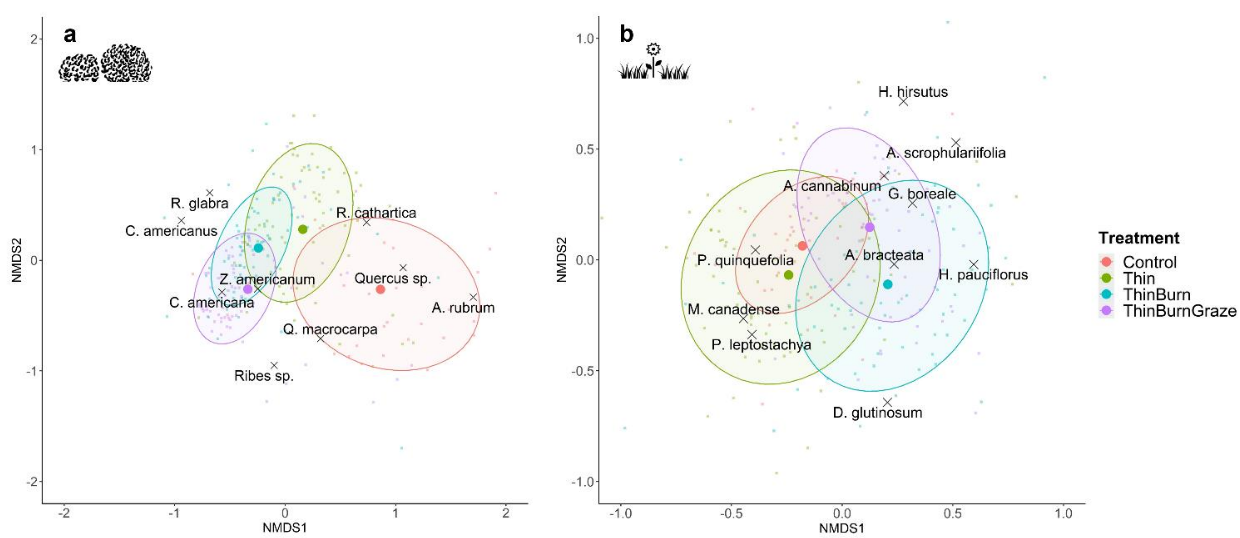

Figure 1-3. *NMDS ordination plots to visualize the a) woody (stress = 0.132) and b) herbaceous (stress = 0.162) communities. Each colored point represents an individual survey plot; points in closer proximity have more similar vegetation communities. Ellipses encompass data within one standard deviation of the centroid. Select species are displayed with a black X; these are the top indicators for each treatment based on indicator species analysis. Note that Quercus sp. represents Q. rubra and Q. ellipsoidalis combined.*

1.4 Discussion

Our objective was to advance the science and practice of oak savanna restoration through an increased understanding of the application of multiple disturbances. To that end, we implemented an observational study to characterize the response of oak savanna vegetation structure and community composition to a gradient of restoration treatments. We found that increasing restoration effort did not produce consistent shifts toward savanna structure but did coincide with a transition from woodland species to savanna associates. Compared to the reference, the additions of thinning and fire increased canopy openness and herbaceous cover, but also increased shrub cover. Low-intensity grazing provided no further benefits, but rather, decreased herbaceous cover and slightly increased shrub cover in comparison to thinning+burning. Each restoration treatment generated a unique species composition, but the most pronounced community differences were between unburned and burned treatments. Burning increased herbaceous richness, diversity, and non-native herb abundance, and decreased non-native shrub density. Overall, our study identifies potential areas for improvement in oak savanna management and recommends a more nuanced approach to studying multiple disturbances that considers site history and treatment specifics.

1.4.1 Structural vegetation changes & challenges

Oak savanna restorations aim to recover historic reference conditions to some extent, the success of which is often measured by key structural vegetation metrics such as canopy openness and herbaceous cover (Dey & Kabrick, 2015). Though the vegetation goals we evaluate here were written for SNWR, they are representative of common targets for Midwestern oak savanna restorations (e.g., Burger et al., 2016). We found that target canopy cover and basal area were achieved in areas that received both thinning and burning, but not thinning alone. This could be because the burned treatments were already more open when thinning was implemented to remove 50% of the standing basal area, though we do not have pre-thinning tree data. Prescribed fires had been ongoing in the burned treatments for 20-30 years at the time of thinning, and repeated, low-intensity burns have been shown to increase canopy openness over decades (Knapp et al., 2015; Peterson & Reich, 2001). Additional tree mortality occurred in the thin+burn treatment during a particularly hot burn in 1998, which top-killed several mature oaks. We note that the canopy openness that defines savannas could be created without fire by simply removing more trees during thinning. However, thinning is not a feasible stand-alone restoration practice as fire is still required to restore an herbaceous-dominated understory (Brudvig & Asbjornsen, 2007, Peterson et al., 2007).

A previous oak savanna study found that vegetative cover increased more in thin+burn treatments than in burn-only treatments, but they lacked a thin-only treatment and did not differentiate between woody and herbaceous plants (Bassett et al., 2020). Here, we found that thinning alone increased both shrub and herbaceous cover compared to the reference, but the increase in herbaceous cover was much greater in the thin+burn treatment. Our results help to disentangle the individual effects of each management action and suggest that thinning and burning interactively increase understory herbaceous cover. We also distinguish between vegetation types, as increased herbaceous cover is a desirable oak savanna restoration outcome but increased shrub cover is not. We found that herbaceous cover increased to the goal of ≥50% in the thin+burn treatment, but shrub cover was not contained to the 5-35% target in any restoration treatment. Instead, shrubs flourished after thinning and seemed to be further stimulated by fire and low-intensity grazing.

Thinning rapidly decreases canopy cover and increases light and nutrient availability, which may favor already established shrubs (Peterson et al., 2007; Vander Yacht et al., 2017). Subsequent low-intensity fires may fail to suppress woody species, particularly “endurer” species with resprouting capabilities such as oaks, aspen, and many shrubs (Abella et al., 2020; Peterson & Reich, 2001). Whether fire controls woody encroachment depends on the frequency and seasonality of prescribed burns. Historically, oak savannas were maintained by indigenous fires with an estimated mean fire interval of 3.7 years (Dey et al., 2004; Wolf, 2004). Interval-burning experiments have found that annual to biennial fires result in the highest cover of grasses and the greatest herbaceous species richness (Peterson & Reich, 2001, 2008; Tester, 1989). A 2-year fire return interval can also maximize woody control (Vander Yacht et al., 2017). Longer fire return intervals of 5-8 years promote woody vegetation, with stem density accumulating over time from repeated top-killing and resprouting (Clatterbuck & Rollins, 2018; Peterson & Reich, 2001). Our study corroborates these findings, as our mean fire interval of 5.2 years is likely longer than the historic norm and has resulted in an overabundance of shrubs and inadequate herbaceous cover. Dense shrub thickets and low fine fuel loads make it difficult to implement fire, which further increases shrub survival (Ratajczak et al., 2011). This leads to a positive feedback loop that promotes the shrub midstory and inhibits the herbaceous layer (Ratajczak et al., 2011), thereby reducing the chance of meeting structural vegetation goals for oak savanna restoration.

Burning seasonality is also important; dormant season fires are common practice, but growing season fires may be more effective at controlling woody vegetation (Burger et al., 2016). A study in Wisconsin found that burning during late August resulted in the highest amount of top-kill and lowest amount of resprouting, while spring burns produced high levels of resprouting (Meunier 2021). In southeastern pine-grasslands, woody resprout growth rates were lower after early growing season burns than after dormant season burns (Robertson & Hmielowski, 2014). At our study site, all but one burn over the past 40 years occurred in the spring dormant season, which may partially explain the high shrub density. While two to three growing season burns are recommended to suppress the woody midstory after a thinning event (Burger et al., 2016), in practice the timing of prescribed burns is limited to days with appropriate fuel and weather conditions (Weir, 2011). Given that fire frequency seems to play a stronger role than fire season in controlling woody species, it is inadvisable to skip burn years while waiting for ideal conditions in the growing season (Knapp et al., 2009).

The addition of low-intensity cattle grazing did not produce any additional improvements in vegetation structure beyond what thinning and burning achieved. To the contrary, average herbaceous cover was lower in the thin+burn+graze treatment than in the thin+burn treatment. It is possible that cattle consumption of herbaceous plants led to lower cover; however, we do not think that is a driving factor based on how grazing was implemented. The cattle were grazed in paddocks that encompassed our study's restoration areas as well as larger areas of prairie. From our own observations and conversations with the grazing cooperator, it is likely that the cattle grazed primarily in the open prairie, using the restoration areas only for shade and water access. We thus suspect that the impact of cattle grazing on the understory of the thin+burn+graze treatment was minimal, and that differences in herbaceous cover between the thin+burn and thin+burn+graze treatments were driven by differences in restoration history (e.g., time since last fire, total number of fires) rather than the presence of cows.

Previous research has shown that cattle grazing can have vegetation impacts that align with savanna restoration goals; for example, a global review of 144 studies concluded that cattle grazing in temperate forests reduces woody abundance and increases grass and forb richness (Bernes et al., 2018). When used in an oak savanna restoration in Wisconsin, cattle halved woody plant density (Harrington and Kathol 2009). The reason we did not see similar vegetation impacts in our study can be explained by differences in grazing management. In Harrington and Kathol (2009), cattle were intentionally managed to reduce shrub stem density; they were stocked at a high density and rotated every two days through small paddocks. In contrast, grazing at SNWR was implemented at a lower stock density, for a longer duration, over a larger area that did not specifically target the savanna restoration sites. This type of low-intensity cattle grazing is likely not reflective of the strong top-down pressure that 30-60 million bison would have historically exerted on vegetation structure (Truett et al., 2001), and our results suggest it may not be an effective approach to restore severely woody-encroached oak savannas.

Given the observational nature of our study, we were not able to control for differences in restoration history. The thin-only treatment was thinned more recently than the thin+burn and thin+burn+graze treatments. Burning began in the thin+burn treatment a decade prior to in the thin+burn+graze treatment, and the thin+burn treatment had a more recent fire (Table 1-1). It is unknown to what extent these management differences influenced the vegetation patterns we saw among treatments. In addition, pre-treatment vegetation data was not available for our study sites, and starting conditions are important to explaining restoration outcomes (Galatowitsch & Bohnen, 2020). Ultimately, conducting observational research at sites with an extensive management history such as ours provides a tradeoff: there are many variables we cannot control, but we gain valuable insight into long-term, large-scale outcomes of applied restoration actions. Future studies on layered restoration approaches may benefit from an experimental design that clearly documents starting conditions and controls for the timing of management actions.

1.4.2 Plant community composition changes

Though increasing restoration effort did not produce consistent shifts toward savanna structure, each restoration treatment did result in distinct species communities. In general, the woody community transitioned from tree seedling species to shrub species as restoration effort increased. Red maple, a shade-tolerant, mesophytic tree species, was an indicator exclusive to the closed-canopy reference site. Bur oak and red oak species were indicators of the reference and the thin-only treatment, but not the thin+burn and thin+burn+graze treatments. While biennial fires are likely necessary to reduce and control shrub density in these areas, managers could consider periodically incorporating a longer burn-free window to allow young oaks to grow above the fire-sensitive threshold (Burger et al., 2016). Frequent fires can then be reinitiated to maintain the advantage of oaks over mesophytes (Brose et al., 2014). Thinning promoted American hazelnut, which was a dominant shrub across all restoration treatments excluding the reference. This is not surprising as American hazelnut is a rhizomatous, thicket-forming shrub that does well in a variety of light and moisture environments (Coladonato, 1993). The defining woody species of the two burned treatments was New Jersey tea, a “best indicator” of oak savannas due to its ability to tolerate drought and recover quickly after fire (Pruka, 1995). Burned treatments also had lower density of common buckthorn, which was the primary non-native shrub recorded in our surveys. Though other studies have found that one or two prescribed fires do not reduce buckthorn resprout (Bisikwa et al., 2020; Meunier et al., 2021), our results suggest that repeated burns over 40 years may effectively suppress buckthorn and promote native shrub species.

We saw similarly distinct communities in the herbaceous layer. The thin treatment was characterized by shade-tolerant, woodland species that prefer moist soil conditions such as Canada mayflower and Virginia creeper. With the addition of fire, the results of our indicator species analysis began to align with lists of species considered savanna indicators or associates (Curtis 1959, Pruka 1995). Ten of the defining thin+burn species were savanna associates including purple giant hyssop, which is a savanna “best indicator” given its preference for recently disturbed areas with patchy shade (Pruka 1995). Characteristic species of the thin+burn+graze treatment included savanna associates that prefer drier, open woodland edges (e.g., northern bedstraw, hairy sunflower) and disturbed areas (e.g., dogbane). This shift toward a more savanna-like species composition came with only a small increase in non-native herbaceous cover, which was low across all treatments. The introduction of non-native species is a common concern associated with cattle grazing; however, non-native cover was lower in the thin+burn+graze treatment than in the thin+burn treatment. We suspect that the sandy, nutrient-poor soils at SNWR help limit the spread of non-native species, keeping their cover well below the restoration goal of <50% in all treatments. Overall, looking at the species composition data allowed us to see subtle community changes that were not apparent in the structural vegetation metrics, underlining the importance of including species-specific goals in restoration plans. These results also provide evidence that different combinations of disturbances leave unique legacies in terms of species composition (Johnstone et al., 2016).

1.4.3 Recommendations for improved restorations

The unifying theme throughout our findings is that the outcomes of restoration depend on the nuances of how the actions were implemented. Restoration research, including our own, often falls into the trap of comparing binaries: thinned vs. not thinned, burned vs. unburned, etc. An assessment of prescribed fire research in rangelands found that >80% of studies reported vague treatment categories (i.e., burned vs. unburned) without sufficient details on the fire characteristics (Limb et al., 2016). We had similar difficulty finding information about the burns conducted at SNWR; the plans contained acceptable prescription ranges for weather, fuel conditions, and fire behavior, but nothing on the actual burn-day conditions or fire intensity. Recording treatment specifics is more common in livestock grazing experiments, which often report animal type, stocking density, season, and duration (Limb et al., 2016; Twidwell et al., 2021). This context is necessary to understand conflicting results among grazing studies and allows managers to implement grazing management with more precision (Limb et al., 2016; Twidwell et al., 2021). Grazing experiments should therefore serve as an example for how to better document other restoration actions such as tree thinning and prescribed burning. Studies like our own that compare only gross treatment effects are oversimplifying to the point that the results are hard to interpret and lose some relevance to managers. We are then left with a series of isolated restoration projects whose findings are nearly impossible to replicate or generalize. Therefore, moving research away from treatment binaries toward explicit methods and standardized metrics will allow us to synthesize disturbance research and improve restoration outcomes across ecosystems (Buma, 2021).

We conclude that layered restoration approaches promote savanna-associated species and some, not all, defining structural features of savannas. Implementing multiple disturbances created an open canopy and a diverse herbaceous understory but had the undesirable effect of stimulating a dense shrub midstory. The generalizability of these results is limited due to using simplified treatment binaries, lacking data on starting conditions, and having only two replicates per treatment. Our work supports previous studies that show interactive effects of thinning and fire (Bassett et al., 2020; Lettow et al., 2014;

Vander Yacht et al., 2017), but does not reveal any additional synergies with low-intensity grazing. This does not indicate that cattle grazing is an ineffective restoration tool, but rather, that livestock management needs to align with the restoration objectives. Managers of woody-dominated sites such as ours could experiment with targeted grazing (Bailey et al., 2019), and manipulate the season, duration, distribution, and intensity of livestock grazing to specifically impact shrubs and saplings. Moreover, burning every 2-3 years and possibly incorporating growing season burns may better target woody species and limit resprout. We wish to reiterate that restoration outcomes are not dictated by *if* a management strategy was applied, but *how* it was applied. Simply reintroducing disturbances does not ensure the successful restoration of ecosystems with historically complex and dynamic disturbance regimes.

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1.6 Supplementary Materials

Supplemental Table 1-1. *Results of the indicator species analyses for woody and herbaceous understory species using the 'multipatt' function from the 'indicspecies' package (De Caceres & Legendre, 2009). Species were considered significant indicators of a treatment at p ≤ 0.05. Woody species were allowed to be indicators of multiple treatments. Based on lists from Curtis (1959), MN DNR (2003), and Pruka (1995), species are marked as prevalent savanna species (+), savanna associate species (++), or savanna indicator species (+++).*

WOODY SPECIES					
Treatment	**Species name**	**Common name**	**stat**	**p value**	**Savanna association**
Unmanaged	*Acer rubrum*	Red maple	0.653	0.001	
	Quercus sp.	Red oak species	0.784	0.001	
	Rhamnus cathartica	Common buckthorn	0.730	0.001	
	Prunus serotina	Black cherry	0.664	0.001	
	Acer negundo	Boxelder	0.283	0.026	
	Diervilla lonicera	Northern bush honeysuckle	0.312	0.01	
	Populus tremuloides	Quaking aspen	0.335	0.019	
	Quercus macrocarpa	Bur oak	0.581	0.002	+
Thin	*Quercus sp.*	Red oak species	0.784	0.001	
	Rhamnus cathartica	Common buckthorn	0.730	0.001	
	Prunus serotina	Black cherry	0.664	0.001	
	Acer negundo	Boxelder	0.283	0.026	
	Zanthoxylum americanum	Prickly ash	0.61	0.001	
	Populus tremuloides	Quaking aspen	0.335	0.019	
	Corylus americana	American hazelnut	0.928	0.001	+
	Quercus macrocarpa	Bur oak	0.581	0.002	+
Thin+Burn	*Rhus glabra*	Smooth sumac	0.368	0.012	+
	Diervilla lonicera	Northern bush honeysuckle	0.312	0.01	
	Ceanothus americanus	New Jersey Tea	0.28	0.034	+++
	Populus tremuloides	Quaking aspen	0.335	0.019	
	Corylus americana	American hazelnut	0.928	0.001	+
Thin+Burn+Graze	*Ribes sp.*	Gooseberry	0.245	0.045	
	Zanthoxylum americanum	Prickly ash	0.61	0.001	
	Ceanothus americanus	New Jersey Tea	0.28	0.034	+++
	Quercus macrocarpa	Bur oak	0.581	0.002	
	Corylus americana	American hazelnut	0.928	0.001	+

HERBACEOUS SPECIES					
Treatment	**Species name**	**Common name**	**stat**	**p value**	**Savanna association**
Unmanaged	*Bromus inermis*	Smooth brome	0.325	0.007	
Thin	*Phryma leptostachya*	American lopseed	0.502	0.001	
	Parthenocissus quinquefolia	Virginia creeper	0.501	0.011	+
	Maianthemum canadense	Canada mayflower	0.499	0.001	
	Galium triflorum	Fragrant bedstraw	0.463	0.001	
	Vitis riparia	Riverbank grape	0.333	0.022	+
	Lysimachia borealis	Starflower	0.329	0.088	
Thin+Burn	*Amphicarpaea bracteata*	Hog peanut	0.536	0.001	++
	Desmodium glutinosum	Pointed-leaf tick-trefoil	0.510	0.001	+
	Helianthus pauciflorus	Stiff sunflower	0.480	0.001	+
	Helianthus tuberosus	Jerusalem artichoke	0.431	0.001	
	Lathyrus ochroleucus	Cream pea	0.427	0.001	++
	Pteridium aquilinum	Eagle fern	0.378	0.001	
	Phalaris arundinacea	Reed canary grass	0.334	0.005	
	Polygonatum biflorum	Smooth solomon's seal	0.322	0.049	+
	Athyrium filixfemina	Lady fern	0.316	0.009	
	Elymus repens	Couch grass	0.310	0.044	
	Andropogon gerardii	Big bluestem	0.309	0.004	+++
	Monarda fistulosa	Wild bergamot	0.302	0.004	+
	Symphyotrichum urophyllum	Arrowleaf aster	0.294	0.011	
	Geranium maculatum	Wild geranium	0.292	0.015	
	Astragalus sp.	Milkvetch	0.262	0.018	
	Agastache scrophulariifolia	Purple giant hyssop	0.242	0.026	+++
Thin+Burn+Graze	*Galium boreale*	Northern bedstraw	0.595	0.001	+++
	Poa sp.	Bluegrass	0.476	0.002	
	Eurybia macrophylla	Large-leaved aster	0.404	0.001	
	Solidago canadensis	Canada goldenrod	0.393	0.019	
	Helianthus hirsutus	Hairy sunflower	0.378	0.001	++
	Apocynum cannabinum	Indian hemp	0.344	0.001	++
	Symphyotrichum cordifolium	Blue wood-aster	0.326	0.001	
	Helianthus strumosus	Woodland sunflower	0.298	0.003	+
	Calamagrostis canadensis	Canada bluejoint	0.279	0.016	

CHAPTER 2

Targeted Cattle Grazing for Shrub Control in Woody-Encroached Oak Savannas

In preparation as:

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Austin M. Yantes: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Supervision, Writing - Original Draft. **Kent L. Solberg:** Conceptualization, Methodology, Resources, Supervision, Writing - Review & Editing. **Rebecca A. Montgomery:** Methodology, Writing - Review & Editing, Project administration.

Chapter 2 Abstract

Woody encroachment threatens savanna ecosystems around the world. In the midwestern United States, remnant oak savannas persist in a woody-encroached state due to the removal of grazing and fire disturbances from the landscape. Restoring oak savannas is challenging because efforts to remove woody vegetation, namely thinning and fire, can promote a dense shrub layer. Therefore, it is necessary to explore other tools to control woody species such as targeted grazing. We conducted an experiment to evaluate the effectiveness of targeted cattle grazing as a shrub control method, and its impacts on the herbaceous community. We used high-density, short-duration grazing in order to target shrubs and minimize negative non-target impacts. We found that this type of cattle management reduced shrub density over the short term, but there was substantial resprout after one year of no grazing. Targeted grazing lowered herbaceous cover and shifted species composition but did not affect herbaceous species density or diversity. We saw no increase in non-native cover during the study, though we documented isolated occurrences of new non-native species in the grazing paddocks. Overall, our study points to the potential of targeted cattle grazing as a viable tool to help restore the understory of woody-encroached ecosystems. Successfully meeting vegetation objectives requires a grazing manager with knowledge of the site, the target species, and livestock care and nutrition, as well as a commitment to adaptive management.

2.1 Introduction

Increasing woody vegetation in grasslands, known as woody encroachment, threatens the persistence of savanna ecosystems around the world (Stevens et al., 2017). Woody encroachment can have negative impacts including altered light, water, and nutrient dynamics, decreased plant species richness, and degraded habitat quality (Knapp et al., 2008; Ratajczak et al., 2012; Scholes & Archer, 1997; Taft, 2009). As a result, there is global interest in finding strategies to manage and restore woody-encroached savannas (Archer et al., 2017). In the central United States, oak savannas once covered millions of hectares from Minnesota to Texas, but now most remnants exist in a woody-encroached state (Gleason, 1922; Nowacki & Abrams, 2008; Nuzzo, 1986). Dynamic interactions between large herbivores and Indigenous fire historically maintained the characteristic park-like structure of oak savannas including a sparse canopy, open midstory, and an exceptionally diverse grass-forb understory (Abrams et al., 2021; Anderson et al., 1999; Bray, 1960; Leach & Givnish, 1999). During European settlement, oak savannas were converted to agriculture, native herbivores (i.e., bison, elk) were nearly extirpated, and Indigenous people were systematically displaced to reservations (Nuzzo, 1986; O'Connor et al., 2020; Vinyeta, 2022). A century of strict fire suppression policies ensued (Abrams et al. 2021). In the absence of grazing and fire disturbances, oak savannas filled in with fire-intolerant, mesic woody species, undergoing succession to closed-canopy woodlands (Anderson 1999; Nowacki & Abrams, 2008).

Today, oak savanna managers are challenged by how best to restore an ecosystem with a dynamic historic disturbance regime in the face of ongoing woody encroachment (Abella et al., 2020). A substantial hurdle for oak savanna restoration is that efforts to remove woody plants can actually stimulate the shrub layer. The most common restoration actions include tree thinning to re-open the canopy and prescribed fire to promote an herbaceous dominated understory (Burger et al., 2016). However, thinning increases light and nitrogen availability in the understory, which favors established woody species (Peterson et al., 2007). Several studies in oak ecosystems report increased woody stem density after thinning due to aggressive resprouting (Brudvig & Asbjornsen, 2007; Vander Yacht et al., 2019). Prescribed fires are recommended to control woody vegetation post-thinning (Burger et al. 2016), but counterproductively, repeated burns under open canopies can increase shrub density (Abella et al., 2020; Hutchinson et al., 2012). Intermediate fire frequencies (4-8 years) particularly favor woody vegetation, causing stem density to accumulate over time from repeated top-killing and resprouting (Clatterbuck & Rollins, 2018; Peterson & Reich, 2001). In fact, burning intermittently can increase the abundance of shrubs more than fire exclusion (Briggs et al., 2002, 2005; McCarron & Knapp, 2003). Our previous work in Midwestern oak savannas found that after tree thinning and burning every 5 years, shrub density doubled compared to no management (Yantes et al., 2023).

Once established, a dense woody midstory further complicates the use of prescribed fire as a restoration tool (Abella et al. 2020). Many native shrub species occurring in Midwestern oak systems spread clonally and are capable of forming dense thickets, such as *Corylus americana* (American hazelnut) and *Rubus* species (raspberries) (Haney & Apfelbaum, 1993). As shrub colonies expand, fine fuel loads are reduced and fire cannot penetrate the thickets (Ratajczak et al., 2011, 2014). Shrubs are thus resistant to future fires, and even if fire top-kills some stems, they can resprout vigorously (Briggs et al., 2005; Heisler et al., 2004). This leads to a self-reinforcing feedback loop that promotes woody dominance, inhibits the herbaceous layer, and makes prescribed fire an increasingly ineffective restoration tool (Ratajczak et al. 2011). Therefore, it is worthwhile to experiment with alternative methods to restore woody-encroached oak savannas.

One potential management option for reducing woody vegetation is targeted livestock grazing. Targeted grazing is a form of adaptive grazing designed to accomplish defined vegetation goals while meeting the nutritional needs of the cattle within the context of the site (Bailey et al., 2019; Launchbaugh & Walker, 2006). Managers achieve specific objectives by manipulating stocking density (animal weight per area), duration, species, distribution, and season of grazing (e.g., grazing at a time when undesirable plants are most vulnerable to defoliation) (Bailey et al. 2019). While goats are most commonly used to control woody vegetation (Marchetto et al., 2021), there is some evidence that cattle can reduce shrubs through trampling and browsing, particularly at high stocking densities (Bernes et al., 2018; Hedtcke et al., 2009; Marquardt et al., 2009). An oak savanna restoration study in the Upper Midwest found that cattle grazing reduced shrub stem density by over 40% (Harrington & Kathol, 2009). Additionally, using cattle rather than goats or a native herbivore (i.e., bison) has many practical incentives including ease of management, profitability, and accessibility to land managers (Allred et al., 2011; Frost et al., 2012).

Despite the potential benefits, grazing cattle in natural areas raises concerns for many land managers. Uncontrolled or continuous cattle grazing has a long history of negative ecosystem impacts due to overutilization, including soil compaction and erosion, altered nutrient cycling, loss of plant diversity, and an increase in invasive species (Bernes et al., 2018; Eldridge et al., 2016; Fleischner, 1994; Lai & Kumar, 2020). To avoid these side effects, conservation-oriented grazing approaches such as targeted grazing use short grazing durations and long recovery periods (Bailey et al., 2019; Teague & Kreuter, 2020). It has been hypothesized that the frequent movement of livestock at high densities should mimic natural herd migrations of large herbivores that historically maintained savannas (Savory, 1983; Teague & Kreuter, 2020). Yet while targeted grazing is growing in popularity as a restoration practice, questions remain around its efficacy and potential unintended ecological impacts (Marchetto et al., 2021).

We evaluated the effectiveness of targeted cattle grazing to reduce shrub density in a heavily encroached oak savanna. We implemented high-density, short-duration grazing to target the shrub layer and minimize negative unwanted ecosystem impacts. Specifically, we address the following questions: 1) Is targeted grazing with beef cattle an effective and feasible shrub reduction method? 2) How does targeted grazing for shrub control impact herbaceous cover, richness, and species composition? By answering these questions, our study provides insight on an alternative or complementary management tool to prescribed fire that may help improve oak savanna restoration outcomes.

2.2 Methods

2.2.1 Study Site Characteristics

Sherburne National Wildlife Refuge (SNWR) is located in the Anoka Sand Plain region of central Minnesota, 80 kilometers northwest of Minneapolis/St. Paul (45°29'45"N 93°41'28"W). Upland soils are deep, excessively drained fine sands of the Zimmerman series (USDA NRCS). This area is the traditional homeland of the Dakota people and was later co-inhabited by the Ojibwe people. Indigenous fire management, droughty soils, and large herbivore grazing maintained oak savanna as the predominant upland vegetation. Europeans settled in the area in the 1870s, converting oak savannas to agricultural fields and introducing livestock grazing. In 1965, the U.S. Fish and Wildlife Service (USFWS) purchased over 300 individual landholdings to form the 12,400-hectare refuge. USFWS managers began restoring degraded savanna remnants around 1980 using prescribed burns, and later tree thinning and conservation grazing.

We selected two ~2-hectare areas of ongoing oak savanna restoration to implement targeted grazing. We chose these sites because of their high level of shrub encroachment, proximity to water sources, and overall accessibility. Spring dormant-season burns had been conducted in these sites since 1980 with a mean fire return interval of 4.7 years. The most recent burns were in 2014 in the north site and 2016 in the south site. Trees were thinned from the north site in 2008 and the south site in 2016, removing 50% of the standing basal area while leaving *Quercus macrocarpa* (bur oak) in place. Low-intensity cattle grazing occurred in 2015 and 2019 with an average stocking density of ~0.5 animal units (AU) per hectare for two to four weeks per summer. During this time, cattle spent the majority of their grazing time in the adjacent prairie, using the present study's woody sites mostly for shade and water access. For controls, we used two areas immediately adjacent to, and with an identical restoration history as, our targeted grazing areas.

Past restoration management has resulted in a tall, dense midstory with shrub cover exceeding 85% in many areas. The dominant shrub species is *Corylus americana* (American hazelnut), with smaller components of *Rubus* species (brambles), *Zanthoxylum americanum* (prickly ash), and *Prunus serotina* (black cherry). The most common herbaceous species are *Amphicarpaea bracteata* (American hog peanut), *Parthenocissus quinquefolia* (Virginia creeper), *Carex pensylvanica* (Pennsylvania sedge), *Fragaria virginiana* (wild strawberry), and *Solidago* species (goldenrods). The main overstory species is bur oak, followed by *Q. rubra* (northern red oak) and *Q. ellipsoidalis* (northern pin oak). Prior to the start of the present study, our control areas had an estimated average shrub cover of 41%, herbaceous cover of 43%, and canopy cover of 30%. The areas that would become our targeted grazing paddocks had an estimated average shrub cover of 55%, herbaceous cover of 51%, and canopy cover of 50% (Yantes et al., 2023).

2.2.2 Grazing Design

A custom grazing company, GrazeTEK, helped develop our grazing plan. Our strategy was to use high-density, short-duration grazing to target the shrub layer. We divided the two study sites into nine paddocks (five in the north site and four in the south) that averaged 0.3-ha in size (Figure 2-1). SNWR managers used a forestry mower to create cutlines through the brush for temporary electric fencing, which consisted of a single strand of polywire with a solar powered energizer. We provided the cattle with mineral feeders, salt blocks, and water as needed.

A complete summary of our targeted grazing management can be seen in Table 2-1. In 2020, we worked with a local cattle owner and a herd of 100 yearling stocker cattle. Both the cattle and the herd were smaller in size than we had initially planned for, so we grazed the research paddocks twice that year to help achieve our desired level of impact on the shrubs. In 2021, we were able to assemble a larger herd of 385 cow-calf pairs from cattle owners in North Dakota. Since our 2021 stocking density (kg/ha) was triple that of 2020, we grazed the research paddocks only once. We typically brought the cattle into the paddocks midday so they could use shade provided by the overstory trees. The cattle were only kept in the shrub-dominated paddocks for a few hours, spending the rest of their time grazing in an adjacent grass-dominated area to meet their nutritional needs and ensure adequate forage intake. Through careful management and strategically timed cattle moves, we were able to balance vegetation management goals with livestock performance.

Table 2-1. *Details of targeted cattle grazing management at Sherburne National Wildlife Refuge.*

	May 2020	**August 2020**	**July 2021**
Dates	05/22-05/27/20	08/03-08/07/20	07/08-07/16/20
Livestock class	Angus yearling stockers	Angus yearling stockers	Angus & Angus cross cow-calf pairs
Herd size	100	100	385
Avg. Stocking Density *(kg/ha)*	71,800	77,500	239,900
Avg. Duration *(hrs/paddock)*	6.3	5.9	4.6

2.2.3 Vegetation Surveys

We monitored vegetation changes using a combination of plot- and transect-based surveys. We established 18 plots inside the grazing area (two per paddock) and 18 plots outside to serve as a reference (Figure 2-1). We collected baseline vegetation data in August of 2019 prior to the start of this study; subsequent surveys occurred in July of 2020, July of 2021 (prior to targeted grazing), and August of 2022. Thus, the herbaceous layer had 2.5 months to recover from grazing before the 2020 survey, and one year to recover before the 2021 and 2022 surveys. We were not interested in herbaceous data from immediately post-grazing because large areas of the ground were bare. We used a 1m x 0.5m quadrat to record all herbaceous species and their estimated cover classes (1= 1%, 2= 2-5%, 3= 6-25%, 4= 26-50%, 5= 51-75%, and 6= 76-100%), noting the percent cover of shrubs in the quadrat using the same scale. At the same survey plot markers, we used a 1-meter fixed radius plot to record shrub species, number of stems, and height class (1= <0.5m, 2= 0.5-1.5m, 3= >1.5m), as well as sapling species and count.

Since the primary target of our grazing management was shrub control, we implemented an additional, more intensive shrub survey within the paddocks. We sampled immediately before and immediately after grazing in August of 2020 and July of 2021, and in August of 2022 after one year of no grazing. We used a line-point intercept method and extended a 50-meter survey tape across the width of the paddock with a north-south orientation. Beginning at 0m, we dropped a pin (thin PVC pipe) to the

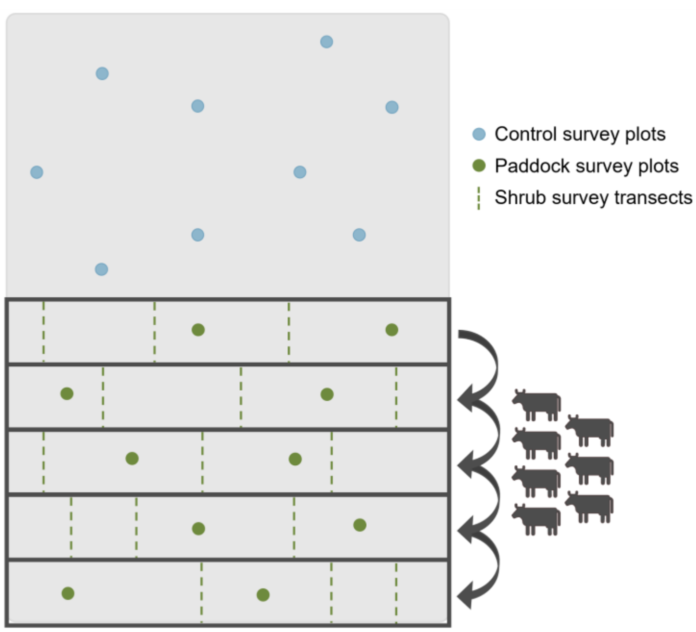

Figure 2-1. *Simplified vegetation survey design at Sherburne National Wildlife Refuge, MN, USA. The figure shows one of two sites. There were 18 control plots split evenly between the two sites. Cattle were rotated through a series of small grazing paddocks (outlined in dark gray). In each paddock, there were two vegetation survey plots and three shrub survey transects.*

ground every 5m. Holding the pipe vertically, we recorded every shrub stem touching the pipe. For each individual stem, we recorded species and height class (1= 0-0.5m, 2= 0.5-1m, 3= 1-1.5m, 4= 1.5-2m), and noted the type and severity of cattle impact. We repeated this process at three transects per paddock, for a total of 27 transects. We measured shrub density as the number of shrub stems per transect, and percent shrub cover as the number of shrub hits divided by the total number of points along the transect.

2.2.4 Statistical Analyses

Prior to statistical analyses, we categorized all woody and herbaceous species as native or non-native. We conducted our vegetation analyses in R version 4.2.0 (R Core Team, 2022), checking assumptions of normality and homoscedasticity using the *simulateResiduals* function in the *DHARMa* package (Hartig, 2022). We used the plot-based data to assess changes in vegetation metrics among treatments and over time. For herbaceous cover, species density, and diversity, and shrub height and stem density, we used linear mixed-effects models (LMM) via the *lmer* function in the *lme4* package (Bates et al., 2015). Treatment, time point, and their interaction were fixed effects, and plot nested within survey site was a random effect to account for repeated measures. For non-native cover, sapling density, and young oak density, we used generalized linear mixed models (GLMM) in the *glmmTMB* package (Brooks et al., 2017). We specified the same fixed and random effects, a tweedie distribution for non-native cover, and a negative binomial distribution with a log link for sapling and young oak density. Due to the ordinal nature of the shrub cover class data, we used a cumulative link mixed model (CLMM) via the *clmm* function in the *ordinal* package (Christensen, 2019).

We used the transect-based shrub assessments to evaluate pre- to post-grazing changes in shrubs within the paddocks over time and in response to grazing management characteristics. We tested for differences in mean shrub density, cover, and height across the five survey time points (2020 pre and post, 2021 pre and post, 2022 follow-up) with LMMs using the *lme4* package. Time point was a fixed effect, and transect nested within paddock was a random effect to account for repeated measures. We also tested if stocking density or grazing duration predicted pre- to post-grazing change in shrub density, cover, or height. We specified LMMs with grazing density/duration as the fixed effect and transect nested within paddock as a random effect. For all vegetation analyses described above, we conducted pairwise comparisons with the Tukey adjustment using the *emmeans* package when models were significant at $\alpha = 0.05$ (Lenth, 2022).

We visualized differences in plant community composition between treatments and across years using non-metric multidimensional scaling (NMDS) via the *metaMDS* function in the *vegan* package (Oksanen et al., 2022). Prior to analysis, we removed species with only one occurrence, and we analyzed the shrub and herbaceous communities separately. We calculated Bray-Curtis distances on species abundances (stem density for shrubs and percent cover for herbs) and specified two dimensions. To test for statistical differences in community composition, we used permutational multivariate analysis of variance (PERMANOVA) via *adonis* in the *vegan* package with Bray-Curtis distances and 999 permutations (Oksanen et al., 2022). We also checked if the treatment groups had homogeneous dispersions using the *betadisper* function. When PERMANOVA results were significant at p=0.05, we carried out pairwise comparisons using the *pairwise.adonis* function from the *pairwiseAdonis* package (Martinez Arbizu, 2017). To identify specific species unique to or missing from the paddocks, we used indicator species analysis (ISA) via the *multipatt* function in the *indicspecies* package (De Caceres & Legendre, 2009). Species were considered indicators at p=0.05.

2.3 Results

2.3.1 Shrub Impacts

From our transect surveys, we were able to see clear impacts of targeted grazing on shrubs that reflected visual changes on the landscape (Figure 2-2). The cattle grazed, broke, or trampled 42% of shrub stems surveyed in 2020 and 88% of stems surveyed in 2021. Shrub density ($F_{4,64}$=9.4; p<0.001) and shrub cover ($F_{4,65}$=11.4; p<0.001) were lower post-grazing in 2021 than at any prior time point (Figure 2-3). Compared to the start of the study, shrub density was 44% lower and shrub cover was 24% lower after targeted grazing in 2021. However, at the end of the study in 2022 (after one year of no grazing), shrub density and cover were only 16% and 13% lower than at the start (Figure 2-3). Cattle stocking density

Figure 2-2. *Vegetation changes due to targeted cattle grazing at Sherburne NWR, MN, USA. (A) Research paddock at the start of targeted grazing in 2021, (B) Immediately after six hours of targeted grazing by 385 cow-calf pairs in 2021, (C) The same paddock in 2022 after one year of no grazing. The goal was to suppress the dense shrub thickets (primarily Corylus americana) that dominated the oak savanna restoration site and promote herbaceous species.*

was a significant predictor of pre- to post-grazing change in shrub density ($F_{1,47}$=9.2; p=0.004) and shrub cover ($F_{1,49}$=17.5; p<0.001), with higher stocking densities leading to a greater decrease. Grazing duration in hours did not influence pre- to post-grazing change in shrub density or cover. There was also no impact of targeted grazing on average shrub height. From our plot-based surveys, we saw no statistical differences in shrub cover, height, and stem density, or sapling density between the paddocks and the controls. The paddocks consistently had 0.5-1.5 fewer oak seedlings+saplings per plot than the controls (χ^2=3.9, df=1, p=0.048); however, there was no directional change in young oak density over time within the paddocks.

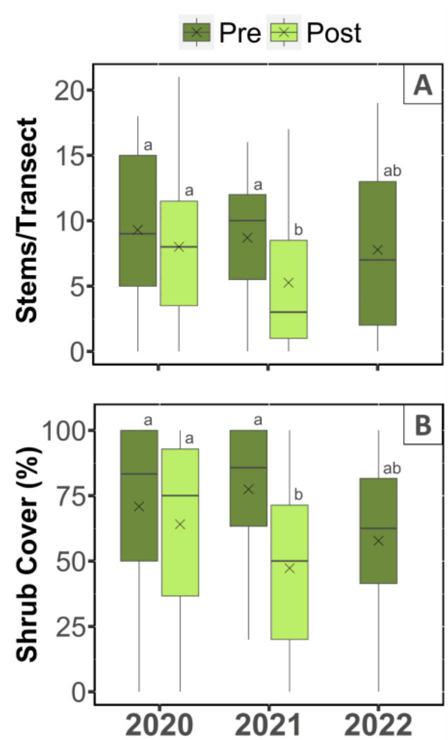

Figure 2-3. *Response of A) shrub density (stems/transect) and B) shrub cover (% of transect points touching shrubs) to targeted cattle grazing. Data were collected immediately pre- and post-grazing in 2020 and 2021, and in 2022 after one year of no grazing. Time points with the same lowercase letter showed no significant pairwise differences in means at α=0.05.*

2.3.2 Herbaceous Response

Herbaceous cover was similar between the paddocks and controls prior to the start of the study (Figure 2-4). In the years following the initiation of targeted grazing, herbaceous cover was significantly lower in the paddocks ($F_{1,38}$=6.09; p=0.018). Though our 2021 and 2022 herb data were collected after a full year of no grazing, herbaceous cover was still 15-23% lower in the paddocks than in the controls (Figure 2-4). However, within the paddocks, herbaceous cover was not statistically different between the start and end of the study (t_{103}=1.8; p=0.279). There was no difference in herbaceous diversity (Shannon index) between the paddocks and controls, nor did diversity change over time within the paddocks. Herbaceous species density (species per plot) also did not change significantly over time within the paddocks, though species density was significantly lower in the paddocks than in the controls in 2020 (t_{100}=2.17; p=0.033) (Figure 2-4). Non-native herbaceous cover did not vary between the paddocks and controls and was under 3% in both areas at the end of the study in 2022. We did, however, record three non-native species in 2022 that were not present in the paddocks in 2019: *Berteroa incana* (hoary alyssum), *Chenopodium album* (lamb's-quarters), and *Cichorium intybus* (chicory). There was only one documentation of each species, and all had less than 8% cover in their respective plots. Year-to-year changes in the herbaceous layer within the paddocks were a direct result of our grazing management, as there were no changes over time in any herbaceous metric in the control area.

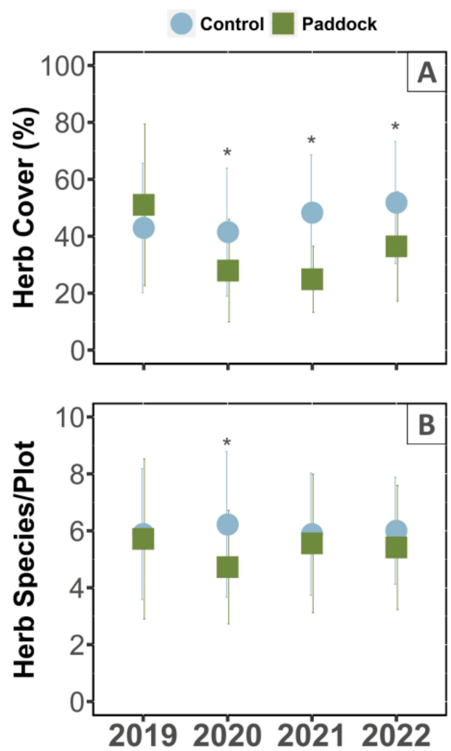

Figure 2-4. *Response of A) herbaceous vegetation cover (%) and B) herbaceous species density (species/plot) to targeted cattle grazing. 2019 baseline data were collected prior to the start of this study. 2020 data were collected 2.5 months after targeted grazing, while 2021 and 2022 data were collected one year after targeted grazing. Stars indicate significant differences in means between control and paddock plots within that year at α=0.05. Error bars represent 1 SD.*

PERMANOVA revealed a significant effect of targeted grazing on herbaceous species composition. Herb community composition was similar between the paddocks and controls in 2020, but it diverged in 2021 and 2022 (Figure 2-5). There were no differences in the dispersions of the control and treatment groups in any year, confirming that significant PERMANOVA results were driven by differences in the group centroids. Indicator species analysis showed that *Helianthus* species (sunflowers) and *Solidago* species (goldenrods) were consistent indicators of the control areas across years, with *Eurybia macrophylla* (large-leaved aster) and *Fragaria virginiana* (wild strawberry) showing up as significant in 2021 and 2022, respectively. There were no indicator species associated with the paddocks until 2022, when *Aquilegia canadensis* (red columbine) and *Conyza canadensis* (horseweed) became significant indicators. There were no differences in shrub species composition between the paddocks and controls in any year.

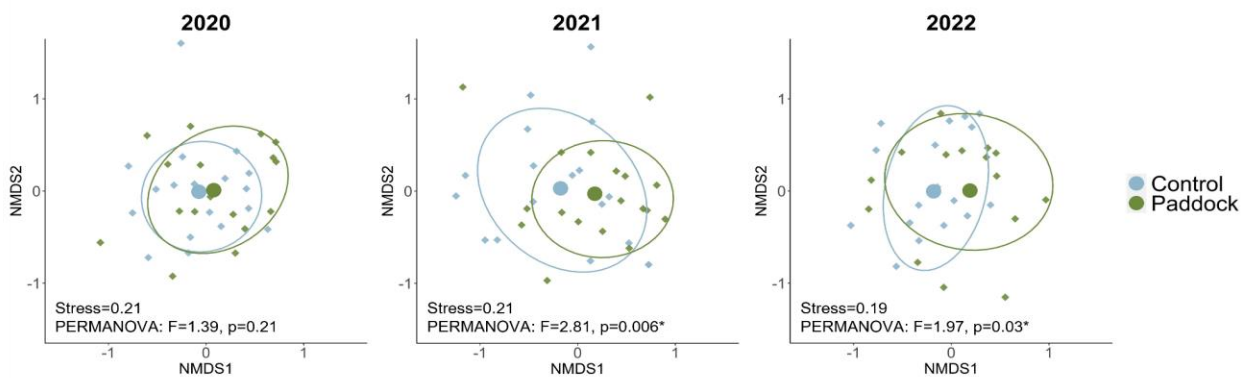

Figure 2-5. *NMDS ordination plots to visualize differences in herbaceous community composition between the control and paddock plots. Data were collected in 2020 (2.5 months after May grazing, before August grazing), 2021 (one year after 2020 grazing, before 2021 grazing), and 2022 (one year after 2021 grazing). Diamond-shaped points are individual survey plots; points in closer proximity have more similar vegetation. Round points are treatment centroids, and ellipses encompass data within 1 SD of the centroid. PERMANOVA revealed significant compositional differences between the paddocks and controls in 2021 and 2022.*

2.4 Discussion

Our goal was to evaluate the effectiveness of targeted cattle grazing as a tool to reduce shrub density and restore woody-encroached ecosystems. We implemented high-density, short-duration cattle grazing in an ongoing oak savanna restoration and tracked the response of vegetation metrics over three years. We found this type of cattle management substantially reduced shrub density, but the impacts were largely transient. Targeted shrub grazing lowered herbaceous cover and produced slight shifts in herb species composition but did not seem to affect herbaceous species density or diversity. There was no increase in non-native herbaceous cover, though we did document isolated occurrences of new non-native species. Overall, our study points to the potential of cattle grazing as a viable restoration tool for shrub control, though questions remain regarding its long-term effectiveness and potential non-target impacts.

We stress that ecological outcomes are not determined by whether or not a site was grazed, but rather, the specifics of how the grazing was implemented.

2.4.1 Targeted cattle grazing temporarily reduced shrub density and cover

Beef cattle are primarily grazers with grasses and forbs making up 70% and 20% of their diet, respectively (Moechnig, 2010). They will consume a small amount of browse (10% of diet) when given the option, but cattle are not typically used for shrub management (Moechnig, 2010; Marchetto et al., 2021). This study demonstrates the ability of Angus and cross-bred cattle to reduce shrub density and cover via targeted grazing under very high stocking densities. We observed the cattle browsing on shrubs, as well as breaking and tramping them. However, there are few long-term studies on targeted grazing, and a key unknown is whether changes in vegetation represent temporary defoliation or actual plant mortality (Marchetto et al., 2021). We resurveyed our paddocks after one year of no grazing and documented substantial shrub resprout, indicating that our shrub impacts may be short-lived. Many shrub species, including *C. americana*, readily resprout after their aboveground parts are damaged or killed, and in some cases, resprouting after top-killing leads to the regrowth of more biomass than was lost(Briggs et al., 2005; Pelc et al., 2011; Peterson & Reich, 2001). Therefore, shrub-dominated systems such as our own are highly resilient to management tools like fire and grazing (Briggs et al., 2005; Silva et al., 2001), making woody encroachment difficult to reverse (Ratajczak et al., 2014).

We may be able to improve long-term shrub reduction by tailoring certain aspects of the grazing design such as season, frequency, and stocking density. For example, a study in Minnesota found that clipping (a proxy for browsing) *C. americana* in late July resulted in much lower and slower resprout than clipping in May or June (Pelc et al., 2011). This suggests that targeted shrub grazing is most effective later in the growing season when more carbohydrates are lost with top-kill, leaving fewer reserves for resprouting (Drewa et al., 2002). However, managers must also consider that plant palatability and digestibility decrease over the growing season, which may affect cattle's willingness to browse (Ammar et al., 2004; Bailey et al., 2019). Besides adjusting the grazing season, implementing multiple targeted grazing events may better suppress shrubs. Previous studies have found no significant decreases in stem density until the second year of grazing management (Harrington & Kathol, 2009; Rathfon et al., 2021). If resprouting stems are repeatedly removed before carbohydrate stores are replenished, the reserves available for resprout could be further reduced by each successive round of grazing (Pelc et al., 2011). Frequent, repeated disturbances historically maintained oak savannas, so it follows that targeted grazing should be viewed as part of an ongoing management plan rather than a "one and done" solution.

A final consideration for maximizing the success of targeted grazing is stocking density (Bailey et al., 2019). We identified that change in shrub density/cover was tied to stocking density but not grazing duration. This result is consistent with the findings of a global meta-analysis on manipulated herbivory in woodlands (Bernes et al., 2018), though we note our grazing duration was measured on the scale of hours. To reduce shrubs with Angus cattle in 4-6 hours, we needed an ultra-high stocking density of over 200,000 kg/ha; we were not successful with a stocking density under 100,000 kg/ha. Another study in Midwestern oak savannas achieved a similar level of shrub reduction using managed grazing at lower stocking densities (900-1,500 kg/ha) for a longer duration (2 days), repeated seven times (Harrington & Kathol, 2008). However, they used Scottish Highland cattle, a breed recognized for being hardy browsers (Hedtke et al., 2009). We suggest that generating equivalent impact with a breed that is less inclined to browse requires small paddocks and high stocking densities to encourage the consumption of less palatable/non-preferred woody vegetation (Bailey et al., 2019; Petersen et al., 2014). Again, we stress that high stocking densities must be coupled with short grazing durations and long recovery periods so as to avoid the negative ecological effects associated with overutilization (Eldridge et al., 2016; Fleishner, 1994; Teague & Kreuter, 2020).

2.4.2 Targeted grazing affected herbaceous cover and composition

There were no differences in herbaceous species density between the paddocks and the control except for in 2020. Sampling in 2020 occurred only 2.5 months after targeted grazing, whereas sampling in 2021 and 2022 took place after a full year of rest. This result indicates that short-term decreases in the number of herbaceous species will dissipate as long as grazing managers incorporate adequate recovery periods. Unlike species density, herbaceous cover did not rebound between 2020 and 2021 and instead was on a downward trajectory. This may be because there was an extreme drought during the growing season of 2021 (Riganti, 2021), which negatively impacts herbaceous regeneration by reducing primary productivity (Carroll et al., 2021; Ciais et al., 2005). Moreover, high-intensity grazing and drought can interact to reduce herbaceous cover, slow recovery, and potentially shift community composition (Loeser et al., 2007; von Keyserlingk et al., 2021). In order to mitigate the potential negative effects of targeted grazing and drought in 2021, we decided to implement a rest year in 2022. This type of flexible management that responds and adapts to ecosystem signals is a key tenet of well-managed grazing (Teague et al., 2013). After one year of no grazing, herbaceous cover had increased though not to pre-grazing baseline levels.

The composition of the herbaceous community in the paddocks diverged from that of the controls in 2021 and remained distinct even after the rest year. Looking at the indicator species analysis results can help us understand these changes in community composition. Sunflower and goldenrod species were the most consistent indicators of the control areas throughout the study. We suspect these sun-loving species were more abundant in the controls from the start due to the lower average canopy cover in the control areas (29%) than in the paddocks (50%). In all years, indicator species of the controls (*E. macrophylla*, *Helianthus sp., F. virginiana, Solidago sp.*) were also present in the paddocks. These results demonstrate that targeted grazing did not eliminate species, but rather, shifted community composition by changing the relative abundance of existing species. Previous studies suggest that grazing can also alter community composition by favoring short-lived, ruderal, and grazing-resistant species, though the response of a community to grazing depends on its evolutionary history of grazing and moisture levels (Milchunas et al., 1988; Oesterheld & Semmartin, 2011; Török et al., 2016). At our site, we saw a flush of *A. canadensis* and *C. canadensis* in 2022 in the paddocks but not in the controls, supporting the idea that targeted grazing may promote disturbance-tolerant natives that thrive in bare soil (Croskery & Lee, 1981; Weaver, 2001).

Over the three-year duration of our study, we saw no increase in non-native herbaceous cover in response to targeted grazing. However, we did record three new non-natives in the paddocks in 2022, two of which (*B. incana* and *C. intybus*) are listed as invasives in Minnesota (MISAC, 2020; MN DNR). *B. incana* and *C. album* were present at SNWR prior to this study and were likely in the seed bank or transported by the cattle into the paddocks from other areas of the Refuge. *C. intybus* may have been introduced from outside of SNWR. Though cattle grazing is often criticized for promoting non-native species (e.g., Chuong et al., 2016; Galleguillos et al., 2018), an increase in non-natives and weedy natives is a well-established response to disturbance that is not unique to grazing (Abella & Springer, 2015; Bartuszevige & Kennedy, 2009). Many studies have evaluated the extent to which restoration activities such as thinning and prescribed burning promote non-natives (Abella & Springer, 2015; Jang et al., 2021; Nelson et al., 2008; Willms et al., 2017), and commonly find that non-native species benefit more from applied disturbances than natives (Davis et al., 2000; Jauni et al., 2015; Pearson et al., 2018).

By nature, oak savanna restoration requires disturbances (e.g., thinning, burning, and grazing) that expose mineral soil and create open conditions with increased light and nutrient availability (Dey & Kabrick, 2015). These are exactly the conditions in which early-successional and non-native species thrive, and therefore an increase in such species is predictable in the early stages of restoration (Dey & Kabrick, 2015; Rossman et al., 2018). Treatment-induced increases in non-natives may dissipate over time as sites undergo natural ecological succession, and do not necessarily represent long-term compositional shifts (Jang et al., 2021). The complete exclusion or eradication of non-native species from restoration sites is unrealistic, especially as we attempt to restore small, remnant ecosystems within a highly altered landscape matrix. Instead, monitoring and controlling invasive species as they appear should be viewed as an obligatory component of ongoing oak savanna management (Dey et al., 2017).

2.4.3 Is targeted cattle grazing a practical option for shrub control?

Cattle maintained body condition and had adequate daily weight gain (Solberg, pers. comm.), indicating that alternating them between the shrubby paddocks and adjacent grass-dominated pasture provided adequate nutritional support. Our study thus demonstrates that livestock productivity and restoration goals can be achieved concurrently. We saw that short-duration targeted grazing was far more effective under higher stocking density, consistent with James et al. (2017). The greatest management potential comes from herds of >200 cattle, which poses a challenge in the Midwest where 73% of ranches have fewer than 100 cattle (Asem-Hiablie et al., 2016). Land managers with smaller herd sizes may be able to achieve some of the same vegetation outcomes by using smaller paddock sizes to increase stocking density. Cattle will congregate around water tanks, salt blocks, and mineral feeders, so these can be intentionally placed in areas of high shrub density to focus grazing without the use of fencing (Bailey et al., 2019). We also note that cattle will perform best in a target grazing application if they are from a herd adapted to a similar climate, forage, and management regime as the restoration site (Solberg, pers. comm.). A final consideration is that targeted grazing is an intensive management approach involving frequent cattle moves (potentially on the time scale of hours), and therefore requires an attentive and adaptable grazing manager.

During our study, implementing a rest year with no grazing resulted in a high degree of shrub resprout with only partial recovery of the herbaceous cover. Therefore, managers of woody-dominated sites may need to implement targeted grazing once or twice per year until shrubs are effectively suppressed before turning their attention to herbaceous layer. In some cases, direct seeding of desired native species may be required (Rathfon et al., 2021). If fine fuel loads were adequate, targeted grazing could potentially be used in the same year as a prescribed burn to limit post-fire shrub resprout. We also note the important influence of canopy cover: native understory plants, particularly grasses, tend to have higher cover under more open canopies (Jang et al., 2021; Leach & Givnish, 1999; Peterson et al., 2007). Canopy cover at our site is relatively high for an oak savanna (50%), so additional tree thinning may be necessary to maintain an herbaceous-dominated understory. However, opening the canopy often favors established woody species (Peterson et al., 2007), so uncertainties remain regarding how to use targeted grazing to shift the competitive balance in favor of grasses and forbs over shrubs (Bailey et al., 2019; Ratajczak et al., 2012).

Many argue that goats are better equipped to reduce shrubs than beef cattle, as they readily browse woody species while minimally impacting herbaceous cover and diversity (Rathfon et al., 2021; Walker et al., 1994). We suggest that goats and cattle could potentially be used in sequence, with targeted goat grazing to reduce dense shrub thickets initially, and short-duration, high-density cattle grazing to suppress woody resprout and maintain herbaceous dominance over time. As a long-term shrub management tool, cattle offer several practical benefits over goats. First, cattle have the potential to be profitable for all parties involved. The cattle owners pay the Refuge for grazing land, rather than the Refuge having to pay for a goat grazing service. In turn, the cattle owners benefit from a substantially lower price than they would pay on private land ($3/AUM compared to $20-25/AUM; IA State Extension, 2022), in addition to the profits from beef. Secondly, cattle are more available than goats in most regions of North America, and they are easier to manage and train; we were able to contain the cattle using a single strand of temporary electric fencing and step-in posts. Third, cattle are, and will continue to be, a dominant pressure on grasslands worldwide (Allred et al., 2011). As long as there is a demand for beef, there is value in finding ways to produce it in a sustainable and regenerative manner. Given the benefits related to economics, accessibility, and practicality, targeted cattle grazing may allow us to have our ecosystems and eat them too.

2.5 Conclusions

We found that targeted cattle grazing successfully reduced shrub density and cover over the short term, with seemingly transient impacts on the herbaceous layer. Our study demonstrates the potential for targeted cattle grazing to help restore the understory of woody-encroached grasslands, woodlands, and savannas. We suggest that targeted cattle grazing may be particularly useful where other restoration actions such as mechanical shrub removal or prescribed fire are not feasible or effective. Once aggressive shrubs are controlled and fine fuels have recovered, prescribed burning can be reintroduced to promote a diverse herbaceous understory (Burger et al., 2016; Peterson et al., 2007). More research is needed on how targeted grazing and fire can be used as complementary tools for the restoration and long-term maintenance of disturbance-dependent ecosystems.

Due to the site-specific, goal-oriented nature of targeted grazing, we cannot make definitive grazing design recommendations to achieve shrub reduction. Targeted grazing schemes should be designed within the context of the restoration site to maximize the control of unwanted species while minimizing non-target impacts. As such, targeted grazing requires a skilled and committed grazing manager with an understanding of the focus ecosystem, the biology/phenology of their target species, and animal husbandry. Like other management strategies, targeted grazing should be viewed as an adaptive process, where iterative application, monitoring, and evaluation refines and improves techniques.

2.6 References

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CHAPTER 3

Butterfly, Bird, and Bat Response to Varying Oak Savanna Restoration Approaches

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Chapter 3 Abstract

Wildlife species associated with disturbance-dependent ecosystems such as oak savannas are decreasing across North America. This trend is seen across multiple taxa and is primarily driven by habitat loss. Restoring oak savannas and their associated fauna requires the reintroduction or simulation of historic disturbances including fire, thinning, and grazing. Restoration success is most commonly measured by vegetation metrics, and therefore our knowledge of how animal communities respond to prescribed disturbances is relatively limited. We conducted a study to assess how efforts to restore oak savanna vegetation impact bird, butterfly, and bat communities. We surveyed areas with increasing levels of restoration intensity: 1) unmanaged, 2) thinning + burning, and 3) thinning + burning + cattle grazing. We found that oak savanna restoration actions increased canopy openness, shrub density and height, and herbaceous cover and diversity. These shifts in vegetation structure corresponded with increases in bird abundance and diversity, but there was little impact on butterfly abundance or the activity of most bat species. We also found that the effect of grazing was minimal compared to thinning and burning, suggesting that cattle grazing can be used to manage savanna vegetation at no detriment to wildlife. Wildlife outcomes were species-specific and context-dependent; therefore, we do not make generalizable management recommendations. However, we provide evidence that carefully managed thinning, burning, and grazing may improve avian habitat without negatively affecting butterfly and bat communities.

3.1 Introduction

Wildlife species associated with disturbance-dependent ecosystems such as savannas are decreasing across North America (Askins, 2001; King & Schlossberg, 2014). An estimated 70% of savanna-associated bird species are undergoing long-term declines, along with many grassland butterfly species (Bussan, 2022; Hunter et al., 2001; S. R. Swengel et al., 2011). The Karner blue butterfly is a case example of a savanna-specialist that was once widespread, but is now listed as federally endangered (Bried et al., 2014). This cross-taxa downward trend is driven primarily by habitat loss (Askins, 2001). In the midwestern USA, the extent of oak savannas has been reduced by ~99% due to agricultural conversion and disturbance suppression (Nuzzo, 1986). Historically, Indigenous fire and grazing by large herbivores such as bison maintained the characteristic open canopy and herbaceous understory of oak savannas (Anderson et al., 1999; Heikens & Robertson, 1994). Fire and grazing also created distinctive habitat features for wildlife including snags, scattered mature trees, and a mosaic of grassy and shrubby vegetation that shifts over space and time (Davis et al., 2000; Heikens & Robertson, 1994). This spatially and temporally heterogeneous habitat structure is utilized differently by different species, thereby promoting biological diversity (Leach & Givnish, 1999). Without fire and grazing disturbances, oak savannas transition into closed-canopy forests, losing their structural heterogeneity and associated wildlife benefits (Vander Yacht et al., 2016). Taken together, the biological uniqueness and geographic scarcity of oak savannas has made restoring these ecosystems an increasingly common management priority in the United States (Dey et al., 2017).

Restoring disturbance-dependent ecosystems and their associated fauna requires the reintroduction or simulation of historic disturbances (Askins, 2001). In oak savannas, this involves some combination of prescribed fire, tree thinning, and grazing by bison or cattle (e.g., Bassett et al., 2020; Harrington & Kathol, 2009). Management is typically focused on restoring the heterogeneous vegetation structure that defines oak savannas; however, these actions also have major implications for wildlife. Fire provides nesting and roosting opportunities for birds and bats by creating snags (Davis et al., 2000; Perry, 2012). Both fire and thinning impact habitat quality for butterflies by increasing the abundance and diversity of floral resources (Lettow et al., 2014). Fire, thinning, and grazing can all reduce below-canopy clutter, which improves foraging conditions for bats (Carr et al., 2020; Perry, 2012; Rainho et al., 2010). Grazing also benefits mineralizing butterflies through the generation of dung (Downes, 1973). In sum, applied disturbances modify habitat structure and composition, which in turn affects visibility, nesting and feeding resources, host plant presence, and more.

Despite the numerous impacts of restored disturbances on wildlife, the success of oak savanna restorations is most commonly measured by vegetation metrics, e.g., canopy cover, shrub density, and herbaceous diversity (e.g., Abella et al., 2004; Bassett et al., 2020; Peterson & Reich, 2001). The assumption is that increased structural heterogeneity and plant diversity is positively correlated with the diversity of faunal species. Restoring savanna disturbance processes should create vegetative patchiness and spatial gradients in environmental conditions and thus a rich suite of microhabitats for animals (Ishii et al., 2004; Leach & Givnish, 1999). This Field of Dreams approach - “if you build it, they will come” - is common in wildlife restoration projects (Fraser et al., 2015). The broader restoration literature also is dominated by vegetation-focused studies; 67% of restoration papers published between 1990-2014 focused on vegetation only, while just 33% incorporated animals (McAlpine et al., 2016). Therefore, our knowledge of how animal communities respond to oak savanna restoration, and prescribed disturbances in general, is relatively limited.

Of the studies that look at the effect of oak savanna restoration on wildlife, most focus on a single taxon, with birds being particularly common (e.g., Au et al., 2008; Brawn, 2006; Vander Yacht et al., 2016). Restoring savannas has been shown to increase overall bird diversity and disturbance-dependent bird species (Au et al., 2008; Vander Yacht et al., 2016). There are comparatively fewer studies on other taxa such as butterflies and bats, though some evidence exists that butterfly richness and bat occupancy may be higher in savannas than in closed-canopy woodlands (Grundel et al., 2020; Starbuck et al., 2015). Birds, butterflies, and bats can serve as good bioindicators (Jones et al., 2009; King & Schlossberg, 2014; Öckinger et al., 2006), and they provide essential ecosystem services including seed dispersal, insect control, nutrient transfer, and pollination (Gaston, 2022; Ramírez-Fráncel et al., 2022). Therefore, looking across multiple taxa gives us a holistic understanding of how ecosystems respond to restoration, not only structurally and compositionally, but also functionally.

The objective of this study was to assess how efforts to restore oak savanna vegetation impact wildlife communities. We used ongoing oak savanna restoration sites at a federal wildlife refuge in central Minnesota, USA where management has largely focused on restoring vegetation structure. We took a comprehensive approach, surveying bird, butterfly, and bat communities across sites that had received differing levels of restoration intensity: 1) unmanaged, 2) thinning + burning, and 3) thinning + burning + cattle grazing. We predicted that butterfly abundance/richness, bird abundance/richness, and bat activity would increase with increasing restoration intensity. We also expected species compositions to change with restoration level, specifically an increase in early-successional, generalist species.

3.2 Methods

3.2.1 Study Site

This study was conducted at Sherburne National Wildlife Refuge (SNWR) in Sherburne County, Minnesota, about 80 km northwest of Minneapolis/St. Paul. The 12,400-ha refuge is located on the Anoka

Sand Plain, a large, flat, sandy outwash. Prior to widespread European settlement in the mid-1800s, the predominant upland vegetation was oak savanna that was maintained by Indigenous fire management, droughty soils, and grazing by bison and elk. At the time of SNWR's establishment in 1965, the landscape was largely covered by cropped fields, with smaller areas of wetlands, mixed hardwood forests, and remnant oak savannas. Remnant savannas had transformed into closed-canopy woodlands due to the disruption of the historic fire and grazing regimes. Refuge managers with the U.S. Fish & Wildlife Service are now working to restore degraded savannas to early 1800s conditions using a combination of tree thinning, prescribed burning, and cattle grazing.

3.2.2 Study Design & Restoration History

For our study, we identified areas of ongoing oak savanna restoration at SNWR that had received three different levels of restoration: 1) unmanaged, 2) thin+burn, and 3) thin+burn+graze. We selected two 13-ha survey sites to represent each restoration level. Within the thin+burn+graze level, there were two 2-ha areas that had received high-density, targeted cattle grazing (Figure 3-1). We used these additional areas to represent a fourth restoration level for our butterfly surveys, i.e., thin+burn+high-graze. We did not distinguish between the low- and high-graze levels for our bird and bat surveys. This is because birds and bats operate at a larger spatial scale than butterflies; the high-graze sites were too small and too close in proximity to the low-graze sites to classify them as distinct bird or bat habitats. Thus, there were four restoration levels (eight survey sites) for butterflies and three levels (six survey sites) for birds and bats.

Prescribed burning has been ongoing at SNWR since the 1980s. Burns were conducted every ~5 years on average in the spring dormant season, with flame lengths of 0.5-3 meters. Thinning was done between 2008-2013 by removing 50% of the basal area of standing trees, leaving bur oaks (*Quercus macrocarpa*) in place. Low-density cattle grazing occurred in the summers of 2015 and 2019; the average stock density in these areas was approximately 0.5 animal units (AU) per hectare for 2-4 weeks per year. High-density cattle grazing was implemented in 2020 and 2021 to target a specific area of dense shrubs. Average stock density in these areas was high (average = 380 AU/ha) for a brief duration (average = 6 hours/year). Additional information on the restoration history of our study sites can be found in Yantes et al. (2023).

3.2.3 Habitat Assessment

Long-term vegetation monitoring plots were established across the four restoration levels as part of a larger research project at SNWR (Yantes et al., 2023). We randomly selected a subset of 15 plots per restoration level (60 plots total) to serve as the basis for the present study (Figure 3-1). At each plot we surveyed the canopy, shrub, and herbaceous layers. We determined canopy cover using a spherical densiometer. We used a 1-m fixed-radius plot to record each shrub species, the number of living stems, and the height class (1= 0-0.5m, 2= 0.5-1.5m, 3= >1.5m). We used a 1-m x 0.5-m quadrat to record all herbaceous species and their estimated cover classes, which were based on a modified Domin scale (1= 1%, 2= 2-5%, 3= 6-10%, 4= 11-25%, 5= 26-50%, 6= 51-75%, and 7= 76-100%). We calculated herbaceous diversity using the Shannon Diversity Index (H).

We conducted all vegetation and wildlife analyses in R version 4.2.0 (R Core Team, 2022), checking for normality and homoscedasticity of residuals using the *simulateResiduals* function in the *DHARMa* package (Hartig, 2022). For all analyses, we conducted pairwise comparisons with the Tukey adjustment using the *emmeans* package when models were significant at $\alpha = 0.1$, (Lenth, 2022). We assessed canopy cover with a linear mixed effect models (LMM) using the *lmer* function in the *lme4* package (Bates et al., 2015), specifying treatment as a fixed effect and survey site as a random effect. We also used LMMs to test differences in herbaceous cover, herbaceous diversity (Shannon index), shrub height, and shrub stem density across restoration levels. We constructed models with restoration level as a fixed effect and plot nested within site as a random effect to account for repeated measures. We included year as a random effect to account for interannual variation in vegetation metrics.

3.2.4 Butterflies

We used the 60 vegetation plots as the center points of our butterfly surveys, thus there were 60 butterfly survey plots (15 per restoration level) (Figure 3-1). We conducted surveys 3 to 4 times per summer (approximately once per month) on days that were sunny or partly cloudy, with temperatures >65°F and <90°F, wind speeds <10 mph, and no rain. We used point-count distance sampling, a method that is well suited to dense, shrub-dominated areas like those at SNWR (Henry et al., 2015). At each plot, we surveyed a 180° arc from a fixed, north-facing vantage point with the arc extending east-west. We recorded all diurnal Lepidoptera (butterflies and moths) observed within this arc for two minutes. The majority of our observations were butterflies, so we use the word 'butterfly' in place of 'lepidopteran' throughout this manuscript for ease of reading. We intended to use distance measurements to estimate population abundance; however, our sample size was ultimately too small for this calculation.

We evaluated our butterfly data using a series of LMMs and generalized linear mixed models (GLMM). For all butterfly models, we included visit number as a random effect to account for temporal variance in butterfly numbers, and plot nested within site to account for repeated measures. We tested the impact of restoration level on butterfly species richness (species per plot) and overall abundance (butterflies per plot) using a GLMM with restoration level as a fixed effect and a negative binomial distribution in the *glmmTMB* package (Brooks et al., 2017). We grouped the 2021 butterfly species record into three different habitat groups: generalist, forest, and grassland (MN DNR; Supplemental Table 3-1).

For each habitat group, we tested differences in abundance among restoration levels using the same model parameters as above. To determine if weather conditions influenced overall butterfly abundance, we used a GLMM with a negative binomial distribution, with temperature, cloud cover, and wind speed as fixed effects. Lastly, we assessed which vegetation metrics influenced overall butterfly abundance with a LMM; canopy cover, herbaceous cover, herbaceous diversity (H), shrub stem density, and shrub height were fixed effects.

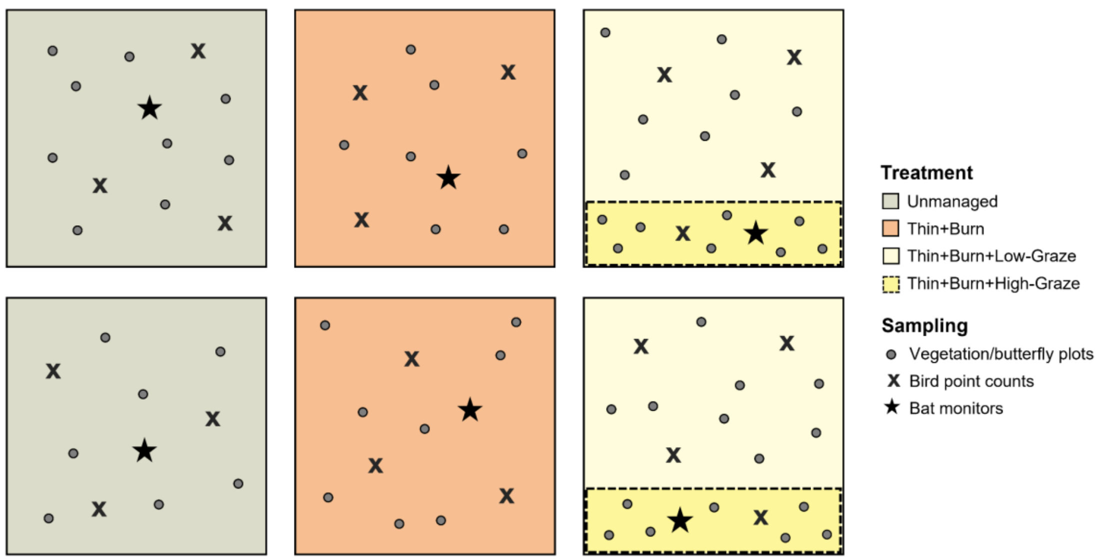

Figure 3-1. *Simplified study design at Sherburne NWR, MN, USA. There were two 13-ha survey areas per restoration level, and two 1.5-ha areas within the thin+burn+low-graze level that received high-intensity grazing. For birds and bats, we did not distinguish between low-graze and high-graze, but rather, combined them into a single 'thin+burn+graze' level.*

3.2.5 Birds

We conducted avian point-count surveys at six points in the unmanaged and thin+burn levels, and eight points in the thin+burn+graze level (two of which were located within the high-graze area, see Figure 3-1). Each survey point had a buffer of 100-meters and was placed using GIS to maximize their distance from one another within the survey area. The center of the point-counts did not align with the vegetation plots, thus we did not make direct plot-scale comparisons between the vegetation and bird communities. We censused each survey point three times over a three week period in June of 2020. Point-counts began 30 minutes before sunrise and finished no later than 10:00 am, following the protocol of Hutto et al. (1986) and Ralph et al. (1995). We arrived at the survey point and silently waited for two minutes before beginning a six-minute census. We recorded all songbird species encountered within a 100 meter radius, including flyovers, by either site or sound. For each individual, we recorded the AOU code and the initial distance where the bird was detected. Point-counts were not conducted in the rain, winds exceeding 18 mph, or if any electrical storm warnings were present.

We tested for differences among restoration levels in three community-level metrics: bird species richness, diversity, and total abundance, as well as in the abundances of frequently detected species (>30 observations, excluding flyovers). We used count as an index for abundance. We used LMMs for community-level metrics and GLMMs with a Poisson distribution for individual species abundances. We fit models with restoration level as a fixed effect and point number nested within survey location as a random effect to account for repeated measures at the same points. We tested for differences in mean bird response variables among restoration levels using a type II Wald chi-square test.

3.2.6 Bats

We used passive ultrasonic bat monitoring with a Song Meter SM4BAT FS Ultrasonic Recorder to survey bats in June-September of 2020 and 2021. We deployed two bat detectors simultaneously in two different restoration levels, so it took three rounds of monitoring to complete each combination of pairs. We then repeated the cycle in each restoration level's second survey site. We set up the bat detectors near the center of the survey site, in a clearing free from tall shrubs and overhanging branches to avoid noise from rustling vegetation. Detectors recorded data every night from 30 minutes before sunset until 30 minutes after sunrise. Our goal was to record data on ≥5 nights with a low temperature above 50°F, wind below 10 mph, and rain duration <30 minutes. We moved the bat detectors between survey sites every 6-10 days, depending on weather conditions. Prior to statistical analyses, we removed data from nights with low temperatures ≤45°F.

We processed the full spectrum acoustic data in Kaleidoscope v. 5.4.8 and Sonobat v. 4.4.5 using the settings in the North American Bat Monitoring Program (NABat) guidelines. To minimize misidentifications, we used the automated species identification from both software programs to reach a consensus identification, similar to the protocol in Moen et al. (2018). We used these consensus IDs to quantify calls per night of each bat species as a measure of activity. Total bat activity (calls/night) is a count of all sound files identified as a bat, including those without species consensus. We compared total activity and individual species activity among restoration levels using a GLMM with a negative binomial distribution. We built a model with activity as the dependent variable, restoration level as a fixed effect, and sampling period and site as random effects. Including sampling period as a random effect accounts for variability in bat activity due to weather or time of year, while site accounts for variability between the two different detector locations within the same restoration level.

3.3 Results

3.3.1 Habitat Assessment

Overall, the thin+burn and thin+burn+low-graze levels had the most savanna-like characteristics (i.e., lowest canopy cover, highest herbaceous cover and diversity; Curtis, 1959). While there were clear proportional differences in raw means (Table 3-1), the nested design limited our power to detect statistical differences in vegetation between restoration levels. Compared to the unmanaged levels, average canopy cover was 42% lower in the thin+burn level and 34% lower in the thin+burn+low-graze level ($F=1.24_{3,5}$, p=0.39). Average shrub stem density was lowest in the unmanaged level and 45-59% higher in all other restoration levels ($F=0.71_{3,4}$ p=0.59). Shrub height followed the same trend and was lower in the unmanaged level than in all other restoration levels ($F=2.90_{3,4}$ p=0.17). Both herbaceous cover ($F=5.56_{3,4}$, p=0.07) and herbaceous diversity ($F=3.69_{3,54}$, p=0.02) differed significantly across restoration levels, and were lowest in the thin+burn+high-graze level. Herbaceous cover in the thin+burn+high-graze level was 8-22% lower than in the other restoration levels (Table 3-1).

Table 3-1. *Habitat characteristics of the four restoration levels at Sherburne National Wildlife Refuge, MN, USA. Data represent 2020-2021 averages and are presented as raw mean ± SD. Canopy cover, shrub density, and herbaceous cover are rounded to the nearest whole number.*

	Unmanaged	**Thin+Burn**	**Thin+Burn+ Low-Graze**	**Thin+Burn+ High-Graze**
Canopy Cover (%)	66 ± 36	24 ± 24	32 ± 29	44 ± 32
Shrub Density (stems/m^2)	12 ± 6	22 ± 9	20 ± 8	19 ± 11
Shrub Height (m)	0.46 ± 0.29	0.72 ± 0.25	0.86 ± 0.24	0.68 ± 0.26
Herbaceous Cover (%)	27 ± 20	41 ± 21	37 ± 21	19 ± 17
Herbaceous Diversity (H)	1.13 ± 0.60	1.42 ± 0.42	1.44 ± 0.40	1.01 ± 0.62

3.3.2 Butterflies

Average butterfly abundance (butterflies/plot) was not significantly different among restoration levels, but was slightly lower in the thin+burn+low-graze level (Table 3-2). Cloud cover was a significant predictor of butterfly abundance (χ^2=3.2, df=1, p=0.07); we observed more butterflies when cloud cover was lower. Shrub density was also a significant predictor of butterfly abundance (χ^2=3.5, df=1, p=0.06), with more individuals at plots with fewer shrub stems (Figure 3-2). We note that butterfly abundance was significantly lower in 2021 than in 2020 (χ^2=22.5, df=1, p<0.001). We observed 337 total individuals in 2020 and only 108 in 2021.

We observed 26 of Lepidopteran species in our 2021 surveys (Supplemental Table 3-1). The most common species were *Danaus plexippus* (monarch), *Megisto cymela* (little wood satyr), *Poanes hobomok* (Hobomok skipper), and *Chlosyne nycteis* (silvery checkerspot) which together made up over half of the individuals observed. Average species richness per plot was 50-65% lower in the grazed restoration levels than in the unmanaged and thin+burn levels (χ^2=5.8, df=3, p=0.12). Our habitat-based analyses revealed no significant differences in the abundances of generalist, forest, or grassland species across restoration levels. Generalist and forest species abundance were highest in the unmanaged level and tended to decrease as restoration effort increased (Table 3-2). In contrast, grassland species abundance was lowest in the unmanaged level and highest in the thin+burn level (Table 3-2).

Table 3-2. *Average butterfly species richness, total abundance, and habitat group abundance per plot across restoration levels. Total abundance includes all individuals observed in 2020 and 2021, while habitat group abundances and species richness include only 2021 observations. Data are presented as raw mean ± SD.*

	Unmanaged	**Thin+Burn**	**Thin+Burn+ Low-Graze**	**Thin+Burn+ High-Graze**
Species Richness	0.6 ± 0.9	0.6 ± 0.8	0.3 ± 0.7	0.4 ± 0.6
Total Abundance	1.2 ± 1.7	1.2 ± 1.6	0.8 ± 1.4	1.1 ± 1.8
Generalist	0.2 ± 0.6	0.2 ± 0.5	0.0 ± 0.1	0.1 ± 0.4
Forest	0.4 ± 1.0	0.3 ± 0.8	0.2 ± 0.5	0.2 ± 0.4
Grassland	0.1 ± 0.3	0.3 ± 0.7	0.2 ± 0.6	0.2 ± 0.5

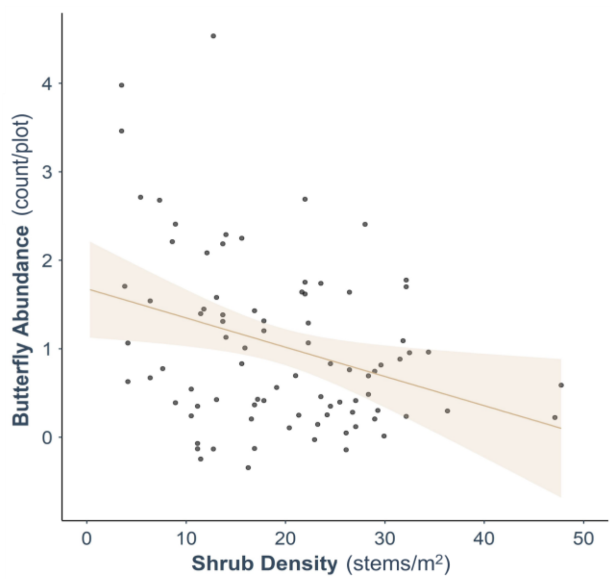

Figure 3-2. *Effect plot showing shrub density (average stems/m^2) versus predicted butterfly abundance (average number/plot). To account for other vegetation variables included in the model, all except shrub density are set to their mean value. The shaded area around the line represents a 95% confidence interval.*

3.3.3 Birds

We recorded 69 bird species including 11 savanna-associates and 17 species listed as Minnesota Species in Greatest Conservation Need (Supplemental Table 3-2). There were differences among restoration levels in total abundance (χ^2= 10.8, df= 2, p=0.005), species richness (χ^2= 13.9, df= 2, p<0.001), and diversity (χ^2= 8.5, df= 2, p=0.015) (Figure 3-3), all of which were significantly higher in the thin+burn and thin+burn+graze levels than in the unmanaged level. We also tested for differences among restoration levels in the abundances of 13 frequently-detected species (those recorded >30 times, excluding flyovers). We found six species to be significantly affected by restoration level: eastern towhee, field sparrow, golden-winged warbler, gray catbird, mourning dove, and yellow warbler (Table 3-3). All six of these species had higher abundances in the thin+burn level than in the unmanaged level. Moreover, 5 of 6 species (not the golden-winged warbler) had higher abundances in the thin+burn+graze level than in the unmanaged level.

Table 3-3. *Mean abundance ± SD of frequently detected bird species (>30 detections) at Sherburne NWR, MN, USA and GLMM outputs. Only species with significant differences among restoration levels are shown (all species shown in Supplemental Table 3-2). Restoration levels with the same superscript letter are not significantly different at α = 0.1. The + symbol denotes oak savanna associates in the Midwest USA (Oak Savannas 2022, USFS 2022) and ∗ denotes MN Species in Greatest Conservation Need (MNDNR 2015).*

	Unmanaged	**Thin+Burn**	**Thin+Burn+Graze**	***Treatment***
Eastern towhee + *Pipilo erythrophthalmus*	0.22 ± 0.43^a	1.83 ± 1.04^b	1.71 ± 1.12^b	*χ^2= 16.4, df= 2* *p<0.001*
Field sparrow +∗ *Spizella pusilla*	0.28 ± 0.67^a	0.89 ± 0.68^b	1.13 ± 0.80^b	*χ^2= 8.3, df= 2* *p=0.016*
Golden-winged warbler ∗ *Vermivora chrysoptera*	0.28 ± 0.46^a	1.22 ± 0.73^b	0.25 ± 0.44^a	*χ^2= 17.4, df= 2* *p<0.001*
Gray catbird *Dumetella carolinensis*	0.11 ± 0.32^a	1.28 ± 0.67^b	1.17 ± 0.96^b	*χ^2= 11.1, df= 2* *p=0.004*
Mourning dove *Zenaida macroura*	0.22 ± 0.43^a	0.89 ± 0.76^b	1.96 ± 1.08^c	*χ^2= 22.1, df= 2* *p<0.001*
Yellow warbler *Setophaga petechia*	0.28 ± 0.57^a	2.39 ± 1.24^b	1.88 ± 1.08^b	*χ^2= 20.3, df= 2* *p<0.001*

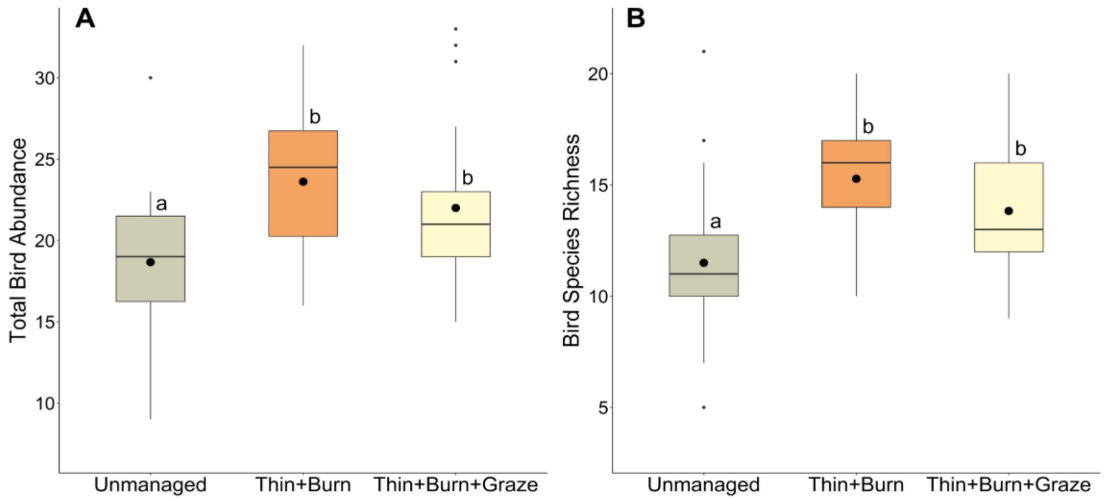

Figure 3-3. *Effect of different restoration levels at Sherburne NWR, MN, USA on A) total bird abundance and B) bird species richness (per point-count). Restoration levels with the same lowercase letters are not significantly different at α = 0.1.*

3.3.4 Bats

We analyzed bat activity from a total of 104 nights and 38,000 call files over the summers of 2020-2021. We reached species consensus identification on ~27,500 call files. We recorded seven of the eight species of bats in Minnesota: *Eptesicus fuscus* (big brown bat), *Lasionycteris noctivagan* (silver-haired bat), *Lasiurus cinereus* (hoary bat), *Lasiurus borealis* (eastern red bat), *Nycticeius humeralis* (evening bat), *Perimyotis subflavus* (tricolored bat), and *Myotis lucifugus* (little brown bat). There were significant differences in total bat activity (calls/night) between restoration levels (χ^2= 5.28, df= 2, p=0.07); average bat activity was 53-60% higher in the thin+burn+graze level than in the thin+burn and unmanaged levels (Supplemental Table 4). Big brown bat was the only species whose activity varied among levels (χ^2= 8.45, df= 2, p=0.01) and was significantly higher in the thin+burn+graze level (Figure 3-4). Little brown myotis activity was two to three times higher in the thin+burn+graze level than in the thin+burn and unmanaged levels, but this was not a statistically significant difference (Figure 3-4).

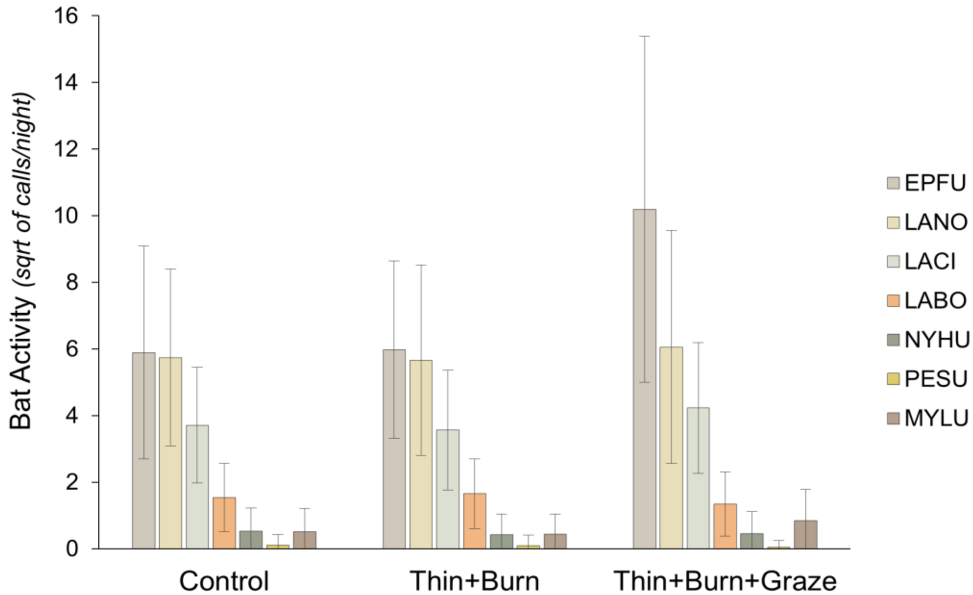

Figure 3-4. *Bat activity (calls/night) across restoration levels for seven species: Big brown bat (EPFU), Silver-haired bat (LANO), Hoary bat (LACI), Eastern red bat (LABO), Evening bat (NYHU), Tricolored bat (PESU), and Little brown myotis (MYLU). Data are square-root transformed in order to visualize all species on the same scale. Untransformed values can be found in Supplemental Table 3-3. Error bars represent 1 SD.*

3.4 Discussion

Our objective was to evaluate if using prescribed disturbances to restore oak savanna vegetation structure translates into changes in wildlife abundance and diversity. We conducted an observational study to determine how 40+ years of vegetation management including burning, thinning, and grazing have affected butterfly, bird, and bat communities. We found that restoration actions created more heterogeneity in vegetation structure; the thin+burn and thin+burn+graze levels had greater canopy openness, shrub density, shrub height, herbaceous cover, and herbaceous diversity than the unmanaged level. These shifts in vegetation corresponded with increases in total bird abundance, richness, and diversity, but had no influence on butterfly abundance or richness, or the activity of most bat species. We conclude that well-managed thinning, burning, and grazing can improve bird habitat quality while minimally impacting other taxa. Our study provides a unique, multi-taxa perspective on how wildlife communities respond to different oak savanna restoration approaches.

3.4.1 Butterflies

Our butterfly surveys included a fourth restoration level, a small area within the thin+burn+graze level that received high-density cattle grazing. Compared to the thin+burn and thin+burn+low-graze levels, the high-graze areas had lower canopy openness, shrub density, herbaceous cover, and herbaceous diversity. Despite the substantial differences in vegetation structure among restoration levels, there was no observed impact of these restoration efforts on butterfly abundance. This result is consistent with a global meta-analysis and a global review that found no effect or largely inconclusive effects of low-intensity fire, thinning+fire, and grazing on total butterfly abundance (Bussan, 2022; Mason et al., 2021). Response to disturbance is highly variable among butterfly species, depending on factors such as life history traits and whether their host plant is favored by the disturbance (Mason et al., 2021; Swengel, 1998; Swengel et al., 2011). Therefore, community-level disturbance responses may not be as apparent as species-level responses. For example, Bussan (2022) found that while the effect of grazing on butterfly communities was mixed, many individual species responded positively. Studies in Wisconsin's extensive oak savannas also conclude that the impact of fire and grazing is species-specific, and no single management approach favors all butterfly species (Swengel, 2001; Swengel & Swengel, 2007). Given that individual species vary greatly in their responses to management, butterfly communities as a whole may be too broad of a taxonomic group for studying the impacts of combined thinning, burning, and grazing (Mason et al., 2021).

Instead of affecting overall butterfly abundance, it is possible that the vegetation changes produced by oak savanna restoration at SNWR shifted the relative abundances of individual species. Grundel et al. (2020) found that canopy cover was a more important predictor of butterfly species composition than of total abundance along a grassland-forest gradient (Grundel et al., 2020). As restoration proceeds, butterfly communities may shift from late-successional to early-successional species while abundance or richness remains unchanged (Mason et al., 2021; Swengel, 1998). We found that thinning and burning weakly promoted grassland butterfly species, while forest and generalist species slightly decreased with increased restoration intensity. However, we also saw a decrease in species richness in response to both low and high-density cattle grazing. Low butterfly numbers in 2021 inhibited our ability to see significant differences between treatments in habitat group abundances and species richness. By August of 2021, central Minnesota was in an extreme drought which can lower butterfly populations though reduced nectar availability, early senescence of host plants, and increased egg mortality (Ehrlich et al., 1980; Klockmann & Fischer, 2017).

Previous research has identified canopy cover and forb cover as determinants of butterfly abundance in oak savannas (Grundel et al., 2020; Hess et al., 2014), whereas we found that shrub density was the only significant vegetative predictor. Consistent with other studies in the Midwest, we saw a strong negative impact of shrub cover on butterfly abundance, likely because shrub-dominated areas typically have fewer nectaring plants and lower forb cover (Hess et al., 2014; McCullough et al., 2019). A limitation of our study is that we did not measure floral abundance (i.e., forbs actively flowering at the time of our butterfly surveys), which would likely be a more important predictor of butterfly abundance than the structural vegetation metrics reported here. Ongoing management to create scattered shrub cover and promote floral resources, such as thinning and burning (Lettow et al., 2014) or livestock grazing (Bernes et al., 2018; Bussan, 2022; Wallis De Vries et al., 2007) may thereby achieve oak savanna vegetation goals while simultaneously increasing butterfly numbers.

3.4.2 Birds

Oak savanna restoration activities increased overall bird species richness, diversity, and abundance. All three metrics were significantly higher in the thin+burn and thin+burn+graze levels than in the unmanaged level. Our results align with the existing body of literature on how restoring oak savannas increases bird abundance, richness, and diversity by creating diverse microhabitats for nesting and foraging (Au et al., 2008; Davis et al., 2000; Mabry et al., 2010). Adding grazing to thinned and burned sites was neither beneficial nor detrimental. Livestock grazing primarily influences birds by altering vegetation type, cover, and structure (Powell et al., 2000), and our surveys showed no significant differences in vegetation characteristics between the thin+burn and thin+burn+low-graze levels. We expect that the continued use of high-density grazing to target the shrub layer may eventually influence the bird community, as the abundance of many bird species is related to shrub density (Reidy et al., 2014). However, our study did not robustly measure the response of birds to targeted grazing at a high stock density, so this remains a topic for future research.

We saw strong responses to restoration level from six bird species, though our point-count surveys were conducted over a single summer and did not account for detection probability. All six species are associated with disturbance-dependent habitats (i.e., scrub, open woodland) and were positively affected by thinning, burning, and grazing. The only species that did not respond positively to grazing was the golden-winged warbler, a species of high conservation concern throughout North America (Roth et al., 2019). This is an important result given that cattle grazing is currently considered a best practice for golden-winged warbler habitat management (GWW Working Group, 2013). The seven species not significantly affected by restoration level have a variety of habitat associations from scrub (common yellowthroat) to second-growth woodlands (American redstart, rose-breasted grosbeak) to forest edges (blue jay, eastern wood-pewee) (Supplemental Table 3-3). These results support a previous study that found restoring oak savannas can increase disturbance-dependent birds while retaining species of later successional habitat types (Vander Yacht et al., 2016). Veerys were a marked exception; we encountered this ground-nesting, mature-forest species exclusively in the unmanaged level. Our results therefore echo other studies that conclude that savanna restoration presents a potential trade-off for avian conservation (Brawn, 2006). However, given the precipitous declines in bird species associated with disturbance-dependent habitats, savanna restoration benefits a group of species with comparatively urgent conservation needs (Brawn, 2006).

3.4.3 Bats

Total bat activity was significantly higher in the thin+burn+graze level than in the other two levels, which is consistent with other studies in the eastern USA that report higher bat activity in thinned oak-hickory forests compared to undisturbed forests (Dodd et al., 2012; Titchenell et al., 2011). However, in our study, this result was driven by exceptionally high big brown bat activity at a single detector location within the thin+burn+graze level. The detector consistently recorded over 100 big brown bat calls/night, and as many as 600 calls/night. This may be due to the proximity of the detector to a wide pool of the St. Francis River, as big brown bats prefer to forage along forest edges over open water (WI DNR). The nights with the highest calls all occurred in mid-June around the time females aggregate into maternity colonies (WI DNR); thus, it is also possible that this detector was unintentionally placed near a big brown bat maternity colony.

The relative activity of different bat species was consistent across all restoration levels, with big brown bat and silver-haired bat being the most active, and tri-colored bat and little brown bat being the least active. The lack of effect of site-level management aligns with a Missouri study that found site occupancy of big brown bats, eastern red bats, and tri-colored bats was largely unrelated to local vegetation structure across a savanna-forest gradient (Starbuck et al., 2015). Instead, landscape-level characteristics such as the amount and distribution of forest, agriculture, and urban cover may be the most important factor driving bat activity (Starbuck et al., 2015). However, our results differ from previous work in Appalachia that found thinned and burned sites had much higher activity of big brown, silver-haired, and eastern red bats than the forest controls due to reduced midstory clutter and improved foraging conditions (Cox et al., 2016; Smith et al., 2020). This discrepancy may be explained by our unmanaged sites having a fairly open midstory with short shrubs and few saplings. Across all restoration levels, tri-colored bat and little brown bat had low activity, likely because these species have declined by 90% over the past 20 years due to white nose syndrome (Cheng et al., 2021).

We did not have any confirmed recordings of the federally-threatened northern long-eared bat (*Myotis septentrionalis*). Interestingly, we identified over one hundred call files as evening bat, recorded evenly across the detector locations. The northern edge of this species' range was once thought to be central Iowa, but recently, reproductive females have been captured in Wisconsin and near Minneapolis, MN (Kaarakka, 2018; Swingen et al., 2016). Moen et al. (2018) also reported two locations in Minnesota where acoustic files were recorded and consensus-identified as evening bats. It is possible our call files were misidentified since eastern red bat has a similar mid-frequency call; however, we used two software programs and conservative settings to reach consensus ID. Therefore, we believe our data contribute to a growing body of evidence that suggests the evening bat range may be shifting northward.

3.5 Conclusions

We documented that actions to restore oak savanna vegetation structure positively influence bird abundance and diversity, while minimally impacting butterfly and bat communities. We also found that the effects of cattle grazing were insignificant compared to thinning and burning, suggesting that cattle grazing may be a viable tool to manage savanna vegetation with little detriment to wildlife. Our study was limited to two years of observational data, and several environmental factors unrelated to restoration level likely influenced our results. Previous research highlights how butterflies, birds, and bats are all highly dependent on the composition and quality of the landscape matrix surrounding restoration sites (Mabry et al., 2010; Starbuck et. al, 2015; Summerville et al., 2005). Therefore, it is important to consider large-scale land cover and connectivity between resource areas (Brückmann et al., 2010; Schultz & Crone, 2005) when drawing conclusions about the effects of restoration on wildlife at the local level. Given that wildlife outcomes are context-dependent and often species-specific, it is difficult to make generalizable, prescriptive management recommendations (Bussan, 2022; Grundel & Pavlovic, 2007; Swengel, 1998, 2001). However, we provide evidence that well-managed thinning, burning, and grazing can all be used to improve avian habitat without negatively affecting butterfly and bat communities. Concerns regarding trade offs among individual species should be balanced with the knowledge that disturbance-dependent species are declining disproportionately across North America, making early-successional habitats such as oak savannas a priority for restoration.

3.6 References

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3.6 Supplementary Materials

Supplemental Table 3-1. *Summary of 108 observations of 26 Lepidoptera species observed in 2021 at Sherburne National Wildlife Refuge, MN, USA. Plant community associations were determined using expert knowledge at the MN DNR and US EPA.*

Common Name	Scientific Name	Observations	Habitat Type
Eight Spotted Forester Moth	*Alypia octomaculata*	1	General
Meadow Fritillary	*Boloria bellona*	1	Grassland
Clover Looper Moth	*Caenurgina crassiuscula*	2	Grassland
Common Wood Nymph	*Cercyonis pegala*	2	Forest
Harris's Checkerspot	*Chlosyne harrisii*	1	Grassland
Silvery Checkerspot	*Chlosyne nycteis*	11	Grassland
Orange Sulpher	*Colias eurytheme*	2	Grassland
Virginia Ctenucha Moth	*Ctenucha virginica*	1	Forest
Monarch butterfly	*Danaus plexippus*	16	General
Northern Pearly Eye	*Enodia anthedon*	3	Forest
Silver Spotted Skipper	*Epargyreus clarus*	1	Forest
White Admiral	*Limenitis arthemis*	5	Forest
Little Wood-Satyr	*Megisto cymela*	16	Forest
Eastern Tiger Swallowtail	*Papilio glaucus*	5	General
Black Swallowtail	*Papilio polyxenes*	3	General
Northern Crescent	*Phyciodes cocyta*	3	Grassland
Hobomok Skipper	*Poanes hobomok*	15	Forest
Yellow-spotted Renia Moth	*Renia flavipunctalis*	2	Forest
Banded Hairstreak	*Satyrium calanus*	5	Grassland
Striped Hairstreak	*Satyrium liparops*	1	Grassland
Eyed Brown	*Satyrodes eurydice*	3	Grassland
Aphrodite Fritillary	*Speyeria aphrodite*	2	Grassland
Great Spangled Fritillary	*Speyeria cybele*	4	Grassland
Red Admiral	*Vanessa atalanta*	1	General
Wavy-lined Fan-Foot Moth	*Zanclognatha jacchusalis*	1	Forest
Northern Broken Dash	*Wallengrenia egeremet*	1	Forest

Supplemental Table 3-2. *Summary of 1,302 detections of 69 bird species observed during 60 point-counts at 20 survey locations within Sherburne National Wildlife Refuge. The ∗ symbol indicates species that are listed as a Minnesota Species in Greatest Conservation Need (MNDNR 2015). Plant community associations were determined using Birds of the World (Cornell Lab of Ornithology; Accessed 8 Apr 2022).*

Species name	**Scientific name**	**Detections**	**Plant community**
Oak savanna associates			
Eastern towhee	*Pipilo erythrophthalmus*	78	Scrub
Field sparrow ∗	*Spizella pusilla*	48	Scrub
Eastern wood-pewee ∗	*Contopus virens*	45	Forests
Indigo bunting	*Passerina cyanea*	19	Open Woodlands
White-breasted nuthatch	*Sitta carolinensis*	15	Forests
Eastern kingbird	*Tyrannus tyrannus*	8	Grasslands
Northern flicker	*Colaptes auratus*	8	Open Woodlands
Chestnut-sided warbler	*Setophaga pensylvanica*	4	Open Woodlands
Mourning warbler	*Geothlypis philadelphia*	2	Forests
Wild turkey	*Meleagris gallopavo*	2	Open Woodlands
Red-headed woodpecker ∗	*Melanerpes erythrocephalus*	1	Open Woodlands
Not associated with oak savanna			
Yellow warbler	*Setophaga petechia*	93	Open Woodlands
Common yellowthroat	*Geothlypis trichas*	82	Scrub
Blue jay	*Cyanocitta cristata*	69	Forests
Mourning dove	*Zenaida macroura*	67	Open Woodlands
American redstart	*Setophaga ruticilla*	60	Forests
Red-winged blackbird	*Agelaius phoeniceus*	56	Marshes
Gray catbird	*Dumetella carolinensis*	53	Open Woodlands
Rose-breasted grosbeak ∗	*Pheucticus ludovicianus*	52	Forests
Golden-winged warbler ∗	*Vermivora chrysoptera*	33	Open Woodlands
American crow	*Corvus brachyrhynchos*	32	Open Woodlands
Veery ∗	*Catharus fuscescens*	32	Forests
Trumpeter swan ∗	*Cygnus buccinator*	30	Lakes and Ponds
Red-eyed vireo	*Vireo olivaceus*	27	Forests
Yellow-throated vireo	*Vireo flavifrons*	27	Open Woodlands
Sandhill crane	*Antigone canadensis*	26	Marshes
Cedar waxwing	*Bombycilla cedrorum*	23	Open Woodlands
Red-necked phalarope	*Phalaropus lobatus*	22	Oceans
Brown-headed cowbird	*Molothrus ater*	20	Grasslands
Great-crested flycatcher	*Myiarchus crinitus*	20	Open Woodlands
Wood thrush ∗	*Hylocichla mustelina*	20	Forests
Song sparrow	*Melospiza melodia*	18	Open Woodlands
Black-capped chickadee	*Poecile atricapillus*	17	Forests
House wren	*Troglodytes aedon*	17	Open Woodlands
Red-bellied woodpecker	*Melanerpes carolinus*	15	Forests
American goldfinch	*Spinus tristis*	14	Open Woodlands
Baltimore oriole	*Icterus galbula*	13	Open Woodlands

Scarlet tanager	*Piranga olivacea*	11	Forests
Swamp sparrow ∗	*Melospiza georgiana*	11	Marshes
Alder flycatcher	*Empidonax alnorum*	10	Scrub
Black-and-white warbler	*Mniotilta varia*	10	Forests
Ovenbird ∗	*Seiurus aurocapilla*	9	Forests
Black tern ∗	*Chlidonias niger*	8	Marshes
Common loon ∗	*Gavia immer*	8	Lakes and Ponds
Pileated woodpecker	*Dryocopus pileatus*	8	Forests
Downy woodpecker	*Dryobates pubescens*	7	Forests
Grasshopper sparrow ∗	*Ammodramus savannarum*	7	Grasslands
American robin	*Turdus migratorius*	5	Open Woodlands
Blue-gray gnatcatcher	*Polioptila caerulea*	3	Forests
Brown thrasher ∗	*Toxostoma rufum*	3	Scrub
Hairy woodpecker	*Dryobates villosus*	3	Forests
Bank swallow	*Riparia riparia*	2	Lakes and Ponds
Canada goose	*Branta canadensis*	2	Marshes
Common grackle	*Quiscalus quiscula*	2	Open Woodlands
Great blue heron	*Ardea herodias*	2	Marshes
Marsh wren ∗	*Cistothorus palustris*	2	Marshes
Northern cardinal	*Cardinalis cardinalis*	2	Open Woodlands
Warbling vireo	*Vireo gilvus*	2	Open Woodlands
Yellow-billed cuckoo	*Coccyzus americanus*	2	Open Woodlands
Yellow-bellied sapsucker	*Sphyrapicus varius*	2	Forests
Black-billed cuckoo ∗	*Coccyzus erythropthalmus*	1	Forests
Belted kingfisher	*Megaceryle alcyon*	1	Lakes and Ponds
Eastern bluebird	*Sialia sialis*	1	Grasslands
Eastern meadowlark ∗	*Sturnella magna*	1	Grasslands
Eastern phoebe	*Sayornis phoebe*	1	Open Woodlands
Mallard	*Anas platyrhynchos*	1	Lakes and Ponds
Pied-billed grebe	*Podilymbus podiceps*	1	Lakes and Ponds
Wilson's snipe	*Gallinago delicata*	1	Marshes

Supplemental Table 3-3. *Raw mean ± SD of bird diversity, richness, and total abundance, abundances of frequently detected species (>30 observations), and model outputs. The + symbol denotes oak savanna associates in the midwest USA (Oak Savannas 2022, U.S. Forest Service 2022) and ∗ denotes Minnesota Species in Greatest Conservation Need (MNDNR 2015). Restoration levels with the same superscript letter are not significantly different at α = 0.1.*

Bird Response Metric	**Unmanaged**	**Thin+Burn**	**Thin+Burn+ Graze**	χ^2	**df**	***P*-value**
Bird species diversity	2.25 ± 0.32[b]	2.59 ± 0.20[a]	2.50 ± 0.22[a]	8.46	2	0.015
Bird species richness	11.5 ± 3.7[b]	15.3 ± 2.7[a]	13.8 ± 2.7[a]	13.96	2	<0.001
Bird total abundance	18.7 ± 4.7[b]	23.6 ± 4.5[a]	22.0 ± 4.6[a]	10.79	2	0.005
American crow *Corvus brachyrhynchos*	0.6 ± 1.0	0.7 ± 0.8	0.4 ± 0.9	0.51	2	0.774
American redstart *Setophaga ruticilla*	0.6 ± 1.1	1.3 ± 1.6	1.1 ± 1.3	1.34	2	0.513
Blue jay *Cyanocitta cristata*	1.4 ± 1.3	0.8 ± 1.0	1.2 ± 1.5	1.32	2	0.516
Common yellowthroat *Geothlypis trichas*	1.1 ± 1.0	1.7 ± 0.9	1.3 ± 1.0	2.59	2	0.273
Eastern towhee + *Pipilo erythrophthalmus*	0.2 ± 0.4[b]	1.8 ± 1.0[a]	1.7 ± 1.1[a]	16.36	2	<0.001
Eastern wood-pewee +∗ *Contopus virens*	1.1 ± 0.6	0.5 ± 0.5	0.7 ± 0.7	3.68	2	0.159
Field sparrow +∗ *Spizella pusilla*	0.3 ± 0.7[b]	0.9 ± 0.7[a]	1.1 ± 0.8[a]	8.26	2	0.016
Golden-winged warbler ∗ *Vermivora chrysoptera*	0.3 ± 0.5[a]	1.2 ± 0.7[b]	0.3 ± 0.4[a]	17.40	2	<0.001
Gray catbird *Dumetella carolinensis*	0.1 ± 0.3[b]	1.3 ± 0.7[a]	1.2 ± 1.0[a]	11.12	2	0.004
Mourning dove *Zenaida macroura*	0.2 ± 0.4[c]	0.9 ± 0.8[b]	2.0 ± 1.1[a]	22.13	2	<0.001
Red-winged blackbird *Agelaius phoeniceus*	1.6 ± 1.9	0.6 ± 1.1	0.7 ± 1.0	0.05	2	0.976
Rose-breasted grosbeak ∗ *Pheucticus ludovicianus*	0.8 ± 1.1	0.9 ± 1.1	0.9 ± 0.8	0.24	2	0.886
Yellow warbler *Setophaga petechia*	0.3 ± 0.6[b]	2.4 ± 1.2[a]	1.9 ± 1.1[a]	20.33	2	<0.001

Supplemental Table 3-4. *Bat activity (calls/night) across restoration levels. Data are presented as raw mean ± SD. Total activity includes bat calls with no species consensus and is therefore not equal to the sum of individual species. Restoration levels with the same superscript letter are not significantly different at α = 0.05.*

	Unmanaged	**Thin+Burn**	**Thin+Burn+Graze**
Big brown bat *Eptesicus fuscus*	44.8 ± 50.4[a]	42.7 ± 32.8[a]	130.3 ± 131.8[b]
Silver-haired bat *Lasionycteris noctivagans*	39.9 ± 31.5	40.1 ± 35.6	48.7 ± 55.8
Hoary bat *Lasiurus cinereus*	16.7 ± 13.0	15.9 ± 13.8	21.6 ± 21.4
Eastern red bat *Lasiurus borealis*	3.4 ± 3.1	3.8 ± 3.4	2.7 ± 3.4
Evening bat *Nycticeius humeralis*	0.7 ± 1.2	0.6 ± 0.97	0.6 ± 1.2
Tricolored bat *Perimyotis subflavus*	0.1 ± 0.4	0.1 ± 0.4	0.0 ± 0.2
Little brown bat *Myotis lucifugus*	0.7 ± 1.2	0.5 ± 0.8	1.6 ± 2.2
Total activity	157.7 ± 95.3	144.9 ± 90.4	272.1 ± 179.4

Epilogue

This dissertation reveals how oak savanna communities respond to different types and combinations of prescribed disturbances. Chapter 1 characterized vegetation response to 40 years of management at Sherburne National Wildlife Refuge across a gradient of restoration intensity. I found that increased restoration effort corresponded with reduced canopy cover and increased savanna-associate species, but also stimulated a dense shrub midstory. These results highlighted the need for an alternative restoration tool to reduce woody vegetation. To that end, Chapter 2 evaluated the effectiveness of targeted cattle grazing for shrub control. Using a high-density, short-duration grazing scheme substantially reduced shrub density, though repeated management will be necessary to control resprouting. Having explored various strategies to restore vegetation structure and composition in the previous chapters, Chapter 3 assessed wildlife response to these restoration actions. The results showed that oak savanna vegetation management with disturbance can positively affect bird communities with minimal impacts on butterflies and bats.

An overarching theme from this work is that restoration outcomes are dictated by the specifics of how management actions are implemented. For instance, prescribed fire is a recommended strategy to suppress woody species and promote an herbaceous understory; however, I saw that spring burns every 5+ years resulted in a dense shrub midstory. Controlling shrubs would have required a shorter fire return interval (1-2 years) that potentially incorporated growing season burns. As a second example, cattle grazing has a notorious reputation for negative ecological impacts due to poor management and overutilization. My work contrasts with this narrative, demonstrating how adaptive and regenerative grazing approaches such as targeted grazing can be used to restore ecosystems. Moreover, I saw that low-intensity grazing did not change vegetation structure, while short-duration grazing under very high stocking densities reduced shrub dominance (at least temporarily). Overall, my results show that restoration success is not determined by if a management strategy was applied, but how it was applied. Or as a wise farmer once said, "It's the how, not the cow."

Even though continuous disturbance variables (e.g., frequency, intensity, duration) are what dictate ecological outcomes, restoration research often falls into the trap of comparing treatment binaries: burned vs. unburned or grazed vs. ungrazed. Such an approach is oversimplified to the point that the findings can't be interpreted in a meaningful way to inform land management decisions. This leads to the problem of n=1: a series of isolated restoration case studies that are nearly impossible to replicate or generalize. Thus, continuing to work within a binary framework stalls our advancement of restoration science and practices. Instead, we need to emphasize specific treatment details, clearly and explicitly record our methods, and ideally use standardized metrics to facilitate the comparison of restoration outcomes across sites.

Another key takeaway from this project is the value of incorporating ways of knowing outside of the scientific method. Science is not an unbiased source of truth, but rather, an attempt to explain observable phenomena. There are ecological patterns, processes, and histories that cannot be distilled into numbers and graphs. For example, applying disturbances for the purpose of restoration requires a deep knowledge of the focus ecosystem, considering both the current landscape context and the evolutionary history of the community with fire and grazing. Yet researchers like myself often have a relatively limited understanding of their study sites that reflects the three-year duration of their projects. It is therefore important to recognize the value of collaborating meaningfully and respectfully with people who have a long-term connection to the land and deep-rooted, place-based knowledge. In this way, restoration scientists have much to learn from Indigenous land stewardship and lifeways, and from the local ecological knowledge of farmers and other long-time land managers.

My dissertation contributes to decades of savanna research by a multitude of ecologists, all endeavoring to advance the science of restoration in one of the most imperiled ecosystems in the world. Yet these recent efforts comprise only a tiny fraction of the long history of savanna management in North America. Prior to Euro-American colonization and settlement, Indigenous peoples played a keystone role in savannas for over 10,000 years, shaping these ecosystems directly through fire, and indirectly through interactions with herbivores. Thus, contemporary restoration strategies such as tree thinning, prescribed burning, and targeted cattle grazing represent a reintroduction of humans as the primary disturbance agent that promotes savannas. Ultimately, maintaining oak savannas is an intentional choice that requires rebuilding a reciprocal relationship between people and the land, making restoration both an ecological and a cultural act. And so the interconnected story of savannas and people comes full circle.