12-2021

American Burying Beetle, Plant Richness, and Soil Property Responses to Collapse of *Juniperus virginiana* Woodlands with Fire

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Ludwig, Alison, "American Burying Beetle, Plant Richness, and Soil Property Responses to Collapse of *Juniperus virginiana* Woodlands with Fire" (2021). *Department of Agronomy and Horticulture: Dissertations, Theses, and Student Research*. 225.
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AMERICAN BURYING BEETLE, PLANT RICHNESS, AND SOIL PROPERTY RESPONSES TO COLLAPSE OF JUNIPERUS VIRGINIANA WOODLANDS WITH FIRE

by

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A THESIS

Presented to the Faculty of
The Graduate College at the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Master of Science

Major: Agronomy

Under the Supervision of Professors Dirac Twidwell and Craig R. Allen

Lincoln, Nebraska

December 2021

AMERICAN BURYING BEETLE, PLANT RICHNESS, AND SOIL PROPERTY RESPONSES TO COLLAPSE OF JUNIPERUS VIRGINIANA WOODLANDS WITH FIRE

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University of Nebraska, 2021

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Grasslands are declining in the Great Plains due to land use changes, woody plant encroachment, and loss of historic fire cycles. Prescribed burn associations have utilized prescribed fire to collapse invading woodlands and allow the restoration of grasslands. This fire is considered “extreme” because it is capable of changing the structure and function of an ecosystem. Our study site is the Loess Canyons Experimental Landscape, a long-term, ecoregion-scale experiment to apply prescribed fire across the region to restore grasslands. The Nebraska Natural Legacy Project established the Loess Canyons ecoregion as a Biologically-Unique Landscape in 2005 with the state’s wildlife action plan to stop habitat loss due to woody encroachment and prevent reductions in the federally-threatened American burying beetle. We use 13 years of beetle monitoring data and multi-spatial landcover data of perennial forbs/grasses, trees, croplands, and litter in a Bayesian N-mixture model to estimate the relative abundance of ABB at permanent trapping locations. We use the Bayesian latent indicator scale selection method to select the best-performing spatial scale for each landcover type in the model. We apply a space-for-time substitution design across the Loess Canyons to allow sampling across a time-since-fire gradient of 17 years. We sample herbaceous plant richness, basal percent cover, soil compaction, and infiltration rates in grasslands restored with fire, uninvaded grasslands, and unburned woodland. We apply an NMDS analysis to examine changes in functional groups over time among sites. The abundance and distribution of the ABB in the Loess Canyons is mapped with the four landcover types. This study is the first to document increases in the ABB due to management with fire. ABB are positively associated with perennial forbs/grasses, and negatively associated with trees at >10% cover and cropland at 0.5% cover. Herbaceous species richness and basal cover in grasslands restored with extreme fire are comparable to uninvaded grasslands. Soil compaction and infiltration rates are similar between restored grasslands and uninvaded grasslands. Extreme prescribed fire restores ABB habitat and herbaceous plant communities that were lost to woody encroachment. Soil properties are not adversely impacted by fire, a positive outcome for the soil-dwelling American burying beetle.

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DEDICATION

To the American burying beetle—a uniquely charismatic insect who has been with me since the start of this journey.

To the forbs, grasses, soils, and wildlife of the Loess Canyons—you have been a joy to study (and an occasional terror).

To the regenerative power of fire on the land in the right place at the right time.

To the stewards of the land who do their best to create a healthy and productive landscape for us and for the future.

ACKNOWLEDGEMENTS

I would like to thank my advisors, Dr. Dirac Twidwell and Dr. Craig R. Allen. Their varied and deep ecological knowledge helped me turn this project into a scientific work I am proud of. I want to thank my committee members, Dr. Rhae A. Drijber and Dr. Daniel R. Uden. They helped me immensely in working through problems and gave me encouragement and insight. I want to thank Dr. Nancy C. Shank who served on my committee but retired before I finished. Your direction into organizational behavior and public policy will prove to be invaluable.

I want to thank the members of the Twidwell Lab, the Allen Lab, and the NRT (INFEWS) program. I especially want to thank Victoria M. Donovan and Caleb P. Roberts for helping me get out of the mire of statistics. Thank you to Dillon T. Fogarty and Christine H. Bielski for their help in study design and site selection. Many thanks to Conor D. Barnes and Christopher T. Fill for their tireless aid in data collection in the field, despite the heat waves and hard soils.

Many thanks are owed to the researchers who have studied the American burying beetle before me and laid a strong foundation for this work. Thanks especially to those beetle researchers who have given me insight, encouragement, and advice, Dr. Jessica D. Jurzenski, Dr. Brett C. Ratcliffe, and Dr. W. Wyatt Hoback.

A huge thanks to the Nebraska Game and Parks Commission for providing over ten years of data on the American burying beetle. I want to give a special thanks to T. J. Walker of the NGPC who is responsible for the initiation of beetle monitoring in the

Loess Canyons and for this treasure trove of data. Many thanks go out to Andy Moore and Adam Kester of the NGPC, whose hard work has kept the beetle monitoring going. I want to thank Shaun Dunn, who has helped coordinate the sampling of this once-endangered, now-threatened beetle. Many thanks to the dozens of volunteers who have helped with the annual beetle trapping.

I would like to thank the ranchers and landowners of the Loess Canyons Rangeland Alliance (LCRA) for their tirelessness and ingenuity in returning fire to our grasslands. Special thanks to Scott Stout for his organizational and leadership skills. Many thanks to the ranchers who kindly allowed us to sample vegetation and soil on their lands and who made sure I didn’t get lost.

Lastly, I thank my family for being there for me during this multi-year journey. Rachel, Derek, and Danielle, for always being willing to talk, hang out virtually, and provide unconditional support. Mom and Dad, for loving me and supporting me in any way you could, from helping me move to Lincoln, Nebraska, (750 miles from home) to helping me finish field work despite the difficult conditions. I couldn’t have done it without you.

GRANT INFORMATION

This work was supported by the National Science Foundation (NSF) National Research Traineeship program, the Nebraska Game and Parks Commission (NGPC), and the University of Nebraska-Lincoln’s (UNL) Institute of Agriculture and Natural Resources. The Center for Grassland Studies at UNL provided partial support for this work through the competitive Arthur W. Sampson Fellowship.

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PREFACE

INTO THE WORLD OF THE AMERICAN BURYING BEETLE

When I first told my parents that I had accepted a research assistantship to study an endangered beetle in Nebraska, they asked with surprise, “Beetles? You don’t like bugs though. Won’t this make you the “bug person” in future jobs?”

I have to say, they were right to be surprised. I’ve never been overly fond of insects, with few exceptions. One insect I’ve never minded handling is the firefly, the magic of its glow overcoming my discomfort in feeling its six legs and two antennae poking and prodding my cupped hand. Going into the program, I was wary of the idea of handling shockingly large numbers of insects but heartened by the fact I could bring my previous experience to bear in my other chapters focusing on plants and soils. With that, I dove into the literature on the beetle.

What I found was a beautiful and fascinating insect, whose complex life cycle was both grisly and admirable. The more I read, the more excited I was to be working with this insect. I began sharing the nitty-gritty details of its life cycle and behavior to anyone who would listen: my family, peers, and even my dentist. The thought of being the “bug person” no longer bothered me.

As I learned about the beetle, I also learned about the land it lives on and the people who are its neighbors. The terrain is rough, though not as rough as some. It is hot and dry, though not as hot and dry as others. This place lies at the crossroads between north and south, east and west; sharing eastern species and western species, with climate neither southern nor northern. Torn between these identities, it forges a new identity from the shreds of the previous. This identity rubs off on the folks who live here, an idiosyncratic bunch who collect culture and norms piecemeal and aren’t afraid to be trailblazers. As it happens, the peculiar nature of the landscape and its people built a refuge for the American burying beetle, an endangered insect which has clung to the fringes of its historic range and remains threatened today.

If anything, the American burying beetle is a perfect mascot to display the resilience of the Loess Canyons and its social and ecological communities. Although found in less than 10% of its historic range, the beetle has been increasing in abundance in the Loess Canyons over the years. Similarly, the grasslands of the Loess Canyons have shifted to woodland as eastern redcedar trees continue to encroach. Despite this encroachment, landowners have fought to keep their grasslands by reintroducing fire onto the landscape. They have successfully reduced eastern redcedar abundance and halted the encroachment. Despite pressures to collapse and change to an alternative state, the grasslands and the American burying beetle have persisted here. Such a model of success is inspiring not only to those who have worked hard to conserve flora and fauna of the Loess Canyons, but to others in the Great Plains and elsewhere who wish to follow in their footsteps.

CHAPTER 1

WOODY ENCROACHMENT AND THE AMERICAN BURYING BEETLE: GAPS IN SCIENTIFIC KNOWLEDGE AND MANAGEMENT[1]

1.1 Introduction

The difficulty of obtaining long-term data for rare and endangered species can leave considerable gaps in knowledge about those species' role in an ecosystem and how a rapidly changing environment impacts them (Schaffer-Smith et al., 2016). These knowledge gaps add to the challenge of managing for rare species in regions undergoing rapid shifts, such as afforestation, land use changes, or climate change (Wilcove et al., 1998; Wilkening et al., 2019). Among these species is the American burying beetle (*Nicrophorus americanus*) (ABB), which was listed as federally endangered under the Endangered Species Act in 1989 (Federal Register 54:29652-55) and downgraded to threatened in 2020 (Federal Register 85:65241-61). It is considered a habitat generalist (Lomolino et al., 1995) and is only found on the periphery of its former range, which once stretched across the entire eastern U.S. and up into Canada (Leasure and Hoback,

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[1] Ludwig, A. K., and D. Twidwell. (2021). Woody encroachment and the American burying beetle: Gaps in scientific knowledge and management. Prepared manuscript for research journal submission.

AKL contributed to conceptualization, literature review and visualization, all writing aspects, and project administration. DT contributed to conceptualization and critical revisions.

2017; Sikes and Raithel, 2002). However, knowledge gaps have made it difficult to manage for the beetle since its listing in 1989 (Crawford and Hoagland, 2010).

The American burying beetle also appears to have different habitat preferences on the periphery of its range than in the historic core of its range. Many of the eastern states that hold historical records of the ABB were primarily deciduous forest, including Illinois, Michigan, and Tennessee (Anderson, 1982). However, its current range is in areas that are primarily grassland: Nebraska and Oklahoma in the Great Plains and Block Island (part of Rhode Island) on the northeastern coast (Leasure and Hoback, 2017). Many of these grasslands are undergoing rapid change to woodland and shrubland by encroaching woody species (Kinnebrew et al., 2020; Twidwell et al., 2013b), leaving the future of the ABB in doubt.

Given the inconsistencies in behavior and habitat use of many species, including the ABB, when found on the periphery of their range, the ongoing encroachment of woody plant species may pose a severe threat to the beetle. In the Great Plains region, *Juniperus virginiana* is the primary woody species encroaching into grasslands (Twidwell et al., 2013b). *J. virginiana* woodlands have a different understory and denser canopy than the deciduous-dominated forests that have been shown to support the ABB in other regions (Leasure, 2017). Although ABB were found in forested areas within the core of their range historically, there is no historical precedent that ABB on the periphery of their range can thrive in *Juniperus* woodlands instead of deciduous woodlands.

This chapter's objectives are to provide an overview of the American burying beetle and its conservation status, introduce the background of woody encroachment in the range of the ABB, present the scientific literature on woody plant encroachment and the American burying beetle, and identify four knowledge gaps and misconceptions in the science that impact conservation for the ABB. To help fill this gap, we discuss why woody encroachment has not been perceived as a serious threat to the ABB until now.

1.2 Overview of the American burying beetle and conservation status

The American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae) is exceptional in many ways. It is the largest carrion beetle in North America (Ratcliffe, 1996). It requires vertebrate carrion, a relatively rare "boom and bust" resource (Smith and Merrick, 2001), throughout its life cycle (Lomolino et al., 1995). A breeding male-female adult pair will work together to bury carrion that is ideally 100-300 grams in size (Lomolino and Creighton, 1996) and construct an underground brood chamber around it to raise their young (Ratcliffe, 1996). They display biparental care of their larvae, a rare trait in beetles (Lomolino et al., 1995). They play an important role in the ecosystem as decomposers and their activities enrich soil nutrients (Hoback et al., 2020).

Populations of the beetle have seriously decreased over the past decades. The ABB's historic range covered approximately the eastern half of the United States and some parts of Canada (Ratcliffe, 1996). By the 1980s, it had noticeably declined to cover less than 10% of its former range (Lomolino et al., 1995), leading to its listing as federally endangered in 1989 (Bedick et al., 1999). In 2020, the U.S. Fish and Wildlife Service (USFWS) downgraded the ABB from endangered to threatened (U.S. Fish and Wildlife Service, 2020). Although surveying has found new pockets of ABB in neighboring states and documented the increase of the beetle population in Oklahoma, the beetle is still only found in the periphery of its former range (U.S. Fish and Wildlife Service, 2019).

The cause for the ABB's decline is unclear, with multiple proposed causes being possible. Widespread use of pesticides such as DDT may have played a role in local extinctions, but they are probably not the primary cause of decline since other species of carrion beetles are still extant throughout the range (Sikes and Raithel, 2002). Light pollution is a proposed cause that has not been well studied, but recent research has found that ABB capture rates were negatively influenced by increased moonlight, suggesting that light pollution may play a role (Wormington et al., 2017). Extinctions and declines in some ideally-sized prey species such as the passenger pigeon (*Ectopistes migratorius*) and the bobwhite quail (*Colinus virginianus*) have led to a decreasing prey base to support the beetle (Sikes and Raithel, 2002). This in turn has led to increased competition from other species of carrion beetles as well as vertebrate scavengers, including raccoons, opossums, and coyotes (Sikes and Raithel, 2002). Since carrion beetles in general are susceptible to desiccation and larger-bodied beetles like the ABB are especially susceptible (Bedick et al., 2006), projected changes in climate (such as hotter and drier weather) may be unfavorable to the large-bodied ABB, now and into the future (Jurzenski et al., 2014). Lastly, the loss and fragmentation of habitat in its remaining range through widespread woody encroachment and conversion of natural land to agriculture have played a major role in the beetle's decline (Sikes and Raithel, 2002).

The beetle was initially thought to be a forest specialist (Anderson, 1982) but further research later determined it is a habitat generalist (Lomolino et al., 1995;

Ratcliffe, 1996). Given its generalist nature, it seems unintuitive that woody encroachment would have such a negative impact on the beetle, but research has confirmed that some woody plant species, such as the dense canopies of *Juniperus* forest, are harmful to the ABB (Walker and Hoback, 2007). Therefore, it is vital to understand the drivers of woody encroachment within the ABB's range and the impacts woody species may have on the beetle.

1.3 Background of woody encroachment in the range of the ABB

Across the ABB's range, the main driver behind woody encroachment is generally the loss or suppression of historic fire cycles, which allows the spread of woody species in grassland and savanna ecosystems (Twidwell et al., 2016b). The loss of grazing herbivores is also a factor in woody encroachment (Allred et al., 2012). Increased temperatures and change in weather patterns brought on by climate change are known to expand the range of many species beyond their historic limits (Twidwell et al., 2013b). Lastly, an often overlooked vector for the spread of woody species is human dispersal. Intentional plantings of woody species including eastern redcedar (*Juniperus virginiana*) in grasslands is aiding in the conversion of grasslands into woodlands (Briggs et al., 2002).

Within the Great Plains, the current range of the ABB can be split into the northern region (primarily Nebraska with some adjacent portions of South Dakota) and the southern region (primarily eastern Oklahoma with some adjacent portions of Kansas, Arkansas, and Texas) (Harms et al., 2020; U.S. Fish and Wildlife Service, 2019). In the northern region, the Sandhills and Loess Canyons of Nebraska host large populations of the beetle (Jurzenski et al., 2014; Walker and Hoback, 2007) and are relatively intact grasslands (Raynor et al., 2017). Recently, concern has spread over the encroachment of eastern redcedar in these areas (Donovan et al., 2018; Walker and Hoback, 2007).

In the southern region of the Great Plains, studies regarding woody encroachment date back to at least 1969 (Dalrymple, 1969), suggesting the persistence of a longstanding problem. Two species of *Juniperus* (*J. virginiana* and *J. ashei*) are encroaching in the grasslands of the southern Great Plains (Qiao et al., 2017; Twidwell et al., 2013a). In Texas, the ABB has not been recorded since 2008 (U.S. Fish and Wildlife Service, 2019), while the encroachment of woody species such as honey mesquite (*Prosopis glandulosa* var. glandulosa) is well-documented in the region (Martin and Asner, 2005).

In the northeastern United States, the eastern extent of its former range, the ABB remains on only a few islands in the Atlantic: an independently surviving population on Block Island (Raithel et al., 2006) and an introduced population on Nantucket Island (Mckenna-Foster et al., 2016). The coastal grasslands of this region have been undergoing encroachment from several native woody species, such as black huckleberry (*Gaylussacia baccata*) and common greenbrier (*Smilax rotundifolia*) (Kinnebrew et al., 2020). These woody species are a threat to the persistence of the region's coastal grasslands as well as several species of fauna and flora. Woody species may also pose a threat to the populations of ABB on Block Island and Nantucket Island (Kinnebrew et al., 2020), but that has not been studied as of yet.

Much research and modelling effort has focused on the habitat requirements of the ABB throughout its current range (Bedick et al., 1999; Crawford and Hoagland, 2010;

Creighton et al., 1993; Jenkins et al., 2018; Jurzenski et al., 2014; Leasure and Hoback, 2017; McPherron et al., 2012; Peyton, 2003; Schnell et al., 2014, 2008). In addition, there is a wide variety of research on woody encroachment in locations throughout their current range and its impacts on soil systems (Kinnebrew et al., 2020; Martin and Asner, 2005), hydrology (Qiao et al., 2017), and plant communities (Kinnebrew et al., 2020; Msanne et al., 2017), among many other topics. However, as our review of the literature illustrated, there is very little research that directly examines the impacts of woody encroachment on American burying beetle abundance (Walker and Hoback, 2007). These knowledge gaps make appropriate management for the ABB challenging.

1.4 Scientific literature on woody encroachment and the ABB

Only one publication explicitly explored the impacts of woody encroachment on the American burying beetle (Walker and Hoback, 2007) (Table 1.1). This study, centered on the Loess Canyons region of Nebraska, captured significantly more ABB in open grassland sites than in closed woodland sites dominated by eastern redcedar (*Juniperus virginiana*). They concluded that woody encroachment in the region has had a negative impact on the ABB.

Four other publications explored ABB habitat preferences that included areas of woodland or forest, without investigating the impacts of woody encroachment (Table 1.1). The first of these studied ABB movements between grassland and deciduous woodland habitats at two military bases in Oklahoma and Arkansas (Creighton and Schnell, 1998). They found that beetles were highly mobile between habitat types, but did not determine if the beetles had a preference between habitat types. The second of these

Table 1.1 Summary of scholarly articles relating to *Nicrophorus americanus* and woody encroachment.

Article Title	Author(s)	Journal	Date	Search Terms	Result
Effects of Invasive Eastern Redcedar on Capture Rates of *Nicrophorus americanus* and Other Silphidae	Walker, Hoback	*Environmental Entomology*	2007	"nicrophorus americanus" AND "encroachment"	Juniperus reduces the numbers of ABB*‡
Short-term movement patterns of the endangered American burying beetle, *Nicrophorus americanus*	Creighton, Schnell	*Biological Conservation*	1998	"nicrophorus americanus" AND "wood*"	ABB move between grassland and woodland†
Identifying priority conservation areas for the American burying beetle, *Nicrophorus americanus* (Coleoptera:Silphidae), a habitat generalist	Jurzenski, Jorgensen, Bishop, Grosse, Riens, Hoback	*Systematics and Biodiversity*	2014	"nicrophorus americanus" AND "wood*"	ABB negatively associated with woodland in model‡
Landsat to monitor an endangered beetle population and its habitat: Addressing annual life history and imperfect detection	Leasure	*Insect Conservation and Diversity*	2017	"nicrophorus americanus" AND "wood*"	Grassland and open-canopy woodland associated with ABB abundance†
Factors affecting overwinter survival of the American burying beetle, *Nicrophorus americanus* (Coleoptera:Silphidae)	Schnell, Hiott, Creighton, Smyth, Komendat	*Journal of Insect Conservation*	2008	"nicrophorus americanus" AND "wood*"	No difference in ABB overwintering survival in grassland or woodland†
Ecology and conservation of the endangered American burying beetle (*Nicrophorus americanus*)	Lomolino, Creighton, Schnell, Certain	*Conservation Biology*	1995	"nicrophorus americanus" AND "*forest*"	ABB is a habitat generalist, preferring neither grassland nor forest†
Habitat selection, breeding success and conservation of the endangered American burying beetle, *Nicrophorus americanus*	Lomolino, Creighton	*Conservation Biogeography*	1996	"nicrophorus americanus" AND "*forest*"	ABB prefer mature forest over clearcuts§

Effect of forest removal on the abundance of the endangered American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae)	Creighton, Bastarache, Lomolino, Belk	*Journal of Insect Conservation*	2009	"nicrophorus americanus" AND “*forest*”	Forest removal (i.e., disturbance) had negative impact on ABB abundance**§**
Distribution and habitat of endangered American burying beetle in northern and southern regions	Leasure, Hoback	*Journal of Insect Conservation*	2017	"nicrophorus americanus" AND “*forest*”	ABB associated with several habitat types including grassland, forest, wetland**†**
Distribution of the Endangered American Burying Beetle at the Northwestern Limit of its Range	Jenkins, Hoback, Leasure, Mulder, Davis	*Insect Systematics and Diversity*	2018	"nicrophorus americanus" AND “*forest*”	ABB positively associated with wet grassland; negatively with forest and open water**‡**

***ABB and woody encroachment**
†ABB uses areas of woodland and grassland
‡ABB negatively associated with forest
§ABB negatively impacted by forest removal/disturbance

studies created a habitat suitability model using selected landscape components and beetle surveys within the Sandhills region of Nebraska (Jurzenski et al., 2014). They found through their model that woodland areas have a negative relationship with the ABB. The third of these studies investigated habitat characteristics related to ABB abundance at a military base in Arkansas (Leasure, 2017). They found that ABB were positively associated with grassland and open-canopy deciduous woodlands, whereas they were negatively associated with closed-canopy bottomland forests (defined as >60% canopy cover). The final of these four studies explored overwintering survival rates of ABB at grassland and woodland sites within a military base in Arkansas (Schnell et al., 2008). They found no differences between grasslands and woodlands when determining ABB winter survival rates, but suggested that differences in habitats may affect other aspects of the beetle's life cycle.

Further exploration of the scientific literature found five publications that studied the habitat generalist nature of the ABB and impacts of disturbance through tree removal (Table 1.1). The first publication focused on the ABB in the far northern portion of the Sandhills, on a distinct population straddling the border of Nebraska and South Dakota (Jenkins et al., 2018). They found that ABB were positively associated with wet grasslands and open prairie, and negatively associated with forest, open water, and human development. The next two publications found that ABB are habitat generalists across their range, having no strong preference for one habitat type. The first of these studied beetle habitat preferences at two military bases in Oklahoma and Arkansas (Lomolino et al., 1995). It found that ABB had no strong preference between the grassland and mixed deciduous forest sites on the bases and concluded that the beetles are habitat generalists. The second article explored ABB habitat preferences between beetle populations centered in Nebraska and Oklahoma (Leasure and Hoback, 2017). They found that although there were some differences between geographical locations, ABB were positively associated with a range of habitat types including wetlands, grasslands, and forest, but negatively associated with urban development and croplands. This result suggests the ABB may avoid areas that are heavily disturbed by human activities.

The final two publications explored the impact of disturbance events on the ABB and found that disturbances, specifically tree removal, had negative impacts on the ABB. The first studied ABB habitat preferences across the eastern half of Oklahoma at local and regional scales and found that at local scales, ABB were positively associated with mature forest and negatively associated with clearcuts (Lomolino and Creighton, 1996). At the regional scale, they found that ABB were positively associated with areas combining forest, shrub cover, and deep soils. The second article studied the impacts of oak-pine forest removal on ABB in the Ouachita National Forest in Oklahoma (Creighton et al., 2009). They found that ABB declined significantly in areas that had undergone forest removal while remaining steady in areas that did not undergo forest removal. They concluded that habitat loss and fragmentation have negatively impacted the ABB across its range.

To summarize, we found one scholarly article that explicitly investigated the link between the ABB and woody encroachment in grasslands (Walker and Hoback, 2007). They found that woody encroachment is negatively associated with the ABB. Other articles found that beetles will move between habitat types (Creighton and Schnell, 1998), are habitat generalists (Leasure, 2017; Leasure and Hoback, 2017; Lomolino et al., 1995), and use both grassland and woodland to survive the winter (Schnell et al., 2008). Two explored the negative impacts of tree removal and forest clearcuts on the ABB in Oklahoma (Creighton et al., 2009; Lomolino and Creighton, 1996). Lastly, two articles concluded that ABB are negatively associated with forest and in some cases positively associated with grassland in areas of Nebraska and South Dakota (Jenkins et al., 2018; Jurzenski et al., 2014). Since we could only find one article directly exploring the relationship between the ABB and woody encroachment, we can conclude that there is a gap in scientific knowledge on the impacts of woody encroachment on the American burying beetle.

This review of the scientific literature was conducted in December 2020. Literature related to the impacts of woody encroachment on the American burying beetle was searched via the Web of Science. Topic searches included the Boolean search string (“Nicrophorus americanus” AND “encroachment”), and derivative strings associated with woody encroachment: (“Nicrophorus americanus” AND “invasive”), (“Nicrophorus americanus” AND “wood*”), and (“Nicrophorus americanus” AND “*forest*”). A total of 19 publications were gathered across all search strings. We first removed duplicate articles, then removed results that were deemed irrelevant. Irrelevant results included articles on invasive elytral clipping on the beetle, studies of other *Nicrophorus* species that did not include the ABB, and studies that did not make relevant habitat comparisons (e.g., grassland vs woodland). After this removal process, the literature was distilled down to ten publications. We reviewed these ten articles and noted their key results (Table 1.1). We then assigned each article to one of four topic categories: 1) Evidence that the ABB is negatively impacted by woody encroachment (one publication); 2) evidence of the ABB using both grasslands and woodlands without strong preference (five publications); 3) evidence that the ABB is negatively associated with forest (two publications); and 4) evidence that the ABB is negatively impacted by forest removal (e.g., clearcutting) (two publications).

1.5 Misconceptions and Knowledge Gaps

1) Early scientific views of the ABB hypothesized it was a forest specialist that required the deep, loose soils of primary forest to survive and that its decline in the eastern U.S. was due to widespread deforestation (Anderson, 1982; Creighton et al., 1993). By 1995 this hypothesis was rejected and it was determined that the ABB is a habitat generalist (Lomolino et al., 1995). Since the ABB uses forest habitat to some extent as a generalist, it can be difficult to determine which forests the beetle prefers and which it avoids. There are also regional differences in ABB's habitat preferences. In the northern Great Plains, ABB were found to prefer wetter grassland areas whereas in the southern Great Plains they preferred sandier soils, grasslands and hayfields, and native forests (Leasure and Hoback, 2017). The history of associating the ABB with forest in addition to the variations in habitat preferences across its range may contribute to assumptions that woody encroachment is not a threat to the beetle.

2) The threats that woody species pose to the flora and fauna of grasslands, and to the very existence of grasslands, is often ignored or not dealt with effectively. This has been shown by the persistent encroachment of ashe juniper in Texas for over 50 years (Dalrymple, 1969; Yang and Crews, 2020), the spread of eastern redcedar in much of the Great Plains (Miller et al., 2017), and the continued planting of eastern redcedar in prairies (Briggs et al., 2002). Not only is woody encroachment a threat to grasslands

(Twidwell et al., 2013b) but it is also a threat to the beetle (Walker and Hoback, 2007). The costs associated with managing woody encroachment in grasslands cascade and make it more difficult to successfully manage for the ABB in the Great Plains.

3) In a milestone work signaling the decline of American burying beetle, researchers proposed that a climax community of mature forest was the only habitat suitable for the ABB (Anderson, 1982). Later studies have echoed the idea that ABB prefers late-successional or climax communities (Creighton et al., 1993; Leasure et al., 2012). However, climax communities and linear ecological succession are older frameworks (Briske et al., 2003) that should not be applied to the ABB, its habitat preferences, or woody encroachment within its range. Modern ecological theory including alternative states, adaptive cycles, and multi-scale approaches along with adaptive management are required to understand the complex forces shaping the landscape and the ABB's interactions within it.

4) Studies of the ABB tend to focus on a small area of a local or regional landscape such as the Sandhills (Jenkins et al., 2018), Loess Canyons (McPherron et al., 2012; Walker and Hoback, 2007), military bases or national forests, (Crawford and Hoagland, 2010; Creighton et al., 1993), or an isolated island in the Atlantic (Mckenna-Foster et al., 2016; Raithel et al., 2006). These studies are necessary, but broader studies at the biome-level (e.g., Great Plains) may prove insightful as well. A study of the range wide impacts of woody encroachment on the ABB would help paint a clearer picture of the beetle as it is in its current habitat as well as the potential habitat that remains, and allow land managers to adjust accordingly.

1.6 Summary

Research investigating the impacts of woody encroachment on the ABB is sparse. Within the literature there is only one article exploring this question (Walker and Hoback, 2007). Other research on explored ABB habitat preferences including woodland or forest, without investigating the impacts of woody encroachment (Creighton and Schnell, 1998; Jurzenski et al., 2014; Leasure, 2017; Schnell et al., 2008). Three publications econcluded that the ABB is a habitat generalist (Jenkins et al., 2018; Leasure and Hoback, 2017; Lomolino et al., 1995). Two publications found that disturbances due to forest removal had negative impacts on the ABB (Creighton et al., 2009; Lomolino and Creighton, 1996).

The lack of scientific publications exploring the impacts of woody encroachment on the American burying beetle leaves four identifiable knowledge gaps and misconceptions in the science. This may be due in some part to persistent misunderstandings about the beetle's habitat preferences. The legacy of the ABB as a forest specialist has lingered despite conclusive evidence that it is a habitat generalist. Additionally, many species alter their behavior at the periphery of their ranges and will generalize or specialize as needed, for example bullsnakes (Kapfer et al., 2008), mountain lions (Gigliotti et al., 2019), and Canada lynx (Squires et al., 2013). The ABB seems to also alter its habitat preferences based on geography, for example between Nebraska and Oklahoma (Leasure and Hoback, 2017), or in the extreme northern extent of its range (Jenkins et al., 2018), leading to continued uncertainty about its habitat needs.

Another misconception relates to ecological succession and climax communities. Older research supposed that the ABB relied entirely on climax forest communities, not open grassland habitat. However, this research has found that beetles are often positively associated with grasslands, suggesting they do not rely solely on developed forests. Additionally, woody encroachment is often not seen as a threat to grasslands in its early stages. These two views taken together mean that encroaching forests are not seen as a threat to grasslands in general or to beetles specifically. Habitat managers then fail to address the problems for flora and fauna that arise from woody plant encroachment in grasslands.

Finally, many studies of the ABB focus on a limited spatial scale. They focus on small local scales but do not explore broader scales across the biome. Studies across the range of the ABB to understand the state of its current habitat as well as potential habitat could inform restoration activities. Additionally, studies across the temporal scale of the beetle could provide novel insights into its relationship with the landscape over time.

Future studies of the beetle should employ modern ecological theories, including studies of woody encroachment and the ABB at multiple scales and cross-scale interactions as found in Panarchy theory (Allen et al., 2014). It must also embrace modern technologies to aid these broad, multi-scale studies (Jones et al., 2020). Woody encroachment has been shown to have negative impacts on the ABB in a significant portion of its range (Walker and Hoback, 2007), and other studies have shown that beetles are positively associated with open grassland and negatively with closed-canopy woodlands (Jenkins et al., 2018; Jurzenski et al., 2014; Leasure, 2017). There is a need for additional studies in diverse parts of the ABB’s range in order to inform land managers of appropriate goals and directions to pursue in order to conserve ABB populations. Once the American burying beetle is better understood in its current range, we can take the next step to reintroduce the beetle across its historic range.

CHAPTER 2

LARGE-SCALE GRASSLANDS INCREASE ABUNDANCE OF THE THREATENED AMERICAN BURYING BEETLE (*NICROPHORUS AMERICANUS*)[2]

2.1 Introduction

Large-scale landscape initiatives for threatened and endangered species conservation are a relatively new development for natural resource management. As a result, there are few success stories on which to model restoration efforts. One example of successful large-scale restoration efforts for threatened and endangered species comes from the Sage Grouse Initiative in western sagebrush ecosystems. In the Warner Mountain Landscape of southern Oregon, land managers succeeded in increasing sage-grouse populations by 12% as part of a large-scale effort to remove encroaching conifers from the sagebrush steppes (Olsen et al., 2021). Their efforts provide empirical evidence of successful management for a threatened species and inform land managers how to best target conservation efforts. However, there are few if any examples for successful landscape conservation initiatives for threatened and endangered insect species in rangelands and

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[2] Ludwig, A. K., C. P. Roberts, D. R. Uden, E. F. Stuber, D. T. Fogarty, and D. Twidwell. (2021). Large-scale grasslands increase abundance of the threatened American burying beetle (*Nicrophorus americanus*). Prepared manuscript for research journal submission.

AKL contributed to conceptualization, data collection and curation, formal analysis, visualization, all writing aspects, and project administration. CPR contributed to formal analysis, data curation, visualization, and writing selected sections. DRU contributed to data collection and curation, formal analysis, and visualization. EFS contributed to formal analysis and visualization. DTF contributed to conceptualization, data collection, and visualization. DT contributed to conceptualization, visualization, and critical revisions.

grasslands undergoing woody plant encroachment, as evidenced by the absence of insect species of concern from assessments of rangeland wildlife conservation (Krausman et al., 2011). For the threatened American burying beetle (*Nicrophorus americanus*), no ecoregion-scale conservation outcomes have been documented following the initiation of a landscape restoration initiative.

Globally, grassland species are facing multiple threats, including agricultural land conversion, woody plant encroachment, and altered disturbance regimes (Bonanomi et al., 2019; Daru et al., 2013; Dirzo et al., 2014; Fogarty et al., 2020; Gallardo and Aldridge, 2012; Knapp, 1996; Twidwell et al., 2020; Wilcove et al., 1998). For threatened species whose last population strongholds lie in shrinking grassland landscapes, such as the American burying beetle, it is critical to understand the spatial scales at which these threats are affecting their populations (Henry et al., 2020) and inform management responses at the appropriate scales.

The shift from grassland biome to woodland in the Great Plains is well-documented and results directly from human activities (Briggs et al., 2002; Limb et al., 2010). European settlers on the Plains instituted the total suppression of the historic fire cycle established by indigenous peoples (Twidwell et al., 2020) as well as drastically disrupting previous cycles of herbivory (Fogarty et al., 2020; Starns et al., 2019). Subsequently, woody plant species such as eastern redcedar (*Juniperus virginiana*) began encroaching into the grasslands of North America and converting grasslands into woodland (Streit Krug et al., 2017; Van Auken, 2009). The conversion of grassland to woodland puts the Great Plains biome at risk and threatens the ecosystem services that it provides. Water resources are negatively impacted due to less soil moisture and surface runoff, leading to less groundwater recharge and streamflow (Zou et al., 2018). Woody encroachment and conversion of grasslands also increases the risk of wildfires, which negatively impact human settlements (Donovan et al., 2020). Woody encroachment on the Great Plains poses a direct threat to livestock production, the primary human use for grasslands (Anadón et al., 2014), creating a less resilient food production system. Lastly, woody encroachment negatively impacts biodiversity, since it disrupts the grasslands that many plant and animal species require in their life cycles (Ratajczak et al., 2012).

Recent research has discovered a widespread decrease in bird abundance globally, nowhere more significantly than in the grasslands of the world (Inger et al., 2015; Rosenberg et al., 2019; Sekercioglu et al., 2004). Results include a 74% decrease in grassland bird species and a 53% loss of individual grassland birds (Rosenberg et al., 2019). The lesser prairie chicken (*Tympanuchus pallidicintus*) has faced steep declines over the past 100 years due primarily to woody encroachment (Fuhlendorf et al., 2002), and has been considered for listing under the Endangered Species Act (ESA) (Twidwell et al., 2013b). Many other grassland-obligate species are threatened by woody encroachment, including the greater prairie chicken (*Tympanuchus cupido*) (Svedarsky et al., 2000), mountain plover (*Charadrius montanus*) (Vickery et al., 1995), the western prairie fringed orchid (*Platanthera praeclara*) (Bjugstad and Fortune, 1989), and the blowout penstemon (*Penstemon haydenii*) (Stubbendieck et al., 1989). The potential loss of the grassland biome due to woody plant encroachment threatens all grassland species.

In the grasslands of the Great Plains, the American burying beetle (ABB) is known to be threatened by woody encroachment (Walker and Hoback, 2007). As the largest carrion beetle of North America, the American burying beetle once ranged across the eastern half of the United States (Ratcliffe, 1996). It was listed as federally endangered in 1989 (Federal Register 54:29652-55) after it was found to be present in less than 10% of its former range (Lomolino et al., 1995). In 2020, the ABB was downgraded to federally threatened (Federal Register 85:65241-61) and remains rare or extirpated throughout most of its former range (U.S. Fish and Wildlife Service, 2020). The beetle exists primarily in the Great Plains region, with the largest populations found in Nebraska and Oklahoma. Additionally, a small but enduring presence can be found on two islands in the Atlantic Ocean off the coasts of Rhode Island and Massachusetts (U.S. Fish and Wildlife Service, 2019). For ABBs in the Great Plains, the impacts of woody encroachment are not well-studied but initial assessments show that woody encroachment is detrimental to them (Walker and Hoback, 2007). In addition, the impacts on the ABB of prescribed fire and other management practices used to combat woody encroachment are unknown (U.S. Fish and Wildlife Service, 2019). Within the current literature, there are no examples of successful conservation of the ABB within the ongoing expansion of woody encroachment in the Great Plains.

Only a few regions within the Great Plains still support the ABB. One such region is the Loess Canyons Experimental Landscape (LCEL). This region in south-central Nebraska was established in 2005 with the goal of returning fire across the landscape to manage woody encroachment, conserve productivity of privately-held working rangelands, and benefit the ABB (which was listed as endangered at the time). Establishment of the LCEL led to a partnership between scientists, landowners, and agency personnel and has produced over a decade of ABB monitoring data. The LCEL is a biologically-unique landscape (BUL) in the state, making it a part of the Nebraska state wildlife action plan developed in 2005 with specific emphasis on the conservation of the ABB (Schneider et al., 2011). The BUL action plan was one of the first in the Great Plains to plan conservation at the landscape scale. Such broad-scale conservation planning in an area that is mostly privately-owned requires investment and cooperation between private landowners and public agencies for success.

The scale at which ABB are associated with various habitat types is unclear for land managers and conservation planners. It is also unclear which habitat types are more or less desirable to the beetle at those scales. Management for the ABB at broad scales given the rapid woody encroachment of grasslands across the Great Plains biome remains a key concern.

Like much of the Great Plains, the Loess Canyons are undergoing change due to woody encroachment and land managers have turned to prescribed fire to halt the conversion of grasslands (Fogarty et al., 2020). The advent of prescribed burn associations (PBAs) in the region along with the establishment of the LCEL coincides closely with the start of annual beetle monitoring in 2007. The Loess Canyons is a notable landscape that has been dominated by decades of broad-scale woody encroachment and annual high-intensity prescribed fires.

The long-tern experiment within the LCEL was established alongside the state’s wildlife action plan with the following objectives for the American burying beetle: (1) improve the distribution and availability of grassland habitat and prevent habitat loss associated with woody encroachment, and (2) prevent reductions in American burying beetle populations. This study applies thirteen years of beetle monitoring data alongside remotely-sensed landcover changes at multiple spatiotemporal scales to determine the distribution, abundance, and habitat preferences of the American burying beetle. It quantifies whether beetle population abundance trends are meeting conservation objectives and measures the spatial scales and directionality of ABB abundance responses to land cover covariates within the LCEL. Lastly, it visualizes the current state of American burying beetle abundance across the landscape together with land cover trajectories.

2.2 Methods

2.2.1 Study Site Description

The Nebraska Natural Legacy Project was established in 2005 as the state's wildlife action plan. It was designed with the goals of 1) reversing the decline of at-risk species in the state, 2) aiding in the recovery of currently listed species, 3) keeping common species common, and 4) conserving the state's natural communities (Schneider et al., 2011). As part of this statewide effort, a network of regional-scale landscapes were designated as conservation priorities. Among them was the Loess Canyons ecoregion. This region hosts a robust population of the federally-threatened American burying beetle (Schneider et al., 2011), an insect that once was found across the eastern U.S. but now remains only on the periphery of its range (Bedick et al., 1999; U.S. Fish and Wildlife Service, 2019) (Figure 2.1). The Loess Canyons are part of the northern Great Plains population of American burying beetles, along with the Sandhills and parts of South Dakota. The southern Great Plains population is densely centered in eastern Oklahoma, with some populations found in bordering states. Finally, the last naturally-surviving populations of ABB are on the opposite side of its former range, on Block Island and Nantucket Island in the Atlantic Ocean, just off the northeastern coast (U.S. Fish and Wildlife Service, 2019). Within the

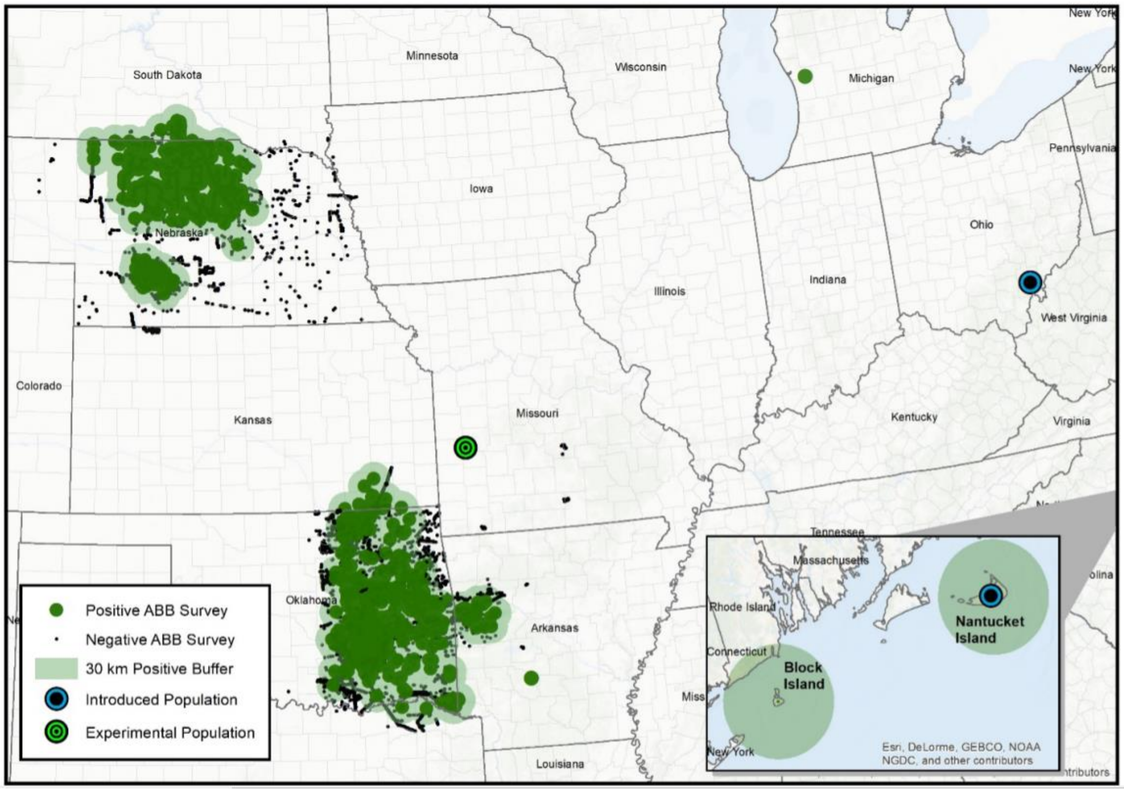


Figure 2.1 Current distribution of the American burying beetle based on 2001-2015 survey data. (Figure adapted from (U.S. Fish and Wildlife Service, 2019)).

Loess Canyons ecoregion, there is evidence that woody encroachment by eastern redcedar has negative impacts on the ABB (Walker and Hoback, 2007). Once designated as a high-priority conservation area, it became a key objective for land managers to halt woody encroachment and prevent losses in ABB habitat. Thus, the implementation of prescribed fire to meet large-scale restoration goals in the region was driven in part by the American burying beetle.

The LCEL is a long-term experiment implementing extreme prescribed fire across the entire Loess Canyons ecoregion (Bielski et al., 2021). Since 2002, private landowners of the Loess Canyons Rangeland Alliance (LCRA) have worked in tandem with public land managers and researchers from the University of Nebraska's Institute of Agriculture and Natural Resources to restore fire to the landscape, reverse woody encroachment, maintain prairie, and co-produce science on working lands (Fogarty et al., 2020; Naugle et al., 2020; Twidwell et al., 2013b). In order to produce fire on the landscape capable of eliminating invasive eastern redcedar trees, fire practitioners first prepare the fuels by cutting down outlying trees and placing them just within the borders of a dense stand of eastern redcedar. When selecting the day to implement a prescribed burn, they choose weather conditions that create sufficient fire intensity to exceed juniper mortality thresholds (Twidwell et al., 2013a) and meet objectives of restoring grassland productivity (Bielski et al. 2021). This restoration effort has successfully halted the spread of eastern redcedar at large scales in the Loess Canyons (Fogarty et al., 2020) (Figure 2.2).

The LCEL is located within the Loess Canyons ecoregion of south-central Nebraska, which spans three counties (Lincoln, Dawson, and Frontier). The Loess Canyons ecoregion spans 121,405 hectares and is classified as a biologically-unique landscape (BUL) in the state. The region supports several species of significance that are known to be negatively impacted by woody encroachment, including the American burying beetle (*Nicrophorus americanus*), regal fritillary (*Speyeria idalia*), burrowing owl (*Athene cunicularia*), greater prairie-chicken (*Tympanuchus cupido*), and Bell’s vireo (*Vireo bellii*) (Schneider et al., 2011). The experimental landscape spans 72,843 hectares within the ecoregion, and 27,176 ha have been burned from 2002 to 2019. The majority of prescribed fires have taken place in the central and southern portions of the Loess Canyons, whereas prescribed fire occurrences are rare in the northwestern and southeastern portions of the ecoregion (Figure 2.3).

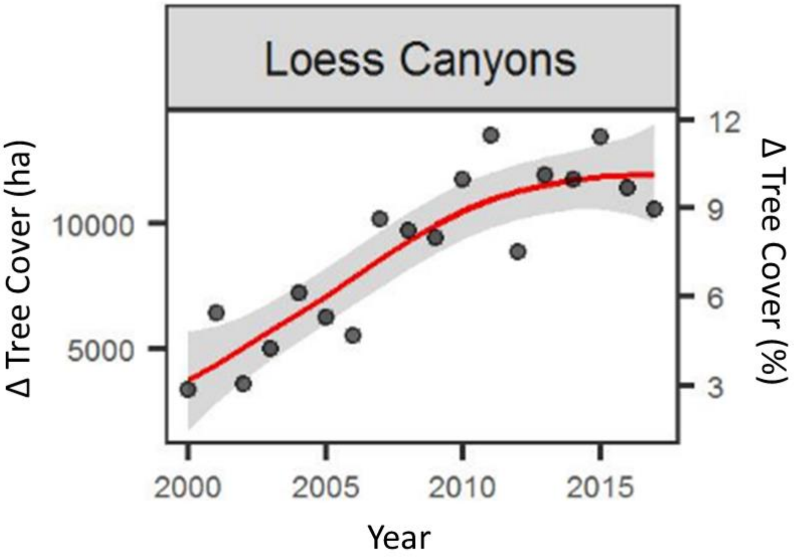


Figure 2.2 Change in tree cover in the Loess Canyons from 2000 to 2017. Tree cover increased over time since 2000 but leveled out starting in 2014. (Figure adapted from (Fogarty et al., 2020)).

Historically, the ecoregion was dominated by mixed-grass prairie, while trees were mostly limited to areas that burned infrequently (i.e., riparian zones, steep hillsides, and draws (Roos et al., 2018)). In recent decades, disruption of the fire cycle has allowed tree species, primarily eastern redcedar (*Juniperus virginiana*), to encroach into prairie landscapes (Twidwell et al., 2016b). This has caused much of the region to shift from grassland to woodland (Fogarty et al., 2020; Twidwell et al., 2016b). Common grass and forb species include blue grama (*Bouteloua gracilis*), big bluestem (*Andropogon gerardii*), needle-and-thread grass (*Hesperostipa comata*), common sunflower (*Helianthus annuus*), and hoary vervain (*Verbena stricta*) (Bedick et al., 1999; Schneider et al., 2011).

The Loess Canyons topography is characterized by steep-sided hills and sloping canyons that mostly run north-south; soil consists of an easily eroded loess-sand mixture (Bedick et al., 2004, 1999; McPherron et al., 2012). Parent material is primarily silt loams

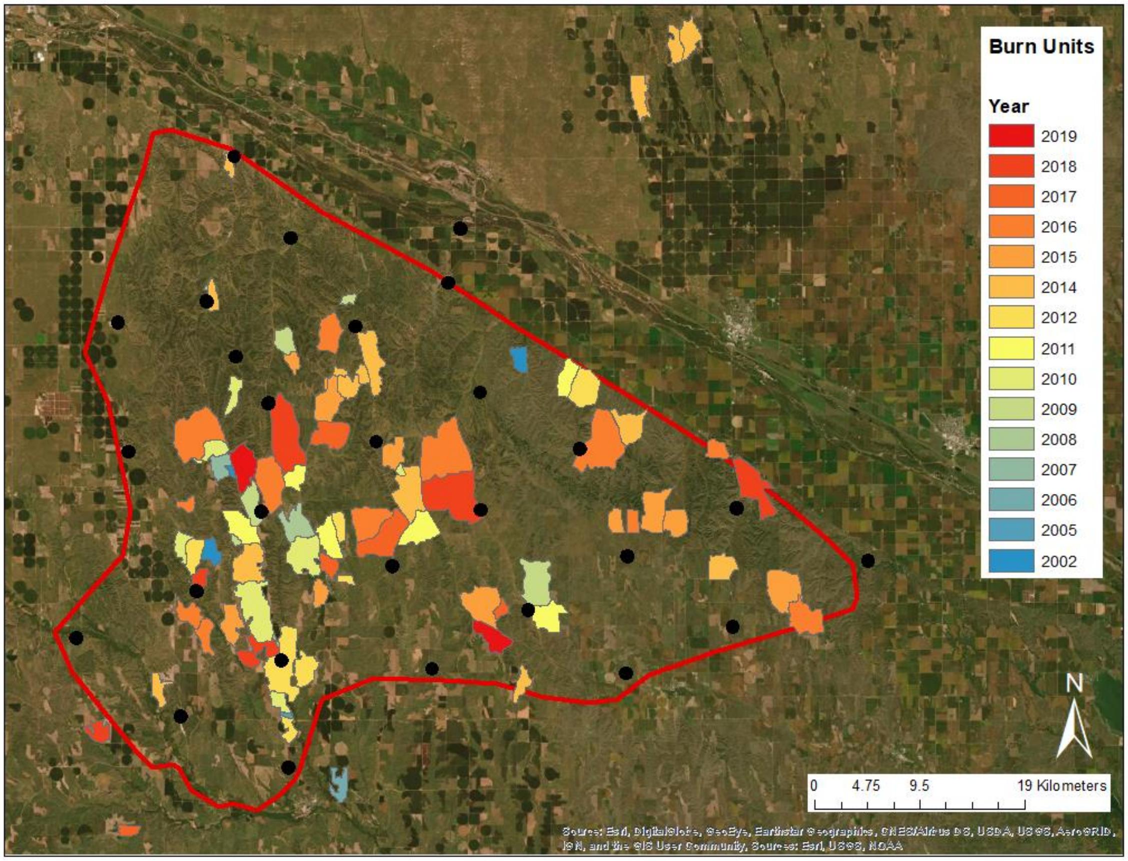


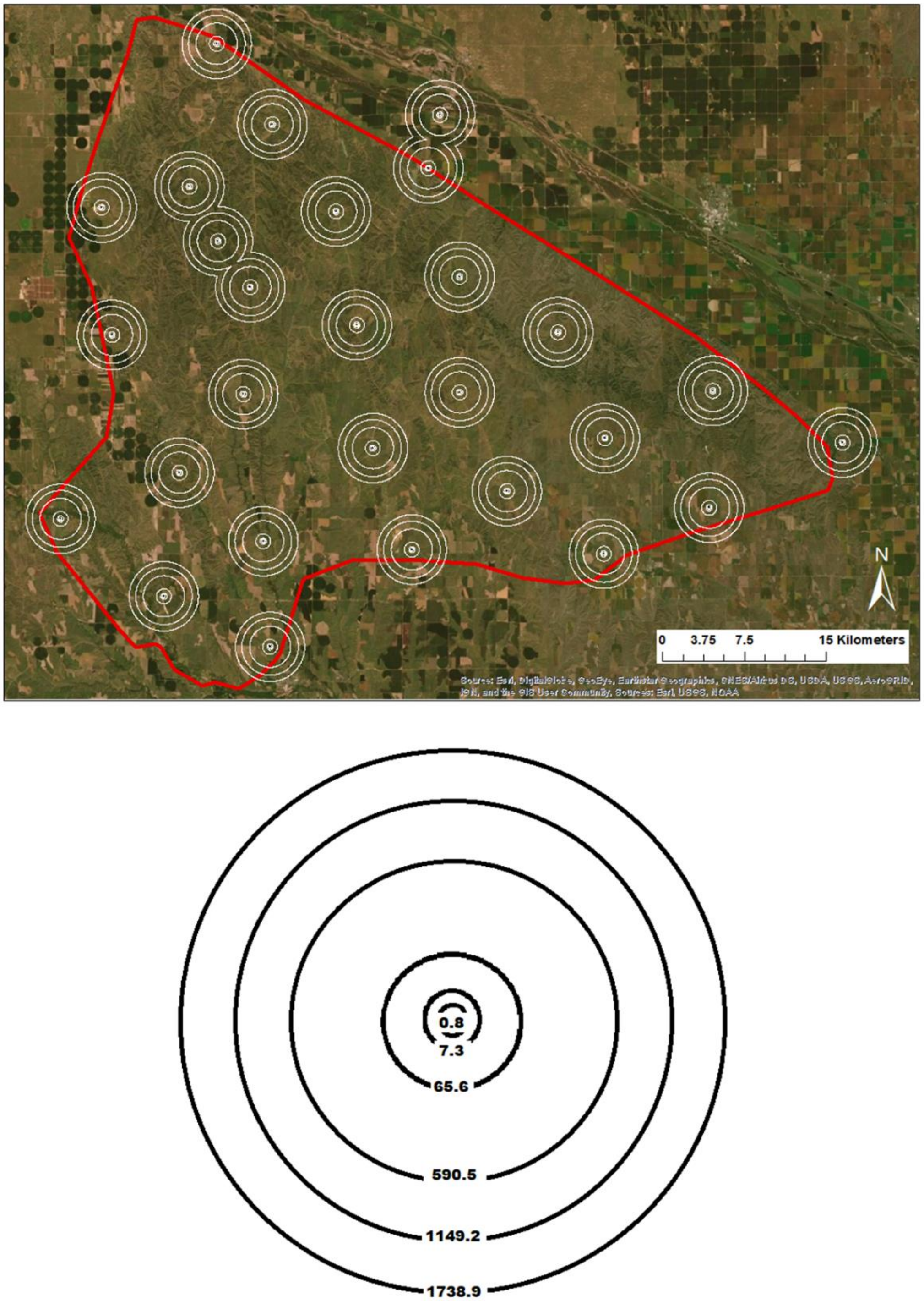
Figure 2.3 Burn units in the Loess Canyons from 2002 to 2019. Black dots show permanent ABB trap locations. Traps were sampled annually since 2007.

of the Coly soil series (Soil Survey Staff, 2021). Most of the land is used for grazing livestock, although small pockets of agriculture are found in areas with flatter topography (McPherron et al., 2012; Schneider et al., 2011). Mean annual temperature is 9.4°C (Arguez et al., 2012), with an average annual high of 18.3°C and low of 1.4°C (McPherron et al., 2012). Mean annual rainfall is 52.8 cm (Arguez et al., 2012).

2.2.2 Beetle Sampling Protocol

An ecoregion-scale long-term sampling protocol was initiated in 2007 to monitor American burying beetle populations across the Loess Canyons ecoregion (Figure 2.4). Permanent trapping locations were established and spaced approximately 8 km apart to ensure sampling independence and to avoid individual beetles dispersing among trap locations (American burying beetles can travel 1.2 km overnight (Bedick et al., 2004; Creighton and Schnell, 1998)). A total of 28 traps were distributed in permanent locations across the 121,405 ha Loess Canyons ecoregion. Trapping occurred annually across the LCEL from 2007 through 2019. Some traps were not used in all years, but a minimum of 24 traps were used every year. Beetle trapping took place for four to five consecutive nights in August. A total of 1,654 American burying beetles were captured during the 13-year trapping effort.

All sampling was coordinated by Nebraska Game and Parks Commission, the state wildlife agency, and followed trapping protocols established by U.S. Fish and Wildlife Service (USFWS) guidelines (U.S. Fish and Wildlife Service, 2018). Sampling occurred annually every August, which corresponded to a period when most old and young adults had emerged from their summer brood chambers but had not yet burrowed underground for hibernation. For each trap, a food-grade, 5-gallon bucket was buried in the ground. The rim of the bucket was left about one inch above the soil surface and a ramp of soil was pushed up to the rim. Buckets were covered with a wire mesh to deter scavengers from tampering with the bucket but with large enough gaps to allow entry of carrion beetles. A lid covered the bucket’s opening, propped up on two wooden blocks with a 1-2 inch gap below that allowed beetle entry. The lid served to prevent beetle escape while also keeping rainfall and sunlight out of the bucket to prevent the drowning and desiccation of beetles. Moist, but not wet, soil was placed in the bottom of the bucket to allow beetles to burrow and hide and to keep the bucket’s environment cool and moist. An aged lab rat carcass (procured fresh from a laboratory supply company and aged in a



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Sources: Esri, USGS, NOAA

Figure 2.4 American burying beetle trap locations. Rings illustrate the multiple scales at which each landcover type was sampled. Landcover types sampled were perennial forb/grass cover, tree cover, cropland cover, and litter cover. Area within each circle indicated in hectares.

sealed bucket for at least 3-5 days) was placed in the trap. When placing the lid on top of the trap, additional stakes were used to secure the apparatus from outside disturbances.

Traps were deployed, baited, and then left overnight. Traps were checked the following morning at first light. All traps were to be checked by noon, per USFWS guidelines. Captured ABB were removed from the traps and held in a separate container in moist, cool conditions until they could be processed. Each beetle’s length was measured from tip-to-tip and from its mandibles to the end of its elytra. The width of its pronotum was also measured. Each beetle was then marked with a bee tag. The number and color of the bee tag was recorded alongside each beetle’s measurements to track any recaptures. Other species of carrion beetles (silphids) were removed from the trap, identified, tallied, and placed in a larger holding container. After all beetles were removed, the trap was reset and additional bait added if necessary. Marked ABB were released about 200 m from the trap at which they were caught, following USFWS guidelines that they be released within 609 m of their trap location (U.S. Fish and Wildlife Service, 2018). Other silphid species were released at least a mile from the trap at which they were caught. All endangered beetles were trapped and handled in the field per established USFWS guidelines to avoid unnecessary mortalities. In addition, efforts were made to reduce mortalities of other silphid species that were caught.

2.2.3 Landcover Data

Landcover data were compiled for vegetation functional groups known to be influential to American burying beetle habitat and their distributions (Leasure and Hoback, 2017; Lomolino and Creighton, 1996; Walker and Hoback, 2007). Landcover data included cropland (%), perennial forbs and grasses (%), tree cover (%), and litter (%) using geospatial data sources measured at a 30-m resolution. Cropland (%) cover was acquired from the USDA NASS cropland data layers, accessed through Google Earth Engine (USDA National Agricultural Statistics Service Cropland Data Layer, 2020). Data were collected for the region from 2006 to 2019. Pixels with values less than or equal to 61 were classified as cropland. Rangeland vegetation data were acquired from the Rangeland Analysis Platform and included annual measures from 2006 to 2019 (RAP; (Allred et al., 2021; Jones et al., 2020; Uden et al., 2019)). Roads, water, and developed areas as defined in the National Land Cover Database (Multi-Resolution Land Characteristics Consortium, 2011) were masked out of the datasets. A moving window algorithm was used to calculate the mean values of the chosen land cover types across the different window sizes. Window sizes around each trapping location (Figure 2.4) were: 0.81 ha (3x3 window), 7.29 ha (9x9 window), 65.61 ha (27x27 window), 590.49 ha (81x81 window), 1149.21 ha (113x113 window), and 1738.89 ha (139x139 window). This provided a continuous raster for all locations that were not masked out. Each trap location had a 60 m buffer surrounding it that calculated the average pixel value from the raster within that buffer for each of the window sizes. One cover value for each land cover type at was extracted from the continuous raster using a 60 m buffer around each trap. Thus, each sampling location (i.e., beetle trap) was assigned six landcover values for each of the four landcover types, for a total of 24 land cover values at six spatial scales.

2.2.4 Analysis

To estimate the relative abundance of American burying beetles at trapping locations in the Loess Canyons, we used a Bayesian N-mixture model (Royle et al., 2007). We assumed closure of individuals for each trap within each year (Royle, 2004). As fixed effect predictors for the ecological process of the N-mixture model, we included four land cover covariates: crop cover, litter cover, perennial forb/grass cover, and tree cover. We also included time (year) as a fixed effect predictor in the ecological process portion of the model. The ecological process is the portion of the model that relates beetle abundance to the four land cover covariates. To allow abundance-predictor relationships to change signs, we added quadratic terms to all predictors in the ecological process. As linear predictors for the detection process of the N-mixture model (i.e., detection probability), we used average wind speed, presence/absence of fog, minimum temperature, and amount of precipitation. This weather data was obtained through NOAA's Climate Data Online archive for the beetle sampling date range. To account for variability in surveyor crews over time and effects of this variability on detection probability, we set year (2007 – 2019) as a random effect for the detection portion of the model. Year may be used as a fixed effect in the ecological process and as a random effect in the detection process of the model without causing issues with collinearity. The detection process is the portion of the model that accounts for and models imperfect detection of the beetles.

To determine at which scale our land cover covariates best explained ABB abundance, we used the Bayesian latent indicator scale selection (BLISS) method (Stuber et al., 2017). BLISS is a model selection approach that simultaneously evaluates all possible combinations of spatial scales for the ecological process predictor variables, selects the best-performing scale for each variable, and estimates the effects of predictors (Stuber et al., 2018). BLISS outperforms other model selection approaches because it is not sensitive to collinearity among scales for a single predictor or to collinearity between predictors (Stuber and Fontaine, 2019).

We conducted our analysis in the R programming environment (R 3.6.3) using JAGS (Just Another Gibbs Sampler (Plummer, 2003)) via the R package rjags (Plummer, 2019; R Core Team, 2021). We used normally distributed priors with zero-means and large variance for all ecological process predictor variables and all detection probability predictor variables—except for the binomial 'fog' variable for which we used the beta distribution as a prior. For the six candidate spatial scales, we used discrete uniform priors (Stuber et al., 2018). For initial starting values for MCMC sampling, we generated random values via a Poisson distribution capped at the maximum observed count across all traps and years. We ran 200,000 iterations for posterior simulations, with a burn-in period of 100,000. Per the BLISS approach, we considered the spatial scale with the highest posterior probability as the 'best-performing' scale for each predictor variable (Stuber et al., 2018, 2017; Stuber and Fontaine, 2019).

2.2.5 Mapping Visualization

To visualize the geographic distribution of American burying beetles and their association with land cover types at preferred scales of selection, we synthesized our results into a map of the region. This map shows the four cover types chosen for the model (perennial forb/grass, tree, cropland, and litter), the predicted beetle abundance for each trap location per the model, and the actual percent cover of each cover type at the scale preferred by the beetle.

2.3 Results

2.3.1 American burying beetle abundance in the Loess Canyons

A total of 1,654 American burying beetles were trapped and marked during the 13 years of sampling. The most beetles caught in one year was in 2016 with a total of 318 beetles captured, and the least beetles caught in one year was in 2007 with a total of 32 beetles.

The results of our N-mixture model show changes in American burying beetle abundance from 2007 to 2019 (Figure 2.5). Beetle abundance appears to increase and decrease from year-to-year. Despite this fluctuation in American burying beetle abundance, our results show that beetle abundance has increased over time from 98 estimated beetles when annual sampling began in 2007 to 152 estimated beetles in 2019, an increase of 55%. The model estimates a peak beetle abundance of 220 beetles in 2011, and a low beetle abundance of 90 in 2013.

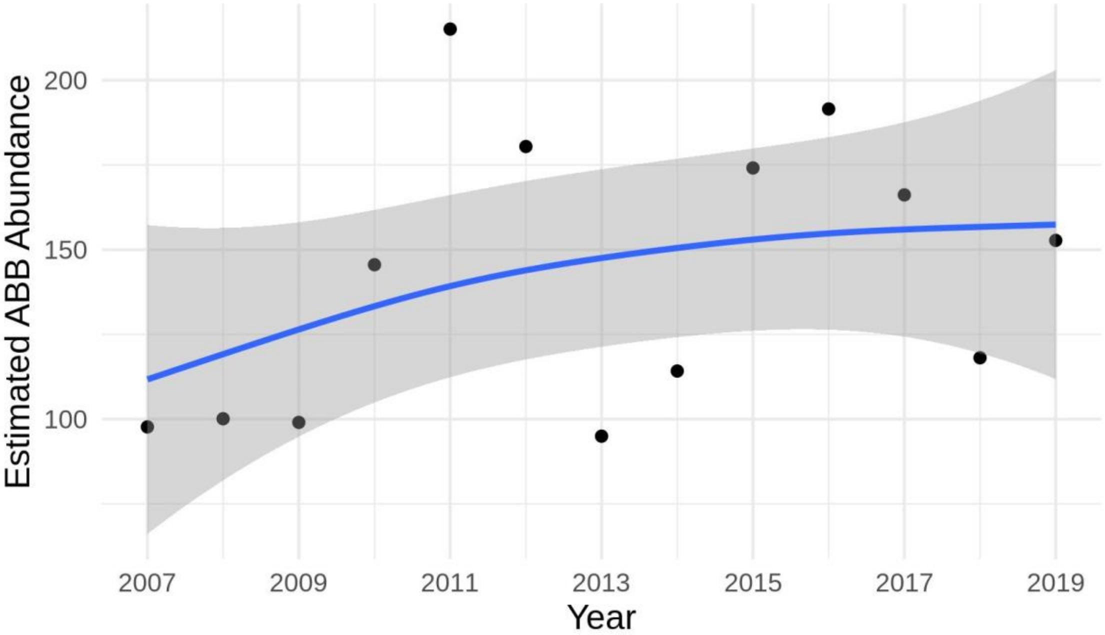


Figure 2.5 GAM plot of American burying beetle abundance in Loess Canyons, Nebraska. Beetle abundances estimated by Bayesian N-mixture model for trap years 2007-2019. A Bayesian approach was used in the modelling which does not use tests of significance. The trend in the plot shows beetle abundance increasing over time.

2.3.2 Scale selection across land cover types

BLISS revealed that the scales of analysis best estimating American burying beetle abundance varied across land cover types. A moderately-sized scale of analysis was the best performing spatial scale for mean perennial forb and grass cover and predicted beetle abundance (Figure 2.6a; posterior probability of highest ranking scale = 0.98; 590.49 ha). For mean tree cover, a single scale of analysis (7.29 ha) was the best supported scale (Figure 2.6b; posterior probability = 1.00). The largest scale of analysis (1738.89 ha) was the best predictor for mean cropland cover (Figure 2.6c; posterior probability = 0.94), whereas the finest scale of analysis (0.81 ha) was the best predictor for mean litter cover (Figure 2.6d; posterior probability = 0.99).

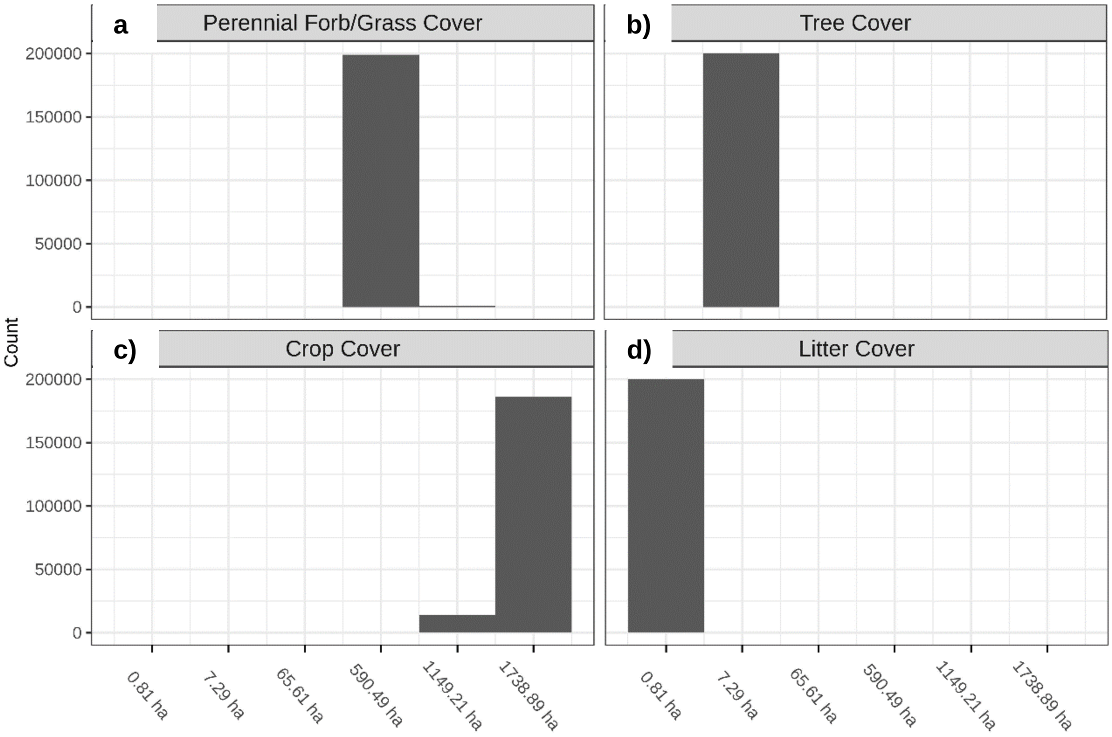


Figure 2.6 Posterior distributions of the spatial scales (in hectares) for land cover abundance predictor variables estimated via the BLISS approach for American Burying Beetle in the Loess Canyons, Nebraska.

The results of our scale selection method help determine what scales of habitat ABB associate with and how they perceive and interact with different land cover types on the landscape (Figure 2.6). In our model, mean percent tree cover was the only predictor variable whose result settled on only one scale. That scale was the second smallest scale in our model, covering 7.29 hectares. All other predictor variables were split between two scales, although in some cases only very slightly. Mean cropland cover was split at the largest scales (1149.21 ha and 1738.89 ha); litter cover was split at the smallest scales (0.81 ha and 7.29 ha); and perennial forb and grass cover was split at mid-to-large scales (590.49 ha and 1149.21 ha).

Modeling results demonstrate American burying beetles exhibit strong, scale-dependent sensitivities to land cover change. Relative abundance of American burying beetles was highest for perennial grass/forb cover occurring at moderately large scales (Figure 2.7a). Increases in perennial grass/forb cover was the only land cover covariate to have a strictly positive effect on relative beetle abundance (Figure 2.7). Beetle abundances exhibited strong negative associations to slight increases in tree cover at fine scales (7 ha) and crop cover at broad scales (1739 ha) (Figure 2.7b-c). Negative effects on relative beetle abundances were observed once tree cover exceeded 10% (Figure 2.7b). At tree cover values of 22% or greater, the mean number of beetles estimated by the model fell to < 1 per trap (Figure 2.7b). Cropland cover was the only covariate to have a strictly (i.e., linear) negative effect (Figure 2.7c). Relative abundance was always < 1 per trap for all cropland cover values and dropped markedly even under very small increases in percent crop cover at the largest scale of analysis (Figure 2.7c). Litter cover also had negative effects on relative abundance, once cover values exceeded 8% (Figure 2.7d).

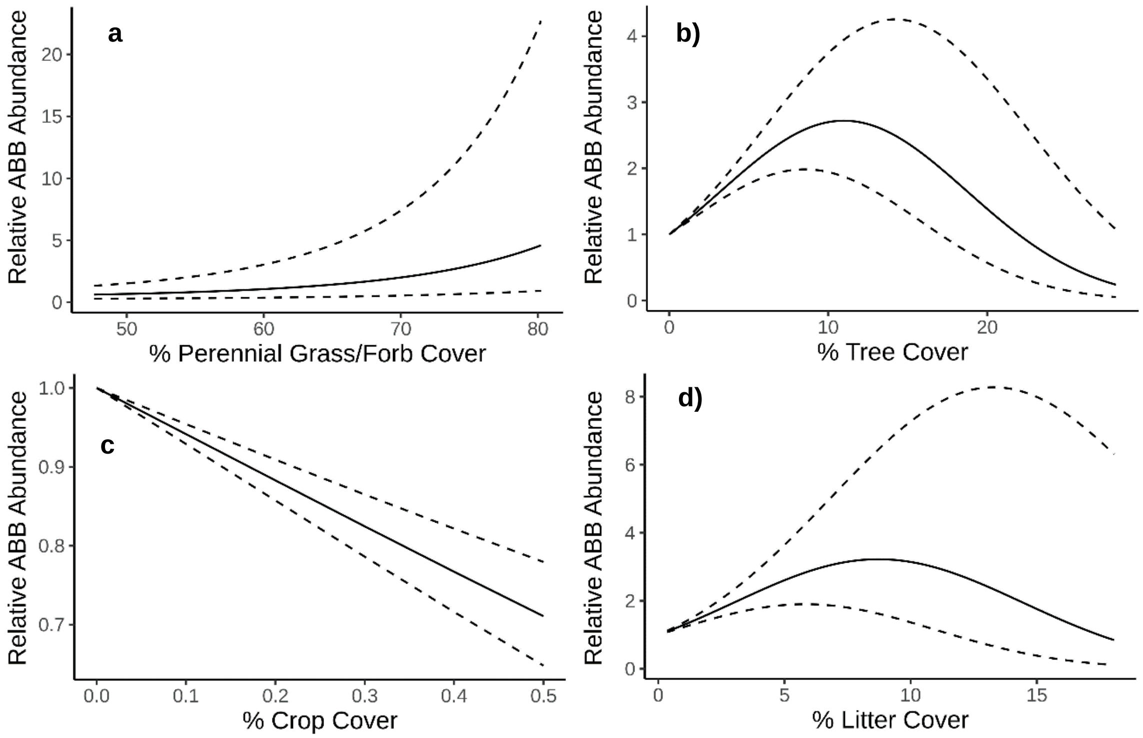


Figure 2.7 Marginal effects (mean: black line; 80% CI: dashed lines) of land cover abundance predictors at the best-supported scales on relative abundance of American Burying Beetle in the Loess Canyons, Nebraska. X-axis ranges for each predictor represents observed ranges of predictors measured as proportions.

2.3.3 Mapping Visualization

Mapping spatial variability in the relative abundances shows the spatial complexity of the American burying beetle's response to scale-specific patterns for different land cover types. Spatial patterns of abundance demonstrate that highest numbers occur where grassland-dominated areas (Figure 2.8a) have been minimally impacted by scale-specific changes in trees, cropland, or litter (Figure 2.8b, 2.8c, 2.8d). This occurs in the central portion of the Loess Canyons (Figure 2.8a) and contains 67% of the total estimated American burying beetle abundance across the ecoregion. Tree cover is highest in the northern portion of the Loess Canyons (Figure 2.8b), a densely forested area that contains 11% of total American burying beetle abundance in the ecoregion. Cropland cover surrounds the perimeter of the ecoregion with the most cultivation occurring in the southwestern and southeastern corners of the Loess Canyons (Figure 2.8c). Litter cover is densest in pockets along the Loess Canyon’s southern border and in areas in the northwestern quadrant (Figure 2.8d).

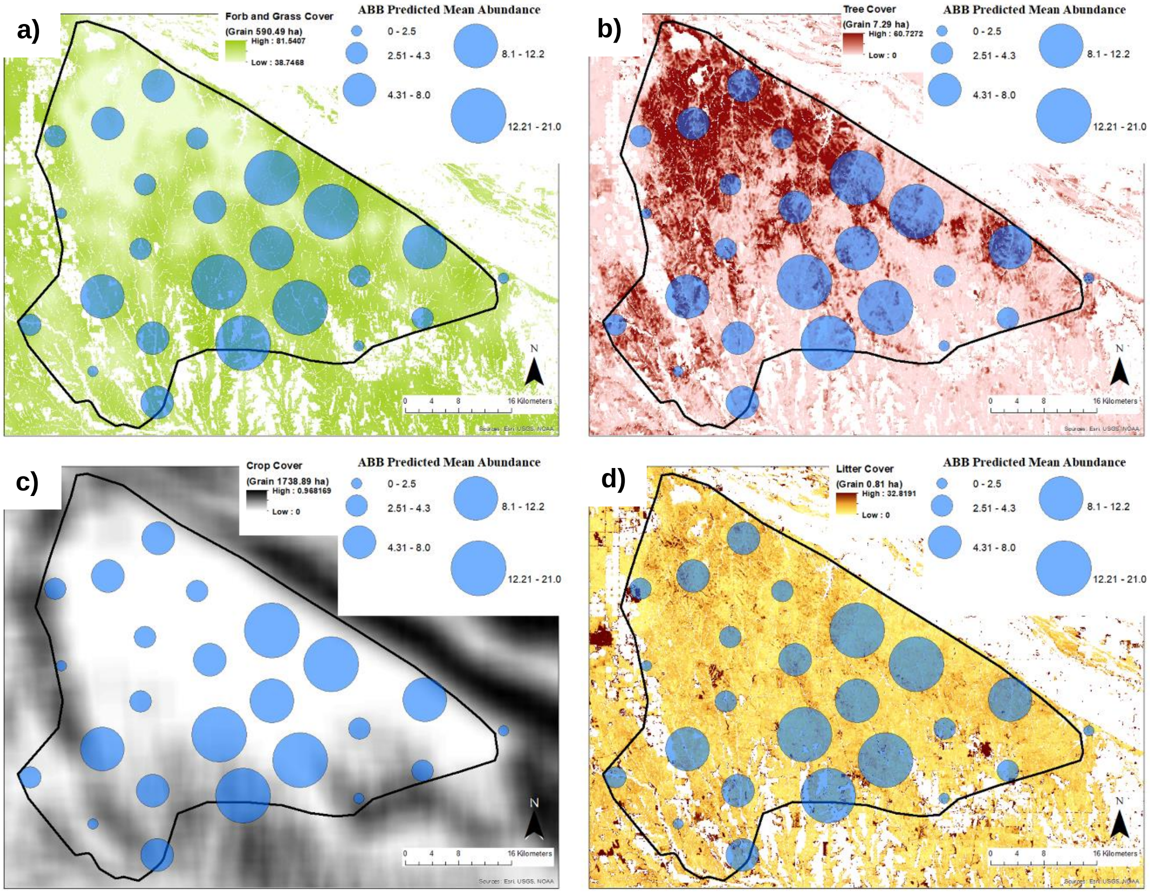


Figure 2.8 Spatial patterns of predicted American burying beetle abundance across 24 permanent trapping locations in the Loess Canyons, Nebraska. Cover types are shown at the spatial grain size most relevant for the beetle as determined by BLISS (Bayesian latent indicator scale selection) model. Cover data shows the state of cover in 2019.

2.4 Discussion

The Bayesian analysis and N-mixture model found that American burying beetle abundances have increased since annual trapping began in 2007 (Figure 2.5). The model showed that beetles have increased by 55% as of 2019. Our study illustrates the first documented increase in the American burying beetle, a federally-threatened species, in an ecoregion managed extensively with prescribed fire. In addition, this is within a working landscape that is multi-use, supporting widespread livestock grazing and recreational activities while meeting conservation goals.

Conservation activities in the Loess Canyons Experimental Landscape have been ongoing since the establishment of the Nebraska Natural Legacy Project in 2005. The Project’s goals of improving the distribution and availability of grassland habitat, preventing habitat loss from woody plant encroachment, and averting reductions in American burying beetle populations have been instrumental in directing conservation activities in the region. We measured the directionality of beetle abundance responses to land cover covariates at six spatial scales. This allowed us to determine the distribution and abundance of American burying beetle populations in the Loess Canyons Experimental Landscape, their habitat preferences, and whether conservation objectives have been met. We found that the American burying beetle is distributed throughout the Loess Canyons, with the most abundant populations in the central region (Figure 2.8). Beetles are most abundant in areas with high perennial forb and grass cover (Figure 2.8a) and are less abundant in areas with high tree cover (Figure 2.8b). Areas of high forb and grass cover in the central Loess Canyons are less impacted by large increases in cropland or litter cover (Figure 2.8c, 2.8d).

Perennial forb and grass cover is positively related to ABB abundance (Figure 2.7a) at mid-to-high spatial scales (Figure 2.6a). Our model suggests that beetles may be more abundant in highly intact grasslands and prairies, which agrees with other studies in the northern Great Plains (Jenkins et al., 2018; Jurzenski et al., 2014; Walker and Hoback, 2007). Tree cover is negatively associated with ABB abundance at greater than 10% tree cover (Figure 2.7b), with the greatest impact at lower spatial scales (Figure 2.6b). This result agrees with previous work in the Loess Canyons which found that ABB populations declined at 20-40% tree cover (Walker and Hoback, 2007). Our finding also suggests that small amounts of tree cover may be beneficial to the ABB. The American burying beetle is a habitat generalist and may be able to use trees as shelter from heat, desiccation, or other extreme weather. Some trees may also support ideally-sized prey species for the beetle, such as certain birds and rodents. Studies in other regions of the beetle's range have found that oak-hickory forest is an important habitat for the beetle (Creighton et al., 1993). However others have shown that the *Juniperus* forest of the Loess Canyons has a different understory than deciduous oak-hickory forest (Walker and Hoback, 2007) so its utility to the beetle in this region may be limited.

Increasing crop cover has an entirely negative impact on ABB abundance (Figure 2.7c) and is impactful at the highest spatial scales (Figure 2.6c). Litter cover is negatively associated with ABB abundance at greater than 8% litter cover (Figure 2.7d) and is impactful at the lowest spatial scales (Figure 2.6d).

The negative impacts of woody encroachment on the ABB in the Loess Canyons have been known for over a decade (Walker and Hoback, 2007). This study shows that management actions to reverse woody encroachment have had a subsequent positive outcome for the beetle. There are several other studies that have explored habitat characteristics correlated to beetle abundance or decline, or have created habitat suitability models to inform future land management efforts (Jurzenski et al., 2014; Leasure and Hoback, 2017; McPherron et al., 2012). However, ours is the only study we know of that investigates the impacts of real-world woody plant management on American burying beetle populations.

Our model shows the sensitivity of American burying beetles to scale-specific changes associated with woody plant encroachment and cropland conversion. The split between the smallest scales of litter cover may indicate that beetles use litter cover at smaller spatial scales than accounted for in the model (Figure 2.6d). For cropland cover, the split in the model between the two largest spatial scales could indicate that beetles are interacting with that cover type at a larger scale than what was accounted for in the model (Figure 2.6c). The sensitivity of the American burying beetle to cropland conversion is supported by many other studies of the beetle (Jenkins et al., 2018; Jurzenski et al., 2014; Leasure and Hoback, 2017; Schnell et al., 2008). Additionally, the scale of tree cover chosen by the model (7.29 ha; Figure 2.6b) is associated with how woody plant encroachment fragments intact grassland over time.

Conservation efforts in the Loess Canyons ecoregion need to prioritize the area with the greatest American burying beetle stronghold. The central Loess Canyons holds the greatest abundance of ABB (Figure 2.8), and this area overlaps closely with ongoing restoration activities in the region (e.g., brush management and prescribed fire). However, this stronghold of beetles in the Loess Canyons is vulnerable to woody plant encroachment and dependent on the continued actions of land managers through prescribed fire. Conversely, these ABB in the central Loess Canyons are far less vulnerable to cropland conversion because of soil types and topography. High litter cover is also less of a threat to the American burying beetles in the central Loess Canyons. We expect higher litter cover in areas that have not been burned recently, and the central Loess Canyons is the most actively burned area in the ecoregion (Figure 2.1). Additionally, litter cover appears to be the most heterogeneous cover type on the landscape, with patches of high and low cover beside each other across the landscape (Figure 2.8d). Grazing practices of individual landowners may impact litter cover in the Loess Canyons and make relationships with ABB abundance unclear. Land managers should aim to prevent increases in tree, cropland, and litter cover in the beetle's central stronghold in order to avoid major depletion of beetle abundances. Once that stronghold is secured, conservation efforts can grow from that foundation to increase beetle abundance across the ecoregion and reduce the negative impacts of trees, cropland, and litter at critical scales of importance to the beetle.

It is important for large-scale conservation planning to deal with large-scale threats (e.g., woody plant encroachment across the Great Plains). The threat of woody encroachment at the biome-scale also creates a threat to the ABB at the ecoregion-scale (Walker and Hoback, 2007). This holds true for the beetle's scale-dependent associations to other land cover types. The two land cover types with strong negative impacts to the beetle (tree cover and cropland cover) have been identified as the leading threats to wildlife conservation in the Great Plains biome (Natural Resources Conservation Service, 2021). The Loess Canyons Experimental Landscape provides evidence that private lands conservation efforts can operate at the necessary scales to achieve the broad conservation outcomes needed to sustain threatened and endangered species facing such threats. More strategic implementation of conservation investments can build upon current efforts in this experimental landscape.

2.5 Conclusions

The ABB in the Loess Canyons strongly prefer areas of perennial forbs and grasses at intermediate spatial scales (Figure 2.7a), suggesting that their habitat of choice is primarily open grasslands. Since these grasslands require disturbances from a fire regime to avoid woody invasions, our results suggest that prescribed fire has an overall positive impact on the ABB despite the fear that fire will cause mortality to the beetle. Fire clears away the dense, closed-canopy eastern redcedar woodland and restores open grasslands. This allows the beetle to move more freely while seeking carrion to feed and reproduce. The majority of prescribed burns in the Loess Canyons occur early in the spring, before the beetle emerges from hibernation. Additionally, since the beetles are nocturnal they spend most of their time during the day underground, the same time when prescribed fires are actively burning. Prescribed fire appears to cause little direct mortality to the ABB while having positive impacts on beetle habitat. For the Great Plains biome, an area undergoing widespread woody encroachment, these results are encouraging. Prescribed fire can be a powerful tool for grassland managers grappling with woody encroachment. It can also help create habitat for rare, threatened, or endangered species that depend on grasslands.

CHAPTER 3

RESTORATION OF GRASSLAND RICHNESS FOLLOWING COLLAPSE OF *JUNIPERUS* WOODLAND WITH EXTREME FIRE[3]

3.1 Introduction

In the Great Plains, woody plant encroachment is a growing concern. Much of the region has been converted from grasslands to woodlands, resulting in a regime shift throughout the biome (Briggs et al., 2002; Twidwell et al., 2013a). A regime shift is the rapid change of an ecosystem from one state to an alternative state that has its own unique processes and feedbacks (Beisner et al., 2003; Scheffer et al., 2001). Additionally, such regime shifts in grasslands are often hysteretic (Bielski et al., 2021; Fogarty et al., 2021), requiring more effort to return to the original grassland regime than was needed to shift to the alternative woodland regime (Carpenter et al., 1999; Scheffer et al., 2001). This is because the woodland regime establishes positive feedback loops that enhance its own stability and also prevent the conditions needed for a grassland regime (Twidwell et al., 2013a). In order to return to a grassland regime, restoration practitioners must use

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[3] Ludwig, A. K., V. M. Donovan, C. R. Allen, and D. Twidwell. (2021).Restoration of grassland richness following collapse of *Juniperus* woodland with extreme fire. Prepared manuscript for research journal submission.

AKL contributed to conceptualization, data collection and curation, formal analysis, visualization, all writing aspects, and project administration. VMD contributed to formal analysis, data curation, visualization, and writing selected sections. CRA contributed conceptualization and critical revisions. DT contributed to conceptualization, visualization, and critical revisions.

alternative pathways to break the positive feedback loops of the woodland regime or else risk the consequences of woody encroachment (Twidwell et al., 2013a).

In the Great Plains, the consequences of shifting to a woodland regime can be severe. Livestock production can decrease as much as 75% (Fuhlendorf et al., 2008). The risk of wildfire increases, destroying homes, increasing the cost of suppression, and threatening human lives (Twidwell et al., 2013b). Biodiversity and endangered species across the Plains are impacted by woody encroachment, from grassland birds (Chapman and Engle, 2004; Fuhlendorf et al., 2002) and small mammals (Reddin, 2016), to the federally-listed American burying beetle (Walker and Hoback, 2007) and herbaceous plant species (Briggs et al., 2002; Limb et al., 2010). Streamflow can be drastically reduced by woody encroachment (Starks and Moriasi, 2017; Zou et al., 2018), which decreases the region's resilience to drought. After a grassland has undergone a regime shift to a woodland, restoration can be difficult.

The difficulty of restoring the lost biodiversity and communities of Great Plains grasslands is complex and in some cases may be impossible. Restoration efforts must account for lost keystone species (Kotliar et al., 1999; McMillan et al., 2019), create preferred habitat for grassland species (Madden et al., 2000; Walker and Hoback, 2007), reduce habitat fragmentation (Adhikari and Hansen, 2018; Fuhlendorf et al., 2002; Johnson, 2001), and reestablish the lost patterns and processes that formed the Great Plains (Fuhlendorf et al., 2009; Twidwell et al., 2020). Lost biodiversity includes not only extirpated and endangered animal species, but also common species that have declined and the lost plant assemblages that create the foundation for diverse animal life (Samson et al., 2004; Van Auken, 2009). Woody encroachment is a direct threat to grassland plant assemblages and therefore a threat to the species, patterns, and processes of grasslands (Twidwell et al., 2013b; Van Auken, 2009). Two approaches have emerged that have successfully restored grasslands that were lost to woody encroachment at large scales: (1) prescribed burn associations (PBAs), and (2) extreme fire.

In response to the threat of woody encroachment across the Great Plains, prescribed fire has gained widespread traction among landowners as a cost-effective, useful tool in grassland restoration (Bielski et al., 2021; Twidwell et al., 2013b). Landowner-driven PBAs are well-suited to restoration in the Great Plains, a region that is mostly privately-owned with complex patterns of ownership across the landscape (Augustine et al., 2019). Though relatively small on their own, cumulative restoration actions at the scale of the individual landowner have an upward cascading effect across the landscape (Allen et al., 2014) and become more efficient as more landowners participate in PBA activities (Twidwell et al., 2013b). Thus, PBAs in the Great Plains are an effective mechanism to respond to hysteretic regime shifts and restore grasslands (Bielski et al., 2021). It was previously hypothesized that encroachment of juniper woodlands was irreversible with prescribed fire alone, but this was demonstrated to be a social artifact stemming from a narrow range of accepted burn conditions and fire intensities (Twidwell et al., 2020). Studies have shown that conducting burns above juniper mortality thresholds can successfully collapse alternative juniper woodland states and restore grassland processes (Twidwell et al., 2016a, 2013a, 2009). Such high intensity fires are described as “extreme” in the sense that the fire behaves erratically, undergoes sudden and rapid changes, and fundamentally alters the structure and functioning of an ecosystem (Twidwell et al., 2016a). However, following such prescribed burns it is unclear whether grassland plant biodiversity and herbaceous communities are restored to grassland systems that had been converted to juniper woodland.

While studies have shown restoration is possible using fire in juniper woodland and that grassland biomass recovers following burning with extreme fire (Bielski et al., 2021), studies have not been conducted to assess whether biodiversity patterns following fire mimic grassland reference sites. In addition, landscape studies are extraordinarily rare in grassland fire ecology, yet are critical to better understanding the complexity in post-fire community responses (Fuhlendorf et al., 2009; Smit et al., 2016). Using a long-term, ecoregion-scale experiment (17 years of treatments on 220,000 acres in the Loess Canyons Experimental Landscape; Bielski et al. 2021), we utilize a space-for-time substitution design to (1) quantify how herbaceous community characteristics and herbaceous species richness respond to extreme fire-based restoration treatments in *J. virginiana* woodlands and compare those to reference grassland states, (2) determine how herbaceous community characteristics and species richness change with time-since-fire (tsf) treatments compared to unburned reference sites.

3.2 Methods

3.2.1 Study Site: Loess Canyons Experimental Landscape

The Loess Canyons Experimental Landscape (LCEL) covers 72,843 ha in central Nebraska and is the result of partnerships we initiated between private land managers of the Loess Canyons Range Alliance (LCRA), other local PBAs, and state agencies (Bielski et al., 2021). These groups have partnered to restore fire to the Great Plains and co-produce science studying prescribed fire across its extreme range of variability. The

LCRA has conducted prescribed burns in the region almost annually since 2002, allowing this study to cover a spread of 17 years of fire (Figure 3.1). Annual prescribed burns typically are held in the spring season from February to April. Fuels density is manipulated using the cut-and-stuff technique within eastern redcedar forests (Fogarty et al., 2021). Specific weather conditions are chosen to magnify the fire intensity and ensure forest collapse (Twidwell et al., 2013a).

The region consists of steep, hilly terrain and sandy loess soil that is easily eroded into sloping canyons. Elevations range from 781 to 989 m above sea level. The region receives an average 550 mm of precipitation annually and the mean annual temperature is

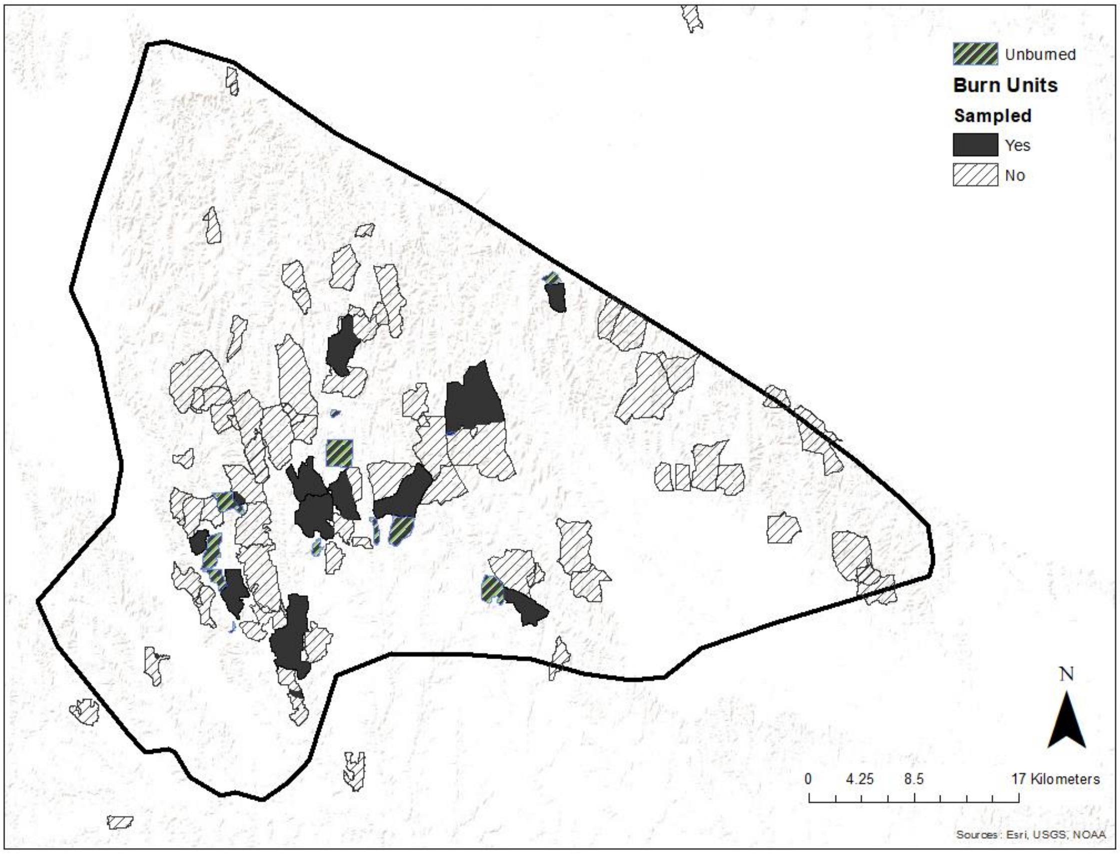

Figure 3.1 Locations of burn units in the Loess Canyons Experimental Landscape. Dark polygons are burn units in which burned grassland and fire-collapsed juniper woodland were sampled. Green and black striped polygons were paired reference sites where unburned grassland and intact juniper woodland were sampled. White and black striped polygons were other burn units in the region that were not sampled.

9.8 ºC (Arguez et al., 2012). It supports mixed-grass prairie as well as several species of significance, such as the federally-listed American burying beetle (Walker and Hoback, 2007). The region is classified by the state as a biologically-unique landscape (Schneider et al., 2011), but in recent years woody encroachment by eastern redcedar has been identified as a threat to the region's ecological significance. Suppression of fire and the disruption of the historical fire-return interval has resulted in woody encroachment of grassland areas (Fogarty et al., 2020).

3.2.2 Experimental Design and Sampling

In the LCEL, we selected 13 burn units across a gradient of 17 years for sampling (Figure 3.1; Table 3.1) to allow for a space-for-time substitution to assess herbaceous species richness and basal cover after extreme fire. Each burn unit was paired with a nearby unburned unit to sample as a reference site. Burn units were chosen based on: 1) the

Table 3.1 Summary of burn units sampled for herbaceous plant richness and percent cover. All units were sampled in 2019.

Burn Unit	Year Burned	tsf (yrs)	Area (ha)	Area (acres)
38_E_2002	2002	17	162	400
40_S_2005	2005	14	28	69
15_N_2008	2008	11	366	904
30_D_2009	2009	10	37	91
14_N_2010	2010	9	505	1248
17_G_2011	2011	8	313	773
5_S_2012	2012	7	751	1856
36_E_2014	2014	5	434	1072
52_S_2015	2015	4	304	751
58_S_2016	2016	3	1041	2572
61_G_2017	2017	2	593	1465
69_D_2018	2018	1	121	299
72_K_2019	2019	0.333	308	761
Total Area Burned:			4963	12261

temporal gradient to ensure a comprehensive spread of years, 2) a wide-ranging spatial spread across the core of fire activity on the landscape, 3) the size of the burn unit to ensure a reasonable number of plots available for sampling, and 4) the availability of a nearby unburned unit to pair as a reference site. Within each of the 26 burned and unburned units, two plots were selected. In the unburned units, one unburned grassland plot and one unburned woodland reference plot were selected (Figure 3.2). In the burned units, one burned grassland plot and one grassland restoration plot were selected. Grassland restoration plots consisted of localized extreme fire in closed-canopy cedar woodlands which caused the collapse of the cedar woodland and restored it to a grassland state, leaving only tree skeletons. A total of 52 plots across 26 units were sampled from July to September 2019. To be selected for sampling, the plots had to be at least

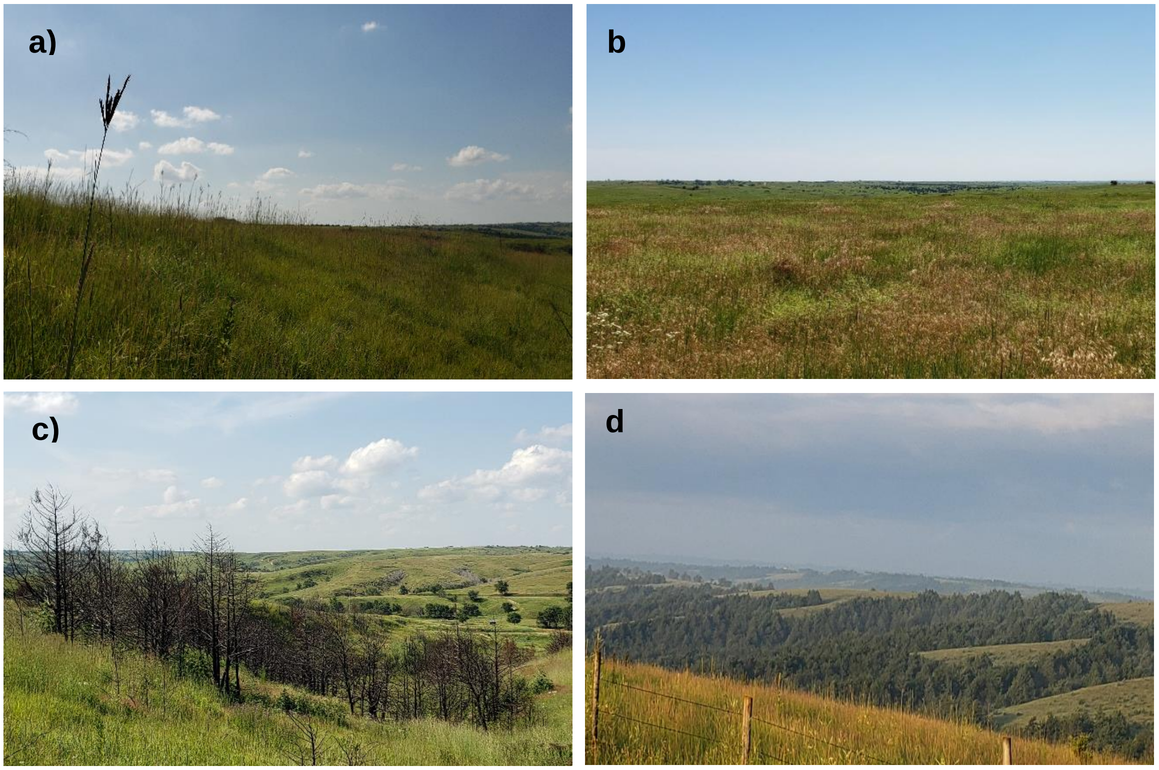

Figure 3.2 Examples of plot types sampled. a) Burned grasslands; b) unburned grasslands; c) restored grassland from fire-collapsed juniper woodland; and d) unburned juniper woodlands.

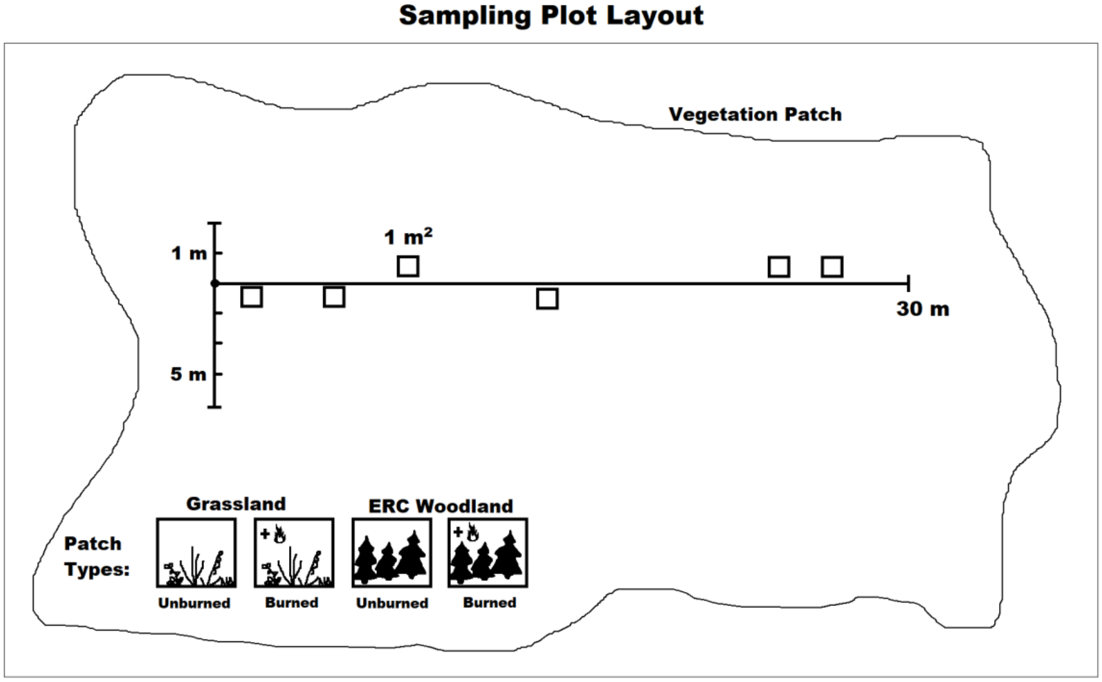

Figure 3.3 Plot sampling layout. The starting point was randomly chosen along a 5 m transect that was laid parallel to the slope, then the main transect laid out perpendicularly from the starting point for 30 m. A 1-m^2 quadrat was placed at six random locations along the transect. Within the quadrat, all herbaceous plants were identified to species. Percent basal cover of each species in the quadrat was estimated.

40 m x 15 m to allow for a minimum 5-meter buffer on all sides of the plot and reduce edge effects. On each plot, a starting point was randomly chosen along a 5 m tape laid parallel to the slope (Figure 3.3). At that point, a 30 m transect was run perpendicularly from the slope across the length of the plot. If the plot was on a hillside, the transect followed the contour of the hill to avoid cresting the top or descending to the bottom so as to reduce variability in sampling, since vegetative communities can vary greatly between the drier crests and wetter troughs of hills. All random numbers were predetermined through a random number generator at [https://www.random.org/] and recorded before beginning field work to avoid sampling biases in the field.

After the 30 m transect was laid out, 6 points were randomly chosen along the entire length of the transect (Figure 3.3). A 1-m^2 sampling quadrat was placed at each randomly chosen point. The quadrat was placed on either the right or left side of the transect at random. Within each quadrat, all herbaceous plant species were identified to the species level, with a few exceptions that were only identifiable to genus and treated consistently as recorded unknowns. The percent basal cover of all herbaceous plants in the quadrat was visually estimated. Herbaceous vegetation must be alive and rooted more than 50% inside the quadrat to be identified and estimated. A complete list of plant species encountered in the field can be found in Appendix A.

3.2.3 Analysis

To examine changes in the herbaceous plant community across time and between site types, we used a non-metric multidimensional scaling (NMDS) analysis in the ‘vegan’ package in R (Oksanen et al., 2020). We averaged percent cover for each plant species across the transect sampled at each site. We then generated a pair-wise distance matrix using the Canberra distance metric. We used the Canberra distance metric reduced over 4 dimensions in our NMDS because this offered the most acceptable stress levels (Kruskal, 1964). Environmental vectors were calculated using the function ‘envfit’ for time since fire and plant functional groups (annual/perennial, native/nonnative, warm/cool season, and forb/grass/sedge/subshrub).

We used PERMANOVA to test for differences in herbaceous plant community composition among the four plot types: unburned grasslands, unburned woodlands, burned grasslands, and grassland restoration sites. We confirmed homogeneity of dispersion among groups by calculating multivariate dispersions within each group using the function ‘betadisper’ and then testing for differences using ANOVA. We then used the function ‘adonis’ to identify differences in community composition among groups.

Total species richness and mean percent basal cover of herbaceous species was calculated across the four plot types. We used non-parametric local regression (loess) smoothing curves to visualize trends in total species richness and mean basal percent cover to compare trends in each of the four plot types relative to time-since-fire. Loess smoothing curves were applied to illustrate trends using the ‘ggplot2’ package in R (Wickham, 2016). All analyses and figures utilized the R statistical software (R Core Team, 2021).

3.3 Results

3.3.1 Herbaceous response to restoration

Differences in community composition among grassland restoration sites, unburned woodlands, burned grasslands, and unburned grasslands were largely distinguished along NMDS axis 1 in our analysis (Figure 3.4). Following axis 1 from left to right there is a woodland-to-grassland gradient, with unburned woodland at the far left, followed by restored grassland (which was woodland collapsed by extreme fire and restored to a grassland state), then unburned grassland, and finally burned grassland at the far right. There was a high level of similarity in herbaceous community composition between burned grasslands and unburned grasslands across sample sites (Figure 3.4; p-value = 0.16; Table 3.2). In contrast, grassland restoration sites within juniper woodlands differed significantly from unburned juniper woodlands (p-value < 0.01; Table 3.2). Grassland restoration sites in juniper woodlands had a community composition that was split between burned and unburned grasslands and unburned woodlands (Figure 3.4).

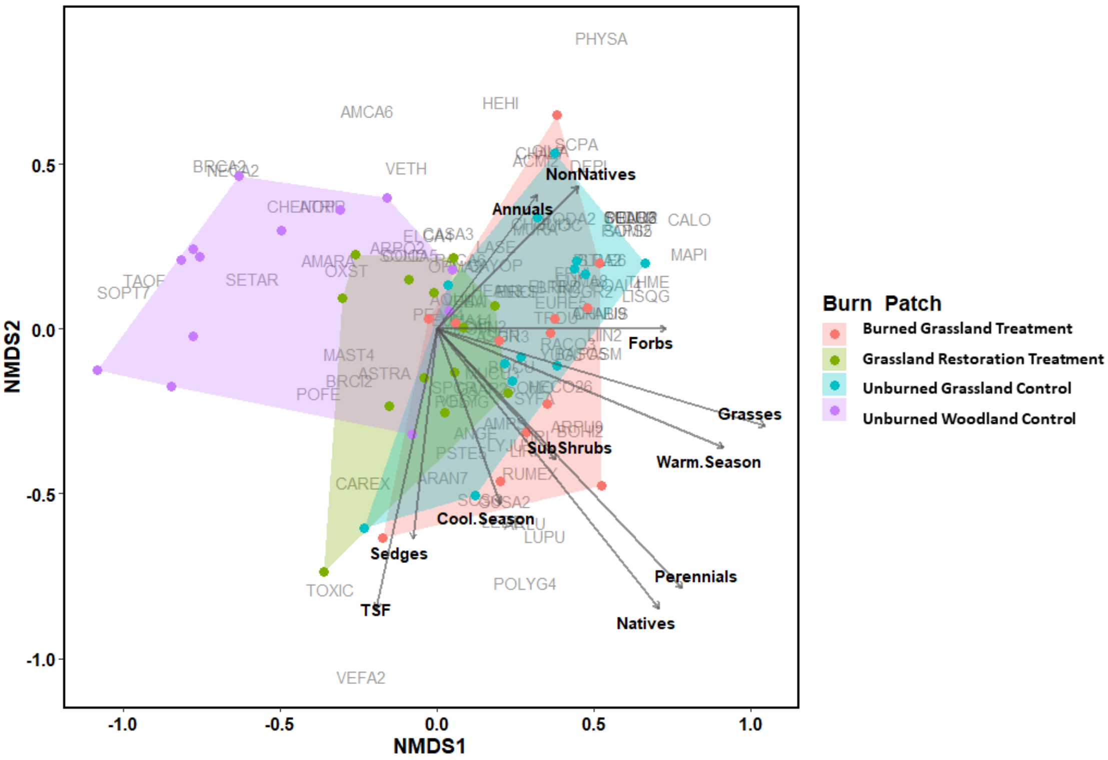

Figure 3.4 Plant community composition of four plot types as shown by non-metric multidimensional scaling (NMDS). Plot shows major axes of the NMDS with continuous vectors showing relationships of plant community functional groups.

Herbaceous community composition within grassland restoration sites was significantly different to burned grasslands (p-value = 0.02; Table 3.2) and unburned grasslands (p-value < 0.01; Table 3.2). Unburned woodlands had largely different community compositions compared to restored grasslands (p-value < 0.01), burned grasslands (p-value < 0.01), and unburned grasslands (p-value < 0.01; Table 3.2).

Species compositions in grassland restoration sites appeared to be a combination of species found in woodland and grassland sites (Figure 3.4). Common dandelion (*Taraxacum officinale*) and West Indian nightshade (*Solanum ptycanthum*) were strongly associated with unburned woodlands. Scaly blazing star (*Liatris squarrosa*), prairie

Table 3.2 Differences in herbaceous species compositions among restored grasslands (RG), unburned woodlands (UW), burned grasslands (BG), and unburned grasslands (UG) indicated by PERMANOVA.

	Df	Sum of Sqs	R^2	F	Pr(>F)
RG x UW	1	1.09	0.11	2.96	<0.01
BG x UG	1	0.43	0.05	1.16	0.16
RG x BG	1	0.50	0.05	1.34	0.02
UW x UG	1	1.41	0.14	3.87	<0.01
RG x UG	1	0.61	0.06	1.65	<0.01
UW x BG	1	1.36	0.13	3.71	<0.01

sandreed (*Calamovilfa longifolia*), and lacy tansyaster (*Machaeranthera pinnatifida*) were more common in burned grasslands and unburned grasslands. The occurrence of forbs, grasses, perennial, native, and warm season species was strongly associated with grassland restoration sites, burned grasslands, and unburned grasslands (Figure 3.4).

Mean herbaceous species richness was over two times greater in grassland restoration sites (17.2 ± 5.4 SD) compared to unburned woodlands (8.2 ± 3.6 SD) (Figure 3.5). Mean species richness was similar between burned grasslands (19.2 ± 4.6 SD), unburned grasslands(18.1 ± 4.4 SD), and grassland restoration sites (17.2 ± 5.4 SD). Burned grasslands, unburned grasslands, and grassland restoration sites all had a maximum species richness of 26 across sites, while unburned woodlands had a maximum species richness of 14 across sites (Figure 3.5). Burned grasslands and unburned grasslands had a minimum species richness of 9 across sites, while grassland restoration sites had a minimum species richness of 6 and unburned woodlands had a minimum species richness of 3 (Figure 3.5).

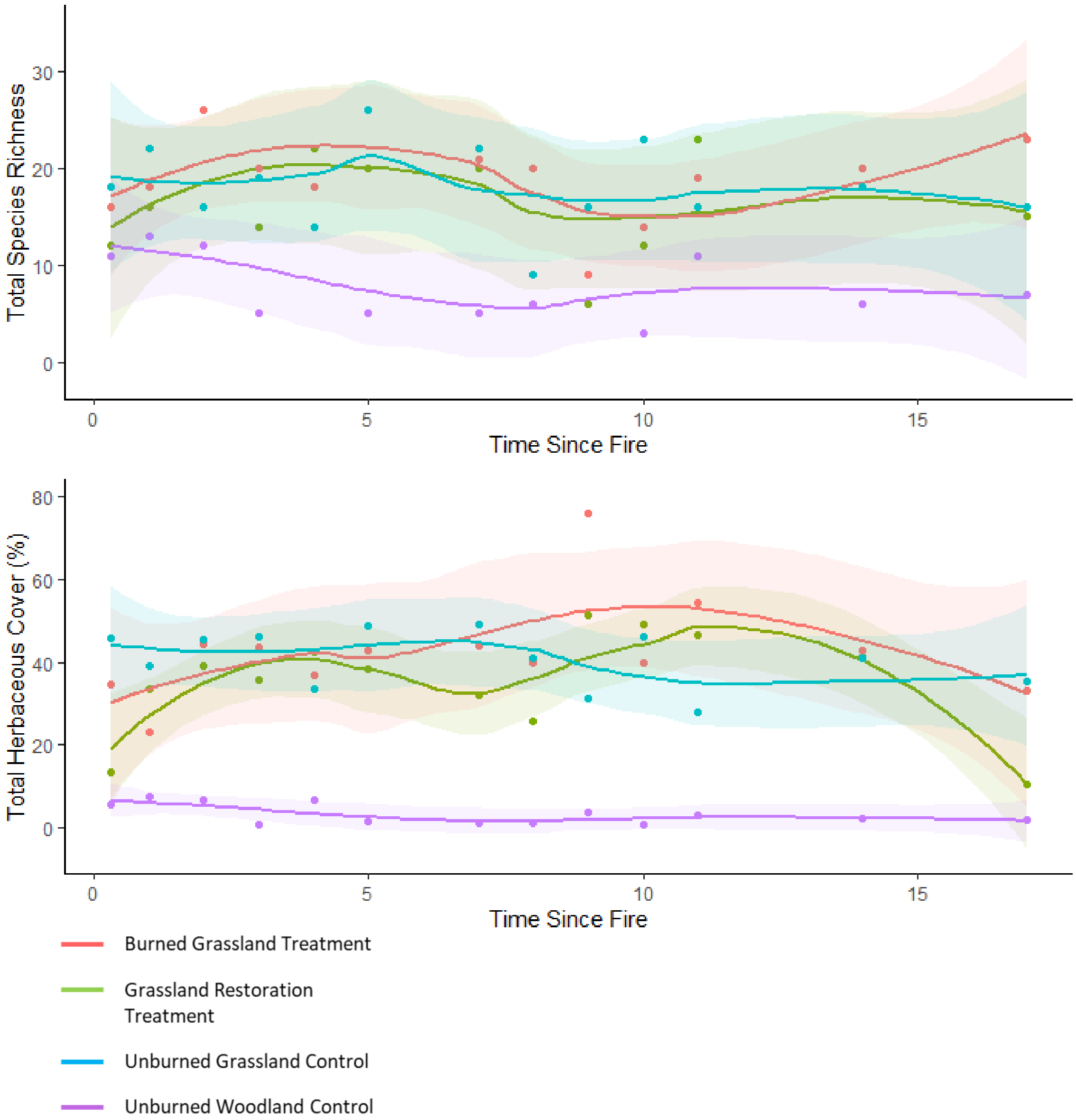

Figure 3.5 The change in total species richness and total herbaceous cover relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

Grassland restoration sites had higher native species richness compared to unburned woodlands (Figure 3.6). Native species richness in grassland restoration sites was similar to burned grasslands and unburned grasslands. Grassland restoration sites had similar nonnative species richness to unburned woodlands, burned grassland sites, and

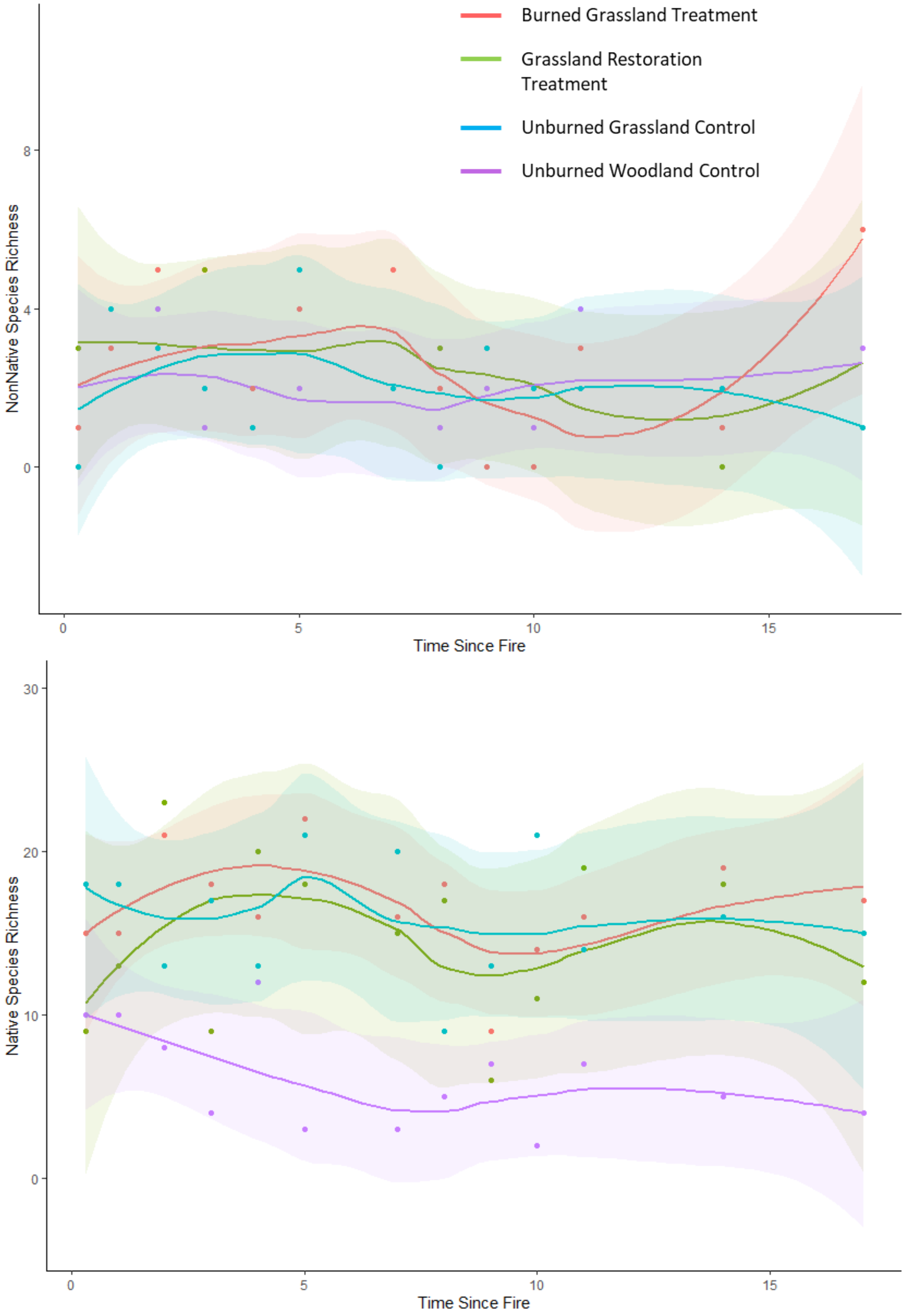

Figure 3.6 The change in native and nonnative species richness at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

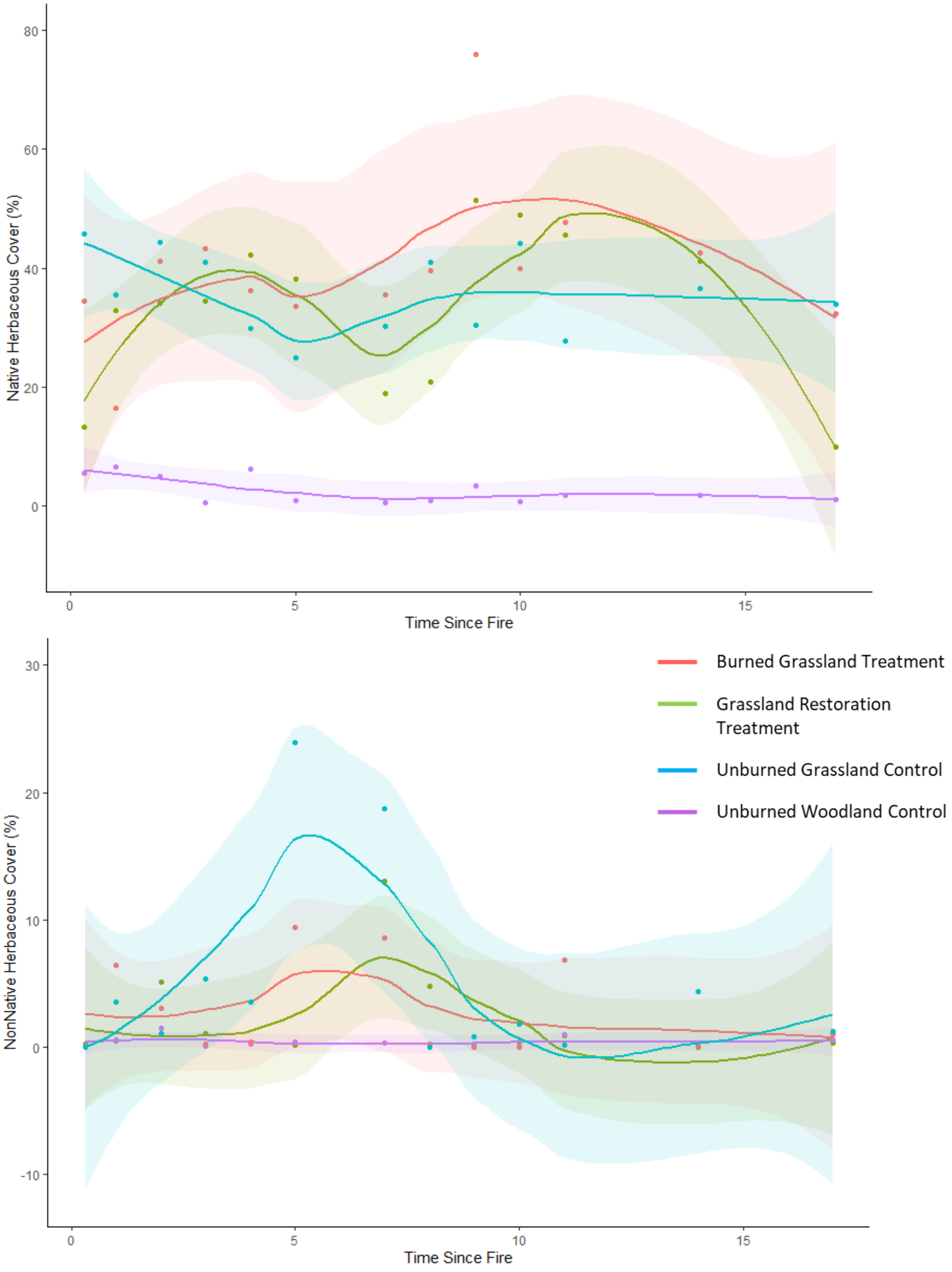

Figure 3.7 The change in Native and Nonnative herbaceous basal percent cover at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

unburned grasslands. Grassland restoration sites had higher native percent cover compared to unburned woodlands (Figure 3.7). Burned grasslands in general had higher or similar native percent cover to unburned grasslands.

Mean herbaceous cover in grassland restoration sites was 12 times greater than unburned woodlands (Figure 3.5; 37.3% ± 16.8 versus 3.1% ± 2.5 SD, respectively). Mean herbaceous cover was similar between grassland restoration sites (37.3% ± 16.8 SD), unburned grasslands (40.8% ± 7.0 SD), and burned grasslands (42.7% ± 12.4 SD). Maximum herbaceous cover in grassland restoration sites was 10 times great than unburned woodlands (77.5% versus 7.2%, respectively). Maximum herbaceous cover was similar between grassland restoration sites (77.5%) and burned grasslands (76%). Maximum cover at unburned grasslands (49%) was about two-thirds as much as at grassland restoration sites. Minimum herbaceous cover in restored grasslands was 17 times greater than unburned woodlands (10.25% versus 0.6%, respectively). Minimum herbaceous cover in burned grasslands (22.9%) and unburned grasslands (27.9%) was two and three times as much as in restored grasslands (10.25%), respectively.

3.3.2 Herbaceous response to time since fire

Patterns in NDMS axis 2 were strongly associated with patterns in time since fire (Figure 3.8). Species near the upper-mid quadrant of ordination were most associated with earlier tsf communities, whereas species near lower-mid quadrant were more associated with greater time since fire (Figure 3.8). Sedges, cool season grasses, perennials, and native species were more common with greater time since fire, while annuals and non-native species were more strongly associated with lower time since fire. In the second NMDS

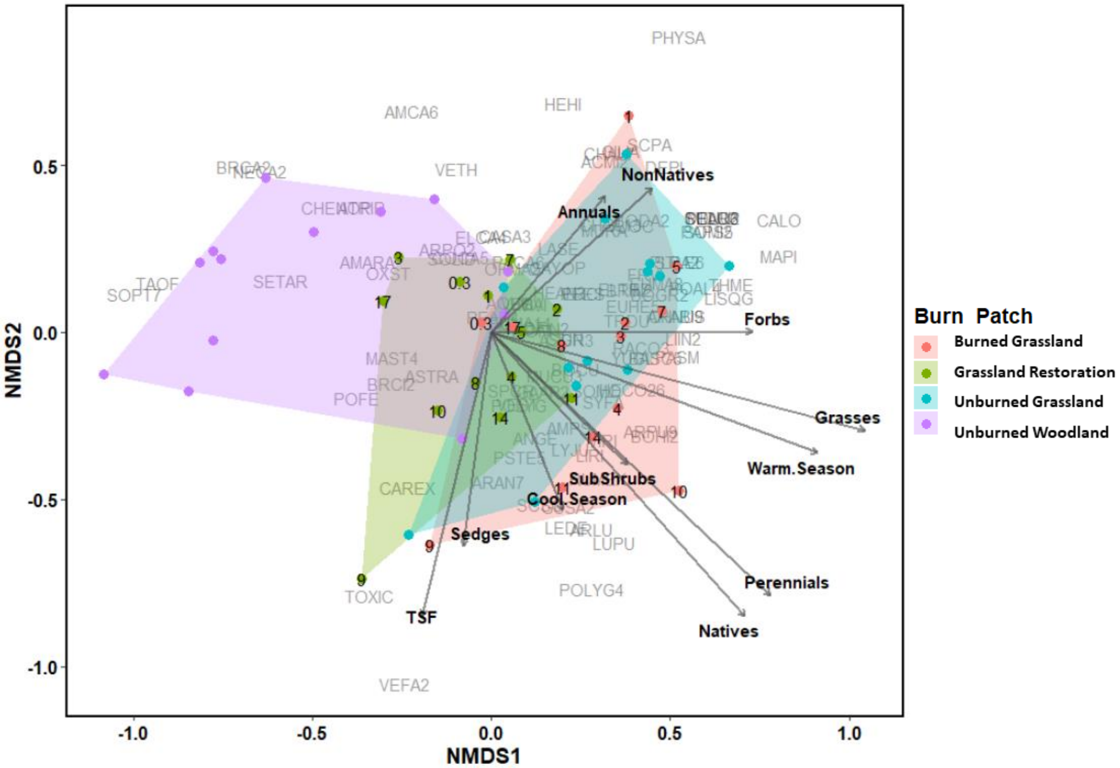

Figure 3.8 Plant community composition of four plot types as shown by non-metric multidimensional scaling (NMDS) with time since fire (tsf) indicated for all burned plots. Plot shows major axes of the NMDS with continuous vectors showing relationships of plant community functional groups.

plot, grassland restoration sites and burned grasslands tended to separate along a time since fire gradient (Figure 3.8). Younger burned areas grouped near the top of the plot, while older burned areas grouped towards the bottom. However, the oldest burned areas (tsf = 17) were near the middle of the NMDS plot, not going strongly in either direction of the tsf gradient (NMDS axis 2).

Grassland restoration sites and burned grasslands had similar patterns in species richness response to time since fire, except at the end of our time since fire gradient (~14 years since burning) where burned grasslands increased in species richness while restored grasslands decreased (Figure 3.5). Grassland restoration sites and burned grasslands had higher species richness than unburned woodlands only four months following fire. Mean species richness was highest in restored grasslands 2 years after fire (11.8 ± 2.5 SD) (Figure 3.5). In burned grasslands, mean species richness was also highest 2 years after fire (12.7 ± 1.4 SD). Grassland restoration sites and burned grasslands reached lowest mean species richness 9 years after fire (2.5 ± 1.0 SD; 4.2 ± 1.5 SD, respectively).

Native species richness showed a slight increase through time in grassland restoration sites, while nonnative species richness showed a slight decrease (Figure 3.6). The opposite was true for unburned woodlands. Grassland restoration sites had higher native species richness than unburned woodlands across the entire tsf gradient, except at 0.3 years tsf. Grassland restoration sites had a higher nonnative species richness than unburned woodlands except after 10 years tsf, where restored grasslands had lower nonnative species richness. Burned grasslands and unburned grasslands shared similar trends for both native and nonnative species richness, except at 17 years tsf, where burned grasslands had an increase in nonnative species while unburned grasslands had a decrease. Native percent cover showed a bimodal distribution in grassland restoration sites, increasing and then decreasing at two inflection points at 5 years tsf and 14 years tsf (Figure 3.7). Burned grasslands showed a similar, but dampened trend. Nonnative percent cover was less variable across most of the tsf gradient, especially for unburned woodlands. However, grassland restoration sites, burned grasslands, and unburned grasslands all showed a spike in nonnative percent cover from 5-7 years tsf.

Like species richness, mean herbaceous cover was similar between grassland restoration sites and burned grasslands. Mean herbaceous cover in grassland restoration sites and burned grasslands was highest 9 years after fire (51.5% ± 21.3 SD; 76% ± 12.3

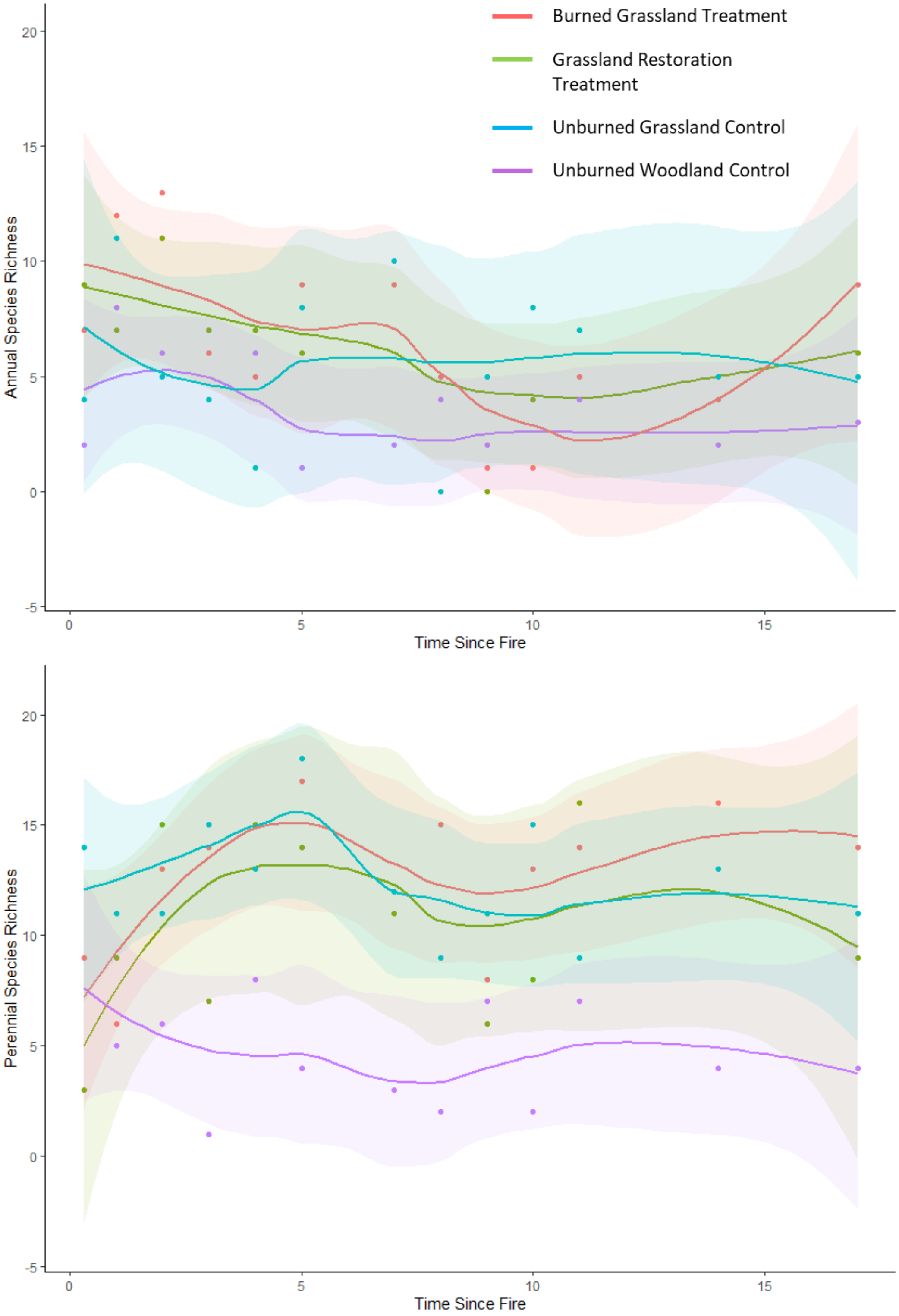

Figure 3.9 The change in annual and perennial species richness at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

SD, respectively; Figure 3.5). However, patterns differed between burned grasslands and grassland restoration sites near the end of our time since fire gradient, with much more drastic declines in herbaceous cover in grassland restoration sites 17 years post fire. The lowest mean cover in grassland restoration sites was 17 years after fire (10.3% ± 4.6 SD). Lowest mean cover in burned grasslands was 1 year after fire (22.9% ± 7.6 SD).

Grassland restoration sites had higher annual and perennial species richness compared to unburned woodlands (Figure 3.9). Annual species richness declines through time in grassland restoration sites, while perennial species richness increases (Figure 3.9). Immediately after fire (tsf < 1 year), perennial species richness was lower in grassland restoration sites compared to unburned woodlands but increased above unburned woodland levels after tsf = 1 year.

3.3.3 Herbaceous functional group responses to restoration

Grassland restoration sites had higher annual and perennial percent cover compared to unburned woodlands (Figure 3.10). Annual and perennial percent cover in grassland restoration sites was more variable, but similar to burned grasslands and unburned grasslands. Annual percent cover largely declines through time in grassland restoration sites, while perennial percent cover increases through time before decreasing after 10 years tsf (Figure 3.10). Annual percent cover for unburned woodlands, burned grasslands, and unburned grasslands remains fairly static through time. Perennial percent cover in burned grasslands increases through time before decreasing after 10 years tsf.

Grassland restoration sites had higher warm and cool season species richness compared to unburned woodlands (Figure 3.11). The warm and cool season species

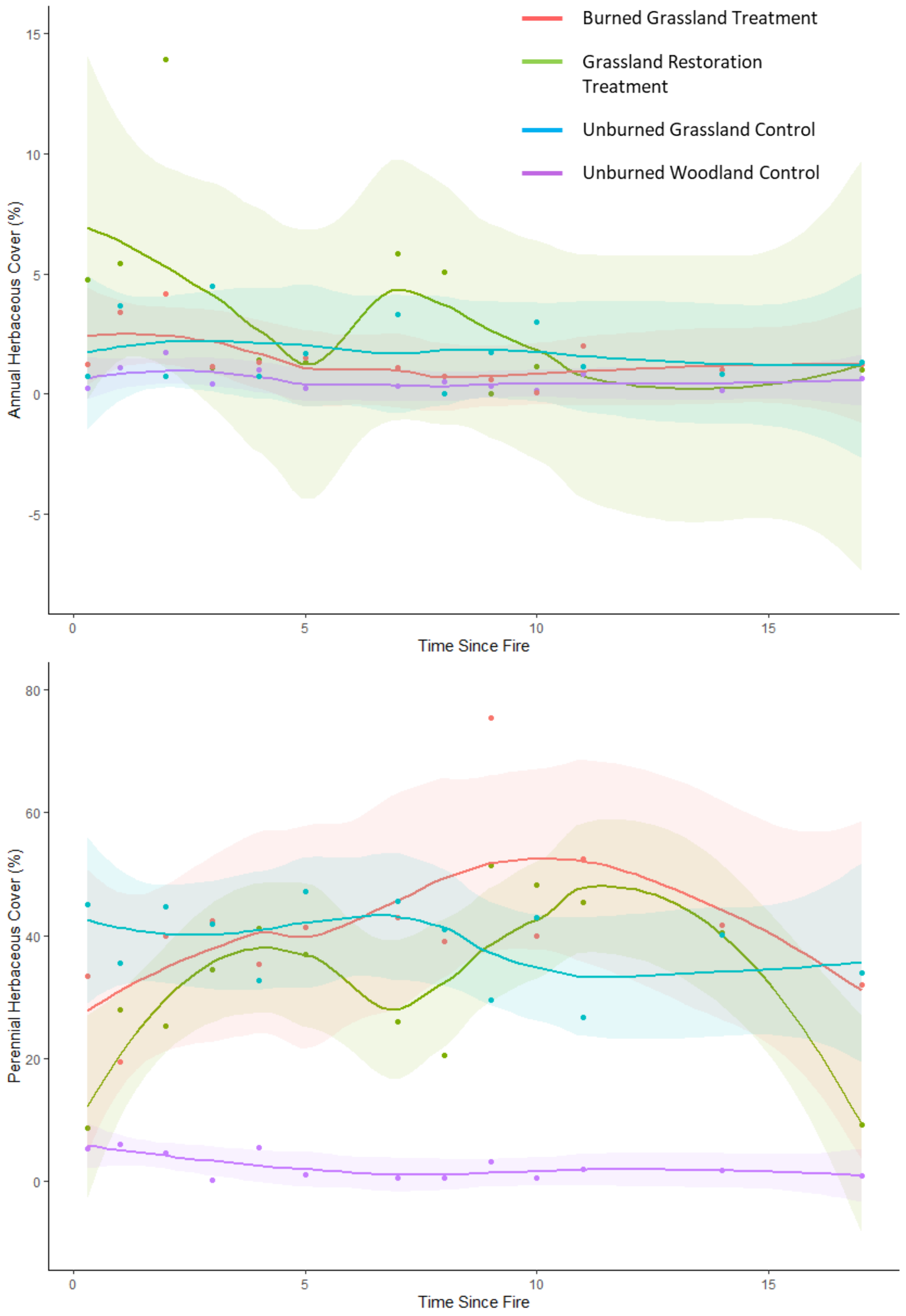

Figure 3.10 The change in annual and perennial herbaceous basal percent cover at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

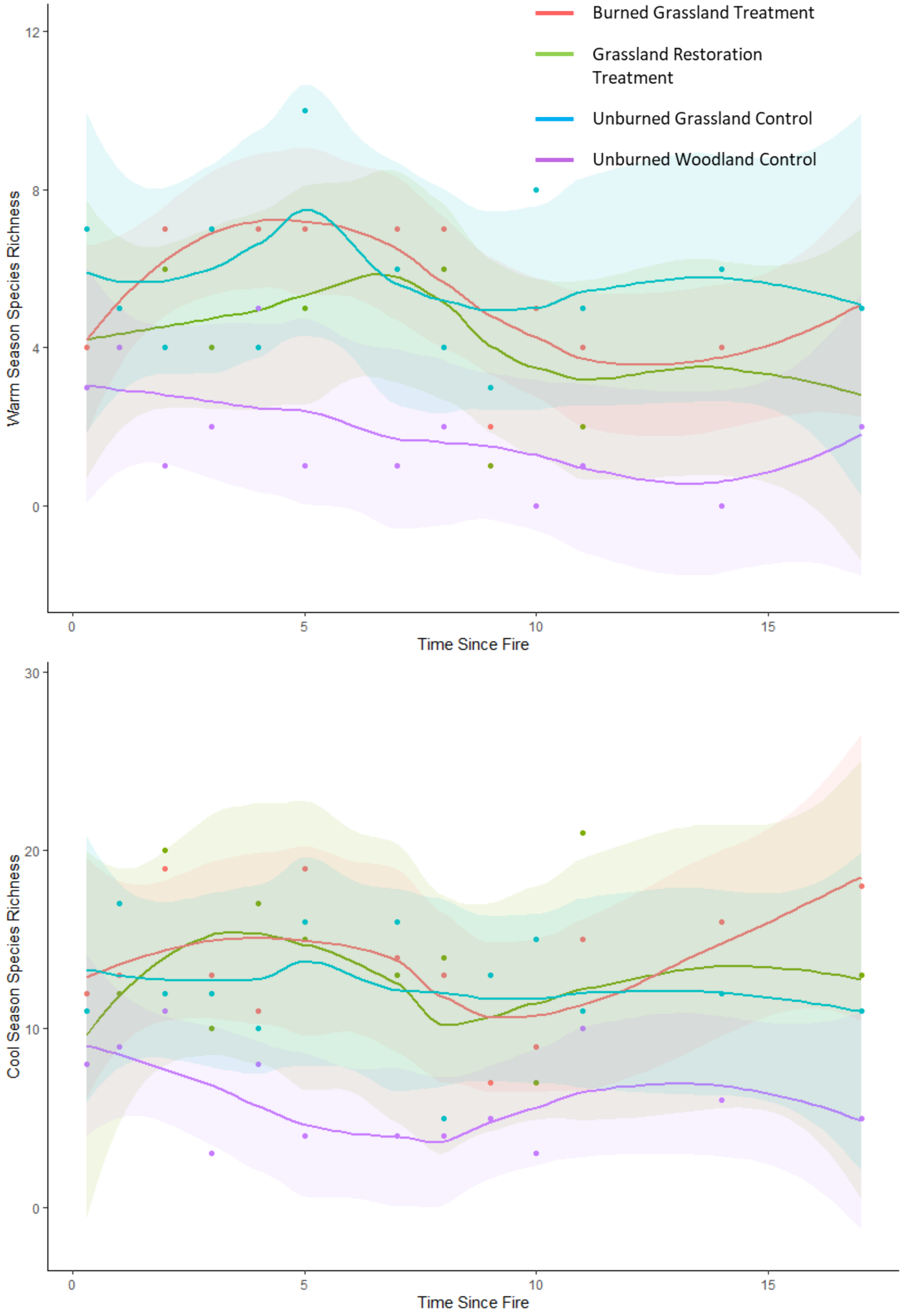

Figure 3.11 The change in warm season and cool season species richness at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

richness in grassland restoration sites was relatively similar to burned grasslands and unburned grasslands. Warm season species richness showed a slight decrease through time in grassland restoration sites, while cool season species richness showed a slight increase (Figure 3.11). Burned grasslands and unburned grasslands largely shared trends for both warm and cool season species richness across tsf.

Grassland restoration sites had higher warm and cool season percent cover compared to unburned woodlands (Figure 3.12). The warm and cool season percent cover in grassland restoration sites was similar to burned grasslands and unburned grasslands. Warm season percent cover in grassland restoration sites was mostly the same through time, with a sudden drop in percent cover at 17 years tsf (Figure 3.12). Cool season percent cover in grassland restoration sites was higher than in unburned woodlands, except at 0.3 years tsf. Burned grasslands and unburned grasslands shared similar trends for both warm and cool season percent cover across tsf.

Grassland restoration sites had higher grass and forb species richness compared to unburned woodlands (Figure 3.13). The grass and forb species richness in grassland restoration sites was relatively similar to burned grasslands and unburned grasslands. Grass species richness showed a slight decrease through time restored grassland, while forb species richness trends remained fairly similar across tsf in grassland restoration sites (Figure 3.13). Burned grasslands and unburned grasslands closely shared trends for grass species richness across tsf, although forb species richness was more variable in burned grasslands across tsf.

Grassland restoration sites had higher grass and forb percent cover compared to unburned woodlands (Figure 3.14). The grass and forb percent cover in grassland

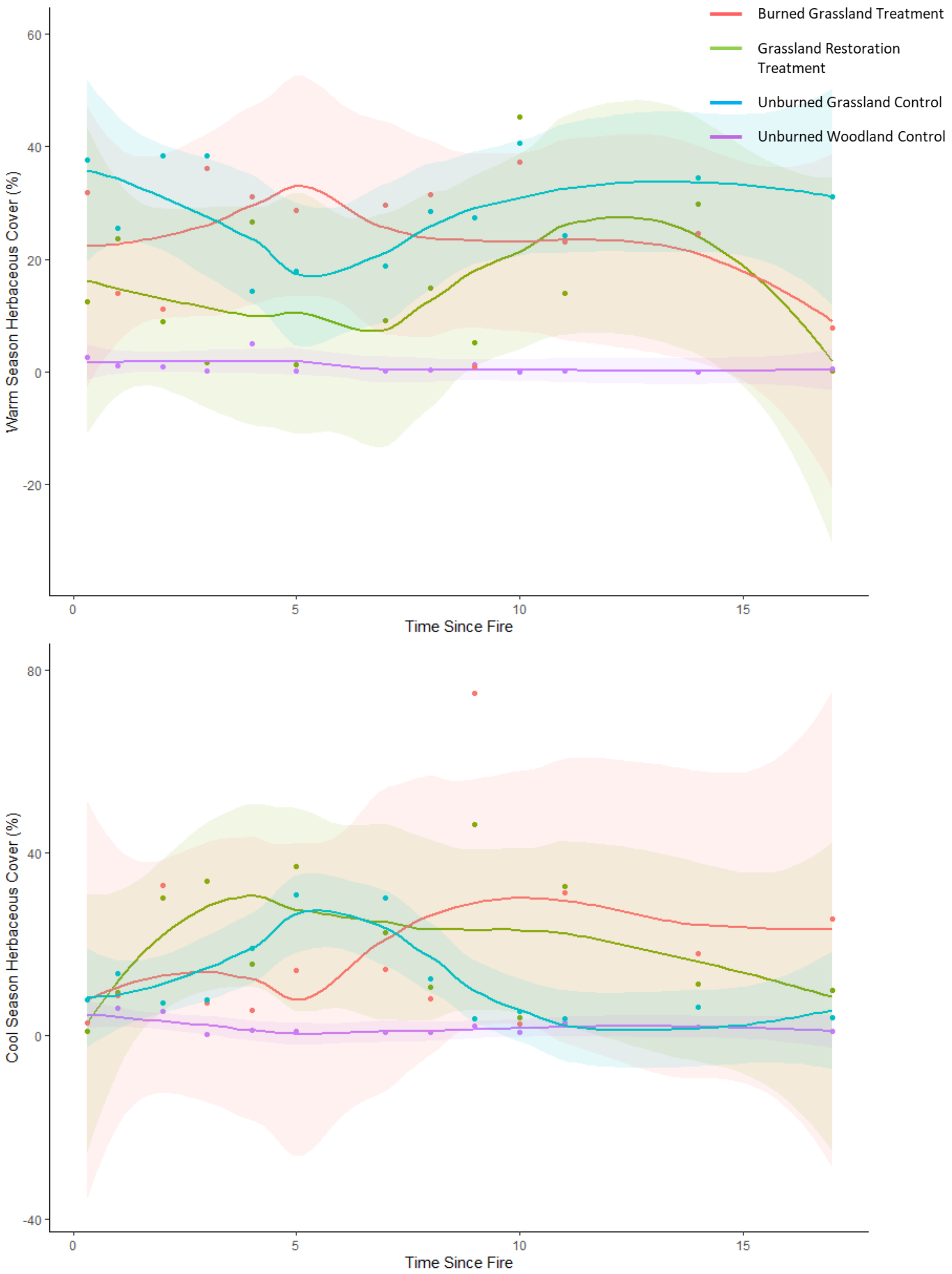

Figure 3.12 The change in warm season and cool season herbaceous basal percent cover at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

restoration sites was relatively similar to burned grasslands and unburned grasslands. Forb percent cover in grassland restoration sites spikes at 2 years tsf, then decreases over time (Figure 3.14). Grass cover decreases over time in grassland restoration sites. Burned grasslands and unburned grasslands had similar trends for grass and forb percent cover across tsf.

All site types had similar levels of subshrub and sedge species richness (Figure 3.15). Subshrub and sedge species richness was mostly static across tsf for all site types (Figure 3.15). Grassland restoration sites had a small increase in subshrub species richness across tsf.

All site types had similar levels of subshrub percent cover (Figure 3.16). Sedge percent cover was similar in grassland restoration sites and burned grasslands, and both were higher than the sedge percent cover in unburned woodlands and unburned grasslands. Subshrub percent cover was mostly static across tsf for all site types (Figure 3.16). Sedge cover in burned grasslands was similar to unburned grasslands in early tsf, but spiked at 9 years tsf. Grassland restoration sites had a similar but smaller increase in sedge percent cover at 9 years tsf.

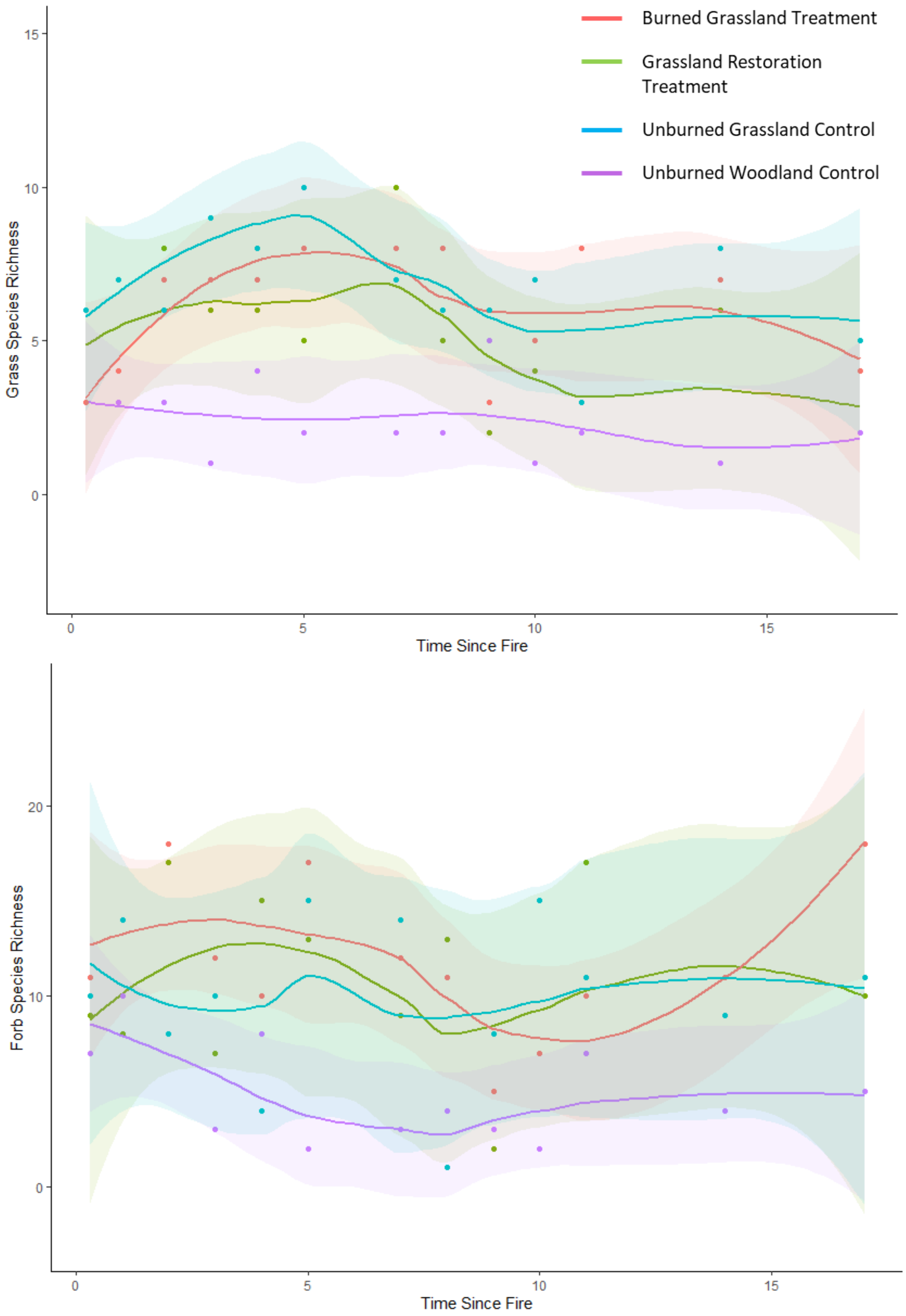

Figure 3.13 The change in forb and grass species richness at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

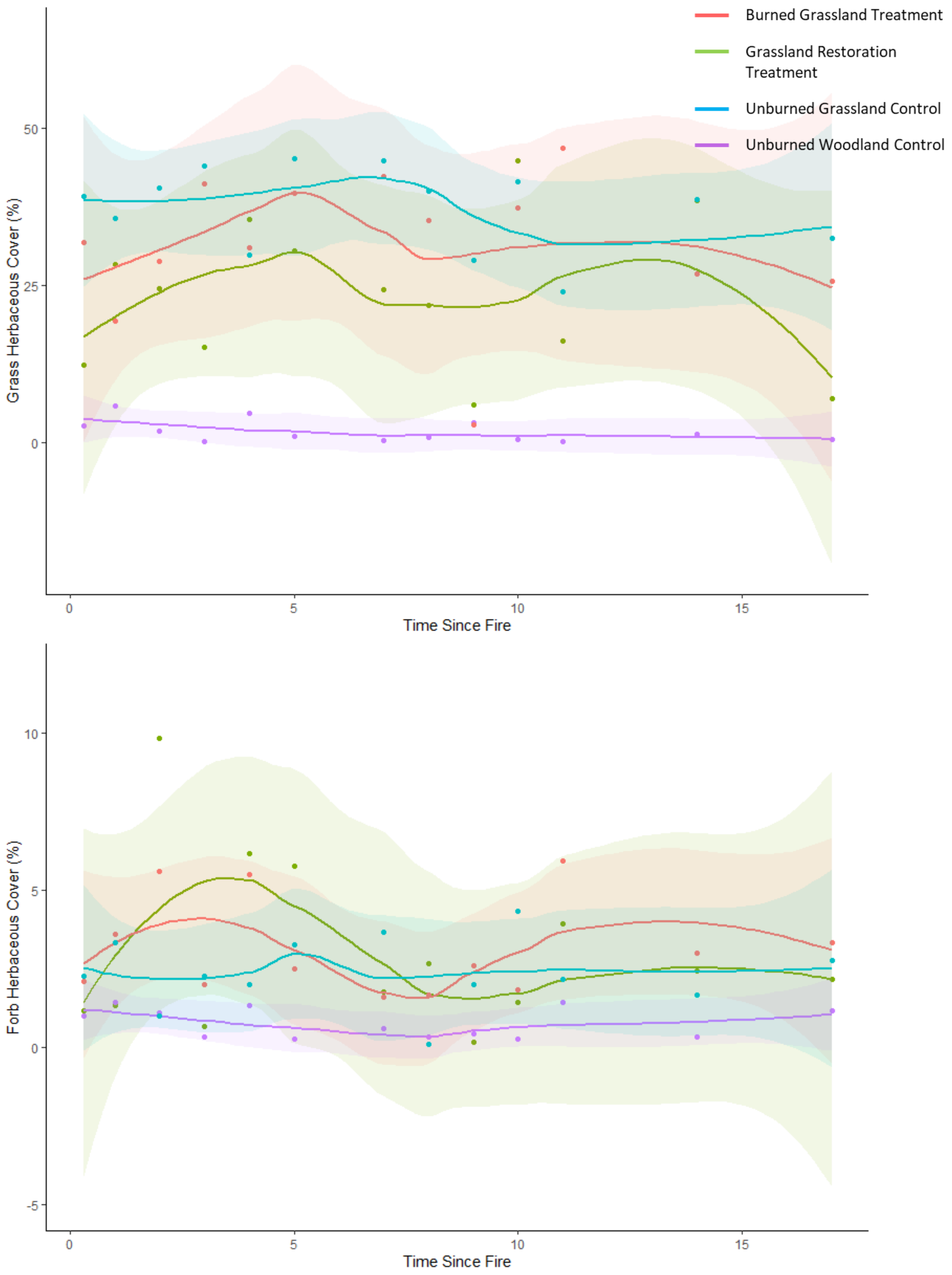

Figure 3.14 The change in grass and forb basal percent cover at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

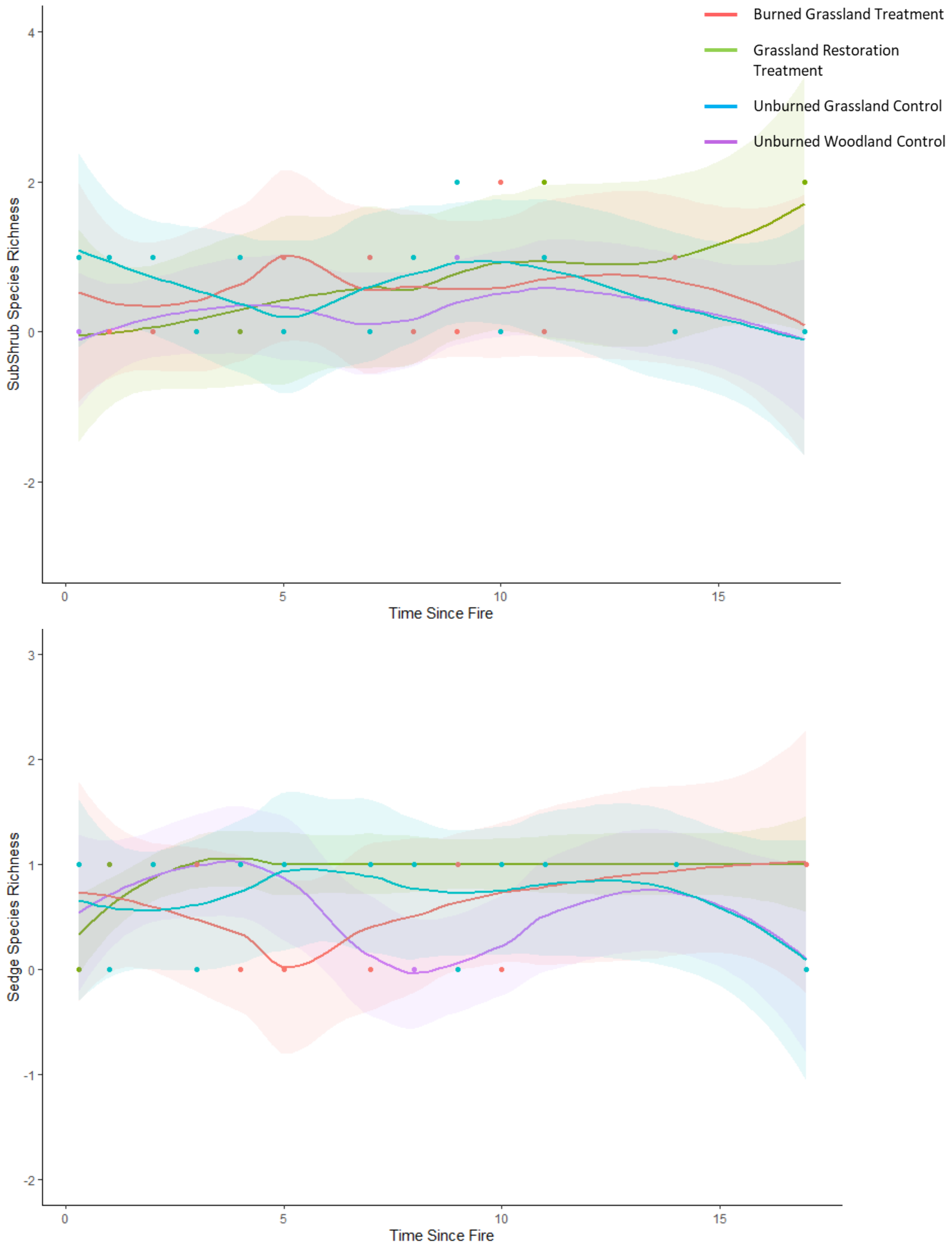

Figure 3.15 The change in subshrub and sedge species richness at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

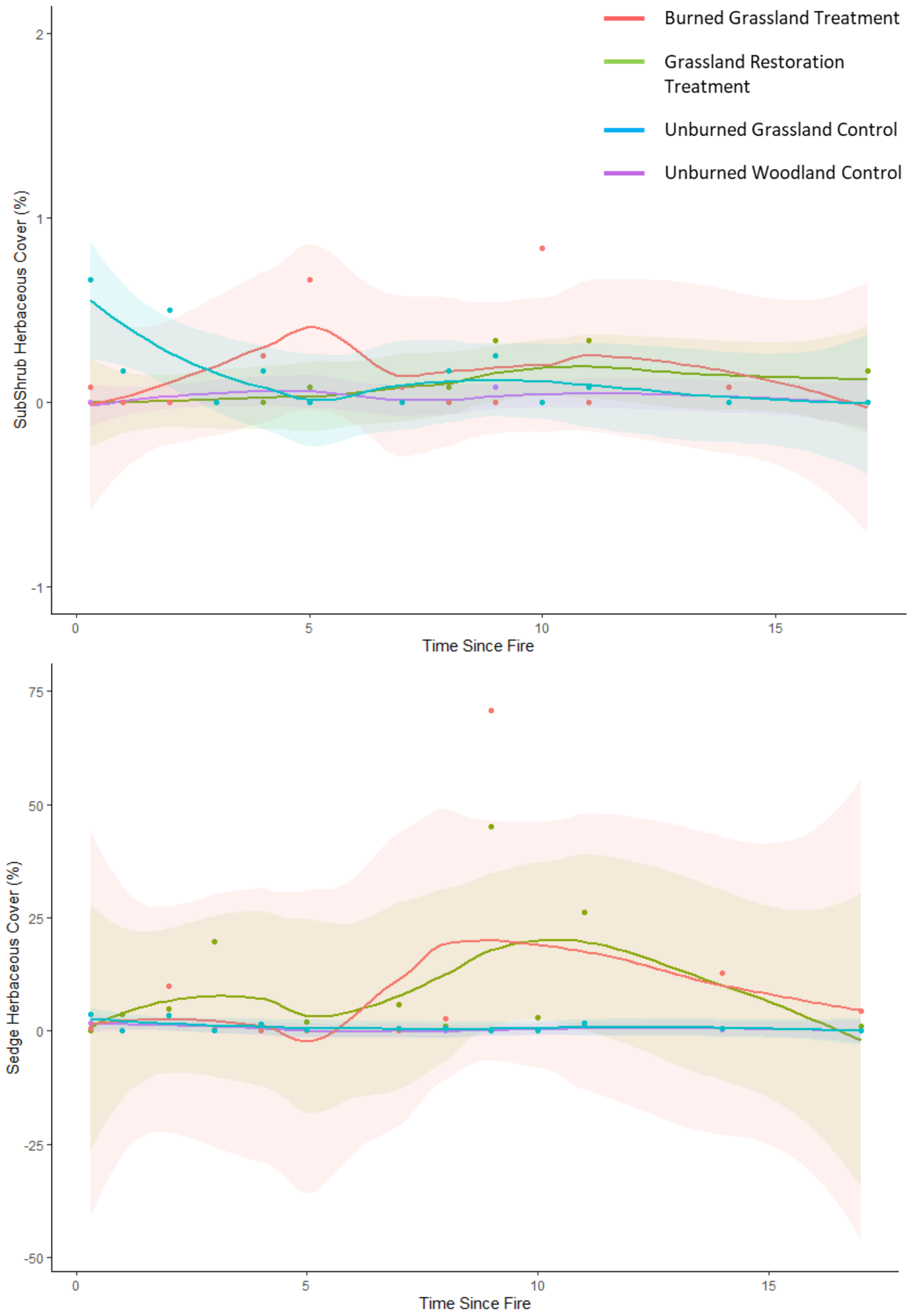

Figure 3.16 The change in subshrub and sedge basal percent cover at sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

3.4 Discussion

There are multiple possible trajectories for reorganization in restored juniper woodland following reset with fire (Allen et al., 2014; Beisner et al., 2003; Garmestani et al., 2020). If the juniper mortality threshold is not overcome by fire, the system could rebound to juniper woodland (Twidwell et al., 2013a). If the juniper mortality threshold is overcome by fire of sufficient intensity, the system could transition to a grassland regime (Bielski et al., 2021). In other cases, neither juniper woodland nor grassland will arise, but rather a novel state emerges, e.g., forb dominance. Our findings agree with other studies that regime shifts between grasslands and juniper woodlands behave hysteretically and that woody encroachment in grasslands is not irreversible (Bielski et al., 2021; Fogarty et al., 2020; Twidwell et al., 2016a, 2013b). In juniper woodlands that have undergone extreme fire-based restoration treatments, we found that herbaceous species richness and percent cover returned to levels comparable to that of reference grassland states. In contrast, unburned juniper woodlands had low levels of herbaceous species richness and percent cover, consistent with other studies (Briggs et al., 2002; Ratajczak et al., 2012; Van Auken, 2009). There are relatively few studies that show herbaceous richness can be restored using only extreme fire treatments, highlighting the importance of this work.

When using prescribed fire in non-resprouting juniper woodlands, diversity responses are contingent upon exceeding the fire intensity-juniper mortality thresholds (Twidwell et al., 2013a). Success or failure is readily apparent shortly after treatment. However, mechanical removal of encroaching juniper woodland has a slower response, with species richness in restored grasslands reaching levels similar to reference grassland communities fire years after treatment (Limb et al., 2014). Although this confirms the richness patterns recorded by our study in restored grasslands for the first five years after extreme fire, it cannot be used to compare the restoration outcomes of mechanical removal and extreme fire ten or more years after restoration. In restored grasslands, studies have found that juniper re-encroachment begins shortly after treatment and can return to previous densities 5-11 years after treatment (Fogarty et al., 2021). Thus, more long-term studies (≥10 years) comparing treatment types and re-encroachment rates in restored grasslands are needed.

Modeling based on decades of data in Australian rangelands has shown that prescribed fire, along with other management activities such as grazing, can reduce some encroaching woody species and successfully restore grasslands (Noble and Walker, 2006). Conversely, other management activities such as mechanical removal through chaining, has failed to restore grasslands and simply replaced one dominant woody species (*Acacia* spp.) with several smaller woody plants (budda, green turkey-bush, and ellangowan poison bush) (Noble and Walker, 2006). In African savannas, the fire return interval was found to play an important role in the structuring of grasslands, second only to mean annual precipitation (Sankaran et al., 2008). Shorter fire return intervals led to a decrease in woody cover, suggesting that more frequent fires (fire return interval <10 years) are vital to restoring and maintaining grassland structure (Sankaran et al., 2008).

While our study demonstrated the relatively rapid restoration response in grasslands following localized extreme fire treatments, restoration success could be short-lived (Fogarty et al., 2021). The emergence of hysteretic system behavior following the transition from a grassland to a juniper woodland could establish positive feedback loops that strengthen the alternative vegetation state and make the transition difficult to reverse

(Bielski et al., 2021). Single restoration treatments are less likely to persist past a 10-year threshold as re-encroachment from external and internal seed sources begins shortly after restoration (Bielski et al., 2021; Fogarty et al., 2021; Noble and Walker, 2006; Sankaran et al., 2008). In the future, grassland restoration activities should explore variability in treatment types, intensities, and timing of application, as well as envisage mixed treatments (e.g., pyric herbivory, herbicide/prescribed fire) over decades versus one-time treatments of a single type.

CHAPTER 4

SOIL COMPACTION AND INFILTRATION RATES FOR ALTERNATIVE GRASSLAND-JUNIPER WOODLAND STATES[4]

4.1 Introduction

In rangeland and fire ecology, a space-for-time substitution provides the opportunity for time-since-fire (tsf) studies. A space-for-time substitution allows for present spatial observations of phenomena that occurred in the past across a temporal spectrum (Blois et al., 2013). In our case, a space-for-time substitution can be used to study extreme fire events that occurred across a span of 17 years and relate observed rangeland characteristics to tsf. The usual focus in the literature is applied treatment vs. control (i.e., burned vs. unburned), and not changes in properties across time-since-fire (Limb et al., 2016).

More recent work has been done to study tsf and fire effects in rangelands, including fire's impacts on herbaceous biomass over time (Bielski et al., 2021) and woody re-encroachment after fire over time (Fogarty et al., 2021). Other studies have explored the relationship of fire effects over time on habitat structure in savannas

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[4] Ludwig, A. K., V. M. Donovan, R. A. Drijber, and D. Twidwell. (2021). Soil compaction and infiltration rates for alternative grassland-juniper woodland states. Prepared manuscript for research journal submission.

AKL contributed to conceptualization, data collection and curation, formal analysis, visualization, all writing aspects, and project administration. VMD contributed to formal analysis, data curation, visualization, and writing selected sections. RAD contributed conceptualization and critical revisions. DT contributed to conceptualization, visualization, and critical revisions.

(Roberts et al., 2020). In addition to broadening temporal scale by applying tsf to their research questions, these studies have broadened the spatial scales under scrutiny (e.g., ecoregion) rather than focusing on small patch dynamics (Fuhlendorf et al., 2009).

The application of extreme fire as a land management technique adds to the toolbox for cutting-edge rangeland restoration. Extreme fire is fire applied to the landscape under specially-selected conditions that favor higher-intensity fire effects (Twidwell et al., 2020). Extreme fires show intense and variable fire behavior and are capable of shifting an ecosystem to an alternative state (e.g., collapsing closed-canopy woodland and allowing grassland re-emergence) and altering its functions (Twidwell et al., 2016a). Although extreme fire aids in management to restore grasslands, it can have negative impacts as well. High-intensity fire can heat the soil to high temperatures that change soil chemical properties, increase soil hydrophobicity, and reduce water infiltration rates (Fuhlendorf et al., 2011). However, the reintroduction to fire to the landscape (including extreme fire) can trigger shifts between alternative states, restore biodiversity, and increase heterogeneity on the landscape (Fuhlendorf et al., 2011).

We apply a space-for-time substitution design to the Loess Canyons Experimental Landscape (LCEL), a 220,000-acre region with over 15 years of fire treatments (Bielski et al., 2021), to create a long-term, ecoregion-scale experiment that will (1) quantify differences in soil compaction and infiltration rates between grasslands that have undergone collapse and reorganization to an alternative state (i.e., extreme fire treatments in woodlands to restore grassland) and grasslands that have undergone the same disturbance treatment but have not undergone reorganization (burned grasslands) and compare them to a reference unburned grassland state, and (2) determine how soil compaction and infiltration rates change with time-since-fire (tsf) treatments in burned grasslands compared to unburned reference sites in grassland and woodland.

4.2 Methods

4.2.1 Study Site

This study takes place in a region of south-central Nebraska called the Loess Canyons Experimental Landscape (LCEL) (Figure 4.1). The LCEL is a biologically-unique area in the state that consists of steep, easily-eroded loess hills and canyons (McPherron et al., 2012). It is managed through partnerships between private landowners, state and federal agencies, and NGOs, with researchers from the University of Nebraska involved in co-producing science to help manage the landscape (Bielski et al., 2021). Through the formation of the Loess Canyons Rangeland Alliance (LCRA), these groups have worked together to return fire to the landscape in order to restore grasslands and manage encroaching woody species such as eastern redcedar (*Juniperus virginiana*). Managers manipulate the fuel density prior to burning in order to increase fire intensity and subsequently collapse encroaching woodlands (Fogarty et al., 2020; Twidwell et al., 2013a). Management with extreme fire has been ongoing since 2002, providing this study with burn sites across a time gradient of 17 years.

The LCEL covers approximately 72,843 ha with elevations ranging between 781 and 989 m above sea level (Bielski et al., 2021). The region's mean annual temperature is 9.8 ºC and mean annual precipitation is 550 mm (Arguez et al., 2012). The soil parent material is primarily loess and alluvium, creating silt loams of the Coly, Coly-Hobbs, and Uly-Coly soil series (Soil Survey Staff, 2021). The landscape is predominantly composed of mixed-grass prairie that supports widespread livestock grazing, with scattered cropland

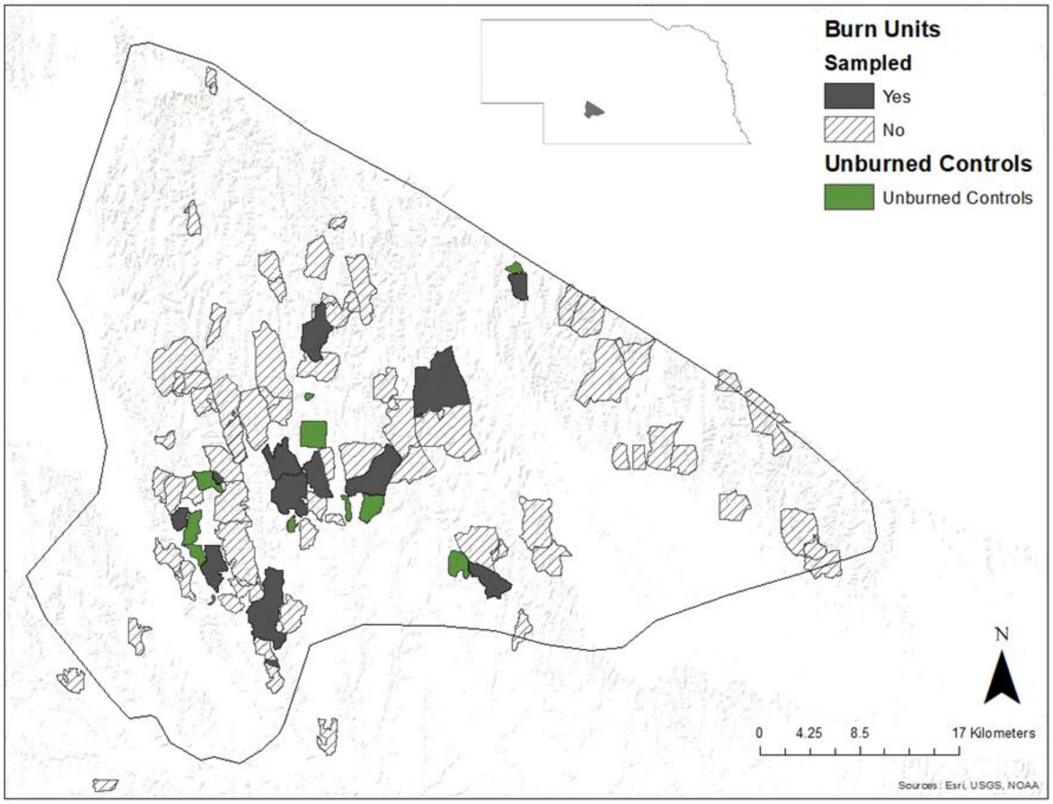


Figure 4.1 Locations of burn units in the Loess Canyons Experimental Landscape. Black polygons are burn units in which burned grassland and fire-collapsed juniper woodland were sampled. Green polygons were paired reference sites where unburned grassland and intact juniper woodland were sampled. White and black striped polygons were other burn units in the region that were not sampled.

in more level areas (Walker and Hoback, 2007). Suppression of historic fire regimes has allowed for the encroachment of eastern redcedar into much of the grasslands, threatening native prairie flora and fauna as well as livestock production (Fogarty et al., 2020).

4.2.2 Experimental design and sampling

Our sampling sites consisted of 13 burned units and 13 unburned reference units (Figure 4.1). Burned units were selected across the 17 year time gradient (Table 4.1), which allowed us to apply a space-for-time substitution to measure soil compaction levels and water infiltration rates after management with fire. Several criteria guided us as we chose burn units to sample: 1) the area of the burn unit must be large enough to provide enough plots for sampling, 2) the spatial spread across the landscape must be broad enough to encapsulate the activities of fire practitioners, 3) the temporal spread across the landscape must encompass the 17 year time gradient, and 4) unburned units must be nearby to serve as paired controls. Within the 13 burned units and 13 unburned units, two plot types were selected. These plot types consisted of a burned grassland and a grassland restoration site in the case of the burn units, and an unburned grassland and unburned woodland in the case of the unburned units (Figure 4.2). Grassland restoration sites are defined as applications of localized extreme fire that collapse closed-canopy cedar woodlands and allow the return of a grassland state. In total, 52 plots were sampled across all units from July to September 2019. Plots were chosen for sampling if they had a minimum area of 40 m x 15 m, to allow for a 5 m buffer on all sides of the plot.

Starting from a random point, a 30 m transect was run across the plot following the contour of the hill, perpendicular to the slope of the hill (Figure 4.2). At 6 regular intervals spaced 5 meters apart along the transect, soil compaction was measured at 6 depths (5 cm, 10 cm, 15 cm, 20 cm, 25 cm, 30 cm) to create a profile of soil compaction across the chosen plot. All compaction readings were taken with a DGSI double-rod static cone penetrometer with a cone tip angle of 60º and section area of 1.5 cm^2. Measurements were read directly on the penetrometer using the cone index (Q_c) gauge that is output in kg/cm^2 with a maximum reading of 70 kg/cm^2.

Table 4.1 Summary of all burn units in the LCEL. Soil compaction and water infiltration rate were sampled in selected units.

Burn Unit	Year Burned	tsf (yrs)	Area (ha)	Area (acres)	Sampled (y/n)
38_E_2002	2002	17	162	400.3	X
9_D_2002	2002	17	171	422.6	
25_G_2002	2002	17	33	81.5	
2_T_2002	2002	17	172	425.0	
40_S_2005	2005	14	28	69.2	X
32_H_2006	2006	13	190	469.5	
8_P_2006	2006	13	477	1178.7	
44_G_2007	2007	12	195	481.9	
15_N_2008	2008	11	366	904.4	X
42_P_2008	2008	11	16	39.5	
28_S_2008	2008	11	9	22.2	
29_B_2008	2008	11	27	66.7	
43_L_2009	2009	10	563	1391.2	
18_N_2009	2009	10	156	385.5	
30_D_2009	2009	10	37	91.4	X
12_M_2009	2009	10	282	696.8	
24_B_2009	2009	10	208	514.0	
31_VR_2009	2009	10	62	153.2	
Sf_conf_2010	2010	9	37	91.4	
14_N_2010	2010	9	505	1247.9	X
41_S_2010	2010	9	130	321.2	
6_S_2010	2010	9	722	1784.1	
11_D_2010	2010	9	159	392.9	
26_G_2010	2010	9	277	684.5	
27_W_2010	2010	9	165	407.7	
39_K_2011	2011	8	247	610.4	
20_L_2011	2011	8	345	852.5	
22_A_2011	2011	8	398	983.5	
17_G_2011	2011	8	313	773.4	X
7_M_2011	2011	8	364	899.5	
13_G_2011	2011	8	283	699.3	
1_W_2012	2012	7	427	1055.1	
19_N_2012	2012	7	62	153.2	

Burn Unit	Year Burned	tsf (yrs)	Area (ha)	Area (acres)	Sampled (y/n)
16_G_2012	2012	7	147	363.2	
3_S_2012	2012	7	134	331.1	
5_S_2012	2012	7	751	1855.8	X
4_NN_2012	2012	7	282	696.8	
10_D_2012	2012	7	230	568.3	
48_NN_2014	2014	5	358	884.6	
49_NN_2014	2014	5	291	719.1	
66_NN_2014	2014	5	267	659.8	
67_NN_2014	2014	5	201	496.7	
68_NN_2014	2014	5	281	694.4	
Sf_conf_2014	2014	5	19	47.0	
Pondo_2014	2014	5	48	118.6	
21_T_2014	2014	5	172	425.0	
33_P_2014	2014	5	477	1178.7	
47_S_2014	2014	5	570	1408.5	
34_F_2014	2014	5	164	405.3	
35_B_2014	2014	5	91	224.9	
45_S_2014	2014	5	136	336.1	
36_E_2014	2014	5	434	1072.4	X
37_C_2014	2014	5	94	232.3	
46_CR_2014	2014	5	457	1129.3	
23_PE_2014	2014	5	203	501.6	
KTKF_2015	2015	4	559	1381.3	
Sf_conf_2015	2015	4	258	637.5	
36_Ef_conf_2015	2015	4	21	51.9	
Bf_conf_2015	2015	4	677	1672.9	
50_B_2015	2015	4	108	266.9	
51_NN_2015	2015	4	163	402.8	
52_S_2015	2015	4	304	751.2	X
73_G_2015	2015	4	271	669.7	
74_G_2015	2015	4	435	1074.9	
76_G_2015	2015	4	150	370.7	
75_NN_2016	2016	3	127	313.8	
Df_conf_2016	2016	3	164	405.3	
Ff_conf_2016	2016	3	436	1077.4	

Burn Unit	Year Burned	tsf (yrs)	Area (ha)	Area (acres)	Sampled (y/n)
58_S_2016	2016	3	1041	2572.4	X
55_R_2016	2016	3	834	2060.9	
57_H_2016	2016	3	568	1403.6	
53_G_2016	2016	3	343	847.6	
59_G_2016	2016	3	457	1129.3	
60_W_2016	2016	3	238	588.1	
56_B_2016	2016	3	90	222.4	
54_V_2016	2016	3	198	489.3	
77_G_2016	2016	3	915	2261.0	
63_N_2017	2017	2	156	385.5	
61_G_2017	2017	2	593	1465.3	X
64_G_2017	2017	2	398	983.5	
62_K_2017	2017	2	85	210.0	
65_JS_2017	2017	2	97	239.7	
SA_fall_2018	2018	1	347	857.5	
78_NN_2018	2018	1	555	1371.4	
69_D_2018	2018	1	121	299.0	X
70_S_2018	2018	1	1032	2550.1	
72_H_2018	2018	1	876	2164.6	
71_JN_2018	2018	1	179	442.3	
MME_spring_2019	2019	0.333	677	1672.9	
72_K_2019	2019	0.333	308	761.1	X
Total Area Burned:			27176 ha	67153 acres	

To measure water infiltration rate, a minimum of two locations on the plot were randomly chosen. Locations had to be within 5 m of the transect and on a reasonably level patch of ground. One location was placed along the first half of the transect and the other placed along the second half. At each location, excess vegetation that could hamper measurements was clipped without disturbing the soil surface. An infiltration ring 6

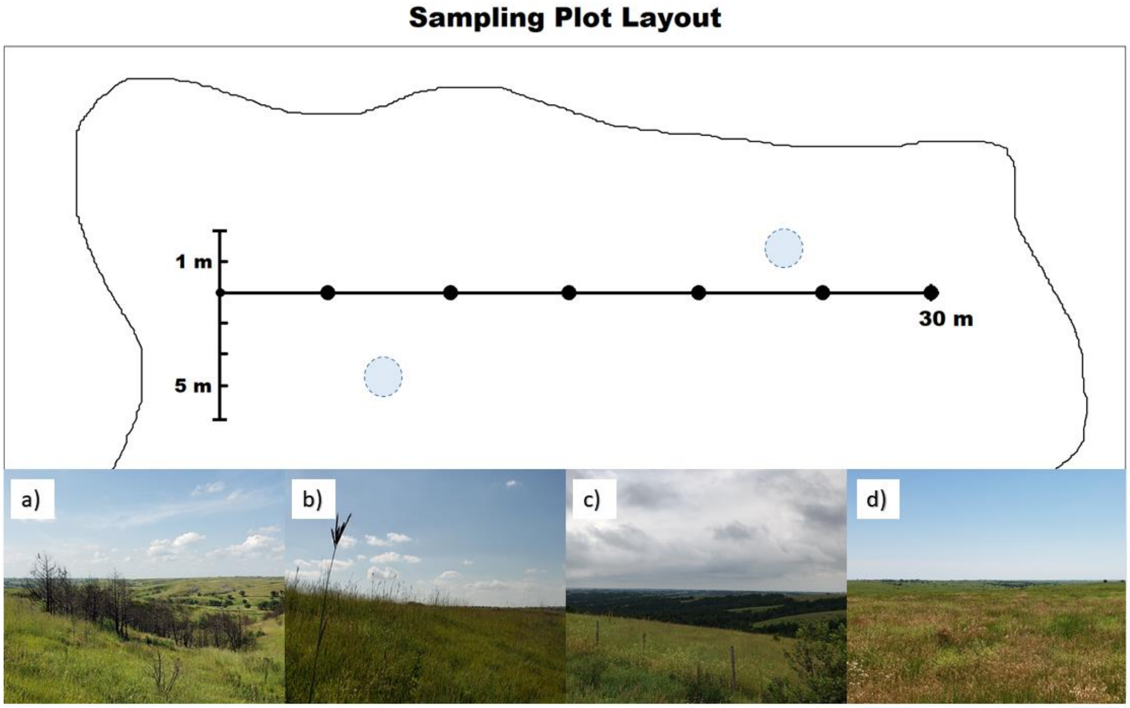


Figure 4.2 Plot sampling layout. The starting point was randomly chosen along a 5m transect, then the main transect laid out perpendicularly from the starting point for 30m. Soil compaction measurements were taken at six regularly-spaced intervals along the transect (black points) and at six depths at each sampling point. Sampling points for water infiltration (blue circles) were taken at a minimum of two random locations that were within 5m of the transect. Examples of plot types sampled: a) restored grassland from fire-collapsed juniper woodland; b) burned grassland; c) unburned juniper woodland; and d) unburned grassland.

inches in diameter was driven 5 cm into the soil. A measuring cup was filled with 444 mL of water and gently poured into the ring to avoid splashing or disturbing the soil surface. Immediately following this, a timer was started to record the time it took for the water to completely soak into the soil. Depth measurements were also recorded every few minutes throughout the trial. If the water took greater than 20 mins to absorb into the soil, a final depth measurement was taken and the final infiltration rate calculated based on that. If the water took fewer than 15 mins to absorb into the soil, additional trials were run until the 20 minute benchmark was reached. This methodology was chosen due to limitations on time spent in the field and the amount of water able to be carried to remote sampling locations.

4.2.3 Analysis

To explore changes in soil compaction across time and between site types, we calculated the average soil compaction for each site at all six depths and plotted them across the time-since-fire gradient. Non-parametric local regression (loess) smoothing curves were applied to the plots to aid in visualizing trends in soil compaction using the ‘ggplot2’ package in R (Wickham, 2016). To further examine relationships in compaction between sites, we selected four comparisons to undergo a two-sided student’s t-test for significant differences. The comparisons were made using mean compaction values of all selected site types, and at each of the six depths. The selected comparisons were: Restored Grassland x Burned Grassland; Restored Grassland x Unburned Woodland; Burned Grassland x Unburned Grassland; and Unburned Grassland x Unburned Woodland. We first compared the variances of the selected sites using the function ‘var.test’ in R (R Core Team, 2021). After determining if the variances were or were not significantly different, we then entered that result into the formula for the t-test, calculated using the ‘t.test’ function in R. If the variances are not equal, then R uses Welch’s t-test. Otherwise it uses a pooled variance between the sites selected for comparison. To further illustrate the differences in mean soil compaction between site types, we created box-and-whisker plots of compaction readings at the four site types and at all depths.

To investigate differences in water infiltration rates across site types and time-since-fire, we calculated each site’s mean infiltration rate across all sampling locations and trials within the respective site. Some infiltration rates were removed from the dataset due to abnormal infiltration rate measurements that did not follow the standard sampling protocol. Calculating mean infiltration rates reduces the effects of any sampling errors made while taking readings in the field. We also calculated the final trial's infiltration rate at each of the sampling locations within a site. Using only the final reading after multiple trials ensures similar levels of soil moisture have been reached at each site, since differences in soil moisture can affect infiltration rates and soil moisture will be inherently different at sites sampled at differing spatial and temporal locations. Final and mean infiltration rates were plotted across the time-since-fire gradient to show trends over time. Loess smoothing curves were applied using the 'ggplot2' package in R (Wickham, 2016) to show trends in water infiltration rates at all sites across time. We then further explored relationships in infiltration rates between sites by selecting four comparisons to undergo t-tests, following the same protocol as outlined in the previous paragraph. Comparison types were the same as those chosen for soil compaction. Tests of variance and t-tests were run using mean infiltration rates and final infiltration rates. Methodology followed that of the soil compaction t-tests using R (R Core Team, 2021). Box-and-whisker plots were made for both mean and final infiltration rates.

4.3 Results

4.3.1 Soil characteristics in alternative grassland states

Mean soil compaction levels were similar in burned grasslands, grasslands restored from eastern redcedar woodland, and unburned reference grasslands at all depths sampled (Figure 4.3). The greatest variation in mean compaction was in unburned grassland reference sites at a depth of 5 cm with values ranging from 8 kg/cm^2 to 44 kg/cm^2. The second largest variation was in burned grasslands at a depth of 30 cm with values ranging

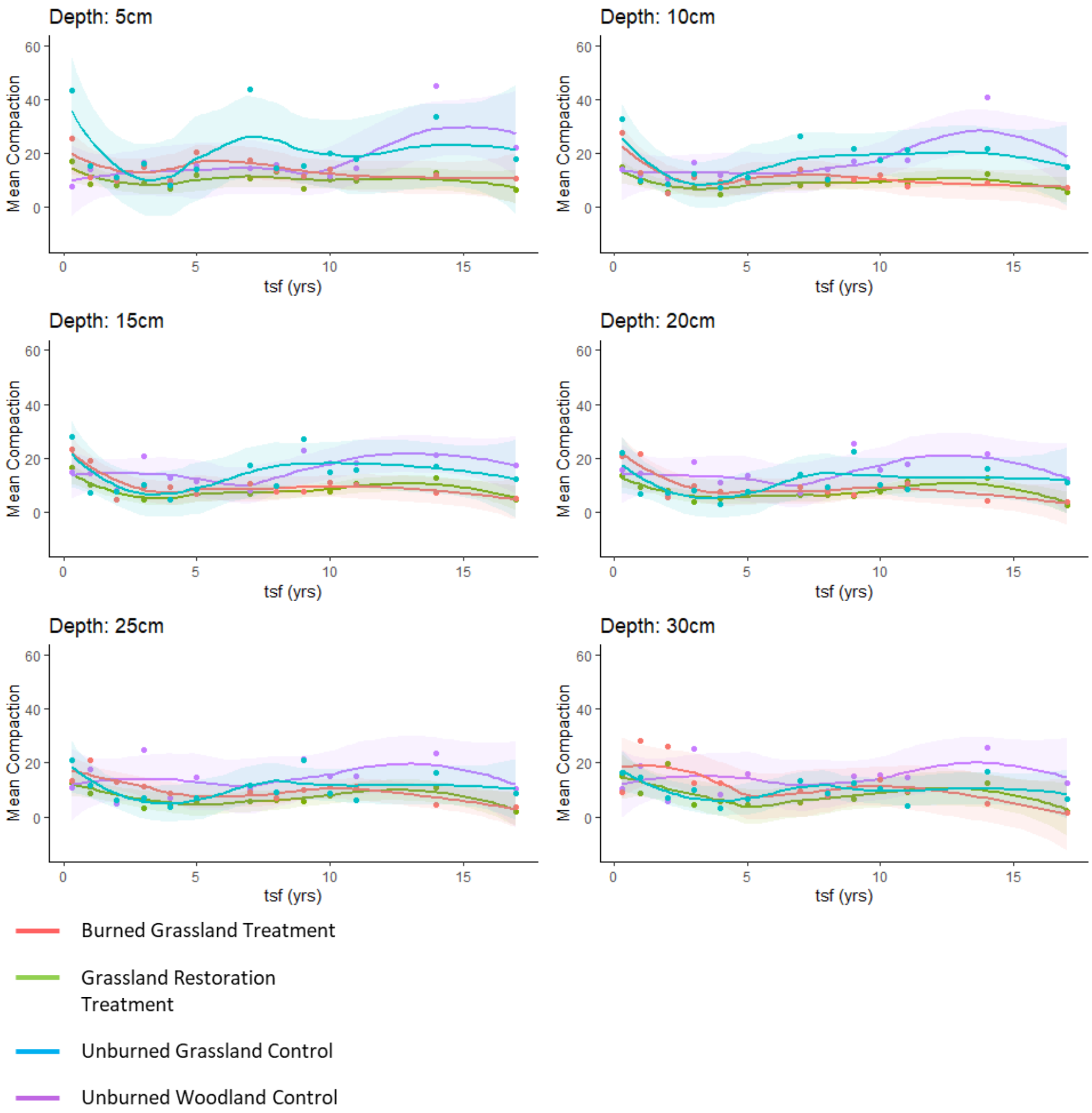


Figure 4.3 The change in mean soil compaction at paired sampled sites relative to time since fire, ranging from a depth of 5 cm to 30 cm. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

from 1.7 kg/cm^2 to 28 kg/cm^2. Grasslands restored through extreme fire in juniper woodland showed the least variation in mean soil compaction levels amongst site types with values ranging from 2 kg/cm^2 to 20 kg/cm^2 at a depth of 30 cm. In unburned grassland reference sites across all depths, the minimum and maximum mean compaction

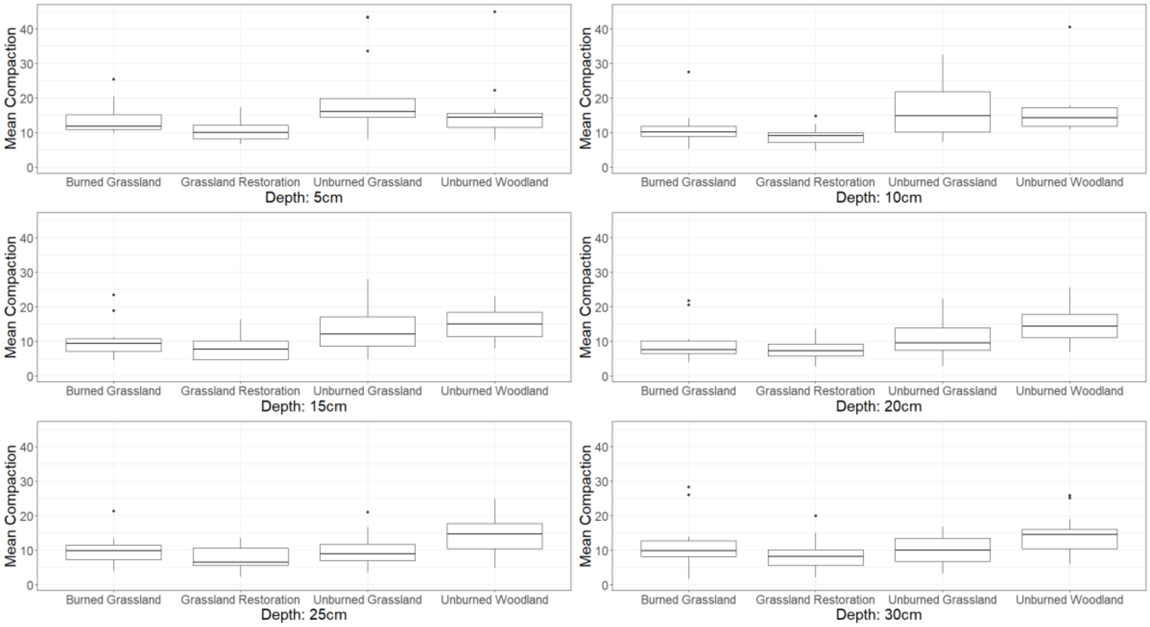


Figure 4.4 Mean soil compaction boxplots for all depths at the four site types. Median compaction values are shown as the solid black line with the box, first and third quartiles are shown as the top and bottom of the box, minimum and maximum compaction values are shown as the whiskers from the box, and outlying data points are shown as black dots.

readings were 2.83 kg/cm^2 and 43.6 kg/cm^2, respectively. In burned grasslands across all depths, the minimum and maximum mean compaction readings were 1.7 kg/cm^2 and 28.3 kg/cm^2, respectively. In restored grasslands across all depths, the minimum and maximum mean compaction readings were 2.1 kg/cm^2 and 19.9 kg/cm^2, respectively. Restored grasslands had the lowest mean compaction readings across all depths compared to other grassland states (Figure 4.4). Burned grasslands consistently had lower mean compaction readings than unburned grasslands at all depths except at 25 and 30 cm, where mean compaction in burned grasslands was equal to or higher than compaction in unburned grasslands.

Mean and final infiltration rates were similar in burned grasslands, grasslands restored from woodland, and unburned grasslands (Figure 4.5). Unburned grasslands had

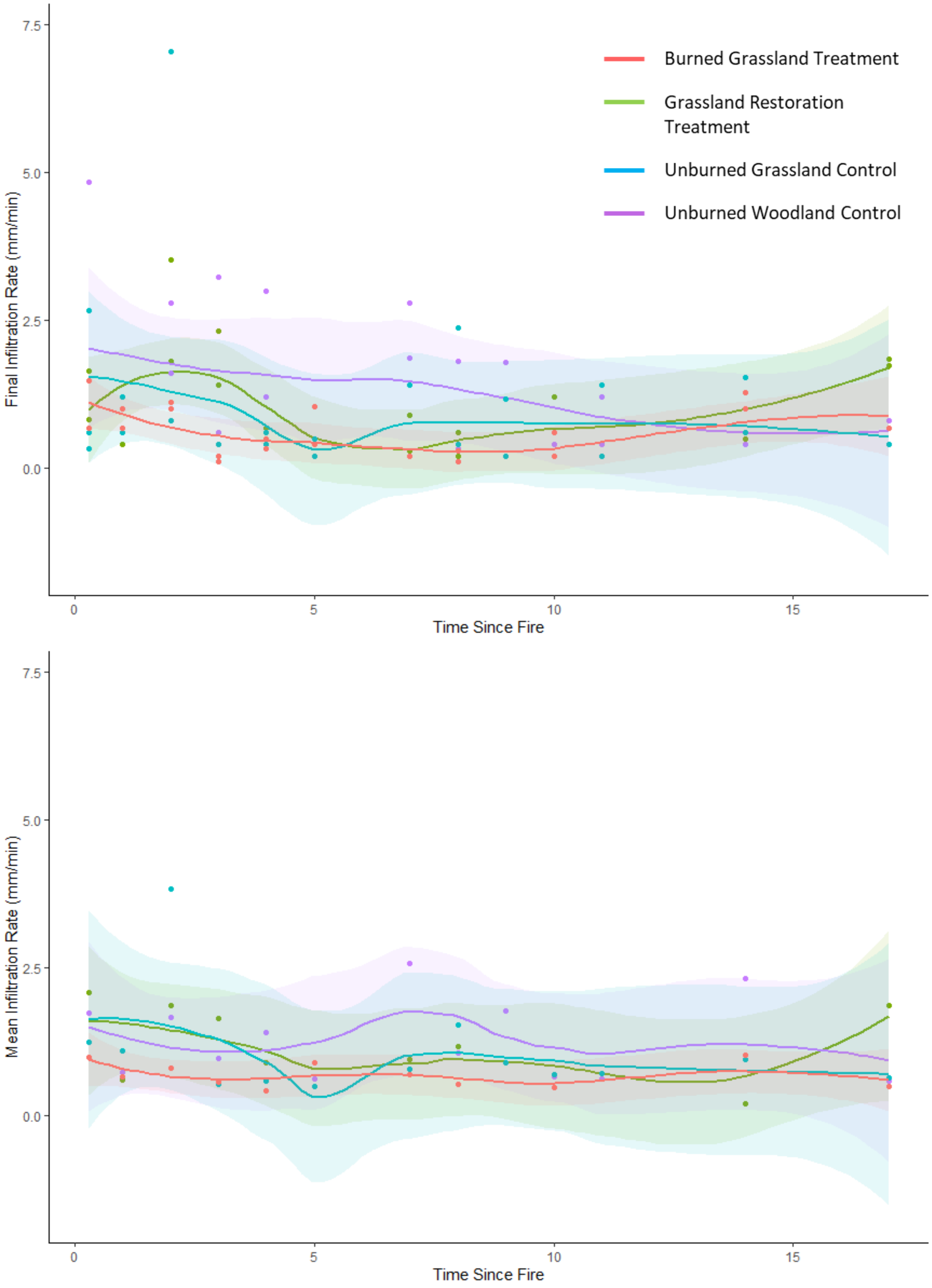


Figure 4.5 The change in final and mean water infiltration rates at paired sampled sites relative to time since fire. Green indicates grassland restoration sites, red indicates burned grasslands, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

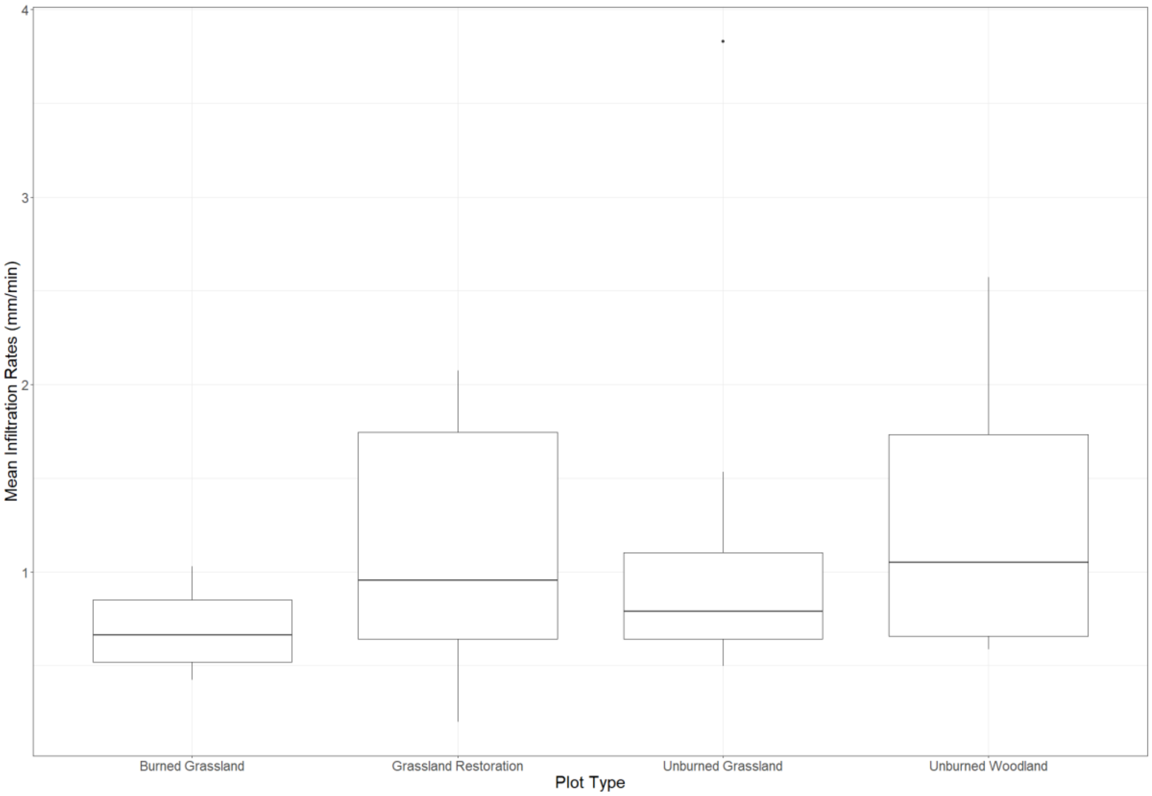


Figure 4.6 Mean infiltration rates for all four site types shown as boxplots. Median infiltration rates are shown as the solid black line with the box, first and third quartiles are shown as the top and bottom of the box, minimum and maximum infiltration rates are shown as the whiskers from the box, and outlying data points are shown as black dots.

the greatest difference in minimum and maximum final infiltration rates, ranging from 0.20 mm/min to 7.04 mm/min. Grasslands restored through extreme fire had the second most difference between minimum and maximum final infiltration rates, ranging from 0.20 mm/min to 3.53 mm/min. Burned grasslands had the least difference between minimum and maximum final infiltration rates, ranging from 0.10 mm/min to 1.48 mm/min. Mean infiltration rates showed even less variation (Figure 4.5). Mean infiltration rates in unburned grassland reference sites had a minimum and maximum of 0.50 mm/min to 3.83 mm/min. Mean infiltration rates in grasslands restored through extreme fire had a minimum and maximum of 0.20 mm/min to 2.08 mm/min. Mean infiltration rates in burned grasslands had the least variation with a minimum and maximum of 0.42 mm/min to 1.03 mm/min. Burned grasslands had the lowest mean infiltration rates compared to other grassland states, followed by unburned grasslands and finally restored grasslands (Figure 4.6).

4.3.2 Changes in soil characteristics over increasing time-since-fire

Grasslands restored through extreme fire and burned grasslands had similar mean soil compaction to one another throughout the 17 years of post-fire treatment and at all depths (Figure 4.3). The largest difference between the two was from 1 to 4 years post-fire at at depth of 30 cm, where burned grasslands had as much as twice the compaction levels of restored grasslands. Unburned grasslands usually had higher compaction levels than both restored grassland and burned grasslands along the time-since-fire (tsf) gradient starting from 6 years tsf to 17 years. From 0.3 tsf to 5 tsf, burned grassland and unburned grassland sites had similar or higher compaction levels. Restored grasslands consistently had some of the lowest compaction levels across the tsf gradient.

Final and mean infiltration rates were similar in alternative grassland states across most of the 17-year tsf gradient (Figure 4.5). Restored grasslands varied the most across tsf, and generally had higher infiltration rates than burned grasslands. It had similar infiltration rates to unburned grasslands, with the greatest difference in mean and final infiltration rates in restored grasslands coming at the end of the 17-year tsf gradient. Burned grasslands generally had the lowest mean and final infiltration rates across tsf. Restored grassland and burned grassland infiltration rates differed the most from 0.3 to 4 years post-fire.

We used two-sided Student’s t-tests to test for significant differences between site types. For mean soil compaction, there was a significant difference between grasslands restored by extreme fire and unburned woodland at all six depths (Table 4.2a-f). P-values ranged from as high as 0.05 at 5 cm to as low as 0.0001 at 20 cm, indicating that mean soil compaction in restored grasslands is significantly different from that in unburned woodlands. We also found a significant difference between restored grasslands and burned grasslands at 5 cm (p-value = 0.02). The only other significant difference in mean soil compaction was between unburned woodlands and unburned grasslands at 30 cm (p-value = 0.04). All other comparisons of mean soil compaction between the chosen site types were not significant.

Table 4.2a Differences in soil compaction at a depth of **5 cm** among restored grassland (RG), unburned woodland (UW), burned grassland (BG), and unburned grassland (UG) indicated by two-sided student's t-test.

	Df	**95% CI**	**t**	**p-value**
RG x UW	14.5	[-11.74, 0.01]	-2.13	0.05*
BG x UG	15.7	[-14.22, 0.57]	-1.96	0.07
RG x BG	24	[-6.99, -0.60]	-2.45	0.02*
UW x UG	24	[-3.84, 13.34]	1.15	0.26

Table 4.2b Differences in soil compaction at a depth of **10 cm**.

	Df	**95% CI**	**t**	**p-value**
RG x UW	15.2	[-12.22, -2.51]	-3.23	0.006**
BG x UG	24	[-10.71, 0.12]	-2.02	0.06
RG x BG	18.1	[-5.91, 1.23]	-1.38	0.19
UW x UG	24	[-5.99, 6.53]	0.09	0.93

Table 4.2c Differences in soil compaction at a depth of **15 cm**.

	Df	**95% CI**	**t**	**p-value**
RG x UW	24	[-10.64, -3.53]	-4.11	0.0004**
BG x UG	24	[-8.93, 1.42]	-1.50	0.15
RG x BG	24	[-5.66, 1.72]	-1.10	0.28
UW x UG	24	[-6.44, 3.72]	-0.55	0.59

Table 4.2d Differences in soil compaction at a depth of **20 cm**.

	Df	**95% CI**	**t**	**p-value**
RG x UW	24	[-10.59, -3.07]	-3.75	0.0001**
BG x UG	24	[-6.22, 3.05]	-0.71	0.49
RG x BG	24	[-5.66, 1.75]	-1.09	0.29
UW x UG	24	[-7.97, 1.40]	-1.45	0.16

Table 4.2e Differences in soil compaction at a depth of **25 cm**.

	Df	**95% CI**	**t**	**p-value**
RG x UW	24	[-10.81, -2.58]	-3.36	0.0026**
BG x UG	24	[-4.63, 3.61]	-0.25	0.80
RG x BG	24	[-5.92, 0.62]	-1.67	0.11
UW x UG	24	[-8.36, 1.27]	-1.52	0.14

Table 4.2f Differences in soil compaction at a depth of **30 cm**.

	Df	**95% CI**	**t**	**p-value**
RG x UW	24	[-10.38, -1.56]	-2.80	0.01**
BG x UG	24	[-3.10, 6.95]	0.79	0.44
RG x BG	24	[-8.50, 1.76]	-1.35	0.19
UW x UG	24	[-8.81, -0.24]	-2.18	0.04*

We also tested for significant differences in mean and final infiltration rates at chosen sites (Table 4.3a-b). The only significant differences were found between restored grasslands and burned grasslands, for both mean infiltration rate (p-value = 0.04) and final infiltration rate (p-value = 0.04). All other comparisons were not significant.

Table 4.3a Differences in MEAN water infiltration rates among restored grassland (RG), unburned woodland (UW), burned grassland (BG), and unburned grassland (UG) indicated by two-sided student's t-test.

	Df	**95% CI**	**t**	**p-value**
RG x UW	22	[-0.70, 0.41]	-0.53	0.60
BG x UG	13.6	[-0.93, 0.16]	-1.52	0.15
RG x BG	12.3	[-0.88, -0.02]	-2.26	0.04*
UW x UG	24	[-0.43, 0.84]	0.67	0.51

Table 4.3b Differences in FINAL water infiltration rates among restored grassland (RG), unburned woodland (UW), burned grassland (BG), and unburned grassland (UG) indicated by two-sided student's t-test.

	Df	95% CI	t	p-value
RG x UW	44	[-0.92, 0.32]	-0.98	0.33
BG x UG	32	[-0.92, 0.22]	-1.24	0.22
RG x BG	29.4	[-0.85, -0.02]	-2.12	0.04*
UW x UG	50	[-0.33, 1.10]	1.08	0.29

4.3.3 Additional results

Plotting all water infiltration rates across the time-since-fire gradient showed similar trends to mean and final infiltration readings (Figure 4.7). Restored grasslands had the highest infiltration rates right after fire (<1 year since fire), but after 1 year since fire their infiltration rates follow a similar trajectory to unburned grasslands. However, after 14 years since fire, infiltration rates in restored grasslands increase again and become the highest of all site types at 17 years since fire. Burned grasslands have the lowest infiltration rates of all site types across the entire tsf gradient. Unburned woodlands vary across tsf, with infiltration rates peaking as the highest of all site types from 5 to 14 years since fire.

Comparing final infiltration rates with all infiltration rates shows much less variation in final infiltration rates than in all infiltration rates (Figure 4.8). Final infiltration readings have far fewer outliers and smaller differences between minimum and maximum readings. Final infiltration rates were chosen as the primary metric due to this perceived stability. Similarly, breaking out all infiltration rates by time since fire highlights the variability seen among all infiltration rates even within the same site type

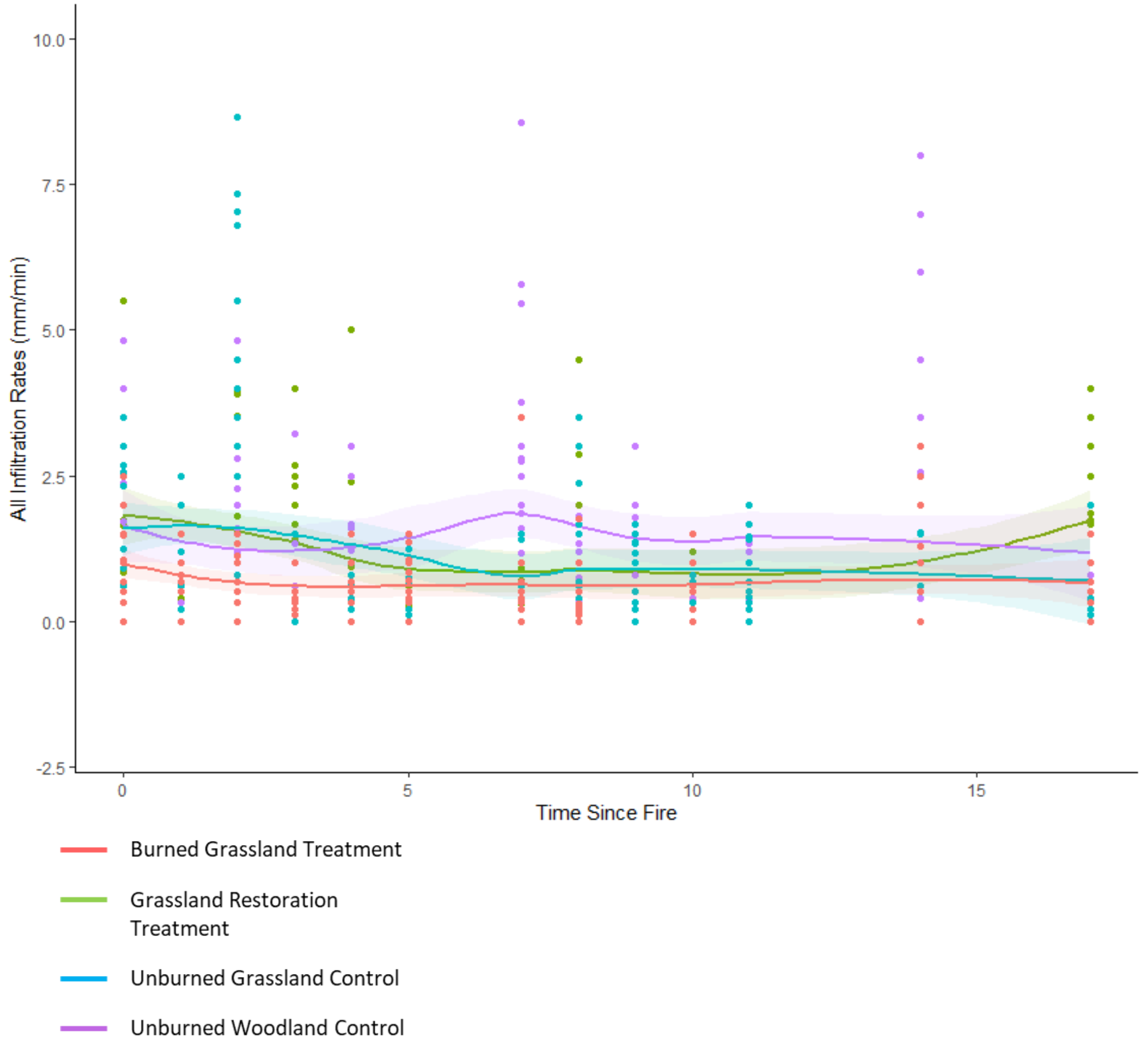


Figure 4.7 All final water infiltration rates relative to time since fire. Red indicates burned grasslands, green indicates grassland restoration site, blue indicates unburned grasslands, and purple indicates unburned woodlands. Trend visualized using loess smoothing method. Shaded areas represented 95% confidence intervals.

(Figure 4.9). Unburned grasslands show exceptionally more variation among all infiltration readings, lending further support to the primary use of final infiltration readings to investigate trends and differences.

Burned grasslands had far lower final infiltration rates than other site types, with the majority of their final infiltration readings falling at or below 1.5 mm/min (Figure 4.10). Final infiltration rates in unburned grasslands primarily fell at or below 3 mm/min,

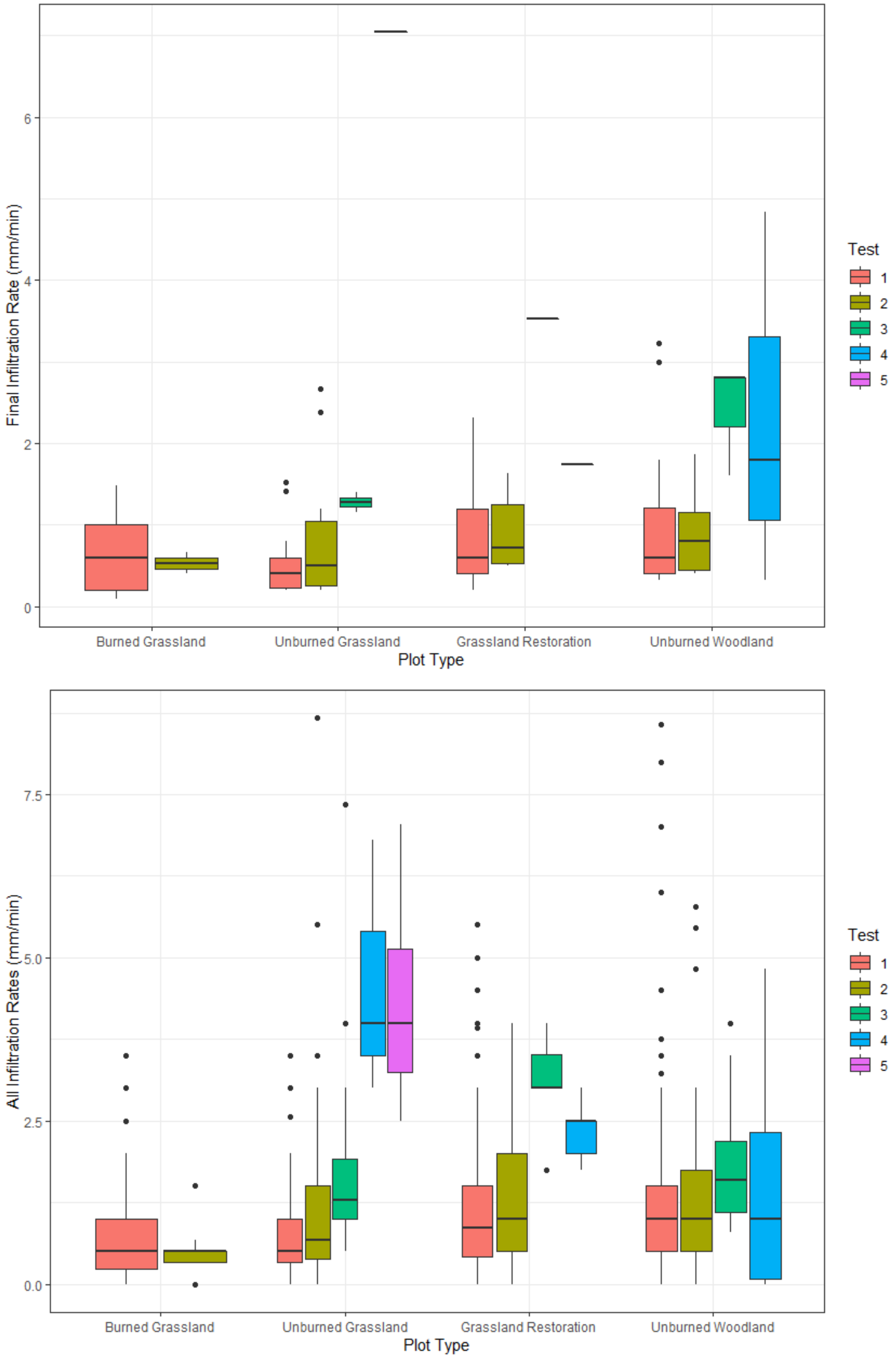


Figure 4.8 Box-and-whisker plots showing final infiltration readings versus all infiltration readings, by site type. Median infiltration rates, first and third quartiles, minimum and maximum infiltration readings are shown. Some sites ran more than two tests per testing location, up to a maximum of five tests.

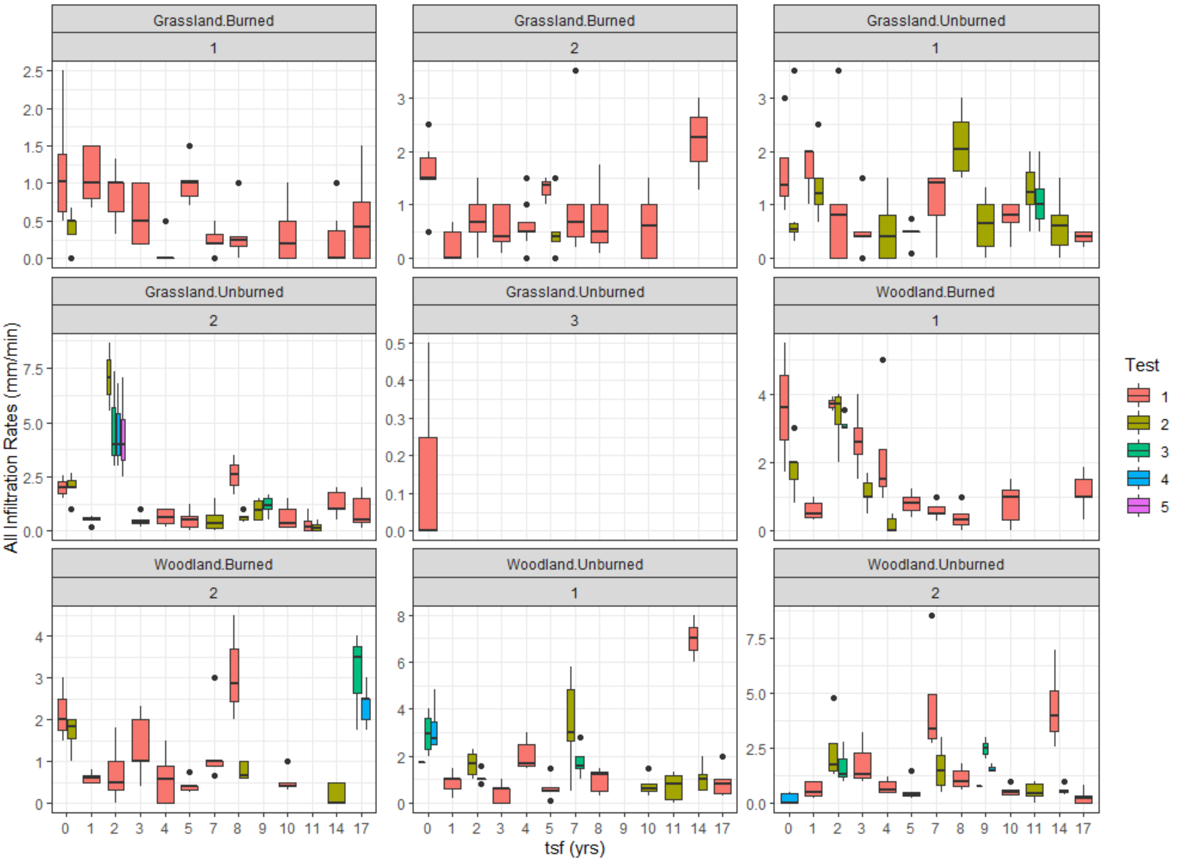


Figure 4.9 Boxplots showing all infiltration readings, broken out by site type then by test location and plotted across the tsf gradient. Median infiltration rates are shown as the solid black line within the box, first and third quartiles are shown as the top and bottom of the box, minimum and maximum infiltration readings are shown as the whiskers from the box, and outlying data points are shown as black dots. Some sites ran more than two tests per testing location, up to a maximum of five tests.

although some readings were as high as 8 mm/min. Final infiltration rates in restored grasslands fell primarily at or below 2.5 mm/min, with some readings at 4 mm/min. Final infiltration rates in unburned woodlands mostly fell at or below 5 mm/min.

Mean infiltration rates in restored grasslands primarily fell at 1 to 2 mm/min (Figure 4.11). Almost all mean infiltration rates in unburned grasslands at or below 1 mm/min. Mean infiltration rates in burned grasslands fell at or below 1.1 mm/min across a fairly consistent frequency (1.0-3.0). Mean infiltration rates in unburned woodlands were mostly low, the majority ranging from 0.5-1.5 mm/min.

Mean compaction readings were similarly distributed across site types at depths of 5 and 10 cm (Figure 4.12a). The majority of mean compaction readings were at or below 20 kg/cm^2 for all site types, with unburned woodlands and grasslands getting the highest readings at 50 kg/cm^2. From depths of 15 to 20 cm, mean compaction readings fell primarily at or below 20 kg/cm^2 and ranged no higher than 30 kg/cm^2 (Figure 4.12b). Mean compaction readings at depths of 25 and 30 cm were similar to previous depths, ranging no higher than 30 kg/cm^2 with the majority of readings falling at or below 15 kg/cm^2 (Figure 4.12c).

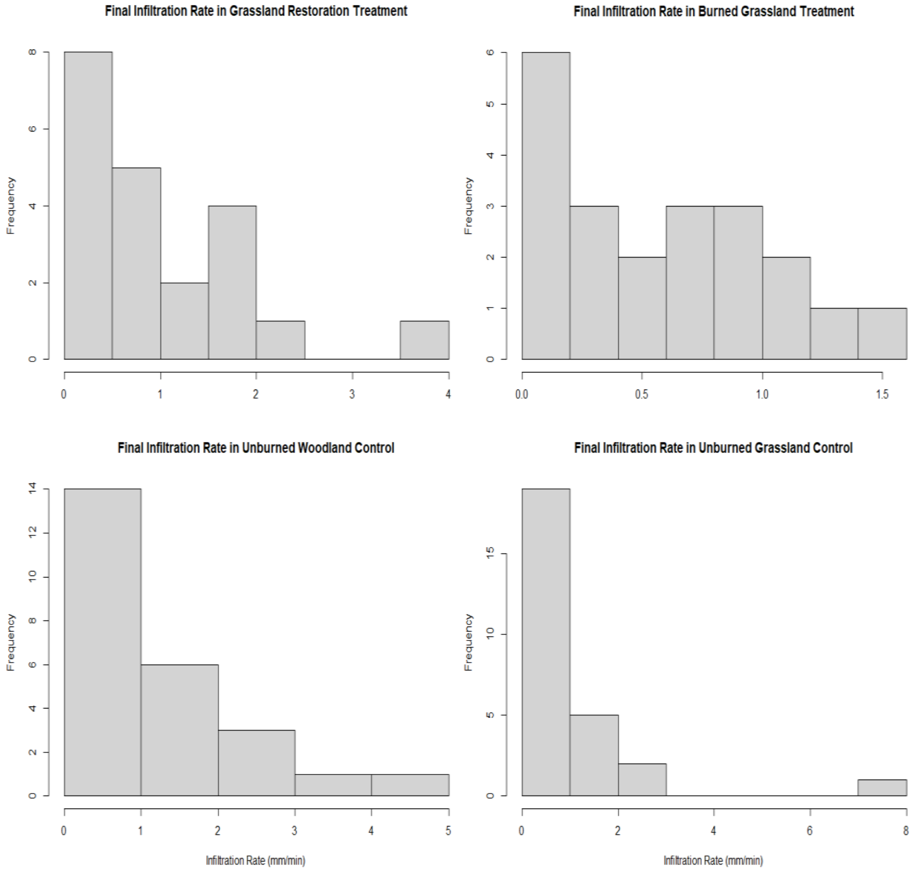
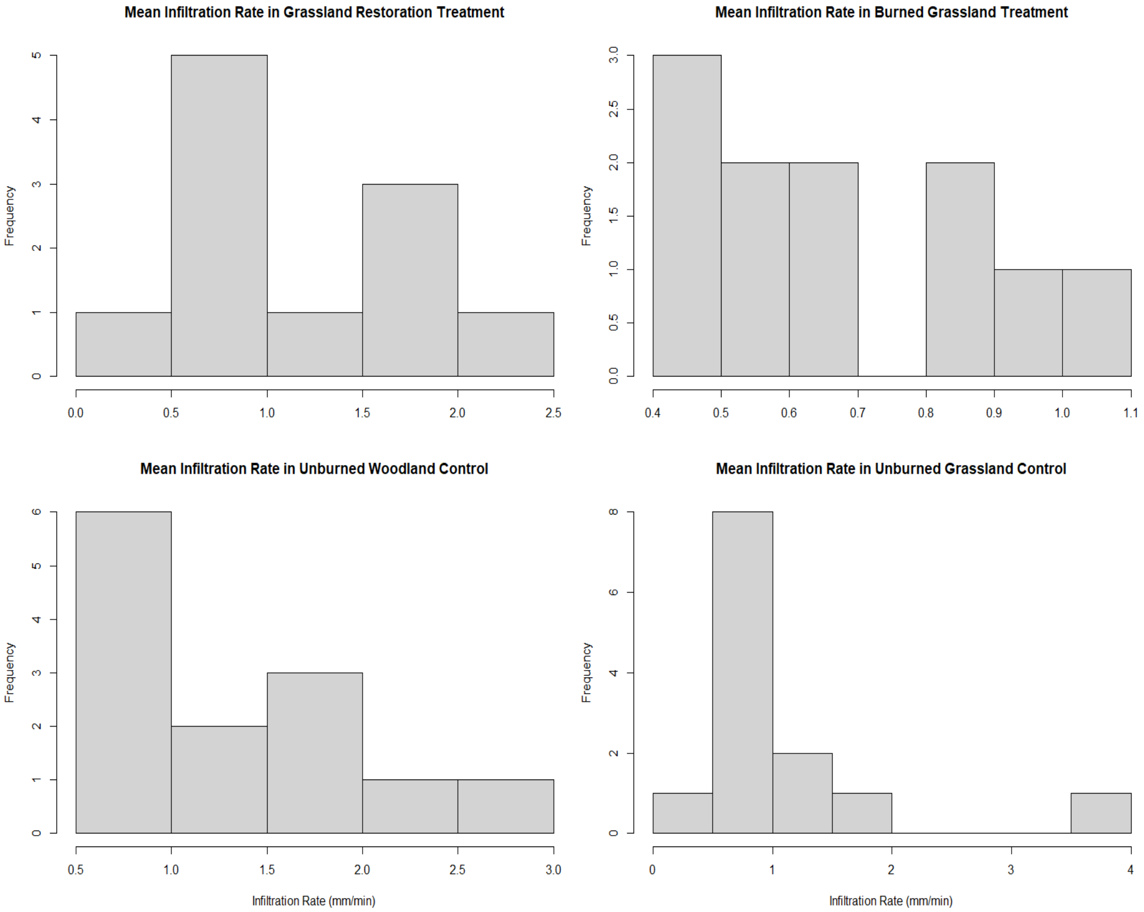


Figure 4.10 Histograms showing the frequency of final infiltration readings broken out by site type.


Mean Infiltration Rate in Grassland Restoration Treatment

Mean Infiltration Rate in Burned Grassland Treatment

Mean Infiltration Rate in Unburned Woodland Control

Mean Infiltration Rate in Unburned Grassland Control

Figure 4.11 Histograms showing the frequency of mean infiltration readings broken out by site type.

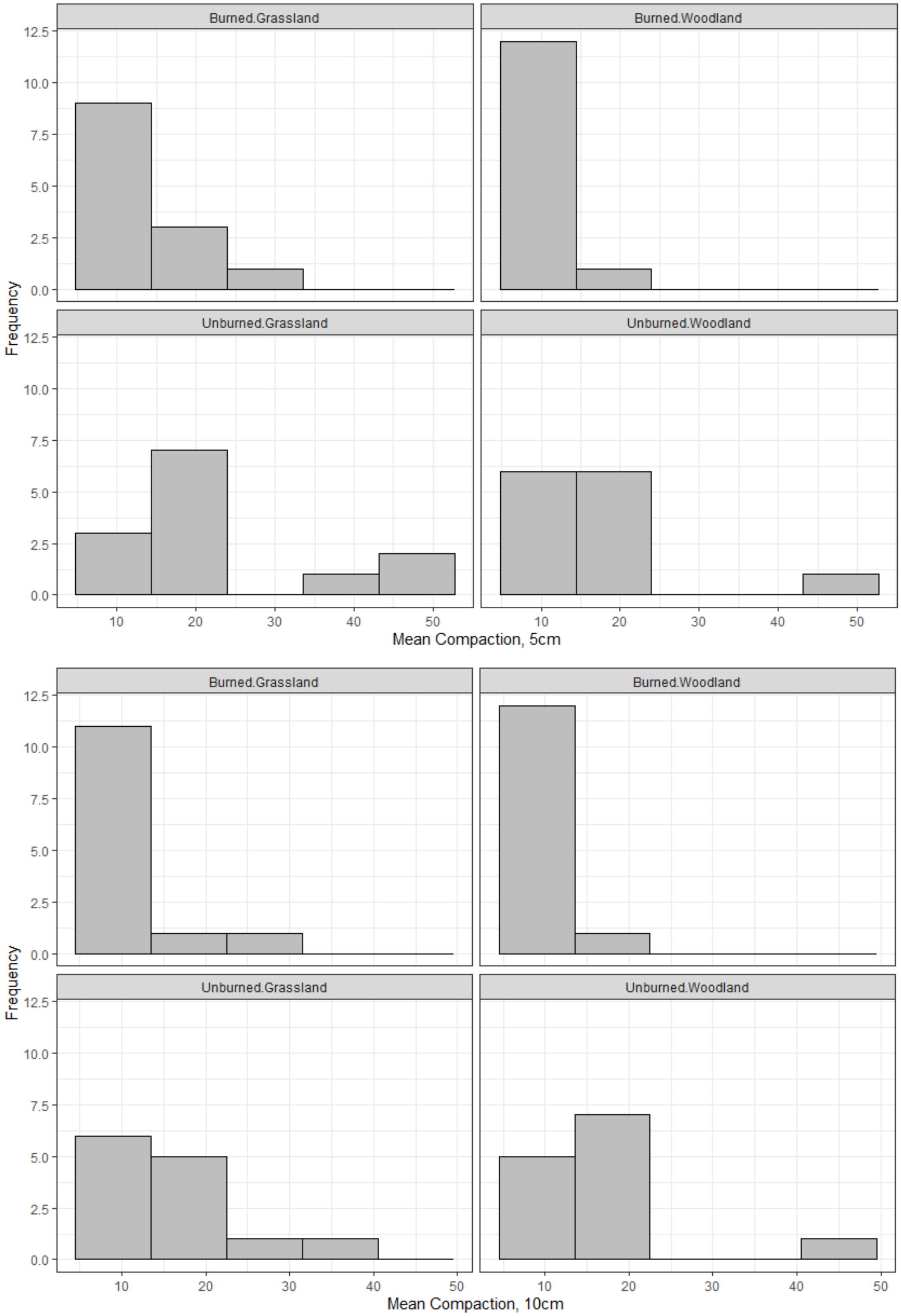


Figure 4.12a Histograms showing the frequency of mean compaction readings broken out by site type. Readings shown are from depths of 5 cm and 10 cm.

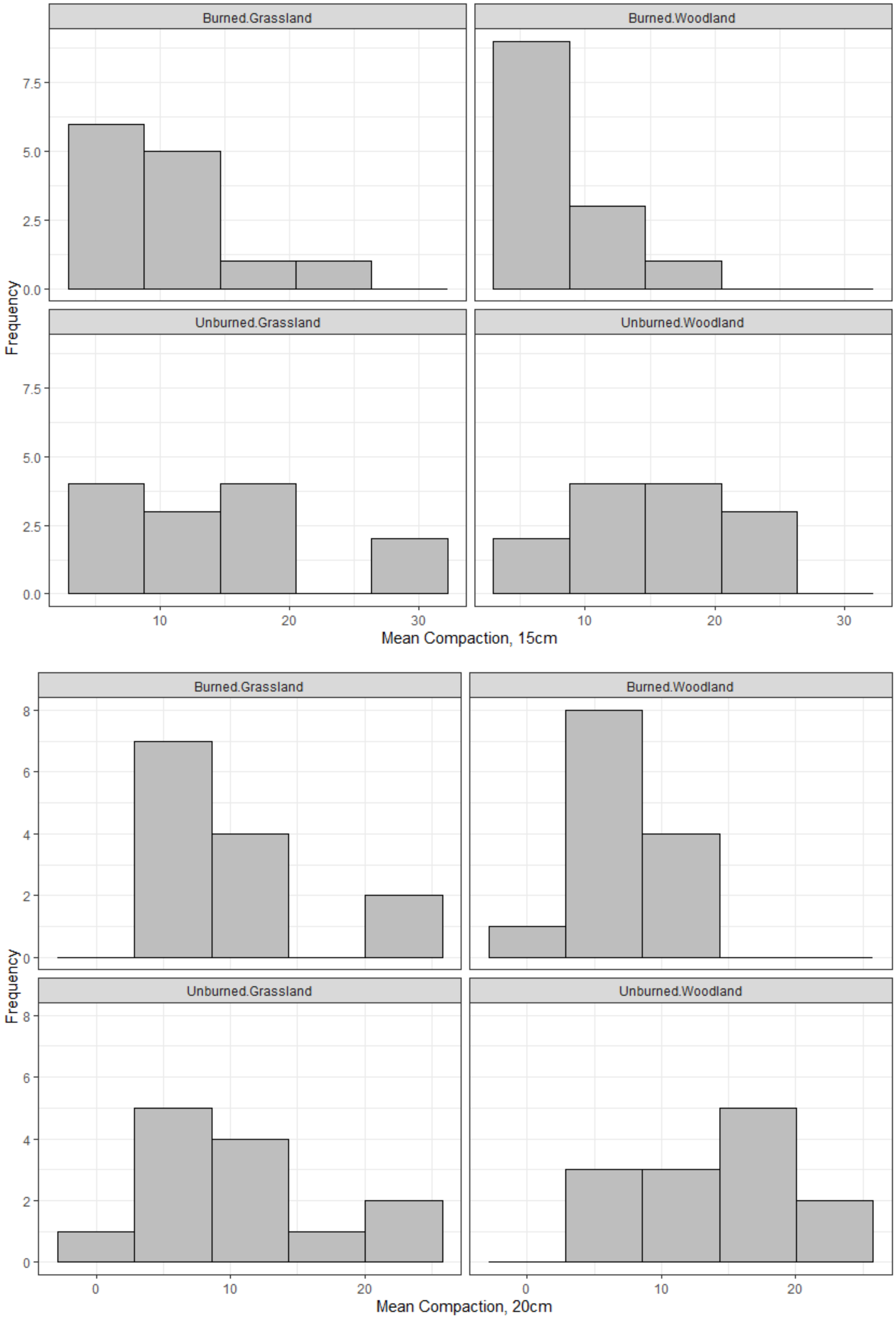


Figure 4.12b Histograms showing the frequency of mean compaction readings broken out by site type. Readings shown are from depths of 15 cm and 20 cm.

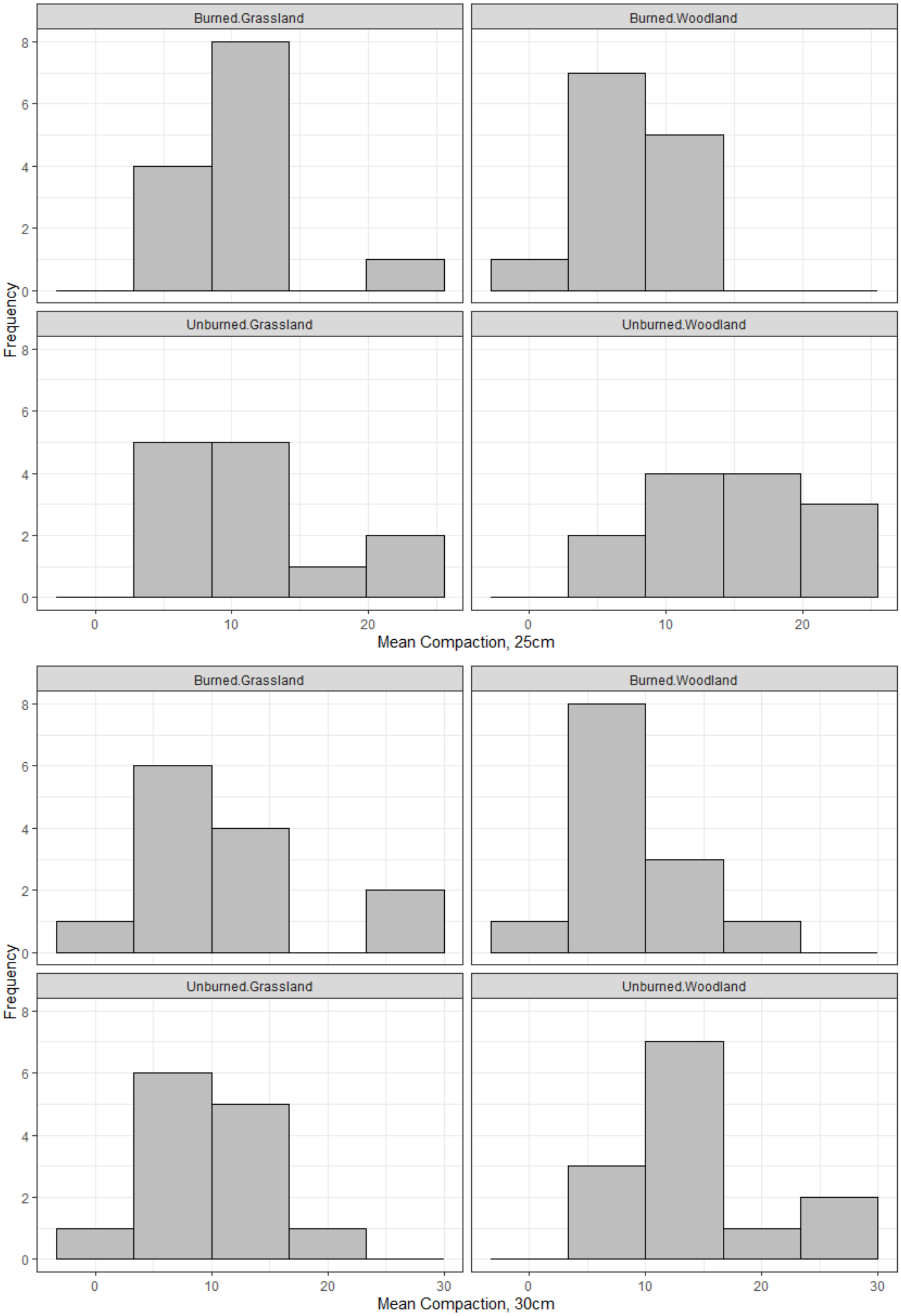


Figure 4.12c. Histograms showing the frequency of mean compaction readings broken out by site type. Readings shown are from depths of 25 cm and 30 cm.

4.4 Discussion

This study aimed to understand dynamic changes in soil properties after regime shifts and across a time-since-fire gradient of 17 years. We compared two alternative states in grasslands (i.e., grasslands treated with prescribed fire and grasslands that emerged following the collapse of juniper woodland with high intensity fire) with one another and against a reference unburned grassland state and a reference unburned woodland state. We compared physical soil properties of burned and unburned grasslands against the properties of grasslands restored from juniper woodland. This allowed us to investigate the changes that can be expected in grassland and juniper woodland soils when applying fire to the landscape. Additionally, we studied how these soil properties change over time after fire has been applied to the system. Lastly, we compared soil properties of alternative grassland states to those of closed-canopy juniper woodland, illustrating the differences in regimes that land managers can expect when undertaking ecological restoration.

We found that the greatest differences in soil compaction were between grasslands restored with extreme fire and unburned woodland sites. Restored grasslands had lower median compaction levels across all depths when compared to unburned woodlands (Figure 4.4) and were significantly different at all depths (Table 4.2a-f). It is noteworthy that restored grasslands were previously closed-canopy juniper woodlands, the same as the unburned woodlands, but had undergone high intensity fire in order to shift from a woodland to a grassland state. In contrast, other studies have found increased compaction in grasslands for two growing seasons post-fire (Snyman, 2002). This partially agrees with our data. In the first growing season after collapse and reorganization (about four months post-fire) we found that restored grasslands had higher soil compaction levels than unburned woodland at almost every depth (Figure 4.3). However, in the second growing season after fire, soil compaction in restored grasslands was consistently lower than in unburned woodlands. The increased compaction in restored grasslands right after burning may be related to the sudden loss of organic matter from the top layer of the soil and the decrease in plant and litter cover (Snyman, 2002). By the second growing season however, soil compaction in restored grasslands has decreased to levels similar to burned and unburned grasslands.

The only significant differences in mean and final infiltration rates were between restored grasslands and burned grasslands (Table 4.3a-b). Restored grasslands had a higher median infiltration rate than burned grasslands (Figure 4.6). Mean infiltration rates in restored grasslands were very similar to those in unburned woodlands, especially within the first and third quartiles. Restored grasslands in our study were once closed-canopy juniper woodlands which had collapsed after extreme fire and reorganized into grasslands. For the first five years after fire, mean infiltration rate in restored grasslands follows a similar trajectory to paired woodland reference sites (Figure 4.5). However, after five years tsf the two begin to diverge, with the strongest differences in mean infiltration seen at 7 and 14 years post-fire. Although their median infiltration rate is high compared to burned and unburned grasslands, restored grasslands had some of the lowest mean infiltration rates overall (Figure 4.6). Studies have found that fire can create soil crusts or hydrophobic soil surfaces that reduce infiltration rates (Snyman, 2002), perhaps explaining the large variation in mean infiltration rates in restored grasslands. Unburned woodlands were also highly variable, but had some of the highest mean infiltration rates.

It is possible that underneath the dense canopy of juniper woodlands, the soil is drier since most rainfall is intercepted by the canopy. This drier soil could lead to higher infiltration rates overall.

There are some limitations to this dataset. Some sites that were sampled were found to have different parent material than other sites, specifically the 38_E_2002 burn unit (Table 4.1). This site is on the northeastern edge of the LCEL and with a different parent material we can expect the soil to have a different chemical makeup, pH, and cation distribution than other soils in the region. Additionally, soil properties are dynamic, changing over time and from season to season. Since not all sites could be sampled at the same month of the year, some variation in soil properties is to be expected.

We chose to sample during the summer season as opposed to other seasons for several reasons. Summer measurements can be used to infer the soil's resilience to hotter and drier conditions, an important factor for landowners managing for drought. Additionally, the LCEL hosts a large population of the federally-listed American burying beetle (*Nicrophorus americanus*). Summer is the peak of the beetle's activities, mainly foraging, breeding, and larval development. The beetle is closely tied to the soil, spending a large portion of time belowground throughout its developmental stages including when constructing underground brood chambers to raise their young. The American burying beetle is also a large-bodied insect and quite susceptible to desiccation, for example during summer drought conditions. Therefore, we deduced that water infiltration rates and soil compaction levels could have outsized impacts on the beetle.

The complexity of the landscape also poses a unique limitation to our study. The area is a working landscape that primarily supports grazers. However, it is almost entirely privately-owned by many different landowners who may each follow different grazing plans and stocking rates. Grazers can impact soil compaction, and since each site is managed differently it is unknown how livestock may have affected these results.

In the LCEL, and when managing systems in general, often the goal of management is to reduce variability and increase stability. Researchers also prefer dampened variability in order to control for unknowns in their studies. However, heterogeneity and variability in the system can be important. These characteristics can increase the system's resilience to extreme events such as wildfire and drought (Arterburn et al., 2018). Heterogeneity can also provide unique niches for wildlife to take advantage of, such as the American burying beetle (Walker and Hoback, 2007). It supports a wider variety of local species and can increase biodiversity in general (Fuhlendorf et al., 2011).

4.5 Conclusions

Select physical soil characteristics do not differ strongly between grassland alternative states. Soils in grasslands restored with extreme, woodland-collapsing fire were similar to soils in grasslands burned with less intense prescribed fire and grasslands that were not burned. A major implication is that land managers who apply a range of fire intensities to the landscape in order to restore or maintain grasslands do not need to worry about negative impacts on these selected physical soil characteristics over time.

CHAPTER 5

SYNTHESIS

The American burying beetle contributes to the flow of nutrients through the ecosystem as it breaks down dead organic matter and returns it to the soil. Its populations boom and bust depending on the availability of carrion, climate factors such as drought, and its ability to raise the next generation. An ABB lives a little over one year, meaning it has one summer to successfully reproduce and raise its young. If anything goes wrong in that season (either to an individual beetle or a local population) and they are unable to raise a successful brood, then that beetle or group of beetles is lost from the gene pool and from the landscape.

For an insect no larger than your thumb, this could be a terrifying prospect. The chances of finding a good-sized piece of carrion on which to raise your brood is slim. Even if you find carrion of the right size, you will have to fight off other carrion beetles to secure it for you and your mate. Then you will have to work together to prepare the carrion for burial, despite its far larger size and weight. Burial and brood chamber construction in the soil is generally 20 to 30 cm deep, and you yourself are no more than 4.5 cm long. After all that, a vertebrate scavenger such as a coyote may dig up that carrion and all your hard work will have been for naught.

Life is hard for these beetles, and it’s getting harder. Predicted increases in extreme weather and drought will make summers hotter and drier, a distinct threat to such a large and easily desiccated beetle. Grassland bird species, generally the perfect size for beetle use, are declining in the Great Plains. This includes the two Great Plains' states that have the most American burying beetles: Nebraska and Oklahoma. The biome is also troubled by an existential threat to its grasslands—woody plant encroachment.

Woody encroachment is not just a threat to some beetle the size of your thumb or to a grassland bird you've never seen. It is a threat to the existence of grasslands and all the ecosystem services they provide. Woody encroachment is the common enemy of all who use or value any components of grasslands. Once woody plants invade grasslands, they shade out forbs and grasses, reducing grassland plant biodiversity and the forage available for grazing. Fewer grassland birds, including common species, provide fewer opportunities for hunters and birders. Woody encroachment provides more aboveground fuel for wildfires, which will become more frequent and threaten more homes and families across the Great Plains.

The worst part of it is that to some it's already too late. Huge swathes of grassland have already been converted to dense woodland, and the cost of mechanically removing those woodlands is impossibly high. Even after mechanical removal, the seed bank remains in the soil to ensure reinvasion within a handful of years. Although the conversion to woodland is not irreversible, it is often hysteretic, requiring more effort to return to the grassland state than was needed to change to the alternative woodland state. Is it any wonder that landowners have begun to ban together across the Great Plains to combat woody encroachment?

Prescribed burn associations have become the solution to the problem of woody encroachment. These groups are returning fire to the Great Plains, a biome that was fundamentally shaped by fire for millennia. This includes the ambitious application of extreme prescribed fire: the use of intense fire that rapidly and unpredictably fluctuates and alters an ecosystem's structure and function. This has been the key to stop woody plant encroachment, restore grasslands, and rebuild grassland structure and ecological functions.

We found that extreme prescribed fire restored herbaceous species richness and basal cover to areas that had been invaded by eastern redcedar woodlands. The plant communities in restored grasslands were similar to uninvaded grasslands. Herbaceous richness and percent cover of functional groups like perennials, grasses, natives, and warm season species were comparable between restored and uninvaded grasslands.

Despite the extreme nature of these prescribed fires, we found that soil characteristics were minimally impacted. Soil compaction in restored grasslands did not differ significantly from uninvaded grasslands except in the top 5 cm of the soil. Grasslands restored through extreme fire had slightly water higher infiltration rates than burned grasslands, but they were comparable across most of the time-since-fire gradient.

Perennial forbs and grasses at large spatial scales have a positive relationship with the American burying beetle, whereas >10% tree cover at small spatial scales negatively impacts ABB abundance. Cropland cover in small amounts (e.g., 0.5%) but at broad spatial scales has strong negative impacts on the beetle. Since 2007, we found that American burying beetle abundances have increased by 55% across our study site, the Loess Canyons Experimental Landscape. Across this site the ABB has been monitored for 13 years and prescribed fire has been applied for 17 years. We found that two-thirds of ABB were found in areas of high forb and grass cover, which coincides with areas of high prescribed fire activity. This is the only study to document increases in American burying beetle abundance alongside management with fire.

There have been many knowledge gaps in the science that have prevented effective management for the beetle across its range. Only one scientific publication has studied the impacts of woody plant encroachment on the ABB. We have confirmed their finding that increasing woody plant cover causes decreases in beetle abundance. We have applied a multi-scale lens to the landscape, in order to better understand at what scales the beetle interacts with grasslands, woodlands, and croplands in its range. Lastly, this study utilizes the ecological framework of alternative states in order to understand how the landscape has changed repeatedly over years of woody encroachment and fire.

Future directions of ABB research should explore the impacts of woody encroachment across the beetle's entire range. Further investigation of the beetle's food web would allow us to better understand what prey species the beetle relies on. The impacts of woody encroachment and prescribed fire on beetle prey species should also be studied. Entomological studies using the same beetle survey data used in this study could apply beetle sex, length, and width measurements to research sexual dimorphism in beetles as well as differences in male-female abundances over time. This data could also be applied to our landcover dataset to determine if there are differences between beetle populations that live in grasslands versus woodlands. Lastly, the human dimensions of American burying beetle conservation should be explored. Our study site is mostly owned and managed by private individuals, as is the case in much of the Great Plains. The interests of landowners must be understood in order to find areas of mutual benefit for them and the beetle.

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Appendix A

Table of Herbaceous Plant Species Encountered

Table A.1: Complete plant species assemblages at sampled sites. Species presence is indicated by an ‘x’ for each of the four site types: Restored Grassland (RG), Unburned Woodland (UW), Burned Grassland (BG), and Unburned Grassland (UG).

USDA Code	Genus	Species	Common Name	*f* group	Life Cycle	Non/Native	Season	RG	UW	BG	UG
ACMI2	*Achillea*	*millefolium*	common yarrow	Forb	Perennial	Native	Cool	x		x	x
AMARA	*Amaranthus*	*sp.*	pigweed	Forb	Annual	Native	Warm	x	x	x	x
AMCA6	*Amorpha*	*canescens*	leadplant	Subshrub	Perennial	Native	Warm		x		
AMPS	*Ambrosia*	*psilostachya*	western ragweed	Forb	Perennial	Native	Cool	x		x	x
ANGE	*Andropogon*	*gerardii*	big bluestem	Grass	Perennial	Native	Warm	x		x	x
AQUIL	*Aquilegia*	*sp.*	columbine	Forb	Perennial	Native	Cool		x		
ARABIS	*Arabis*	*sp.*	rockcress	Forb	Annual	Native	Cool			x	
ARAN7	*Argentina*	*anserina*	silverweed cinquefoil	Forb	Perennial	Native	Cool		x		x
ARLU	*Artemisia*	*ludoviciana*	white sagebrush	Forb	Perennial	Native	Cool	x		x	
ARPO2	*Argemone*	*polyanthemos*	crested pricklypoppy	Forb	Annual	Native	Cool	x			
ARPU9	*Aristida*	*purpurea*	purple threeawn	Grass	Perennial	Native	Warm			x	x
ASTRA	*Astragalus*	*sp.*	milkvetch	Forb	Perennial	Native	Cool	x	x	x	x
ASGR3	*Astragalus*	*gracilis*	slender milkvetch	Forb	Perennial	Native	Cool			x	x
ATRIP	*Atriplex*	*sp.*	saltbush	Forb	Annual	Nonnative	Cool	x			

BASC5	*Bassia*	*scoparia*	burningbush	Forb	Annual	Nonnative	Warm	x		x	x
BOCU	*Bouteloua*	*curtipendula*	sideoats grama	Grass	Perennial	Native	Warm	x	x	x	x
BODA2	*Bouteloua*	*dactyloides*	buffalograss	Grass	Perennial	Native	Warm			x	x
BOGR2	*Bouteloua*	*gracilis*	blue grama	Grass	Perennial	Native	Warm	x	x	x	x
BOHI2	*Bouteloua*	*hirsuta*	hairy grama	Grass	Perennial	Native	Warm			x	x
BRCA2	*Brassica*	*campestris*	field mustard	Forb	Annual	Nonnative	Cool		x		
BRCI2	*Bromus*	*ciliatus*	fringed brome	Grass	Perennial	Native	Cool	x			x
BRIN2	*Bromus*	*inermis*	smooth brome	Grass	Perennial	Nonnative	Cool	x	x	x	x
CAIN2	*Callirhoe*	*involucrata*	purple poppy mallow	Forb	Perennial	Native	Cool	x		x	x
CALO	*Calamovilfa*	*longifolia*	prairie sandreed	Grass	Perennial	Native	Warm				x
CAREX	*Carex*	*sp.*	sedge	Sedge	Perennial	Native	Cool	x	x	x	x
CASA3	*Cannabis*	*sativa*	marijuana	Forb	Annual	Nonnative	Cool	x			
CELO3	*Cenchrus*	*longispinus*	mat sandbur	Grass	Annual	Native	Warm				x
CHENOP	*Chenopodium*	*sp.*	goosefoot	Forb	Annual	Native	Cool	x	x		x
CHAL7	*Chenopodium*	*album*	lambsquarters	Forb	Annual	Nonnative	Cool		x	x	
CHGL13	*Chamaesyce*	*glyptosperma*	ribseed sandmat	Forb	Annual	Native	Warm	x	x	x	x
CHNU9	*Chamaesyce*	*nutans*	eyebane	Forb	Annual	Native	Warm			x	
CIUN	*Cirsium*	*undulatum*	wavyleaf thistle	Forb	Perennial	Native	Cool	x			x
COCA5	*Conyza*	*canadensis*	Canadian horseweed	Forb	Annual	Native	Cool	x	x	x	x
DEPI	*Descurainia*	*pinnata*	western tansymustard	Forb	Annual	Native	Cool	x		x	x
ELCA4	*Elymus*	*canadensis*	Canada wildrye	Grass	Perennial	Native	Cool	x	x	x	
ELTR7	*Elymus*	*trachycaulus*	slender wheatgrass	Grass	Perennial	Native	Cool	x	x	x	x
ERCI	*Eragrostis*	*cilianensis*	stinkgrass	Grass	Annual	Nonnative	Warm	x			
EUHE5	*Euphorbia*	*hexagona*	sixangle spurge	Forb	Annual	Native	Warm	x		x	

EUMA14	*Euphorbia*	*maculata*	eyebane	Forb	Annual	Native	Warm			x	
EUMA8	*Euphorbia*	*marginata*	snow on the mountain	Forb	Annual	Native	Warm	x		x	x
FRVI	*Fragaria*	*virginiana*	Virginia strawberry	Forb	Perennial	Native	Cool	x		x	
GAAP2	*Galium*	*aparine*	bedstraw	Forb	Annual	Native	Cool	x	x	x	x
GAYOP	*Gayophytum*	*sp.*	groundsmoke	Forb	Annual	Native	Cool		x	x	
GILIA	*Gilia*	*sp.*	gilia	Forb	Annual	Native	Cool	x		x	x
GUSA2	*Gutierrezia*	*sarothrae*	broom snakeweed	Subshrub	Perennial	Native	Cool	x		x	x
HEAN3	*Helianthus*	*annuus*	common sunflower	Forb	Annual	Native	Cool	x		x	x
HECO26	*Hesperostipa*	*comata*	needle and thread	Grass	Perennial	Native	Cool	x		x	x
HEHI	*Hedeoma*	*hispida*	rough false pennyroyal	Forb	Annual	Native	Cool	x	x	x	x
LASE	*Lactuca*	*serriola*	prickly lettuce	Forb	Annual	Nonnative	Cool	x	x	x	x
LEDE	*Lepidium*	*densiflorum*	common pepperweed	Forb	Annual	Native	Cool	x		x	
LIIN2	*Lithospermum*	*incisum*	narrowleaf stoneseed	Forb	Perennial	Native	Cool			x	x
LIRI	*Linum*	*rigidum*	stiff flax	Forb	Annual	Native	Cool	x		x	
LISQG	*Liatris*	*squarrosa var. glabrata*	scaly blazing star	Forb	Perennial	Native	Cool			x	
LUPU	*Lupinus*	*pusillus*	rusty lupine	Forb	Annual	Native	Cool			x	
LYJU	*Lygodesmia*	*juncea*	rush skeletonplant	Forb	Perennial	Native	Cool	x		x	x
MAPI	*Machaeranthera*	*pinnatifida*	lacy tansyaster	Subshrub	Perennial	Native	Cool			x	x

MAST4	*Maianthemum*	*stellatum*	starry false lily of the valley	Forb	Perennial	Native	Cool	x	x		
MEOF	*Melilotus*	*officinalis*	sweetclover	Forb	Annual	Nonnative	Cool	x	x	x	x
MIQU2	*Mimosa*	*nuttallii*	Nuttall's sensitive briar	Forb	Perennial	Native	Cool				x
MOFI	*Monarda*	*fistulosa*	wild bergamot	Forb	Perennial	Native	Cool	x			
MUCU3	*Muhlenbergia*	*cuspidata*	plains muhly	Grass	Perennial	Native	Warm	x	x	x	x
MURA	*Muhlenbergia*	*racemosa*	marsh muhly	Grass	Perennial	Native	Warm	x			x
NECA2	*Nepeta*	*cataria*	catnip	Forb	Perennial	Nonnative	Cool	x	x		
OPMA2	*Opuntia*	*macrorhiza*	twistspine pricklypear	Subshrub	Perennial	Native	CAM		x		
OXST	*Oxalis*	*stricta*	yellow woodsorrel	Forb	Perennial	Native	Cool	x	x	x	x
PACA6	*Panicum*	*capillare*	witchgrass	Grass	Annual	Native	Warm	x	x	x	x
PAPS5	*Packera*	*pseudaurea*	falsegold groundsel	Forb	Perennial	Native	Cool				x
PASM	*Pascopyrum*	*smithii*	western wheatgrass	Grass	Perennial	Native	Cool			x	x
PEAN4	*Penstemon*	*angustifolius*	broadbeard beardtongue	Forb	Perennial	Native	Cool	x			x
PEAR6	*Pediomelum*	*argophyllum*	silverlead Indian breadroot	Forb	Perennial	Native	Cool				x
PEES	*Pediomelum*	*esculentum*	large Indian breadroot	Forb	Perennial	Native	Cool	x			
PHYSA	*Physalis*	*sp.*	groundcherry	Forb	Perennial	Native	Cool				x
PLPA2	*Plantago*	*patagonica*	woolly plantain	Forb	Annual	Native	Cool	x		x	x
POFE	*Poa*	*fendleriana*	muttongrass	Grass	Perennial	Native	Cool	x	x	x	x
POAL4	*Polygala*	*alba*	white milkwort	Forb	Perennial	Native	Cool			x	x
POLYG	*Polygala*	*sp.*	milkwort	Forb	Annual	Native	Cool	x			

POLYG4	*Polygonum*	*sp.*	knotweed	Forb	Annual	Nonnative	Cool			x	
PSTE5	*Psoralidium*	*tenuiflorum*	slimflower scurfpea	Forb	Perennial	Native	Cool	x	x	x	x
RACO3	*Ratibida*	*columnifera*	upright prairie coneflower	Forb	Perennial	Native	Cool	x		x	x
RUMEX	*Rumex*	*sp.*	dock	Forb	Perennial	Native	Cool	x		x	
SCPA	*Schedonnardus*	*paniculatus*	tumblegrass	Grass	Perennial	Native	Warm				x
SCSC	*Schizachyrium*	*scoparium*	little bluestem	Grass	Perennial	Native	Warm	x	x	x	x
SETAR	*Setaria*	*sp.*	foxtail	Grass	Annual	Nonnative	Warm	x	x	x	x
SOLID	*Solidago*	*sp.*	goldenrod	Forb	Perennial	Native	Cool	x	x	x	x
SOMI2	*Solidago*	*missouriensis*	Missouri goldenrod	Forb	Perennial	Native	Cool				x
SOMO	*Solidago*	*mollis*	velvety goldenrod	Forb	Perennial	Native	Cool				x
SONU2	*Sorghastrum*	*nutans*	Indiangrass	Grass	Perennial	Native	Warm				x
SOPT7	*Solanum*	*ptycanthum*	West Indian nightshade	Forb	Annual	Native	Cool	x	x	x	
SPCR	*Sporobolus*	*cryptandrus*	sand dropseed	Grass	Perennial	Native	Warm	x			x
STLE6	*Strophostyles*	*leiosperma*	slickseed fuzzybean	Forb	Annual	Native	Cool				x
SYFA	*Symphyotrichum*	*falcatum*	white prairie aster	Forb	Perennial	Native	Cool	x		x	
TAOF	*Taraxacum*	*officinale*	common dandelion	Forb	Perennial	Nonnative	Cool	x	x	x	x
THME	*Thelesperma*	*megapotamicum*	Hopi tea greenthread	Forb	Perennial	Native	Cool			x	x
TOXIC	*Toxicodendron*	*sp.*	poison oak/ivy	Subshrub	Perennial	Native	Cool	x			
TRDU	*Tragopogon*	*dubius*	yellow salsify	Forb	Annual	Nonnative	Cool	x		x	x

VEBA	*Vernonia*	*baldwinii*	Baldwin's ironweed	Forb	Perennial	Native	Cool	x	x	x	x
VEFA2	*Vernonia*	*fasciculata*	prairie ironweed	Forb	Perennial	Native	Cool			x	
VEST	*Verbena*	*stricta*	hoary vervain	Forb	Perennial	Native	Cool	x		x	x
VETH	*Verbascum*	*thapsus*	common mullein	Forb	Annual	Nonnative	Cool	x	x	x	x
VIRI	*Vitis*	*riparia*	riverbank grape	Subshrub	Perennial	Native	Cool	x			
VIVI	*Vicia*	*villosa*	winter vetch	Forb	Annual	Nonnative	Cool	x		x	
VUOC	*Vulpia*	*octoflora*	sixweeks fescue	Grass	Annual	Native	Cool	x		x	x
YUGL	*Yucca*	*glauca*	soapweed yucca	Subshrub	Perennial	Native	Cool			x	x

Appendix B

Communication and Outreach

B.1: Media Communications

Szuch, Susan. The North Platte Telegraph. 2021. Print news article. “Watch now: On the lookout for American burying beetles southeast of North Platte.” [https://nptelegraph.com/news/local/watch-now-on-the-lookout-for-american-burying-beetles-southeast-of-north-platte/article_49e83742-fc8d-11eb-8e47-13837fd99ee2.html]

Reyna, Beatriz. KNOP-TV. 2021. Television news presentation. “American Burying Beetle Research Underway.” [https://twitter.com/ALudwig7/status/1427678623385874438?s=20]

Stromberg, Ronica. University of Nebraska-Lincoln NSF National Research Traineeship Program. 2019. Student spotlight article. “Uncovering buried secrets of an endangered beetle.” [https://nrt.unl.edu/alison-ludwig]

B.2: Presentations and Posters

Ludwig, Alison K., Daniel R. Uden, and Dirac Twidwell. University Nebraska Lincoln Spring Research Fair. 2020. Poster presentation. “Extreme fire as a management tool to combat regime shifts in the range of the endangered American burying beetle.” [https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1203&context=agronhortdiss]

Ludwig, Alison. Nebraska Natural Legacy Conference. 2021. Video presentation. “The role of extreme fire in grassland restoration for the threatened American burying beetle.” [https://youtu.be/IkW0cADIX5A]

Ludwig, Alison. Nebraska Natural Legacy Conference. 2020. Video presentation. “Screening landcover types on a shifting landscape that supports the endangered American burying beetle (*Nicrophorus americanus*).” [https://youtu.be/wURNNuWDEfs]

B.3: Educational Programming

Ludwig, Alison K., Conor D. Barnes, Dillon T. Fogarty, Julie A. Fowler, Katharine F. E. Hogan, Jessica E. Johnson, and Dirac Twidwell. Plant and Soil Sciences eLibrary. 2021. Online educational module. “Ecological Resilience.” [https://passel2.unl.edu/view/lesson/d6c3e24cbc7e]

Barnes, Conor D., Dominic J. Cristiano, Hugh Ellerman, Alexandra Loker, Alison K. Ludwig, Daniel Morales, Alyssa Noble, and Dirac Twidwell. Council for Resilience Education Case Study. 2021. Online educational material. “The Sandville Wind Project: A Case Study for Teaching the Adaptive Cycle.” [https://cre.unl.edu/Teacher%27s%20Notes.pdf] & [https://cre.unl.edu/Student%20Handouts.pdf]

Dillon T. Fogarty, Katharine F. E. Hogan, Conor D. Barnes, Alison K. Ludwig, Julie A. Fowler, Jessica E. Johnson, and Dirac Twidwell. Council for Resilience Education Classroom Game Activity. 2021. Online educational material. “Understanding Resilience with Jenga.” [https://cre.unl.edu/Jenga%20Booklet.pdf]

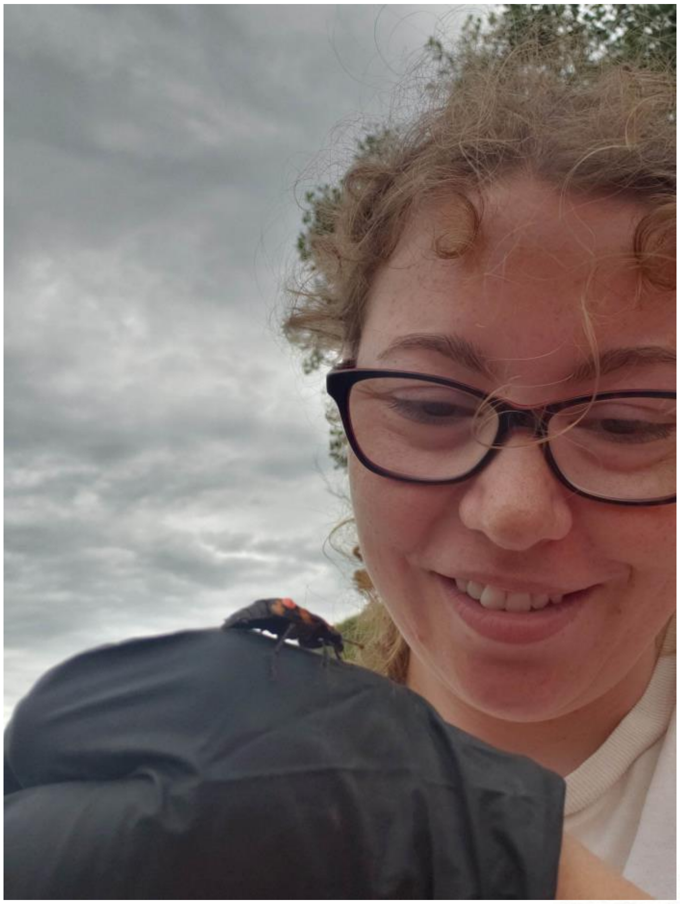
Appendix C

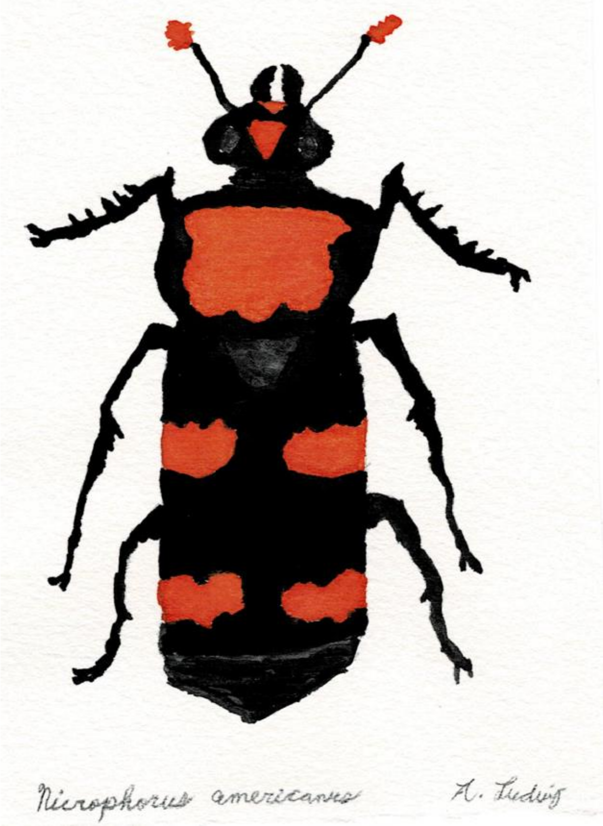
American Burying Beetle Image Gallery

C.1: Photos


7


12




Nicrophorus americanus
A. Ludwig

C.2: Videos

- **American Burying Beetle (Nicrophorus americanus) Grooming Behavior**

  https://youtu.be/EoHmkIoe9_0

- **American Burying Beetle Burrows into Soil**

  https://youtu.be/qLGXqtxIWGg

- **Old American Burying Beetle in Holding Container**

  https://youtu.be/W-e10z4MnHw

- **Carrion Beetles in Baited Bucket Trap**

  https://youtu.be/Cu0JHERWo3I

- **Young American Burying Beetles in Holding Container**

  https://youtu.be/nHbcmB29CPo

- **Inside Bucket Trap - American Burying Beetle**

  https://youtu.be/nHO6HhWVMGg