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Disturbances impose a state of disequilibrium on ecosystems, often leading to the maintenance of ecosystem type and prevention of state shifts. Grasslands serve as a model system for assessing disturbance regime shifts, as they are disturbance-dependent ecosystems. Fire, climate, and herbivory are key disturbances in maintaining grasslands, but these regimes are shifting due to anthropogenic activity. Fire intensity is increasing while frequency is decreasing, and precipitation is becoming more variable, with longer and more intense droughts projected. Moreover, grasslands are being exploited for agricultural use, often resulting in a shift of primary herbivores from native species to cattle grazers while terrestrial arthropods—globally important herbivores—are decreasing in abundance. Thus, we must work to understand how shifts in these regimes will affect future biodiversity and ecosystem function in grasslands.

To explore ecosystem changes as disturbance regimes shift, I focused on the Great Plains of North America where I performed a meta-analysis exploring the effects of fire frequency across multiple abiotic and biotic ecological factors (Chapter II) and used experimental and observational approaches to determine drought effects on plant communities (Chapter III) and assess the effects of cattle grazing and precipitation regime shifts on arthropod communities (Chapter IV). In Chapter II, I found that there is no “one-size-fits-all” fire management strategy to benefit all ecological factors in tallgrass prairie, however fire in unison with grazing creates a heterogeneous landscape, which benefits many ecological factors. In Chapter III, I provide evidence that plant communities in northern mixed-grass prairie are resistant to drought, likely due to shifts in plant species traits; however, this outcome is variable based on site and environmental factors. Finally, in Chapter IV, I demonstrated that precipitation mediates the effects of cattle grazing on arthropod communities, with diversity of arthropods increasing with cattle grazing intensity only in drought years. Overall, my work advances scientific knowledge on how anthropogenic and climate change driven shifts in disturbance regimes impact community dynamics and ecosystem function in Great Plains grasslands. As grasslands make up 40% of the earth's ice-free surface and contribute to the livelihoods of more than 800 million people worldwide through agricultural goods and services, providing evidenced-based information to land managers about how novel disturbance regimes impact grassland biodiversity and function will be critical to promote long-term sustainability of the ecosystem and will increase global food security.

THE ROLE OF DISTURBANCE IN GREAT PLAINS GRASSLAND COMMUNITY DYNAMICS

by

Kathryn J. Bloodworth

A Dissertation
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Approved by

Dr. Sally Koerner
Committee Chair

DEDICATION

To Nana and Papa, Grandmama, Granddad, and Linda. Your love of birds, chipmunks, gardens, and porch sitting, together with my time on The Farm inspired my passion for ecology from an early age.

APPROVAL PAGE

This dissertation written by Kathryn J. Bloodworth has been approved by the following committee of the Faculty of The Graduate School at The University of North Carolina at Greensboro.

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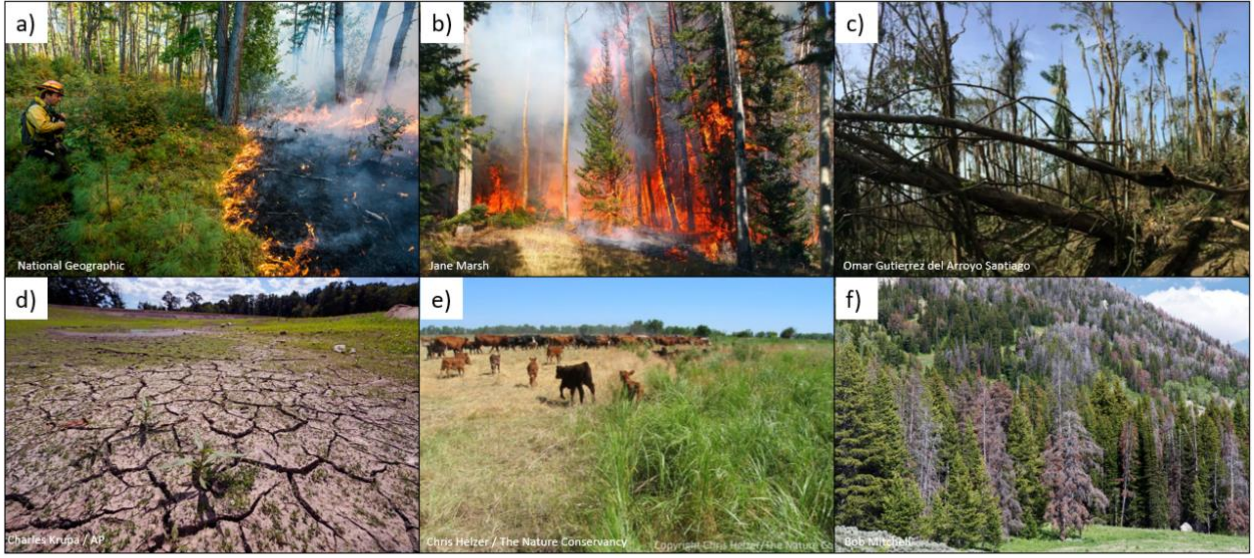
CHAPTER I: INTRODUCTION

Disturbance as an Ecological Driver

Many ecosystems have evolved with and rely on disturbances—defined here as any biomass altering events that result in a restructuring process (Grime, 1980; Jones & Syms, 1998; Rykiel, 1985)—to maintain ecosystem type and prevent state shifts (Beisner et al., 2003; Strömberg, 2011). In grasslands, fire, herbivory, and/or climate disturbances play a large role in maintaining healthy ecosystems (Briggs et al., 2005; Strömberg, 2011). However, the disturbance regimes that once existed are threatened by anthropogenic activity and climate change (Battisti et al., 2016). With humans managing 84.2% of grasslands (Ellis et al., 2021), land managers must be equipped with information on how shifting disturbance regimes will alter ecosystem function and biodiversity to make management decisions ensuring the sustainability of grassland ecosystems.

Disturbances often selectively cause mortality, consume biomass, and displace organisms (Burton et al., 2020). Ranging in length from seconds to years (Burton et al., 2020), disturbances vary in type, frequency, size, and severity (Figure 1.1) (Pickett & White, 1985). They create and alter patch-dynamics through a reduction of biomass and a change in plant species composition (Jentsch & White, 2019; Rykiel, 1985; Willig & Presley, 2018), thereby resulting in changes in biodiversity and ecosystem processes. As such, disturbances are an integral part of many ecosystems worldwide (Burton et al., 2020). For example, fire, herbivory, and climate maintain grasslands by preventing their transformation into forest ecosystems (Briggs et al., 2005). Disturbance is often necessary to slow or prevent competitive exclusion, leading to an ecosystem in which many species can coexist for tens to hundreds of years given periodic disturbance (Connell, 1978; Huston, 1979, 2014).

Figure 1. 1. Diversity of Ecosystem Disturbances



Note. Examples include a (a) healthy and mild forest fire, (b) severe forest fire, (c) category four hurricane, (d) severe grassland grazing, (e) mob grazing where cattle are transferred from paddock to paddock, (f) bark beetle insect damage during a major outbreak. Each disturbance type, frequency, and severity alter the ecosystem in different ways.

Disturbances have been widely recognized as crucial to ecosystem processes and community structure and dynamics for a century (Cooper, 1926; Pickett et al., 1989; Watt, 1947), yet many central ecological theories, such as the competitive exclusion principle (Hardin, 1960), are built on the assumption that communities exist in stable states. While more complex and more difficult to study, many nonequilibrium dynamic theories that include disturbance as a major component are recognized as important in ecological theory (Rapacciuolo et al., 2019)—e.g., intermediate disturbance hypothesis (Connell, 1978) and patch dynamic theory (Hastings, 1980; Tilman, 1994). Intermediate disturbance hypothesis (IDH), although mired in controversy (Fox, 2013a, 2013b; Sheil & Burslem, 2013), has played a large role in shaping disturbance ecology over the last four decades (Moi et al., 2020). IDH states that biodiversity should be highest at intermediate levels of disturbance, allowing colonizer and stress tolerant species to coexist (Connell, 1978). However, the exact frequency of disturbance necessary to maintain high levels of biodiversity is hypothesized to be, in part, dependent upon productivity (i.e., dynamic equilibrium model), —with higher productivity sites requiring higher frequency of disturbance (Huston, 1979)—ecosystem type, and natural climatic variability (Briggs et al., 2005; Johnstone et al., 2016).

The effects of disturbances can be ubiquitous, impacting everything from ecosystem function down to individual trait changes (Pickett et al., 1989). Disturbance helps to maintain higher plant biodiversity through both indirect mechanisms—by increasing heterogeneity—and direct mechanisms—by causing the death of a dominant species, resulting in greater opportunity for non-dominant species (Battisti et al., 2016; Thom & Seidl, 2016). The effects of disturbance on primary producers have cascading consequences for other taxa (Griffiths & Brook, 2014; Michalski & Peres, 2007). For example, an increase in plant diversity can lead to greater diversity of arthropods, especially those that rely on plant species for food or shelter (Ebeling et al., 2018), leading to an increase in food sources for higher trophic levels (Neff et al., 2020). This can increase indirect and direct pressure on plant species, creating a cyclical nature of disturbance effects on the ecosystem (Hewitt & Onsager, 1983).

While disturbances alter ecosystems, ecosystem components also respond and acclimate or adapt to disturbances over time. Adaptive strategies range from an individual level to a species level and can range in time from immediately post disturbance to over many generations (Battisti et al., 2016). Disturbances can cause a response of (1) regulation—quick and reversible changes to an individual, (2) acclimation—longer-term but reversible morphological changes, (3) development—longer-term and irreversible change throughout an individual’s development, or (4) evolution (Battisti et al., 2016). Disturbances create evolutionary pressure by selecting for or against specific traits (Jentsch & White, 2019). Therefore, disturbances can increase plant functional diversity (Battisti et al., 2016) because evolutionarily, more functional traits—attributes that influence plant fitness (Reich et al., 2003)—within a community allow for a higher probability of ecosystem resilience (ability to recover) following a disturbance and resistance (ability to withstand) to a disturbance. However, disturbances can also simplify plant functional diversity, as they may reduce redundancy within the community by selecting for only traits that can survive the disturbance thereby making the system more vulnerable to future disturbances (Battisti et al., 2016). Although disturbances initially kill individuals or remove biomass within the ecosystem, they can ultimately lead to increases or decreases in biodiversity and ecosystem function depending on the ecosystem type and disturbance type, frequency, and intensity (Jones & Syms, 1998; Pickett & White, 1985).

Ecosystem Function and Community Dynamics

Disturbances can alter community composition, increasing, decreasing, or having no effect on diversity (Battisti et al., 2016; Koerner et al., 2018). Changes in community composition within the ecosystem may result in changes in ecosystem function (Cardinale & Palmer, 2002) with disturbances orchestrating interactions between biodiversity and ecosystem function by increasing emergent properties (properties of the whole system) or by decreasing the selection-probability effect (ecological processes controlled by one group of species) (Cardinale & Palmer, 2002). There is evidence that diversity is positively correlated with certain ecosystem functions, such as nutrient retention (Schwartz et al., 2000). Numerous theories exist to explain the biodiversity-ecosystem function relationship, such as niche complementarity (Tilman et al., 1997) or the sampling effect (Cardinale et al., 2006; Huston, 1997). However, a positive association between diversity and ecosystem function is not always present and other factors leading to ecosystem function are important to consider (Schwartz et al., 2000). For example, studies that find that increased plant species richness results in higher ecosystem function may be observing that increased functional diversity results in higher ecosystem function; it is not necessarily due to the increase of the number of plant species alone (Naeem et al., 1994; Schwartz et al., 2000). Moreover, we see that on a small scale, structural heterogeneity enhances ecosystem function, suggesting that patchy disturbances may be most useful in increasing ecosystem function (Sitters et al., 2015).

As disturbances facilitate changes in the plant community and species diversity, we see cascading effects within the ecosystem. Changes to forage quantity and quality can affect a broad range of ecological variables, including nutrient availability in the system (Schaub et al., 2020), arthropod abundance (Ebeling et al., 2018), and grazer health and weight (Ortega et al., 1997). While changes in overall species richness and diversity in the community are important, we must also consider how species turnover and changes in abundance leads to changes in ecosystem function. Altering the identity of species within an ecosystem can lead to changes in ecosystem function because of differing niche spaces that are occupied by a given species (Slade et al., 2017). However, when species turnover occurs one species that occupies a specific niche space may be replaced with another that occupies a similar niche space, leading to no change in functional diversity and therefore no change in ecosystem function (Schwartz et al., 2000). It is crucial to understand not only which species are being replaced within a community under varying disturbance regimes but also what niche spaces each species occupies within the ecosystem.

Global Change Factors Alter Disturbance Regimes and Ecosystem Function

As we continue to unveil how disturbances and ecosystem functions relate, we must add global change factors into the equation, because changes in the disturbance regimes (how often, how intense, and how large the disturbance) that are already and will continue to result from global change and anthropogenic activity will lead to changes in the response of the environment (Battisti et al., 2016). For example, herbivory is changing drastically with the decrease in native mega-fauna (Ripple et al., 2016) and their replacement with non-native domesticated species, such as cattle. Currently, cattle grazing pressure is increasing because of increased demand for protein with our growing human population (*FAO*, 2022). This combined with the global decline of terrestrial arthropods (Seibold et al., 2019; van Klink et al., 2020; Wagner et al., 2021)—a group that includes important herbivores (Hewitt & Onsager, 1983)—is leading to a multifaceted change in herbivory disturbances. Additionally, fire disturbances are changing because of anthropogenic activity, though this change is region specific. For example, fires in Australia are less frequent but more intense due to fire suppression (Clarke et al., 2013), whereas fires in the contiguous United States are more intense and larger when they naturally begin and they have become more frequent over a longer period with anthropogenic ignitions (Cattau et al., 2020). Finally, precipitation regimes are becoming more variable, resulting in an increase in drought intensity and frequency in many ecosystems (Stocker et al., 2013). To preserve ecosystem function, we must attempt to conserve or actively manage natural disturbance regimes in the face of the rapid change induced by anthropogenic activity (Newman, 2019). If disturbance regimes cannot be entirely conserved, it will be more important than ever to develop evidence-based adaptive management strategies that evolve with changing disturbance regimes (Newman, 2019).

Grasslands as a Model Ecosystem

Grasslands provide a model ecosystem for studying disturbances because of their disturbance-dependent nature, importance in human agriculture and biodiversity, and changing disturbance regimes. Grasslands are thought to have evolved with disturbances and cannot exist or persist without some level of regular disturbance (Strömberg, 2011). Historically, they covered more terrestrial land than any other single biome, once making up 40% of the earth's ice-free surface (Lehmann et al., 2019; Panunzi, 2008; White et al., 2000). Additionally, they contribute to the livelihoods of more than 800 million people worldwide, primarily through agricultural goods and services (Lehmann et al., 2019), and they provide a vast array of ecosystem services (e.g., carbon cycling and habitat for diverse plants and animals) (Grace et al., 2006; Parr et al., 2014). Further, grasslands are easy to experimentally manipulate, have rapidly observable dynamics (Blair et al., 2014), and have a rich plant trait history (Eriksson & Jakobsson, 1998; Poschlod et al., 2003; Purschke et al., 2012).

The North American Great Plains (hereafter, Great Plains)—a region stretching across the central United States and south-central Canada (Figure 1.2)—provide 25% of the annual crop and animal production in the United States (Rosenberg & Smith, 2009), while maintaining high levels of biodiversity (Blair et al., 2014). The Great Plains can be divided into three grassland ecosystem types: shortgrass prairie (furthest west), mixed-grass prairie, and tallgrass prairie (furthest east). The plant communities in these ecosystem types vary because of the natural precipitation gradient, with the shortgrass prairie being most xeric (precipitation limited) and the tallgrass prairie being the most mesic (high precipitation). While not strictly defined, grasslands have high graminoid cover, including grasses, sedges, and rushes, and are generally open landscapes with varying abundances of trees, shrubs, and forbs. Despite being dominated by graminoid species in terms of biomass, forb species make up much of the high plant diversity. Grassland soils are highly fertile because of their high plant diversity and the extensive root systems of the graminoid species, which has led to a long history of exploitation for agricultural purposes (Ellis et al., 2010).

Figure 1. 2. Range of the North American Great Plains

Note. Highlighted in dark green (data source: US Environmental Protection Agency). Map created in ArcGIS.

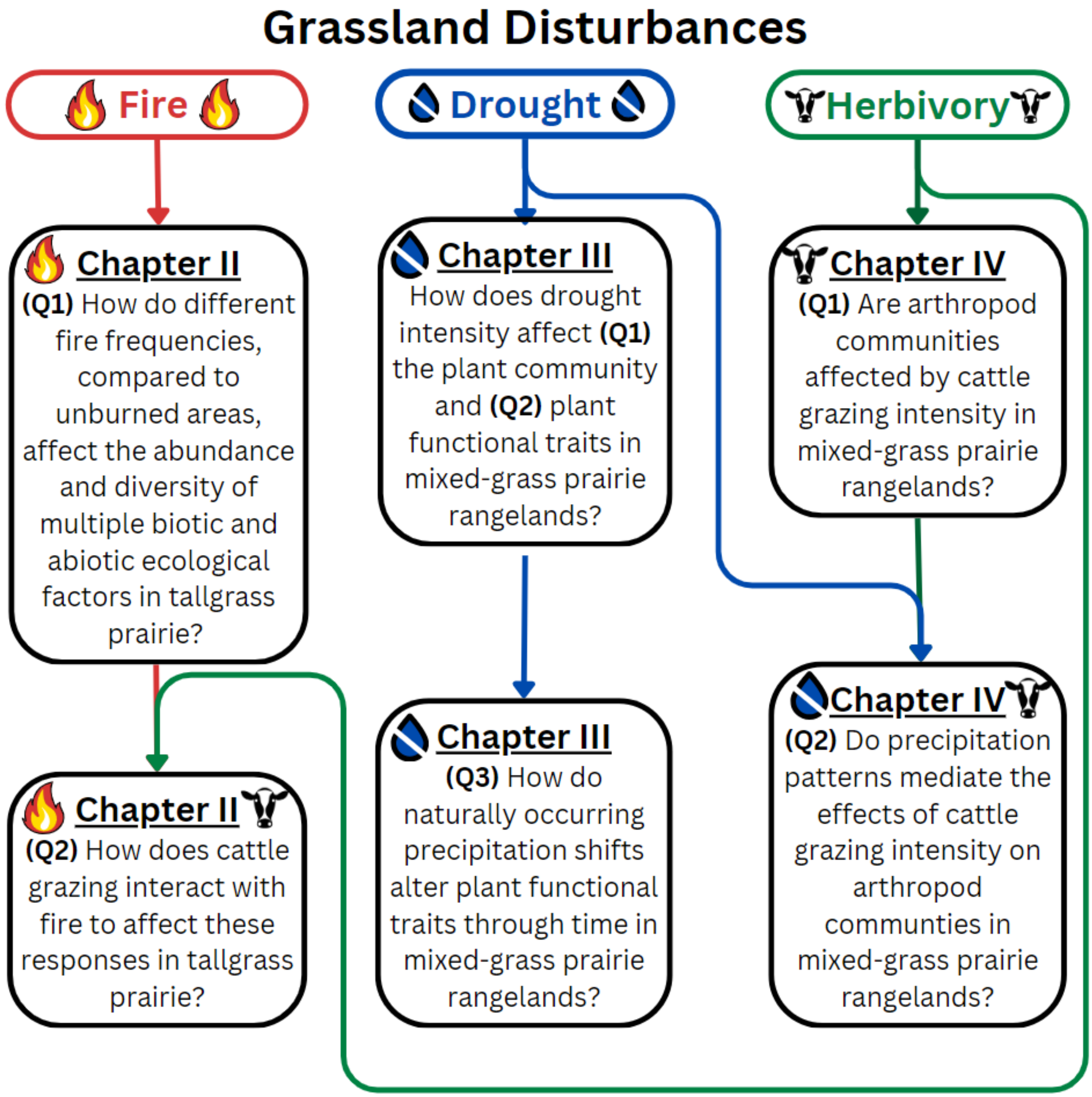
Like many grasslands, the Great Plains are threatened by multiple types of anthropogenic activity and climate change, including land use change for agricultural expansion, increases in nitrogen deposition and invasive species, degradation because of overgrazing (i.e., herbivory of herbaceous plants), fire suppression, and increases in drought occurrence (Stocker et al., 2013; Vickery et al., 2000). In fact, grasslands in the Great Plains are considered some of the most endangered ecosystems in North America (Blair et al., 2014; Hoekstra et al., 2005; Ricketts et al., 1999). As a result of anthropogenic activity, the disturbance regimes that grasslands have evolved with will no longer be the status quo (Newman, 2019). It is critical to understand how these changes may alter ecosystem function in grasslands, which may lead to a need for different management strategies to conserve the native North American grassland ecosystems.

Dissertation Aims and Significance

My dissertation research uses grasslands as a model system to explore how community dynamics and community traits respond to both natural and anthropogenic changes in disturbance regimes through three chapters (Figure 1.3). First, I performed a meta-analysis assessing the effects of fire on multiple ecological factors (e.g., plants, animals, and soil properties) in tallgrass prairie to create a guide for land managers as they make decisions about fire management strategies (Figure 1.3: Chapter II). Second, I used a combination of experimental and observational research to assess the effects of drought and rainfall variability on mixed-grass prairie rangeland plant communities (Figure 1.3: Chapter III). Finally, I used both an experimental and observational approach to assess the effects of cattle grazing and the interaction of cattle grazing and precipitation variability on the arthropod community in mixed-grass prairie rangelands (Figure 1.3: Chapter IV).

My dissertation work answers major outstanding questions in disturbance ecology and contributes to the field of disturbance ecology by adding to a growing body of literature assessing how anthropogenic and climate mediated disturbance regime shifts will affect important grassland ecosystems. My work is also applied in nature and provides land managers with vital information. 84.2% of grasslands are actively managed for diverse human-centric ecosystem services (Ellis et al., 2021) and only 4.6% of temperate grasslands are protected (Juffe-Bignoli et al., 2014). As grasslands are pressed into service to feed the growing global population, my work will assist land managers in making evidence-based management decisions that ultimately lead to greater sustainability of important but endangered grassland ecosystems.

Figure 1. 3. Dissertation Research Outline



Chapter II
(Q1) How do different fire frequencies, compared to unburned areas, affect the abundance and diversity of multiple biotic and abiotic ecological factors in tallgrass prairie?

Chapter II
(Q2) How does cattle grazing interact with fire to affect these responses in tallgrass prairie?

Chapter III
How does drought intensity affect **(Q1)** the plant community and **(Q2)** plant functional traits in mixed-grass prairie rangelands?

Chapter III
(Q3) How do naturally occurring precipitation shifts alter plant functional traits through time in mixed-grass prairie rangelands?

Chapter IV
(Q1) Are arthropod communities affected by cattle grazing intensity in mixed-grass prairie rangelands?

Chapter IV
(Q2) Do precipitation patterns mediate the effects of cattle grazing intensity on arthropod communities in mixed-grass prairie rangelands?

Note. Fire, grazing, and drought drive and maintain the disturbance dependent grassland ecosystems of the Great Plains. My dissertation explored grassland community shifts in response to altered disturbance regimes in the age of the Anthropocene.

CHAPTER II: FIRE FREQUENCY DRIVES TRADEOFFS AMONG CONSERVATION PRIORITIES IN TALLGRASS PRAIRIE

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Abstract

Disturbance is a natural part of all ecosystems and often creates a balance of resistance-resilience amongst taxa. Grassland ecosystems, and in particular tallgrass prairie, are model systems for studying the outcomes of disturbance regime shifts because they are disturbance dependent (i.e., maintained by fire, grazing, and/or climate). The effects of changing disturbance intensities and frequencies, such as fire in mesic grasslands, are often assessed based on one or a few taxa. However, to support diverse management goals land managers must understand the effects of their choices for many taxa. In this study, we addressed this gap using a meta-analysis of 37 studies to assess the effects of different fire frequencies on ecological factors (i.e., arthropods, birds, plants, small mammals, and soil properties) and the interactive effects of fire frequency and grazing, another important disturbance in tallgrass prairie. As expected, abundance and diversity of taxa were affected by different fire frequencies. However, the directionality of the change varied among taxonomic groups, indicating that there is no "one-size-fits-all" fire management strategy to maintain and improve habitat for grassland taxa. Annual fires promoted small mammal abundance but decreased plant abundance and diversity. Meanwhile, intermediate fire frequencies promoted plant abundance but at the cost of plant diversity, arthropod abundance, and soil total carbon and nitrogen. Finally, grazing promoted plant abundance while reducing arthropod and obligate grassland bird abundance. Our study revealed research gaps, with critical data missing or lacking from small mammals, birds, soil properties, and eastern tallgrass prairie.

Synthesis and Applications: Quantifying the differential responses of ecological factors to fire frequency can inform tallgrass prairie management strategies. Here we provide an example of the potential for land managers to manipulate disturbance frequencies to meet diverse management goals. We outline the important tradeoffs associated with management strategies using fire frequency and highlight the potential for fire to be used in unison with grazing to create a more heterogenous landscape conducive to tallgrass prairie. While there is still much work to be done, this study addresses questions of harnessing the power of prescribed fire to increase sustainability and health of mesic grasslands worldwide.

Keywords: Biodiversity, burn, disturbance, ecosystem management, grassland, grazing, Great Plains, soil health

Introduction

Ecological disturbances—defined here as biomass-altering abiotic or biotic events that result in a restructuring process (Grime, 1980; Jones & Syms, 1998; Rykiel, 1985)—are agents of natural selection: affecting species composition, structure, and the distribution of species (Battisti et al., 2016; Pickett et al., 1989). Disturbances are often used as land management techniques (Long, 2009; North & Keeton, 2008) and are widely recognized as important ecological processes (see Connell, 1978; Hastings, 1980; Rapacciuolo, Rominger, Morueta-Holme, & Blois, 2019; Tilman, 1994). Yet, the frequency of disturbance that is beneficial for meeting management goals varies based on many factors including ecosystem type, natural climatic variability (Briggs et al., 2005; Johnstone et al., 2016), productivity (Huston, 1979), and desired outcomes (e.g., butterfly diversity or soil health). Therefore, there is likely no “one-size-fits-all” disturbance frequency when it comes to ecosystem management.

Species often exhibit either resistance or resilience to disturbances—with some species tolerating the effects of disturbance (resistance) while others respond quickly post-disturbance (resilience) (Miller et al., 2011; Miller & Chesson, 2009; Seifan et al., 2013). This leads to potentially diverging responses of ecological factors (i.e., arthropods, birds, plants, small mammals, and soil properties) to disturbance, mediated in part by trophic level interactions (Kadin et al., 2019). For example, responses of plant communities are generally consistent with the intermediate disturbance hypothesis (Connell, 1978), whereas consumer responses are more variable (Wootton, 1998), with top-down and bottom-up food web processes shifting in the presence of disturbances (Jellyman & McIntosh, 2020). In addition, soil nutrient levels vary across disturbance regimes with frequent burning resulting in decreased soil carbon and nitrogen through time (Pellegrini et al., 2018). This alters other ecological factors such as primary productivity (Augustine et al., 2003; Koorem et al., 2014). These varying effects of disturbance on ecological factors must therefore be thoughtfully weighed, and cascading effects accounted for within an ecosystem (Kadin et al., 2019) when making management decisions. However, to date most studies assess disturbance effects on one or two ecological factors, likely because of logistical constraints (see Benson, Dinsmore, & Hohman, 2007; Li, Knops, Zuo, & Laungani, 2014; O’Connor, Taylor, & Nippert, 2020; Vogel, Debinski, Koford, & Miller, 2007; Wessman, Bateson, & Benning, 1997).

Grasslands are dependent on disturbance and thus are excellent ecosystems for addressing diverging responses of abiotic and biotic ecological factors due to often-conflicting management goals such as cattle production and grassland bird conservation. Grasslands historically covered more terrestrial land than any other biome (Lehmann et al., 2019; Panunzi, 2008; White et al., 2000), and they currently contribute to the livelihoods of more than 800 million people worldwide, primarily though agricultural goods and services (Lehmann et al., 2019; Liu et al., 2022). Additionally, grasslands provide diverse ecosystem services such as storing approximately one-third of the world's carbon, playing a key role in global biogeochemical cycles (Bai & Cotrufo, 2022; White et al., 2000) and providing habitat for diverse plants and animals (Grace et al., 2007; Parr et al., 2014).

Disturbances such as fire, herbivory, and climate contribute to grassland conditions worldwide (Brockway et al., 2002; James et al., 1905; Umbanhowar, 1996). Highly flammable plant litter, open landscapes, and typical windy conditions lead to the occurrence of periodic large-scale fires (Blair et al., 2014). Fires often move quickly through grasslands, burning aboveground biomass and leaving belowground buds and meristems protected under the soil (Blair et al., 2014). Grazing also plays a vital role in shaping the plant communities of nearly all grasslands (Strömberg, 2011), with moderate grazing typically increasing plant diversity, but decreasing grass cover in mesic grasslands (Koerner et al., 2018). In many grasslands, fire and grazing combined can increase structural heterogeneity (Ricketts & Sandercock, 2016), which can lead to increases in diversity and/or abundance of native species (Hovick et al., 2014; Joern, 2005). This ultimately increases overall ecosystem function. As with other disturbances, fire can differentially affect ecological factors depending on the frequency of the disturbance (Knapp et al., 1998) and co-occurrence with other disturbances. Therefore, land managers can harness fire frequency to obtain desired land management outcomes.

Grasslands are some of the most threatened ecosystems worldwide (Scholtz & Twidwell, 2022), with the tallgrass prairies of central North America being a particularly endangered ecosystem. The tallgrass prairie once stretched from south-central Canada down to Texas, USA, covering 7 million hectares, with only ~13.4% of the original extent remaining (Robertson et al., 1997; Samson et al., 2004; Samson & Knopf, 1994), and with some estimates putting the remaining area as low as 1% (Helzer, 2009; Quijas & Balvanera, 2013; Samson & Knopf, 1996). As management of remaining tallgrass prairie continues and restoration efforts of tallgrass prairie expand, land managers can rely on natural disturbances such as fire and grazing to meet their management goals.

Historically in the tallgrass prairie, fires occurred due to lightning strikes (Blair et al., 2014), but likely even more significant were the fires set by Indigenous Americans largely to lure bison and other game (McClain et al., 2021) because large grazers are attracted to the new growth of grass post-burn. This resulted in a shifting, heterogenous landscape (Souther et al., 2023). Following the genocide, displacement, and forced cultural assimilation of Indigenous Americans by European settlers, Traditional Ecological Knowledge was largely abandoned, and land management strategies were altered (Nelson, 2014). While fires continued to occur across North American tallgrass prairie, they were rarer and mainly occurred because of accidental expansion of small fires or to clear land for agricultural use. By the late 1800s, the tallgrass prairie ecosystem was so fragmented that fires were largely extinct (McClain et al., 2021). One exception was the Flint Hills of Kansas and Oklahoma, where a landscape of tallgrass prairie was preserved due to underlying geology of limestone and chert, and where a culture of prescribed burning was adopted by many in the ranching community. Fragmentation of remnant tallgrass prairie, even in portions of the Flint Hills, led to a further decline with less frequent and intense fires favoring shrub- or woodland in lieu of grasses (Blair et al., 2014; Knapp & Seastedt, 1986). As the plant community lays the foundation for many ecological services, including cattle production, carbon sequestration, and wildlife habitat provisioning, fire effects on the primary production and plant community structure can have cascading consequence for other ecological factors (Griffiths & Brook, 2014; Michalski & Peres, 2007).

Prescribed fire is a powerful tool for land managers to effectively manage and restore tallgrass prairie for ecological, cultural, and economical benefits, especially when used in combination with light to moderate grazing. Yet, because different taxa are sensitive to different frequencies of disturbance, the fire frequency that will have the most positive consequences for the most ecological factors is unknown. Here we examine the effects of fire frequency on a wide range of ecological factors, performing a meta-analysis to ask: **(Q1)** How do fire frequencies compared to unburned areas affect the abundance and diversity of multiple biotic and abiotic ecological factors? And **(Q2)** How does grazing interact with fire to affect these responses? We hypothesized that there would not be a "one-size-fits-all" fire frequency, but instead we would see diverging effects amongst and within ecological factors, given that fire frequency differentially affects many ecological factors (Johnson & Matchett, 2001; Koerner & Collins, 2014; Wallner, Molano-Flores, & Dietrich, 2012). Moreover, given the historical nature of grazing and fire interactions in tallgrass prairie systems, we hypothesized that fire and grazing combined would increase heterogeneity (Fuhlendorf & Engle, 2004), thereby benefiting many ecological factors.

Materials and Methods

Literature Review: We performed a systematic literature review using Web of Science to search for peer-reviewed journal articles published between 1950 and 2020. The search included key words that required locations in the tallgrass prairie range, ecosystem terms for tallgrass prairie, fire, and at least one ecological factor of interest: the abundance, diversity, and/or rarity of arthropods, birds, plants, and small mammals and soil metrics (total carbon [TC], total nitrogen [TN], and soil microbial biomass). The full search term list can be found in Table A.2.1. This search resulted in 1,158 peer reviewed journal articles, 492 of which were studies where fire frequency was assessed within tallgrass prairie.

Inclusion Criteria: In assessing the 492 papers for inclusion in our study the study must have (1) occurred within the tallgrass prairie range, (2) measured effects of at least one fire frequency treatment, (3) measured effects of an unburned area (no burn for >20 years), and (4) measured at least one ecological factor of interest. We chose to use unburned areas as our reference treatment so that we could determine effect sizes, making the data comparable across studies because the methodology of data collection techniques varies drastically across researchers. However, we could have also chosen an annual fire frequency—an especially common management practice in eastern tallgrass prairie—as our reference; however, that choice would have eliminated many studies which were included with the selection criteria. We anticipated that using annual fire frequency would result in a similar number of studies for the final analysis. In short, we could not do both within the scope of this single study. In assessing ecological factors, we included arthropod, bird, plant, and small mammal studies if they assessed abundance, diversity, and/or rarity data, although no studies that included rarity met other criteria. For soil metrics, studies were included if soil TN or TC, or soil microbial biomass was studied, although no studies that included soil microbial biomass met other criteria. We used the *metagear* package version 0.7 (Lajeunesse, 2016) in R 4.2.1 (R Core Team & Computing, 2021) to filter studies based on inclusion criteria.

Data Extraction: For each of the articles that met criteria, we categorized fire frequency and extracted means, standard errors, and sample size from both the fire treatment and unburned area. We determined means and standard error using Plot Digitizer (Huwaldt, 2020). In cases where confidence intervals were reported, we converted them to standard error. Then, we converted all standard error values to standard deviation. Fire frequency categories ultimately included annual burning, burning every 2-4 years, and fire with grazing. While we attempted to capture 5-10-year and 10–20-year fire frequencies, as they are common management strategies, we were unable to do so. This was likely because most studies that assessed effects of 5+ year fire frequencies did not also assess effects of 20+ year fire frequencies, therefore eliminating them from our study as they did not have an unburned reference area. We also noted coordinates of each study for later comparison across latitudinal and longitudinal gradients.

Meta Analysis: All analyses were performed in R 4.2.1 (R Core Team & Computing, 2021). To avoid methodological mismatching between studies, we calculated the effect size Hedges' *g* (Hedges, 1981; Hedges et al., 1999) for each sample using the equation:

$$Hedges'g = \frac{(Mean_{treatment} - Mean_{control})}{\sigma_{pooled}}$$

where

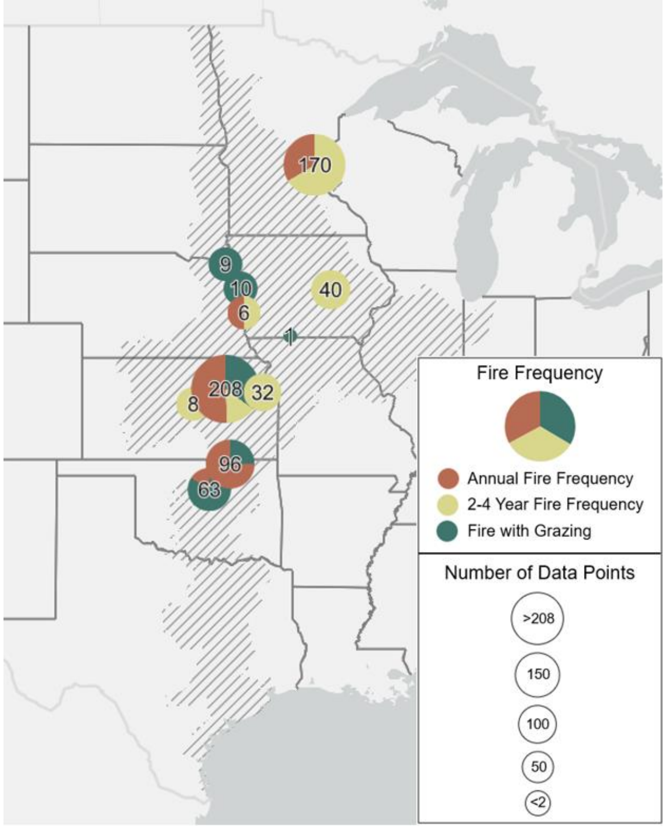
$$\sigma_{pooled} = \sqrt{\frac{(n_{treatment} - 1) \times \sigma^2_{treatment} + (n_{control} - 1) \times \sigma^2_{control}}{(n_{treatment} + n_{control} - 2)}}$$

Treatment refers to either annual fire frequencies, 2–4-year fire frequencies, or a fire with grazing treatment. Control refers to our reference treatments; annual fire frequencies were compared to unburned, ungrazed areas, 2–4-year fire frequencies were compared to unburned, ungrazed areas, and grazing with fire was compared to unburned areas that were grazed. σ refers to the standard deviation and n refers to the sample size. In studies where n was reported as a range, we took the average of the range. Hedges’ *g* effect sizes were then averaged across ecological factor and fire frequency. An average Hedges’ *g* effect size ± 95% CI > 0 indicates a positive effect of a given fire frequency on a given ecological factor compared to the reference area. Alternatively, an average Hedges’ *g* effect size ± 95% CI < 0 indicates a negative effect of a given fire frequency on a given ecological factor compared to the reference area. All data and code can be found in a GitHub Repository (link to be provided upon acceptance).

Results

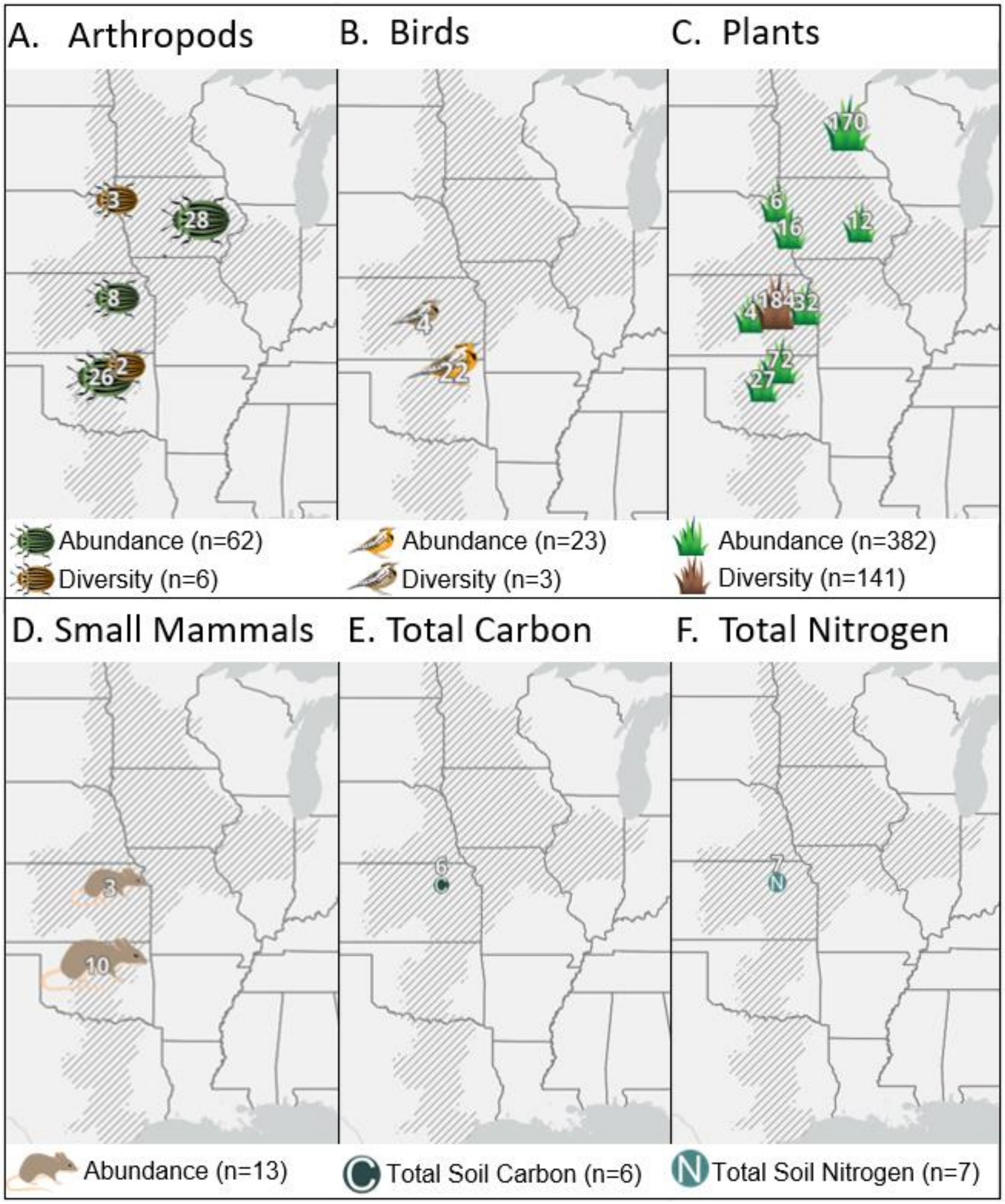
Following screening, 37 articles, published from 1988-2020 remained in this study (Table A.2.2). From those studies, there were 643 pairwise comparisons made. Specifically, there were 247 comparisons (effect sizes) derived from 21 studies at 5 locations assessing responses to annual fire frequencies compared to unburned areas (Figure 2.1). There were 226 comparisons (effect sizes) derived from 14 studies at 7 locations assessing responses to 2-4-year fire frequencies compared to unburned areas (Figure 2.1). Finally, there were 170 comparisons (effect sizes) derived from 16 studies at 10 locations assessing responses to fire with grazing compared to unburned areas with grazing (Figure 2.1). Most of the fire with grazing treatments occurred on an annual or tri-annual basis using patch burn grazing or pyric herbivory. Soil TC and TN and the diversity and abundance of arthropods, birds, plants, and small mammals were assessed across some but not all fire frequencies (Figure 2.2).

Figure 2. 1. Map of the Distribution of all Ecological Factors.



Note. Data are from annual fire frequency (orange), 2-4-year fire frequency (yellow), and fire with grazing (blue) across the tallgrass prairie region (hatched lines; data obtained from USDA Forest Service). Numbers inside circles represent the number of pairwise comparisons in each area, scaled by size where larger circles have more pairwise comparisons.

Figure 2. 2. The Distribution of Data Points by Ecological Factor.



Note. (A.) Arthropods, (B.) birds, (C.) plants, (D.) small mammals, (E.) soil total carbon, and (F.) soil total nitrogen across the tallgrass prairie region (hatched lines; data obtained from USDA Forest Service). Abundance and diversity are represented as different colors in panels A, B, and C. Numbers inside icons represent the number of pairwise comparisons in each area, scaled by size where larger circles have more pairwise comparisons.

Data collection methods varied across studies. In studies that assessed arthropods, abundance was reported as a count, density, relative abundance, or biomass, assessing all arthropods, functional groups, or arthropod orders. Arthropod diversity was reported as species richness, alpha diversity, or Shannon-Weiner diversity and was assessed within an arthropod order or across insects. Sample size was less than five for arthropod abundance in annual fire and arthropod diversity in 2-4-year fire and fire with grazing treatments. Bird abundance was reported as the number of detections, number of eggs per female, or number of young per successful nest across grassland obligate bird species (e.g., dickcissels, grasshopper sparrows, eastern meadowlarks). Bird diversity was reported as species richness, Shannon-Weiner diversity, or evenness of breeding grassland-obligate species. Sample size was less than five for bird abundance and diversity in 2-4-year fire treatments. Plant abundance was reported as the total aboveground net primary productivity (ANPP), cover, biomass, or stem density across all plants, functional groups, species, or native status. Plant diversity was reported as richness, Shannon-Weiner diversity, or evenness of all plants, functional group, or native status. Small mammal abundance was reported as number of individuals by species. Sample size of small mammals was less than five in 2-4-year fire treatments. Soil TC and soil TN were reported as grams per meter squared, micrograms per sample, or metric tons per hectare. Sample size was less than five for soil TC and TN in all fire frequencies.

Data did not span a longitudinal gradient across tallgrass prairie (Figure 2.1), as our methodological approach ultimately removed most studies in the eastern tallgrass prairie, where unburned areas are not common land management practices. In eastern tallgrass prairie, burning, especially in the absence of haying or grazing is widely recognized as important to the ecosystem health and consequently, areas with >20 years without burning are rare. Therefore, we were unable to assess changes in the effect of fire frequency longitudinally.

We found that annual fire compared to unburned areas resulted in a lower abundance and diversity of plants (Table 2.1; Figure 2.3A and B, respectively), but an overall increase in abundance of small mammals (Table 2.1; Figure 2.3A) and no change in arthropod abundance (Figure 2.3A). Soil TC and soil TN were not affected by annual fire frequencies compared to unburned areas (Table 2.1; Figure 2.4). Two-to-four-year fire frequencies compared to unburned areas reduced arthropod and bird abundance (Table 2.1; Figure 2.3C) but did not affect arthropod or bird diversity (Table 2.1; Figure 2.3D). Plant abundance increased with 2–4-year fire frequencies compared to unburned areas while plant diversity decreased (Table 2.1; Figure 2.3C and D, respectively). Small mammal abundance was not affected by the 2–4-year fire frequencies compared to unburned areas (Table 2.1; Figure 2.3C). Soil TC and TN were both reduced with 2–4-year burn frequencies compared to unburned areas (Table 2.1; Figure 2.4).

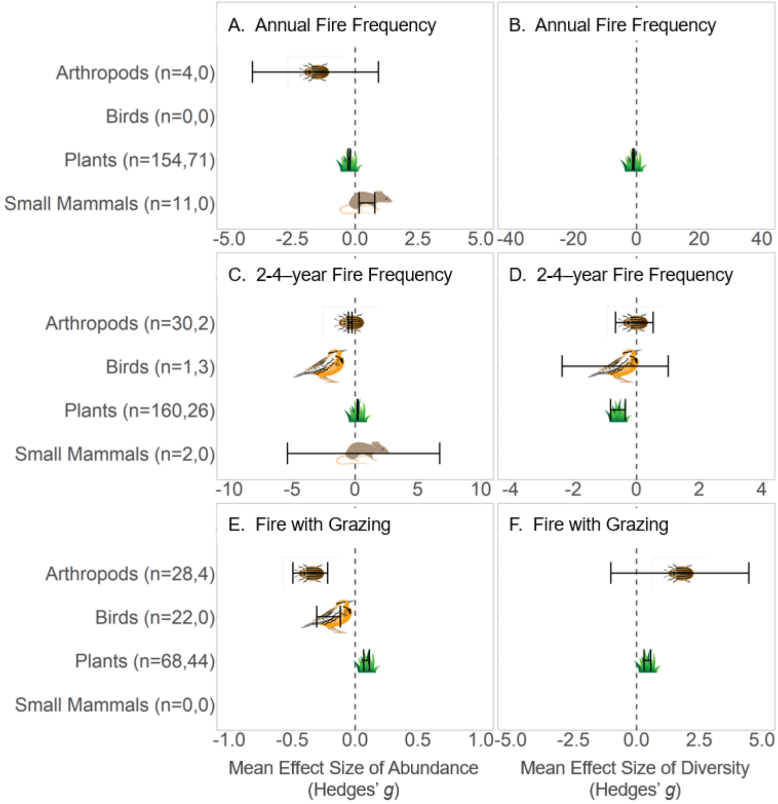
When comparing fire with grazing to unburned areas with grazing, abundance of arthropods and birds decreased, but plant abundance increased (Table 2.1; Figure 2.3E). Moreover, plant diversity increased, and arthropod diversity did not change when fire was paired with grazing compared to unburned areas with grazing (Table 2.1; Figure 2.3F). Finally, soil TC and soil TN were not affected by fire with grazing compared to unburned areas with grazing (Table 2.1; Figure 2.4). The consequences of fire did not vary with latitude except for plant abundance at 2–4-year fire frequencies compared to unburned areas, where higher latitude corresponded with decreased plant abundance; due to minimal effects, latitude analyses are not presented further.

Table 2. 1. The Average Effect Size (Hedges' *g*) of Annual Fire Frequencies and 2–4-Year Fire Frequencies Compared to Unburned Areas and Fire with Grazing Compared to Unburned Areas with Grazing

Ecological Factor		Annual Fire Frequency			2–4-year Fire Frequency			Fire with Grazing		
		Hedges' *g*	n	95% CI	Hedges' *g*	n	95% CI	Hedges' *g*	n	95% CI
Arthropod	Abun	-1.58	4	-4.08 to 0.93	-0.39	30	-0.54 to -0.25	-0.36	28	-0.49 to -0.22
	Div	-	-	-	-0.07	2	-0.67 to 0.53	1.73	4	-1.02 to 4.47
Bird	Abun	-	-	-	-2.73	1	-	-0.21	22	-0.31 to -0.12
	Div	-	-	-	-0.68	3	-2.37 to 1.01	-	-	-
Plant	Abun	-0.24	154	-0.28 to -0.20	0.19	160	0.16 to 0.22	0.09	68	0.07 to 0.11
	Div	-1.00	71	-1.24 to -0.77	-0.58	26	-0.82 to -0.35	0.44	44	0.31 to 0.57
Small Mammal	Abun	0.47	11	0.15 to 0.78	0.67	2	-5.39 to 6.74	-	-	-
	Div	-	-	-	-	-	-	-	-	-
Total Soil Carbon		-0.86	3	-2.30 to 1.28	-2.33	1	-	1.67	2	-13.30 to 16.64
Total Soil Nitrogen		-1.62	4	-4.19 to 0.96	-2.86	1	-	0.77	2	-6.18 to 7.73

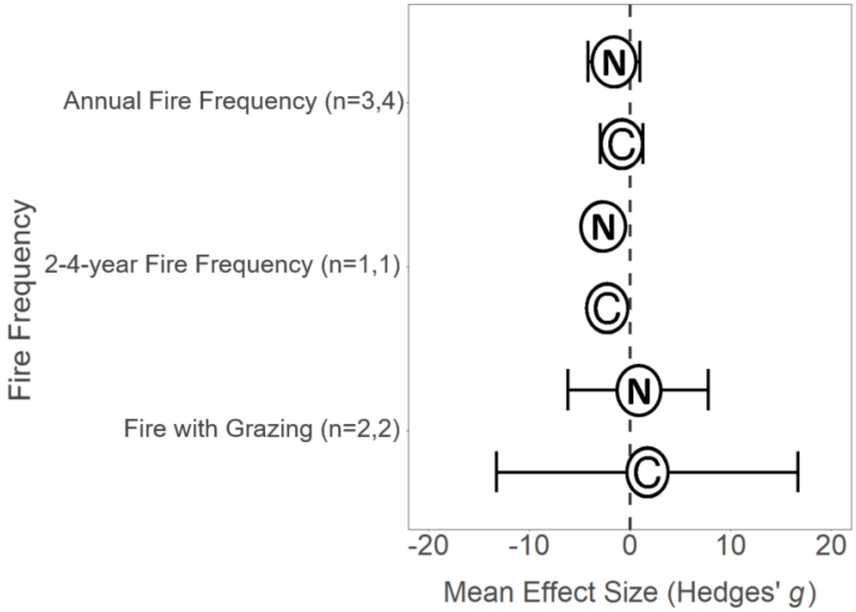
Note. Abundance (Abun) and diversity (Div), effect sizes (Hedges' *g*), sample size (n), and 95% confidence intervals (95% CI) are reported.

Figure 2. 3. Fire Frequency Effect Sizes (Hedges' *g*) for Biotic Ecological Factors



Note. The mean effect size (Hedges' *g*) of the abundance and diversity of each biotic ecological factor given annual fire frequencies compared to unburned areas (A, B), 2-4-year fire frequencies compared to unburned areas (C, D), and fire with grazing compared to unburned areas with grazing (E, F). The dotted line represents no difference in the given fire return interval from reference areas. Points that occur to the left of the dotted line indicate a reduction in abundance/diversity of the ecological factor, while points that occur to the right of the dotted line indicate an increase in abundance/diversity of the ecological factor. Icons represent the mean and bars represent +/- the 95% confidence interval; in the instance where the 95% confidence interval does not overlap with the dotted line at zero, this indicates a difference in the given fire frequency compared to the reference area. Sample size (number of pairwise comparisons) is noted in the y-axis labels for abundance and diversity, respectively, for each ecological factor. For clarity of the log response ratios, each panel is reported with a different scale on the x-axis.

Figure 2. 4. Fire Frequency Effect Sizes (Hedges' *g*) for Soil Variables



Note. The mean effect size (Hedges' *g*) of the total soil nitrogen (N) and total soil carbon (C) in response to annual fire frequencies compared to unburned areas, 2-4-year fire frequencies compared to unburned areas, and fire with grazing compared to unburned areas with grazing. The dotted line represents no difference in the given fire return interval compared to the reference area. Points that occur to the left of the dotted line indicate a reduction in response to the given fire frequency, while points that occur to the right of the dotted line indicate an increase in response to the given fire frequency. Sample size (number of pairwise comparisons) is noted in the y-axis labels for total soil nitrogen and total soil carbon, respectively for each fire frequency.

Discussion

Here we identify fire frequency effects on a broad suite of abiotic and biotic responses to advise fire management in tallgrass prairie. We found that the fire frequency that provides the greatest plant diversity, a common management goal in tallgrass prairie (Wright Morton et al., 2010), was fire with grazing. However, we found three main tradeoffs of management using fire frequency that are crucial to understand and carefully weigh when determining management plans for tallgrass prairie conservation and restoration.

First, in ungrazed systems, annual fires (compared to unburned areas) promoted small mammal abundance at the expense of plant abundance and diversity. The response of small mammals here is expected, as small mammal abundance typically increases in recently burned areas though this outcome may be driven by the increase in abundance of common species of small mammals (e.g., Deer mouse, *Peromyscus maniculatus*) (Burke et al., 2020). With more comprehensive small mammal diversity data, we may have seen that the increased small mammal abundance was the result of decreased diversity (Guiden et al., 2021) because grassland specialists (e.g., Prairie vole, *Microtus ochrogaster*) lose critical habitat with frequent burning, allowing common species to increase in abundance (Burke et al., 2020). Frequent fires, especially in wet years and at the beginning of growing seasons, reduce the overall diversity of plant species; this is typically attributed to increased growth of grasses and total plant productivity, which changes the microclimate and resource availability when detritus is removed via burning (Blair et al., 2014; Knapp & Seastedt, 1986). The reduction in plant abundance seen here may be caused by the beneficial reduction in woody encroachment: a common issue in tallgrass prairie, where native or non-native woody shrubs increase in abundance, outcompeting native grasses and forbs (Archer et al., 2017). Therefore, fire is often used in tallgrass prairie to clear woody areas and minimize woody encroachment (Miller et al., 2017; O’Connor et al., 2020; Twidwell et al., 2013).

Second, intermediate fire frequencies (compared to unburned areas) supported plant growth at the detriment of plant diversity and arthropod abundance. This can be attributed to the typically seen increase in soil temperature, surface light, and soil nitrogen resulting in greater plant growth (Hulbert, 1988) and the warm season C_4 grasses outcompeting forbs, reducing plant diversity (Gibson et al., 1993). This reduction in plant diversity may lead to a reduction in arthropod abundance because of the expected lower structural heterogeneity and fewer available host species for herbivorous insects (Kelleher & Choi, 2020). However, fire has differential effects on the abundance of arthropods, with increasing fire frequency increasing the abundance of Hemiptera (true bugs), decreasing the abundance of Thysanoptera (thrips), and not affecting the highly mobile Diptera (flies), Hymenoptera (bees, wasps), Lepidoptera (butterflies, moths) (Hartley et al., 2007), or Coleoptera (Beetles) (Mason et al., 2021). Orders such as Orthoptera (grasshoppers), are often species specific in their response to fire (Joern, 2004). Thus, even within major taxonomic groups, there is no one fire regime that supports the highest diversity and abundance of all taxa.

Third, in the presence of grazing, burning (compared to unburned areas in the presence of grazing) promoted plant abundance and diversity at the cost of arthropod and bird abundance. The increase in plant diversity may be a result of the preferential consuming of grasses by large-bodied grazers such as bison or cattle, reducing the competitive ability of grass and leaving niche space for diverse forbs (Elson & Hartnett, 2017; Ratajczak et al., 2022). This is interesting given that grassland-obligate bird species typically do well with the increased structural heterogeneity that results from burning and grazing (Askins et al., 2007; Glass & Eichholz, 2023). Reduction in arthropod abundance could be the result of increased plant diversity leading to the stabilization of arthropod communities (i.e., fewer arthropod outbreaks) (Haddad et al., 2011).

Land managers have varied and disparate conservation goals covering more ecological factors than we were able to address in this study. While we set out to assess the effects of fire frequency across a broader range of fire return intervals and with more ecological factors, this study highlights the variability in study design and the gaps in scientific understanding and research, in particular collecting rigorous scientific data on ecological variables that are directly important to land managers. The literature to date effectively describes effects of fire frequencies on plant diversity and abundance, which can often explain changes among other ecological factors (Ebeling et al., 2018; Haddad et al., 2011; Neff et al., 2020). However, there was not representation of all other ecological factors across fire frequencies. We found a dearth of literature addressing questions of species rarity across biotic ecological factors and of microbial biomass, as well as a lack of spatial representation, with all soil TC and TN data coming from Konza Prairie Biological Station in Kansas, USA. Increasing ecological research with a focus on rarity studies could help scientists to better understand the ecological implications of management for threatened taxa. While we were also only able to include a small number of studies on birds and small mammals, this was likely a result of methodological mismatch between our study and those that addressed these questions. Often, we found that small mammal studies addressed questions of time since fire (e.g., (Clark & Kaufman, 1990; Kirchner, Green, Sergeant, Mink, & Wilkins, 2011), not fire frequency, which indicates important differences between taxa and how they respond to disturbances. As grassland research advances, ecologist must continue to broaden their work to include the effects of fire frequency on multiple ecological factors within a given study. Further, we need comprehensive, long-term fire management data reported with studies, allowing us to address questions in relevant ways to each taxon.

Originally, we hoped to identify latitudinal responses across the tallgrass prairie range which correspond to a precipitation gradient. However, we did not have enough data to address this question as our methodology led to the removal of many studies in eastern tallgrass prairie.

Eastern tallgrass prairie studies rarely, if ever, included unburned areas. While incorporating these studies was outside the scope of this project, we acknowledge that they still provide important information regarding fire management in tallgrass prairie. It is well established in eastern tallgrass prairie that not burning land at regular intervals in the absence of haying or grazing, especially, is detrimental to the tallgrass prairie ecosystem. Therefore, there is no need to test the idea that unburned land degrades the ecosystem. This is especially important given that eastern tallgrass prairie has experienced some of the highest losses of native grassland (Askins et al., 2007). Moreover, efforts to study this question would have large costs and labor requirements. Thus, the scientific community needs to acknowledge the experiences that lead to management decisions that are not robustly reported in peer-reviewed literature but are understood and supported by evidence known to current land managers and from Traditional Ecological Knowledge (Berkes et al., 2000; Kimmerer & Lake, 2001; Souther et al., 2023).

Overall, we show the diverging and synergistic responses to fire, enabling land managers to make evidence-based prioritizations of specific land management concerns. For example, many land managers seek to increase herbaceous plant biomass for grazing while reducing large woody species (Wright Morton et al., 2010); our study supports the idea that burning grazed land will increase plant abundance, likely leading to increased forage availability. Land managers also seek to conserve or increase native grassland plant species in restoration efforts (Rowe, 2010). We provide evidence of an increase of small mammal abundance with more frequent fires, which may have cascading effects on food webs as small mammals can act as both predators of native seeds (Schneider et al., 2017) and prey. In addition to management for native plant species and increased herbaceous plant abundance, restoration practitioners are interested in restoring other native species to the tallgrass prairie. Though information on grassland-obligate bird species is important for restoration practitioners, we did not have enough data in this study to draw important conclusions here. Although arthropods are rarely included in land management goals, they play an important role in ecosystems, contributing to nutrient cycling, pollination, and herbivory (Wagner et al., 2021). Again, here we see that including fire with grazing management may be an important technique for reducing arthropod abundance without affecting arthropod diversity, which is important given the reduction in native arthropods globally (van Klink et al., 2020; Wagner et al., 2021). In many ways, our study highlights the synergy that can exist between desired land management outcomes and conservation or restoration of the tallgrass prairie ecosystem. We further show that integrated land management using grazing and fire may be the best approach. Integrating fire and grazing across both space and time will lead to a further heterogeneous landscape, thereby benefiting many ecological outcomes, despite their diverging needs.

Conclusion

Grassland land managers must be equipped with knowledge of fire frequency effects across ecological factors to better inform ecologically desired outcomes. Our study begins to tackle this previously unaddressed question for mesic warm-season grass dominated grasslands globally, as tallgrass prairie serves as a representative of that group (Forrestel et al., 2017; Lehmann et al., 2019). We did not find evidence of one ideal fire return interval across all ecological factors but instead found support for tradeoffs in land management strategies between and within ecological factors. Our results also supported the idea that the structural heterogeneity that results from fire management in unison with grazing is ecologically beneficial in tallgrass prairie. Future research directions include (1) increasing the body of work that shows empirical evidence of fire management strategies across time, space, and a broad range of taxa (2) assessment of other grassland types, (3) exploration of shifts in responses to fire frequency under changing climate scenarios (IPCC, 2023), and (4) consideration of other aspects of fire management such as fire intensity and seasonality (Shea et al., 2004). Harnessing fire as a land management tool across mesic grasslands around the world will likely lead to greater conservation and restoration of the highly endangered, yet vastly important grassland ecosystem.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Bloodworth, Bach, Kazanski, and Koerner conceived the ideas and designed methodology; Bloodworth and Gora collected the data; Bloodworth analyzed the data and drafted the manuscript. All authors advised the project contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

All data and annotated code will be made available in our GitHub Repository upon acceptance.

CHAPTER III: MIXED EFFECTS OF DROUGHT ON SPECIES-LEVEL TRAITS AND PLANT COMMUNITY COMPOSITION IN MIXED-GRASS PRAIRIE RANGELANDS

Bloodworth, K.J., Komatsu, K.J., Porensky, L.M., Reinhart, K.O., Vaarre-Lamoureux, K., Wilcox, K.R., Koerner, S.E. Mixed effects of drought on species-level traits and plant composition in mixed-grass prairie rangelands. In preparation for submission to *Ecology*.

Abstract

Precipitation variability is increasing globally which will have complex consequences for ecosystem dynamics. Droughts in the northern mixed-grass prairies of North America are predicted to become more frequent and more intense. The effects of drought on plant communities are routinely assessed, but plant functional traits (community- and species-level) are also important as they may allow us to gain a greater understanding of the complexity of ecosystem dynamic shifts in responses to ecosystem level disturbances. We conducted a manipulative drought field experiment and an observational study to assess both species composition and functional traits at a community- and species-level in two mixed-grass prairie field sites. The experimental design consisted of a complete block design with five rainfall reduction treatments and three grazing treatments, replicated in three blocks at each site. Drought treatments occurred for two years and recovery from drought occurred for three years. We measured plant community shifts and community level functional traits using community weighted means and functional dispersion. The observational study was conducted at the same two sites and consisted of measuring plant functional traits of five focal plant species at each site across four years to assess changes in plant functional traits with a natural precipitation gradient. We found that the plant communities at both sites are tolerant of drought, with the plant community having only subtle and occasional shifts and no appreciable shift in community level functional traits. In contrast, natural shifts in precipitation were associated with shifts in plant functional traits of individual species. Specifically, reductions in rainfall were associated with drought avoidance or tolerance traits such as greater leaf thickness and lower leaf dry matter content and leaf area. Importantly, changes in the plant community and in plant functional traits (or lack thereof) were site specific. Our study indicates that species-level traits may shift in response to drought while plant communities and community-level traits remain stable.

Keywords: Functional trait, functional dispersion, community weighted mean, precipitation variability, grassland, disturbance, Grazing Management for Drought Resistance

Introduction

Precipitation variability is predicted to increase globally, with some areas receiving more precipitation while others will experience more frequent and more intense droughts (IPCC 2023). Increased frequency and intensity of droughts will have complex consequences for ecosystems (Basara et al., 2013, Johnstone et al., 2016), ranging from species level trait shifts (Fay et al., 2003) to species turnover and community level trait shifts (Griffin-Nolan et al., 2019) to changes in ecosystem function (Basara et al., 2013). These consequences will likely be temporally dynamic, shifting during a drought and/or during recovery from drought (Moran et al., 2014, Frost et al., 2023). Changes in the primary producers via shifts in traits or community structure during drought or recovery from drought will have cascading effects on ecosystem processes. Therefore, it is important to understand how drought will affect the plant community via species shifts and plant functional traits during drought and during recovery from drought.

Plant functional traits influence plant fitness (Reich et al., 2003), link plant species richness to functional diversity (Diaz et al 2007), predict ecosystem level responses to disturbances (Griffin-Nolan et al., 2018), and respond quickly to ecosystem change (Mouillot et al., 2013). More specifically, plant functional traits can give insight into how plants acquire and use resources (Wright et al., 2004, Reich 2014). This acquisition and use of resources then alters other trophic levels, ultimately altering ecosystem function (Kattge et al., 2011). While plant communities have long been studied (Watt 1947) and are important in understanding ecosystem dynamics (Naeem et al., 1994, Tilman et al., 1997), plant functional trait changes are often better predictors of ecosystem processes than metrics such as species diversity and richness (Tilman et al., 1997, Naeem et al., 2012). They also allow us to assess plant performance at a community scale (Griffin-Nolan et al., 2019) and are therefore a valuable tool to assess community dynamic shifts with changes in environmental conditions, especially when combined with the plant community structure (Violle et al., 2007).

One common way of assessing changes in plant functional traits is through community weighted traits and functional diversity. Community weighted traits combine plant functional traits with plant species relative abundances, informing functional composition across a community (McGill et al., 2006). Functional diversity measures the distribution of trait values in a community (Villéger et al., 2008), which links species composition with consequences for ecosystem function (Sitters et al., 2015). One metric of functional diversity is functional dispersion, which measures the mean distance of a plant functional trait of an individual species to the centroid of all species in multivariate space (Laliberte and Legendre 2010). Community weighted traits and functional diversity metrics allow us to scale up from organismal fitness obtained through studying plant species composition and plant functional traits independently to community level fitness (Violle et al., 2007), ultimately uncovering information about community level resistance and resilience to changes in environmental conditions (Griffin-Nolan et al., 2019). In both indices, plant functional trait values are fixed for a given species and changes in community weighted traits and functional diversity metrics depict changes in the plant community via species turnover, changes in dominance, or changes in abundance. Alternatively, we can assess intraspecific variation, by tracking the functional traits of a species through time, as environmental conditions change. This method allows us to assess the rapid response of plants to environmental conditions and does not require species loss or change to have occurred within the community, thereby potentially giving advance warning of shifts in environmental conditions (Mouillot et al., 2013).

Plant functional traits that are a proxy for plant tolerance, resistance, or resilience to drought can help us to understand how shifts in drought intensity and frequency may affect plant communities and ecosystems (Willson et al., 2008, Lehmann et al., 2019). For example, increases in leaf thickness and leaf dry matter content (Blumenthal et al., 2020) and decreases in specific leaf area (Reich 2014) and leaf area (Anyia and Herzog 2004) are indicators of drought tolerance or avoidance. Although leaf area and plant height are more commonly associated with herbivore defenses (Blumenthal et al., 2020), they may have interacting effects when herbivory and drought coincide. However, the effects of drought on plant functional traits are highly dependent upon the plant community type (Zuo et al., 2021). Therefore, ecosystem specific studies may be necessary to draw accurate conclusions about ecosystem resilience and resistance to drought.

In northern mixed-grass prairie, a grassland ecosystem in the Great Plains of North America, understanding plant community and plant functional trait responses to drought are critical as droughts are projected to increase in frequency and intensity in the coming years (Andresen et al., 2012). The mixed-grass prairie ecosystem contributes to a significant portion of rangeland used for cattle in the United States (National Agricultural Statistics Service 2022) and is economically important. Understanding functional trait changes in mixed-grass prairie will give insight into the resilience and resistance of this community to shifts in precipitation regimes. We tested for plant community and plant functional traits change with increased drought intensity on two working rangelands in northern mixed-grass prairie. First, we used an experimental approach to determine if the plant community changes during a two-year imposed drought with five drought levels or during recovery years from the imposed drought. Then, we determined if that change resulted in a shift in plant functional traits at the community level using community weighted traits and functional dispersion. We hypothesized that the plant community would shift towards species with plant functional traits that indicate drought resistance or resilience. Moreover, we hypothesized that functional dispersion would decrease, thereby converging on traits that increase drought resistance or resilience. We also conducted an observational study to measure how natural shifts in annual precipitation alter plant functional traits of five focal plant species. We hypothesized that plant species would shift plant functional traits (either via phenotypic plasticity or changes at the population level) to favor traits that increase drought resistance and resilience.

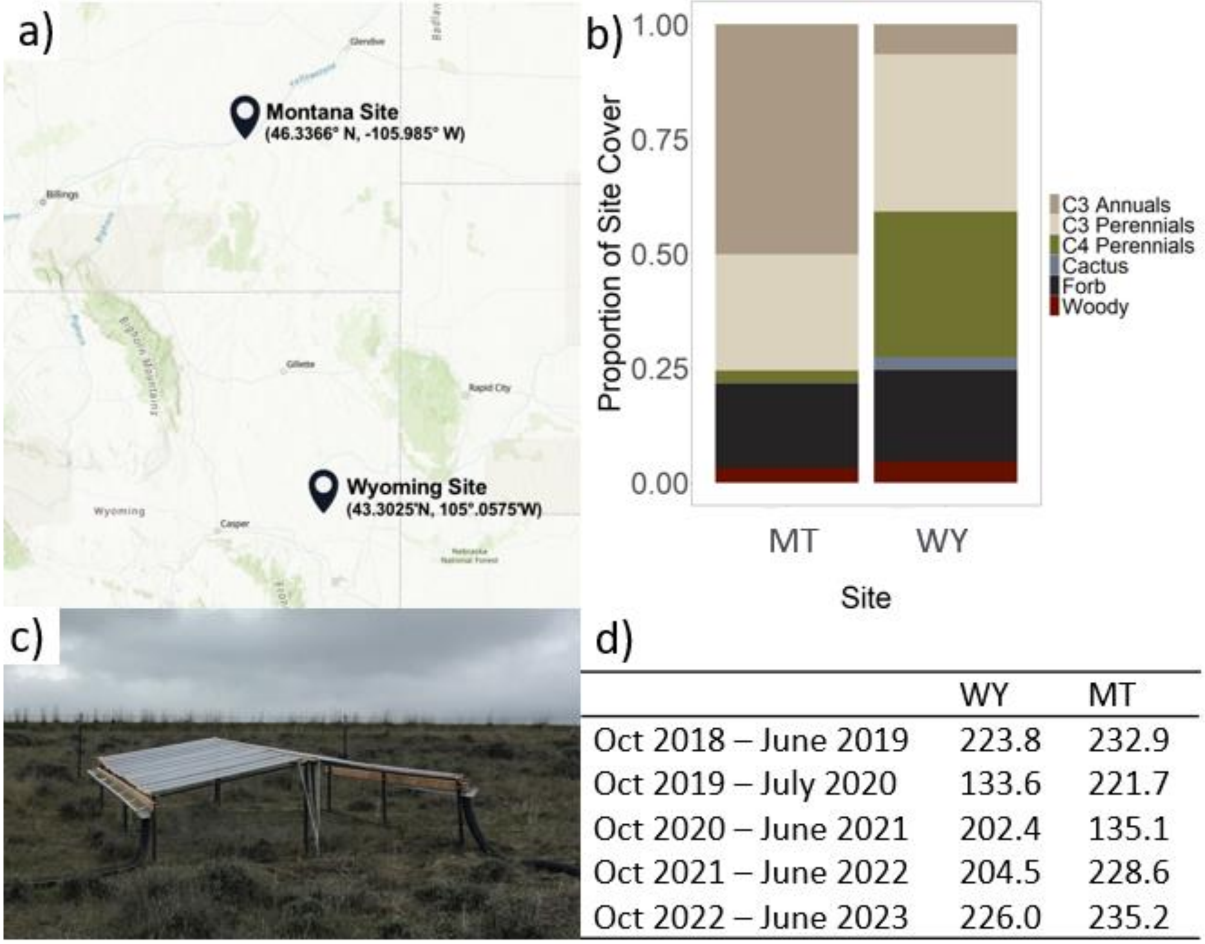
Materials and Methods

Site Description

Plant community and plant functional trait shifts during drought and recovery from drought were assessed in two mixed-grass prairie sites, Thunder Basin Ecoregion and Fort Keogh Livestock Range and Research Laboratory. Thunder Basin Ecoregion is an area spanning nearly 2.9 million acres, from Colorado to Wyoming, consisting of both USDA Forest Service and privately-owned land. This study was carried out in eastern Wyoming on a privately-owned mixed-grass prairie rangeland (43.3025° N, -105.0575° W) (Figure 3.1a). The mean annual precipitation and temperature at the WY site are 350 mm and 6.0ºC, respectively. The frost-free growing season is mid-May through mid-September, approximately 115 days per year. Prior to the start of this experiment, the WY site was dominated by native C_3 perennial graminoids (primarily *Pascopyrum smithii*, *Carex filifolia*, and *Koeleria macrantha*) and the native C_4 perennial graminoid, *Bouteloua gracilis* (Figure 3.1b).

Fort Keogh Livestock Range and Research Laboratory is a United States Department of Agriculture Agricultural Research Service site in eastern Montana (46.3366° N, -105.985° W) (Figure 3.1a). The mean annual precipitation and temperature are 320 mm and 7.8ºC, respectively. Fort Keogh Livestock Range and Research Laboratory has approximately 50,000 acres of native rangeland consisting of both mixed-grass prairie and sagebrush steppe; the work presented here occurred on a working rangeland in mixed-grass prairie. The frost-free growing season is early May to early October, approximately 150 days per year. In typical years, by the beginning of July, 90% of aboveground net primary production has been reached at this site, making the beginning of July the peak of aboveground biomass (Vermeire et al., 2009). Prior to the start of the experiment, the MT site was dominated by C_3 annual grasses, most of which are invasive bromes (*Bromus arvensis* and *Bromus tectorum*), and C_3 perennials including a common sedge (*Carex filifolia*) and grass (*Hesperostipa comata*) (Figure 3.1b).

Figure 3. 1. Methodological Figure Depicting Site Location, Plant Community Cover, Rainout Shelter, and Annual Precipitation



	WY	MT
Oct 2018 – June 2019	223.8	232.9
Oct 2019 – July 2020	133.6	221.7
Oct 2020 – June 2021	202.4	135.1
Oct 2021 – June 2022	204.5	228.6
Oct 2022 – June 2023	226.0	235.2

Note. (a) Thunder Basin Ecoregion is in eastern Wyoming (Wyoming Site) and Fort Keogh Livestock Range and Research Laboratory is in eastern Montana (Montana Site). Map created in ArcGIS. (b) The plant community composition in 2018 prior to the start of the experiment was different in Montana compared to Wyoming. (c) An example rainout shelter is shown here with gutters that remove precipitation from plots to mimic a drought at 99% rainfall reduction, similar shelters were erected for all other rainfall reduction treatments. (d) Precipitation (mm) from October of the previous year through the month when measurements were taken throughout the experiment. In 2020 only, measurements were collected in mid-July rather than mid-June.

Experimental Study Design

We conducted a randomized complete block design with five drought treatments replicated three times per block within grazing treatment paddocks (40.4×30.5 m), and with three blocks (80.8×61.0 m) per site. The three grazing treatments included a light, moderate, and heavy grazing regime. Grazing is not assessed in this study and is therefore not elaborated on further. The drought treatment included five levels: 0% (control), 25%, 50%, 75%, and 99% rainfall reduction, achieved with 3×4 m rain-out shelters erected over 2×2 m plots (Figure 3.1c). Within each grazing paddock, there were two control treatments (0% rainout) which were averaged together prior to analysis. Rainfall reduction treatments were applied during the growing season from May to October in 2019 and 2020, except during a short period when cattle grazed in each paddock in July in WY and August in MT. Then from 2021-2023 no rainfall reduction treatments were applied. At each site, n=45 (5 drought treatments×3 grazing paddocks×3 blocks). See Frost et al., (2023) for further details regarding the experimental design.

Within site and site-to-site variation was documented throughout the experiment. Elevation and soil texture varied within site and was accounted for by assigning spatial cluster categories to each paddock. During the imposed drought (2019-2020), there was a 24.1% (2019) and 25.2% (2020) reduction in soil moisture from the control treatment compared to the 99% rainfall reduction treatment in WY (Frost et al., 2023). Whereas in MT, there was a 42.2% (2019) and 43.6% (2020) reduction in soil moisture between the control treatment and 99% rainfall reduction treatment (Frost et al., 2023). Further differentiating the sites, WY experienced a natural drought in 2020, whereas MT experienced a natural drought in 2021. This caused soil water deficit durations and recovery periods to vary between the two sites. In MT, the soil water deficits created by rainfall reduction treatments (2019-2020) were likely extended into the natural drought (2021). Thus, treatment plots in MT effectively experienced three consecutive years of rainfall reduction, and sites had different recovery years (WY: 2021 to 2023; MT: 2022 to 2023).

Field Measurements: To determine plant community changes, we measured foliar plant community composition using the pin-drop method in a designated 1 m^2 subplot within each 2×2 m plot (Frost et al., 2023) in each year of the experiment (2019-2023). To assess functional trait changes across the community, we collected plant functional traits on the top 90% of plant species based on plant species composition data from each year at each site. Functional trait data were collected once in 2022 on nine individuals of each species found in ambient rainfall conditions across the landscape at each site. Plant functional trait measurements occurred during the peak growing season for each species: C_3 graminoid and forb trait measurements were collected in May and C_4 graminoid and shrub trait measurements were collected in late June. Collected traits included plant height, leaf thickness, leaf dry matter content (LDMC), leaf area, and specific leaf area (SLA). Plant height was measured to the tallest stretched vegetative point. Leaf thickness of the second fully expanded leaf from the top was measured using a micrometer caliper (0.25-0.01 mm United Scientific PMSET04 Precision Measuring Micrometer Caliper). Using the same leaf, LDMC was measured as the dry weight of the leaf (dried at 60°C for at least 1 week) divided by the wet weight of the leaf. Again, using the same leaf, we measured leaf area by scanning the leaf and using ImageJ (Rasband 2021) to find the area of the leaf. SLA was calculated by dividing the leaf area by the dry weight of the leaf.

Community Weighted Means and Functional Diversity Metrics: Using the plant species composition data, we calculated the relative cover of each species within a plot by dividing the cover of each species by the total vegetative cover within a plot. We then determined an average value for each trait of each species at each site. Using the average trait value and relative cover of each species within a plot, we calculated the community weighted mean (CWM) of each trait in a plot. To determine functional dispersion (FDis) (Laliberte and Legendre 2010, Griffin-Nolan et al., 2019) we used the *dbFD* function in the *FD* package version 1.0-12 (Laliberté et al., 2014). FDis is measured as the mean distance of species traits to the centroid of the community traits (Laliberte and Legendre 2010). We assessed FDis of each individual trait and across multivariate trait space.

Data Analysis: We used R version 4.2.1 (R Core Team 2021) to conduct all analyses for the experimental and observational studies. We removed outliers when needed based on the interquartile range (IDR) criterion and using Rosner's Test (Rosner et al., 1975, Rosner 1983) in the *EnvStats* package version 2.8.1 (Millard and Kowarik 2023). We then assessed normality of residuals using the Shapiro-Wilk, Anderson-Daring, Cramer-von Mises, and Kolmogorov-Smirnov tests within the *Olsrr* package version 0.5.3 (Hebbali 2023) and transformed data when needed to reach approximate normality (Table A3.1 and A3.2).

We used relativized plant community data to determine plant species richness (count of unique species in each plot), diversity (Shannon Diversity Index) (Shannon, Claude E. & Weaver 1964), and evenness (Evar) (Smith and Wilson 1996). We used the *lme4* package version 1.1-34 (Bates et al., 2015) to run linear mixed-effects models with drought as our fixed effect and block and the assigned spatial cluster of the plot nested within block as our random effects. We used assigned plot spatial cluster nested within block as our random effect in lieu of paddock nested within block, as it more accurately accounted for local variability that was not accounted for in the layout of paddock within block. Response variables were relative cover, plant species richness, diversity, and evenness, and the CWM and FDis of each trait. We then performed an analysis of variance (ANOVA) on the linear mixed-effects model to determine the differences across drought treatments with a significance cutoff value of P=0.05 after correcting for multiple comparisons (correction value of 5 for each year). In cases when the ANOVA was significant, we performed a Tukey's multiple comparisons analysis using the *multicomp* package version 1.4-25 (Hothorn et al., 2008), adjusting for multiple comparisons using the Benjamini-Hochberg method (Benjamini and Hochberg 1995). Separate models were run for each site, year, and community metric or functional trait. Differences in multivariate FDis were also assessed using the same analytical method.

We used the relative plant community to calculate Bray-Curtis dissimilarity values for all pairwise combinations of plots to assess overall plant compositional dissimilarity. Using the Bray-Curtis dissimilarity values we ran a permutational multivariate analysis of variance (perMANOVA) to determine plant compositional differences with drought treatments as a fixed effect and block and the assigned spatial cluster of the plot nested within block as our random effects. We then ran a permutational test for homogeneity of variance (permDISP) based on Bray-Curtis dissimilarity values to determine compositional similarity among replicate plots across drought treatments. Finally, the CWM of all traits were combined into principal components using a principal component analysis (PCA) for each year and site.

Observational Study Design

At the same locations in WY and MT, we collected the same plant functional traits on three common grasses and two common forbs at each site from areas within the experimental blocks but in areas that received ambient rainfall. The focal plant species in WY were *B. gracilis* (Blue grama: native, C_4 perennial bunchgrass), *K. macrantha* (Junegrass: native, C_3 perennial bunchgrass), *P. smithii* (Western wheatgrass: native, C_3 perennial grass), *Logfia arvensis* (Field cottonrose: nonnative, annual forb), and *Vicia americana* (American vetch: native, perennial forb). The focal plant species in MT were *B. arvensis* (Field brome: invasive, C_3 annual grass), *H. comata* (Needle-and-thread grass: native, C_3 perennial bunchgrass), *K. macrantha*, *Sphaeralcea coccinea* (Scarlet globemallow: native, perennial forb), and *Tragopogon dubius* (Yellow salsify: nonnative, annual or biennial forb). For each plant species, we collected nine individuals from across blocks during peak growing season (late June or early July) of 2019-2022. Using the same techniques as in the experimental study, we collected plant height, leaf thickness, LDMC, leaf area, and SLA. Leaf thickness was not collected in 2020.

Throughout the observational study, natural precipitation patterns changed (Figure 3.1d) allowing us to assess shifts in plant functional traits of common species with annual precipitation levels. Yearly precipitation levels in this study were obtained from local precipitation gauges (within 2 miles of the site) for the WY site and from a NOAA weather station in Miles City, MT (within 15 miles of the site) for the MT site. Precipitation was calculated as the total precipitation from October of the previous year through the month when measurements were collected. In 2019, 2021, and 2022, measurements were collected in June. In 2020 due to delays because of the COVID-19 Pandemic measurements were collected in July.

Data Analysis: To assess shifts in plant functional traits across precipitation levels, we used the lme4 package version 1.1-34 (Bates et al., 2015) to run a linear mixed-effect model with yearly precipitation as the fixed effect and block as a random effect. We then performed an ANOVA on the model to determine the differences across precipitation levels. Separate models were run for each site and functional trait.

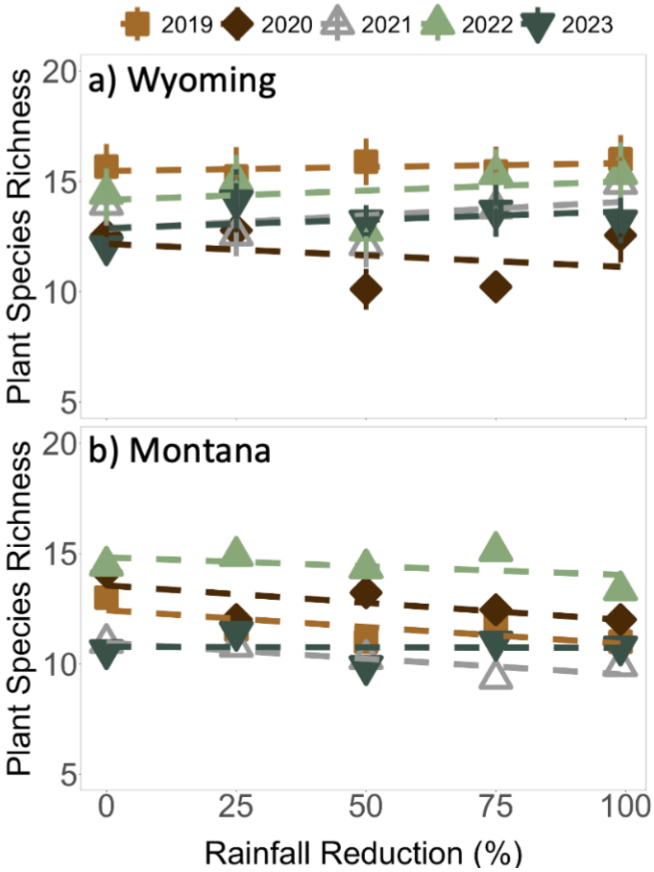
Results

Experimental Study

Plant Community Composition: Drought did not alter the relative cover, richness (Figure 3.2), or diversity of the plant community in WY in any year of the experiment (Table 3.1). Moreover, drought did not alter the evenness in the plant community in any year, except during the first year of recovery from imposed drought (2021) when plant species evenness increased with drought intensity ($F_{35.6,1}$=8.13, P=0.04) at the WY site (Table 3.1). The perMANOVA and permDISP showed no difference in plant communities or their dispersion across drought treatments in any year of the experiment in WY (Table 3.1). .

At the MT site, imposed drought did not alter relative cover, richness (Figure 3.2), or diversity of the plant community (Table 3.1). The evenness of the plant community was not affected by imposed drought except during the first year of recovery from the experimental drought—during the natural drought (2021)—when plant species evenness increased with drought intensity ($F_{33.6,1}$=6.58, P=0.05) in MT (Table 3.1). We also found no appreciable effect of rainfall reduction treatments on plant community composition during the drought years (2019-2020) or in the first year of recovery from experimental drought, when a natural drought occurred (2021). Two- and three-years after imposing drought treatments (2022, 2023), the plant community composition shifted (pseudo$F$=3.46, P=0.03 and pseudo$F$=5.08, P=0.01, respectively; Table 3.1) based on perMANOVA tests. We found no differences in dispersion of the plant community with imposed drought in any year (Table 3.1).

Figure 3. 2. The Mean +/- Standard Error of Plant Species Richness in Wyoming and Montana



Note. Measurements occurred during two consecutive imposed droughts (browns) and one year of natural drought (grey) and two years of recovery (greens) in MT and three years of recovery (grey and greens) in WY across five different rainfall reduction treatments. Shapes and colors represent year and lines represent regressions using a linear model. Note that no regressions depicted indicate significant relationships.

Table 3. 1. Linear Mixed-Model Analysis of Variance of the Plant Community Responses to Five Levels of Drought from 2019-2023 in Wyoming and Montana

		2019		2020		2021		2022		2023	
Site		*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
WY	Relative Cover	0.16	1	0.29	1	0.03	1	0.10	1	0.36	1
	Richness	0.01	1	0.84	1	0.56	1	0.29	1	0.22	1
	Evenness	0.78	1	1.12	1	8.13	**0.04**	1.68	1	0.03	1
	Diversity	0.30	1	0.12	1	0.77	1	<0.01	1	1.76	0.95
	PerMANOVA	0.28	1	0.42	1	1.82	0.55	1.63	0.80	0.91	1
	PermDISP	0.12	1	0.42	1	0.65	1	0.76	1	1.12	1
MT	Relative Cover	1.33	1	2.02	0.80	1.29	1	0.52	1	0.44	1
	Richness	2.95	0.50	2.43	0.65	3.89	0.30	1.59	1	<0.01	1
	Evenness	0.15	1	0.15	1	6.58	**0.05**	0.10	1	0.37	1
	Diversity	5.72	0.10	1.45	1	1.16	1	0.37	1	1.73	1
	PerMANOVA	1.39	1	0.97	1	2.91	0.20	3.46	**0.03**	5.08	**0.01**
	PermDISP	0.47	1	1.14	1	1.12	1	2.19	0.50	3.63	0.10

Note. Drought was implemented in 2019 and 2020 (grey). A natural drought occurred in MT in 2021 and recovery from drought occurred from 2022-2023 and recovery from drought occurred from 2021-2023 in WY. Bold values represent significant effects of drought after adjusting for multiple comparisons. For relative cover, richness, evenness, and diversity the *F* statistics and *P* values are reported and for the perMANOVA and permDISP, the pseudo*F* statistics and *P* values are reported.

Community Weighted Means & Functional Dispersion: In WY imposed drought did not alter the CWM or DFis of height, leaf thickness, LDMC, leaf area, or SLA in any year of the experiment (Table 3.2). There was also no change in CWM in multivariate space or multivariate FDis with drought treatments during any year of the experiment except in the second year of recovery from imposed drought (2022) when multivariate functional dispersion was higher with a greater intensity of drought ($F_{39.4,4}$=4.33, *P*=0.03; Table 3.2). Likewise, in MT we saw no change in the CWM or FDis of height, leaf thickness, LDMC, leaf area, or SLA with drought treatments, except during the second year of the rainfall reduction treatments (2020) where we saw an increase in the CWM of leaf area ($F_{45.5,4}$=5.13, *P*<0.01), and three years after the implemented drought treatments (2023) when we saw an increase in the FDis of SLA with rainfall reduction ($F_{47,4}$=4.12, P=0.03; Table 3.2). Drought treatments did not alter the CWM in multivariate space or multivariate FDis in any year of the experiment at either site (Table 3.2).

Table 3. 2. Linear Mixed-Model Analysis of Variance of the Community Weighted Means (CWM) and Functional Dispersion (FDis) of Traits with Five Levels of Drought from 2019-2023 in Wyoming and Montana

			2019		2020		2021		2022		2023	
Site			*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
WY	CWM	Height	0.30	1	1.07	1	0.99	1	1.38	1	1.74	0.79
		Leaf Thickness	0.27	1	0.43	1	0.22	1	0.93	1	0.75	1
		LDMC	0.53	1	0.83	1	1.00	1	0.83	1	0.73	1
		Leaf Area	1.11	1	0.74	1	1.28	1	0.79	1	0.44	1
		SLA	0.73	1	0.56	1	0.15	1	0.38	1	1.99	0.55
		PerMANOVA	0.26	1	1.66	0.61	1.62	0.87	0.92	1	0.40	1
	FDis	Height	1.03	1	0.67	1	0.26	1	0.50	1	0.76	1
		Leaf Thickness	0.32	1	0.13	1	1.16	1	0.15	1	0.08	1
		LDMC	0.38	1	0.14	1	1.88	0.65	0.77	1	0.76	1
		Leaf Area	3.00	0.14	1.24	1	1.64	0.90	1.57	1	1.40	1
		SLA	0.76	1	1.63	0.91	1.72	0.80	2.12	0.47	0.80	1
		Multivariate	2.20	0.42	0.77	1	1.45	1	4.33	**0.03**	0.46	0.38
MT	CWM	Height	0.49	1	0.73	1	2.83	0.17	1.43	1	2.23	0.67
		Leaf Thickness	0.39	1	0.47	1	1.90	0.63	1.67	0.87	0.78	1
		LDMC	0.21	1	0.15	1	0.42	1	1.42	1	1.83	0.69
		Leaf Area	1.59	0.98	5.13	**<0.01**	2.01	0.54	0.68	1	0.55	1
		SLA	1.63	0.90	2.39	0.30	0.15	1	0.81	1	078	1
		PerMANOVA	0.18	1	0.12	1	0.17	1	0.20	1	0.46	1
	FDis	Height	0.37	1	1.81	0.71	0.98	1	1.79	0.73	1.60	0.95
		Leaf Thickness	1.18	1	0.58	1	0.70	1	0.91	1	0.77	1
		LDMC	1.47	1	0.57	1	1.28	1	2.36	0.33	0.62	1
		Leaf Area	1.03	1	0.60	1	1.86	0.66	0.44	1	2.52	0.26
		SLA	2.83	0.18	1.18	1	0.44	1	1.33	1	4.12	**0.03**
		Multivariate	2.08	0.49	1.35	1	0.61	1	0.79	1	0.51	1

Note. Drought was implemented in 2019 and 2020 (grey). A natural drought occurred in 2021 and recovery from drought occurred from 2022-2023 in MT and recovery from drought occurred from 2021-2023 in WY. Bold values represent significant effects of drought after adjusting for multiple comparisons. For independent CWM and FDis functional trait analysis and the multivariate FDis analysis the *F* statistics and *P* values are reported and for the perMANOVA the pseudo*F* statistics and *P* values is reported.

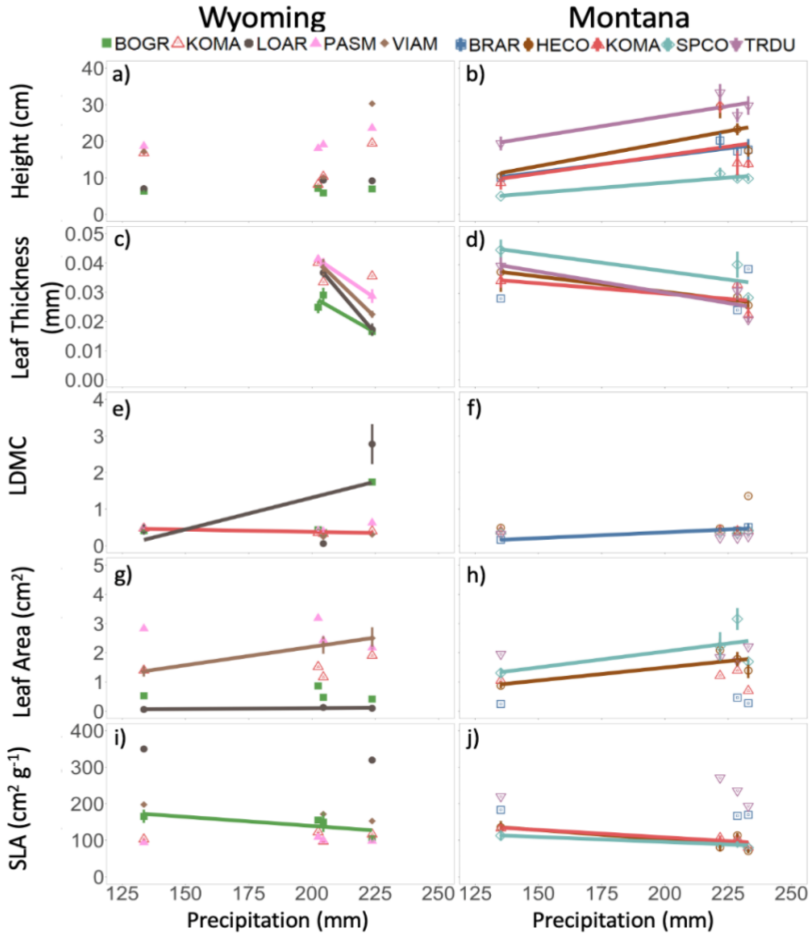
Observational Study

In the observational study in WY, *B. gracilis* showed no change in height, LDMC, leaf area, or SLA with increased precipitation but there was a 32% decrease in leaf thickness ($F_{22.1,1}$=20.76, P<0.001) (Figure 3.3, Table A3.3), although leaf thickness data were not collected during the year with the lowest precipitation (2020). *K. macrantha* exhibited a 56% decrease in LDMC ($F_{33.1,1}$=10.24, P<0.001) but no change in height, leaf thickness, leaf area, or SLA with increased precipitation (Figure 3.3, Table A3.3). Leaf area and LDMC increased by 66% and 533%, respectively, with precipitation in *L. arvensis* ($F_{23,1}$=5.77, P<0.01 and $F_{25,1}$=5.34, P=0.03, respectively) while leaf thickness decreased by 31% ($F_{14,1}$=100.46, P<0.001) and height and SLA were not affected (Figure 3.3, Table A3.3). Due to the removal of outliers, no data from 2021 were included in the analysis of *L. arvensis* and leaf thickness was not collected in 2020, the year with the lowest precipitation. *P. smithii* showed a 29% decrease in leaf thickness ($F_{23,1}$=33.50, P=0.01) but no change in height, LDMC, leaf area, or SLA with increased precipitation (Figure 3.3, Table A3.3), though leaf thickness in the year with the lowest precipitation (2020) was again not collected. *V. americana* exhibited a 107% increase in leaf area ($F_{23,1}$=8.16, P<0.01) and a 44% decrease in leaf thickness ($F_{14,1}$=34.87, P<0.001) but no change in height, LDMC, or SLA (Figure 3.3, Table A3.3). Again, leaf thickness was not assessed during the year with the lowest precipitation (2020) and due to removal of outliers, there were no data from *V. americana* in 2021 included in the analysis.

In MT, increased precipitation resulted in increased height and decreased leaf thickness in *H. comata* [66%; $F_{32,1}$=27.08, P<0.001 and 30%;$F_{25,1}$=4.79, P=0.04, respectively], *K. macrantha* [60%; $F_{32,1}$=23.33, P<0.001 and 33%; $F_{24,1}$=4.36, P=0.03, respectively], *S. coccinea* [98%; $F_{34,1}$=34.91, P<0.001 and 74%; $F_{25,1}$=12.45, P<0.01, respectively], and *T. dubius* [54%;

$F_{31.9,1}$=14.79, P<0.001and 48%; $F_{23,1}$=16.79, P<0.001, respectively] (Figure 3.3, Table A3.3). *B. arvensis* exhibited a 499% increase in height ($F_{31.1,1}$=16.41, P<0.001) and a 183% increase in LDMC ($F_{18,1}$=19.84. P<0.001) with increased precipitation but no change in leaf thickness, leaf area, or SLA (Figure 3.3, Table A3.3). *H. comata*, *K. macrantha, S. coccinea* also exhibited a 48% [$F_{29.5,1}$=4.3, P=0.05], 40%, [$F_{31,1}$=14.38, P<0.001] and 30%[$F_{25,1}$=5.89, P=0.02] decrease in SLA, respectively but no change in LDMC with increased precipitation Figure 3.3, Table A3.3). *H. comata* and *S. coccinea* showed a 60% and 30% increase in leaf area with increased precipitation, respectively ($F_{29.8,1}$=8.10, P<0.01 and $F_{24.1,1}$=11.05, P<0.01, respectively). *T. dubius* did not exhibit a change in SLA, LDMC, or leaf area with increased precipitation (Figure 3.3, Table A3.3).

Figure 3. 3. The Mean +/- Standard Error of Height, Leaf Thickness, Leaf Dry Matter Content (LDMC), Leaf Area, and Specific Leaf Area (SLA) of Five Focal Species in Wyoming and Montana



Note. Plant species in Wyoming include *Bouteloua gracilis* (BOGR), *Koeleria macrantha* (KOMA), *Logfia arvensis* (LOAR), *Pascopyrum smithii* (PASM), and *Vicia americana* (VIAM). Plant species in Montana include *Bromus arvensis* (BRAR), *Hesperostipa comata* (HECO), *Koeleria macrantha* (KOMA), *Sphaeralcea coccinea* (SPCO), and *Tragopogon dubius* (TRDU). Shapes and colors represent the five focal species at each site. Lines represent regressions using a linear model where $P < 0.05$ when the linear mixed-model analysis of variance was evaluated (see Table A.3.3). Precipitation was calculated as the mm of precipitation from October of the previous year through the month of sampling each year (see Figure 3.1d).

Discussion

The plant community, and therefore CWM and FDis, were not greatly affected by the imposed drought at either site, although there were subtle changes in the plant community with increased drought intensity in MT. In MT, plant species evenness increased with drought during the first year of recovery from imposed drought, when a natural drought occurred (2021), and the overall plant community was different between controls and 99% rainfall reduction two and three years after the imposed drought (2022 and 2023). Despite these changes in the plant community, we saw little evidence of changes in the CWM or FDis of the plant community during those years. Although, there was an increase in the FDis of SLA with increased drought intensity three years after the imposed drought (2023), indicating small shifts in the functional traits within the community. In WY, there was no evidence of changes in the plant community with increased rainfall reduction, except during the first year of recovery (2021) where plant species evenness increased with drought intensity. As a result, we saw no changes in CWM or FDis, as both metrics require changes in the plant community in order to change. MT showed functional resistance to drought and functional redundancy as there were shifts in the plant community with intense drought treatments, but there were few resulting changes in plant functional traits at the community level. On the other hand, WY showed resistance to drought by not shifting the plant community, and therefore not shifting community level functional traits. We hypothesize that site and experimental differences played a large role in the different degrees and mechanisms of resistance and resilience to drought in MT compared to WY.

The sites experienced different combinations of imposed and natural drought and were dominated by different community types which likely contributed to the site-specific plant community and community level trait responses to drought. Because of the natural drought in

2021 in MT, plots that experienced the imposed rainfall reduction from 2019-2020 effectively experienced three consecutive years of drought compared to the two years of imposed drought in WY. Moreover, the MT site experienced approximately double the soil moisture reduction with drought treatments compared to WY (Frost et al., 2023). In addition to the less intense and shorter drought experienced by the WY plots compared to the MT plots, the WY site was dominated by the native *B. gracilis*, a highly drought resistant C_4 grass (Mueller and Weaver 1942), while the MT site was dominated mainly by invasive bromes (*B. tectorum and B. arvensis*). These differences in experimental conditions and dominant species at the two sites may account for the different responses of the plant community to imposed drought and recovery from imposed drought. Therefore, we cannot say with certainty whether differences in plant community responses to imposed drought resulted because MT was dominated by invasive species whereas WY was dominated by native species, or because of the more intense and longer lasting drought in MT compared to WY, or a combination of both factors.

While plant communities at the two sites were relatively resistant to change induced by drought conditions, focal plant species at both sites exhibited shifts in plant functional traits in response to precipitation variability. LDMC increased as precipitation increased in a dominant grass species in MT (*B. arvensis*) and a common non-native forb in WY (*L. arvensis*) but decreased with increased precipitation in a common grass in WY (*K. macrantha*). Interestingly, this may indicate lower drought tolerance but greater drought avoidance for *B. arvensis* and greater drought tolerance for *K. macrantha* (Blumenthal et al., 2020). This aligns with findings from our experimental study indicating that WY and MT have different strategies for addressing drought. While *L. arviensis* had a higher LDMC with increased precipitation, data were missing as a result of outliers. Leaf area and precipitation exhibited a positive relationship in the two common forb species in WY (*L. arvensis* and *V. americana*) and in a common grass and forb species in MT (*B. arvensis* and *S. coccinea*, respectively). This indicates an increased leaf relative water content (Anyia and Herzog 2004) which can assist in resistance to drought conditions. Leaf thickness had a negative relationship with precipitation in all focal species in WY and MT except *B. arvensis* in MT. This result is unsurprising given that plants tend to increase leaf thickness with drought as a means of increasing water holding capacity, thereby avoiding drought (Blumenthal et al., 2020). However, leaf thickness data was not collected in 2020, which leaves us with potentially important data missing during the year with lower precipitation levels in WY. There was a significant negative relationship between precipitation and SLA in *B. gracilis* in WY and *S. coccinea* in MT. The SLA of *K. macrantha* was negatively related to precipitation in MT but not WY. Even though SLA is commonly used as a metric to indicate drought tolerance (Wellstein et al., 2017, Griffin-Nolan et al., 2019), there is inconsistent evidence of changes in SLA with increased precipitation (Griffin-Nolan et al., 2018) and the changes can be functional group and ecosystem dependent (Wellstein et al., 2017). Some reports support a positive relationship between SLA and precipitation (Fonseca et al., 2000, Reich et al., 2003, Cunningham et al., 2016, Wellstein et al., 2017), while others show evidence of a negative relationship (Wellstein et al., 2017, Melo et al., 2021), while others still, indicate no correlation between SLA and precipitation (Wellstein et al., 2017).

Interestingly, height was not consistent across the two sites: height increased with precipitation in all focal species in MT but there was no correlation in any plant species in WY. Typically, we would expect to see an increase in plant height with increased precipitation (Fonseca et al., 2000, Stears et al., 2022). This difference in relationship between plant height and precipitation at each site may be a species-specific difference, though we cannot conclude this within the framework of this study.

Using both community and species level plant functional traits, we have shown that mixed-grass prairie ecosystems tend to resist short-term (2-3 yr) drought, this may be because of phenotypic plasticity or genetic variability within the community resulting in the increase of drought avoidant or tolerant functional traits when precipitation decreases. Often studies focus on community level plant functional trait changes via community weighted traits or functional diversity metrics or plant functional traits changes through time (Fay et al., 2003, Griffin-Nolan et al., 2019, Blumenthal et al., 2020). In this study we provide evidence for the importance of using both techniques to study plant functional traits. Without assessing both mechanisms for functional trait changes, we omit evidence of changes (or lack thereof) in our communities and can potentially draw incomplete conclusions as to the effect of environmental changes on plant communities and therefore ecosystem function.

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This work was funded by the United States Department of Agriculture (USDA NIFA 2018-68002-27922), the University of North Carolina Greensboro's Graduate School, and Biology Department.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

SEK, KJK, LMP, KOR, KRW designed the experimental platform. KJB designed the trait-based study within the experimental platform. All authors collected data. KJB performed analyses and wrote the manuscript with input and editing from all authors.

Data Availability Statement

All data and annotated code will be made available in our GitHub Repository upon acceptance.

CHAPTER IV: CATTLE GRAZING ALTERS ARTHROPOD DIVERSITY DURING DROUGHT IN NORTHERN MIXED-GRASS PRAIRIE

Bloodworth, K.J., Reinhart, K.O., Baker, T., Mann, W., Vaarre-Lamoureux, K., Mota, S., White, K., Koerner, S.E., Cattle grazing alters arthropod diversity during drought in northern mixed-grass prairie. In preparation for submission to *Ecosphere.*

Abstract

Arthropods make up ~78.5% of all animal species and are crucial to ecosystem services such as pollination and decomposition. Terrestrial arthropods are declining due to anthropogenic activity (e.g., land use change for agriculture) and climate change (e.g., precipitation variability). Changing precipitation regimes may alter the relationship between the arthropod community and cattle grazers, which is often dependent upon ecosystem, location, and arthropod feeding guild. Changing cattle grazer and arthropod interactions with precipitation regimes are especially important in grassland ecosystems, such as northern mixed-grass prairie in the Great Plains of North America, where cattle make up most of the grazers and droughts are predicted to become more frequent and more severe, limiting forage availability. Here, we assessed (1) the effects of cattle grazers on arthropods in mixed-grass prairie and (2) how this relationship shifts through time with changing precipitation. We collected arthropods on a working rangeland in eastern Montana, USA for three years within an experimental design that manipulated cattle grazing intensity, with three cattle grazing regimes (rest [no grazing], light, and high impact). Eastern Montana experienced near normal rainfall in 2020 and 2022 and drought conditions in 2021. During the drought year, increased grazing intensity led to an increase in the diversity of arthropods. However, during years with near normal rainfall, cattle grazing intensity did not alter the arthropod community. Our study indicates that the arthropod-cattle grazer relationship may depend on growing season precipitation. As the climate continues to change and droughts become more intense and more frequent in mixed-grass prairie, the arthropod-cattle grazer relationship may become more intertwined.

Keywords: grassland, precipitation variability, grazing management regimes, Montana, insect, herbivores

Introduction

Arthropods are the most diverse group of animals on earth, with approximately 78.5% of all species in the kingdom Animalia belonging to the phylum Arthropoda (Zhang, 2013). Arthropods provide a vast array of ecosystem services including provisioning, regulating, supporting, and cultural services (Noriega et al., 2018). For example, arthropods are important pollinators of native and crop species (Katumo et al., 2022; Klein Goldewijk & Ramankutty, 2004), are critical to decomposing organic matter (Seibold et al., 2021), and consume large amounts of plant biomass (Shorthouse & Larson, 2010; Tscharntke & Greiler, 1995). Therefore, the approximated 8.81% decline in terrestrial arthropod abundance per decade (van Klink et al., 2015) because of anthropogenic activity and climate change factors such as changing precipitation regimes (Wagner et al., 2021), could lead to unforeseen consequences. Insects—the largest class in the phylum Arthropoda—are being particularly threatened by agricultural activity and drought (Wagner et al., 2021), two factors that are of particular importance in grassland ecosystems.

Rangelands (here defined as a grassland used for livestock such as cattle) cover approximately 19% of the earth’s surface and over 50% of grasslands globally (Ellis et al., 2010). In rangelands, cattle directly affect arthropod communities through accidental ingestion

(Berman & Inbar, 2022) or by altering food sources (van Klink et al., 2015). Further, livestock grazing (herbivory, treading, and manuring) may alter plant community structure and composition (Morris, 2000), which may indirectly alter arthropod communities by affecting their food and shelter (Kruess & Tscharntke, 2002). Cattle grazing changes the microenvironment where arthropods reside by altering the plant community (Morris, 2000), which can have important consequences for arthropod communities. Importantly though, studies assessing the interaction between cattle and arthropods have highly variable results, with some showing that intermediate levels of grazing result in the highest diversity (Guan et al., 2023), while others show that cattle grazing has a negative relationship with arthropod diversity (Kruess & Tscharntke, 2002; Wang & Tang, 2019) or no relationship at all (Rambo & Faeth, 1999). Moreover, large grazers like cattle typically reduce arthropod abundances (Rambo & Faeth, 1999; Wang & Tang, 2019), but this can be dependent on the functional group of the arthropods (Farrell et al., 2015). Overall, studies find that the relationship between large grazers and arthropods are highly dependent upon the patch size, intensity, and frequency of grazing (Duffy, 1975) and on the arthropod feeding guild (Zhu et al., 2023).

As precipitation variability continues to increase across grassland ecosystems (IPCC, 2023), droughts are likely to become more frequent and intense in US rangelands (Andresen et al., 2012), which may alter the relationship between large grazers and arthropods. During a drought, rangelands may become more severely grazed because of cattle grazers and/or arthropod herbivory. Net primary productivity is reduced during drought years, leading to an increase in cattle grazing intensity, as cattle remove a greater proportion of biomass via grazing if they are not provided with supplemental feed. While this may indirectly affect the arthropod community, arthropods are also affected by variable rainfall alone. Grasshoppers—an important herbivore in rangelands that annually consume ~20% of available forage (Hewitt & Onsager, 1983)—typically benefit during dry years and their populations collapse during cool, wet years (Joern & Gaines, 1990). Therefore, dry years may lead to an increase in both cattle grazing intensity and grasshopper herbivory, resulting in severely grazed rangelands and potentially having consequences for the arthropod community.

With conflicting results and an intensifying climate, exploring large grazer impacts on arthropod communities is imperative at a local scale and across a range of precipitation levels. Here, we addressed two main questions: (Q1) Are arthropod communities affected by cattle grazing intensity? (Q2) Do shifts in precipitation mediate these effects? We addressed these questions in a working rangeland in mixed-grass prairie, where we collected arthropods across three cattle grazing regimes including: 1) rest from grazing, 2) light grazing sequence (moderate, light, and light grazing intensities [2019-2021]), and 3) high impact grazing sequence (heavy, heavy, and moderate [2019-2021]). We hypothesized that as grazing intensified, arthropod richness and abundance would decrease because mixed-grass prairie has relatively low productivity, leading to higher competition for resources. Furthermore, we hypothesized that this pattern would be most apparent in years where precipitation is lower due to a reduction in annual net primary productivity leading to higher competition between herbivore types. Alternatively, we may see that grazing intensity does not affect arthropod communities during drought years, as forage will be so limited that the effects of grazing are not apparent.

Materials and Methods

Site Description: This study took place on a working rangeland in northern mixed-grass prairie at the Fort Keogh Livestock and Range Research Laboratory (hereafter, Fort Keogh) in Montana, USA (46.3366° N, -105.985° W). This experimental rangeland is managed by the

United States Department of Agriculture Agricultural Research Service. Fort Keogh has approximately 50,000 acres of native rangeland consisting of both mixed-grass prairie and sagebrush steppe; the work presented here occurred in mixed-grass prairie only, which is dominated by C_3 grasses (Vermeire et al., 2009). The growing season is approximately 150 days per year, from early May to early October. Peak aboveground net primary production (90% of ANPP reached) occurs by the beginning of July in typical years (Vermeire et al., 2009). In the three years that this study was conducted (2020-2022), the total precipitation from October of the previous year through the time of data collection (late June or early July) was 221.7 mm, 135.1 mm, and 228.6 mm, respectively. Precipitation data were retrieved from the NOAA Weather Station ~15 miles from the experimental site. Mean precipitation between 1901-2000 from October through June in the county of sampling, Custer County, was 242.8 mm (NOAA, 2023). Therefore, 2020 and 2022 had near average precipitation while a drought occurred in 2021, with a >55% reduction in precipitation from average.

Experimental Design and Data Collection: Arthropods were collected in late June or early July during peak growing season in 2020, 2021, and 2022 across three cattle grazing regimes. Cattle grazing occurred in August of each growing season. Therefore, we report the cattle grazing levels from 2019-2021, as arthropods collected in one year were affected by the grazing treatment from the previous year. Grazing regimes included (1) rest from grazing, where cattle did not graze from 2019-2021, (2) light grazing, where cattle were grazed at a moderate level in 2019 and then a light level in 2020 and 2021, and (3) high impact grazing, where cattle grazed at a high level in 2019 and 2020, and then a moderate level in 2021 (Table 4.1). Each grazing regime paddock was 40.4×30.5 m, nested within a replicate block (80.8×61.0 m) replicated three times.

Table 4. 1. Cattle Grazing Levels in Animal Unit Days (AUD)

	2019	2020	2021
Rest from Grazing	0	0	0
Light Grazing	41	14	5
High Impact Grazing	82	106	11

Note. Light and high impact grazing regimes were based on grazing scenarios during drought conditions. Grazing levels are reported in animal unit days (AUD) and were averaged across the three replicate blocks. 2019-2021 grazing is reported because arthropod collection occurred before grazing each year.

Arthropods were collected using a modified leaf blower (Stewart & Wright, 1995), where five temporary 1 m^2 plots were used to sample each cattle grazing paddock in peak growing season for 3 years (2020, 2021, 2022). Following collection, all arthropods were stored in a -20ºC freezer until identification. Arthropods were morphologically identified, counted, and separated by order (hereafter: arthropod order abundance) and then dried at approximately 30°C for at least 72 hours and weighed to determine arthropod order biomass differences across cattle grazing regimes.

To determine the proportional contribution of each order or each feeding guild (e.g., herbivore or predator) of a grazing treatment, we divided total treatment order (or feeding guild) biomass (or abundance) by total treatment biomass (or abundance). Using arthropod order biomass, we then determined the average arthropod order richness (count of unique orders in each plot), diversity (Shannon Diversity Index) (Shannon, Claude E. & Weaver, 1964), and evenness (Evar) (Smith & Wilson, 1996) for each 1m^2 plot. Diversity and evenness were calculated using the *codyn* package version 2.0.5 (Hallett et al., 2018). All metrics were then averaged across cattle grazing paddocks (n=3 per grazing treatment).

Data Analysis: All analyses were conducted in R version 4.2.1 (R Core Team & Computing, 2021). We used linear mixed-effects models (*lme4* package version 1.1-30) (Bates et al., 2015) with grazing regime as a fixed effect and block as a random effect to determine differences between grazing regimes for the variables of interest (arthropod biomass, arthropod abundance, proportional biomass or abundance of each order or feeding guild and arthropod order). An analysis of variance (ANOVA) was then used to determine differences between grazing regimes with a cutoff of *P*=0.05. In cases where the ANOVA indicated significant differences among grazing regimes, Tukey's multiple comparisons analysis was performed using the *multcomp* package version 1.4-25 (Hothorn et al., 2008), adjusting for multiple comparisons using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995). Separate models were run for each year and variable of interest.

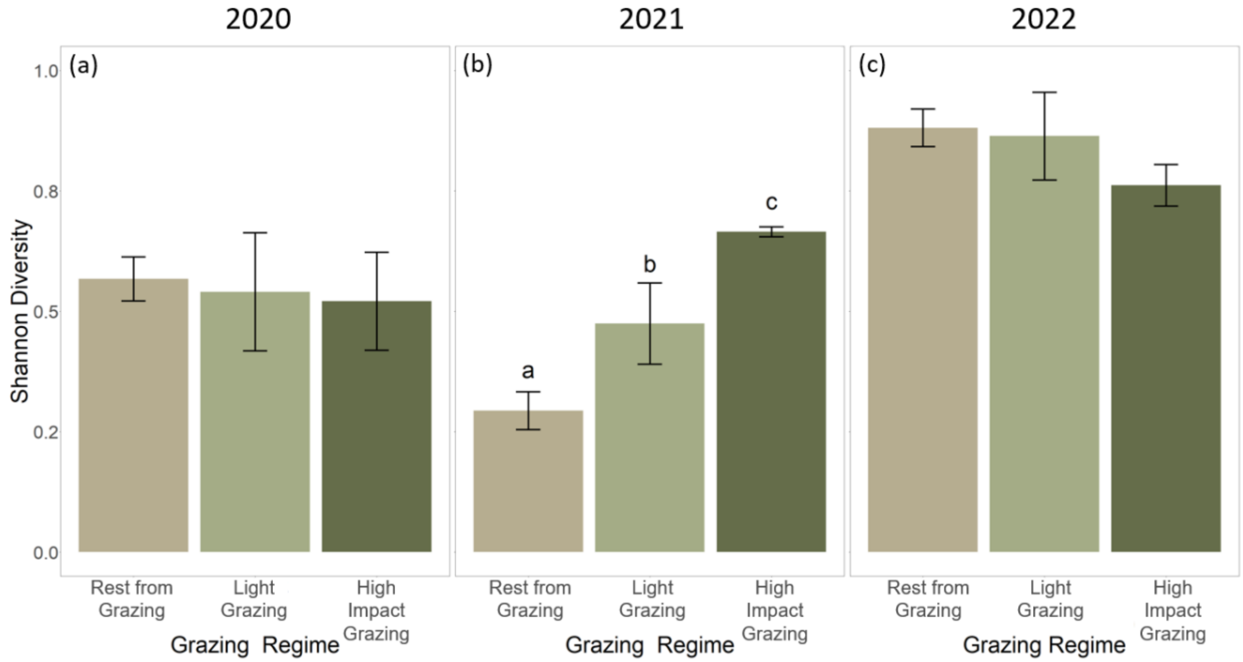
We also assessed arthropod community-level differences in multidimensional space. Using relativized order biomass (individual order biomass divided by total plot biomass), averaged across cattle grazing paddock, we calculated a Bray-Curtis dissimilarity matrix to assess overall arthropod compositional dissimilarity between grazing regimes via a permutational multivariate analysis of variance (perMANOVA) (Anderson, 2005). We then ran a permutational test for homogeneity of variance (permDISP) based on the Bray-Curtis dissimilarity values to determine compositional similarity among replicate plots across grazing regimes. Differences in multivariate space were visualized through non-metric multidimensional scaling (NMDS).

We assessed normality of residuals using the Shapiro-Wilk, Anderson-Daring, Cramer-von Mises, and Kolmogorov-Smirnov tests within the *Olsrr* package version 0.5.3 (Hebbali, 2023) and tested the assumption of homoscedasticity using Levene's test for equality of variances (Levene, 1960) in the *CAR* package version 3.1-1 (Fox & Weisberg, 2019) prior to analyses. When necessary, we transformed the data to fit the assumptions of models and reach approximate normality and homoscedasticity (Table A4.1).

Results

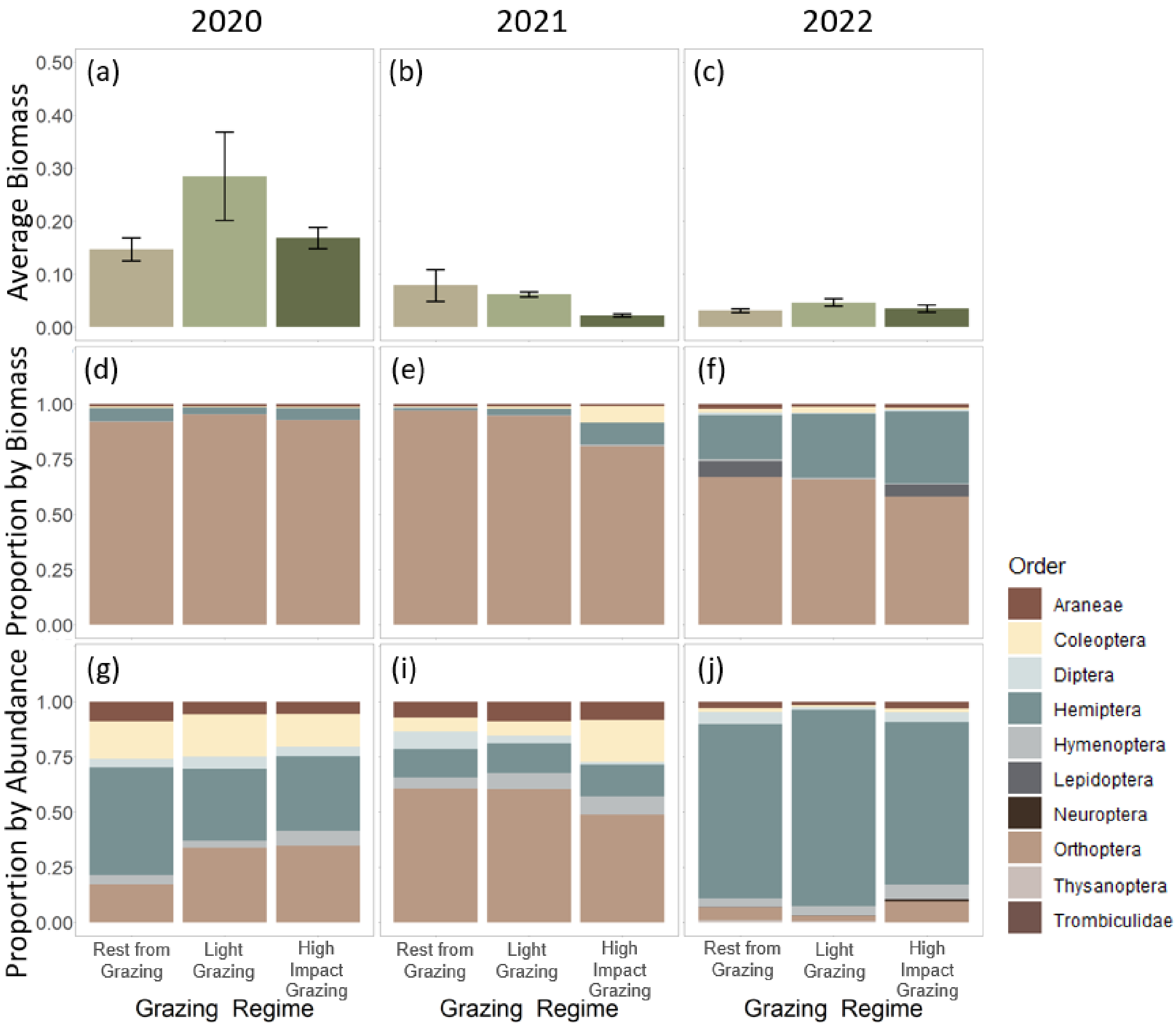
Arthropod diversity did not differ across grazing regimes in 2020 or 2022 (Table A2); however, in 2021 increased cattle grazing intensity resulted in an increase in diversity of arthropod orders ($F_{2,4}$=15.36, *P*=0.01) (Figure 4.1; Table A4.2). There was no difference in arthropod order richness or evenness across grazing regimes in any year (Figure A4.1). Similarly arthropod biomass did not differ across grazing regime in any year of the experiment (Figure 4.2a-c; Table A4.2). Orthoptera (grasshoppers, etc.) made up the majority of arthropod biomass in all years of the experiment (Figure 4.2d-f) and arthropod abundance in 2020 and 2021 (Figure 4.2g-i), though not in 2022 when Hemiptera (true bugs) made up the majority of the abundance (Figure 4.2j). In addition to Orthoptera and Hemiptera, we identified arthropods in the orders of Araneae (spiders), Coleoptera (beetles), Diptera (flies), Hymenoptera (bees and wasps), Lepidoptera (butterflies and moths), Neuroptera (net-winged insects), Thysanoptera (thrips), and Trombidiformes (mites) (Figure 4.2d-j).

Figure 4. 1. Shannon Diversity Index of Arthropods in 2020, 2021, and 2022



Note. Average diversity based on arthropod biomass by order across grazing regimes. Bars represent +/- the standard error. Letters represent significant differences between grazing regimes during that year (*P*<0.05).

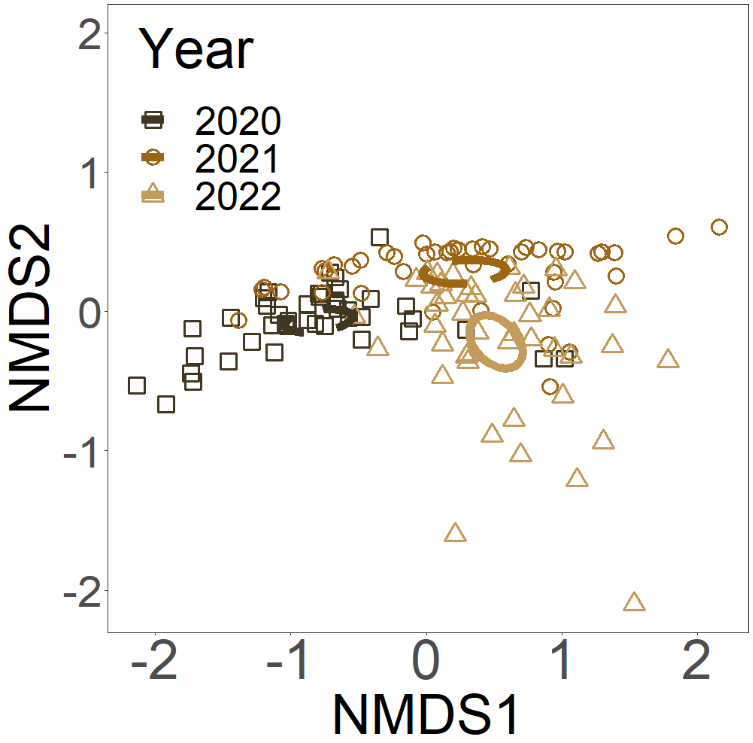
Figure 4. 2. Arthropod Biomass and Composition in 2020, 2021, and 2022



Note. (a-c) Average arthropod biomass across grazing regimes. Bars represent +/- the standard error. (d-f) Arthropod community composition showing the proportion of each arthropod order by biomass across grazing treatments. (g-i) Arthropod community composition showing the proportion of each arthropod order by abundance across grazing treatments. Colors indicate different arthropod orders.

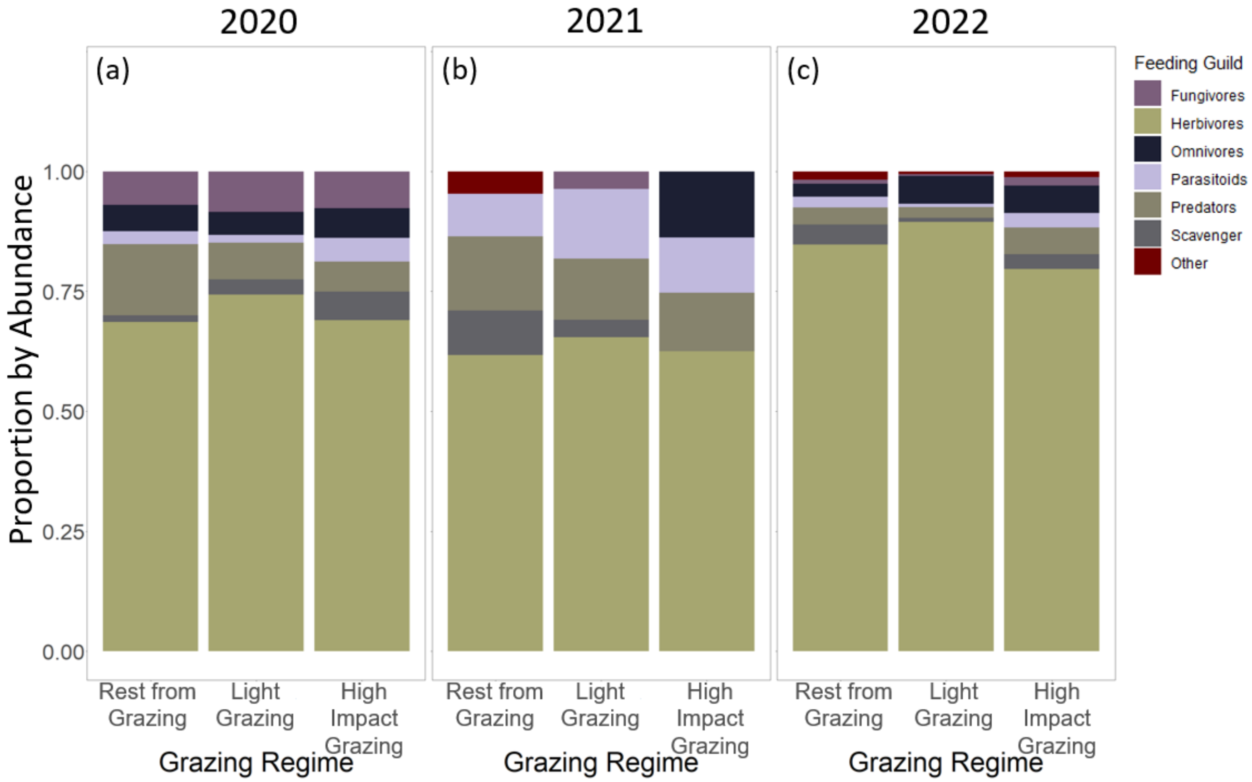
The perMANOVA indicated that there were significant year-to-year differences in the arthropod communities (pseudo$F_{2,18}$=31.12, P=0.001; Figure 4.3a). However, there were not differences in cattle grazing regimes within a given year. There were also no differences in dispersion between years or cattle grazing treatments (data not shown). When assessing changes in the proportion of the plot that was made up by each feeding guild, we saw that in the year prior to drought (2020) and during drought (2021), cattle grazing treatments did not alter any arthropod feeding guild ($F_{28,10}$=1.13, P=0.37 and $F_{18,5}$=0.23, P=0.94, respectively) (Figure 4.4). However, cattle grazing did differentially affect arthropod feeding guilds one year following the drought (2022; $F_{34.4,12}$=2.37, P=0.02) (Figure 4.4). Fungivores increased with high impact grazing while parasitoids, predators, and scavengers decreased with light grazing (Figure 4.4).

Figure 4. 3. Nonmetric Multidimensional Scaling (NMDS) Analysis



Note. NMDS is based on Bray-Curtis dissimilarity values representing the relative abundance based on arthropod biomass of orders across years. Point symbols represent years. Ellipses represent the standard error of the arthropod community composition.

Figure 4. 4. Proportion of Arthropod Abundance by Feeding Guild in 2020, 2021, and 2022



Note. Colors indicate different arthropod feeding guilds.

Discussion

Increased cattle grazing intensity led to increased arthropod diversity when precipitation was below average (2021). Arthropod communities were not affected by cattle grazing intensity in mixed-grass prairie grasslands in years with near average precipitation (2020 and 2022). Therefore, we saw evidence of precipitation mediating the effects of cattle grazing on arthropod diversity. Previous studies show that forage quantity is reduced during droughts (Batbaatar et al., 2021) and increased cattle grazing intensity interacts with drought to further reduce forage quantity (Batbaatar et al., 2021; Prather et al., 2020). Therefore, we hypothesized that lower forage quantity may have led to increased competition between cattle grazers and common herbivorous arthropods such as Orthoptera, releasing subdominant arthropods from intense competition with dominant arthropods (van Klink et al., 2015), thereby resulting in increased arthropod diversity.

Interestingly, we found that the effects of cattle grazing were not dependent upon arthropod feeding guild during the year prior to or during drought, opposing other studies (Farrell et al., 2015; Zhu et al., 2023). However, we did see a difference in the effect of cattle grazing intensity on arthropod feeding guild in the year following the drought, with Fungivorous arthropods (families within Coleoptera) increasing with cattle grazing intensity, while parasitic arthropods (families within Hymenoptera and Trombiculidae), predatory arthropods (families within Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Neuroptera), and scavengers (families within Coleoptera and Diptera) all decreased with light grazing regimes. Cattle grazing typically, but not always, reduces predators, parasitoids, and scavengers because of the decreased plant quantity or the changes in microclimate associated with increasing cattle grazing intensity (Zhu et al., 2023). It is interesting that this pattern is not observed with high impact grazing and may be the result of variability in the data coupled with low sample size.

The effects of cattle grazing did not alter arthropod biomass during years with average or below average precipitation. This is not surprising given that the effects of cattle grazing on arthropod biomass are highly variable depending on the location (Zhu et al., 2023; Farrell et al., 2015). Interestingly, we did see an overall reduction in arthropod abundance and biomass—driven by Orthoptera—during the drought (2021) compared to the year prior to the drought (2020) when typically, Orthoptera abundance increases during drought years (Shorthouse & Larson, 2010). The proportion of arthropod abundance made up by Orthoptera decreased from the drought year (2021) to the year following drought (2022), which follows previously seen patterns (Shorthouse & Larson, 2010) while Hemiptera interestingly increased in abundance following the drought.

Arthropod communities changed more from year to year than with cattle grazing intensities, supporting the idea that abiotic factors are strong drivers of arthropod communities, especially Orthoptera (Branson et al., 2006; Joern, 2005; Powell et al., 2007). We saw a general reduction in overall arthropod abundance and biomass during the drought year compared to the year before the drought. Despite this trend, we saw that precipitation levels mediated cattle grazing effects on arthropod diversity, with increased cattle grazing pressure resulting in higher arthropod diversity only when precipitation levels were below average. Here we provide further evidence that grasslands are overwhelmingly climate-controlled ecosystems (Ren et al., 2018). As grassland ecosystems experience a greater frequency and intensity of drought, the relationship between cattle grazers and arthropods may become more intertwined.

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This work was funded by the United States Department of Agriculture (USDA NIFA 2018-68002-27922), the University of North Carolina Greensboro's Graduate School, and Biology Department.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

SEK and KOR designed the experimental platform. KJB designed the arthropod study within the experimental platform. KJB, KVL, WM, KW, TB, and SM collected data. KJB performed analyses and wrote the manuscript with input and editing from all authors.

Data Availability Statement

All data and annotated code will be made available in our GitHub Repository upon acceptance.

CHAPTER V: CONCLUSIONS

Disturbance regimes play a large role in shaping ecosystems (Beisner, Haydon, & Cuddington, 2003; Burton, Jentsch, & Walker, 2020; Strömberg, 2011), and therefore alterations to these regimes because of global change and anthropogenic activity (Battisti, Poeta, & Fanelli, 2016) will have major consequences for ecosystems around the world. My dissertation research aimed to increase understanding of global change and anthropogenic-driven disturbance regime shifts in grassland ecosystems. I contributed substantially to the field of disturbance and community ecology, and my work advanced literature surrounding multi-taxa studies and provided important information on effective management strategies to land managers in grassland ecosystems.

Anthropogenic activity has greatly altered fire regimes in grassland ecosystems (McClain, Ruffner, Ebinger, & Spyreas, 2021; Nelson, 2014), leaving grasslands that require fire to maintain ecosystem dynamics, like tallgrass prairie, in peril (Helzer, 2009; Quijas & Balvanera, 2013; Samson & Knopf, 1996). However, fire can be harnessed as a land management tool for land managers who are tasked with preserving the small portion of remaining tallgrass prairie, those who are involved in restoration, and those that manage the land for alternative uses such as cattle grazing (Wright Morton, Regen, Engle, MIller, & Harr, 2010). In Chapter II, I assessed the effects of fire frequency across multiple ecological factors to assist land managers in effectively managing tallgrass prairie. I found that (Q1) there are tradeoffs when it comes to management techniques that use fire frequency, with some biotic or abiotic ecological factors benefiting from increased fire frequency, while others do not. This indicates the usefulness of site-specific management plans based on management priorities. I also found that (Q2) grazing and fire interact to create a heterogenous landscape that likely benefit most abiotic and biotic ecological factors through temporal and spatial heterogeneity. While there is no “one-size-fits-all” management strategy for prescribed fire frequencies, this study will equip land managers with the information needed to make evidenced-based decisions for their land. Serving as a framework for mesic grassland management worldwide, this research helps to increase the sustainability of our vastly important, but threatened, mesic grasslands.

In northern mixed-grass prairie, drought is expected to become more frequent and more intense (IPCC, 2023). This will have major implications for our rangeland ecosystems in northern mixed-grass prairie, which host ~20% of the United States beef cattle (National Agricultural Statistics Service, 2022). In Chapter III, I sought to understand the effects of changing drought disturbance regimes in northern mixed-grass prairie by using an experimental and observational approach. I found increased drought intensity does not drastically alter the (Q1) plant community or (Q2) community-level traits in two working rangelands in mixed-grass prairie. However, I found that (Q3) individual plant species are changing with decreased precipitation, shifting their traits towards those that provide resistance to droughts. This study signifies a shift in species specific population level plant traits with drought in mixed-grass prairie rangelands and provides evidence that despite more intense and more frequent droughts, mixed-grass prairie rangelands are resistant to drought. I also saw evidence of native plant communities being more resistant to drought than invasive dominated plant communities, which provides important information to land managers as they decide whether to manage for invasive species and how to create a more sustainable ecosystem for cattle ranching in the face of more intense and more frequent droughts.

Finally, as terrestrial arthropods continue to decline because of anthropogenic activity and climate change (van Klink, van der Plas, van Noordwijk, Wallisdevries, & Olff, 2015;

Wagner, Grames, Forister, Berenbaum, & Stopak, 2021) and droughts become more frequent and more intense (IPCC, 2023), the relationship between cattle grazers and arthropod communities in the northern mixed-grass prairie may shift. Therefore, in Chapter IV, I experimentally assess the effects of cattle grazers on arthropod communities and observationally assessed how this relationship was mediated by natural precipitation variability. I found that (Q1) cattle grazing intensity does not affect the arthropod community except during (Q2) below average precipitation years, when arthropod diversity increases under greater cattle grazing pressure. This study provides evidence that precipitation mediates the relationship between cattle grazers and arthropods. As precipitation becomes more variable the interactions between cattle grazers and arthropod communities will strengthen. Increased interannual variability in precipitation alone is also likely to decrease the stability of arthropod communities. With terrestrial arthropods declining in abundance by 8.81% on average each decade (van Klink et al., 2015) and the predicted interaction of cattle grazers and arthropod communities in mixed-grass prairie rangeland, these findings indicate the importance of ecosystem specific studies regarding arthropod and cattle relationships prior to management decisions to inform cattle grazing management strategies that prioritize arthropod community conservation.

Through my dissertation work, I led teams of ecologists who study the Great Plains region and taught lab, field, and statistical techniques and writing skills to twelve undergraduate and post-baccalaureate researchers. In Chapter II, I led a team of 11 tallgrass prairie ecologists through to manuscript submission. I also instructed three undergraduate researchers and one post-baccalaureate researcher in meta-analysis data extraction protocols, one of whom is a co-author on the manuscript. In Chapter III, I led three undergraduate researchers in learning plant trait data collection protocols, two of whom curated independent research projects under my instruction and within my greater project structure and one of whom is a co-author on the manuscript. Finally, in Chapter IV, I instructed nine undergraduate researchers in arthropod identification and arthropod collection protocols, five of whom are co-authors on the manuscript.

Grasslands are critical ecosystems, covering 40% of the earth's ice-free surface (White, Murray, & Rohweder, 2000), contributing globally to over 800 million people's livelihoods (Lehmann et al., 2019), and providing a vast array of ecosystem services (Bengtsson et al., 2019). Only 4.6% of the world's temperate grasslands are protected (Juffe-Bignoli et al., 2014), while 84.2% of grasslands around the world are actively managed for human-focused ecosystem services (Ellis et al., 2021). However, multi-functional landscapes are becoming increasingly important as society grapples with the reality of climate change and biodiversity loss from poor ecosystem management. This work strived to disentangle the complex and intertwining nature of land management strategies with changing climate patterns and anthropogenic activity, leading to increased effectiveness of management, conservation, and restoration efforts in multiple grassland ecosystems. As such, my dissertation research adds to both foundational knowledge—about grassland responses to climate and anthropogenic induced changes—and applied knowledge—helping to generate evidence-based adaptive management strategies. My dissertation research has led to options for more sustainable land management strategies in the Great Plains and globally, helping to conserve the multifaceted function of grasslands into the future.

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APPENDIX A: SUPPLEMENTARY MATERIALS

Chapter II Supplemental Materials

Table A.2. 1. Search Terms Used in Web of Science to Identify Peer Reviewed Journal Articles of Interest Published Between 1950 and 2020

Location		Ecosystem		Study of Fire		Response Variable	
	AND		AND		AND	Category	Search Term
North America		grassland*		burn*		Arthropods	arthropod*
Canada		prairie*		fire*			herbivor*
United States		rangeland*					insect*
Arkansas		savanna*					invertebrate*
Illinois		tallgrass NEAR/n prairie					pollinator*
Indiana							soil NEAR/n foodweb
Iowa						Birds	bird*
Kansas							grouse*
Manitoba							pheasant*
Michigan							quail*
Minnesota							shorebird*
Missouri							songbird*
Nebraska							turkey*
North Dakota							waterfowl*
Ohio						Plants	plant NEAR/n biomass
Oklahoma							plant NEAR/n community
South Dakota							plant NEAR/n diversity
Texas							plant NEAR/n product*
Wisconsin							vegetat*
							brush*
							shrub*
							woody NEAR/n encroach*
						Small Mammals	mammal*
							mammal* NEAR/n abundance*
							mammal* NEAR/n richness
							small NEAR/n mammal*
						Soil Metrics	microbial NEAR/n biomass

	soil NEAR/n carbon
	soil NEAR/n nitrogen
Herbivory	brows*
	graz*
Status	exotic*
	introduc*
	invas*
	non-native*

Note. NEAR/n finds records containing both words indicated within 5 words of each other. * Represents any number of letters at the end of the search term and therefore finds records with any version of the search term. AND indicates requirement to have at least one of the search terms in each category.

Table A.2. 2. Peer Reviewed Papers Used in Meta Analysis

			Response Variable	Location (US State)	Fire Return Interval Comparison		
Author	Year	Title			Annual Fire: Unburned	2-4-year Fire: Unburned	Fire & grazing: Unburned & grazing
Benson TJ et al	2007	Responses of plants and arthropods to burning and disking of riparian habitats	Arthropod Abundance & Diversity Plant Abundance & Diversity	IA		X	
Brudvig LA et al	2007	Evaluation of central north American prairie management based on species diversity, life form, and individual species metrics	Plant Abundance & Diversity	IA			X
Callaham Jr MA et al	2003	Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass	Arthropod Abundance	KS	X		
Carson CM et al	2019	Soil fungal community changes in response to long-term fire cessation and N fertilization in tallgrass prairie	Plant Abundance & Diversity	KS	X		
Collins SL et al	1998	Modulation of diversity by grazing and mowing in native tallgrass prairie	Plant Abundance & Diversity Total Soil Nitrogen	KS	X		X
Coppedge BR and Shaw JH	1998	Bison grazing patterns on seasonally burned tallgrass prairie	Plant Abundance	OK	X		
Davis CA et al	2016	Effect of pyric herbivory on source-sink dynamics in grassland birds	Bird Abundance	OK			X
Dickson TL et al	2019	Effects of 34 years of experimentally manipulated burn season and frequencies on prairie plant composition	Plant Abundance	NE	X	X	
Dunham JW et al	1996	Comparison of nadir and off-nadir multispectral response patterns for six tallgrass prairie treatments in eastern Kansas	Plant Abundance	KS		X	

Eby S et al	2014	Loss of a large grazer impacts savanna grassland plant communities similarly in North America and South Africa	Plant Diversity	KS	X		X
Engle DM et al	2008	Invertebrate Community Response to a shifting mosaic of habitat	Arthropod Abundance Plant Abundance	OK			X
Evans HW	1988	Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography, and vegetation	Arthropod Abundance	KS	X	X	
Fay PA	2003	Insect diversity in two burned and grazed grasslands	Arthropod Diversity	OK			X
Forrestel EJ et al	2014	Convergent phylogenetic and functional responses to altered fire regimes in mesic savanna grasslands of North America and South Africa	Plant Diversity	KS	X	X	
Fuhlendorf SD et al	2004	Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie	Plant Abundance	OK			X
Fuhlendorf SD et al	2010	Pyric-herbivory to promote rangeland heterogeneity: Evidence from small mammal Communities	Plant Abundance	OK			X
Griffith JA et al	2000	A multivariate analysis of biophysical parameters of tallgrass prairie among land management practices and years	Plant Abundance	KS		X	
Hobbs TN et al	1991	Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets	Plant Abundance	KS			X
Knapp AK et al	2012	A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing	Plant Abundance	KS	X		X
Koerner SE et al	2014	Plant community response to loss of large herbivores differs between North American and South African savanna grasslands	Plant Diversity	KS			X

Koerner SE and Collins SL	2013	Small-scale patch structure in North American and South African grasslands responds differently to fire and grazing	Plant Abundance & Diversity	KS	X		X
Li W et al	2014	Carbon and nitrogen cycling are resistant to fire in nutrient-poor grasslands	Plant Abundance	MN	X	X	
Li W et al	2013	Different fire frequency impacts over 27 years on vegetation succession in an infertile old-field grassland	Plant Abundance & Diversity	MN	X	X	
Lochmiller RL et al	1991	Response of cottontail rabbit populations to herbicide and fire applications on cross timbers rangeland	Small Mammal Abundance	OK	X		
Manning GC et al	2005	Effects of Grazing and Fire Frequency on Floristic Quality and its Relationship to Indicators of Soil Quality in Tallgrass Prairie	Plant Diversity Total Soil Carbon Total Soil Nitrogen	KS	X	X	X
O’Connor RC et al	2020	Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland	Plant Abundance	KS		X	
Ojima DS et al	1994	Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie	Total Soil Carbon Total Soil Nitrogen	KS	X		
Powell AFLA	2013	Effects of grassland management on breeding birds at the Western Edge of the Tallgrass Prairie ecosystem in Kansas	Bird Abundance & Diversity Plant Abundance	KS		X	
Rehmeier RL et al	2005	Long-term study of abundance of the hispid cotton rat in native tallgrass prairie	Small Mammal Abundance	KS	X	X	
Ricketts	2015	Patch-burn grazing increases habitat heterogeneity and biodiversity of small mammals in managed rangelands	Plant Abundance	KS			X
Scasta JD et al	2012	Pyric-Herbivory to manage horn flies (Diptera: Muscidae) on cattle	Arthropod Abundance	OK			X
Silletti A and Knapp, AK	2002	Long-term responses of the grassland co-dominants	Plant Abundance	KS	X	X	

		Andropogon gerardii and Sorghastrum nutans to changes in climate and management					
Smith MD and Knapp AK	1999	Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure	Plant Abundance & Diversity	KS	X		
Smith MD and Knapp AK	2001	Size of the local species pool determines invasibility of C4-dominated grassland	Plant Abundance & Diversity	KS	X		
Turner CL and Knapp AK	1996	Responses of a C4 grass and the three C3 forbs to variation in nitrogen and light in tallgrass prairie	Plant Abundance	KS	X		
Vogel JA et al	2007	Butterfly responses to prairie restoration through fire and grazing	Arthropod Abundance & Diversity Plant Abundance	IA			X
Wessman CA et al	1997	Detecting fire and grazing patterns in tallgrass prairie using spectral mixture analysis	Plant Abundance	KS	X	X	X

Note. Data from 37 peer-reviewed journal articles published between 1988 and 2020 that assessed at least one response variable of interest across a fire regime and an unburned regime were used in this study.

Chapter III Supplemental Materials

Table A.3. 1. Transformation of Data for Experimental Study

			2019	2020	2021	2022	2023
Wyoming	Plant Community	Richness	-	-	-	-	-
		Evenness	-	-	-	1/sqrt	-
		Diversity	-	-	-	-	-
	CWM	Height	1/ln	1/ln	ln	ln	1/ln
		Leaf Thickness	inv	-	-	-	-
		LDMC	1/sqrt	ln	inv	inv	inv
		Leaf Area	ln	ln	sqrt	ln	sqrt
		SLA	-	ln	ln	ln	ln
	FDis	Height	-	-	-	-	-
		Leaf Thickness	-	ln	-	-	-
		LDMC	ln	ln	ln	ln	ln
		Leaf Area	ln	ln	sqrt	-	ln
		SLA	-	ln	-	-	-
		Multivariate	ln	ln	-	-	-
Montana	Plant Community	Richness	-	-	-	-	-
		Evenness	1/sqrt	-	-	-	-
		Diversity	-	exp	-	-	-
	CWM	Height	1/ln	1/ln	ln	1/ln	1/ln
		Leaf Thickness	-	ln	-	-	-
		LDMC	ln	ln	ln	inv	ln
		Leaf Area	-	-	-	-	ln
		SLA	ln	-	ln	ln	ln
	FDis	Height	-	-	-	-	-
		Leaf Thickness	-	-	exp	-	-
		LDMC	ln	-	ln	-	-
		Leaf Area	-	-	ln	-	-
		SLA	1/sqrt	-	-	ln	1/sqrt
		Multivariate	-	-	-	-	-

Note. Transformation of the plant community, community weighted mean (CWM), and functional dispersion (FDis) data.

Table A.3. 2. Transformation of Data for Observational Study

		BOGR	KOMA	LOAR	PASM	VIAM
Wyoming	Height	-	1/ln	ln	sqrt	ln
	Leaf Thickness	1/sqrt	ln	-	sqrt	sqrt
	LDMC	ln	1/ln	ln	1/sqrt	ln
	Leaf Area	-	1/exp	ln	sqrt	sqrt
	SLA	1/sqrt	1/ln	inv	sqrt	1/ln
		BRAR	HECO	KOMA	SPCO	TRDU
Montana	Height	ln	ln	1/ln	ln	-
	Leaf Thickness	-	1/sqrt	1/ln	ln	-
	LDMC	ln	1/sqrt	1/ln	1/ln	ln
	Leaf Area	1/ln	ln	1/sqrt	ln	ln
	SLA	ln	ln	ln	1/sqrt	ln

Note. Plant species in Wyoming include *Bouteloua gracilis* (BOGR), *Koeleria macrantha* (KOMA), *Logfia arvensis* (LOAR), *Pascopyrum smithii* (PASM), and *Vicia americana* (VIAM). Plant species in Montana include *Bromus arvensis* (BRAR), *Hesperostipa comata* (HECO), *Koeleria macrantha* (KOMA), *Sphaeralcea coccinea* (SPCO), and *Tragopogon dubius* (TRDU).

Table A.3. 3. Linear Mixed-Model Analysis of Variance (*F* Statistics and *P* Values) Showing the Effects of Precipitation on Plant Functional Traits of Five Common Plant Species in Wyoming and Montana

		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
		BOGR		KOMA		LOAR		PASM		VIAM	
WY	Height	0.17	0.69	1.98	0.17	1.35	0.26	1.41	0.24	0.89	0.36
	Leaf Thickness	20.76	**<0.001**	1.15	0.30	100.46	**<0.001**	33.49	**<0.001**	34.87	**<0.001**
	LDMC	2.53	0.12	10.24	**<0.001**	5.34	**0.03**	1.63	0.21	2.82	0.11
	Leaf Area	0.01	0.91	0.04	0.84	5.77	**0.02**	0.98	0.33	8.16	**<0.01**
	SLA	4.36	**0.04**	0.93	0.34	0.51	0.55	0.08	0.78	1.92	0.18
		BRAR		HECO		KOMA		SPCO		TRDU	
MT	Height	16.41	**<0.001**	27.08	**<0.001**	23.33	**<0.001**	34.91	**<0.001**	14.79	**<0.001**
	Leaf Thickness	<0.001	0.98	4.79	**0.04**	4.36	**0.05**	12.45	**<0.01**	16.79	**<0.001**
	LDMC	19.84	**<0.001**	0.47	0.50	0.06	0.81	0.78	0.38	0.06	0.81
	Leaf Area	3.50	0.07	8.10	**<0.01**	2.08	0.16	11.05	**<0.01**	0.01	0.96
	SLA	0.11	0.75	4.3	**0.05**	14.38	**<0.001**	5.89	**0.02**	0.17	0.68

Note. Plant species in WY include *Bouteloua gracilis* (BOGR), *Koeleria macrantha* (KOMA), *Logfia arvensis* (LOAR), *Pascopyrum smithii* (PASM), and *Vicia americana* (VIAM). Plant species in MT include *Bromus arvensis* (BRAR), *Hesperostipa comata* (HECO), *Koeleria macrantha* (KOMA), *Sphaeralcea coccinea* (SPCO), and *Tragopogon dubius* (TRDU). Bold values represent significant effects of yearly precipitation. Precipitation was calculated as the mm of precipitation from October of the previous year through the month of sampling each year (see Figure 3.1d).

Chapter IV Supplemental Materials

Table A.4. 1. Transformation of Data

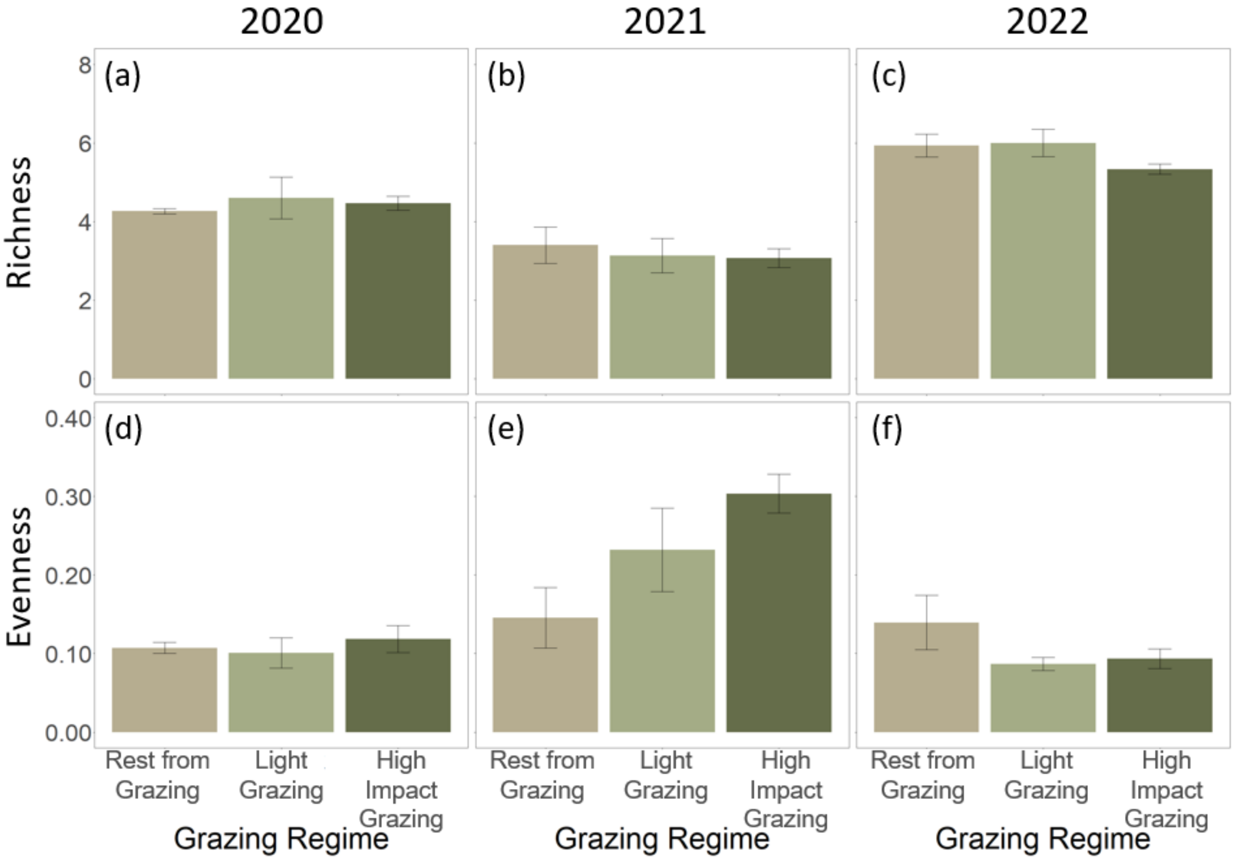
	2020	2021	2022
Richness	-	-	-
Diversity	-	-	-
Evenness	inv	-	-
Biomass	-	-	-
Feeding Guild	log	log	log

Table A.4. 2. Linear Mixed-Model Analysis of Variance of the Effects of Cattle Grazing Intensity on the Arthropod Community from 2020-2022 at Fort Keogh in Eastern Montana

	2020		2021		2022	
	F-value	*P-statistic*	*F-value*	*P-statistic*	*F-value*	*P-statistic*
Richness	0.26	0.77	0.20	0.82	3.64	0.13
Diversity	3.26	0.10	15.36	**0.01**	2.44	0.20
Evenness	0.36	0.71	3.01	0.34	3.01	0.14
Biomass	2.11	0.20	3.09	0.15	1.69	0.26

Note. Bold values represent significant effects (*P*<0.05) of grazing intensity. Bold values represent significant effects of cattle grazing intensity.

Figure A.4. 1. Arthropod Order Richness and Evenness in 2020, 2021, and 2022



Note. Arthropod order richness (a-c) and evenness (d-f) averaged by plot across grazing treatments. Bars represent +/- the standard error.