Examining contingencies of the plant community–grazing relationship at multiple scales across North America

by

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ABSTRACT

Defoliation is a globally ubiquitous driver of plant community structure and function. However, plant community responses to defoliation remain challenging to predict as they are highly context-dependent. Following defoliation, plant community diversity and production may increase, decrease, or display no change depending on climate, plant neighbors, and the disturbance's timing, frequency, and location. In this thesis, I disentangle the role of these three core contingencies in mediating the plant community–defoliation relationship across a broad spectrum of scales in time and space. First, I test the assumption that defoliation instigates higher plant production and diversity when applied using high-intensity, short-duration holistic grazing management across the northern great plains. I find holistic grazing management supports fewer vascular plant species at both local and landscape scales despite no difference in plant community composition and variability. However, holistically managed ranches showed markedly higher plant community production than their regionally typical counterparts, with 20% higher aboveground biomass, 26% higher litter mass, and equivalent amounts of surface root biomass. Second, I examined how varying the proportion and patchiness of defoliation disturbances impacted community-wide competition and production using experimental mesocosms. I found that defoliation intensity strongly interacted with the proportion of the plant community disturbed to influence whole-community production and competition. Increased defoliation intensity negatively affected mesocosm production (aboveground, belowground, and total biomass) when all individuals were defoliated but positively affected production where half the mesocosm was defoliated. Finally, I used a meta-analysis of grazing studies across North America to examine how the consequences of grazing exclusion on plant community production and richness vary depending on the weather at the sampling time, climate, year, and study location. Study location and sampling time mediated the effects of grazing exclusion on plant community production and richness. Plant richness, not plant abundance, responded to grazing exclusion differently depending on mean annual precipitation, with less positive effects of exclusion found when precipitation was higher. Data collection within an unusually wet year detected less positive effects of grazing exclusion. Our results demonstrate that climate and weather drive the effects of grazing exclusion on plant communities and that these effects are growing more deleterious toward plant abundance over time. Overall, the results of this thesis promote a new understanding of how grazing management, plant-plant interactions, and study location in time and space modify the plant community–defoliation relationship.

PREFACE

This thesis is an original work by Jessica Grenke.

Chapter 2 of this thesis was published in the *Journal of Applied Ecology* in 2022:

> Grenke, Jessica SJ, Edward W. Bork, Cameron N. Carlyle, Mark S. Boyce, and James F. Cahill. “Limited impacts of adaptive multi-paddock grazing systems on plant diversity in the Northern Great Plains.” Journal of Applied Ecology 59, no. 7 (2022): 1734-1744.

I was responsible for idea conception, data collection, analysis, and manuscript writing. EWB, CNC, MSB, and JFC provided significant input on the conception of ideas and feedback on the manuscript.

Chapter 3 of this thesis has been submitted to *Agriculture, Ecosystems & Environment* in December 2023:

> Grenke, Jessica SJ, Edward W. Bork, Cameron N. Carlyle, Mark S. Boyce, and James F. Cahill. “Intensive grazing management systems increase plant productivity: evidence for the grazing optimization hypothesis.” Agriculture, Ecosystems & Environment.

I was responsible for idea conception, data collection, analysis, and manuscript writing. EWB, CNC, MSB, and JFC provided significant input on the conception of ideas and feedback on the manuscript.

Chapter 4 of this thesis is intended for publication as “Grenke, Jessica SJ, Emily M. Holden, and James F. Cahill. Proportion matters and pattern does not: Spatial placement of defoliation influences plant community production and structure.” I was responsible for idea conception, data collection, analysis, and manuscript writing. EMH provided feedback on the manuscript. JFC provided significant input on the conception of ideas, experimental design, and feedback on the manuscript.

Chapter 5 of this thesis is intended for publication as “Grenke, Jessica SJ, Amgaa Batbaatar, Anabel Dombro, Emily M. Holden, Alessandro Filazzola, and James F. Cahill. The effects of grazing on plant abundance and richness depend on climate and weather.” I was responsible for idea conception, data collection, analysis, and manuscript writing. AD, EMH, and AB assisted with data extraction. AF and JFC provided significant input on the conception of ideas, experimental design, and feedback on the manuscript.

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To Sauer Lake

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Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

Defoliation (the removal of plant tissue) is a primary mechanism governing plant performance and ecosystem functionality (Liu et al., 2015; Lezama and Paruelo, 2016). The seemingly simple short-term effects of defoliation—removal, and thus, reduction in biomass—belie the plethora of possible consequences to plant community function it entails (McNaughton, 1983). Defoliated individuals are subject to the removal of photosynthetic capacity, nutrients, stored resources, and capacity for growth (Wang et al., 2021). These factors reasonably entail a reduction in relative growth rate and total plant biomass (Penner and Frank, 2021), and such a relationship has been observed in many classical experiments (e.g., Belsky, 1987; Painter and Belsky, 1993; Verkaar, 1986). However, the reduction in relative growth rate or final biomass following defoliation may be less than proportional to the live biomass removed (Hawkes and Sullivan, 2001). Defoliation may even increase targeted plants' growth rate or final biomass (McNaughton, 1983). This process is called overcompensation, with perfect compensation entailing an equivalency between final biomass and biomass at the time of defoliation (Agrawal, 2000).

Although the effects of defoliation on individual plants have been exhaustively studied, the ubiquity and importance of compensatory growth responses remain under debate and examination using theoretical and experimental approaches (Ferrero and Oesterheld, 2002). Predominant theories vary based on the scale considered (individual plant species, plant community, or global) and the core contingencies assumed to be of importance. At an individual plant level, Grime et al.'s (1997) C-S-R plant strategy theory bins plant species into three groups depending on the degree of both disturbance (factors that destroy plant biomass after it has formed) and stress (factors that restrict initial plant production such as limited nutrients, light, water, or temperatures) the individual plant is subjected to. Species adopting the ruderal-type strategy occur where stress is low and disturbance is high, with these ample available resources allowing for sustainable recovery of plant tissues following defoliation. As such, these are tolerant species that prioritize organs and physiological traits that allow for regrowth following defoliation, as opposed to avoidance or resistance (Diaz et al., 2007). A more recent analysis of plant traits globally has validated this theory, though direct integration of stress and disturbance remains to be completed (Diaz et al., 2007).

Connell's Intermediate Disturbance Hypothesis (IDH) is commonly used (1978) to predict and explain plant community-wide diversity and production responses to defoliation disturbances, usually within a grazing context. This theory states that the diversity and production of competing species will be highest at intermediate intensities and/or disturbance frequencies. Key assumptions of this theory are that: (1) similar to the C-S-R, competitive and disturbance tolerant traits are mutually exclusive, and (2) increased species diversity entails more complete use of available niche space, thus increasing community-wide production. According to the IDH, plant diversity is limited at low levels of disturbance by competitive exclusion and at high levels by the physiological limits of plant tolerance.

The MSL model (Milchunas et al., 1988; Milchunas et al., 1993) applies the IDH to a global grazing context. It does so by integrating two core contingencies governing the shape of the generally unimodal IDH: the evolutionary history of grazing and aridity. Broadly, the classically symmetrical IDH applies in humid areas with a long evolutionary history of grazing, with an increasing right skew to the point of linearity with humid areas with short evolutionary histories of grazing, arid areas with short evolutionary histories of grazing, and arid areas with a long evolutionary history of grazing. Cingolani et al. (2005) expanded upon the MSL to integrate a state-and-transition framework, where areas with short grazing histories are prone to irreversible changes to plant community diversity due to a lack of evolution of grazing-tolerant traits. Generally, in humid areas showing high plant productivity, the IDH and, thus, MLS is strongly supported (Gao and Carmel, 2020). However, arid areas are consistently more strongly governed by stress than disturbance factors (Belsky, 1992). Thus, the climate is expected to hold a greater sphere of influence over plant diversity and production than plant-plant interactions and/or grazing disturbances, where it is extreme and/or variable (de Bello et al., 2006).

These core theories vary significantly in scale and core assumptions but share their identification of two core contingencies governing the expression of compensation: the defoliation's nature and the defoliated plant's background conditions, including the social environment, abiotic stress levels, and resource availability.

Characteristics of defoliation

The effects of defoliation will vary depending on its: *frequency*, or number of defoliation events per growing season; *duration*, or the length of time a specific area is defoliated for; and *intensity*, or the absolute or relative amount of plant tissue removed (Bailey et al., 1996; Hart et al., 1993). While frequency and intensity apply equally to individual plants and plant communities, duration is applicable only to plant communities, as its assumed mechanisms lay in the proportion and evenness of the plant community removed (Bailey et al., 1996). Each mechanism corresponds with a broadly simple linear relationship with plant production (i.e., increasing defoliation frequency reduces plant biomass and vice versa) when considered alone (Matches, 1992). However, stimulation of plant community-wide compensatory ability by increasing one aspect of defoliation (typically intensity) while decreasing another (i.e., defoliation and/or duration) has shown support on a theoretical and experimental basis (Holechek, 1983; Taylor et al., 1993). The origin of this theory dates back as far as 1957 with Andre Voison's '*Productivité de l'herbe*' but was most comprehensively formalized within McNaughton's 'Grazing Optimization Hypothesis' (GOH; 1979). The GOH posits that grazing shifts plant communities towards grazing-tolerant species and stimulates increased nutrient cycling through trampling. Trampling of forage can aerate the soil and physically incorporate nutrient-rich litter faster than under biological and abiotic decomposition (Milchunas and Lauenroth, 1995). Hypothetically, this increases the possible production rates of a plant community via enhanced mineralization, which frees available nutrients for new growth (Olofsson and Oksanen, 2002). Livestock management systems that emulate these aspects of historical disturbance regimes may also generate greater forage production per unit area than other management systems (McNaughton et al., 1996). Despite the promise of enhanced plant biomass through high-intensity, short duration grazing practices, there is also abundant evidence that, in many cases, the stimulation of plant production comes at the expense of root growth, potentially increasing vulnerability to drought, suggesting over-compensatory plant responses may be short-lived (Gao et al., 2008; Gong et al., 2015).

High-intensity, short-duration grazing management

As maximizing levels of defoliation while maintaining sustainable plant community production is a primary goal of grazing management, the broad applicability of instigating the GOH by implementing high-intensity, short-duration grazing is of great management interest. Grazing management systems following these principles fall under a variety of names, including high-intensity, low-frequency; holistic grazing; short-duration grazing; time-controlled grazing; cell grazing; and adaptive multipaddock grazing (AMP hereafter; de Virgilio et al., 2019). Though such systems have been predicted to increase plant productivity with minimal consequences to other ecological goods and services, such as plant diversity (Savory, 1978; Savory and Parsons, 1980), controlled studies of its influences on plant growth and diversity are limited and empirical support for these claims is sparse (Briske et al., 2008; Hawkins, 2017). In Chapters 2 and 3, I seek to fill this discrepancy by comparing the plant diversity and production of high-intensity, short-duration ranches compared to their regionally typically managed neighbors.

Social context of defoliation

Realized individual plant responses to defoliation are complicated by the social context under which defoliation occurs (Song et al., 2020). In environments where the relative growth rate of the plant is limited by competition, grazing of both the focal individual and its neighbor can relax these competitive constraints and allow for a diversity of less competitively adapted traits to be expressed (Díaz et al., 2016). This release is associated with higher relative growth rates for the focal plant and the entire plant community (Ritchie and Penner, 2020). In some cases, community-wide relative growth rates increase following defoliation to such an extent that production of the defoliated community is equivalent to or exceeds that of the undefoliated community (known as compensatory responses; McNaughton, 1976; Ramula et al., 2019).

Three generalized mechanisms mediate plant community responses to defoliation: (1) following defoliation, resources are freed to allow for the reallocation of energy from competitive strategies (i.e., exudate production) into strategies that maximize growth and fitness (Alward and Joern, 1993; Milchunas and Noy-Meir, 2002). (2) Competition and compensatory functions are unlikely to positively correlate as the resources associated with these strategies are often opposed, as demonstrated across various climates, species, and grazing histories (Järemo et al., 1996; Ramula et al., 2019; Peng et al., 2023). Thus, defoliation promotes compensatory strategies, which is expressed as (3) a higher community-wide relative growth rate that accumulates over the growing season such that the negative effect of defoliation on biomass is proportionally less than the actual biomass removed (Ferraro and Oesterheld, 2002; Hilbert et al., 1981). It is important to note that the spatial placement of defoliation across a community creates vastly differing competitive arenas (Laca, 2000). Defoliation across natural landscapes is highly heterogenous (Adler and Lauenroth., 2001). Increasing the specificity of defoliation (i.e., single plant defoliation versus increasing patch size of defoliation) will likewise increase the average size inequality between neighbors within a community (Agrawal et al., 2006; Crawley and Weiner, 1991; Marquis, 1992). As size-asymmetry mediates the nature and outcomes of aboveground plant-plant interactions (Brown and Cahill Jr., 2022; Weiner, 1990), the spatial patchiness of defoliation can be assumed to have a strong influence on community-wide compensatory responses. Specifically, defoliated plants located closer to the edge of a defoliated patch will be subjected to greater competition for light and nutrients than plants located closer to the center of a defoliated patch ('border effect'; Semmartin and Oesterheld, 2001). This border effect would be expected to be most influential on total plant community production when the proportion of community defoliated is 50%. Additionally, since the border-to-area ratio of patches is greater in smaller patches, the border effect is expected to increase in importance with smaller patch sizes. Though strongly articulated at a landscape scale (Fuhlendorf et al., 2001), the importance of the defoliation-patchiness and plant-plant interaction effects on mediating community-level biomass remains unclear. In Chapter 4, I examine the effects of effects of the proportion and patchiness of plant community defoliated on total community production and plant-plant interactions.

Climate and defoliation

Climate is a fundamental contingency governing plant community responses to defoliation (Campbell et al., 2000; Allred et al., 2014). Plant community production on grazing lands is highly climate dependent, with precipitation and temperature linked strongly to plant community dynamics under grazed conditions (Ellis and Swift, 1988). In areas with climates highly conducive to plant growth (high precipitation and moderate temperatures), the intermediate disturbance hypothesis is well supported, suggesting that under such conditions, grazing suppresses the dominance of highly competitive species, allowing for community-wide diversity and production to increase (Gao and Carmel, 2020). Climates supporting lower plant productivity generally show a stronger influence of precipitation variability on plant diversity and production than grazing (Olff and Ritchie, 1998). Climate variability is generally an essential driver of plant community dynamics as the absolute amount of precipitation, supported by non-equilibrium theories within rangeland ecology (Briske et al., 2003; Illius and O'Connor, 1999). As increased resources for plant growth allow for a more complete plant community recovery from grazing, areas with increased precipitation, lower temperatures, and low climatic variability show greater resilience to grazing disturbances (Milchunas et al., 1988). While the climate contingencies of the grazing-plant community relationship have been well established through global meta-analysis (e.g., Gao and Carmel, 2020; Filazzola et al., 2020), the weather-dependent nature of this relationship remains less understood. As grazing studies are typically of relatively short duration (predominantly five years or less; de Virgilio et al., 2019), and local variability of climate shows a critical role in plant community responses to grazing (Fuhlendorf et al., 2001), the role of weather at the time of data collection could be expected to strongly influence plant community responses to grazing exclusion across North America. In Chapter 5, I examine how grazing exclusion effects on plant community abundance and diversity vary depending on the climate and weather at the time of sampling.

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Chapter 2: Limited impacts of adaptive multi-paddock grazing systems on plant diversity in the Northern Great Plains

INTRODUCTION

Grazed lands cover approximately half (~3.4 billion hectares) of the earth's land area (McGuire, 2015) and are a source of sustenance and livelihood for millions of people across the globe (Havstad et al., 2007). Grazed grasslands are also vital sources of ecological goods and services, including biodiversity, nutrient cycling, carbon sequestration, and water cycle regulation (McMichael et al.). However, due to low levels of protection and high rates of land-use conversion, grasslands are the most threatened ecosystem in the world (Carbutt et al., 2017).

As grassland ecosystems are disturbance-mediated, conserving their remaining area is contingent on maintaining a disturbance regime that provides desired biological outcomes (Perkins et al., 2019). Primary historical disturbance regimes of the northern Great Plains were fire and roaming herds of large ungulates, in addition to periodic drought (Fuhlendorf et al., 2009). With the modern advent of fire suppression and the replacement of free-ranging bison (*Bison bison*) with spatially confined herds of livestock, grassland disturbance regimes have changed, posing challenges for the maintenance of these ecosystems (Fuhlendorf et al., 2009). Ranch-level management practices have substantial effects on the ecological and economic viability of grasslands, which can extend outwards to a regional level (Hulme, 2005). These effects can enhance or degrade biodiversity depending on the length, duration, and timing of grazing across the landscape.

A grazing system growing in popularity among ranchers, known as Adaptive Multi-Paddock (AMP) grazing, employs high animal densities within small areas for short periods of time (Briske et al., 2008) followed by a long recovery period before subsequent grazing (Bork et al., 2021). In theory this practice allows heightened control for land managers to target how long, and at what intensity, livestock grazing occurs (Briske et al., 2008; Teague et al., 2013). AMP grazing is intended to emulate aspects of the historical grazing patterns of herding ruminants, and thus restore ecological functioning (Savory, 1983). However, replicated empirical assessment of the ecological consequences of AMP grazing are limited to studies small in scale and with treatments having more restricted adaptivity compared to actual working ranches (Teague et al., 2013). Although there exists some evidence that in certain climates, AMP grazing is associated with increased aboveground production, its influence on plant diversity is largely unknown (Hawkins et al., 2017). This knowledge gap is due to both the generality of theoretical frameworks explaining grazing effects on plant communities (i.e., the intermediate disturbance hypothesis, Connell 1978), and the overall lack of empirical tests of such conceptual theories linking grazing effects to ecosystems. Understanding the effects of grazing on plant diversity is of high priority because plant diversity is broadly associated with increased ecosystem resilience (Mori et al., 2013). Plant diversity has been shown to increase, decrease, or remain static in the presence of grazing (De Bello et al., 2006; Kinnebrew et al., 2019) and this ambiguity presents difficulties in implementing grazing to achieve conservation goals (Milchunas & Lauenroth 1993).

High intensity grazing (i.e. high density and/or duration of grazing) is broadly associated with declines in plant diversity (Olff & Ritchie 1998) and this might indicate intensive systems of grazing management (i.e. those with finely tuned application of grazing disturbances) will have similar effects. However, this is not necessarily the case with AMP grazing. First, the practice of AMP grazing results in localized placement of dense herds of livestock for brief periods of time, with long periods thereafter in which no animals are placed in defoliated paddocks. Thus, the season-long grazing intensity (measure of animals per unit area per unit time; also known as stocking rate) of AMP grazing across the entire ranch is not necessarily different from those of its neighbours, though this is rarely measured. Second, the ecological consequences of the uniform application of grazing disturbance under AMP grazing are unclear. Uniform grazing could serve as an ecological filter selecting for plant species that can withstand short-bursts of grazing and reduce diversity, but might also suppress competitive dominants (Díaz et al., 2001 & 2007) and thereby increase diversity via competitive release. Not all vegetation changes due to grazing systems have the same implications for conservation and sustainability. Of particular conservation interest will be AMP grazing effects on native plant species (Maron & Vilà 2001), which may (Dorrough et al., 2007) or may not (Porensky et al., 2020) respond similarly to introduced species in response to defoliation. As native species diversity does not necessarily increase with net species diversity it is necessary to consider this group separately (de Bello et al., 2006).

The key to disentangling these potential mechanisms lies in distinguishing between livestock density (number of animals per unit area at a single point of time) and stocking rate. These aspects of grazing systems have distinct environmental consequences (Coffin & Lauenroth 1988) and might vary independently under AMP grazing (Hawkins et al., 2017). Even if AMP grazing does not lead to increases in grazing intensity, its underlying intent of causing uniform grazing within each paddock is expected to modify plant heterogeneity and associated diversity. The uniform disturbance of vegetation through animal consumption and trampling by hooves associated with AMP contrasts with patchier grazing commonly observed in conventional systems (Chamane et al., 2017). AMP grazing should cause more uniform (i.e., less selective) pressure on plants, as is typical of grazing lawns (McNaughton, 1984), thereby reducing microsite heterogeneity and niche space (Briske et al., 2008). Thus, regardless of the influence of AMP grazing on local and landscape diversity, it would be expected to lead to higher species-evenness within plots and lower beta-diversity among plots. Further, if AMP grazing imposes a consistent ecological filter in multiple ecological contexts (e.g. different ranches), we would also expect to see decreased beta-diversity among ranches.

To test the effects of AMP management on plant diversity, we conducted a large-scale vegetation survey across grasslands of the northern Great Plains using a paired design, which linked to a larger study reporting on grazing practices across 64 ranches in western Canada (Bork et al., 2021). To our knowledge, this study is the first of its kind to compare the real-world consequences of AMP management with regionally-typical practices on ranch-scale diversity across a broad geographic expanse. Here we collected grazing management and plant community data for 18 ranch pairs, each consisting of one AMP and one locally representative (neighbouring-AMP; N-AMP) ranch. With these data, we asked: 1) Do AMP and locally representative neighbouring (N-AMP) ranches employ distinct management systems?; 2) Does AMP-type grazing result in lower community heterogeneity (lower beta-diversity and higher evenness)?; and 3) Does AMP grazing alter plant species diversity and composition?

MATERIALS AND METHODS

Study area

Sampling took place on 36 cattle ranches located across a broad geographic gradient (over 360 000 km^2) of Western Canada (Alberta, Saskatchewan, and Manitoba). 16 ranch-pairs fell within the Aspen-Parkland ecoregion (Figure 2-1), a savanna-type ecoregion consisting of aspen poplar patches surrounded by a larger matrix of grasslands. The remaining two ranch pairs were located in the mixed-grass prairie. This distribution of ecoregions reflects our pool of potentially suitable ranches (see below), rather than an intentional focus on the Parkland habitat. Across all ranches, the average annual precipitation ranged from 300 to 660 mm/year and mean annual temperature ranged from 1.8 to 4.8°C (Canadian Climate Normals 1981-2010; Environment and Climate Change Canada).

The vegetation on most of the study ranches included a diversity of introduced species which likely originated through a mixture of intentional agronomic seeding (*Bromus inermis, Phleum pratense, Dactylis glomerata*) or through invasion across the landscape (*Taraxacum officinale*).

Sampling design and measurements

Overview

To control for spatio-temporal differences associated with the large study extent we used a paired ranch design of actively managed farms across the Northern Great Plains. Each ranch using AMP grazing was paired with a neighboring ranch using more conventional management practices (N-AMP). In this sense, N-AMP ranches represented a random subset of regional ranches. AMP ranches were defined as those using a grazing system with a minimum of 20 paddocks per herd and self-identification by the managers of high adaptability—that is, high flexibility of cattle placement in response to changing environmental conditions.

Ranch selection

Initial recruitment of potential ranch operators/owners using AMP management occurred at the Organic Alberta grazing management conference (2017). At this conference, the project was introduced, and a list of cattle ranch managers interested in participating was compiled. Of the initial candidates, phone and field interviews were used to determine further suitability for inclusion (Appendix 2-S3). This assessment excluded ranches that did not match our AMP classification criteria (Appendix 2-S3) or where no neighboring ranches existed for comparison. In almost all cases, the first neighbouring ranch identified was eligible for inclusion. Neighbouring ranches were excluded from study only if the manager did not wish to participate (i.e. privacy concerns) or if no comparable area suitable for sampling was present. All ranches were screened to ensure current grazing management practices had been in place for a minimum of 10 years.

Sampling area selection and data collection

Once suitable neighbouring ranches (within 20 km) were identified, study sites within each ranch pair were checked via field surveys to ensure they were placed in similar ecosites sharing the same soil series type, coarse topological characteristics, and cultivation histories (e.g. areas showing either no historical tillage, or where both areas had been seeded at least 10 years prior). We randomly placed our 10-hectare sampling site within these areas of broadly comparable topo-edaphic features and cultivation histories. Specifically, a point was randomly placed within the eligible area polygon drawn within our mapping system, and a 10-hectare area created surrounding that point. No measures of cattle management were used to determine the study site. Average ranch sizes and paddock area varied greatly (Appendix 2-S5).

Plant community data collection

Vegetation sampling was conducted by randomly placing five 0.5 metre x 0.5 metre quadrats within each of three relative landscape positions, for a total of 15 quadrats per study site. Each sampled plot within the site was randomly assigned a “high”, “medium” or “low” status. They were determined by first walking to the randomized coordinate, splitting the localized drainage basin into top, medium, and bottom thirds, then placing the final sampling point at the closest point matching the slope position assigned to that point. Plots were permanently marked between the two years of sampling using wooden stakes to allow for accurate repeat sampling. As a result of our prioritization of sampling many pairs of ranches instead of intensive sampling within each study site, rarefaction curves for each 10-hectare study site did not fully saturate (Appendix 2-S4). Plant species counts should therefore be considered as relative values as opposed to a complete tally of plant species present.

Vascular plant species abundance was collected using visual estimation of percent canopy cover in each quadrat. At all sites non-senesced vascular plants were identified to species as defined by the USDA PLANTS database (USDA, NRCS 2021). Study sites within each pair were sampled within a 24-hour period during the peak growing seasons of both 2017 and 2018, typically between June 15 and July 15. To reduce noise in our diversity estimates associated with single point sampling over such a large spatial extent, we pooled the vegetation data across the two years of sampling. Thus, estimates of quadrat-level composition consist of the average cover of each species found in a permanently marked single quadrat in the same location across both years of sampling. Estimates of plant species richness represent the total number of species identified across the two years of sampling at each quadrat (alpha diversity) or study site (gamma diversity), rather than the average number of species observed each year. This procedure was conducted following analysis which verified that there was no significant difference between year of sampling on our plant community metrics ($P>0.1$).

To compare diversity over different spatial scales, we calculated estimates of alpha, beta, and gamma diversity for each study site. Alpha diversity was calculated as the average species richness measured with the 15 quadrats within each study site. Gamma diversity was calculated as the total number of unique species found among the 15 study plots within each study site. Beta diversity was calculated both among plots within the study site (local beta-diversity) and among all ranches of a given management practice (AMP and N-AMP; regional beta-diversity). Local beta diversity was calculated as the mean dissimilarity among plots within each study site (Pearse et al., 2014). Regional beta diversity was calculated as the mean dissimilarity between each study site relative to all other study sites of a given management practice (Pearse et al., 2014). Plant community evenness within each study site was calculated using the Shannon evenness index of all plots within each ranch (vegan v1.0-0 package, R v.3.2, R Core Team 2013).

Species were categorized as "introduced" or "native" following USDA Plant database guidelines, though in the four cases where a species was classified as "both", expert opinion was used to classify the species as either "introduced" or "native" (Appendix 2-S1).

Management data

Data of whole-ranch management practices were collected through a phone survey directed to all 36 ranch managers with 100% participation (Human Ethics Survey #RES0032548; Appendix 2-S2). Our survey focussed on specific management practices across the entire ranch area hypothesized to impact patterns of plant diversity and species composition: stocking rate (weight standardized number of animals/hectare/month) and stocking density (average weight standardized number of animals/hectare at the ranch level; Appendix 2-S2). Though the sampled areas always shared equivalent seeding status between pairs, we also collected data on the presence of seeding anywhere within the entire ranch extent.

Statistical analysis

All analyses were performed using R v.3.2 (R Core Team 2020). Throughout this manuscript P-values less than 0.1 were considered significant due to relatively low statistical power compared to controlled experimental conditions, given our prioritization of attaining widespread regional data coverage over capturing in-depth coverage of the plant community within each ranch.

To assess whether AMP and N-AMP neighbours utilized different management practices we performed a PERMANOVA (Oksanen et al., 2019) of AMP/N-AMP status as a function of management metrics (stocking rate, stocking density and seeded status across entire ranch). We used linear mixed models with pair as a random effect to determine whether stocking density, stocking rate, and ranch-wide seeded status differed between AMP and N-AMP ranches (nlme package, Pinheiro et al., 2020).

To determine whether AMP and N-AMP grazing had differential impacts on local and regional beta-diversity, we constructed linear mixed models using the spatial dissimilarity metrics outlined above (nlme package, Pinheiro et al., 2020). Lower levels of this metric indicate increased homogeneity of plant diversity within either the study site for each ranch (i.e., local) or among study sites from each ranch (i.e., regional scale). Beta diversity and evenness were included in separate linear mixed models as response variables, with AMP status as a fixed effect and ranch pair as a random effect.

To assess the role of AMP systems as a biotic filter on grassland composition we tested for differences in plant community structure between AMP and N-AMP ranches. PERMANOVA (vegan package, Oksanen et al., 2019) was used to identify differences in the overall plant community composition between AMP and N-AMP ranches. Additionally, each of our plant diversity metrics (alpha and gamma diversity of all plants, and of native and introduced species individually) were included in separate linear mixed models, with AMP status as a fixed effect and ranch pair as a random effect. To assess whether particular species might be indicative of AMP management we performed an indicator species analysis on species assembly data (indicspecies package; De Caceres & Legendre, 2009). To further visualize the community composition for each ranch, we used nonmetric multidimensional scaling (NMDS) using the metaMDS procedure (vegan package; Oksanen 2011).

RESULTS

A PERMANOVA analysis (Oksanen et al., 2019) of plant composition as a function of slope position across all ranches found no influence on plant community composition ($P = 0.98$, $R^2=0.008$), and slope position was therefore not included in further analyses.

Our survey found generally low species richness, with an average of 9 species per sampling quadrat in AMP ranches and 10 species per sampling quadrat in N-AMP ranches (Figure 2-3). The same pattern was evident at a study site level, with an average of 23 species in AMP ranches and 27 species in N-AMP ranches. The trend of lower species richness in AMP ranches relative to N-AMP also applied to both introduced-only and native-only species groups (Figure 2-3).

Do AMP and N-AMP ranches use distinct management systems?

The combination of management practices used on AMP and N-AMP ranches was significantly different (PERMANOVA: $P < 0.001$, $R^2 = 0.36$). Compared to N-AMP ranches, AMP ranches had higher stocking densities (Table 2-1; Figure 2-2) but no significant difference in stocking rates or seeded status, though stocking rate trended higher (Tables 2-1 and 2; Figure 2-2). 72% of AMP ranches (n=13) compared to 61% of N-AMP ranches (n=11) were seeded over their entire spatial extent within the preceding decade.

Do AMP grazing systems result in decreased community heterogeneity (β-diversity)?

In contrast to our expectation of AMP being a more uniform ecological filter on plant diversity than the neighboring ranches, we found no influence of AMP status on beta diversity either locally ($P = 0.76$) or regionally ($P = 0.86$; Figure 2-3). Plot-level evenness of the plant community also did not differ between AMP and N-AMP ranches (Figure 2-3).

Do AMP grazing systems alter vegetation structure compared to N-AMP?

In contrast to the lack of effects of AMP grazing on beta-diversity, there was clearly lower alpha and gamma diversity on AMP ranches compared to neighbouring ranches (Figure 2-3). AMP ranches had approximately 13% fewer species at the plot level, and 18% fewer species at the landscape level, compared to their N-AMP neighbours ($P < 0.09$; Figure 2-3). No individual management metrics - including seeded status - were associated with study site-level diversity ($P > 0.1$).

Both native and introduced species had a trend towards lower species richness within AMP grazing systems at both the local and study site (landscape) scale (Table 2-4; Figure 2-3). However, these sub-group analyses were only significant for native species at the landscape scale (Table 2-4; Figure 2-3). In contrast, PERMANOVA analysis of plant community composition as a function of AMP/N-AMP status was not significant ($P = 0.84$, $R^2 = 0.02$). Similarly, indicator species analysis found no particular species were characteristic of AMP or N-AMP grazing systems ($P>0.1$). The lack of influence of AMP management on plant community composition is further illustrated in Appendix 2-S6.

DISCUSSION

This work represents an extensive survey of grassland diversity as a function of operational grazing practices across the Northern Great Plains. We found that cattle ranchers using Adaptive Multi-Paddock grazing reported management practices differing from neighbouring ranches, particularly their use of higher stocking densities (Figure 2-2). AMP grazing was associated with lower plant diversity at the plot and landscape level, with the greatest effects on native diversity at the landscape scale. In contrast to expectation (Olff & Ritchie, 1998), there was no impact of AMP grazing on plot or landscape level heterogeneity in plant biodiversity. Combined, we find evidence that AMP operations employ functionally different management operations compared to their neighbouring operations, and their ability to maintain plant diversity is questionable (Briske et al., 2003).

Do AMP and N-AMP ranches use distinct management systems?

While stocking density was much higher under AMP systems, stocking rates did not differ between AMP and N-AMP ranches (Table 2-1; Figure 2-2). Higher stock densities applied by AMP operators are consistent with the underlying strategy of AMP grazing. Cases of higher stocking densities with equivalent stocking rates are possible when grazing occurs during a shorter period of time. As high stocking densities are considered to be the primary mechanism uniquely indicative of AMP grazing, rather than absolute levels of livestock present per area per time (Sherren & Kent 2019), the equivalent stocking rates is understandable. From a social standpoint, AMP grazing is often publicized as enabling higher stocking rates (Hawkins et al., 2017), though such differences in stocking rates were not found in this particular study. This contrast between expectation and application highlights the value of measuring potential environmental consequences of modified grazing systems from working, rather than hypothetical, cattle operations (Venter et al., 2019).

Stocking density was higher in AMP ranches compared to N-AMP ranches, and was paralleled by other differentiating factors, such as a longer grazing season, shorter grazing periods, and increased rest after grazing in spring and early summer (Bork et al., 2021). What remains unclear is how these factors alter plant diversity, which is otherwise known to respond to grazing intensity (i.e., stocking rate), a response that further varies depending on the moisture regime and tolerance of vegetation to herbivory (Milchunas & Lauenroth, 1993).

We also found higher incidences of total ranch seeding within AMP systems as opposed to N-AMP systems. As our paired design screened out differences in seeding and cultivation at the study site level, we are unable to draw further conclusions on this specifically. Our study design does not allow us to determine whether those ranches who seeded may have been more likely to adopt AMP grazing, or whether AMP grazing use itself led to increased use of seeding.

Do AMP systems decrease plant community heterogeneity?

In contrast to ecological filtering theory, we found no evidence of biotic homogenization due to AMP management (Table 2-2; Figure 2-3). Previous field trials (Earl & Jones, 1996) and theoretical arguments (Teague et al., 2013) assume that high stocking densities employed under AMP grazing decrease the ability of cattle to select forage, thus increasing the evenness of biomass removal (Distel et al., 1995). However, our results indicate that even if this occurred, it did not lead to lower spatial heterogeneity in species composition within these grasslands, either within or among ranches. One possible explanation for this null result is that because AMP and N-AMP ranches did not differ in stocking rate, they do not actually differ in grazing selectivity within these grasslands. However, behavioural studies of animal selection are needed to address critical related hypotheses. For example, if cattle selection of forage is higher at lower stocking densities, it is possible that N-AMP systems will have greater patchiness in the short term (Adler et al., 2001) but not across the entire season because overall stocking rates become equivalent (Porensky et al., 2021). Another possibility is that AMP operators might not have been applying high enough densities or durations of grazing to change the uniformity of cattle use within these grasslands relative to their N-AMP counterparts. Future research is needed within these northern temperate grasslands to establish the broader role of stocking densities, as encompassed by different grazing management systems, on grassland composition and diversity.

Do AMP systems act as a biotic filter to influence the plant community in other ways?

AMP ranches did not differ in overall plant community composition but had lower plot and study-site level plant species richness, including lower counts of native species, compared to the N-AMP ranches (Tables 2-2; Figure 2-3). We therefore conclude that AMP management practices function as a unique ecological disturbance in this respect (Milchunas & Lauenroth, 1993), and filters the number and types of viable plant strategies present (HilleRisLambers et al., 2012). Consistent with expectations due to the imposition of a more uniform ecological filter, we found lower numbers of plant species present at both the local and study-site levels within grasslands subject to AMP management. While the trend of lower species richness in AMP compared to N-AMP systems was consistent, analysis subdividing plants by origin found that only native species at a landscape level were significantly lower under AMP management (Table 2-4). Our species richness counts were relatively low compared to regional plant community surveys due to the agronomic (seeded) history of most of our sites (Pyle et al., 2021). Despite this, site level counts of native species accounted for the majority of plant species present overall (Figure 2-3).

The combination of greater stocking densities for shorter periods of time is the practical realization of the classical "pulse" disturbance described by grazing theorists dating back to Voisin (1957) and lately expanded into the "pulse" versus "press" disturbances concept (Ratajczak et al., 2017). This relatively brief but extreme application of grazing to a small area is thought to simplify the plant community by reducing plant diversity to those species that are relatively more tolerant of such disturbances (Zhu et al., 2020). Simplification of the plant community is particularly pronounced among native species, pointing to their possible disadvantage within such systems compared to introduced species (McIntyre & Lavorel, 1994). The simplification of the plant community under ‘pulse’ disturbances have been demonstrated at a theoretical and experimental basis within the bounds of controlled studies (Cingolani et al., 2005). We now demonstrate that such dynamics between grazing systems and the plant community are at play within operational systems across a broad geographic spectrum.

Our examination of real-world effects is an important step towards understanding how operational grazing management shapes plant communities across multiple spatial scales. Though increased stocking densities may have contributed to the lower plant species richness present within AMP grazed ranches, the mechanisms driving changes to the plant community fall outside the theory that heterogeneity mediates this relationship. In particular, the role of specific grazing management systems, including AMP grazing, at influencing variability of the plant community structure should be further investigated, preferably through a lens explicitly examining livestock selectivity, including how this varies over time. Additionally, AMP grazing is characterized by two factors: the highly elastic response of management to environmental conditions, and the high stocking density exerted on the land area. While the former would be expected to preserve plant diversity (Prato, 2012), the latter would be expected to reduce plant diversity (Wang & Tang, 2019). As the adaptive nature of AMP management is intended to counteract the environmental impacts of increased stocking densities, it is possible this lack of an AMP environmental ‘footprint’ is due to these two forces neutralizing each other. We call for research that examines both, including independently and in concert, the impact of adaptive grazing methods and increased grazing density (Derner et al., 2021).

Additionally, we highlight the potential confounding role of larger ranch sizes found under AMP management. AMP ranches were larger on average compared to their N-AMP counterparts (Bork et al., 2021). While it is beyond the scope of this work to parse out the interactive influence of grazing management and total ranch size on the resulting plant communities (Supplementary Figure 2-5), we note that larger and contiguous areas of land under the same management regime may foster increased plant diversity. The latter could occur due to enhanced diversity of the surrounding vegetation, and therefore lead to a more diverse seed pool. We call for research explicitly examining these factors.

Our results suggest that when examined under operational conditions, these grazing systems showed distinct differences between plant communities though these effects were limited to reduced plant richness with little to no influence on overall community composition. The environmental influences of AMP management systems are only lately emerging and include many potential benefits such as increased methane uptake potential in soils (Shrestha et al., 2020) and improved water infiltration (Döbert et al., 2021). We suggest that while AMP grazing might have many associated benefits in the northern Great Plains, these do not include increased plant biodiversity.

SYNTHESIS AND APPLICATIONS

This work contributes to an increasing consensus that AMP management systems ultimately show negligible differences in ecological goods and services where stocking rate is kept equivalent (Hawkins et al., 2017). The results of this study indicate that policy intended to promote ecosystem resilience through higher levels of species diversity should not place emphasis on AMP management as defined within this work and expressed operationally across the Northern Great Plains.

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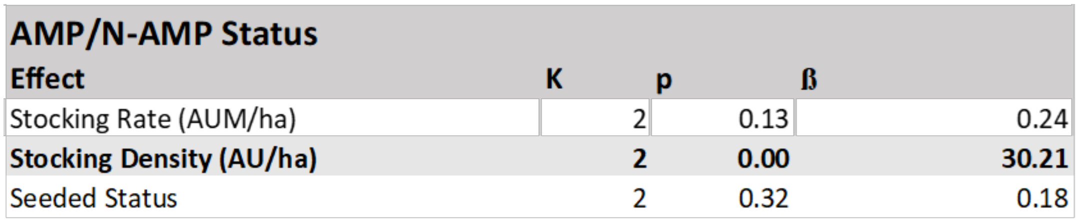
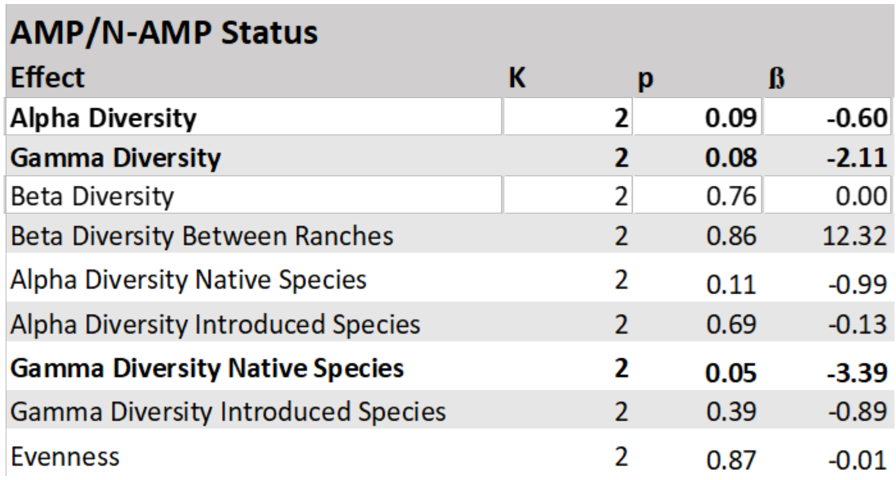
Table 2-1. Number of terms (k), p-value, and beta coefficients (β) for linear mixed models examining the relationship between grazing management style and individual management factors. Positive coefficients indicate higher values in AMP ranches than non-AMP ranches.



AMP/N-AMP Status			
Effect	**K**	**p**	**ß**
Stocking Rate (AUM/ha)	2	0.13	0.24
Stocking Density (AU/ha)	**2**	**0.00**	**30.21**
Seeded Status	2	0.32	0.18

Table 2-2. Number of terms (k), p-value, and beta coefficients (β) for linear mixed models. Negative sign beta coefficients represent less diversity with AMP status compared to N-AMP neighbours. See Figure 3 for visual representation of these results.



AMP/N-AMP Status

Effect	K	p	ß
Alpha Diversity	**2**	**0.09**	**-0.60**
Gamma Diversity	**2**	**0.08**	**-2.11**
Beta Diversity	2	0.76	0.00
Beta Diversity Between Ranches	2	0.86	12.32
Alpha Diversity Native Species	2	0.11	-0.99
Alpha Diversity Introduced Species	2	0.69	-0.13
Gamma Diversity Native Species	**2**	**0.05**	**-3.39**
Gamma Diversity Introduced Species	2	0.39	-0.89
Evenness	2	0.87	-0.01

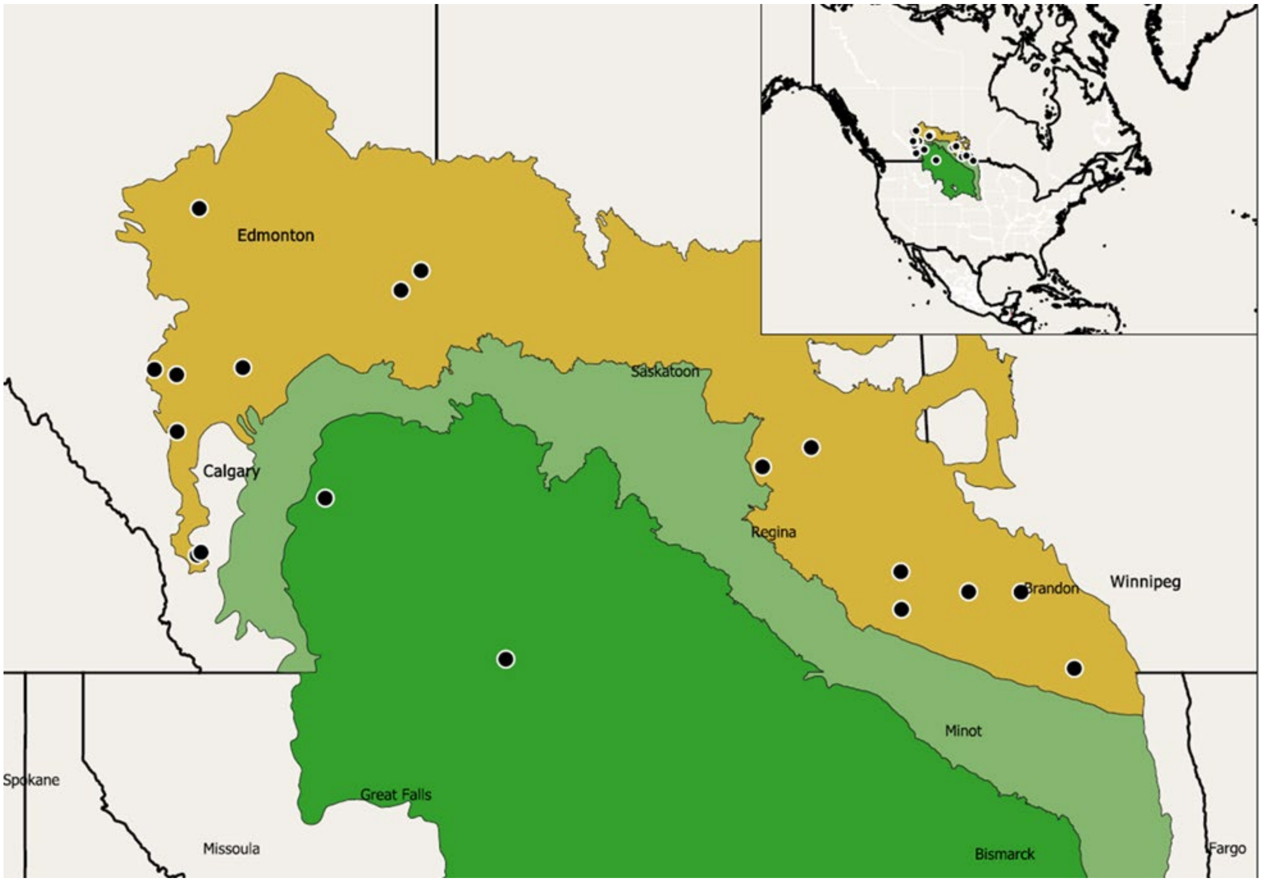


Figure 2-1. Location of ranch pairs across Western Canada. Ranch pairs are represented by black circles. The coloured regions represent ecoregions. Dark yellow represents the Aspen Parkland, light green represents the moist mixed-grass prairie, and dark green represents the mixed grassland.

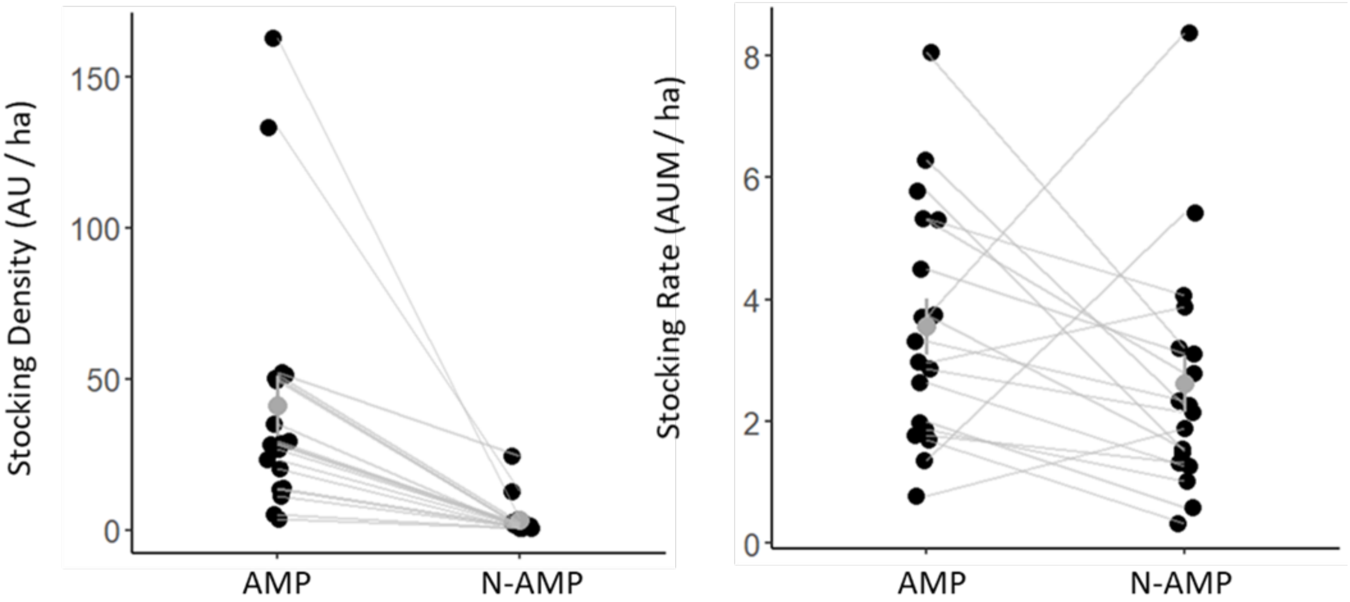


Figure 2-2. Plots contrasting stocking density and stocking rate as a function of AMP or N-AMP status. The gray centre point represents the group mean and the gray outer whiskers represent standard error. Dots represent the values for each sampled ranch. Grey lines connect paired ranch points, illustrating total directionality of response to grazing management.

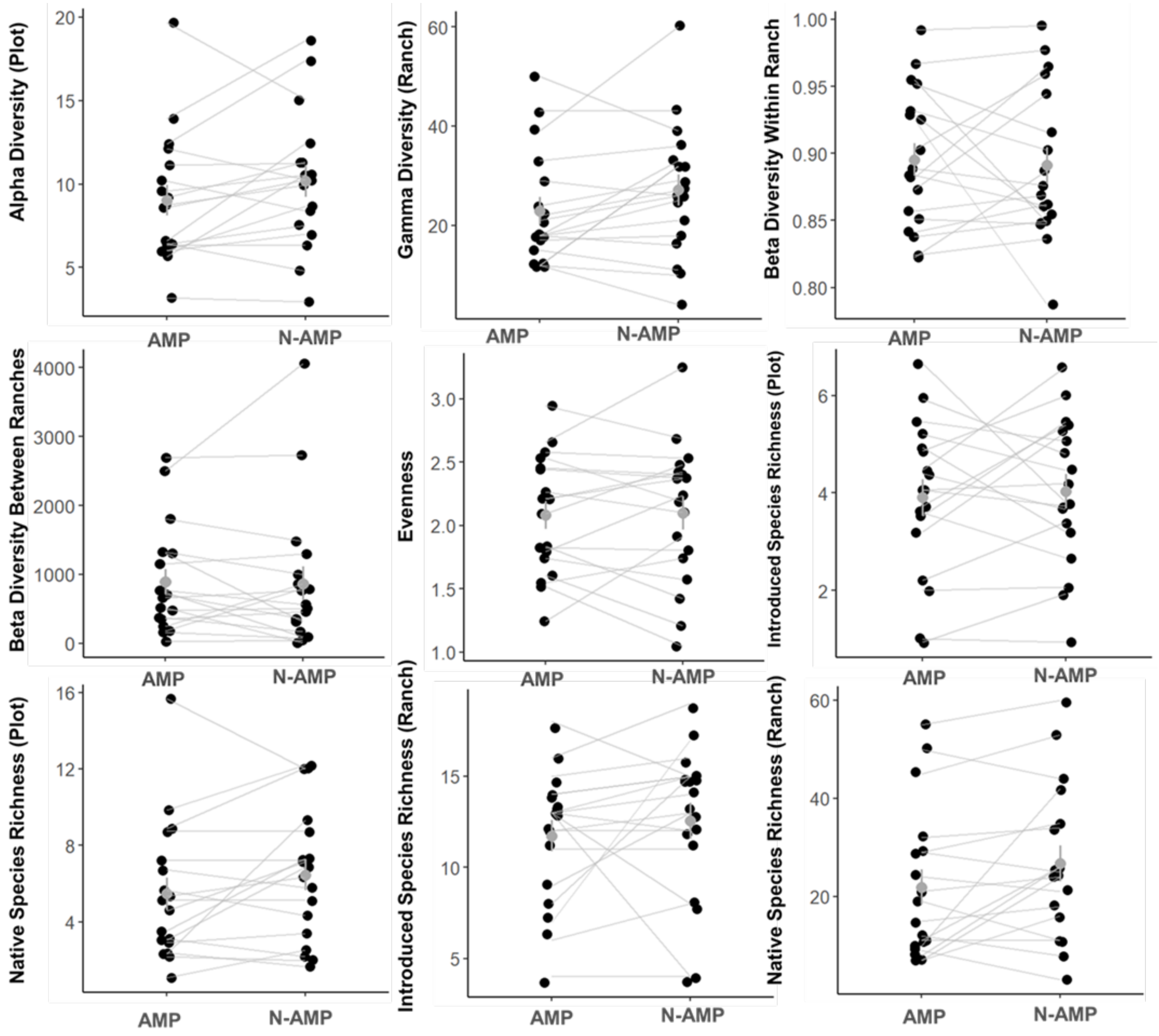


Figure 2-3. Plots contrasting all plant community metrics as a function of AMP or N-AMP status. The gray centre point represents the group mean and the gray outer whiskers represent standard error. Dots represent average values for each sampled ranch. Grey lines connect paired ranch points, illustrating total directionality of response to grazing management.

Chapter 3: Intensive grazing management systems increase plant productivity: evidence for the grazing optimization hypothesis

INTRODUCTION

Grassland ecosystems supply a variety of ecosystem goods and services including livestock production, carbon sequestration, water filtration, maintenance of biodiversity, and provision of cultural-spiritual significance (Briske et al., 2017; Evans et al., 2017). In the Anthropocene, grasslands are among the most heavily modified ecosystem-types (Carbutt et al., 2017) and are widely converted to croplands or used to support livestock production. For example, nearly all extant grasslands support domestic livestock grazing (McSherry and Ritchie, 2013) with half the diet of global livestock consisting of graminoid forages (Herrero et al., 2013). Contemporary livestock production systems are often located on lands with historically analogous patterns of grazing disturbance; for example, by the vast bison herds of the North American great plains and the multi-species complementary grazing across the Serengeti (Frank and Tracy, 1998). Decades of ecological research, and millennia of cultural understanding, provide clear evidence that changes in grazing management practices, such as the type, intensity, and timing of grazing can lead to marked changes in plant functional and species diversity (Díaz et al., 2007), as well as production (Lauenroth, 1979). Over the last century, global livestock numbers have more than doubled while the global extent of grasslands has declined substantially (Goldewijk et al., 2017). Sustaining increased numbers of livestock across a shrinking land base necessitates a greater understanding of grazer impacts on plant productivity. One management system that is growing in popularity is Adaptive Multi-Paddock (AMP) grazing, which is intended to emulate historical grazing regimes by employing dense herds of livestock quickly rotated through a series of small pastures, relative to regionally typical management practices (Briske et al., 2008). Though such systems have been predicted to increase plant productivity with minimal consequences to other ecological goods and services, such as plant diversity, controlled studies of its influences on plant growth are limited (Briske et al., 2008; Hawkins 2017). Recent works tackling this question on research ranches have included Derner et al.'s (2021) Collaborative Adaptive Rangeland Management Experiment, which has found that the adaptive component of AMP grazing may increase livestock production, and Venter et al. (2019 and 2021) who found greater evenness of grazing pressure in AMP systems and increased forage production in AMP systems so long as soils were fertile. While controlled experimental studies intended to mimic operational practices are vital to understand the mechanisms driving observed on-the-ground results, our understanding of the real-world consequences of on-farm AMP grazing remains limited.

Although a typical plant community response to grazing is a reduction in subsequent productivity (Zhang et al., 2018), there is substantial evidence that under some conditions grazing may be neutral or stimulatory to subsequent productivity (Milchunas and Lauenroth, 1993; Milchunas et al., 1988). For example, the 'grazing lawn' concept that drives the classical 'grazing optimization' hypothesis (GOH) of McNaughton (McNaughton et al., 1996) postulates that grazing shifts plant communities towards grazing tolerant species and stimulates increased nutrient cycling through trampling. Trampling of forage can aerate the soil and physically incorporate nutrient-rich litter at a faster rate than under biological and abiotic decomposition (Milchunas et al., 1995). Hypothetically, this increases the possible production rates of a plant community via enhanced mineralization, which frees available nutrients for new growth (Olofsson and Oksanen, 2002). Livestock management systems that emulate these aspects of historical disturbance regimes may also generate greater forage production per unit area than other management systems (McNaughton et al., 1996). Despite such promise of enhanced plant biomass through intentional grazing practices, there is also abundant evidence that in many cases the stimulation of plant production comes at the expense of root growth, potentially increasing vulnerability to drought, suggesting over-compensatory plant responses may be short-lived (Gao et al., 2008; Gong et al., 2015).

AMP practices are presented as a potentially more sustainable management regime due to their intended objective of emulating historical disturbance regimes. AMP grazing consists of rapidly rotating dense herds of livestock through many small paddocks; thereby increasing the spatial and temporal heterogeneity of grazing disturbance at the landscape scale while suppressing spatial and temporal heterogeneity at the local scale (Wang et al., 2020; Bork et al. 2021). This practice contrasts with many conventional livestock management systems utilizing ‘continuous’ (or season-long) grazing that employ much less effort to control when, where and how often livestock graze. The underlying premise of the AMP grazing management style is that such regimented management acts as an ecological filter (eg. HilleRisLambers et al., 2012) that promotes plant productivity as AMP avoids the extreme homogeneity of patch level grazing common under continuous (or slow rotational) grazing. The relatively long recovery periods of vegetation within each paddock between grazing events under AMP and the use of an earlier grazing date (increasing the time-since-disturbance for each paddock; Bork et al., 2021) allows for enhanced recovery of the plant community before subsequent grazing by livestock, despite the higher absolute levels of biomass removed by livestock; a process thought to emulate aspects associated with migratory behavior of bison and wildebeest (Frank and Tracy, 1998). Thus, in AMP systems absolute biomass removed is hypothesized to be greater, while proportional biomass removed is hypothesized to remain equivalent to conventional systems. On this basis AMP could theoretically accord with the GOH because plant productivity would increase relative to non-AMP systems despite higher localized biomass removal (Hawkins, 2017). However as outlined above more generally, it is important to determine whether such stimulation of aboveground biomass is at the expense of belowground biomass as the latter has implications for total system sustainability. Overcompensation is also context dependent with a greater likelihood of occurrence within mesic systems dominated by grazing tolerant, introduced plant species (Gao et al., 2008; Gong et al., 2015). Our earlier work (Grenke et al., 2022) also suggests that AMP systems slightly reduce plant diversity, especially of native species. It remains unknown whether these modest composition changes under AMP grazing have measurable impacts on plant productivity and whether productivity is influenced by proportional changes in native:introduced species abundance ratios.

To test the consequences of AMP grazing on plant community production and biomass removal, we conducted a large-scale survey of plant production and biomass removal, comparing AMP grazed ranches with paired regionally representative neighbors. This work is part of a larger study reporting on grazing practices across western Canada (Bork et al., 2021). The objectives of this study were to: 1) determine how AMP grazing influences aboveground biomass, litter mass, belowground biomass, and biomass allocation; 2) determine how these changes influence broader plant community dynamics of biomass allocation, biomass variability, and biomass removal; and 3) determine whether changes in production were associated with increased abundance of specific species types (i.e. introduced/native species and graminoid/non-graminoid species).

METHODS AND MATERIALS

This study was a part of a larger initiative to understand the ecological impacts of AMP grazing in the northern grasslands of North America (Bork et al., 2021). The design of the plant sampling was discussed in detail in Grenke et. al (2022).

Study area

Sampling took place on 36 cattle ranches located across the Northern Great Plains of Western Canada spanning approximately 360 000 km^2. On 16 of 18 pairs (see below) seeding had previously occurred (likely supplemented by invasion from surrounding areas) with all grasslands therefore dominated by common non-native forage species (e.g., *Bromus inermis*, *Phleum pratense*, and *Dactylis glomerata*; see Grenke et al., 2022 for a full list of species). Throughout the study region, average annual precipitation ranged from 300 to 660 mm/year, and mean annual temperatures ranged from 1.8 to 4.8°Celcius (Canadian Climate Normals 1981-2010; Environment and Climate Change Canada).

Sampling design and measurements

Overview

To minimize confounding effects of spatio-temporal differences among ranches independent of grazing practices, we paired each of our focal AMP-grazed ranches with an adjacent neighbor ranch employing regionally representative management (N-AMP). In this sense, N-AMP ranches comprised a subset of cattle ranches using regionally typical management practices. Ranches were grouped in pairs following a vetting process described in more detail below (see also Grenke et al., 2022).

Ranch selection

Ranch operators/owners using AMP grazing were first recruited at the Organic Alberta grazing management conference (2017) from across the Northern Great Plains (Appendix 3-S1). A list of cattle managers interested in participating was compiled following an introduction to the project. Candidates were then screened using phone and field interviews to determine eligibility and were further subject to a random selection process to minimize bias and keep the sampling pool within our logistical capabilities (details in Appendix 3-S2). Grazing management practices currently used (e.g., AMP) had to have been in place for a minimum of 10 years. Stocking rate and management experience were similar between AMP and N-AMP pairs (Bork et al., 2021; Grenke et al., 2022).

Site selection

Sample areas within each ranch pair were stratified to ensure they were placed in similar ecosites sharing identical soil series type, coarse topological characteristics, and cultivation histories (e.g. areas showing either no historical tillage, or where both areas had been seeded at least 10 years prior). Ranches were not excluded based on any characteristic of the plant community. Our final pool of ranches consisted of 36 ranches organized into 18 pairs.

Individual ranches in our study varied greatly in size, ranging from 32 to over 10000 hectares. Management practices were not expected to be uniform over the entire area nor was it feasible to fully sample 36 ranches of this size in a short timeframe. Thus, we limited our sampling to 10 hectare (ha) focal areas randomly placed in each ranch but excluded water bodies, roads, and supplemental feeding (i.e. bale grazing) areas. All field data were collected from within these 10 ha study areas.

Study area designation and data collection

Plant community data collection

To capture plant community responses to AMP grazing relative to regionally typical management, we established 0.5 × 0.5 meter quadrats in which we identified plant community abundances and biomass estimates. As outlined in Grenke et al. (2022), due to our prioritization of sampling many pairs of ranches rather than conducting intensive sampling within each ranch, rarefaction curves for each of our study sites did not saturate. Therefore, plant community measures should be considered on a relative rather than an absolute basis.

To determine the potential for specific components of the plant community to influence biomass production we assessed community composition. Composition was sampled by randomly placing five quadrats within each of three landscape positions, for a total of 15 quadrats per study site. Sampling was stratified by topographic landscape position in order to capture potential topographically sourced heterogeneity, with landscape designations representative of relative positioning within the context of each ranch pair. Areas were designated as "low" if they occurred within the bottom third of a local relief, "high" if they occurred within the top third of the local relief, and "medium" if they occurred within the middle third of the landscape relief.

To assess how vascular plant species composition may have influenced biomass production we recorded vascular plant species abundance (percent cover) at every site using a 0.5 meter × 0.5 meter quadrat. All non-senesced vascular plants within the quadrat were identified to species (USDA, NRCS 2021). Vascular plant species abundances were collected over two years, during the peak growing seasons of both 2017 and 2018, typically between June

15 and July 15. To reduce variance in our diversity estimates, we pooled data across the two years of sampling. Further details can be found in Grenke et al. (2022).

Plant community biomass estimates

We measured plant biomass (aboveground biomass, litter mass, and roots from soil cores) using three randomly selected quadrats from each of the three landscape positions within the ranch (9 quadrats per ranch). Biomass data were taken from a randomly determined half of the plant composition quadrat (0.25 meter × 0.5 meter total). Plant biomass measures were collected during the peak growing season of 2018 at the same time as vascular plant species abundance sampling (June 15 - July 15). Litter mass was removed using hand raking, followed by clipping all standing plants to ground level (aboveground biomass). Two soil cores (6 cm diameter, 15 cm deep) were then taken within the same area and pooled within a quadrat, with roots later sieved out and washed. All biomass and litter mass was dried to constant weight at 70°C, weighed, and standardized to g/m^2. The resulting root biomass measures were lower than would be reasonably expected from these systems (e.g., see Bork et al., 2019). This was likely due to extensive fine-root degradation in transport as well as breakage during the washing process. As such, root biomass measures represent the within-study relative treatment effects, not absolute indicators of total root biomass present. Neither landscape position nor the landscape position × management interaction significantly influenced aboveground biomass, litter mass, or belowground biomass (Table 3-1).

To measure aboveground biomass and biomass removal by livestock, we required approximate measures of plant growth with and without current-year grazing. The adaptive nature of ranch operations at our sites, as well as the geographic breadth of the sampling area, precluded us from systematically placing exclusion cages prior to grazing. Thus, at each plot, we installed an exclosure cage (1 × 1 meter) located 2 meters away from the non-exclosed plot a minimum of 2 weeks before plant community sampling. Biomass (aboveground, litter mass, and soil cores) and vascular plant species composition were sampled at the excluded and non-excluded sites within each pair. Subsequent analysis and discussion of biomass refer to those data collected from exclosure cages to mitigate the confounding influence of short-term grazing. Data collected from the non-exclosed quadrats were used to estimate the vegetation removed by grazing, detailed below.

We measured two aspects of biomass removal by cattle: the absolute magnitude (amount of biomass removed) and the intensity of biomass removal as estimated by the proportion of available biomass removed. Magnitude of biomass removal was calculated as the following:

$$Magnitude\ Removed = Exclosure\ biomass - NonExclosure\ Biomass$$

between paired quadrats. This metric provides an estimate of the amount of aboveground biomass removed by cattle before plant community sampling. We calculated the intensity of grazing as the following:

$$Intensity\ Removed = \ln\left(\frac{NonExclosure\ Biomass}{Exclosure\ Biomass}\right) * -1$$

where lower values correspond to lower proportional biomass removal.

We did not impose a standard level of grazing on quadrats, but instead individual quadrats experienced grazing as per the ranch managers' typical grazing regime. While this allowed us to sample ranches in a temporally equivalent way, the recovery period for each plot following grazing remained uncertain, complicating the interpretation of our biomass removal measures.

Statistical analysis

All statistical analyses were performed using R v.3.2 (R Core Team 2013). Using a series of linear mixed models (nlme package, RStudio v.3.2), we included above and belowground biomass and plant litter mass as the response variables, with AMP status, landscape position, and the interaction between AMP status × landscape position as fixed effects. Because the interaction between status and landscape position was weakly significant for litter mass (p=0.1), this interaction was included in all further analyses. To assess the influence of the grazing system and landscape position on the intensity and magnitude of biomass removed, we performed the same analysis using either magnitude or intensity as response variables. To assess the potential for specific components of the plant community to influence biomass production, we performed a series of linear mixed models with the total canopy cover for each type of plant species (total, introduced/native species, and graminoid/forb species) as the response variable with grazing management and landscape position as fixed effects. Ranch identity nested within pair and pair were included as random effects.

To determine whether increases in aboveground biomass under AMP systems were at the expense of belowground biomass, we assessed the effects of AMP grazing on biomass allocation using an additional linear mixed model. Shoot biomass served as the response variable, with root biomass, management, landscape position, and the interaction terms included as fixed-effects. Ranch nested within pair and pair served as random effects. An impact of grazing management on the relative allocation to shoots would be indicated as a significant root × management interaction term.

To assess whether any growth increases associated with AMP grazing were due to increased representation of non-native species, we assessed the variability of the native:introduced (N:I) species canopy cover ratio as a function of the AMP system. Specifically, we used a linear mixed model with N:I as the response variable, and total canopy cover, aboveground biomass, litter mass, belowground biomass, and grazing management, as well as the interaction of all of the preceding with grazing management, as fixed effects. Ranch identity nested within pair and pair were included as random effects.

RESULTS

Ranches using AMP systems had greater aboveground biomass (20% more) and litter (21% more) mass compared to paired N-AMP ranches (Table 3-1; Figure 3-1). In contrast, root biomass did not differ as a function of management, suggesting enhanced AMP shoot growth occurred despite stable root systems (Table 3-1; Figure 3-1). In our follow-up analysis of the allocation of aboveground biomass, the latter was primarily influenced by both belowground biomass, the grazing management system, and the interaction between landscape position × belowground biomass (Table 3-2; Figure 3-4). As belowground biomass exhibited markedly higher values at lower landscape positions, the latter interaction term is understandable (Figure 3-1). Both aboveground biomass and the ratios of above:belowground biomass were consistent across a productivity gradient (Figure 3-4), indicating that increases in aboveground productivity were not at the expense of shallow belowground root biomass.

AMP ranches had a greater amount and proportion of forage removed at the time of sampling in mid-summer relative to N-AMP ranches (Table 3-3; Figure 3-2), consistent with expected outcomes of high-density grazing management systems. Although AMP ranches produced an average of 20% more aboveground biomass than N-AMP pairs, there was also a 75% increase in biomass removal (Table 3-3; Figure 3-2) under AMP grazing, suggesting forage use was influenced by more than simply forage production. The interaction between grazing system and landscape position was also a significant driver for both the absolute and proportional biomass removal of aboveground biomass (Table 3-3). This was expressed as higher absolute and proportional aboveground biomass removal at higher landscape positions in AMP systems, and lower absolute and proportional aboveground biomass removal at elevated landscape positions within N-AMP systems (Figure 3-2).

Levels of absolute and proportional litter mass removal were not influenced by grazing system (Table 3-3; Appendix 3-S3). Absolute amounts of litter mass removal were instead a function of the landscape position × grazing management system interaction (Table 3-3). There were greater amounts of absolute litter mass removal at higher landscape positions within AMP systems, with no biomass removal × landscape position interaction present in N-AMP systems (Appendix 3-S3). Absolute differences in belowground biomass between exclosed and non-exclosed quadrats did not vary due to landscape position, grazing system, or the interaction of these two terms (Table 3-3; Appendix 3-S4). However, proportional biomass removal for belowground biomass was significantly influenced by landscape position (Table 3-3). At elevated landscape positions, proportional biomass removal of belowground biomass trended higher (Appendix 3-S4).

Increases in plant community production were not associated with any identified species groups, including those associated with plant community origin (introduced/native) or growth form (graminoid/non-graminoid); instead, only AMP status was a significant factor in those models (Table 3-1; Figure 3-3). The proportion of native:introduced species canopy cover was also not related to aboveground or belowground biomass (Table 3-4). However, the proportion of native:introduced species canopy cover increased with higher levels of litter mass and was influenced by the litter × grazing management system interaction term (Table 3-4).

DISCUSSION

Our results indicate that AMP grazing management practices in the Northern Great Plains promote overcompensation of aboveground plant biomass and litter mass when compared to their regional N-AMP counterparts. There was also no evidence that increased aboveground biomass within AMP systems came at the cost of reduced root biomass (Table 3-1; Figure 3-1), and instead, AMP ranches supported greater aboveground biomass per-unit root mass than N-AMP ranches. Moreover, increased aboveground biomass was associated with increased biomass removal in AMP ranches, in both absolute and relative amounts. There was no evidence these effects were isolated to a single plant group, and instead appear to be representative of the entire grassland plant community. We note that our study ranches have employed AMP grazing for at least one decade, such that species intolerant to these grazing practices may have been filtered out, consistent with prior findings of modest reductions in plant species diversity among these AMP ranches (Grenke et al., 2022).

Evidence for overcompensation in AMP systems

Proponents of AMP often suggest that AMP systems support higher livestock production by stimulating greater plant production (Teague et al., 2011). Our work here strongly supports this, as absolute total plant biomass production was higher in grasslands subject to AMP grazing compared to their paired neighbors. This contrasts with previous reviews of intensive rotational grazing systems (Briske et al., 2008; Hawkins 2017), which concluded that such systems support fewer or equivalent plant production compared to conventional systems. Interpretation of this lack of difference in plant productivity under AMP-type grazing has suggested that it is simply an ecological consequence of the reliance of aboveground production on belowground resource ‘banks’ (Briske et al., 2008). In other words, plant production increases only in the short term after grazing by drawing on resources stored belowground, which depletes belowground biomass and the capacity for future regrowth over time. However, our work examining grazing systems in place for a minimum of 10 years found increased aboveground biomass despite no negative impact on belowground plant biomass (albeit shallow) under AMP systems. Belowground biomass was instead influenced solely by landscape position, suggesting that micro-site factors are more important than grazing management for root development within these grasslands (Table 3-1). This suggests that while aboveground biomass responses within these grazed grasslands are controlled by top-down processes, belowground biomass responses are more strongly controlled by bottom-up ecological processes (i.e. microsite nutrients and resource availability; Mayel et al., 2021; Mohanbabu and Ritchie, 2021). Because belowground biomass frequently responds differently to grazing compared to aboveground biomass (Oñatibia et al., 2017) further research examining the mechanisms behind these differences is warranted. The need for a greater understanding of these differential responses is particularly urgent as the general sustainability of AMP-type systems will depend on the ability of plants to maintain belowground root mass.

The grazing lawn hypothesis originally developed by McNaughton (1984) may better explain these results. This hypothesis assumes that the carrying capacity of grasslands subject to specific grazing systems is dependent on the grazing animals themselves, specifically, that intensive grazing coupled with adequate recovery periods increases whole-plant net productivity (McNaughton 1984). These responses are generally thought to be possible where grazed systems are characterized by tall, un-grazed vegetation close to steady-state biomass (Frank et al., 2002; Ritchie and Penner, 2020). In such circumstances grazing lowers the plant-community-wide maintenance costs, allowing for new growth via negative density dependence (Ritchie and

Penner, 2020). This new growth is further supplemented by nutrient (N) mobilization (e.g. via trampling into the soil promoting mineralization) and this dynamic is presumably maintained due to extended recovery times in between grazing events, which allow enough time for the plant community to fully utilize these available nutrients in advance of the next seasonal grazing event (Frank et al., 2002; McNaughton 1984). The partial stimulation of aboveground biomass we found within AMP-managed grasslands agrees with this framework. As this work takes place in highly productive grasslands dominated by defoliation-tolerant introduced plant species, the potential for light limitation to limit productivity before grazing disturbance is high (Borer et al., 2014). Our work demonstrated higher litter mass in AMP grazing systems (Table 3-1) and greater evenness of forage use at elevated landscape positions in contrast to N-AMP systems (Appendix 3-S3). Under this whole-systems model, the increased amount of litter under AMP grazing may contribute to further primary plant productivity (Deutsch et al., 2010) by being trampled via high densities of livestock into the soil at greater rates and in a more uniform way across the landscape, thereby accelerating mineralization (Frank et al. 2002; McNaughton 1984). However, greater litter under AMP systems will also be a simple by-product of increased plant production. We highlight that as this is fundamentally an observational field study we call for further experimental work to test the mechanisms behind our findings, especially as late-season plant growth and re-growth were not examined.

Evidence for enhanced forage provisioning in AMP systems

AMP systems demonstrated greater absolute and relative plant biomass removal (Tables 3-3 & 3-4). As AMP managers in this region practice an earlier initial date of grazing compared to their N-AMP counterparts (21 days earlier on average, Bork et al., 2021), and our sampling was not standardized across recovery periods following a grazing event, these results are not surprising. Our work suggests the possibility that by initially grazing earlier in the season and providing extended recovery periods between grazing events, AMP managers can produce significantly more aboveground biomass compared to their N-AMP neighbors. Specifically, there was 75% greater plant biomass removed by livestock from grasslands in AMP ranches compared to N-AMP neighbors across our broader dataset, which was accompanied by longer recovery periods between grazing events. In agreement with the purported benefits of AMP impacts (Savory and Butterfield, 2016), the higher aboveground biomass found within AMP grazed systems appears to have been converted into feed for livestock, despite no differences in canopy cover or native/introduced and graminoid/forb cover (Table 3-1). This implies that the increased biomass removal under AMP-type systems was a function of greater aboveground biomass regardless of plant community identity. Notably, AMP ranches demonstrated greater aboveground biomass with equivalent total canopy cover to N-AMP ranches, suggesting greater densities (e.g., more vertical layers of vegetation) of plant community biomass may exist in grasslands managed with AMP grazing. This finding is also in agreement with McNaughton's (1976) hypothesis that dense grazing increases energy flows of grassland systems, permitting more aboveground biomass per unit area due to increased mobilization of nutrients. We note that this mechanism appears to be contingent on an earlier initial grazing date.

As expected, aboveground grassland biomass was strongly influenced by belowground biomass (Table 3-2). However, the influence of grazing system and the interaction of landscape position with belowground biomass were just as strong an influence on aboveground biomass (Table 3-2). This is most strikingly illustrated in Figure 3-4 where the landscape position of the lines between aboveground and belowground biomass remained constant between AMP and N-AMP systems. The relatively disjointed relationship between above and belowground biomass further outlined in the differing responses of the two factors to AMP grazing above speaks to the overriding influence of grazing system in regulating grassland production. Despite the key influence of high-intensity pulsed grazing under AMP management, the lack of stimulation in root biomass here under AMP grazing is in contrast to the whole-plant stimulation response found by Frank et al. (2002). In their examination of intensive migratory grazing within Yellowstone, Frank et al. (2002) found stimulation of both aboveground plant productivity and belowground roots, with root responses nearly seven times higher than aboveground responses. In contrast to the high belowground:aboveground biomass ratios of grasslands in Yellowstone National Park, the vegetation studied here is pre-dominantly introduced forage species with a smaller proportion of total biomass belowground; these baseline ecological differences likely account for these differing responses. We also note that our study of root biomass was limited to the topsoil (15 cm) only, leaving it unclear whether and how AMP systems may alter the mass of roots below this depth. Regional studies have found that deep and shallow root responses to simulated herbivory differ (Coupe et al., 2009), leaving open both the possibility that the whole-plant stimulation (i.e. Frank et al., 2002) is occurring at a larger scale, or that supplementation of aboveground biomass via depletion of root resources is occurring when taking the entire plant into account (Briske et al., 2008). Belowground biomass is relatively understudied compared to aboveground processes, and this work highlights the consequences of ignoring these factors despite their clear multi-trophic impacts.

Minimal impact of AMP systems on plant community composition

AMP management did not act as an ecological filter (eg. HilleRisLambers et al., 2012) to modify any measured aspect of plant community identity, including the contribution of different growth forms (graminoid/non-graminoid) and plants of contrasting origin (introduced/native;

Table 3-1). Though partially explained by the energy flow hypothesis of McNaughton (1976), this finding is surprising in the context of a growing understanding that AMP systems are most likely to exhibit sustainable ecological responses in highly productive, humid systems (Hawkins, 2017), including those dominated by introduced (e.g., grazing tolerant) forage species (Sollenberger et al., 2012). Key to consider is the observational nature of this work, which does not permit disentangling of extant species before grazing management initiation, and grazing management encouragement of certain (e.g., grazing adapted, including invasive) plant species. Most of the ranches studied here contained grassland communities dominated by introduced species regardless of management practice, which further limits our ability to parse apart species identity and AMP management effects on aboveground biomass.

A previous examination of these study sites found reduced site and landscape-level plant diversity across AMP as compared to N-AMP grazed grasslands, which further supports our findings that AMP systems correspond to low diversity systems dominated by a few highly productive forage species, and thus occur at the expense of more diverse, non-forage species (Grenke et al., 2022). As theoretical models of the influence of high-intensity grazing on aboveground biomass rely on intra-specific competition as a key mechanism regulating vegetation dynamics (Ritchie and Penner, 2020), establishing a mechanistic linkage between conspecific competition and aboveground processes is required within these grasslands.

AMP management differs from conventional management in two key aspects: 1) it involves highly responsive changes in management practices to changing operational circumstances (the “adaptive” component); and 2) it often is associated with higher stocking densities (Hawkins et al., 2017; Bork et al., 2021). These two factors are imbricate within an operational context, and historical efforts to examine the ecological consequences of AMP-type grazing have often confounded higher stocking densities with higher levels of managerial involvement (Briske et al., 2008). Recent studies using innovative methodologies to separate the two factors have found indications that each factor does indeed show distinct ecological consequences (Augustine et al., 2020; Derner et al., 2021; Venter et al., 2019 and 2021). The objective of this work was simply to provide an operational understanding of the ecological consequences of AMP grazing across grasslands of the Northern Great Plains. As such, future investigations are needed to further examine AMP impacts on the plant community over time because we are currently unable to determine whether AMP systems are equally successful when applied to areas already hosting highly productive forage species, or if they specifically promote such communities through their use.

CONCLUSIONS

We conclude that within grasslands of the Northern Great Plains, AMP grazing corresponds with higher aboveground biomass and litter. Coincident with AMP managers using an earlier initial grazing date, greater absolute and relative forage removal was observed with AMP grazing. Notably, greater levels of aboveground biomass within AMP systems compared to neighbor ranches did not correspond with differences in belowground biomass, which instead remained stable. We also found that AMP systems supported greater aboveground:belowground biomass ratios across all productivity levels compared to neighboring ranches. These results lend strong indirect support for the use of AMP grazing within the Northern Great Plains for grassland managers interested in maximizing forage production and use.

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Table 3-1. Response of plant biomass and cover to grazing management system and landscape position.

AMP/Non-AMP Status				
Effect	**Term**	**DF**	***F*-value**	***p*-value**
Aboveground				
	Status	**1**	**6.850**	**0.009**
	Landscape Position	2	0.159	0.853
	Status* Landscape Position	2	0.112	0.894
Belowground				
	Status	1	0.037	0.847
	Landscape Position	2	0.972	0.380
	Status* Landscape Position	2	0.153	0.858
Litter				
	Status	**1**	**4.231**	**0.041**
	Landscape Position	2	0.256	0.775
	Status* Landscape Position	**2**	**2.648**	**0.073**
Total % Plant Cover				
	Status	1	0.201	0.654
	Landscape Position	2	1.890	0.153
	Status* Landscape Position	2	0.556	0.574
Introduced Species Cover				
	Status	1	0.000	0.989
	Landscape Position	2	1.559	0.213
	Status* Landscape Position	2	0.726	0.485
Native Species Cover				
	Status	1	1.079	0.300
	Landscape Position	2	0.565	0.569
	Status* Landscape Position	2	0.013	0.987
Graminoid Cover				
	Status	1	0.005	0.942
	Landscape Position	2	1.397	0.249
	Status* Landscape	2	1.291	0.277

	Position			
Forb/Shrub Cover	**Status**	1	1.125	0.290
	Landscape Position	2	0.491	0.613
	Status* Landscape Position	**2**	**2.685**	**0.070**

Footnote: Degrees of freedom (DF), F-value, and p-value for terms within overall linear mixed models. Results of analysis testing for the effects of grazing system and landscape position on plant biomass and absolute and relative canopy cover of forage species. Grazing system and landscape position were included as fixed effects. Ranch identity and ranch identity nested within pair identity were included as random effects. Values in boldface represent significant differences ($p<0.1$).

Table 3-2. Test of aboveground biomass as a function of major hypothesized causal factors.

Aboveground Biomass ~ Belowground Biomass + Grazing System + Landscape Position			
Term	**DF**	***F*-value**	***p*-value**
Belowground Biomass	**1**	**3.648**	**0.057**
Status	**1**	**7.103**	**0.008**
Status*Belowground Biomass	1	0.551	0.459
Landscape Position	2	0.184	0.832
Landscape Position*Belowground Biomass	**2**	**4.894**	**0.008**

Footnote: Degrees of freedom (DF), F-value, Beta coefficients (ß) and p-values for terms within overall linear mixed models. Results of analysis testing for the effects of the interaction of grazing system with belowground biomass on aboveground biomass. Grazing system, belowground biomass, landscape position, and applicable interaction terms were included as fixed effects. Ranch identity and ranch identity nested within pair identity were included as random effects. Values in boldface represent significant differences ($p<0.1$).

Table 3-3. Test of biomass removed metrics as a function of grazing management system and landscape position.

Aboveground Biomass Removed ~ Grazing System + Landscape Position				
Effect	**Term**	**DF**	***F*-value**	***P*-value**
Magnitude Biomass Removed				
	Status	**1**	**6.811**	**0.010**
	Landscape Position	2	0.013	0.987
	Status* Landscape Position	**2**	**2.335**	**0.099**
Intensity Biomass Removed				
	Status	**1**	**7.352**	**0.007**
	Landscape Position	2	0.334	0.716
	Status* Landscape Position	**2**	**3.296**	**0.039**
Litter Mass Removed ~ Grazing System + Landscape Position				
Effect	**Term**	**DF**	***F*-value**	***P*-value**
Magnitude Mass Removed				
	Status	1	2.311	0.130
	Landscape Position	2	0.430	0.651
	Status* Landscape Position	**2**	**2.717**	**0.068**
Intensity Mass Removed				
	Status	1	0.049	0.826
	Landscape Position	2	0.656	0.520
	Status* Landscape Position	2	0.559	0.573
Belowground Biomass Removed ~ Grazing System + Landscape Position				
Effect	**Term**	**DF**	***F*-value**	***P*-value**
Magnitude Biomass Removed				
	Status	1	0.000	0.989
	Landscape Position	2	1.392	0.250

	Status* Landscape Position	2	0.428	0.652
Intensity Biomass Removed	**Status**	1	0.103	0.748
	Landscape Position	**2**	**2.622**	**0.075**
	Status* Landscape Position	2	1.245	0.290

Footnote: Degrees of freedom (DF), F-value, Beta coefficients (ß) and p-values for terms within overall linear mixed models. Results of analysis testing for the effects of grazing system and landscape position on plant biomass removed. Grazing system and landscape position were included as fixed effects. Ranch identity and ranch identity nested within pair identity were included as random effects. Sets of models were run for both overall intensity and magnitude of biomass removed. Values in boldface represent significant differences ($p<0.1$).

Table 3-4. Test of the ratio of native:introduced species canopy cover as a function of total plant canopy cover, aboveground biomass, litter mass, belowground biomass, and grazing management.

N:I ~ Total Canopy Cover + Grazing System + Total Canopy Cover*Grazing System			
Term	DF	*F*-value	*P*-value
Total Canopy Cover	1	0.210	0.647
Grazing System	1	1.181	0.278
Total Canopy Cover*Grazing System	1	0.729	0.394
N:I ~ Aboveground Biomass + Grazing System + Aboveground Biomass*Grazing System			
Term	DF	*F*-value	*P*-value
Aboveground Biomass	1	0.431	0.512
Grazing System	1	1.711	0.192
Aboveground Biomass*Grazing System	1	0.261	0.610
N:I ~ Litter + Grazing System + Litter*Grazing System			
Term	DF	*F*-value	*P*-value
Litter	**1**	**11.154**	**0.001**
Grazing System	**1**	**4.449**	**0.036**
Litter*Grazing System	**1**	**10.096**	**0.002**
N:I ~ Belowground biomass + Grazing System + Belowground biomass*Grazing System			
Term	DF	*F*-value	*P*-value
Belowground Biomass	1	0.012	0.914
Grazing System	1	0.969	0.326
Belowground biomass*Grazing System	1	2.578	0.110

Footnote: Degrees of freedom (DF), F-value, Beta coefficients (ß) and p-values for terms within overall linear mixed models. Values in boldface represent significant differences ($p<0.1$).

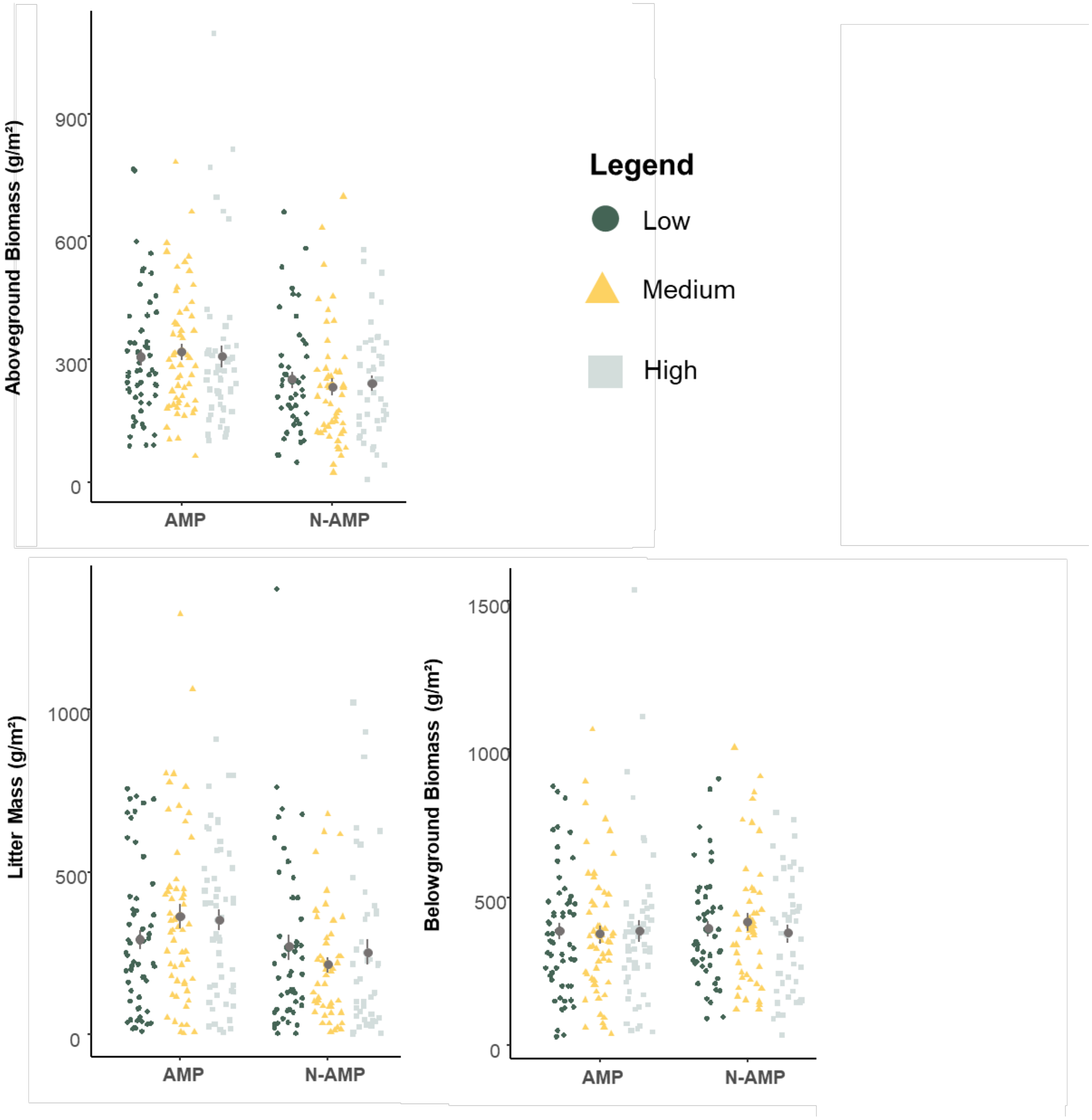

Figure 3-1. Summary figures showing aboveground biomass, litter mass, and belowground biomass as a function of grazing system and landscape position. Grey dots represent the mean and outer grey whiskers represent the mean standard error.

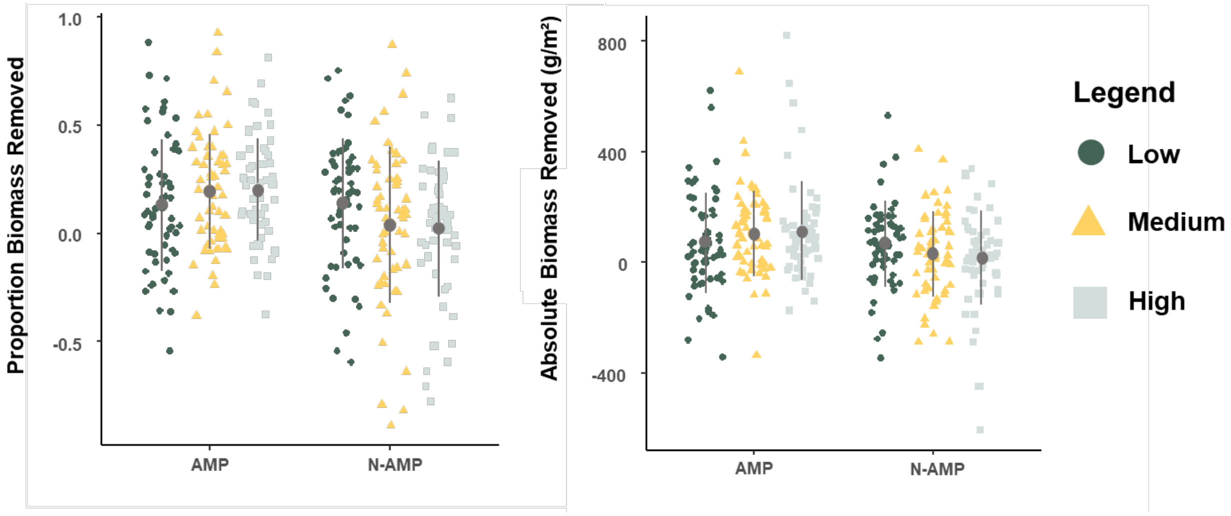

Figure 3-2. Summary figures of aboveground biomass removed by grazing as a function of grazing system and landscape position. The proportion of biomass removed (intensity) is the natural log of the non-excluded plot biomass over the excluded plot biomass multiplied by a negative one. Smaller values represent lesser intensities of biomass removal. Absolute biomass removed (magnitude) is the biomass of excluded plot less the biomass of the non-excluded plot. Small dots represent data derived from each plot. Grey dots represent the mean and outer grey whiskers represent the mean standard error.

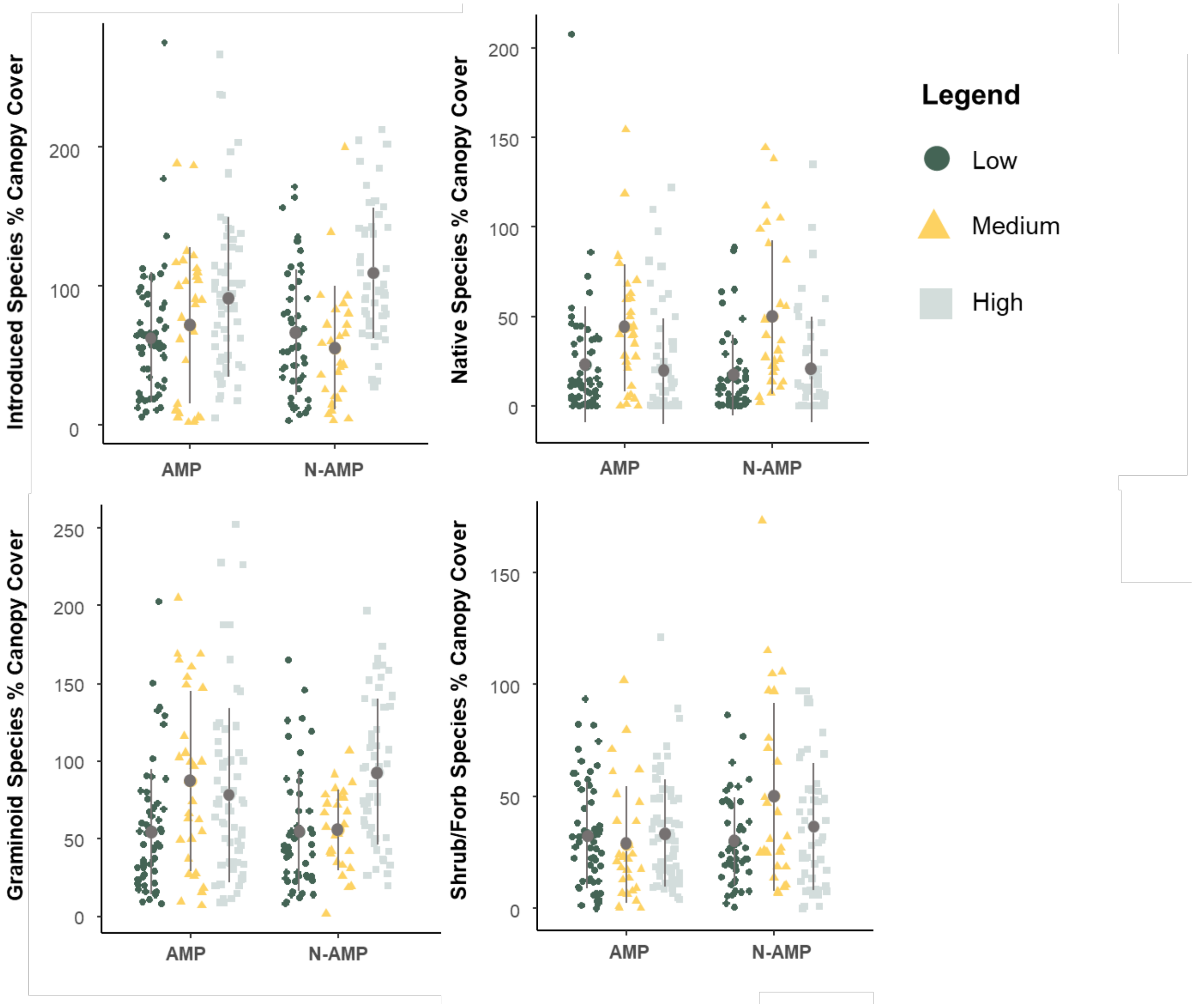

Figure 3-3. Summary figures of canopy cover forage species, non-forage species, and relative cover forage species as a function of grazing system and landscape position. Introduced, native, graminoid, and shrub/forb species were classified using the USDA Plants database. Small dots represent data derived from each plot. Grey dots represent the mean and outer grey whiskers represent the mean standard error.

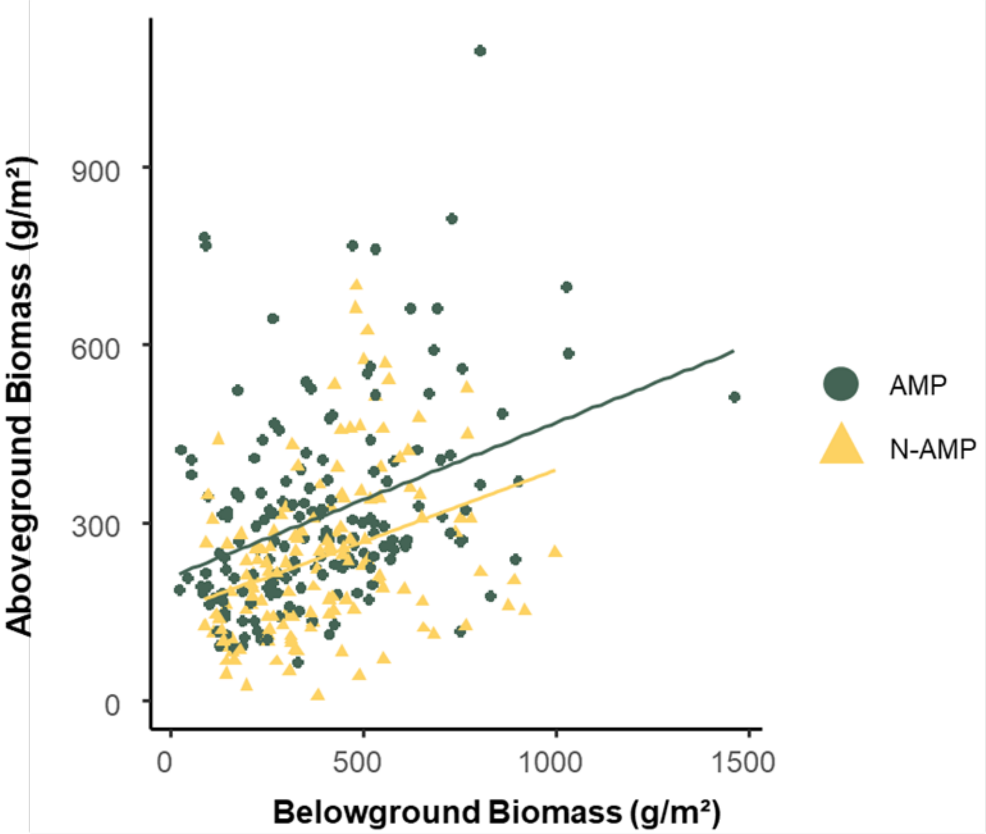

Figure 3-4. Scatterplot showing the relationship between aboveground biomass and belowground biomass per each plot. Each point represents data from an individual plot. The shape represents the grazing system of each sample. Trendline represents an exponential fit to overlaying all data.

Chapter 4: Proportion matters and pattern does not: Spatial placement of defoliation influences plant community production and structure

INTRODUCTION

Defoliation (the removal of plant tissue) is a primary mechanism governing plant performance and ecosystem functionality within grasslands (Liu et al., 2015; Lezama and Paruelo, 2016). Defoliation disturbances are highly variable in scale and location and are thus expected to modify plant competitive plant interactions by direct (changes to neighbor size) and indirect (changes to neighbors' ability to forage) avenues (Ferrero and Oesterheld, 2002; Yang et al., 2018; Zhang et al., 2022). However, the results of the interaction between defoliation and competition are highly unpredictable as positive, negative, and neutral consequences to plant community composition and structure have been observed (Hao and He, 2019; Stevens et al., 2020; Venter et al., 2021). Defoliated individuals are subject to the removal of nutrients, stored resources, and capacity for growth (Wang et al., 2021), all of which typically leads to a reduction in relative growth rate (Penner and Frank, 2021). However, plant responses to defoliation range from negative to positive and are complicated by the social context under which defoliation occurs (Song et al., 2020). In environments where the relative growth rate of the plant is limited by competition, defoliation of both the focal individual and its neighbor can modify these competitive constraints and allow for less competitively adapted traits to be expressed (Díaz et al., 2016). This release is associated with higher relative growth rates for the focal plant and potentially the entire plant community (Ritchie and Penner, 2020). In some cases, community-wide relative growth rates increase following defoliation to such an extent that production of the defoliated community is equivalent to or exceeds that of the undefoliated community (known as compensatory responses; McNaughton, 1976; Ramula et al., 2019).

Three generalized mechanisms mediate plant community responses to defoliation: (1) following defoliation, resources are freed to allow for the reallocation of energy from competitive strategies (i.e., exudate production) into strategies that maximize growth and fitness (Alward and Joern, 1993; Milchunas and Noy-Meir, 2002). (2) Competition and compensatory functions are unlikely to positively correlate as the resources associated with these strategies are often opposed, as demonstrated across various climates, species, and grazing histories (Järemo et al., 1996; Lennartsson et al., 2017; Peng et al., 2023). Thus, defoliation promotes compensatory strategies, which is expressed as (3) a higher community-wide relative growth rate that accumulates over the growing season such that the negative effect of defoliation on biomass is proportionally less than the actual biomass removed (Ferraro and Oesterheld, 2002; Hilbert et al., 1981).

It is important to note that the spatial placement of defoliation across a community creates vastly differing competitive arenas (Laca, 2000). Defoliation across natural landscapes is highly heterogenous (Adler and Lauenroth., 2001). Increasing the specificity of defoliation (i.e., single plant defoliation versus increasing patch size of defoliation) will likewise increase the average size inequality between neighbors within a community (Agrawal et al., 2006; Crawley and Weiner, 1991; Marquis, 1992). As size-asymmetry mediates the nature and outcomes of plant-plant interactions (Brown and Cahill Jr., 2022; Weiner, 1990), the spatial patchiness of defoliation may influence community-wide compensatory responses. Specifically, defoliated plants located closer to the edge of a defoliated patch would likely be subjected to greater competition for light and nutrients than plants located closer to the center of a defoliated patch ('border effect'; Semmartin and Oesterheld, 2001). This border effect would be expected to be most influential on total plant community production when the proportion of community defoliated is 50%. Additionally, since the border-to-area ratio of patches is greater in smaller patches, the border effect is expected to increase in importance with smaller patch sizes.

In this study, we disentangle the role of plant-plant interactions by controlling for species identity and traits as well as soil, nutrient, light, and water availability within and between mesocosms. We measured plant growth among individuals grown individually and with neighbors, subjected to several defoliation regimens. To assess the role of the proportion and patterning of defoliation on plant community biomass and structure, we designed a mesocosm experiment where ten graminoid species were subject to varying community-wide proportions (all or half defoliated) and patchiness (blocked or discrete defoliation) of defoliation. We conducted these defoliations at two intensities (high and low). With this approach, we address the following questions: Do the effects of defoliation intensity on plant community biomass, biomass evenness, and strength of competition vary in interaction with the: a) proportion and b) patterning of defoliation disturbances?

MATERIALS AND METHODS

Species selection

Graminoid species were exclusively used for this work as they account for the majority of locally adjacent grassland biomass (Lamb and Cahill Jr., 2008); as such, impacts to them will have the most significant impacts on the total system. In addition, species were selected to allow for equal representation of contrasting root structures (bunchgrass versus rhizomatous) and points of origin (introduced versus native), as mixtures of these traits are standard within naturalized grassland communities. Our ten selected species can be found in Appendix 4-S1. Seeds were sourced from Apache Seeds, Edmonton AB and Wild About Flowers, Okotoks AB.

Experimental design

Our experiment was located on the rooftop adjacent to the University of Alberta Biotron in Edmonton, Alberta, Canada. We applied two defoliation intensity treatments (i.e., high and low defoliation intensity), two proportions of defoliation treatments (uniform and half-defoliated), and three defoliation patterning treatments (i.e., random, blocked, and all, in increasing order of disturbed patch size) across 35 experimental mesocosms (Figure 4-1). We also grew plants alone in pots and subjected them to all three defoliation intensity treatments (i.e., high, low, and control) to observe the effects of treatments in the absence of neighbors and to derive a competition index. Pots and mesocosms were distributed using a randomized block design, with each of the five blocks containing one replication of each of the seven mesocosm treatments and 60 pots of the intensity single-plant treatment. (Figure 4-1). The experiment consisted of 35 mesocosms and 300 individually grown plants.

Planting

We sowed seeds into flats filled with potting soil (Pro-Mix Organic Moisture Mix) and germinated them in a greenhouse. Transplantation to mesocosms occurred once all species had grown several leaves, approximately ten days after germination. Seedlings were planted into each mesocosm and pot on June 1, 2019. Sown seedlings were randomly selected from among those that appeared healthy.

Mesocosm containers were rectangular plastic tubs (15.75 x 12.5 inches) filled with 6 inches of soil (1 : 2 ratio of topsoil : sand). First, we divided each mesocosm into twenty equally sized planting units (four rows of five planting units; Figure 4-1). Then, one of each (10) species was randomly placed within a lengthwise half (Figure 4-1; two adjacent lengthwise rows) of each mesocosm. This way, we could control for species identity throughout patchiness defoliation treatments.

Pots were 6 inches in diameter and filled with 6 inches of soil (1 : 2 ratio of topsoil : sand). Per block, we sowed six pots with one plant from each of the ten focal species (Figure 4-1). Within species, two pots per block were subject to each of the three defoliation treatments (i.e., high, low, and undefoliated). Species identity and defoliation treatment for each pot were randomly assigned within a block. As soil volume per plant varied between the pot and mesocosm treatments, we cannot compare the absolute sizes of plants between the two growing conditions. Instead, we assume that the underlying biological responses to treatments did not vary with access to soil volume and compare relative growth differences between treatments.

Defoliation

Defoliation treatments were imposed 45 days (July 15, 2019) after transplanting, representing the approximate midway point of the growing season. Due to increasing rates of plant growth throughout the growing season, the defoliated plants were small relative to their final biomass (average height at the time of clipping was 4.07 cm while the average height at harvest was 9.35 cm). All defoliated leaves were collected, dried, and weighed, allowing for subsequent measures of total shoot growth over the growing season.

High-intensity defoliation entailed defoliating the individual to 1 centimeter above the soil surface. Low-intensity defoliation entailed defoliating the individual to 4 centimeters above the soil surface. Clipping heights are proportionally equivalent to those used in local grassland studies and recommended local grazing management practices (Burkinshaw et al., 2009; White et al., 2014). Plants in the control defoliation treatment were not defoliated.

In both defoliation patterning treatments, one plant of each of the ten species (half the individuals per mesocosm) was cut, with the two treatments differing only in how the individual being cut was selected. The 'randomly' defoliated mesocosms comprised one of the two individuals of the ten species randomly selected for defoliation. In the 'blocked' defoliation treatment, we cut all individuals in the upper two rows and no individuals in the lower two rows (Figure 4-1).

To calculate the relative growth rate of plants, we measured the standing height of all plants (pots and mesocosms) after 14, 30, 60, and 90 days of growth post-transplanting. First, we harvested plants at the end of the growing season after 90 days of growth (September 2, 2019). Next, each plant was defoliated to the soil surface, dried at 70°C, and weighed. Finally, we measured belowground biomass by removing the sandy soil from around the roots, separating the twenty individuals, washing away the remaining soil, and then drying and weighing each root system. This complicated process was facilitated by overturning each mesocosm over a 2mm sieve to remove most of the soil and carefully disentangling root systems.

Total biomass was the sum of clipped, standing, and belowground biomass. Total aboveground biomass was the sum of biomass removed by defoliation and the standing aboveground biomass at harvest time. We calculated biomass measures for each plant (within mesocosms and in pots) and at the community level in each mesocosm (sum of all plants per mesocosm). Species evenness within each mesocosm was measured using Simpson's Index (Smith and Wilson, 1996), with higher values representing greater similarity in biomass production of each plant across the focal mesocosm.

Competition index

We measured the intensity of competition experienced by plants grown within a mesocosm environment using competitive response ratios (Weigelt and Jolliffe, 2003):

$$Competitive\ intensity\ =\ \ln(\mathrm{X_{NN}}/\mathrm{X_{WN}})$$

, where NN is the plant grown without neighbors, and WN is the plant grown with neighbors (Goldberg et al., 1999). Values above zero indicate net competition, and values below zero indicate net facilitation. Two methods were used to derive mesocosm-wide and species-specific competition indexes.

We calculated a mesocosm-wide competition index to measure the intensity of competition on mesocosm-wide production. In this case, WN represents the actual total biomass of each mesocosm, and NN consists of a dummy variable representing the total potential mesocosm biomass if all 20 plants grew in the absence of plant-plant interactions:

$$X_{NN} = \sum_{i=1}^{10} 2\bar{x}_{Species/Block}$$

To construct this, we summed the average biomass of plants grown alone (pots) per block per species multiplied by two (as there were two individuals per species per mesocosm) with equivalent defoliation intensities to the focal mesocosm (i.e., if the focal mesocosm was moderately clipped, we used moderately clipped individual plants).

Relative growth rate

We calculated the standardized rate of growth using the heights of each individual plant using the index of relative growth rate (Hunt, 1982):

$$Relative\ Growth\ Rate\ = \frac{\ln(H_2) - \ln(\ H_1)}{t_2 -\ t_1}$$

, where H2 and H1 are the individual plant heights at times t_2 and t_1. We calculated relative growth rates (RGR) over the entire growing season and between each sampling interval (i.e., between t_30 and t_14, between t_60 and t_30, et cetera). Mesocosm-wide measures for RGR were calculated by averaging the RGR for all plants within the respective mesocosm. Heights were used as a proxy for biomass production, as is common where destructive sampling would be logistically prohibitive (Oesterheld and McNaughton., 1991).

Data analysis

Do the effects of defoliation intensity on plant community biomass, biomass evenness, and strength of competition vary in interaction with the proportion of defoliation disturbances?

To determine whether the effects of defoliation intensity varied with the proportion of plant community defoliated, we used a series of linear mixed models (*nlme* package; Pinheiro J, Bates D, R Core Team 2022). The random and blocked patchiness treatments defoliated half (10 plants per mesocosm) of the plants per mesocosm, while the undefoliated and all treatments were equally imposed on each plant within the mesocosm. Thus, we considered the "all-defoliated" (all with undefoliated mesocosms as a control) and "half-defoliated" (random and blocked mesocosms) groups separately throughout analysis and visualization. In separate models, total biomass, aboveground biomass, belowground biomass, biomass evenness, and the competition index served as response variables, while defoliation intensity was the fixed effect. Block was included as a random factor in all models. A significant effect of defoliation intensity would indicate that the amount of biomass clipped influenced our respective response models. We then compared the consistency of responses to defoliation intensity between the half and all defoliated treatments.

We tested whether the effects of defoliation patterning interacted with defoliation intensity using the "half-defoliated" group (consisting of random and blocked patchiness treatments). In separate models, total biomass, aboveground biomass, belowground biomass, biomass evenness, and the competition index served as response variables with intensity, patchiness, and the intensity x patchiness interaction term included as fixed effects. Block was included as a random factor in all models.

We assessed the influence of defoliation intensity treatments on mesocosm-wide relative growth rate using two-way repeated measures ANOVA tests (*aov* function, R Core Team., 2022). We used a linear mixed model to assess for potential differences in relative growth rate between the defoliated and undefoliated individuals in interaction with patchiness treatments (random and blocked treatments only). The relative growth rate per plant was the response variable with defoliated status, patchiness, and the defoliated status x patchiness interaction term included as fixed effects. Block was included as a random factor.

RESULTS

Clipped biomass corresponded tightly with the relative intensity and proportion of community defoliated (Appendix 4-S2). The average biomass clipped per mesocosm was five times greater in the high-intensity treatment than in the low-intensity treatment (0.92 grams for the all-defoliated, high-intensity treatment to 0.18 grams for the blocked defoliated, low-intensity treatment). Average root-to-shoot ratios were close to 1 for all treatments (average ratio of 0.98).

Plant community responses to the proportion of community defoliated

Defoliation intensity had contrasting effects on mesocosm biomass dependent upon whether all or only half of the individuals were defoliated (Table 4-1; Figure 4-2). Within the "all-defoliated" mesocosms increasing intensity of defoliation reduced total mesocosm biomass, aboveground biomass, and belowground biomass (Figure 4-2b; Table 4-1) while also increasing the overall strength of competition (Figure 4-2b; Table 4-1). In contrast, when only half of the plants were defoliated, increased defoliation intensity caused mesocosm-wide increases in total, above, and belowground biomass (Figure 4-2a; Table 4-1) and was associated with decreased competition. Despite these impacts on overall biomass production, defoliation intensity did not affect species evenness in the full or half-defoliated mesocosm (Figure 4-3).

The relative growth rate increased between sampling intervals and throughout the growing season in "all-defoliated" ($F = 30.94$, $p = 0.028$) and "half-defoliated" mesocosms ($F = 3.37$, $p = 0.00004$). However, the relative growth rate did not vary with defoliation intensity for either the "all-defoliated" ($p = 0.17$) or "half-defoliated" ($p = 0.20$) mesocosms.

Mesocosm responses to the pattern of defoliation

In mesocosms where only half of the individuals were defoliated, we found no effects of the spatial pattern of defoliation as a main effect or in interaction with defoliation intensity for any of our measured response variables (Figure 4-2 and 4-4; Table 4-2). The strength of competition also varied with defoliation intensity alone but not with defoliation patchiness or the patchiness x intensity interaction term (Figure 4-2; Table 4-2). The evenness of mesocosm biomass did not differ among intensity treatments, patchiness treatments, or their interaction term (Figure 4-2; Table 4-2).

In patchy-defoliated mesocosms, undefoliated individuals showed significantly higher relative growth rates than their defoliated counterparts (Table 4-3). However, the patchiness treatment and the patchiness x defoliation status interaction did not significantly influence individual relative growth rates (Table 4-3).

DISCUSSION

In contrast to expectation, we found no impacts of defoliation patterning and unexpected interactions between the intensity and number of plants defoliated. Increased defoliation intensity negatively affected mesocosm production (total, above, and belowground) when all individuals were defoliated but positively affected production (total, above, and belowground) where half the mesocosm was defoliated (Table 4-1; Figure 4-2). An increase in production when half-defoliated mesocosms were defoliated with increasing intensity was found for aboveground, belowground, and total plant production (Table 4-1; Figure 4-2). Defoliation did not modify competition intensity within mesocosms where every individual was subject to the same disturbance conditions (all-defoliated; Table 4-1). However, when we defoliated half the individuals of each community, competition decreased with higher defoliation intensities of defoliation, even as community production increased (Tables 4-1 and 4-2). The relative growth rate did not change with defoliation intensity or patterning within the half-defoliated mesocosms but did increase at lower defoliation intensities within all-defoliated mesocosms (Tables 4-1 and 4-2). Even within half-defoliated mesocosms, defoliated individuals did not express a higher relative growth rate than their undefoliated counterparts (Table 4-3). Thus, we conclude that in half-defoliated mesocosms, increased defoliation intensities reduced the intensity of competition, thus allowing plants to reallocate resources for growth and promoting increased overall production. In all-defoliated mesocosms, increasing defoliation intensities did not impact competition but lowered the relative growth rate, reducing whole-plant production. Combined, we demonstrate that relatively modest changes to defoliation regimes alter the strength of plant competition, with impacts for over and under-compensation at the community level.

One of the intriguing results found here is that the overall strength of competition experienced within the mesocosms was contingent on the combination of defoliation intensity and the proportion of community defoliated. There are several possible mechanisms by which defoliation intensity and the proportion of plants defoliated can shift plant community responses along the compensation continuum. Prevailing understanding holds that the production consequences of defoliation are most commonly negative and increase in severity with increasing amounts of biomass removed. Compensatory abilities are expressed only where defoliation catalyzes conditions that support greater relative growth rates (Mueggler, 1967; Grime, 1977; Whittaker, 1979). These higher relative growth rates are commonly catalyzed by the defoliation-induced reduction in net plant community competition, which frees available resources from competitive strategies (i.e., exudate production) into strategies that maximize growth and fitness (Alward and Joern, 1993; Milchunas and Noy-Meir, 2002). Of our candidate mechanisms driving the defoliation–production relationship, only competition significantly varied within the half-defoliated mesocosms, and only the relative growth rate varied within our all-defoliated mesocosms (Tables 4-1 and 4-2). The all-defoliated mesocosms thus follow the classical relationship described above, where resources are more efficiently captured towards net biomass production without defoliation disturbances (Belsky, 1986; Ferraro and Oesterheld, 2002). Within the nutrient-limited mesocosm environment, it is unsurprising that increasing defoliation disturbances lowers possible biomass production as biomass loss lowers the community-wide capacity to use the resource pool (Wang et al., 2021).

These pathways point to competition as an overall limiting factor to growth within the half-defoliated mesocosms and resource availability as an overall limiting factor to growth within the all-defoliated mesocosms. The half-defoliated mesocosms follow a defoliation–production relationship indicative of compensatory responses to disturbance. Compensatory responses to defoliation occur when plant production is equivalent within defoliated and undefoliated circumstances (McNaughton, 1976). Half-defoliated mesocosms defoliated at high intensities showed equivalent production to entirely undefoliated mesocosms (Figure 4-2), likely due to the relaxation of competitive pressure at higher levels of defoliation (Trlica and Rittenhouse, 1993). As competition was constant among defoliation treatments, its importance within half-defoliated mesocosms must be due to size inequities introduced by these defoliation treatments, which occurred regardless of defoliation patterning.

The inverse relationship between competition and niche overlap is well-supported theoretically and empirically (Zuppinger-Dingley et al., 2014). Our mesocosm communities were selected to contain graminoid species with as widely varying functional traits and strategies as possible (Díaz et al., 2016). By introducing heterogeneous disturbance across an otherwise abiotically uniform environment, it is possible that the variety of ecological strategies within our mesocosm communities could be better expressed (Schwinning and Weiner, 1998). For example, a plant belonging to a species well-adapted to defoliation disturbances (i.e., forage species such as *Dactylis glomerata*) had a higher chance of being defoliated adjacent to an undefoliated plant whose species was well-adapted to nutrient-limited conditions in the absence of disturbance (i.e., native species such as *Boutaloua gracilis*; Cullen et al., 2006; Smith, 1998). When this circumstance occurred, both individuals could grow within their optimal realms of ecological strategy, take full advantage of their differentiating disturbance niches, and optimize community-wide resource use (Zuppinger-Dingley et al., 2014). As the inverse circumstance had an equal chance of occurrence (i.e., a defoliation-intolerant plant defoliated adjacent to a defoliation-tolerant plant), this hypothesis assumes the benefits of the former circumstance are more significant than the losses arising from the latter. In support of this hypothesis is that end-of-season production evenness was equivalent between the defoliation intensity and defoliation patchiness treatments, implying that treatment-induced community inequalities were negated within a fairly tight timeframe (Table 4-1; Figure 4-2). We call for further work that explicitly examines these mechanisms to clarify our findings.

We conclude that the effects of defoliation on plant community production, competition, and relative growth rates depend on the proportion, but not the patterning, of the plant community disturbed. When half of the plant community was defoliated, increasing defoliation intensity corresponded to lowered competition and increased whole-plant production. When all members of the plant community were defoliated, increasing defoliation intensity corresponded to a lowered relative growth rate and whole-plant production. The social context of the defoliation–production relationship is contingent on the equity of spatial disturbance distribution of disturbance. This is further evidence of the complexity of plant community responses to disturbance. Combined, we demonstrate that relatively modest changes to defoliation regimes alter the strength of plant competition, with impacts for over and under-compensation at the community level.

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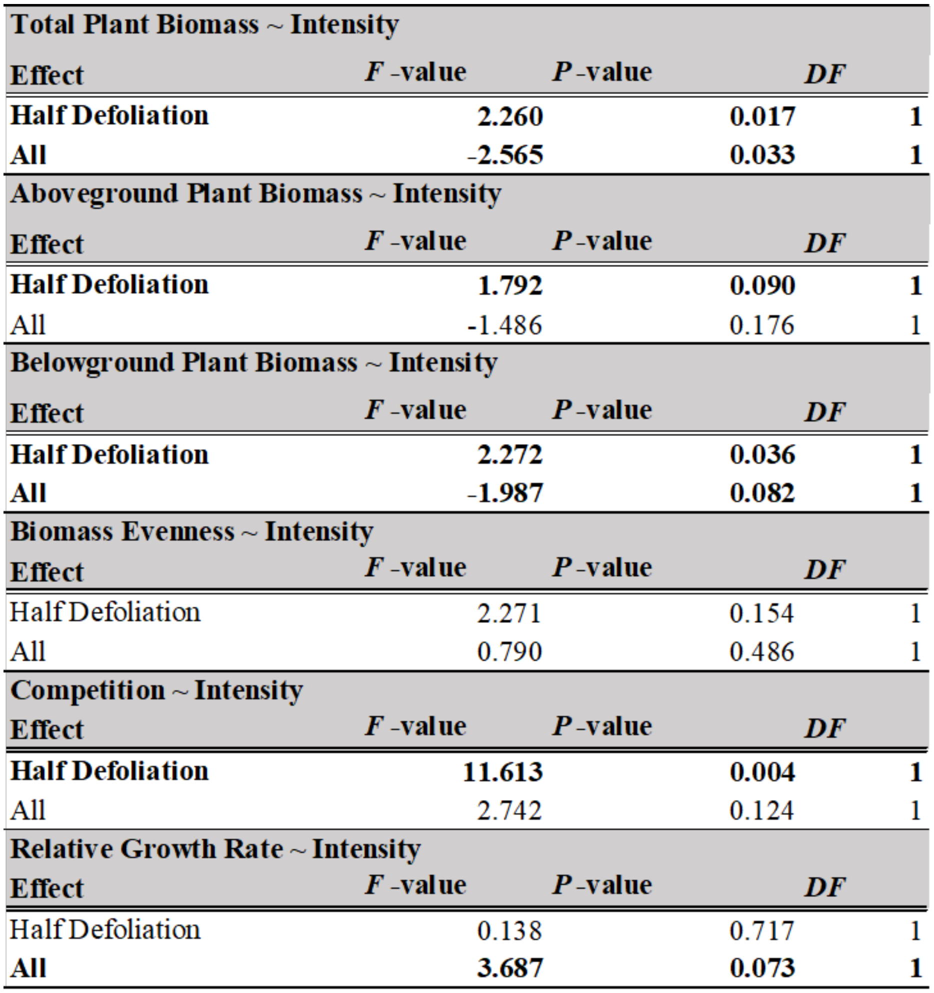
Table 4-1. Results of analysis testing for the effects of defoliation intensity on total mesocosm production, biomass evenness, competition, and relative growth rate. Separate analyses were conducted for mesocosms with half of all plants defoliated (half defoliation) and those where all plants in each mesocosm had equivalent treatment (all).



Total Plant Biomass ~ Intensity

Effect	*F* -value	*P* -value	*DF*
Half Defoliation	**2.260**	**0.017**	**1**
All	**-2.565**	**0.033**	**1**

Aboveground Plant Biomass ~ Intensity

Effect	*F* -value	*P* -value	*DF*
Half Defoliation	**1.792**	**0.090**	**1**
All	-1.486	0.176	1

Belowground Plant Biomass ~ Intensity

Effect	*F* -value	*P* -value	*DF*
Half Defoliation	**2.272**	**0.036**	**1**
All	**-1.987**	**0.082**	**1**

Biomass Evenness ~ Intensity

Effect	*F* -value	*P* -value	*DF*
Half Defoliation	2.271	0.154	1
All	0.790	0.486	1

Competition ~ Intensity

Effect	*F* -value	*P* -value	*DF*
Half Defoliation	**11.613**	**0.004**	**1**
All	2.742	0.124	1

Relative Growth Rate ~ Intensity

Effect	*F* -value	*P* -value	*DF*
Half Defoliation	0.138	0.717	1
All	**3.687**	**0.073**	**1**

Table 4-2. Results of analysis testing for the effects of defoliation intensity and spatial patterning on total mesocosm production, biomass evenness, competition, and relative growth rate. The analysis only includes mesocosms with half of all plants defoliated (half defoliation).

Total Mesocosm Biomass ~ Intensity + Patchiness			
Effect	***F*-value**	***P*-value**	***DF***
Intensity	**7.441**	**0.018**	**1**
Patchiness	0.367	0.556	1
Intensity*Patchiness	0.128	0.777	1

Aboveground Mesocosm Biomass ~ Intensity + Patchiness			
Effect	***F*-value**	***P*-value**	***DF***
Intensity	**3.092**	**0.098**	**1**
Patchiness	0.179	0.678	1
Intensity*Patchiness	1.150	0.300	1

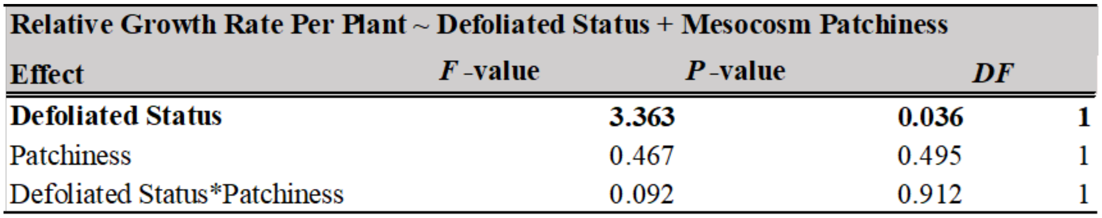
Belowground Mesocosm Biomass ~ Intensity + Patchiness			
Effect	***F*-value**	***P*-value**	***DF***
Intensity	**5.007**	**0.040**	**1**
Patchiness	1.317	0.268	1
Intensity*Patchiness	0.145	0.708	1

Biomass Evenness ~ Intensity + Patchiness			
Effect	***F*-value**	***P*-value**	***DF***
Intensity	2.096	0.167	1
Patchiness	0.312	0.584	1
Intensity*Patchiness	1.351	0.262	1

Competition ~ Intensity + Patchiness			
Effect	***F*-value**	***P*-value**	***DF***
Intensity	**10.935**	**0.006**	**1**
Patchiness	0.545	0.474	1
Intensity*Patchiness	0.405	0.537	1

Relative Growth Rate ~ Intensity + Patchiness			
Effect	***F*-value**	***P*-value**	***DF***
Intensity	0.118	0.739	1
Patchiness	0.261	0.621	1
Intensity*Patchiness	0.127	0.729	1

Table 4-3. Results of analysis testing for the effects of mesocosm-wide defoliation patchiness treatments and individual defoliated status on the whole-season relative growth rate for individual plants. Block was included as a random effect.



Relative Growth Rate Per Plant ~ Defoliated Status + Mesocosm Patchiness			
Effect	***F* -value**	***P* -value**	***DF***
Defoliated Status	**3.363**	**0.036**	**1**
Patchiness	0.467	0.495	1
Defoliated Status*Patchiness	0.092	0.912	1

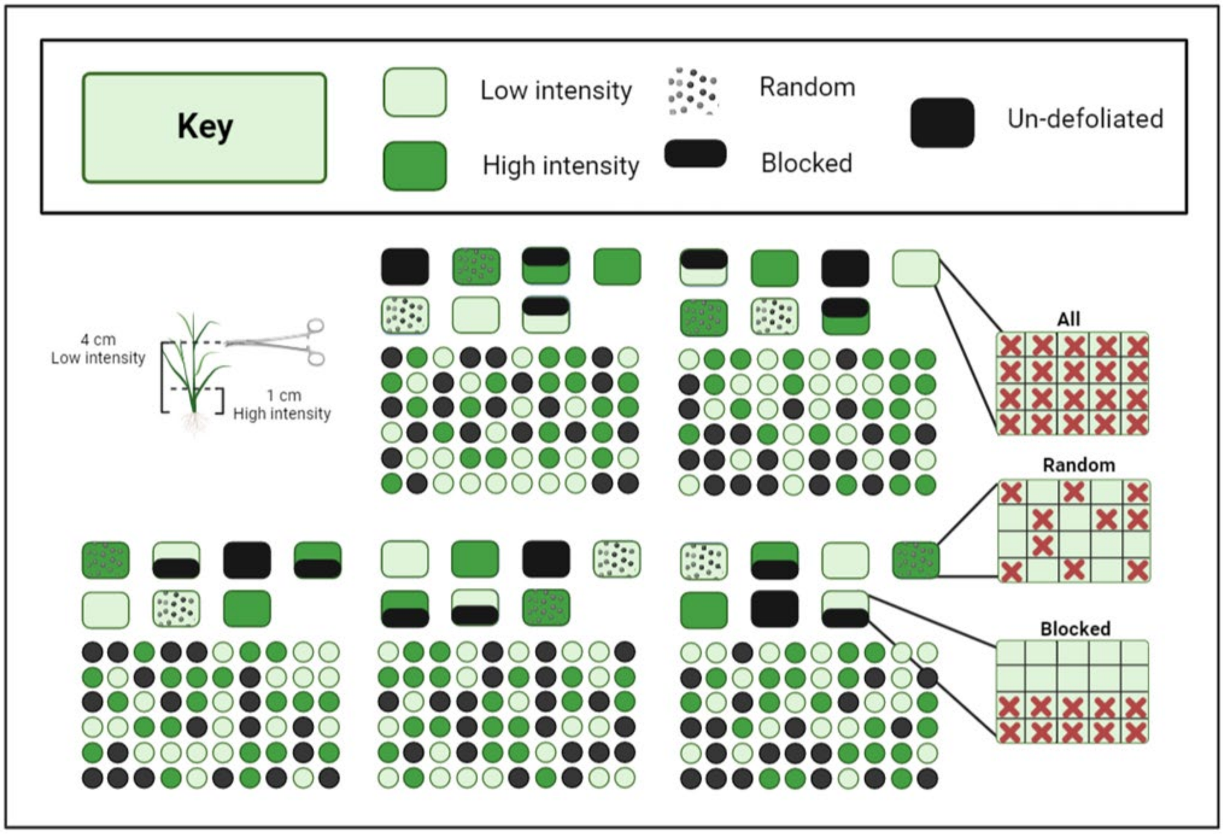
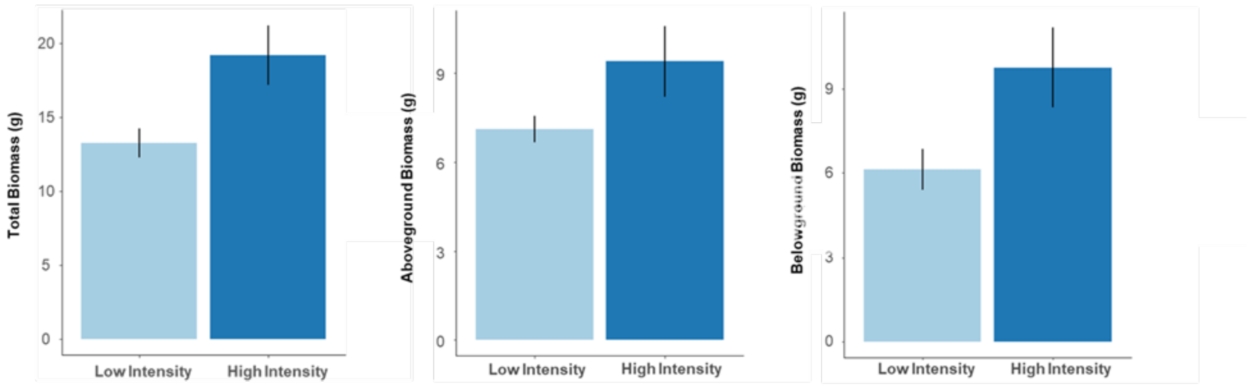
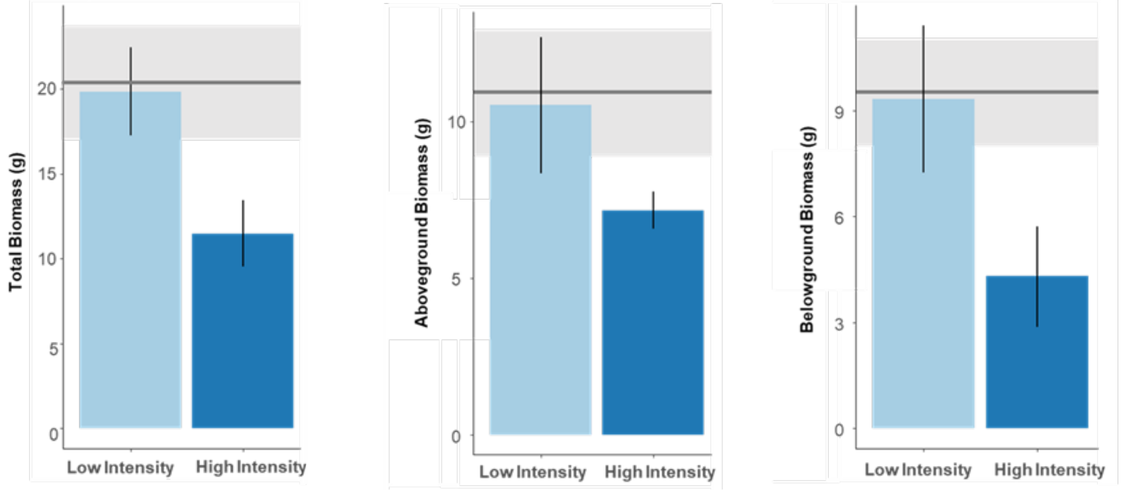


Figure 4-1. Schematic of experimental treatment design. Mesocosms (rectangles) were arranged in five blocks of seven mesocosms which were each assigned an intensity-patchiness treatment (intensity indicated by color: low, high, or undefoliated; patchiness indicated by pattern: random, blocked, or all). Patchiness treatments are shown in greater detail on the right. Each cross indicates the location of a defoliated individual plant. Each lengthwise half of the mesocosms contained one individual of each of the ten species (Appendix 4-S1) studied. Pots (circles) were arranged in five blocks of sixty pots each. Each pot was assigned an intensity treatment (intensity indicated by color: low, high, or undefoliated). Each pot contained one individual grass plant. Two pots for each of the ten species studied (Appendix 4-S1) were included at each treatment level per block.



a) Half-Defoliated



b) All-Defoliated

Figure 4-2. Effect of defoliation intensity on mesocosm biomass (total, aboveground, and belowground). Each bar represents the mean for each treatment. The error bars are the standard error for each treatment. Section a includes mesocosms where half of the individuals were defoliated, while section b includes mesocosms where each individual plant within the mesocosm was subject to identical defoliation treatments. The dark grey horizontal lines and lighter grey rectangles in section b represent the mean and standard error for undefoliated mesocosm treatments.

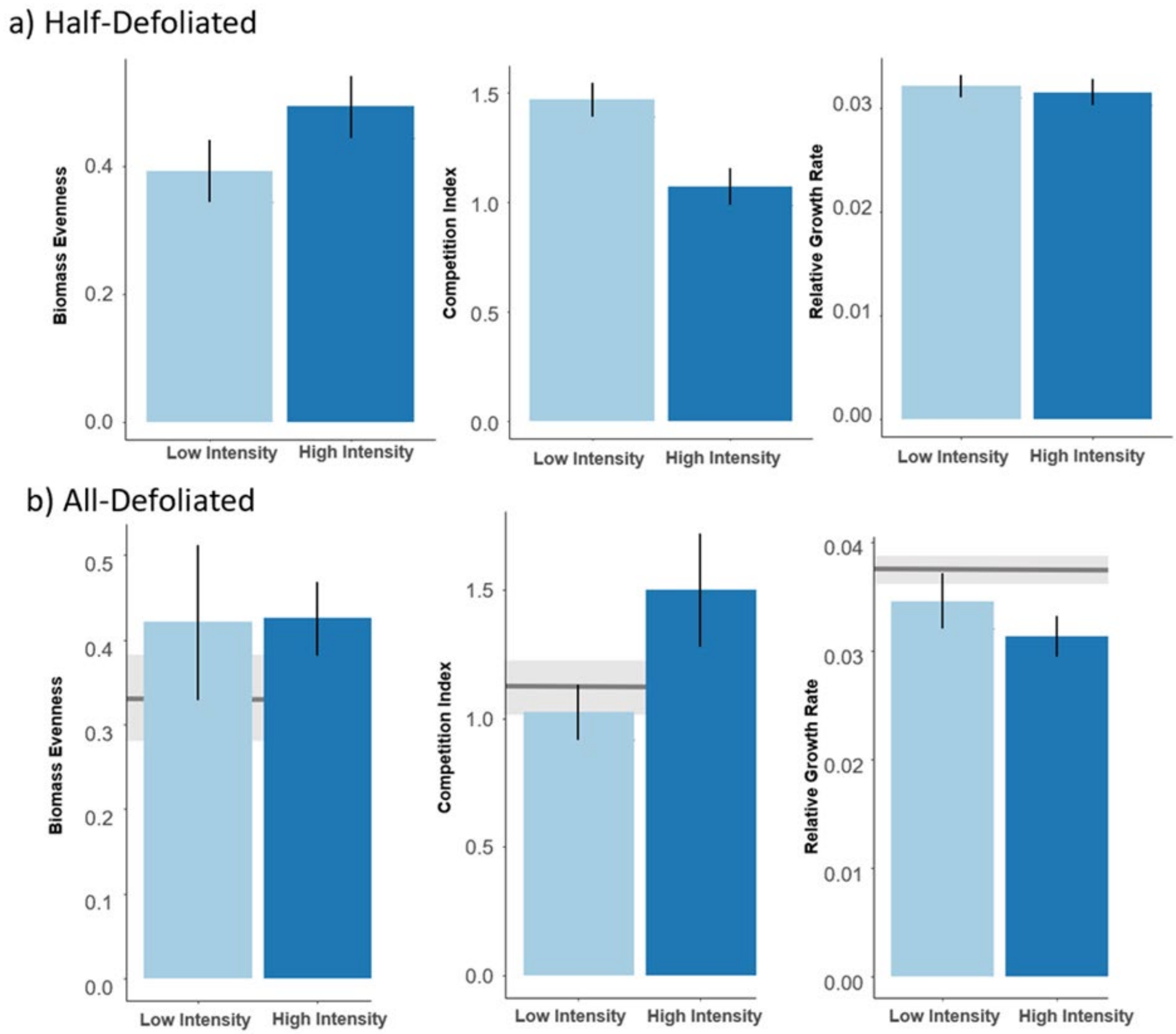


Figure 4-3. Effect of defoliation intensity on mesocosm biomass evenness, competition, and relative growth rate. Each bar represents the mean for each treatment. The error bars are the standard error for each treatment. Section a includes mesocosms where half of the individuals were defoliated, while section b includes mesocosms where each individual plant within the mesocosm was subject to identical defoliation treatments. The dark grey horizontal lines and lighter grey rectangles in section b represent the mean and standard error for undefoliated mesocosm treatments.

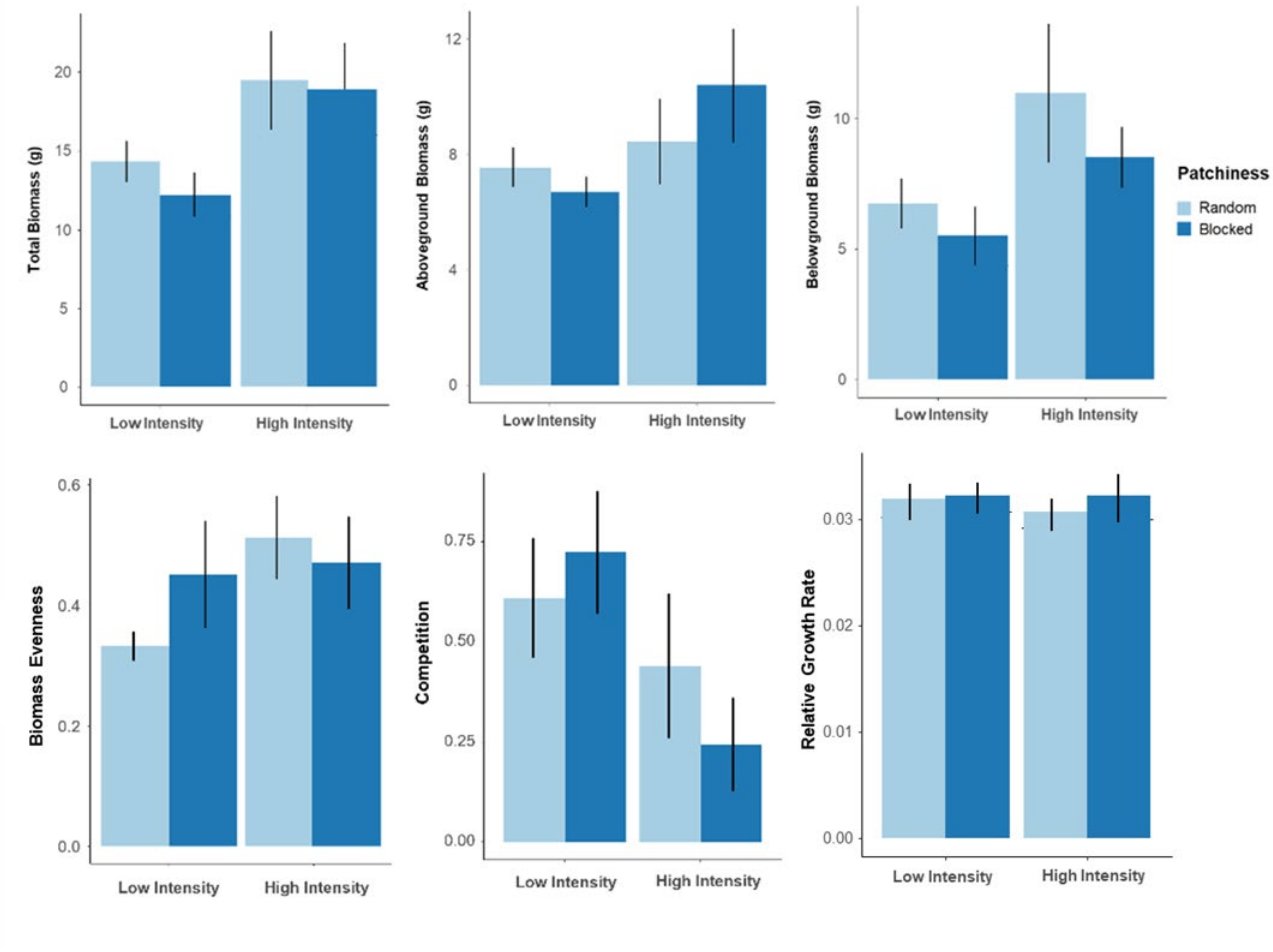


Figure 4-4. Effect of defoliation patchiness and intensity treatments on mesocosm biomass (total, aboveground, and belowground), biomass evenness, competition, and relative growth rate. Each bar represents the mean for each treatment. The error bars are the standard error for each treatment. Only mesocosms where half the individuals were defoliated are represented.

Chapter 5: Effects of grazing on plant abundance and richness are dependent on climate and weather

INTRODUCTION

Grazing is a spatially extensive land-use type, covering 40 million km² worldwide (Lambin and Meyfroidt, 2011). As grazed lands are often maintained within an unmodified state relative to other human land-uses, they provide a range of ecological goods and services (Hewins et al., 2018). Decades of research and millennia of cultural understanding provide clear evidence that grazing has massive potential to complement or hamper these ecological goods and services, which include carbon sequestration, water filtration, maintenance of multi-trophic biodiversity, provision of cultural-spiritual significance, and production of livestock products (Soussana et al., 2014; Herrero et al., 2011; Vågen and Winowiecki, 2013). As demand for livestock products is expected to double by 2050 (Scholes et al., 2018), understanding the circumstances under which grazing harms or supports the provision of these critical ecological goods and services are necessary to support the strategic development of sustainable grazing practices (Sollenberger, 2015).

Grazing most directly impacts plant communities by removing biomass and trampling (Huntly, 1991). The plant community is a crucial mediator of grazing effects on multiple trophic levels and most ecological goods and services (Petersen et al., 2004; Schon et al., 2011; Wilson et al., 1999). As such, the effects of grazing on plant community richness and abundance are well documented, with the established consensus holding that several key abiotic contingencies govern the plant community-grazing relationship (Olff and Ritchie, 1998). These core contingencies are broadly understood to include climate (Li et al., 2018; Wilcox et al., 2015), the endemic status of the grazing species (Bagchi and Ritchie, 2010; Milchunas et al., 1998; Ware et al., 2014), and study site (Briske et al., 2011). However, the identity (Bakker et al., 2006) and relative importance of these contingencies remain subject to debate (Price et al., 2022). Key to this discussion is determining the scale (in time and space) over which meaningful generalizations of the grazer-plant community relationship, and its relationship with climate, are defensible (Ritchie, 2009; Seabloom et al., 2021). Insights into how the study site location in time and space interacts with climate and weather during sampling will enhance our ability to manage these communities (Filazzola et al., 2020; Gao and Carmel, 2020a; Herrero-Jáuregui and Oesterheld, 2018).

The role of the site in mediating plant community responses to grazing is likely to be highly contingent on climate (Campbell et al., 2000; Allred et al., 2014). Plant community production on grazing lands is highly climate dependent, with precipitation and temperature linked strongly to plant community dynamics under grazed conditions (Ellis and Swift, 1988). In areas with climates highly conducive to plant growth (high precipitation and moderate temperatures), the intermediate disturbance hypothesis is well supported, suggesting that under such conditions, grazing suppresses the dominance of highly competitive species, allowing for community-wide diversity and production to increase (Gao and Carmel, 2020b). Climates supporting lower plant productivity generally show a stronger influence of precipitation variability on plant diversity and production then grazing (Olff and Ritchie, 1998). Climate variability is generally an essential driver of plant community dynamics as the absolute amount of precipitation, supported by non-equilibrium theories within rangeland ecology (Briske et al., 2003; Illius and O'Connor, 1999). As increased resources for plant growth allow for a more complete plant community recovery from grazing, areas with increased precipitation, lower temperatures, and low climatic variability show greater resilience to grazing disturbances (Milchunas et al., 1988). While the climate contingencies of the grazing - plant community relationship have been well established through global meta-analysis (e.g., Gao and Carmel, 2020a; Filazzola et al., 2020), the weather dependent nature of this relationship remains less understood. As grazing studies are typically of relatively short duration (predominantly five years or less; de Virgilio et al., 2019), and local variability of climate shows a significant role in plant community responses to grazing (Fuhlendorf et al., 2001), the role of weather at the time of data collection could be expected to strongly influence plant community responses to grazing exclusion across North America.

The role of grazer type in mediating grazing effects on plant communities likewise appears to be highly contingent on study site locationality. While domestic livestock and native herbivores share many traits, including preferences for consuming dominant graminoid species in grasslands (Allred et al., 2011; Kohl et al., 2013), they commonly exhibit several distinct differences in foraging behavior, which show strongly divergent consequences within the plant community. Domestic livestock graze non-grass forage more heavily than native grazers (Schwartz and Ellis, 1981; Van Yuren, 1984; Plumb and Dodd, 1993). As non-graminoid forage is often key to supporting plant community biodiversity, this increased pressure on non-graminoids can mean more severe grazing impacts on species richness within areas grazed by domestic grazers than native ones (Towne et al., 2005). Many landscapes posses a latent potential for increased species richness under grazing, with up to 86% increases in species richness recorded under the reintroduction of native herbivores, compared to an increase of 30% for domestic herbivores (Ratajczak et al., 2022). However, only a handful of studies have quantified the differences between domestic and introduced grazing species (i.e., Schwartz and Ellis, 1981; Van Yuren, 1984; Plumb and Dodd, 1993), with an accounting of their prospective influence on study results still poorly understood.

Here we use a meta-analysis to investigate how the location of sampling effort in time and space might modify the effect of grazing on plant community abundance and richness. We examined articles where grazing was excluded in North America and where the authors recorded vegetative community responses to this treatment. We then tested how the effect of grazing exclusion on these plant community variables varied with climate preceding sampling effort, year of sampling, ecoregion, and grazer status. We hypothesized that grazing exclusion would support greater plant community abundance and richness across North America due to the removal of biomass and nutrients from adjacent grazed areas and that drier and hotter conditions would increase the magnitude of this effect. We also hypothesized that the effect of grazing would be milder in unusually wet and cool years, where plant abundance and richness are expected to be high in both grazed and ungrazed plots. Conversely, in dry and hot years, grazing will have a larger effect because the plant community is more sensitive to plant removal from grazing. Finally, we hypothesized that studies occurring in ecosystems with extremes in precipitation and temperature would show greater sensitivity to grazing exclusion.

METHODS

Systematic review

We conducted a literature search within the Web of Science database. Our search was conducted on September 26, 2022 for all peer-reviewed articles published between 1900 and 2022. We selected articles based on location in North America, study design, and collection of plant response variables. Limiting site location to North America allowed us to capture a large amount of climatic variability while taking advantage of the similar continental biogeography, patterns of human colonization, and management practices of North America relative to the global context. An article was included if it recorded a quantitative plant response to grazing exclusion using exclusion equipment specific to that purpose (i.e., ' grazing exclosures'). As 'ungrazed' conditions often allow for herbivory of the site by non-target herbivores (i.e., wildlife grazing in pastures that are not livestock), we only included articles that specified 'exclusion' of grazing and/or lack of grazing access for all large herbivores. We used the following search to capture articles that compared plant responses between grazing excluded areas to those un-excluded: graz* OR livestock AND defol* OR intensity OR stubble OR gradient OR stocking rate OR exclusion OR exclude* OR ungrazed OR fallow* OR fence* OR pasture* OR field AND diversity OR richness OR community structure AND plant OR vegetation NOT aquatic OR marine OR lake OR algae OR mollusc OR wetland. This search initially did not discriminate based on location, among terrestrial herbivores, or grazing exclusion methods. Using these search terms, we identified 11,973 published articles. As sites outside North America were by far the greatest criteria for exclusion, these articles were individually screened by JG for identification of a site outside North America within the title. This effort resulted in a pool of 7,137 published articles subject to full-text screening by EH, BA, AD, and JG for the remaining criteria. During this stage, articles were only included if the article was available in English, original data were reported, the study site was located in North America, plant responses to grazing exclusion were recorded (including variances), and large herbivores implemented grazing. We were able to identify 106 studies that fulfilled these requirements. To ensure our criteria for inclusion were consistently applied and clear across the team, two individuals not involved with the initial screening validated a subset of the studies.

Data compilation

The 106 included articles were reviewed to determine the measured response variable, the data extraction year, and study site coordinates. We categorized plant response variables as either abundance or richness. To prevent pseudo replication, in cases where multiple levels of response variables were reported, we included only variables at the highest level (i.e., in lieu of including shrub and total biomass, only total biomass would be included). All original reported response variable categories can be found in Appendix 5-S1. The final 106 articles encompassed 336 unique comparisons. A unique comparison consisted of a unique study, unique study site, unique sampling year, and measured either abundance or richness. The location of each unique comparison was then assigned an ecoregion category using the EPA Ecoregion II classifications. Unique comparisons belonging to ecoregions with less than 5% representation within the broader dataset (n = 19) were removed from subsequent analysis to enable cross-ecoregion comparisons (resulting in 336 total unique comparisons). Plant abundance consisted of the majority of unique comparisons (n = 236) followed by richness (n = 81). Details of our workflow and rationale for the exclusion of each manuscript, including a PRISMA report, can be found in Appendix 5-S2, Appendix 5-S3, and Appendix 5-S4. We extracted the mean, standard deviation, and number of replicates for each comparison. In studies where raw data were provided, those statistics were derived. To compare responses to grazing by livestock identity, we grouped reported grazing species into livestock only, non-livestock, and both livestock/non-livestock categories.

Meta-analysis

We compared the effects of grazing exclusion on plant abundance and richness using the data extracted from relevant studies. The 336 comparisons were categorized based on the response variable (abundance or richness; Appendix 5-S1). To quantify differences between grazed and grazing-exclosed areas, we calculated the log-transformed ratio of means - LRR (Lajeunesse 2011; equation 1).

$$Log\ Tranformed\ Ratio\ of\ Means = \ln\left(\frac{\overline{X}_{\text{grazing non-excluded}}}{\overline{X}_{\text{grazing excluded}}}\right) \quad (1)$$

Equation 1 was used to calculate this metric for each unique comparison (function escalc, package metafor) (Viechtbauer 2010). Positive values of the LRR indicate that vegetation abundance or richness is decreased by grazing exclusion. Alternately, positive values indicate that livestock presence increases plant abundance or richness relative to an excluded site. Conversely, negative values of the LRR indicate that vegetation abundance or richness increase when grazing is excluded.

We used random models with effect size determined from each unique comparison to determine how the strength and direction of plant responses to herbivore exclusion changed across space, time, and climates. Separate analyses were run for the vegetation abundance (n = 236) and richness (n = 81) response data. Effect sizes were included as the response variable, with sampling variances included as the error term. To assess the influence of the study site ecoregion, the ecoregion as defined by EPA Level II was included as a fixed effect. In addition, we tested for the influence of year on sampling by likewise including this as a fixed effect.

We tested whether mean annual climate and inter-annual variations in climate mediated the vegetative response to herbivore exclusion by comparing effect sizes with mean annual temperature (MAT) and mean annual precipitation (MAP) as fixed effects. Using the spatial coordinates for each unique comparison, we extracted the MAT and MAP for the 30, 60, and 90 years preceding the year of sampling from the Climate NA database (Wang et al. 2016). MAP and MAT were selected as they are commonly used to predict plant community responses to grazing (Filazzola et al. 2020; Gao and Carmel 2020a; Herrero-Jáuregui & Oesterheld 2017). To further examine whether climate variability influenced vegetative responses to grazing exclusion, we derived the standard deviation for each MAT and MAP, then included those as fixed effects. Standard deviation was chosen as it is a fundamental measure of variability and was normally distributed.

Anomalous weather conditions during sampling might further be expected to drive the vegetative response to herbivore exclusion (Compagnoni et al. 2021). Thus, we also calculated the degree of an anomaly for MAT and MAP at the time of sampling using the method introduced by Compagnoni et al. (2021; equation 2).

$$AnomalityMAT30 = \frac{[MAT.sampling - \bar{x}(MAT30)]}{\sigma(MAT30)} \tag{2}$$

This equation assigns a standardized Z-score for the degree of either MAT or MAP anomaly. Thus, an anomaly of one entails that the weather metric at the time of sampling was one standard deviation above the reference mean. Anomalies for MAT and MAP were included as fixed effects with effect size as the response variable.

We generated funnel plots that compare the observed mean effect and standard error from a random effects model of grazing exclusion on plant abundance and richness. Study distribution of the abundance dataset was confirmed as random by a regression test for asymmetry (z = -0.078, p = 0.94), indicating no bias in study selection (Egger et al. 1997; Appendix 5-S5). The study distribution for the richness dataset displayed marginally random tendencies using a regression test for asymmetry (z = -2.11, p = 0.034), indicating potential asymmetry (Egger et al. 1997; Appendix 5-S6). As visual inspection revealed no categorically confounded outliers, we proceeded with further analysis (Appendix 5-S5 and Appendix 5-S6).

RESULTS

Patterns of grazing exclusion in North America

Grazing exclusion treatments were widely distributed across North America, with a slightly heavier presence in the west (Appendix 5-S7). This western bias is represented by the relatively high proportion of unique comparisons in the Great Plains ecoregion (41% abundance, 18% richness). North American deserts represented the next well-represented ecoregion across the entire dataset (22% abundance, 14% richness), followed by northwestern forested mountains (15% abundance, 17% richness), temperate sierras (10% abundance, 27% richness), eastern temperate forests (7% abundance), southern semi-arid highlands (6% abundance), and tropical dry forests (24% richness). Exclusion treatments were located across a wide variety of climates with mean annual temperatures ranging from 0°C to 23°C and mean annual precipitation ranging from 147 mm to 1564 mm.

The majority of unique comparisons took place in systems grazed exclusively by livestock (83% abundance, 76% richness), followed by both livestock/non-livestock (12% abundance, 18% richness) and non-livestock (5% abundance, 6% richness). Unique comparisons with only livestock identified as grazers were located in significantly warmer locations for both abundance (MAT 11°C versus 7°C) and richness (MAT 13°C versus 7°C) datasets. Sites with only non-livestock identified as grazers were located in areas with much greater mean annual precipitation for abundance (936 mm versus 533 mm) and richness (725 mm versus 524 mm) datasets.

Grazing effects by study locationality

Exclusion of grazing increased plant abundance (mean effect ± SE = 0.12 ± 0.03; t218 = 0.14, p < 0.0001; I2= 84.31%) and plant species richness (mean effect ± SE = 0.005 ± 0.03; t71 = 0.03, p < 0.0001; I2= 65.53%) across all unique comparisons. The year in which sampling took place significantly influenced the effect of grazing exclusion for abundance (mean effect ± SE = 0.01 ± 0.0006; p < 0.0001) but not species richness (mean effect ± SE = -0.0018 ± 0.0019; p = 0.35). The overall effect of grazing exclusion on plant community abundance decreased over time (Figure 5-1).

The effect of grazing exclusion was contingent on ecoregion for both plant abundance (I^2=81.65%, Qm=14.41, p = 0.013) and richness (I^2=59.71%, Qm=16.24, p = 0.003). Grazing exclusion effects for plant abundance were significantly different within the north American deserts (mean effect ± SE = -0.32 ± 0.15, p = 0.037) and southern semi-arid highlands (mean effect ± SE = -0.37 ± 0.18, p = 0.034) ecoregions. Compared to the remaining ecoregions with higher MAP, the effect size for abundance was markedly lower (Figure 5-2a). The effect of grazing exclusion on plant richness was significantly different for tropical dry forests (mean effect ± SE = -0.25 ± 0.08, p = 0.004) alone, with significantly lower effect sizes than remaining ecoregions (Figure 5-2b).

The reported grazer excluded from each treatment did not influence the effect of grazing exclusion on plant abundance (mean effect ± SE = 0.14 ± 0.2; t218 = 2.19, p = 0.33; I2= 84.04%) or plant species richness (mean effect ± SE = 0.03 ± 0.01; t71 = 3.72, p = 0.16; I2= 64.55%) (Figure 5-3).

Grazing effects by study climate

The effects of grazing exclusion on plant abundance were contingent on the mean annual temperature for the 30, 60, and 90 years preceding sampling (Table 5-1). Mean annual precipitation for the 30, 60, and 90 years prior to the sampling year did not influence the response of plant abundance to grazing exclusion (Table 5-1). The interaction of mean annual temperature with mean annual precipitation for the 30, 60, and 90 years preceding sampling likewise did not influence the effect of grazing exclusion on plant abundance (Table 5-1).

Plant species richness responses to grazing exclusion depended on mean annual temperature for the 30, 60, and 90 years preceding sampling (Table 5-1). Mean annual precipitation for the 30, 60, and 90 years preceding sampling also significantly influenced the species richness responses to grazing exclusion (Table 5-1). Neither the interaction of mean annual precipitation with mean annual temperature for the 30, 60, and 90 years prior to sampling significantly influenced the response of plant species richness to grazing exclusion (Table 5-1).

As the mean annual temperature increased, the overall effect of grazing exclusion on plant abundance increased (Figure 5-4a), while the effect of grazing exclusion on plant richness decreased (Figure 5-4b). This relationship indicates that grazing exclusion had a more negative effect on plant abundance at higher temperatures but a more negative effect on plant species richness at lower temperatures. The effect of grazing exclusion on plant species richness increased with mean annual precipitation (Figure 5-4b), indicating that grazing exclusion had less positive effects on plant species richness with increasing precipitation.

The degree of anomaly of the mean annual temperature at the time of sampling significantly influenced the effect of grazing exclusion on plant abundance (t218 = 0.13, p = 0.013) and species richness (t71 = 0.03, p = 0.064). However, the degree of anomaly for mean annual precipitation at the time of sampling did not influence the effect of grazing exclusion on plant abundance (t218 = 0.14, p = 0.46) or species richness (t71 = 0.03, p = 0.24).

As the degree of anomaly of mean annual temperature at the time of sampling increased, the effect of grazing exclusion on plant abundance (Figure 5-5a) and species richness (Figure 5-5b) decreased. This relationship indicates that sampling occurring during unusually cooler years corresponded with a less positive effect of grazing exclusion on plant abundance and species richness.

DISCUSSION

The presence of grazing significantly lowered plant community abundance and richness across North America. Across a broad spectrum of climates, we found that livestock versus non-livestock status did not significantly drive plant community responses to grazing (Figure 5-3). Mean annual temperature effects were equivalent regardless of the normal baseline considered (30 versus 60 versus 90 years). We found evidence that grazing exclusion had a less positive effect on plant abundance when temperatures were higher, while plant richness showed a less positive response to grazing exclusion when temperatures were lower. Plant richness, not plant abundance, responded to grazing exclusion differently depending on mean annual precipitation, with less positive effects of exclusion found when precipitation was higher.

We further observed that study locationality within time and space significantly changed the plant community response to grazing exclusion. More recent studies found increasingly neutral effects of grazing exclusion on plant community abundance but not species richness (Figure 5-1). Data collection within an unusually wet year detected less positive effects of grazing exclusion (Figure 5-5). Our results demonstrate that climate and weather drive the effects of grazing exclusion on plant communities and that these effects are growing more deleterious toward plant abundance over time.

Grazing effects and study locationality

Grazing exclusion research was predominantly located within the northern great plains and North American deserts. This was expected as these regions have a high ecological and social grazing footprint through a robust livestock industry (Hopton and White, 2012) and a high proportion of parks hosting native grazing species (Ibisch et al., 2016). Experimental sites were widely distributed across North America and were roughly proportional to the presence of grazing across the continent (Raynor et al., 2021). We suggest that biases in grazing exclusion studies relative to grazing distribution are slight across North America. Experimental sites were located over a range of climates representative of the climatic spectrum of grazed North America. The studies analyzed spanned regions with mean annual temperature differences of over 20°C and mean annual precipitation differences exceeding 1000 mm.

Livestock grazing is an economically and socially vital industry (Robinson et al., 2007; FAO, 2005). As such, it is not surprising that grazing research primarily considered the impacts of livestock as opposed to non-livestock or co-occurring non-livestock/livestock grazing. Non-livestock grazers were located primarily within the eastern half of the continent, accounting for the higher precipitation co-occurring at these experimental sites. Livestock grazing was also predominantly located within the Northern Great Plains and North American deserts, which likewise accounts for the higher temperatures associated with these sites. However, livestock/non-livestock status did not influence how plant community abundance or richness responded to grazing exclusion. This contrasts with recent (Pryke et al., 2016) and historical (Heitschmidt and Stuth, 1991; McNaughton, 1986; Schwartz and Ellis, 1981) work, which has outlined clear differences between the vegetative footprint of domestic and native herbivores. Native herbivores are thought to promote greater heterogeneity, and thus species richness; mechanically integrate standing vegetative biomass more thoroughly; and display greater selectivity of ingested forage (Schwartz and Ellis, 1981). Presumably, vegetation that has only recently experienced livestock-style grazing has had insufficient time to adapt to this distinct type of grazing and thus shows more marked effects of grazing than a native grazing species (Oesterheld and Semmartin, 2011). Our results and those of Gao and Carmel (2020a) point to an alternate hypothesis. The intense grazing practices of the previous century have likely created highly modified plant communities which are now homogenized in both community composition and response to grazing (Gao and Carmel, 2020a). This alternation of plant community composition would mask any pre-existing distinct effects of domestic versus wild grazing. The relative importance of the domestic versus wild grazer contingency has always been subject to debate, with many other regional factors, including vegetation type (Isbell and Wilsey, 2011), grazing intensity (Herrero-Jáuregui and Oesterheld, 2018), and climate (Díaz et al., 2007) frequently shown to exert equal or greater effects on varying scales.

Interaction of grazing, climate, and weather

Our results show that temperature is an important driver of plant community responses to grazing exclusion. However, plant species richness and abundance showed contrasting responses of effects to grazing disturbance across a temperature gradient (Figure 5-4). While richness showed more positive responses to grazing exclusion under cooler climates and more negative responses to grazing exclusion under warmer climates, the inverse relationship was true for plant abundance (Figure 5-4). We can thus conclude that the global trends of increasingly severe effects of grazing within arid climates (Gao and Carmel, 2020a) hold true for species richness only across the broad climatic gradient of North America. Previous models have held that high-stress environments correspond with intense effects of grazing disturbance as plant communities within such systems have traits that facilitate stress tolerance, not grazing disturbances (Grime, 1977; Oksanen et al., 1981). Our results provide nuance to this hypothesis by demonstrating that the directional response of the plant community to these disturbances varies when considering richness or abundance and extreme cold or extreme heat. Similar to Filazzola et al.'s (2020) findings at a global scale, plant richness responses to grazing exclusion were more negative within cooler climates. As cooler climates typically support fewer plant species than warmer climates (Gaston 2000), the absolute ability of grazing to lower richness is likely lower within cooler climates. Although not tested here, cooler climates typically have a shorter growing season and, thus, grazing season, which may protect against the sustained grazing pressures associated with large-scale plant community compositional changes (i.e., richness; Tubiello et al., 2007). We also note that grazing exclusion effects on species richness were strongly positive within the extremely warm tropical dry forests ecoregion in particular. Grazing practices within this region vary quite markedly from those within central North America (Gill, 2006; Stern et al., 2002) and are broadly recognized as having unusually severe effects on species diversity in part due to differing management goals (Quisehuatl-Medina et al., 2019). Further work examining the intent of grazing practices and a finer-scale consideration of management practices is necessary to further untangle these factors' role in mediating the grazing exclusion – temperature – plant diversity relationship across this region.

In contrast, the effects of grazing exclusion on plant abundance became less positive with increasingly cool climates. The shorter growing season, slower nutrient cycling, and reduced relative growth rate associated with cooler climate plant communities likely reduce plant community capacity to recover from grazing effects (Hou et al., 2020; Kreft and Jetz, 2007). Interestingly, grazing exclusion was most beneficial to plant abundance within the southern semi-arid highlands and the North American deserts, two ecoregions distinguished by unusually high variability of minimum intra-annual temperatures (NOAA., 2023). This suggests that climates with more erratic minimum temperatures support plant species with traits that are specialized to tolerate unpredictably cool conditions, at the expense of traits that allow for grazing tolerance. When taking the relative scarcity of resources available to support growth and, thus, recovery from grazing into additional account, it becomes apparent why such climates show high sensitivity to grazing effects (Cingolani et al., 2005).

The effects of grazing exclusion were precipitation contingent on plant species richness but not plant abundance (Figure 5-4). This work supports previous findings that climate is a strong driver of plant species richness compared with other variables (Milchunas et al., 1988; Olff and Ritchie, 1998; De Bello et al., 2007; Gao and Carmel, 2020a), though this effect may be contingent on grazing intensity (Herrero-Jáuregui and Oesterheld, 2018). This work provides further evidence that when sampling breadth is limited to an area of equivalent precipitation regimes, grazing exclusion effects will likely be limited to plant abundance (particularly in cooler areas). If sampling occurs across multiple climatic zones (across a meaningful spectrum of temperature and/or precipitation), grazing exclusion effects for species richness and abundance are likely to be detected. Our results align with the hypothesis describing the highly resource-limited nature of potentially successful plant traits (Díaz et al., 2007) and the role of precipitation as a pre-eminent and increasingly limiting resource for plant growth worldwide (Novick et al., 2016). Traits governing species presence do not necessarily correspond with species abundance (Cingolani et al., 2007). Our work suggests that plant traits that govern presence across a spectrum of precipitation are more closely tied to the ability to tolerate grazing than those traits governing abundance.

The effects of livestock exclusion on plant abundance and diversity were not only influenced by climate but were also contingent on anomalous weather conditions during sampling (Figure 5-5). Predictably, these contingencies were similar to the effects of climate with benefits of grazing as opposed to grazing exclusion apparent during anomalously cool years and grazing exclusion becoming increasingly beneficial to plant diversity and abundance during unusually warm years (Figure 5-5). However, weather-driven effects of grazing exclusion were limited to temperature only, with no differences in the effects of grazing exclusion as a function of anomality of precipitation apparent (Figure 5-5). As climate change will entail increasingly variable weather conditions (Ghahramani et al., 2019), our results indicate that detailed accounting for anomalous weather conditions at the time of sampling is needed to fully qualify the results of grazing exclusion studies. Not only was the magnitude of the effect contingent on anomalous weather, the plant community directional response to grazing exclusion varied with anomalous weather conditions. We call for a transparent and standardized method of reporting the degree of weather anomaly to be included in future grazing literature.

Interaction of grazing and year of study

Grazing exclusion showed universally positive effects on plant abundance (increasing by 12% on average) and species richness (0.5% on average). This supports previous work, which has found that grazing decreases diversity on a global scale and across multiple trophic levels (Filazzola et al., 2020; Gao and Carmel, 2020a; Herrero-Jáuregui and Oesterheld, 2018). However, the climate contingencies illustrated above are one example of how grazing may increase plant abundance and diversity under certain circumstances. A somewhat unexpected contingency we identified was the year of sampling itself. Over time, the effects of grazing exclosures on plant community abundance become more neutral (Figure 5-1a). Plant diversity responses to grazing exclusion did not vary with the year of sampling (Figure 5-1b). Several possibilities may explain this finding. First, the widespread degradation of grazed lands throughout the continent is well documented (Box, 1990). Though significant recovery has occurred, the original degradation of plant communities due to the introduction of invasive species, overgrazing, grazing during inappropriate seasons, and grazing in especially vulnerable ecosites (i.e., adjacent to riparian areas) has resulted in drastically altered plant communities (Smith et al., 2016; Ganjegunte et al., 2005; Belsky and Gelbard, 2000). Evidence indicates that pre-colonial native grasslands were well-adapted to the extensive grazing of native herbivores (McNaughton, 1984). Our results indicate that modern grazing practices fail to mimic that historical relationship.

Additionally, the widespread loss of grazing lands to intensive agriculture (i.e., crops) and urban development is in serious conflict with the rising global demand for livestock products (Davison et al., 2021; Oritz et al., 2021; Sala et al., 2000; Vitousek et al., 1997). This conflict results in an increasing necessity to increase the amount of product produced per unit area, which may entail increasingly intense grazing pressures (Beckmann et al., 2021). Though intensive grazing does not necessarily decrease plant diversity or abundance when applied inappropriately, it can accelerate degradation of grazed areas through loss of plant productivity, richness, soil erosion, and water cycling capabilities (Zhang et al., 2021). Therefore, increasing rates of grazing across North America are compatible with the increased benefits of grazing exclusion over time identified here (Figure 5-1).

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Table 5-1. The influence of mean annual temperature (MAT) and mean annual precipitation (MAP) on the effect of grazing exclusion on plant abundance and species richness (effect size). MAT and MAP and their interactive effect for the previous 30, 60, and 90 years were tested.

Abundance		
Effect Size ~ MAT		
Effect	***T***	***p*-value**
30 Year	0.13	0.03
60 Year	0.14	0.03
90 Year	0.14	0.03
Effect Size ~ MAP		
Effect	***T***	***p*-value**
30 Year	0.14	0.49
60 Year	0.14	0.32
90 Year	0.14	0.33
Effect Size ~ MAT*MAP		
Effect	***T***	***p*-value**
30 Year	0.14	0.25
60 Year	0.14	0.43
90 Year	0.14	0.48
Richness		
Effect Size ~ MAT		
Effect	***T***	***p*-value**

30 Year	0.03	0.0001
60 Year	0.03	0.0001
90 Year	0.03	0.0001

Effect Size ~ MAP

Effect	***T***	***p*-value**
30 Year	0.03	0.02
60 Year	0.03	0.03
90 Year	0.03	0.04

Effect Size ~ MAT*MAP

Effect	***T***	***p*-value**
30 Year	0.02	0.56
60 Year	0.02	0.60
90 Year	0.02	0.58

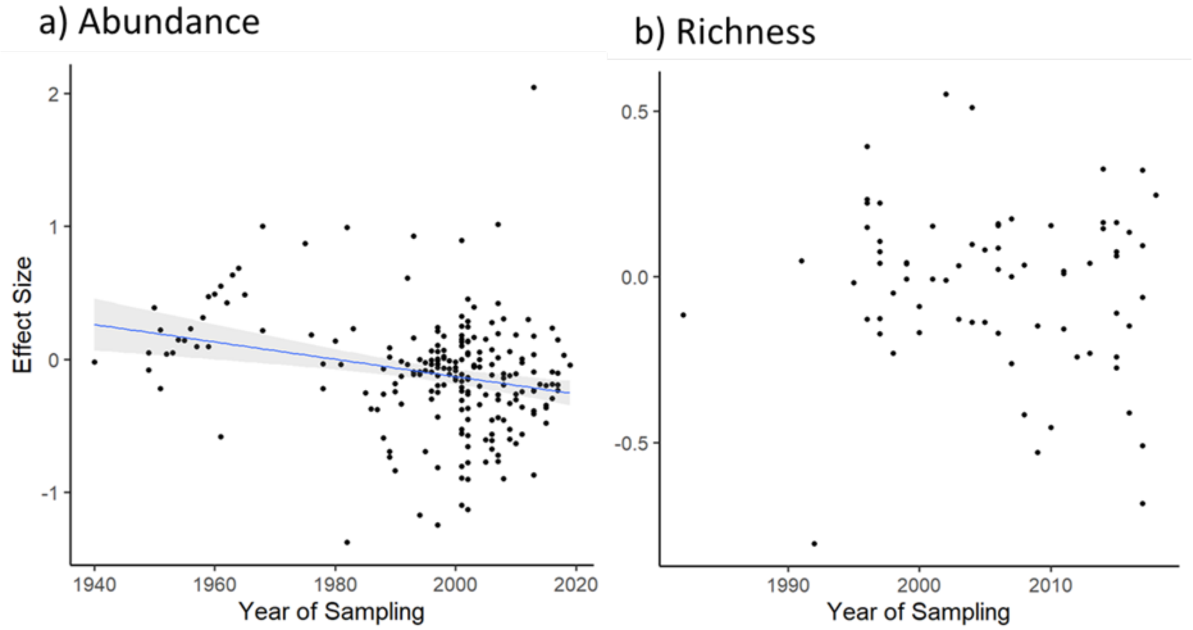


Figure 5-1. Effect sizes of grazing exclusion for plant abundance (a) and richness (b) over sampling year.

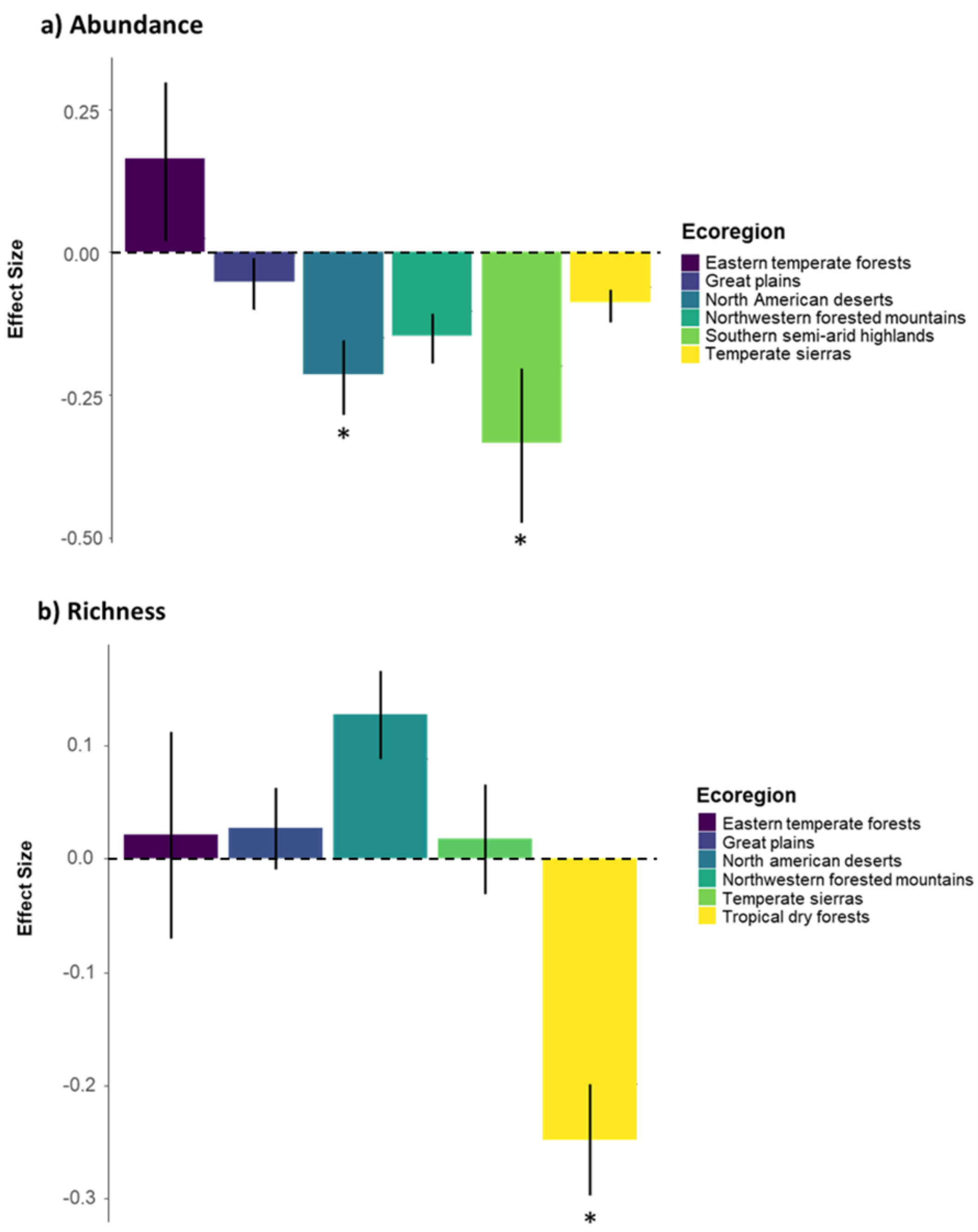


Figure 5-2. Effect sizes of grazing exclusion for plant abundance (a) and richness (b) for respective ecoregion. Mean effect sizes that are significantly different from zero are denoted by an asterisk (* < 0.05). Effect sizes below zero indicate grazing exclusion increased plant abundance (a) or richness (b). Effect sizes above zero indicate grazing exclusion decreased plant abundance (a) or richness (b).

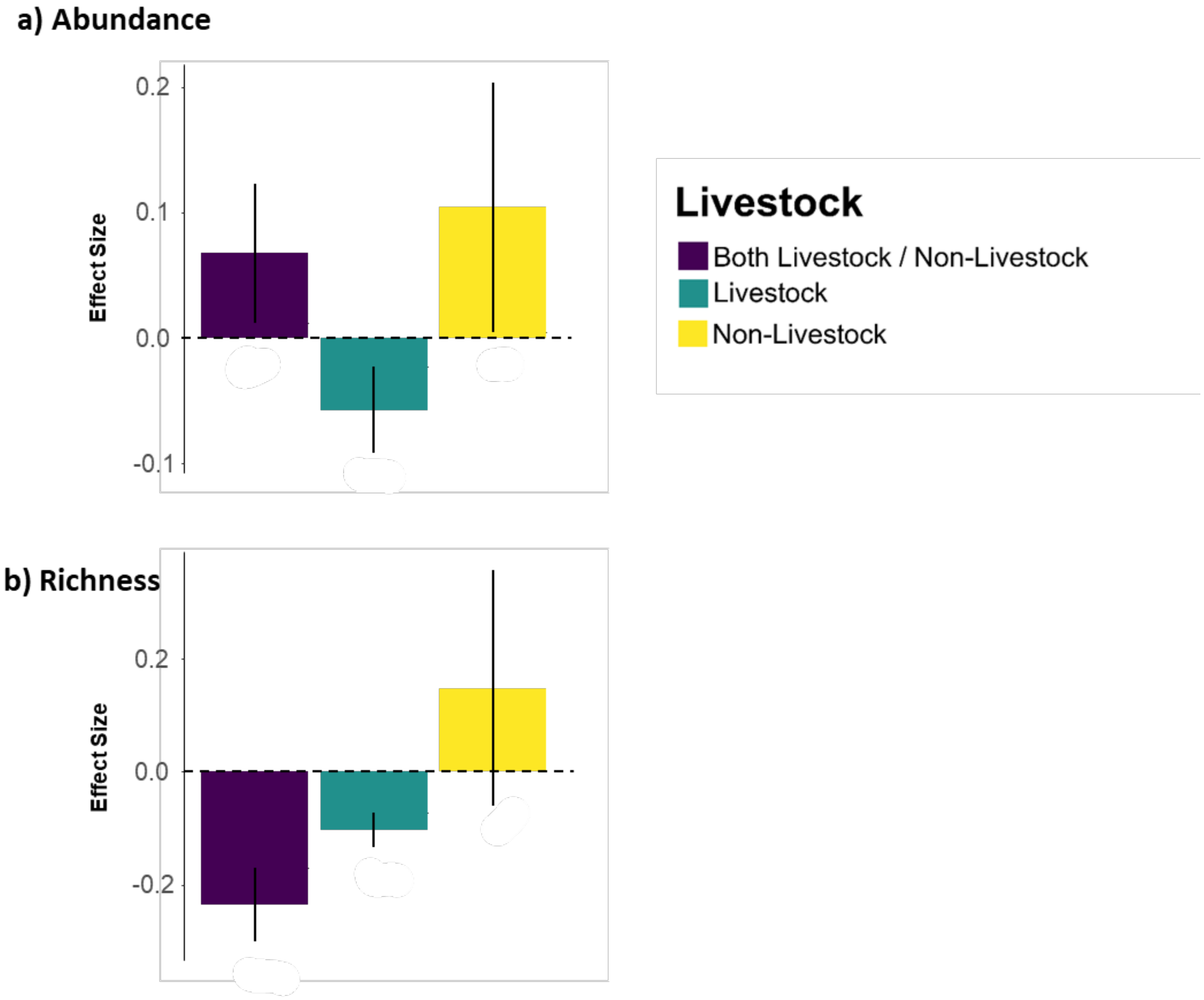
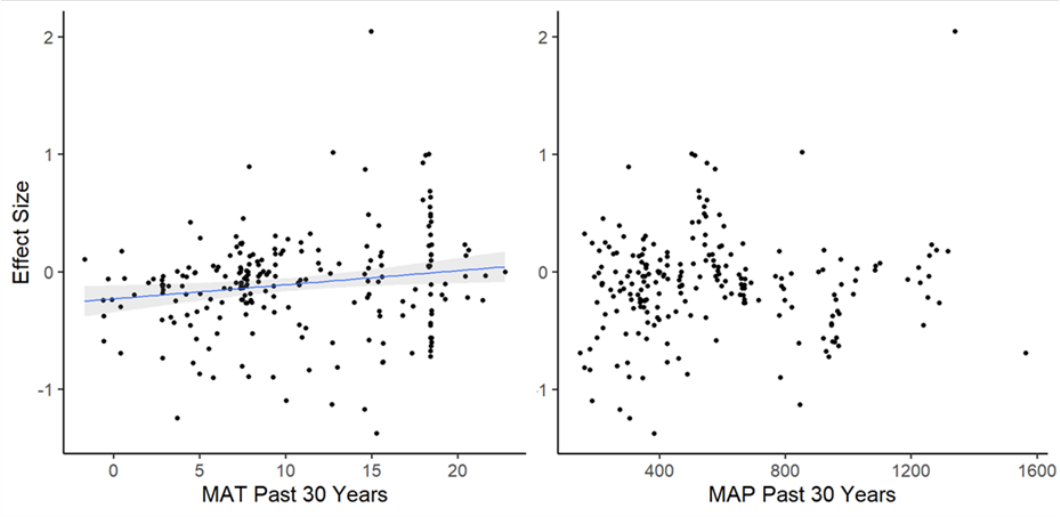


Figure 5-3. Effect sizes of grazing exclusion on plant abundance (a) and richness (b) for respective reported grazer types. No significant effect of grazer identity was found to influence the effects of grazing exclusion for plant abundance (a) or plant species richness (b). Effect sizes below zero indicate grazing exclusion increased plant abundance (a) or richness (b). Effect sizes above zero indicate grazing exclusion decreased plant abundance (a) or richness (b).

a) Abundance



b) Richness

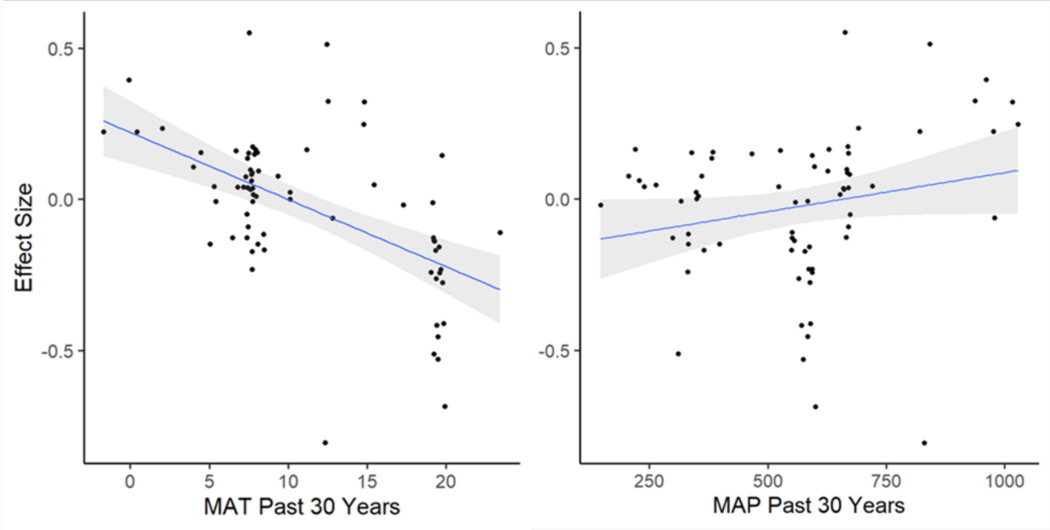
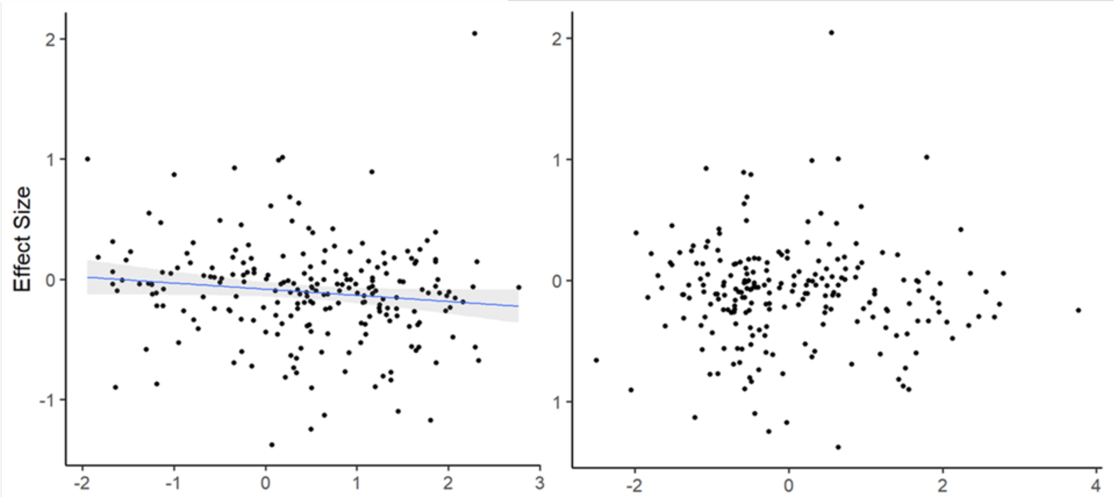


Figure 5-4. Effect sizes of grazing exclusion on plant abundance (a) and richness (b) across the spectrum of mean annual temperature (MAT) and mean annual precipitation (MAP) for the 30 years preceding sampling. Solid lines represent the linear regression model fit of MAT or MAP (where $p < 0.1$) on the effect size of grazing exclusion. Shaded areas represent 95% confidence intervals. Effect sizes below zero indicate grazing exclusion increased plant abundance (a) or richness (b). Effect sizes above zero indicate grazing exclusion decreased plant abundance (a) or richness (b).

a) Abundance



b) Richness

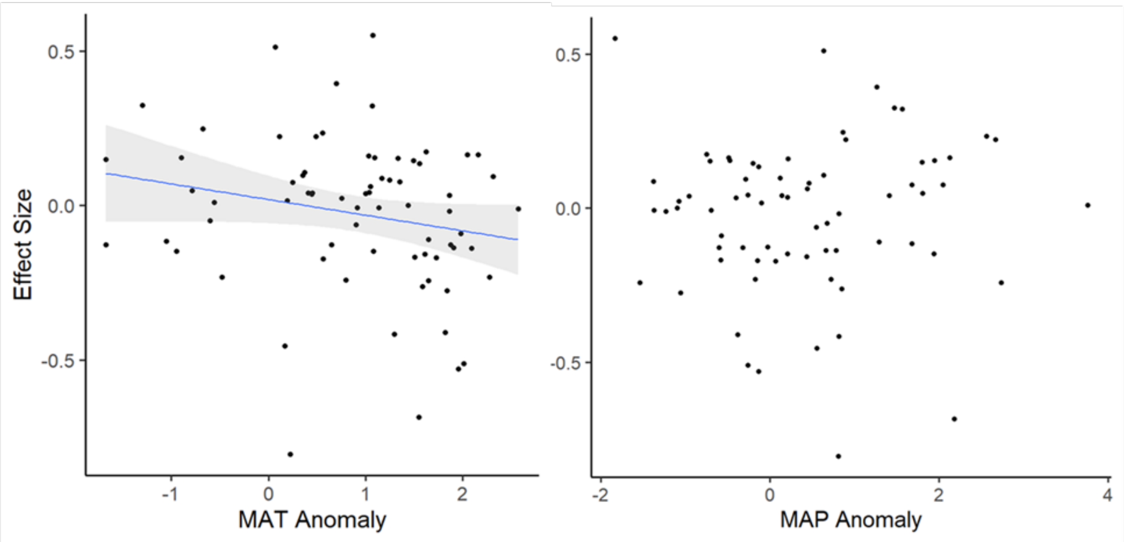


Figure 5-5. Effect sizes of grazing exclusion on plant abundance (a) and richness (b) across the spectrum of mean annual temperature (MAT) and mean annual precipitation (MAP) anomality for the 30 years preceding sampling. Solid lines represent the linear regression model fit of MAT or MAP (where $p < 0.1$) on the effect size of grazing exclusion. Shaded areas represent 95% confidence intervals. Effect sizes below zero indicate grazing exclusion increased plant abundance (a) or richness (b). Effect sizes above zero indicate grazing exclusion decreased plant abundance (a) or richness (b).

Chapter 6: General Discussion

This thesis's primary objective was to elucidate better the primary contingencies governing the defoliation–plant community relationship. Classical literature has emphasized the importance of the nature of defoliation (intensity, frequency, and duration), the role of plant-plant interactions, and climate, in particular (Bakker., 1998; Fuhlendorf and Engle, 2012; Fuhlendorf et al., 2001; Hutchings and Gordon, 2001; Jaramillo and Detling, 1988; Stoddard and Smith, 1955). Through this thesis, I advance this work by providing direct and indirect evidence that a localized understanding of the site is imperative to contextualize the effects of defoliation on plant diversity and production. In Chapters 2-3, I find that adaptable grazing management tailored to each site mimicked the grazing optimization hypothesis, with 20% higher aboveground biomass, 26% greater litter mass, no change in belowground biomass, and minimal reductions in local plant species richness, compared to regionally typical management. In Chapter 4, I find that small-scale variation in the proportion of community defoliated, but not defoliation patterning, influences whole community production and competition. In Chapter 5, I find that climate and weather preceding sampling effort of each site change the effects of grazing exclusion on plant community production and diversity. Chapter 5 introduces a new contingency to consider when qualifying the effects of defoliation: the year of sampling. More recent studies found increasingly positive effects of grazing exclusion on plant community abundance. In this general conclusion, I further summarize some of this thesis's most important findings.

Adaptive, high-intensity grazing management is associated with increased production and minimal loss of species diversity

Though grazing typically causes reductions in plant growth, understanding the unique circumstances under which grazing by vertebrates can increase community-level plant productivity has implications for both natural and managed ecosystems (Knapp et al., 2012; Mipam et al., 2019). A livestock management system characterized by highly adaptive and controlled grazing (hereafter Adaptive Multipaddock Grazing; AMP) may allow for increased plant biomass production with minimal changes to the plant community richness, following predictions of the grazing optimization hypothesis (Painter and Belsky, 1993; Stinner at al., 1997; Venter et al., 2021). Despite increasing popularity among livestock producers, understanding the whole-plant response to AMP under operational circumstances is still generally lacking (Briske et al., 2014). In Chapter 2, I demonstrate that there were fewer plant species in AMP grasslands at the plot and landscape scale compared to N-AMP ranches despite no overall difference in plant community composition. Management type did not alter the variability of plant community composition (beta diversity) or plot-level species evenness. Although there were trends for lower diversity of native and introduced species at both spatial scales, a significant effect was found only for native species at the landscape scale. Chapter 3 demonstrates that consistent with the grazing optimization hypothesis, grasslands exposed to AMP grazing had 20% higher aboveground biomass, 26% higher litter mass, and equivalent amounts of surface root biomass (15 cm depth) relative to conventionally managed grasslands. These findings show significant aboveground growth stimulation without apparent losses to supportive root tissues. This work also suggests that the increased aboveground biomass observed in AMP-grazed grasslands corresponded with greater biomass removed by livestock, both in absolute amounts and as proportional removal of available forage. Further, these growth responses were consistent across species types and did not vary among native/introduced species or graminoid/forbs. These results indicate that AMP grazing can potentially increase forage production in northern temperate grasslands and aligns with a growing body of evidence that such practices may be useful in achieving management goals. However, the impacts of AMP grazing system management included a minor reduction in plant diversity, with a modest decline in native species richness. We conclude that the benefits of AMP grazing in the northern Great Plains do not include the maintenance of plant diversity, and this system could hinder the conservation of remaining native plant species.

The results of Chapter 2 and 3 demonstrate that higher forage production, regardless of plant community identity, can be sustainably maintained by using AMP grazing management practices across the Northern Great Plains. As demand for livestock products increases even as the land-area needed to support this production decreases, there is increasing pressure for livestock managers to do more with less (Goldewijk et al., 2017; Turner et al., 2013). Where vascular plant diversity is of lower management priority then plant production, AMP management is one option for increasing ranch-wide efficiency.

Proportion matters and pattern does not: Spatial placement of defoliation influences plant community production and structure

Plant communities regularly encounter patchy defoliation, ranging in scale from selective defoliation of a single plant tissue to removing clustered groups of neighboring plants (Ferraro and Oesterheld, 2002; Parsons et al., 2000; Yang et al., 2018; Zhang et al., 2022). Patchy defoliation is expected to modify plant-plant interactions by direct (changes to neighbor size) and indirect (changes to neighbors' ability to forage) means (Adler and Lauenroth, 2001; Laca, 2000). However, though patchy defoliation is ubiquitous in natural communities, the consequences of this change to the social environment for the broader plant community have been given limited attention (Semmartin and Oesterheld, 2001). As the distribution of defoliation would be expected to modify plant-plant interactions and thus community-wide production, this literature gap is of concern. In Chapter 4, I find no changes in plant production or competition among neighbor plants as a function of the patterning of defoliation. However, defoliation intensity interacted with the proportion of community disturbed to influence whole-community production and competition in unexpected ways. Increased defoliation intensity negatively affected mesocosm production when all individuals were defoliated but positively affected production where half the mesocosm was defoliated. This defoliation-induced increase in production applied to aboveground, belowground, and total plant production, indicating it was not simply a growth reallocation response. Consistent with the growth responses, increased defoliation in the half-defoliated mesocosms caused a reduction in the overall strength of competition, while it did not alter competitive dynamics in the entirely defoliated treatment.

Effects of grazing on plant abundance and richness are dependent on climate and weather

The effects of grazing on plant community abundance and richness are globally important and are strongly dependent on precipitation and aridity (Ellis and Swift, 1988; Li et al., 2018; Wilcox et al., 2015). As climate change increases climate variability and the frequency of anomalous weather, understanding how the consequences of grazing on plant communities change with this changing climate is of high conservation concern (Briske et al., 2003; Gao and Carmel, 2020; Filazzola et al., 2020; Illius and O'Connor, 1999). In Chapter 5, I assess how the weather and climate preceding sampling effort mediate the effects of grazing exclusion on plant community abundance and diversity across North America. Grazing, regardless of the livestock status of the grazer, reduced plant abundance and species richness. Study location within time and space significantly changed the plant community response to grazing exclusion. More recent studies found increasingly positive effects of grazing exclusion on plant community abundance but not species richness. Grazing exclusion had a less positive effect on plant abundance when temperatures were higher, while plant richness showed a less positive response to grazing exclusion when temperatures were lower. Plant richness, not plant abundance, responded to grazing exclusion differently depending on mean annual precipitation, with less positive effects of exclusion found when precipitation was higher. Data collection within an unusually wet year detected less positive effects of grazing exclusion. These results demonstrate that climate and weather drive the effects of grazing exclusion on plant communities and that these effects are growing more deleterious toward plant abundance over time.

Synthesis and implications

Useful predictions outlining how defoliation will influence plant production, abundance, and diversity rely on the considered identification and integration of qualifying factors (McNaughton, 1983). Depending on the spatial and temporal scale of understanding needed, these contingencies are commonly understood to include climate, the nature of defoliation itself, and plant-plant interactions (Bakker., 1998; Fuhlendorf and Engle, 2012; Fuhlendorf et al., 2001; Hutchings and Gordon, 2001; Jaramillo and Detling, 1988; Stoddard and Smith, 1955). Overall, the results of this thesis provide a new understanding of the relevancy of these core contingencies across varying scales. Chapters 2-3 validate the usefulness of the grazing optimization hypothesis at a ranch-level scale across the Northern Great Plains of Canada. The production benefits of adaptive high-intensity, short-duration grazing management are marked and of high management interest, though this intensive grazing practice did not promote increased vascular plant species diversity. Further work is required to elucidate the mechanisms responsible for these findings on working landscapes. Chapter 4 sheds new light on the highly fine-scale defoliation-mediated plant-plant interactions responsible for community-wide changes in production. Overcompensation to defoliation was catalyzed by defoliating half the plant community to the point where the proportion of the community defoliated was more important than the amount of biomass removed in determining total community production. Finally, Chapter 5 expands upon the well-defined, critical role of climate in mediating the grazing–plant community relationship to include weather at the time of sampling and the year in which the research was conducted.

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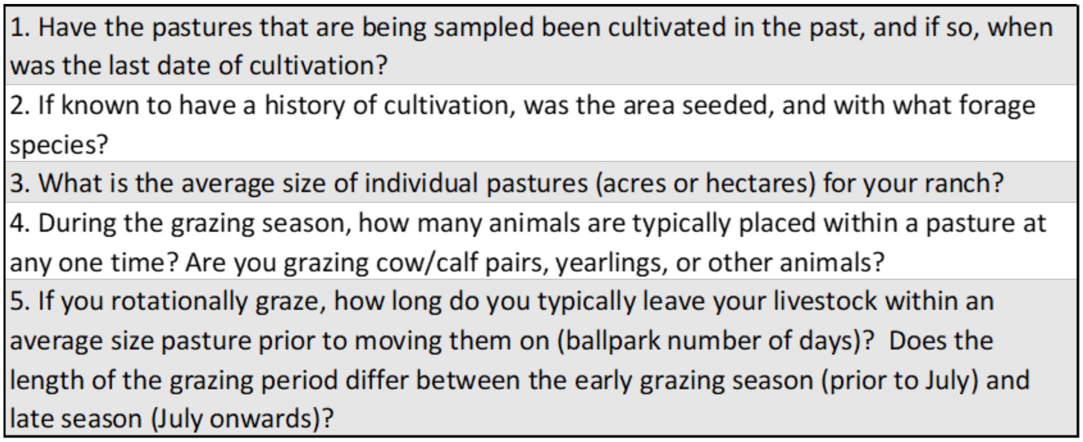
APPENDICES

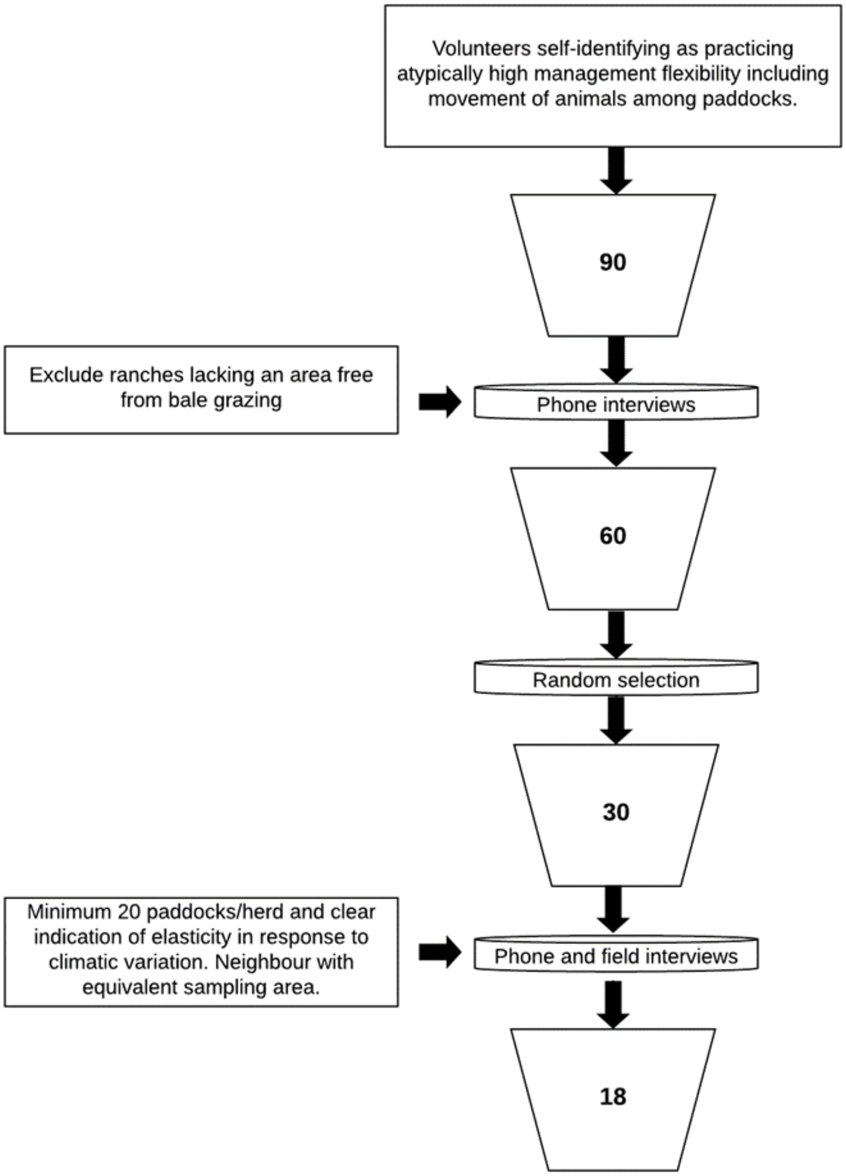
Appendix 2-S1. Inventory of vascular plant species identified on studied ranches. Binomial nomenclature follows the USDA plants database guidelines.

Specific Epithet	Status	Specific Epithet	Status	Specific Epithet	Status	Specific Epithet	Status	Specific Epithet	Status	Specific Epithet	Status	Specific Epithet	Status
*Achillea millefolium**	N	*Bouteloua gracilis*	N	*Echium vulgare*	I	*Hieracium albiflorum*	N	*Monardia fistulosa*	N	*Potentilla diversifolia*	N	*Sphenopholis obtusata*	N
Agoseris glauca	N	*Bromus carinatus*	N	*Elymus trachycaulus*	N	*Hieracium umbellatum*	I	*Moss*	N	*Potentilla norvegica*	B	*Sporobolus airoides*	N
Agopyrum dasystachyum	N	*Bromus ciliatus*	N	*Equisetum arvense*	N	*Hordeum jubatum*	N	*Onobrychis vicifolia*	I	*Potentilla recta*	I	*Sporobolus cryptandrus*	N
Agropyron cristatum	I	*Bromus commutata*	N	*Equisetum hymale*	N	*Juncus sp.*	N	*Opuntia polyacantha*	N	*Prunus sp.*	N	*Stanleya pinnata*	N
Agrostis scabra	N	*Bromus inermis**	I	*Equisetum sylvaticum*	N	*Juniperus horizontalus*	N	*Oxytropis deflexa*	N	*Ranunculus acris*	I	*Stellaria media*	I
Aprogropyron spicatum	N	*Bromus japonicus*	I	*Erigeron caespitosus*	N	*Koeleria macrantha*	N	*Oxytropis monticola*	N	*Ratibida columnifera*	N	*Stipa viridula*	N
Agrostis stolonifera	I	*Bromus subsecumdum*	I	*Erigeron philadelphicus*	N	*Lathyrus ochroleucus*	N	*Oxytropis sericea*	N	*Rosa sp.*	N	*Symphoricarpos albus*	N
Agropyron trachycaulum	N	*Bromus tectorum*	I	*Erigeron pumilus*	N	*Lathyrus purpurea*	N	*Pascopyrum smithii*	N	*Rubus chamaemorus*	N	*Symphoricarpos occidentalis*	N
Allium textile	N	*Calamovilfa longifolia*	N	*Erysimum cheiranthoides*	I	*Lathyrus venosus*	N	*Petasites palmatus*	N	*Rubus idaeus*	N	*Tanacetum vulgare*	I
Allium schoenoprasum	N	*Calamagrostis rubescens*	N	*Euphorbia esula*	I	*Leuecanthemum vulgare*	I	*Petasites sagittatus*	N	*Rudbeckia hirsuta*	N	*Taraxacum officinale*	I
Alopecurus pratensis	I	*Campanula rotundifolia*	N	*Festuca elatior*	I	*Liatrus punctata*	N	*Phalaris arundinacea*	N	*Rumx crispus*	I	*Thalictrum venulosum*	N
Amaranthus californicus	N	*Capsella bursa*	I	*Festuca rubra*	N	*Linum lewisii*	N	*Phleum pratense*	I	*Salsola iberica*	I	*Thermopsis rhombifolia*	N
Amelanchier alnifolia	N	*Carduus nutans*	I	*Festuca idahoensis*	N	*Linaria vulgaris*	I	*Phlox hoodii*	I	*Salix sp.*	N	*Thinopyrum intermedium*	I
Anenome canadensis	N	*Carex sp.*	N	*Fragaria virginiana*	N	*Lithospermum ruderale*	N	*Phragmites australis*	N	*Schizachyrium scoparium*	N	*Tragopogon dubius*	I
Antennaria parvifolia	N	*Chamaenerion angustifolium*	N	*Gallardia aristata*	N	*Lolium perenne*	I	*Plantago major*	I	*Selaginella densa*	N	*Trifolium pratense*	I
Arnica cordifolia	N	*Chenopodium album**	I	*Galium boreale*	N	*Lonicera involucrata*	N	*Plantago patagonica*	N	*Setaria viridis*	I	*Trifolium repens*	I
Artemisia frigida	N	*Cirsium arvense*	I	*Geranium bicknellii*	N	*Lotus corniculatus*	N	*Poa fendleriana*	N	*Shepherdia canadensis*	N	*Trifolium hybridum*	I
Artemisia ludoviciana	N	*Cirsium flodmanii*	N	*Geum triflorum*	N	*Lupinus argenteus*	N	*Poa pratensis**	I	*Silene alba*	N	*Trifolium purpurascens*	I
Astragalus cicer	I	*Comandra umbellata*	N	*Glycyrrhiza lepidota*	N	*Malanthemum canadense*	N	*Poa sandbergii*	N	*Sisyrinchium montanum*	N	*Valeriana dioica*	N
Aster ericoides	N	*Convolvulus arvensis*	I	*Grindelia squarrosa*	N	*Medicago lupulina*	I	*Poa secunda*	N	*Sonchus arvensis*	I	*Vicia americana*	N
Aster laevis	N	*Cornus sericea*	N	*Haplopappus spinulosus*	N	*Medicago sativa*	I	*Polygonum odoratum*	N	*Solidago canadensis*	N	*Viola adunca*	N
Astragalus missouriensis	N	*Dactylis glomerata*	I	*Helictotrichon hookeri*	N	*Melilotus officinalis*	I	*Populus balsamifera*	N	*Solidago missouriensis*	N	*Viola glabella*	N
Avenula hookeri	I	*Descurainia pinnata*	N	*Heterotheca villosa var. hispida*	N	*Melica spectabilis*	I	*Populus tremuloides*	N	*Sphaeralcea coccinea*	N	*Zigadenus elegans*	N

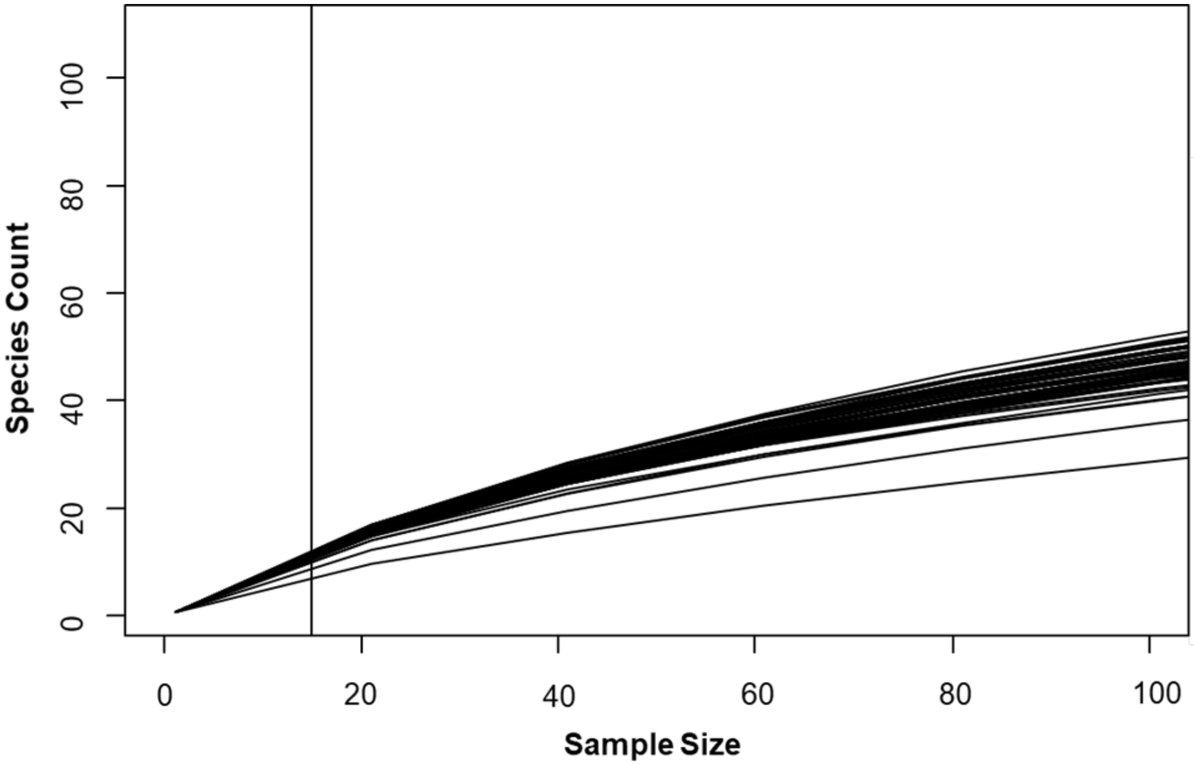
Appendix 2-S2. Questions asked of the primary ranch manager for each ranch. Management metrics were derived from the resulting data following formulas outlined intext. All questions referring to the paddocks used refer specifically to the sampled study area. These data refer to management practices as averaged over the previous 10 years.



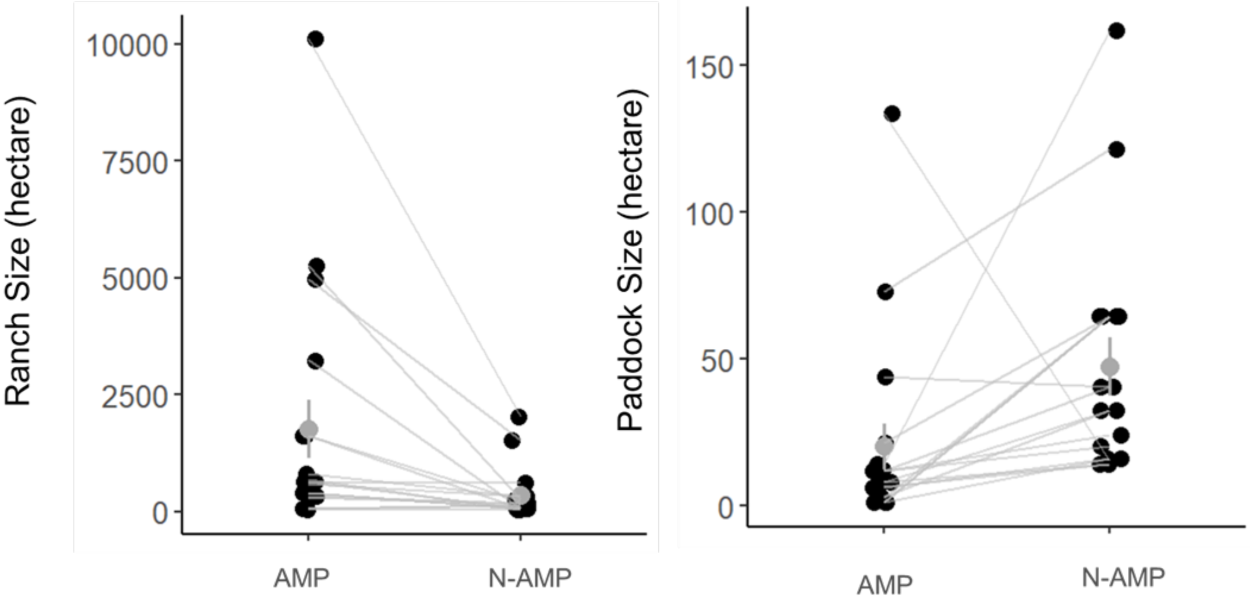
1. Have the pastures that are being sampled been cultivated in the past, and if so, when was the last date of cultivation?
2. If known to have a history of cultivation, was the area seeded, and with what forage species?
3. What is the average size of individual pastures (acres or hectares) for your ranch?
4. During the grazing season, how many animals are typically placed within a pasture at any one time? Are you grazing cow/calf pairs, yearlings, or other animals?
5. If you rotationally graze, how long do you typically leave your livestock within an average size pasture prior to moving them on (ballpark number of days)? Does the length of the grazing period differ between the early grazing season (prior to July) and late season (July onwards)?



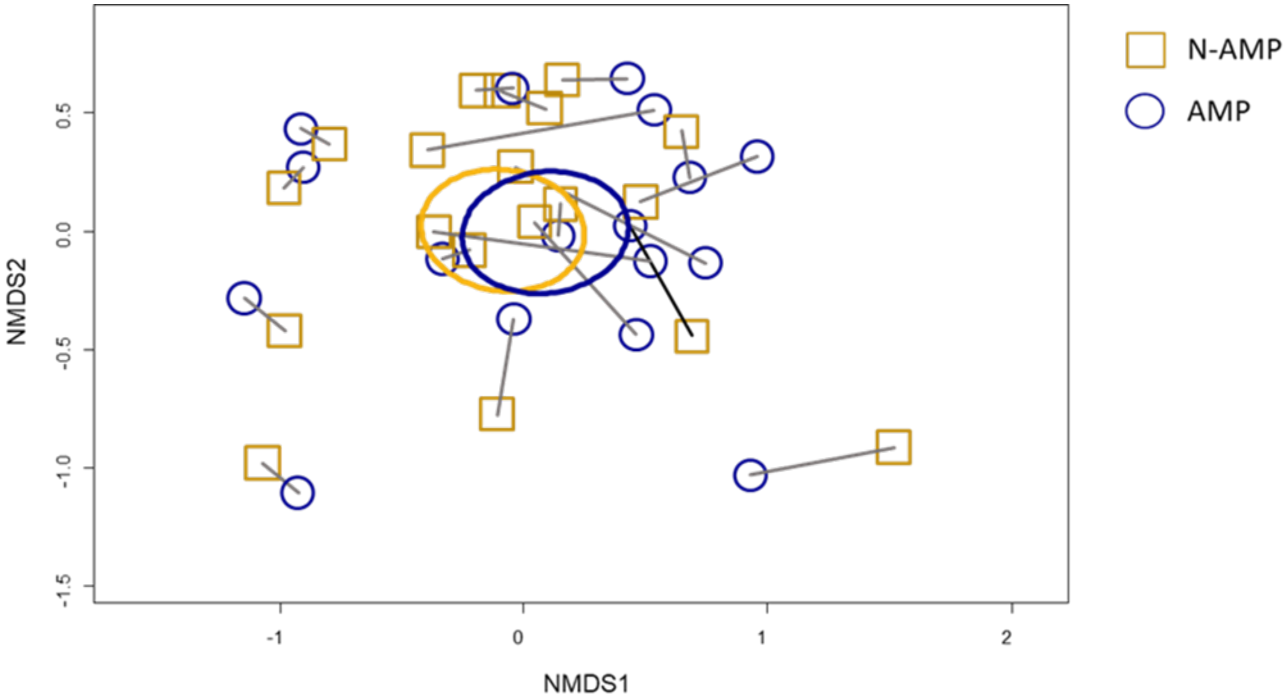
Appendix 2-S3. Schematic illustrating ranch selection and screening processes. Numbers represent counts of potentially "AMP" ranches eligible following each screening stage. Screens represent the criteria by which each selection stage was administered. Boxes to the left outline the specific criteria.



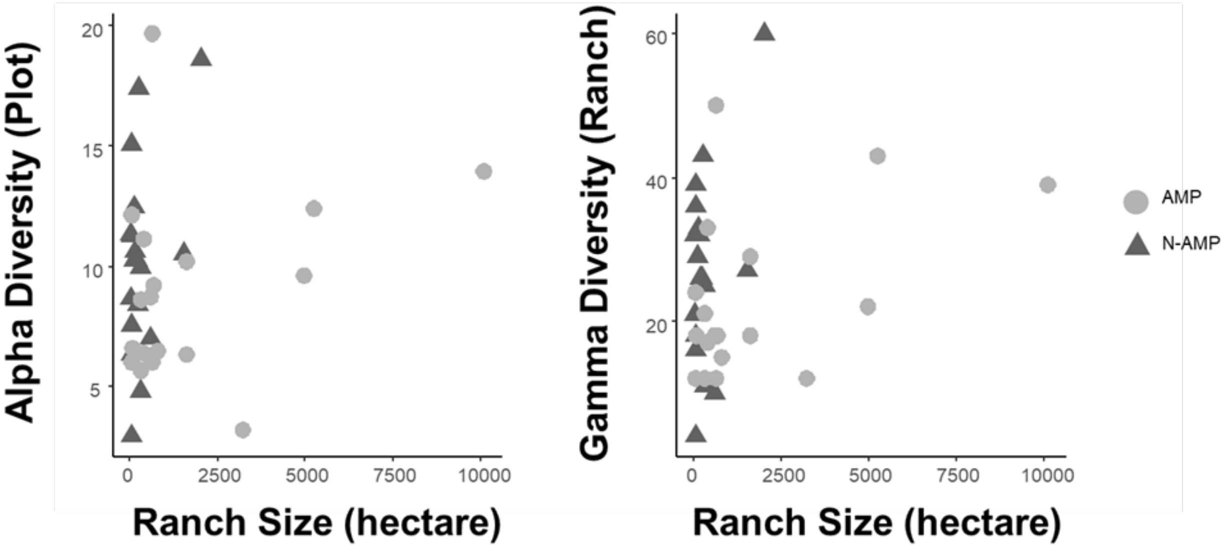
Appendix 2-S4. Rarefaction curve for each ranch sample site, showing relationship between increasing sampling effort and total species captured. Vertical line at simple size of 15 indicates the actual sampling effort undertaken (interpolation) while data beyond that point represents extrapolation.



Appendix 2-S5. Self-reported sizes for the total area of each studied ranch (left) and average size of paddock for each studied ranch (right). The gray centre point represents the group mean and the gray outer whiskers represent standard error. Grey lines connect paired ranch points, illustrating total directionality of response to grazing management.

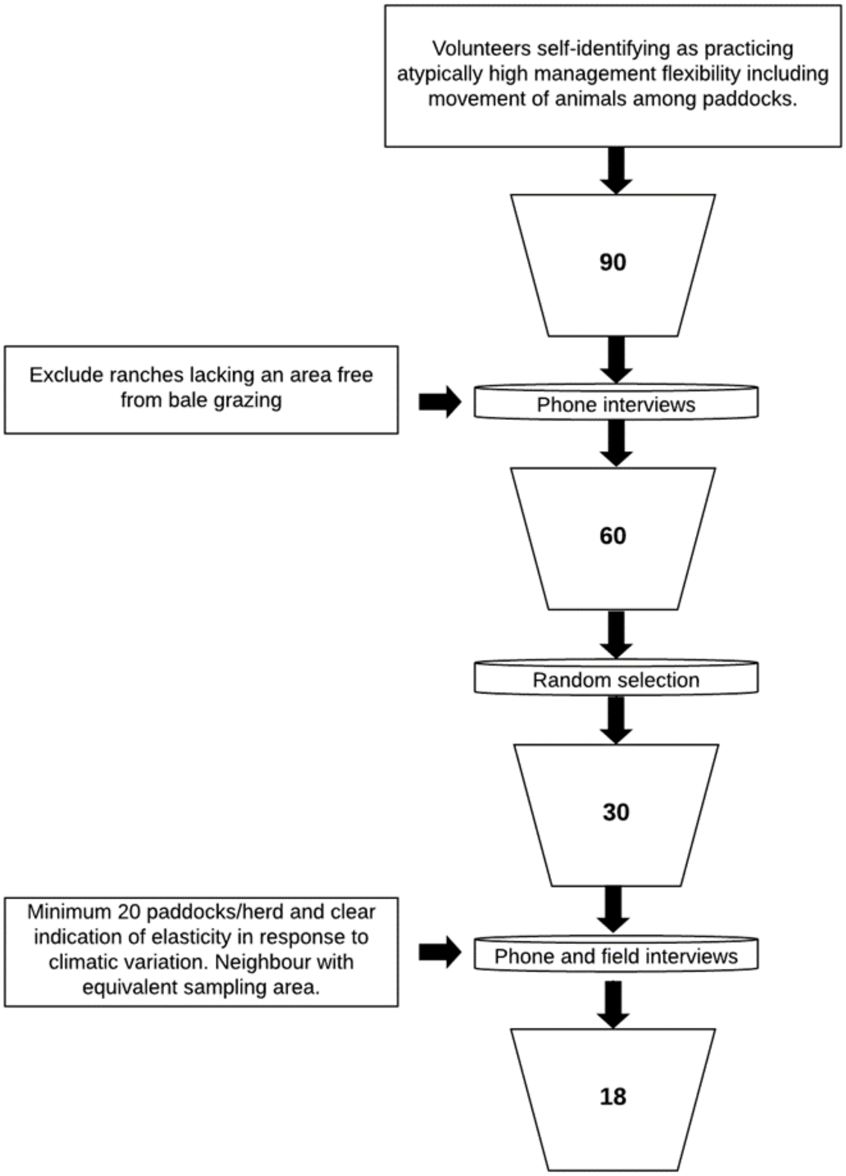


Appendix 2-S6. Non-Metric Multidimensional Scaling ordination representing the dispersion of ranches within plant community generated ordinal space. Each point represents a study site/ranch and ordination base layer was created using vegetation composition data. Ellipses represent the 95% standard error intervals for respective categories. Paired N-AMP and AMP ranches are connected by grey lines. Two axes were included, and ordinal stress was 0.16 with a non-metric fit (R^2) of 0.97. More detailed methods are reported above in-text.

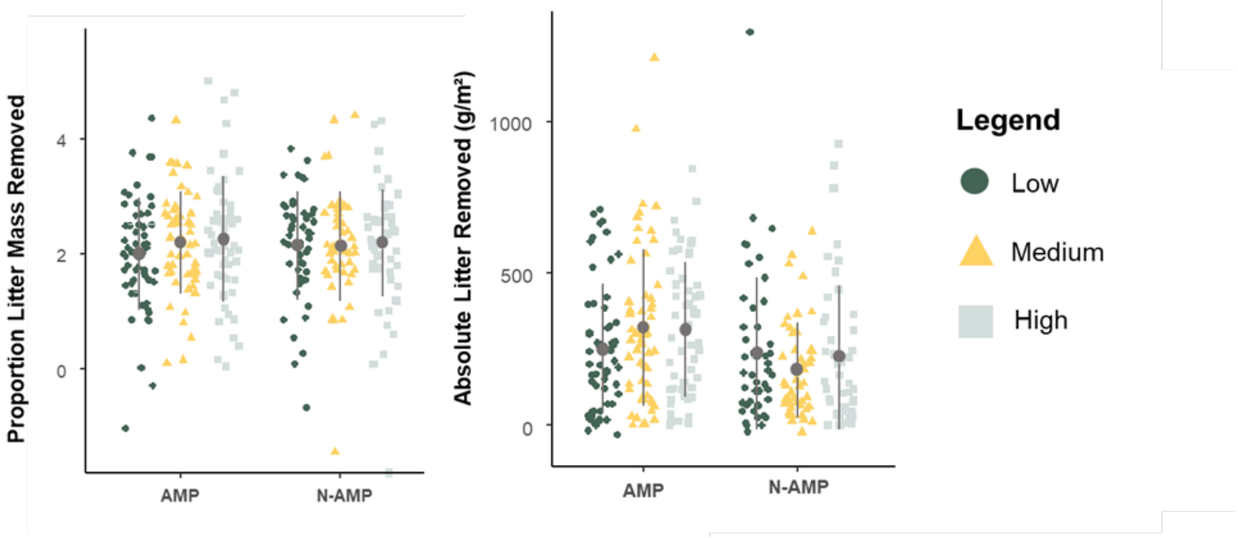


Appendix 2-S7. Scatterplot displaying the relationship between both alpha diversity (plot level) and gamma diversity (ranch level) with total ranch size (hectare).

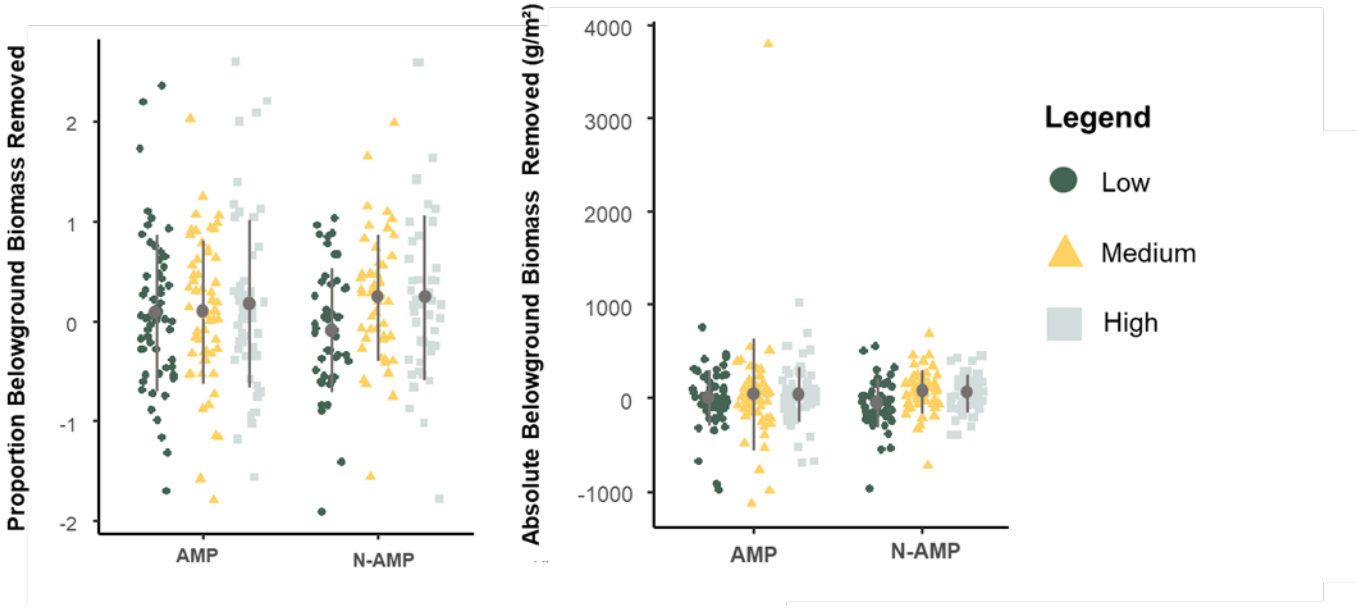
Appendix 3-S1. Photograph demonstrating the size and placement of exclusion cages at our study sites. The cage (i.e. excluded site) was placed 2 meters from the non-excluded paired site.



Appendix 3-S2. Schematic illustrating ranch selection and screening processes. Numbers represent counts of potentially "AMP" ranches eligible following each screening stage. Screens represent the criteria by which each selection stage was administered. Boxes to the left outline the specific criteria.



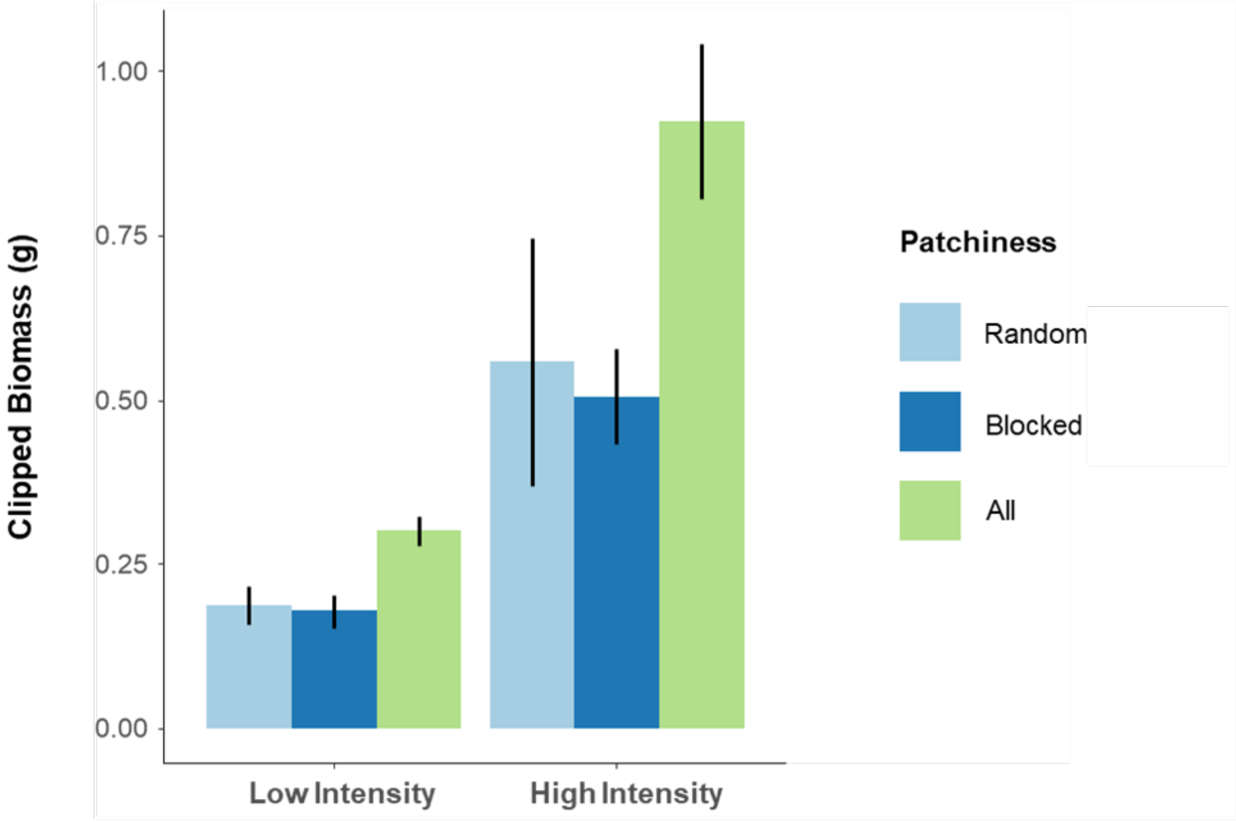
Appendix 3-S3. Summary figures of litter mass removed by grazing as a function of grazing system and landscape position. The proportion of biomass removed (intensity) is the natural log of the non-excluded plot mass over the excluded plot mass multiplied by a negative one. Smaller values represent lesser intensities of mass removal. Absolute mass removed (magnitude) is the mass of excluded plot less the mass of the non-excluded plot. Small dots represent data derived from each plot. Grey dots represent the mean and outer grey whiskers represent the mean standard error.



Appendix 3-S4. Summary figures of belowground biomass removed by grazing as a function of grazing system and landscape position. The proportion of biomass removed (intensity) is the natural log of the non-excluded plot biomass over the excluded plot biomass multiplied by a negative one. Smaller values represent lesser intensities of biomass removal. Absolute biomass removed (magnitude) is the biomass of excluded plot less the biomass of the non-excluded plot. Small dots represent data derived from each plot. Grey dots represent the mean and outer grey whiskers represent the mean standard error.

Appendix 4-S1. Species descriptions for all ten used within this study.

Species	Common Name	Origin	Root Structure
Stipa comata	Needle and thread	Native	Bunchgrass
Deschampsia cespitosa	Hairgrass	Native	Bunchgrass
Koeleria macrantha	Junegrass	Native	Bunchgrass
Agrostis scabra	Ticklegrass	Native	Rhizomatous
Dactylis glomerata	Orchardgrass	Introduced	Bunchgrass
Festuca ovina	Sheep fescue	Introduced	Bunchgrass
Phleum pratense	Timothy	Introduced	Rhizomatous
Pascopyrum smithii	Western wheatgrass	Native	Rhizomatous
Bromus inermis	Smooth brome	Introduced	Rhizomatous
Bouteloua gracilis	Blue grama	Native	Rhizomatous



Appendix 4-S2. Barplot showing total clipped biomass per mesocosm as a function of mesocosm intensity and patchiness treatments. Error bars represent standard error (n=5 per bar).

Appendix 5-S1. Original reported values for vegetation data and their corresponding assignment into generalized groups to allow for comparison between articles.

Original response variable	**Generalized group**
abiesbiomass	Abundance
abovegroundbiomass	Abundance
abudanceperennialgrass	Abundance
Abundance10sppSown	Abundance
Abundance10sppWeed	Abundance
Abundance4sppSown	Abundance
Abundance4sppWeed	Abundance
AbundanceAcerRubrum	Abundance
abundanceannualgrass	Abundance
abundanceannuals	Abundance
AbundanceArisaemaTriphyllum	Abundance
abundanceavena	Abundance
AbundanceBerberisThunbergii	Abundance
abundancebromushordeaceus	Abundance
abundancebromusrubens	Abundance
AbundanceCarexArundinacea	Abundance
AbundanceCarexGracillima	Abundance
AbundanceCarexIntumescens	Abundance
AbundanceCarexLaxiculmis	Abundance
AbundanceCarexRadiata	Abundance

AbundanceCarexSwanii	Abundance
AbundanceCelastrusOrbiculatus	Abundance
AbundanceCircaeaCanadensis	Abundance
AbundanceDactylisGlomerata	Abundance
AbundanceEuonymusAlatus	Abundance
AbundanceEurybiaDivaricata	Abundance
AbundanceExotic	Abundance
AbundanceFraxinusAmericana	Abundance
AbundanceGaliumTriflorum	Abundance
AbundanceGeum	Abundance
AbundanceGlyceriaStriata	Abundance
AbundanceIlexVerticillata	Abundance
AbundanceImpatiensCapensis	Abundance
AbundanceLeersiaVirginica	Abundance
AbundanceLinderaBenzoin	Abundance
AbundanceLiriodendronTulipifera	Abundance
abundanceloliummultiflorum	Abundance
AbundanceMaianthemumCanadense	Abundance
AbundanceMicrostegiumVimineum	Abundance
AbundanceMitchellaRepens	Abundance
AbundanceMonoSown	Abundance
AbundanceMonoWeed	Abundance
AbundanceNative	Abundance

AbundanceOxalisStricta	Abundance
AbundanceParthenocissusQuinquefolia	Abundance
abundanceperennial	Abundance
abundanceperennialforb	Abundance
abundanceperennialgrass	Abundance
abundanceperennialshrub	Abundance
AbundancePersicariaLongiseta	Abundance
AbundancePersicariaSagittata	Abundance
abundanceplantago	Abundance
AbundancePolystichumAcrostichoides	Abundance
AbundancePrunusSerotina	Abundance
AbundanceRanunculusRecurvatus	Abundance
AbundanceRosaMultiflora	Abundance
AbundanceRubusFlagellaris	Abundance
AbundanceRubusPhoenicolasius	Abundance
AbundanceSymplocarpusFoetidus	Abundance
AbundanceToxicodendronRadicans	Abundance
AbundanceTrilliumErectum	Abundance
AbundanceViolaSororia	Abundance
AbundanceVitis	Abundance
abundancevulpiamicrostachys	Abundance
Achillea.millefoliumpercentcover	Abundance
Achnatherum.hymenoidespercentcover	Abundance

Achnatherum.speciosapercentcover	Abundance
achnathpercentcover	Abundance
Agropyron.cristatumpercentcover	Abundance
aliveArtemisia.tridentata/ha	Abundance
alsikecover	Abundance
Ambrosia.artemisiifoliapercentcover	Abundance
Anisantha.tectorumpercentcover	Abundance
annualbromespercentfoliarcover	Abundance
annualforbbiomass	Abundance
annualforbcover	Abundance
annualforbdensity	Abundance
annualgrassbiomass	Abundance
annualgrasscover	Abundance
annualgrassdensity	Abundance
anpp	Abundance
anppmeadow	Abundance
anppriparian	Abundance
anppwillow	Abundance
Antennaria.alpinapercentcover	Abundance
Antennaria.pulcherrimapercentcover	Abundance
Antennaria.spppercentcover	Abundance
Arenaria.spppercentcover	Abundance
aristidacover	Abundance

Artemisia.canapercentcover	Abundance
Artemisia.frigidapercentcover	Abundance
artemisiapercentcover	Abundance
artempercentcover	Abundance
artistpercentcover	Abundance
Astragalus.spppercentcover	Abundance
atripercentcover	Abundance
barbinodiscover	Abundance
bareground	Abundance
baregroundpercent	Abundance
baresoilcover	Abundance
baresoilpercentcover	Abundance
bbcover	Abundance
belowgroundbiomass	Abundance
betulabiomass	Abundance
Biomass	Abundance
Biomass10sppSown	Abundance
Biomass10sppWeed	Abundance
Biomass4sppSown	Abundance
Biomass4sppWeed	Abundance
BiomassC3	Abundance
BiomassC4	Abundance
biomassforb	Abundance

BiomassForbArthropods	Abundance
BiomassForbBurned	Abundance
BiomassForbNoArthropods	Abundance
BiomassForbUnBurned	Abundance
biomassgrass	Abundance
BiomassGrassArthropods	Abundance
BiomassGrassNoArthropods	Abundance
BiomassMonoSown	Abundance
BiomassMonoWeed	Abundance
BiomassSnakeweed	Abundance
biomasstotal	Abundance
bluegrasscover	Abundance
bout2percentcover	Abundance
boutcover	Abundance
Bouteloua.gracilispercentbasalcover	Abundance
Bouteloua.gracilispercentplantcover	Abundance
boutelouabasalcover	Abundance
bouteloupercentcover	Abundance
boutelouaseedviability	Abundance
boutelouaseedweight	Abundance
boutelousplantdiameter	Abundance
boutpercentcover	Abundance
bromustectorumbiomass	Abundance

bromustectorumcover	Abundance
bromustectorumdensity	Abundance
buckbrushcover	Abundance
c3graminoidrelativeabundance	Abundance
c3grassbiomass	Abundance
c3perengrassbiomass	Abundance
c4graminoidrelativeabundance	Abundance
c4grassbiomass	Abundance
c4perengrassbiomass	Abundance
C4perennialgrassespercentbasalcover	Abundance
C4perennialgrassespercentfoliarcover	Abundance
Campanula.rotundifoliapercentcover	Abundance
canopy	Abundance
canopycover	Abundance
canopycoverpercent	Abundance
canopypercentcover	Abundance
canopysizeacompactacovered	Abundance
canopysizeacompactapartialcover	Abundance
canopysizeacompactauncovered	Abundance
canopysizeberectacovered	Abundance
canopysizeberectapartialcover	Abundance
canopysizeberectauncovered	Abundance
canopysizeeglandulosacovered	Abundance

canopysizeeglandulosapartialcover	Abundance
canopysizeeglandulosauncovered	Abundance
canopysizeheleganscovered	Abundance
canopysizeheleganspartialcover	Abundance
canopysizehelegansuncovered	Abundance
canopysizelgraveolenscovered	Abundance
canopysizelgraveolenspartialcover	Abundance
canopysizelgraveolensuncovered	Abundance
Carex.spppercentcover	Abundance
carexpercentcover	Abundance
Centaurea.maculosapercentcover	Abundance
Chondrosium.gracilepercentcover	Abundance
Chrysopsis.villosapercentcover	Abundance
Chrysothamnus.depressuspercentcover	Abundance
Chrysothamnus.viscidifloruspercentcover	Abundance
cornusbiomass	Abundance
Cover	Abundance
CoverAcalyphaRhomboidea	Abundance
CoverAchnatherumHymenoides	Abundance
CoverAchnatherumSpeciosa	Abundance
CoverAgropyronCristatum	Abundance
CoverAmbrosiaArtemisiifolia	Abundance
CoverAmbrosiaConfertiflOra	Abundance

CoverAnisanthaTectorum	Abundance
CoverAnnualForb	Abundance
CoverAnnualGrass	Abundance
CoverAntennariaSpp.	Abundance
CoverAristidaLongiseta	Abundance
CoverArtemisiaFrigida	Abundance
CoverAsterPilosus	Abundance
CoverAstragalusSpp.	Abundance
CoverAstragalusWingatanus	Abundance
CoverAtriplexCanescens	Abundance
coverbareground	Abundance
CoverBgracilisIN	Abundance
CoverBgracilisOUT	Abundance
CoverBoutelouaDactyloides	Abundance
CoverBoutelouaEriopoda	Abundance
CoverBoutelouaGracilis	Abundance
CoverC.Nutans	Abundance
CoverCactiIN	Abundance
CoverCactiOUT	Abundance
CoverCarduusAcanthoides	Abundance
CoverCarexDuriuscula	Abundance
CoverCarexSpp.	Abundance
CoverCelastrusScandens	Abundance

CoverCerastiumVulgatum	Abundance
CoverCheatgrass	Abundance
CoverChenopodiumLeptophyllum	Abundance
CoverChondrosiumGracile	Abundance
CoverChrysopsisVillosa	Abundance
CoverChrysothamnusDepressus	Abundance
CoverChrysothamnusViscidiflorus	Abundance
CoverCrust	Abundance
CoverCryptanthaMinima	Abundance
CoverDaucusCarota	Abundance
CoverDeadVegetation	Abundance
CoverE.Canadensis	Abundance
CoverElymusElymoides	Abundance
CoverEphedraViridis	Abundance
CoverEricameriaCervinea	Abundance
CoverEricameriaNauseosa	Abundance
CoverErigeronAnnuus	Abundance
CoverErigeronSpp.	Abundance
CoverEriogonumEffusum	Abundance
CoverEriogonumSpp.	Abundance
CoverEriogonumWrightii	Abundance
CoverExoticsIN	Abundance
CoverExoticsOUT	Abundance

CoverFestucaIdahoensis	Abundance
CoverFestucaSpp.B	Abundance
CoverForb	Abundance
CoverForbIN	Abundance
CoverForbOUT	Abundance
CoverGrass	Abundance
CoverGrassIN	Abundance
CoverGrassOUT	Abundance
CoverGutierreziaSarothae	Abundance
CoverGutierreziaSarothrae	Abundance
CoverHelianthusPetiolaris	Abundance
CoverHesperostipaComata	Abundance
coverintroduced	Abundance
CoverKoleriaMacrantha	Abundance
CoverKrascheninnikoviaCeratoides	Abundance
CoverLactucaScariola	Abundance
CoverLarrea	Abundance
coverleaves	Abundance
CoverLeptodactylonPungens	Abundance
CoverLitter	Abundance
CoverLoosestrifePost	Abundance
CoverLoosestrifePre	Abundance
CoverLupinusSp.	Abundance

CoverLygodesmiaGrandiflOra	Abundance
CoverMelilotusOfficinal	Abundance
covermixed	Abundance
CoverMuhlenbergiaSpp.C	Abundance
CoverMuhlenbergiiTorreyi	Abundance
covernative	Abundance
covernonnative	Abundance
CoverOenotheraSpp.	Abundance
CoverOpuntiaPolyacantha	Abundance
CoverOpuntiaPolycantha	Abundance
CoverOpuntiaSpp.	Abundance
CoverOryzopsisHymenoides	Abundance
CoverOtherForbs	Abundance
CoverOtherGrass	Abundance
CoverOtherShrubs/Cactus	Abundance
CoverOxalisEuropaea	Abundance
CoverOxytropisSpp.	Abundance
CoverPackeraMultilobatus	Abundance
CoverParthenium	Abundance
CoverPascopyrumSmithii	Abundance
CoverPediocactusSimpsonii	Abundance
CoverPenstemonCaespitosus	Abundance
CoverPenstemonSpp.	Abundance

CoverPerennialForb	Abundance
CoverPerennialGrass	Abundance
CoverPhloxSpp.	Abundance
CoverPhysalisSubglabrata	Abundance
CoverPlantagoPatagonica	Abundance
CoverPlantagoRugelii	Abundance
CoverPleuraphisJamesii	Abundance
CoverPoaFendleriana	Abundance
CoverPoaSpp.	Abundance
CoverPseudoroegnariaSpicatum	Abundance
CoverPsoralidiumTenuiflorum	Abundance
CoverRhusRadicans	Abundance
coverroots	Abundance
CoverSalsolaKali	Abundance
CoverSalsolaTragus	Abundance
CoverSeriphidiumSpp.A	Abundance
CoverShrub	Abundance
CoverShrubIN	Abundance
CoverShrubOUT	Abundance
CoverSidaSpinosa	Abundance
CoverSolanumCarolinense	Abundance
CoverSolidagoCanadensis	Abundance
CoverSphaeralceaCoccinea	Abundance

CoverSporobolusCryptandrus	Abundance
CoverTaraxacumOfficinale	Abundance
CoverTrifoliumPratense	Abundance
CoverTrifoliumSpp	Abundance
CoverVerbascumThapsus	Abundance
CoverVerbenaUrticifolia	Abundance
CoverWeed	Abundance
CoverWeedIN	Abundance
CoverWeedOUT	Abundance
CoverWoody	Abundance
CoverWoodyDebris	Abundance
CoverYuccaBaccata	Abundance
CoverZinnia	Abundance
creosotecanopyshrubcover	Abundance
creosoteperennialgrasscover	Abundance
cryptandruspercentcover	Abundance
currentyearbiomass	Abundance
curtipendulacover	Abundance
cyrptandruspercentcover	Abundance
dandelioncover	Abundance
Danthonia.intermediapercentcover	Abundance
deaddwarfshrubbiomass	Abundance
deadforbbiomass	Abundance

deadgrassbiomass	Abundance
deciduousabundance	Abundance
densityalnus	Abundance
DensityAmbrosiaConfertiflOra	Abundance
DensityAstragalusWingatanus	Abundance
DensityAtriplexCanescens	Abundance
DensityBouteloua Eriopoda	Abundance
DensityBromusRubens	Abundance
DensityEphedraViridis	Abundance
DensityEricameriaCervinea	Abundance
DensityEriogonumSubreniforme	Abundance
DensityEriogonumWetherilli	Abundance
DensityEriogonumWrightii	Abundance
DensityGutierreziaSarothrae	Abundance
DensityLate	Abundance
DensityLygodesmiaGrandiflOra	Abundance
DensityMid	Abundance
DensityOGF	Abundance
DensityOpuntiaPolycantha	Abundance
DensityOryzopsisHymenoides	Abundance
DensityPlantagoPatagonica	Abundance
DensityPleuraphisJamesii	Abundance
densitypopulus	Abundance

DensityRecent	Abundance
densitysalix1	Abundance
densitysalix2	Abundance
densitysalix3	Abundance
DensitySalsolaKali	Abundance
DensityShrub	Abundance
DensitySnakeweed	Abundance
DensityStephanomeriaExigua	Abundance
DensityVulpiaOctoflOra	Abundance
DensityYoung	Abundance
DensityYuccaBaccata	Abundance
Descurainia.spppercentcover	Abundance
devauxiicover	Abundance
eintercover	Abundance
Elymus.elymoidespercentcover	Abundance
elymuspercentcover	Abundance
epilobiumbiomass	Abundance
Erigeron.spppercentcover	Abundance
Eriogonum.spppercentcover	Abundance
eriopercentcover	Abundance
eriopodacover	Abundance
eriopodapercentcover	Abundance
evergreenabundance	Abundance

exoticbiomass	Abundance
exoticgrasscover	Abundance
fescuecover	Abundance
fescuecoverrm	Abundance
Festuca.campestrispercentplantcover	Abundance
Festuca.hallipercentplantcover	Abundance
Festuca.idahoensispercentcover	Abundance
Festuca.scabrellapercentcover	Abundance
floweredshootscniveuscovered	Abundance
floweredshootscniveuspartialcover	Abundance
floweredshootscniveusuncovered	Abundance
FoliarCover	Abundance
foliarcoverforb	Abundance
foliarcovergraminoid	Abundance
foliarcoverother	Abundance
foliarnmass	Abundance
forbbiomass	Abundance
forbfernfrequency	Abundance
forbheight	Abundance
forbpercentcanopycover	Abundance
forbpercentcover	Abundance
forbpercentfoliarcover	Abundance
forbrelativeabundance	Abundance

forbweedbasalcover	Abundance
forestspeciespercentcover	Abundance
Fragaria.spppercentcover	Abundance
FrequencyCrust	Abundance
FrequencyForb	Abundance
FrequencyGrass	Abundance
FrequencyShrub	Abundance
fringecover	Abundance
Galium.spppercentcover	Abundance
Geranium.viscosissimumpercentcover	Abundance
Geum.triflorumpercentcover	Abundance
goldenrodcover	Abundance
gracilispercentcover	Abundance
graminoidabundance	Abundance
graminoidbiomass	Abundance
graminoidheight	Abundance
graminoidpercentcanopycover	Abundance
grass	Abundance
grassbiomass	Abundance
grassfrequency	Abundance
grassherbcover	Abundance
grassherbheight(cm)	Abundance
grasslikefrequency	Abundance

grasspercentcover	Abundance
grasspercentfoliarcover	Abundance
greenvegetationindex	Abundance
groundcoverpercent	Abundance
gutierreziacover	Abundance
Haplopappus.armeriodespercentcover	Abundance
heightaeschynomenecompactacovered	Abundance
heightaeschynomenecompactapartialcover	Abundance
heightaeschynomenecompactauncovered	Abundance
heightalnus	Abundance
HeightBgracilisIN	Abundance
HeightBgracilisOUT	Abundance
heightbouvardiaerectacovered	Abundance
heightbouvardiaerectapartialcover	Abundance
heightbouvardiaerectauncovered	Abundance
heightechinopteryseglandulosacovered	Abundance
heightechinopteryseglandulosapartialcover	Abundance
heightechinopteryseglandulosauncovered	Abundance
HeightGrass	Abundance
heighthibiscuseleganscovered	Abundance
heighthibiscuseleganspartialcover	Abundance
heighthibiscuselegansuncovered	Abundance
heightlippiagraveolenscovered	Abundance

heightlippiagraveolenspartialcover	Abundance
heightlippiagraveolensuncovered	Abundance
heightpopulus	Abundance
heightsalix	Abundance
heightsalix2	Abundance
heightsalix3	Abundance
heliomerispercentcover	Abundance
herbaceouscover	Abundance
hesperopercentcover	Abundance
Hesperostipa.comatapercentcover	Abundance
Hesperostipa.comatapercentplantcover	Abundance
Hieracium.spppercentcover	Abundance
hilariapercentcover	Abundance
igrasscover	Abundance
indexofobstruction	Abundance
invaderbiomassleafyspurge	Abundance
invaderbiomassspottedknapweed	Abundance
kbcover	Abundance
Koeleria.macranthapercentcover	Abundance
Koeleria.macranthapercentplantcover	Abundance
Koeleria.pyramidatapercentcover	Abundance
lbcover	Abundance
leadplantcover	Abundance

leafdrymattercontent	Abundance
leaflittercover	Abundance
legumebiomass	Abundance
legumerelativeabundance	Abundance
Leptodactylon.pungenspercentcover	Abundance
lichenpercentcover	Abundance
Linaria.vulgarispercentcover	Abundance
litter	Abundance
litterbiomass	Abundance
littercover	Abundance
littercoverpercent	Abundance
LitterIN	Abundance
LitterOUT	Abundance
litterpercentcover	Abundance
livecoverpercentcover	Abundance
livedwarfshrubbiomass	Abundance
liveforbbiomass	Abundance
livegrassbiomass	Abundance
lodgepolecover	Abundance
lowwoodypercentcover	Abundance
Lupinus.spppercentcover	Abundance
maxleafheight	Abundance
Melilotus.officinalpercentcover	Abundance

monoculturebiomass	Abundance
Muhlenbergia.spppercentcover	Abundance
nativeannualgrasspercentfoliarcover	Abundance
nativecoveroakunderstoryagrifoliadominated	Abundance
nativecoveroakunderstorylobatadominated	Abundance
nativecoveropengrasslandagrifoliadominated	Abundance
nativecoveropengrasslandlobatadominated	Abundance
nativeforbbiomass	Abundance
nativeforbcover	Abundance
nativegrassbiomass	Abundance
non-grassherbcover	Abundance
nonplantednativegrassbasalcover	Abundance
nyieldForb	Abundance
nyieldgraminoid	Abundance
olddeadmass	Abundance
olddeadmassfire	Abundance
olddeadmassnofire	Abundance
oldfieldgrassbiomass.seeded	Abundance
oldfieldgrassbiomass.unseeded	Abundance
openspeciespercentcover	Abundance
opunpercentcover	Abundance
Opuntia.spppercentcover	Abundance
oxeyecover	Abundance

Pascopyrum.smithiipercentcover	Abundance
Pascopyrum.smithiipercentplantcover	Abundance
pascopyrumpercentcover	Abundance
Pediocactus.simpsoniipercentcover	Abundance
Penstemon.caespitosuspercentcover	Abundance
Penstemon.proceruspercentcover	Abundance
Penstemon.spppercentcover	Abundance
percentbiomassremaining	Abundance
percentchangestemheightscutellariamontana	Abundance
percentcover	Abundance
percentcovergraminoid	Abundance
percentcovershrub	Abundance
percentgrasscanopy	Abundance
percentshrubcover	Abundance
perennialbunchgrassbiomass	Abundance
perennialbunchgrasscover	Abundance
perennialbunchgrassdensity	Abundance
perennialforbbiomass	Abundance
perennialforbcover	Abundance
perennialforbdensity	Abundance
perennialgraminoidspercentcover	Abundance
perennialgrassdensity	Abundance
pescopercentcover	Abundance

pgccover	Abundance
Phleum.pratensepercentcover	Abundance
Phlox.spppercentcover	Abundance
pitchsagecover	Abundance
plantaincover	Abundance
plantbiomass	Abundance
plantcoverpercent	Abundance
plantednativegrassbasalcover	Abundance
plantheight	Abundance
Poa.fendlerianapercentcover	Abundance
Poa.pratensispercentplantcover	Abundance
Poa.spppercentcover	Abundance
poasecundabiomass	Abundance
poasecundacover	Abundance
poasecundadensity	Abundance
Potentilla.gracilispercentcover	Abundance
Pseudoroegnaria.spicatumpercentcover	Abundance
Pseudorogeneria.spicatapercentcover	Abundance
redtopcover	Abundance
relativeimportancevalueindexseedrain	Abundance
reproductiveorgansacompactacovered	Abundance
reproductiveorgansacompactapartialcover	Abundance
reproductiveorgansacompactauncovered	Abundance

reproductiveorgansheleganscovered	Abundance
reproductiveorgansheleganspartialcover	Abundance
reproductiveorganshelegansuncovered	Abundance
rootbiomass	Abundance
roughcover	Abundance
rubusbiomass	Abundance
sandbergbluegrasscover	Abundance
sandbergbluegrassdensity	Abundance
scleropogonpercentcover	Abundance
sdcover	Abundance
sedgecover	Abundance
SedgwickSourcedSeedMeanBiomass	Abundance
SedgwickSourcedSeedPerformance	Abundance
SeedheadBgracilisIN	Abundance
SeedheadBgracilisOUT	Abundance
SeedheadExoticsIN	Abundance
SeedheadExoticsOUT	Abundance
SeedheadForbIN	Abundance
SeedheadForbOUT	Abundance
SeedheadGrassIN	Abundance
SeedheadGrassOUT	Abundance
SeedheadShrubIN	Abundance
SeedheadShrubOUT	Abundance

SeedheadWeedIN	Abundance
SeedheadWeedOUT	Abundance
seedmass	Abundance
Seriphidium.spppercentcover	Abundance
shootbiomass	Abundance
shortspeciespercentbasalcover	Abundance
shrubbiomass	Abundance
shrubheight	Abundance
shrubpercentcanopycover	Abundance
shrubpercentcover	Abundance
shrubrelativeabundance	Abundance
sideoatcover	Abundance
Silene.spppercentcover	Abundance
soilcover	Abundance
specificleafarea	Abundance
Sphaeralcea.coccinea.percentcover	Abundance
sphapercentcover	Abundance
sporopercentcover	Abundance
Spulchraplantdiameter	Abundance
Spulchraseedlingbiomass	Abundance
Spulchraseednumber	Abundance
standingdeadArtemisia.tridentata/ha	Abundance
standinglitterpercentcover	Abundance

standingn	Abundance
stemdensity	Abundance
Stipa.columbianapercentcover	Abundance
Stipa.richardsoniipercentcover	Abundance
strawberrycover	Abundance
subshrubbiomass	Abundance
tallgrassbiomass.seeded	Abundance
tallgrassbiomass.unseeded	Abundance
tallspeciespercentbasalcover	Abundance
tallwoodypercentcover	Abundance
tarbushcanopyshrubcover	Abundance
tarbushperennialgrasscover	Abundance
totalcover	Abundance
totalcoverpark	Abundance
totalcovertree	Abundance
totalforbcover	Abundance
totalgrasscover	Abundance
totalplantsgrazedscutellariamontanainvasivesintact	Abundance
totalplantsgrazedscutellariamontanainvasivesremoved	Abundance
totalshrubcover	Abundance
totalvegetationcover	Abundance
totalvegetationdensity	Abundance
Tragopogon.dubiuspercentcover	Abundance

treecover	Abundance
treecoverpercent	Abundance
treedensity	Abundance
treediameter	Abundance
treeheight	Abundance
treeheight(m)	Abundance
treepercentcover	Abundance
trifoliumcover	Abundance
understorycover	Abundance
understorypercentcover	Abundance
VAFBSourcedSeedMeanBiomass	Abundance
vegetationcover	Abundance
vegetationheight	Abundance
vegetationheight(cm)	Abundance
vegetativepercentcover	Abundance
vegetativeplantsgrazedscutellariamontanainvasivesintact	Abundance
vegetativeplantsgrazedscutellariamontanainvasivesremoved	Abundance
vegpercentcover	Abundance
verticalobstructionindex	Abundance
vinepercentcover	Abundance
vulpiapercentcover	Abundance

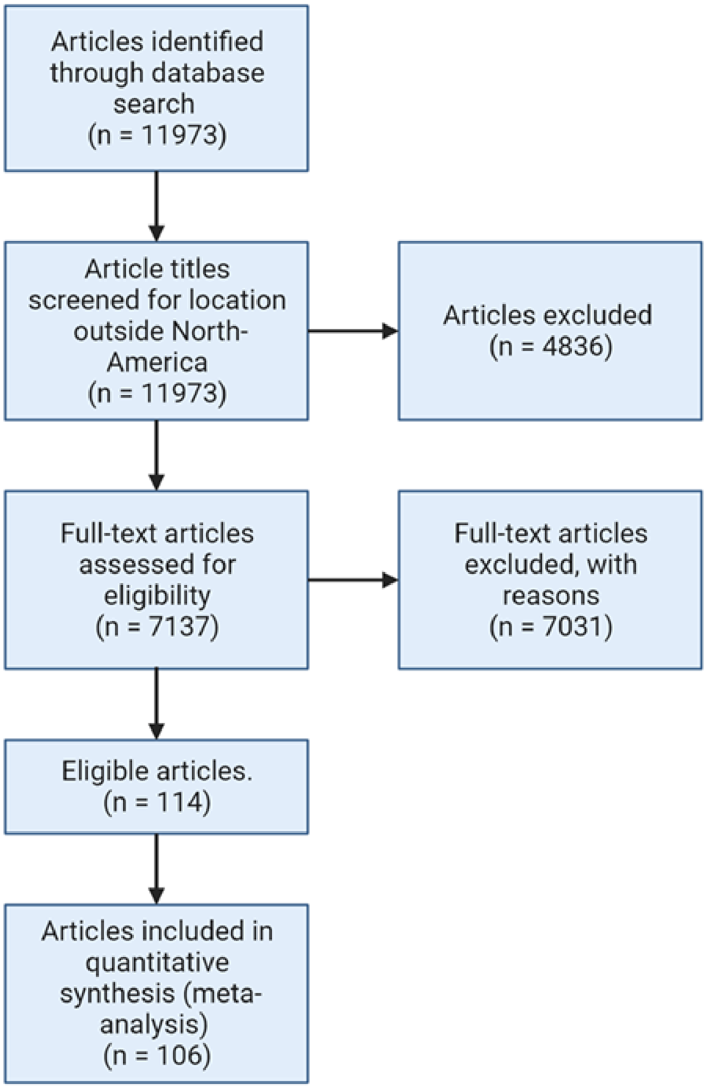
wastercover	Abundance
willowcanopycover	Abundance
willowstemdensity	Abundance
willowstemheight	Abundance
wironweedcover	Abundance
woody	Abundance
woodycount	Abundance
woodypercentcover	Abundance
woodypercentfoliarcover	Abundance
wragweedcover	Abundance
yarrowcover	Abundance
ywscover	Abundance
Zygadenus.spppercentcover	Abundance
Diversity	Richness
diversityannual	Richness
diversityburnedannually	Richness
diversityburnedevery4yrs	Richness
DiversityIN	Richness
diversityindex	Richness
DiversityOUT	Richness
diversityperennial	Richness
exoticrichness	Richness
herbrichness	Richness

managed.annual.forb.richness	Richness
managed.annual.graminoid.richness	Richness
managed.perennial.forb.richness	Richness
managed.shrub.richness	Richness
managed.subshrub.richness	Richness
managed.tree.richness	Richness
mannaged.perennial.graminoid.richness	Richness
nativerichness	Richness
nonnativerichness	Richness
richness	Richness
Richness1	Richness
Richness20	Richness
Richness4	Richness
richnessannual	Richness
richnessburnedannually	Richness
richnessburnedevery4yrs	Richness
richnessdiversity	Richness
Richnessexotic	Richness
richnessforb	Richness
RichnessForbArthropods	Richness
RichnessForbNoArthropods	Richness
richnessforbs	Richness
richnessgraminoid	Richness

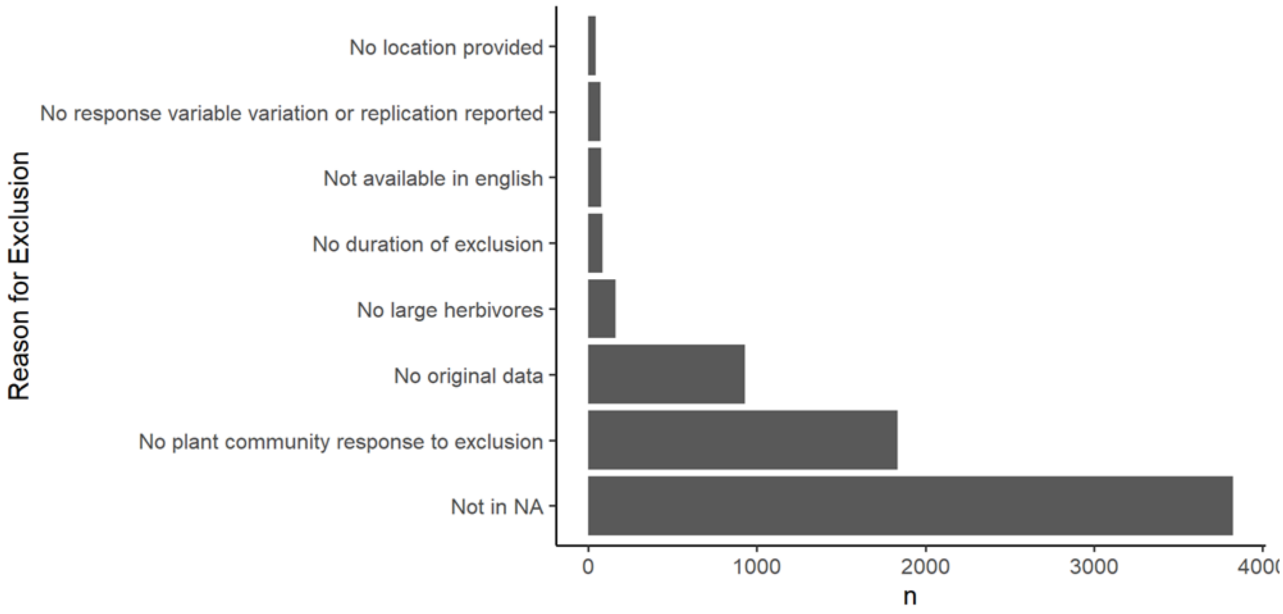
RichnessGrassArthropods	Richness
RichnessGrassNoArthropods	Richness
Richnessherb	Richness
RichnessIN	Richness
richnessintroduced	Richness
RichnessLarge	Richness
RichnessLate	Richness
RichnessMedium	Richness
RichnessMid	Richness
richnessnative	Richness
RichnessOGF	Richness
RichnessOUT	Richness
richnessperennial	Richness
RichnessRecent	Richness
richnessshrub	Richness
RichnessSmall	Richness
richnesstreespecies	Richness
RichnessYoung	Richness
shortspeciesrichness	Richness
speciesdiversity(richness)	Richness
speciesrichness	Richness
tallspeciesrichness	Richness
unmanaged.annual.forb.richness	Richness

unmanaged.annual.graminoid.richness	Richness
unmanaged.perennial.forb.richness	Richness
unmanaged.perennial.graminoid.richness	Richness
unmanaged.shrub.richness	Richness
unmanaged.subshrub.richness	Richness
unmanaged.tree.richness	Richness
woodyrichness	Richness

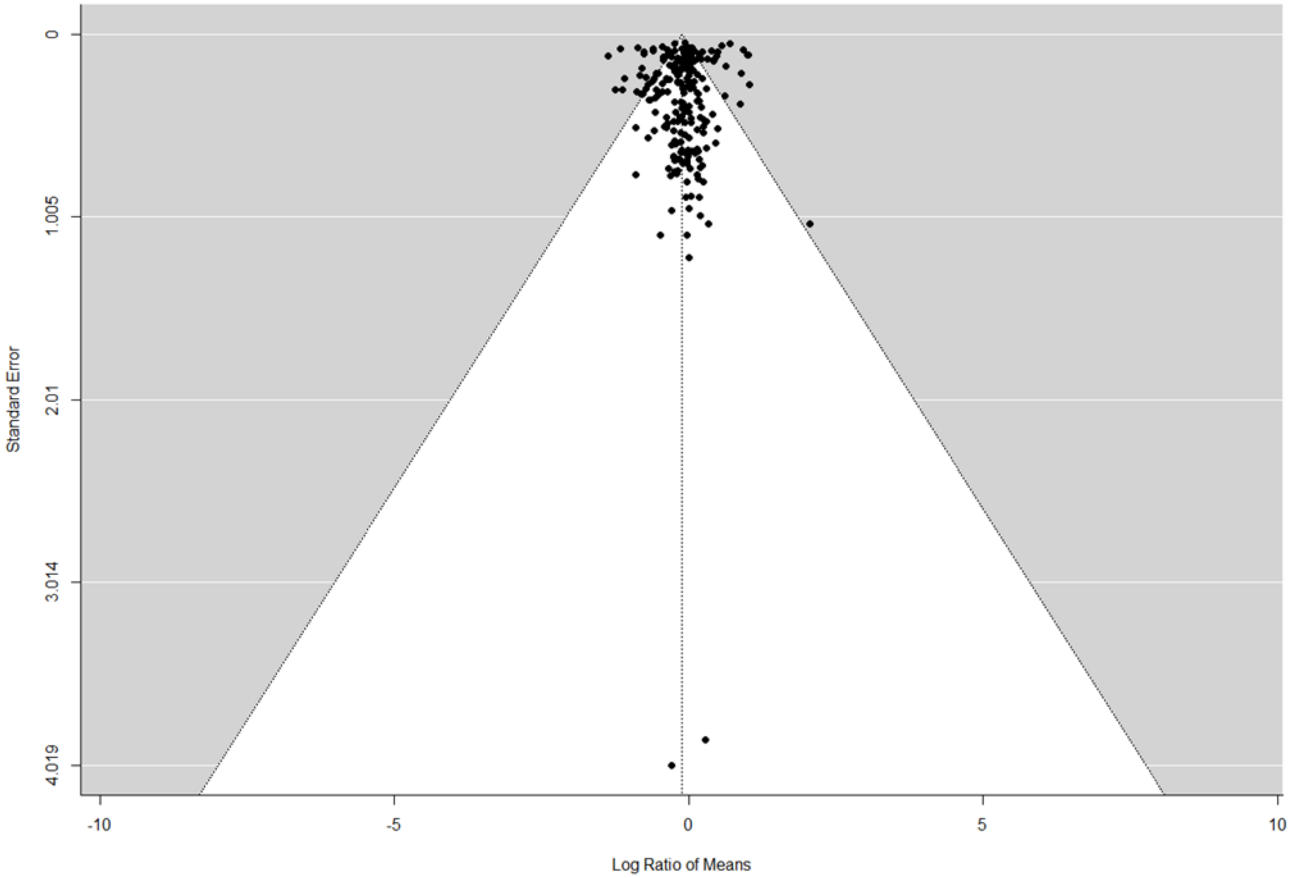
Appendix 5-S2. Workflow for the screening process for inclusion of articles into the meta-analysis comparing the effect of grazing exclusion on North American plant communities. Articles were excluded if any criteria outlined were not met.



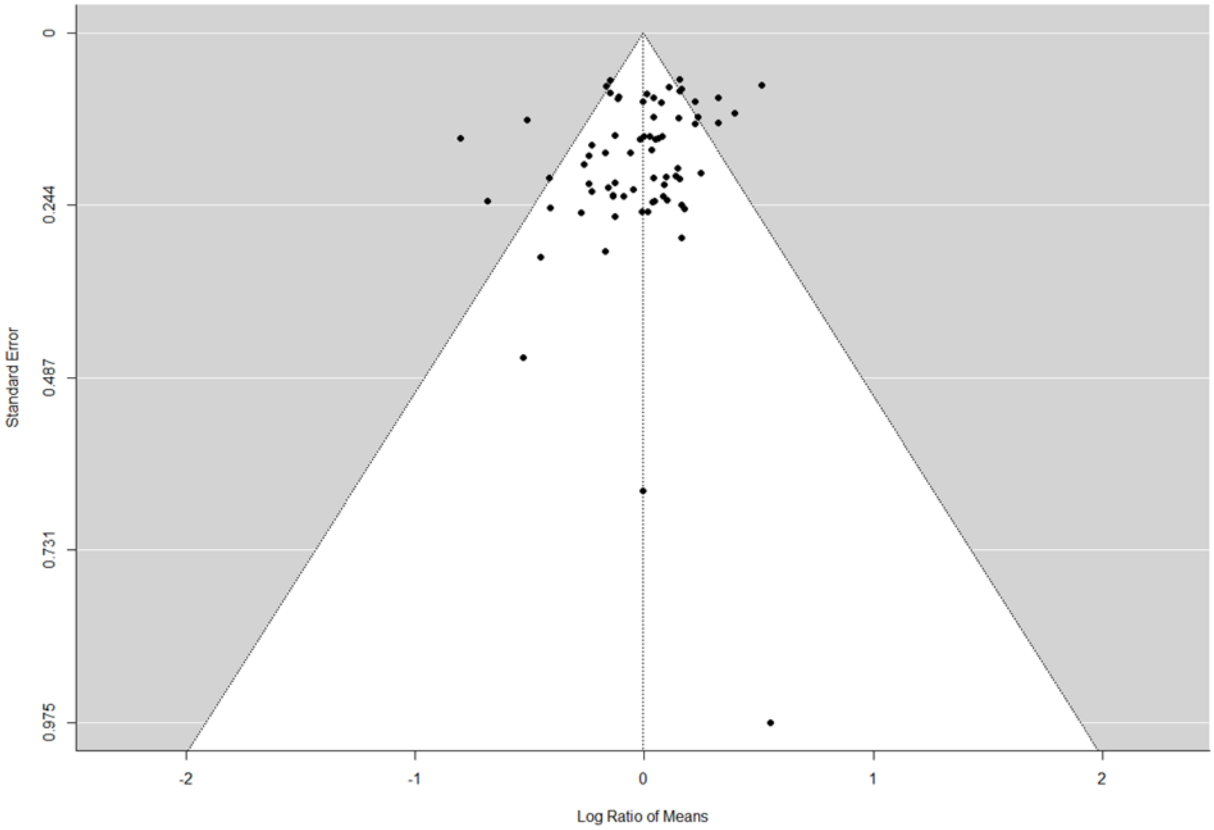
Appendix 5-S3. PRISMA report on the number of studied examined, included, and excluded for each stage of the screening process, Full-text articles were assessed using the criteria outlined in Figure B1. Eight eligible studies sampled vegetative response variables (germination and structure) other than our core focus of abundance and richness. They were not included in our quantitative synthesis to facilitate comparison between studies.



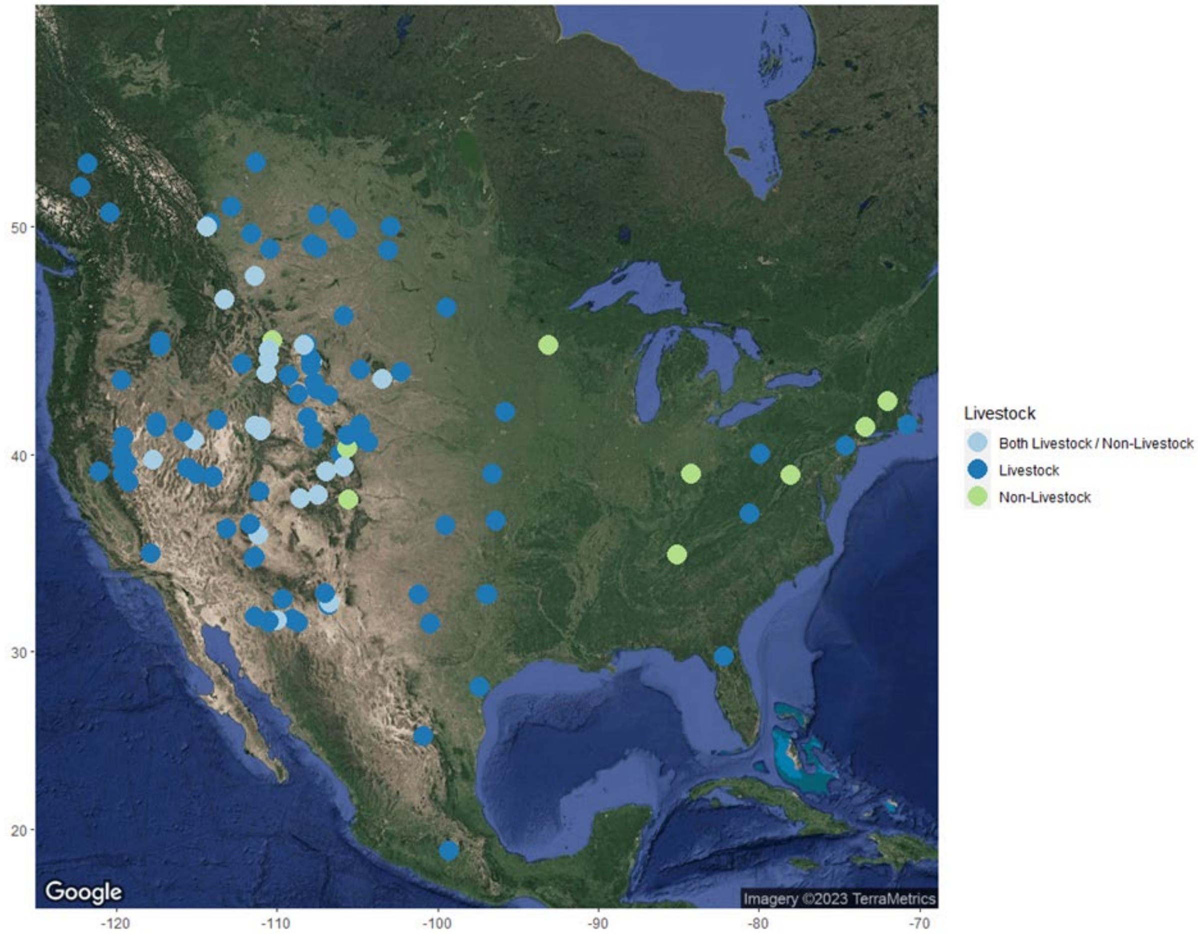
Appendix 5-S4. Count of studies excluded (n) categorized by the reason for exclusion. Due to our comprehensive search strategy, the majority of studies were excluded due to locations outside North America.



Appendix 5-S5. Funnel plot comparing the observed mean effect and standard error from a random effects model of grazing exclusion on plant abundance. Study distribution was confirmed as random by a regression test for asymmetry (z = -0.078, p = 0.94), indicating no bias in study selection.



Appendix 5-S6. Funnel plot comparing the observed mean effect and standard error from a random effects model of grazing exclusion on plant species richness. Study distribution was confirmed as random by a regression test for asymmetry (z = -2.11, p = 0.034), indicating potential asymmetry. Visual inspection reveals no categorically confounded outliers.



Appendix 5-S7. Locations of the 159 grazing exclusion study sites located across North America included within our quantitative review. Color indicates the livestock status of the primary grazers located at each grazing exclusion study site.