FROST, MORGAN D.T. Ph.D. Understanding the consequences of invasive plant species for native rangeland communities in the context of global climate change. (2023)
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Invasive species wreak havoc on nearly every ecosystem on the planet, including grasslands, and are considered currently to be one of the most substantial threats to ecosystems worldwide. Invasive species outcompete native species for resources with far-reaching direct and indirect consequences for the ecosystems they invade. Importantly, invasion is expected to change under global climate change, with global change factors like drought creating complex interactions with invasion, yielding a dire need to understand the widespread consequences of invasion for ecosystem sustainability. My research addresses this, specifically for two invasive grass species in the northern mixed-grass prairies of North America and on a global scale through a meta-analysis of grasslands. Grasslands, which are essential for ecosystem services like providing usable forage for livestock, are one of the most widespread biomes in the world, covering nearly 40% of the land area of the Earth. My dissertation assessed 1) how multi-year, multi-intensity drought and grazing altered two invasive brome grass species, 2) how metrics of stability associated with invasion gradients of two brome grass species, 3) the relationships between multiple trophic levels and gradients of invasion of two brome grass species, and 4) the responses of native and introduced plant species in grasslands to drought.

My dissertation utilized diverse methods to address how invasion will impact ecosystem sustainability. Under a multi-site, long-term, manipulative field experiment, invasive annual bromes decreased in biomass under multiple years of drought, while summer grazing alone did not alter production of these species. Importantly, however, post-drought during recovery, annual bromes increased in biomass, particularly so in the plots which were heavily grazed during the drought (Chapter II). Using an observational field study, I found that invasive brome species tend to destabilize native plant communities, especially functional groups important for forage production, suggesting that invasion has consequences for predictability of yearly forage availability on rangelands (Chapter III). Similarly, in another observational field study, I found plant and insect communities and functional groups, and to a lesser extent, soil microbes, differed with invasion abundance, but relationships between invasive bromes and rangeland communities differed based on the particular invasive species (Chapter IV). Last, using a meta-analysis, I found that under drought, introduced plant species in grasslands tend to fare worse than native plants, but this advantage of native species over introduced species was negated when other global change variables co-occurred (Chapter V). In all, my dissertation shows that invasion destabilizes native communities, has consequences across trophic levels, and alters competition between native and invasive species. This work has implications for ecological theory related to invasions, as well as broad applications for management of our critically important grassland ecosystems.

UNDERSTANDING THE CONSEQUENCES OF INVASIVE PLANT SPECIES FOR NATIVE RANGELAND COMMUNITIES IN THE CONTEXT OF GLOBAL CLIMATE CHANGE

by

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APPROVAL PAGE

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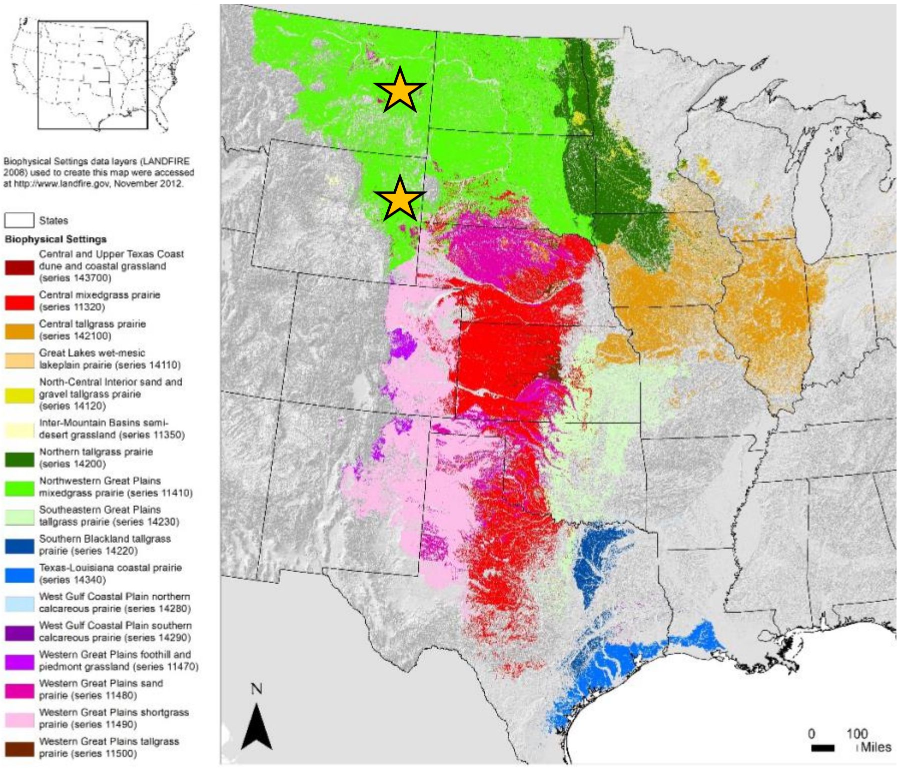
CHAPTER I: INTRODUCTION

Invasive species threaten nearly every ecosystem on the planet, causing harm to biodiversity and ecosystem services globally, often by outcompeting native species for resources (Charles and Dukes, 2007; Pejchar and Mooney, 2009). Environmental damage associated with invasive species costs billions of dollars in damages each year (Tobin, 2018). In particular, invasive plant species are problematic for native ecosystems. While the impacts of invasive plants can be variable (Pyšek et al., 2012), they have been repeatedly shown to have negative impacts on native biodiversity, ecosystem services (Vilà et al., 2011), and temporal community stability (Valone and Balaban-Feld, 2018). Invasive plants decrease plant species richness, hinder nutrient and hydrological cycling, and alter disturbance regimes (Charles and Dukes, 2007; Walker and Smith, 1997). These effects can have large consequences for the agricultural and livestock industry when invasive species dominate the landscape, disrupt soil processes, and transmit diseases (DiTomaso, 2000; Paini et al., 2016). The direct and indirect effects of invasion decrease the quantity and quality of crop and livestock yield, threatening global food security (DiTomaso, 2000; Paini et al., 2016; Pyke et al., 2002).

Grasslands, which cover approximately 40% of the total land area on earth (Gibson, 2009; Suttie et al., 2005; White et al., 2000), are important for numerous ecosystem services (e.g. carbon sequestration, biodiversity, and agriculture), especially for utility in the global livestock industry (Bengtsson et al., 2019; DiTomaso, 2000). In the United States alone, nearly 42% of the terrestrial land area is used as working rangeland (DiTomaso, 2000; White et al., 2000). Grassland ecosystems are dominated by herbaceous and low growing shrub vegetation and are maintained by disturbances of fire, grazing, and drought (Gibson, 2009; Suttie et al., 2005). In North America, grasslands are divided into three prairie ecotypes depending on the dominant grasses - short, tall, and mixed grass prairies (Zouhar, 2021, Figure 1.1). Short grass prairies tend to be dominated by C_3 grasses, while tallgrass prairies mainly consist of C_4 grasses. Mixed grass prairies have the highest diversity and consist of a mix of grass types (Wang et al., 2013). An aridity gradient, driven in part by the rain-shadow effect from the Rocky Mountains, exists across these prairies, causing short grass prairies to be the driest and tallgrass prairies the wettest (Seager et al., 2017). Further, northern mixed-grass prairies in the North American Great Plains are especially important for their services of biodiversity and utility as working range (Martin et al., 1998; Samson and Knopf, 1994; Samson et al., 2004). However, grasslands, including Northern mixed-grass prairies, are threatened by many invasive plant species (DiTomaso, 2000; DiTomaso et al., 2017), and costs associated with invasives on rangelands are high (Pimentel et al., 2000).

Figure 1.1 Map of US Prairies.

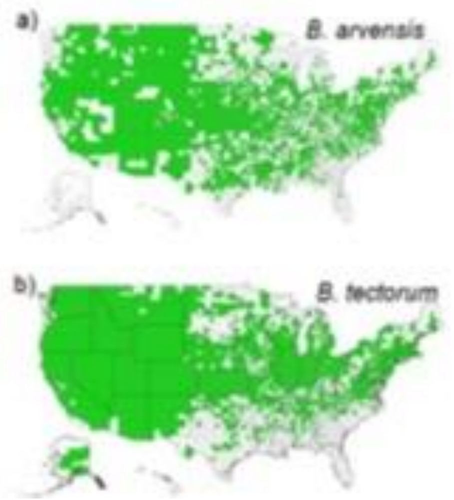


Note. Approximate field locations are marked with stars. Source: Zouhar 2021.

Further, while grassland ecosystems around the globe are well-adapted to, and to an extent are maintained by, recurring droughts, climate change is predicted to increase the frequency and duration of droughts (Sheffield and Wood, 2008) and the long-term effects of increased droughts on rangelands are still unclear. In the Midwest and Northern Great Plains, summer droughts are predicted to increase in frequency and impact (Andresen et al., 2012), with an expected decrease in soil moisture for all seasons of 1-3% in this region (Wehner et al., 2017). Moreover, it is expected that changes in drought regimes as a result of climate change will impact both native and invasive species (Hellmann et al., 2008); however, previous work on the response of native and invasive species to drought is mixed. Evidence exists to support all outcomes in the invasive versus native performance under drought: invasive plants perform better than native species under drought (Ali and Bucher, 2022; Dong et al., 2014), native plants outperform invasives (Blicker et al., 2003; Valliere et al., 2019), or the two perform equally as well (Liu et al., 2017).

Bromus tectorum and *B. arvensis* are two well-established, widespread invasive annual brome grasses in US rangelands (Figure 1.2) (Swearingen and Bargeron, 2016). These C_3, winter annual grasses were both intentionally introduced from Eurasia in the 1800s as forage for cattle. However, upon flowering, which occurs early in the growing season, they are considered very poor quality forage and are known to have negative consequences for native grassland ecosystems (Hulbert, 1955; Klemmedson and Smith, 1964; Oja et al., 2003; Schachner et al., 2008; Vermeire et al., 2009b). Annual brome species can have significant consequences for the production of native plant species (Ogle et al., 2003), which has important implications for overall rangeland health (Hulbert, 1955; Oja et al., 2003; Vermeire et al., 2009b; Wright and Wright, 1948) and forage stability (Landmann, 2017; Ziska et al., 2011). Further, while other invasive plants have been shown to affect animals (Fletcher et al., 2019; Stewart et al., 2021), including insects (Bezemer et al., 2006), soil microbial communities (Xu et al., 2022), and ecological function (Gibbons et al., 2017), our understanding of the consequences for invasive annual bromes across trophic levels of rangelands is limited.

Figure 1.2. Distribution of Two Invasive Bromes.



Note. a) *B. arvensis* and b) *B. tectorum* in the United States. Source: Swearingen and Bargeron 2016.

Through my dissertation research, I aim to understand the consequences of invasive plant species for grassland ecosystems using both a broad meta-analysis as well as focal annual brome invasive species to explore the impacts of invasion on plant stability and across trophic levels, as well as the interaction between invasion and other global change drivers (drought and grazing). To do this, I addressed four specific aims. First, using a long-term large scale field manipulation, I explored how invasion changes under multi-year, multi-intensity drought and grazing conditions in Northern mixed-grass prairies of Montana and Wyoming (Figure 1.3). Second, using an observational field study in Wyoming, I assessed how plant community stability varies with invasion abundance. Third, utilizing observational gradients of invasion in both in the mixed-grass prairies of Wyoming and Montana, I explored how the plant, insect, and soil microbial communities of rangelands change with annual brome abundance. Lastly, using a meta-analysis, I explored how invasive plants from grasslands around the world respond to drought in comparison to native plant species. Overall, my dissertation provides valuable insight into how invasive grass species impact grassland communities and how this may change in the future. Importantly, my work has both theoretical and applied implications. My work contributes to a broader understanding of invasion science, including how invasive species differentially alter native communities, while simultaneously contributing rangeland management by providing critical information to land managers on how invasive will respond to this rapidly changing world.

Figure 1.3. The Picturesque Northern Mixed-Grass Prairies are Invaded by *B. arvensis* and *B. tectorum*.

Note. Images are of field sites from Ch. II-IV. Top) Fort Keogh Livestock and Range Research Laboratory, Miles City, Montana. Bottom) Private land in the Thunder Basin Ecoregion, near Douglas, Wyoming.

CHAPTER II: CONSEQUENCES OF RAINFALL MANIPULATIONS FOR INVASIVE ANNUAL GRASSES VARY ACROSS NORTHERN MIXED-GRASS PRAIRIE SITES

Frost, M. D. T., Komatsu, K. J., Porensky, L. M., Reinhart, K. O., Wilcox, K. R., Koerner, S. E. Consequences of rainfall manipulations for invasive annual grasses vary across northern mixed-grass prairie sites. Accepted with minor revisions to *Rangeland Ecology and Management*. Manuscript number: REMA-D-22-00109.

Abstract

Northern mixed-grass prairie rangelands are threatened by increasing drought severity and invasion by annual grasses. However, it is unclear whether climate change will amplify or dampen this invasion. We tested separate and combined effects of livestock grazing and experimental rainfall manipulation on invasion by annual brome grasses - cheatgrass (*Bromus tectorum* L.) and field brome (*Bromus arvensis* L.) - in two mixed-grass prairie sites (Montana and Wyoming, USA). To provide management-relevant results, we manipulated precipitation at five levels representing a gradient of precipitation reduction and implemented grazing strategies selected by stakeholders to represent realistic management choices – destock, stable, and heavy grazing scenarios. We measured soil moisture and three plant properties of invasive annual bromes (aboveground primary production, percent greenness, and percent cover) during two water manipulation years (2019, 2020) and one recovery year of natural rainfall (2021).

Imposed precipitation reduction generally decreased absolute annual brome biomass and induced earlier senescence. However, during the recovery year, we observed prolonged time to senescence in the formerly droughted plots. In Wyoming, summer grazing had little appreciable effect on annual bromes, perhaps because annual bromes mature early in the growing season (mid-June) and may therefore be less affected by summer grazing. However, in the first year after ending water treatments during a natural drought in Montana, under heavy grazing, annual brome production marginally increased from 32.4 ± 10.6 kg · ha-1 to 130.8 ± 111.8 kg · ha-1 (mean ± standard error) with prior severe precipitation reduction. The magnitude of responses tended to be site dependent, which may be due to inherent vegetation differences between our sites as well as site-scale differences in natural precipitation patterns. Together, these results suggest annual brome abundance may increase in the context of drought combined with heavy grazing, a more likely scenario with continuing climate change.

Keywords: *Bromus arvensis* L.; *Bromus tectorum* L.; Rangeland; Global Change; Precipitation; Drought

Introduction

Grazing lands are the most widespread terrestrial biome in the world (Ellis and Ramankutty, 2008), covering ~40% of the global land surface (Gibson, 2009; Suttie et al., 2005; White et al., 2000). Their structure and diversity are maintained by frequent disturbances including grazing, drought, and fire (Gibson, 2009). The livelihoods and health of >1 billion people worldwide rely specifically on herbaceous systems to graze livestock (Sayre et al., 2013), yet management of these lands is currently challenged by unprecedented climate regimes and intense pressure from invasive species (DiTomaso, 2000; McCollum et al., 2017).

Invasive plant species alter landscapes and plant community dynamics, making management of working rangelands challenging (Belnap et al., 2012). Invasive weeds can harm livestock production due to decreased forage quality and quantity, slower animal weight gain, and decreased land value (DiTomaso, 2000). Simultaneously, invasive plants compete with native plant communities, decreasing native productivity, diversity, and litter decomposition

(Henderson and Naeth, 2005; Ogle et al., 2003). Further, invasive grasses can directly alter soil nutrient content and availability and soil microbial composition (McLeod et al., 2021; Nasto et al., 2022; Parker and Schimel, 2010), which can in turn affect ecosystem functioning and services (McLeod et al., 2021; Parker and Schimel, 2010). Altogether, invasive species on rangelands are responsible for large-scale negative ecological and economic consequences (Pimentel et al., 2005, 2000; Poland et al., 2021).

While climate change and invasive species can independently affect ecosystems, there is also substantial evidence suggesting climate change will have an impact on invasive species (Bezeng et al., 2017; Bradley et al., 2016; Dukes and Mooney, 1999; Hellmann et al., 2008; Mainka and Howard, 2010; Shabani et al., 2020; Ziska et al., 2011). Further, while grasslands are adapted to and depend on disturbances including variable weather, global climate models predict increases in magnitude and frequency of climate extremes (Ades et al., 2020; Rosenzweig et al., 2001; Smith, 2011), which could potentially alter grassland composition and function. Productivity of grasslands in mixed-grass prairies of the United States (US) has a strong positive correlation with spring precipitation (Wiles et al., 2011), so altered precipitation patterns may greatly alter production from these systems. Precipitation patterns are expected to change, with summer droughts in the midwestern US predicted to increase in frequency and impact (Andresen et al., 2012) and surface soil moisture expected to decrease with increasing temperatures across the U.S. (Wehner et al., 2017). With these changes expected in the coming decades, it is critical to understand how increased drought intensity and frequency will impact invasive species on rangeland ecosystems.

The northern mixed-grass prairies of the North American Great Plains are an important ecoregion for biodiversity and livestock (including beef cattle) production (Martin et al., 1998;

Samson and Knopf, 1994; Samson et al., 2004). However, the mixed-grass prairie is threatened by both increased drought severity and invasive species (DiTomaso, 2000; Gaskin et al., 2021; Henderson and Naeth, 2005). Current grazing management practices may not be sustainable as the climate changes, and new approaches to management may be required to uphold land value and prevent overgrazing (Derner and Augustine, 2016; Li et al., 2018). Additionally, across Northern Great Plains rangelands, the invasive grasses field brome (*Bromus arvensis* L.) and cheatgrass (*Bromus tectorum* L.) - hereafter referred together as annual bromes, or separately as field brome (*B. arvensis*) and cheatgrass (*B. tectorum*) - are cause of concern for overall rangeland sustainability (Germino et al., 2016; Vermeire et al., 2009b). *B. arvensis* and *B. tectorum* are two widespread, well established, C_3, winter-annual grass species (Hulbert, 1955; Oja et al., 2003; Wright and Wright, 1948). These species were intentionally introduced as forage for cattle, but while annual bromes provide forage in the spring, the optimal grazing period is short as the protein percentage decreases by ~97% upon maturation in mid-June (Chambers et al., 2007; DiTomaso, 2000; Hulbert, 1955; Morrow and Stahlman, 1984; Oja et al., 2003; Schachner et al., 2008; Vermeire et al., 2009b). Invasive annual brome grasses harm native rangeland communities by decreasing the quality and quantity of forage and competing with native plant species (Ashton et al., 2016; Haferkamp et al., 1998, 1997; Ogle et al., 2003). Intensive cattle grazing of cheatgrass during the boot stage prior to flowering has been shown to significantly reduce annual brome abundance in subsequent years (Diamond et al., 2012; Porensky et al., 2021), and some level of grazing may be required to maintain invasion resistance and native diversity in disturbance-adapted rangelands (Loeser et al., 2007; Porensky et al., 2020, 2013). However, in a Great Basin grassland, after a naturally occurring (single year) severe drought, both heavy grazing and no grazing produced increases in cheatgrass, with heavy grazing resulting in the most dramatic increase (Loeser et al., 2007). Therefore, the relationship between grazing and control of invasive annual bromes is complex, particularly under decreased precipitation conditions.

Uniquely, our study examines the consequences of an experimentally generated gradient of precipitation reduction crossed with varying levels of livestock grazing intensity on the productivity and percent cover of field brome and cheatgrass in northern mixed-grass prairies. Additionally, we assess how annual brome phenology changes under these treatment conditions. We tracked these responses across two years of water reduction treatments (hereafter "precipitation reduction") and the first-year post water reduction treatment (hereafter "recovery year"). Our hypotheses are as follows:

1) We hypothesized that summer grazing and precipitation reduction would have interactive effects on annual brome biomass, percent cover, and senescence. Specifically, we predicted that the combination of severe drought and heavy grazing would result in the largest increases in biomass and percent cover of field brome and cheatgrass, especially during the recovery year. This could be due to high cover of bare space via reductions in perennial plant cover (Porensky et al., 2013). Under heavy grazing following drought, cheatgrass has been shown to significantly increase in abundance and greatly contribute to alterations in plant community composition in similar regions (Souther et al., 2020). Cattle often preferentially graze the non-brome plant community, decreasing perennial plant abundance (Derner and Hart, 2007; Rickard et al., 1975). As grazing intensifies, especially under reduced precipitation conditions, decreases in the non-brome, perennial vegetation, can free up space for invasive annual bromes to increase (Haferkamp, 2001).

2) We hypothesized that during precipitation reduction years, the biomass and percent cover of invasive annual bromes would decrease across precipitation reduction treatments due to the added stress of water loss (Richardson et al., 1989). Likewise, we predicted that precipitation reduction would cause annual bromes to senesce earlier in the season, with average percent green the lowest under the severest water reduction levels (Rice et al., 1992).

3) We hypothesized that in the recovery year following precipitation reduction, biomass and percent cover of invasive annual bromes would increase. We also hypothesized that in the recovery year, precipitation reduction would indirectly cause annual bromes to delay senescence, reflecting a possible drought-avoidance strategy of invasive annual bromes (Rice et al., 1992). After two years of summer precipitation reduction, lowered resistance to invasion via suppression of perennial species under high precipitation reduction could lead to competitive release for bromes in the historically severe precipitation reduction plots (Diez et al., 2012; Jiménez et al., 2011). This could be due to legacy effects in the soil. For example, following drought, soil nitrogen can increase, which annual bromes are better able to utilize than the native plant community, allowing annual bromes to increase in abundance while indirectly suppressing native plant species (Meisner et al., 2013; Souther et al., 2020). In addition, while cheatgrass and field brome are considered winter annuals, they can be relatively plastic in germination timing, especially under altered precipitation, allowing them to better avoid drought-legacy effects in native-suppressed areas (Espeland et al., 2016; Roundy et al., 2007).

Methods

Study Sites

The Northern Great Plains steppe ecoregion is dominated by temperate and semiarid mixed-grass prairie and spans 22 million hectares across five states in the USA and two

Canadian provinces (Martin et al., 1998), covering 38% of grassland area in North America (Chimner and Welker, 2011; Lauenroth, 1979). Most precipitation occurs from May-June, with total average annual precipitation for the region ranging from less than 250 to 500 mm (Reinhart and Vermeire, 2017). This ecoregion is ecologically and economically important, with as much as 50% of the land area being used to support livestock (Holechek et al., 2011; Vold, 2018) and an estimated ~11 million animal unit months of livestock grazing (Reinhart and Vermeire, 2017).

We experimentally manipulated rainfall and cattle management at one site in Custer County in eastern Montana (46.3366° N, -105.985° W) and another in Converse County in northeastern Wyoming (43.3025° N, -105.0575° W). The Montana site is centrally located in the Northern Great Plains steppe ecoregion at the Fort Keogh Livestock and Range Research Laboratory. The Wyoming site is located at the south end of the Northern Great Plains steppe ecoregion on private land within a shrubland-grassland ecotone (known locally as the Thunder Basin ecoregion) (Porensky et al., 2018).

The Montana site has a semi-arid climate (MAP = 342 mm, with mean growing season precipitation of 193 mm and nearly half of the precipitation occurring in May-June) (Peterson and Reinhart, 2012; Wilcox et al., 2015). Mean temperature for this site ranges from -10°C in January to 24°C in July (Waterman et al., 2021) and elevation is 715-860 m above sea level (Peterson and Reinhart, 2012). Ninety percent of annual net primary productivity is completed by July 1 (Vermeire et al., 2009a). In Custer County, MT, annual precipitation in 2019 = 471.7 mm, with April-October precipitation = 417.3 mm; annual precipitation in 2020 = 251.0 mm, with April-October precipitation = 216.9 mm; and annual precipitation in 2021 = 257.3 mm, with April-October precipitation = 222.8 mm (NOAA National Centers for Environmental Information, 2022).

The Wyoming site also has a semi-arid climate (MAP = 250-300 mm/year, with 40-50% of precipitation occurring in April-June) (Curtis and Grimes, 2004). Mean temperature for this site ranges from -5°C in December to 22°C in July and elevation is 1097-1585 m above sea level (Connell et al., 2019; Curtis and Grimes, 2004; Porensky et al., 2018). In Converse County, WY, annual precipitation in 2019 = 390.7 mm, with April-October precipitation = 307.8 mm; annual precipitation in 2020 = 216.4 mm, with April-October precipitation = 155.4 mm; and annual precipitation in 2021 = 341.6 mm, with April-October precipitation = 248.4 mm (NOAA National Centers for Environmental Information, 2022).

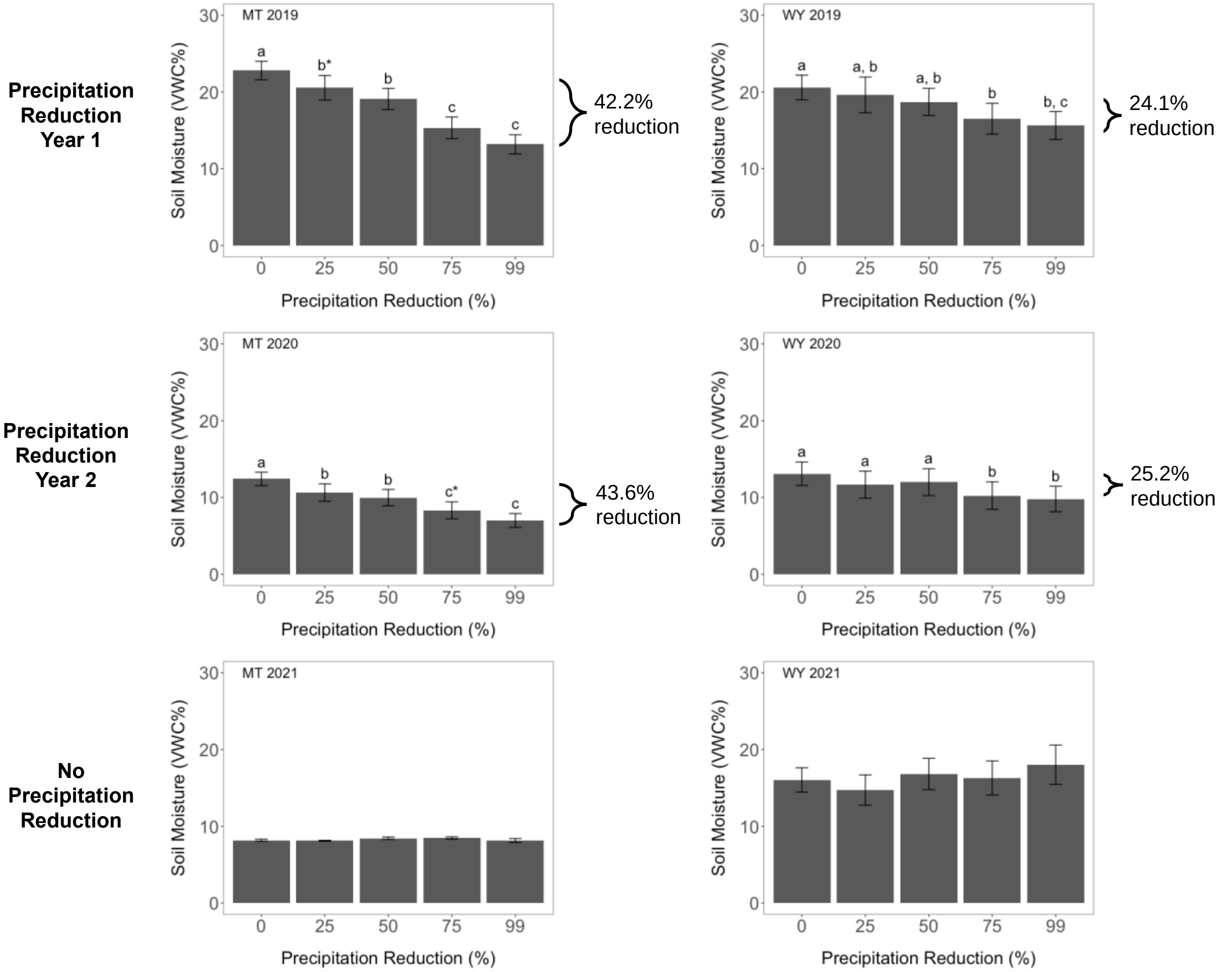
Common plant species at both sites include the shrub, *Artemisia tridentata* Nutt. sp. *Wyomingensis* Beetle and Young (Wyoming big sagebrush); perennial graminoids, *Bouteloua gracilis* (blue grama), *Carex filifolia* Nutt. (threadleaf sedge), *Hesperostipa comata* (needle-and-thread grass), and *Pascopyrum smithii* (western wheatgrass); annual grasses, *Bromus tectorum* (cheatgrass), *Bromus arvensis* (field brome), and *Vulpia octoflora* (Walter) Rydb. (six-week fescue); and the forb, *Plantago patagonica* Jacq. (wooly plantain) (Porensky et al., 2018; Russell et al., 2017). Other reported plant species include the sub-shrub *Artemisia frigida* Wild. (prairie sagewort), the perennial grass, *Bouteloua dactyloides* (Nutt.) J. T. Columbus (buffalograss), and forbs, *Tragopogon dubius* Scop. (yellow salsify), *Logfia arvensis* (L.) Holub (field cottonrose), and *Hedeoma hispida* Pursh. (rough false pennyroyal) in Montana (Russell et al., 2017) and the forbs, *Alyssum desertorum* Stapf (desert madwort), *Lepidium densiflorum* Schrad. (common pepperweed), and *Sphaeralcea coccinea* (Nutt.) Rydb. (scarlet globemallow); and the cactus *Opuntia polyacantha* Haw. (Plains pricklypear) in Wyoming (Porensky et al., 2018).

Experimental design

Experimental design was identical at both sites and consisted of three fully replicated blocks (80.8 × 61.0 m), with three paddocks nested within each block. Paddocks (40.4 × 30.5 m) were randomly assigned to one of three livestock management strategy treatments. Grazing intensity was similar across paddocks in 2018 (pre-treatment), when plots received the conventional practice for the system of moderate summer grazing. However, during precipitation reduction (2019-2020) and recovery (2021) years, grazing intensity varied across the paddocks to correspond with how regional livestock managers might alter their management in response to drought. The ‘control’ grazing strategy was a fixed grazing intensity (moderate) throughout the experiment. The other two grazing treatments varied grazing intensity to reflect destocking or heavy management scenarios (Fig. 2.1).

Figure 2.1. Experimental Design from 2018-2021.

	Forage Utilization % (July – August)				
Grazing Treatment	**Year**	**2018**	**2019**	**2020**	**2021**
Destock		50%	50%	30%	30%
Stable		50%	50%	50%	50%
Heavy		50%	70%	70%	50%



Note. In 2018 (pretreatment), precipitation was ambient, and grazing followed conventional practice; pretreatment data for aboveground biomass and percent cover were collected. Top) Our experiment consisted of three grazing treatments (light – 30%, moderate – 50%, heavy – 70% forage utilization) to represent different livestock utilization methods each year (destock, stable, and heavy, respectively). We imposed grazing in either July or August in each of the three treatment years (2019-2021). Bottom) In 2019 (precipitation reduction year 1) and 2020 (precipitation reduction year 2), we erected rainout shelters during the growing season (April-October) to impose rainfall reduction across a gradient of five levels (0%, 25%, 50%, 75%, 99% precipitation reduction). We did not impose precipitation reduction treatments in 2021; plots were exposed to ambient precipitation (recovery year). Bar graphs show mean +/- standard error of average growing season soil moisture of at Montana (MT) and at Wyoming (WY) across the precipitation reduction treatments through the 3 treatment years. Model fit was assessed using linear mixed-model ANOVAs. Letters indicate significant differences at $p < 0.05$ and asterisks indicate marginal significance at $0.05 < p < 0.1$ based on Tukey HSD.

At each site, we used beef cattle (*Bos taurus*) to implement the grazing treatments. Utilization targets varied by grazing treatment and year according to the experimental design (Fig. 2.1). For each block, different grazing intensities were achieved by varying the number of days a given herd had access to different paddocks within the block. During grazing bouts, we assessed livestock utilization using visual obstruction readings before, during (daily or sub-daily as needed), and after grazing. We used a visual obstruction pole (Robel et al., 1970) with alternating black and white bands modified to a 1-cm increment, a method with application in grasslands broadly (Ganguli et al., 2000). Temporary fencing was used to exclude cows from a given paddock once the target forage utilization (30% for light, 50% for moderate, or 70% for heavy; Fig. 2.1) was achieved. Due to spatial and temporal variation in forage production, this resulted in variable numbers of animals and days of grazing across sites, years, and blocks (summarized in Table S1). Blocks were grazed sequentially, and all grazing was completed within three weeks each year (WY: June 26-July 18, 2019; July 2-15, 2020; July 7-14, 2021; MT: August 13-23, 2019; July 30-August 8, 2020; August 9-12, 2021). Fort Keogh Livestock and Range Research Laboratory's Institutional Animal Care and Use Committee evaluated our experiment and determined that our use of animals was consistent with standard livestock management and did not require special approval for either site.

Within each paddock, six, 2×2 m plots were randomly assigned to different precipitation treatments. Each paddock had two control plots (no precipitation reduction), and one plot for each precipitation reduction level (25%, 50%, 75%, 99% reduction from ambient precipitation), giving a total of 54 plots per site. To achieve our rainfall gradient, we constructed rainout shelters (modified from Yahdjian and Sala, 2002). Rainout shelters were 3×4 m and covered the entire plot. In April 2019 and 2020, rainout shelters were erected. The shelters remained up until October, except for a brief grazing period in July (for Wyoming) or August (for Montana) to allow cattle to graze each paddock. This resulted in varying grazing and water treatments per year. To assess the effectiveness of our precipitation reduction treatments, we tested for water treatment differences in average soil moisture per plot (April-October) for each year and site separately.

Data collection

Each plot was divided into four, 1×1 m subplots used for different sampling approaches, including a permanent 1 m^2 species composition subplot and a 1 m^2 area used for aboveground biomass clipping. We collected all data types annually for three years including the two precipitation reduction years (2019-2020) and the recovery year (2021) from each site. We measured plant species composition in late June each year by visually estimating foliar cover (i.e., calibrated to estimates generated by a 100 pin-point intercept frame) for each species to the nearest percent. Additionally, each year during peak biomass production (mid-late July), we clipped all aboveground biomass from two 0.5×0.2 m quadrats. In Wyoming, where grazing occurred in early July before clipping, biomass plots were protected from same-year grazing using movable grazing cages, and in Montana, grazing occurred after clipping. Thus, both biomass and cover measurements were not affected by current-year grazing treatments but could respond to prior-year treatments. We separated annual grasses (in Montana, consisting largely of annual bromes) and annual bromes (in Wyoming) from the rest of the plant biomass. While ideally annual bromes would have been sorted out from other annual grasses in Montana, this was not done; however, the data is still beneficial for invasive annual bromes as there is only one other annual grass species at the site (*Vulpia octoflora*). This species accounted for less than 0.5% cover on average and has consistently low biomass compared to annual brome production, which can range from low to high biomass at this site (Vermeire et al., 2021). Thus, we feel confident in using this data as a proxy for invasive brome biomass. We collected soil moisture (% volumetric water content [VWC]) and plant phenology (visual estimates of percent of green tissue on randomly selected, individually marked, and ungrazed plants) throughout the growing seasons (April-October) from 2019-2021. Percent of the plant tissue that was green was visually estimated to the nearest 1% based on standard protocols (Blumenthal et al., 2020; Denny et al., 2014; Hoover et al., 2021; USA-NPN National Coordinating Office, 2012). To differentiate between senescence and temporary shifts in color (e.g., due to cold stress), percent green included reddish or purple tinted tissue, but not brown, dried tissue. We minimized bias in percent green measurements by having the same researcher collect the data for each time point across all plots at a site, and often throughout the entirety of each growing season. Plant phenology measurements were done exclusively on field brome in Montana but were done on a combination of field brome and cheatgrass in Wyoming because field brome was not present in all plots.

Statistical analyses

We conducted all calculations and analyses in R version 3.6.2 (R Core Team, 2019) (α = 0.05, but we report results with $0.05 < p < 0.1$ as marginally significant due to low replication of grazing treatments). We used Shapiro-Wilk, Anderson-Darling, Cramer-von Mises, and Kolmogorov-Smirnov tests to assess normality of the residuals of all response variables using the Olsrr package (Hebbali, 2020). We transformed data when necessary to achieve normality (Tables 2.1-3; S1-S2, available online at [insert URL here]). We ran linear mixed-model regressions using the lmerTest package (Kuznetsova et al., 2017), followed by Type III analysis of variance (ANOVA) with Satterthwaite's method (Satterthwaite, 1941). Because water and grazing treatments varied by year (Fig. 2.1), we performed unique tests each year. Further, models include grazing treatments for the prior calendar year because we applied grazing treatments in July-August, after most annual brome data were collected. For 2019 data, we tested only the effect of water treatments, as grazing treatments could not have affected annual brome response variables during that year. For 2020 data, we tested the effect of a second year of water treatments, the two grazing treatments applied in 2019 (two paddocks were moderately grazed and one paddock was heavily grazed; Fig. 2.1), and their interaction. For 2021 data, we tested for water treatment legacy effects, the three grazing treatments applied in 2020 (one paddock was grazed at each of the three grazing intensities - light, moderate, and heavy; Fig. 2.1), and the interaction between water and grazing treatments. We assessed the precipitation reduction treatment as a continuous variable and the grazing treatment as a categorical variable in all analyses. As part of data exploration, we fit non-linear models to all our variables; however, in each instance, linear models fit better based on Akaike’s information criterion with correction for small sample size (AICc). Therefore, only results for linear models are presented here.

To assess how soil moisture changed with our water treatments, we used Type III mixed-model ANOVAs with random effects of block, and paddock nested within block for each site and year separately. We first averaged soil moisture across all time points at each site (collected approximately bi-monthly each year April-October throughout the experiment) to avoid pseudo replication. We then used Tukey's test (Tukey, 1977) adjusted for multiple comparisons using the Benjamini-Hochberg method (Benjamini and Hochberg, 1995) to assess significant differences in soil moisture between precipitation reduction levels.

To assess how aboveground biomass changes with our water and grazing treatments, we used Type III mixed-model ANOVAs with random effects of block, and paddock nested within block for each site and year separately.

We also assessed how annual brome phenology responds to our water and grazing treatments in two ways. To standardize our results, we assessed differences in percent green by comparing each precipitation reduction level (25%, 50%, 75%, 99% reduction) to the corresponding control (0% precipitation reduction) for each paddock (i.e., precipitation reduction treatment – control) at each time point. In Montana, we averaged percent green across both control plots (2 control plots per paddock) first as we only collected percent green data on field brome. In Wyoming, because we collected percent green data on a combination of field brome and cheatgrass, we paired the precipitation reduction plots with control plots for each paddock and time point of the same species (i.e., field brome treatment plots paired with field brome control plots; cheatgrass treatment plots paired with cheatgrass control plots). Then, we analyzed how differences in percent green between precipitation reduction treatments and control plots change with our water and grazing treatments through each summer separately for each site and year. While data collection for percent green occurred from April-October, we conducted data analyses on percent green data collected from May-July only, prior to grazing treatments each year. To do this, we used repeated measures mixed-model ANOVAs with random effects of block, paddock nested within block, and plot nested within paddock. Second, from these phenology results through time, we looked for a single time point in each year that maximized differences in percent green across our water treatments. We then selected the data for this time point only to assess how standardized percent green changes across our treatments at that chosen date. We analyzed this using Type III mixed-model ANOVAs with random effects of block and paddock nested within block separately for each year and site.

Last, we addressed how percent cover of invasive annual bromes respond to water and grazing treatments. In these analyses, we excluded all plots that never included invasive annual bromes, as we cannot attribute this to our treatment conditions. We excluded two plots entirely at our Wyoming site that never contained either field brome or cheatgrass. For analyses with cheatgrass cover, we also excluded eight additional plots at our Wyoming site that never contained cheatgrass. This aligns with previous work (Ashton et al., 2016), and analyses including these plots where invasive annual bromes were never present yielded very similar results but did not fit our distributional assumptions as well (Table S2, available online at [insert URL here]). To determine how percent cover (foliar cover) of field brome and cheatgrass respond to our water and grazing treatments, we used Type III mixed-model ANOVAs with random effects of block and paddock nested within block for each site, year, and species separately. During data exploration, we also assessed how the pretreatment (2018) percent cover data at the Montana site covaried with each year’s response using Type III mixed-model ANCOVAs with random effects of block and paddock nested within block (data not shown). However, AICc scores were similar with and without the covariate, so we proceeded with analyses without the covariate to simplify the models. We also collected pretreatment (2018) percent cover data for the Wyoming site, but we had to move the plots in 2019, so that data could not be compared to subsequent years' data at the plot scale. Results are reported as means +/- standard error (SE), and statistical results are reported as significant when $p < 0.05$ and marginally significant when $0.05 < p < 0.10$.

Results

Soil moisture

At both sites, water manipulations created a gradient of soil moisture during the growing seasons of 2019 and 2020 (water treatment $F_{4,41} = 35.7$, $p < 0.001$ for 2019 in Montana, water treatment $F_{4,41} = 30.1$, $p < 0.001$ for 2020 in Montana, water treatment $F_{4,41} = 6.7$, $p < 0.001$ for 2019 in Wyoming, water treatment $F_{4,41} = 4.6$, $p = 0.004$ for 2020 in Wyoming; Fig. 2.1), though this pattern was somewhat weaker at Wyoming in 2020, when that site was experiencing a natural drought. In 2021, soil moisture was similar across treatments in Montana (water treatment $F_{4,41} = 1.4$, $p = 0.244$), which was experiencing a natural drought. In Wyoming, which experienced wetter conditions in 2021, soil moisture was highest in plots that had previously experienced 99% precipitation reduction (water treatment $F_{4,41} = 1.9$, $p = 0.129$; Fig. 2.1).

Table 2.1. Linear Mixed-Model Analysis of Variance (F Statistics with P-Values) for Aboveground Biomass Responses of Invasive Annual Bromes to Each Year’s Treatment Conditions at the Time of Sampling.

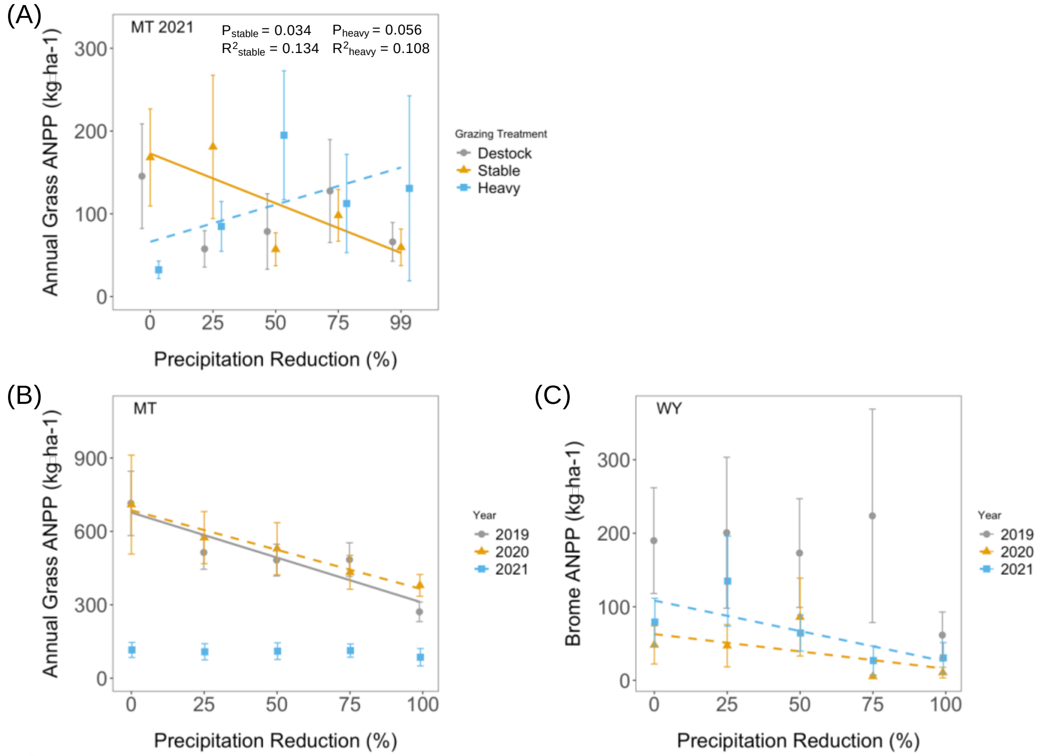
Site		Montana				Wyoming		
Year	Data Transformation	df	F-Value	P-Value	Data Transformation	df	F-Value	P-Value
2019	ln(data + 0.1)				ln(data + 0.1)			
W_{19}		1, 44.00	19.29	**<0.001*****		1, 44.00	0.10	0.76
2020	ln(data + 0.1)				ln(data + 0.1)			
W_{20}		1, 43.00	3.13	**0.08***		1, 43.00	3.93	**0.05***
G_{19}		1, 17.99	0.19	0.67		1, 7.47	0.00	0.98
$W_{20} \times G_{19}$		1, 43.00	0.01	0.92		1, 43.00	0.78	0.38
2021	square root				N/A			
WR_{21}		1, 42.00	0.25	0.62		1, 42.00	3.42	**0.07***
G_{20}		2, 10.10	1.65	0.24		2, 9.72	1.22	0.34
$WR_{21} \times G_{20}$		2, 42.00	3.87	**0.03****		2, 42.00	1.41	0.25

Note. We assessed biomass response to each year’s applicable precipitation reduction and grazing treatments. W = water treatment, G = grazing treatment, WR = water treatment recovery. Numerical subscripts indicate year abbreviations for 2019-2021. Significant values are shown in boldface type, with * indicating $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$.

Annual brome responses

While we found no main effects of grazing on annual brome biomass (Fig. S1, available online at [insert URL here]; Table 2.1), we did find an interactive effect of water treatment and grazing on annual brome biomass in Montana in 2021, where biomass significantly decreased with severe precipitation reduction under stable grazing and marginally increased as precipitation reduction intensified under heavy grazing (Fig. 2.2A, Table 2.1). Under stable grazing conditions, average biomass decreased from 168.2 ± 58.7 kg · ha-1 to 59.5 ± 22.2 kg · ha-1 (64.6% decline) from 0 to 99% precipitation reduction. Conversely, under heavy grazing conditions, average annual brome biomass marginally increased from 32.4 ± 10.6 kg · ha-1 to 130.8 ± 111.8 kg · ha-1 (75.2% increase) from 0 to 99% precipitation reduction (Fig. 2.2A). Further, we found main effects of precipitation reduction on annual brome biomass. Annual brome biomass decreased linearly with precipitation reduction in 2019 (first year of precipitation reduction) in Montana. In contrast, in Wyoming, all treatments maintained similar annual brome biomass except the 99% precipitation reduction treatment, which had on average less than half the biomass of other water treatments (Fig. 2.2B, C, and Table 2.1). In 2020, the second year of precipitation reduction, both sites displayed a marginally significant negative linear relationship between annual brome biomass and precipitation reduction. In Wyoming, this trend was also present in 2021 (recovery year; Fig. 2.2C, Table 2.1). In Montana, water treatments (ambient versus 99% precipitation reduction) reduced average annual brome biomass from 714.2 ± 131.7 kg · ha-1 to 271.2 ± 40.2 kg · ha-1 (62.1% decline) in 2019 and 709.7 ± 202.2 kg · ha-1 to 379.4 ± 44.6 kg · ha-1 (46.5% decline) in 2020 (Fig. 2.2). In Wyoming, water treatments (ambient versus 99% precipitation reduction) reduced average annual brome biomass from 48.1 ± 25.9 kg · ha-1 to 10.6 ± 7.2 kg · ha-1 (78.1% decline) in 2020 and 79.3 ± 32.3 kg · ha-1 to 30.5 kg · ha-1 ± 20.9 (61.5% decline) in 2021 (Fig. 2.2).

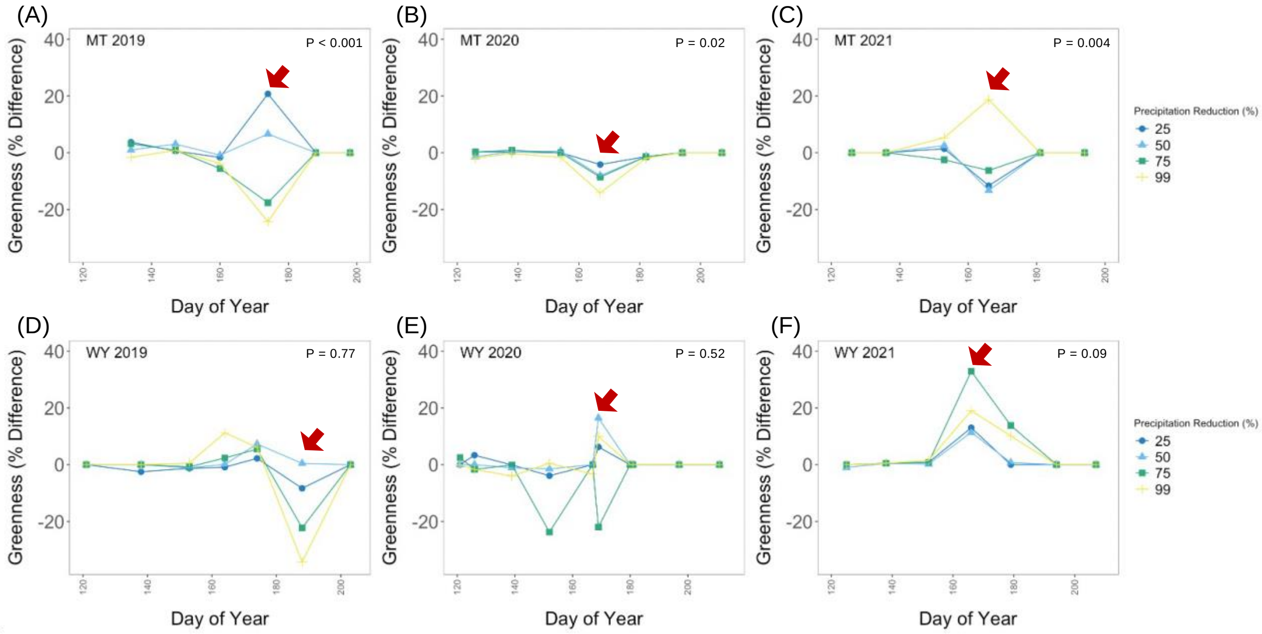
Figure 2.2. Mean +/- Standard Error of Aboveground Net Primary Production (ANPP) of Annual Grass Species for Precipitation Reduction Treatments at Montana (MT) by (A) Grazing Treatment or (B) Year, and (C) of Annual Brome Species at Wyoming (WY) by Year.



Note. (A) P values and marginal R^2 values for grazing treatments with significant or marginally significant precipitation-reduction effects are shown. Solid lines indicate significant main effects of water treatment ($p < 0.05$), and dashed lines indicate marginally significant results ($0.05 < p < 0.1$) as calculated from the linear mixed-model ANOVAs (Table 2.1).

Throughout each growing season, grazing had no direct or interactive impacts on annual bromes percent green, but precipitation reduction treatments did result in within-season changes to brome phenology (Table 2.2). In 2019 and 2020 at Montana, imposed water treatments negatively impacted percent green (Fig. 2.3, Table 2.2). Here, field brome experienced earlier senescence under more extreme precipitation reduction. This pattern was not present in Wyoming (Table 2.2). In contrast, recovery year results revealed significant, positive legacy effects of water treatments in Montana and marginally significant, positive legacy effects of water treatments in Wyoming, with foliar greenness declining earlier in ambient precipitation plots than the most extreme precipitation reduction plots (Fig. 2.3, Table 2.2).

Figure 2.3. Changes in Average Percent Green Difference of Annual Bromes within Each Growing Season (A-C) at Montana (MT) and (D-F) at Wyoming (WY) from 2019-2021.

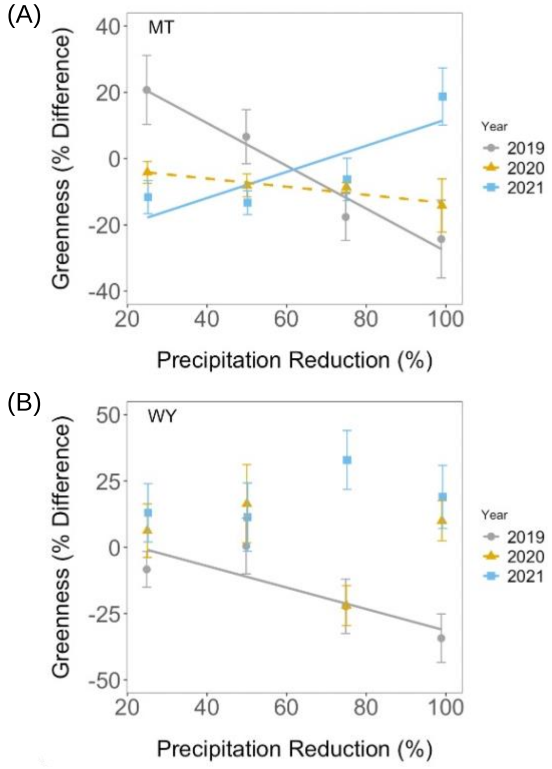


Note. Colored lines represent the water treatments. Julian day of the year is along the x-axis. P values are for the water treatment main effect. Arrow indicates the time point with the greatest difference in standardized percent green among water treatments chosen for further analyses (Table 2.3, Fig. 2.4).

When we assessed a single time point that represented peak differences in percent green across water treatments, these trends tended to persist. In 2019 at Montana, we again found water manipulation significantly decreased percent green of field brome and marginally decreased in

2020, but in 2021, percent green significantly increased with precipitation reduction (Fig. 2.4, Table 2.3). Similar to Montana, in Wyoming in 2019, we found a significant decrease in percent green difference of annual bromes with precipitation reduction (Fig. 2.4, Table 2.3). Additionally, in 2020 in Wyoming, we found an interaction between grazing and precipitation reduction on percent green difference, though post-hoc testing revealed no significant differences. We also found a main effect of grazing on percent green difference of annual bromes in 2020 in Wyoming, where percent green difference significantly decreased from stable to heavy grazing (Table 2.3).

Figure 2.4. Mean +/- Standard Error of Percent Green Difference of Annual Bromes at A) Montana (MT) and B) Wyoming (WY) from 2019-2021.



Note. Data shown is from a single time point representing peak differences in standardized percent green across the water treatments. Dates chosen for MT are June 24, 2019, June 16, 2020, and June 16, 2021, and dates chosen for WY are July 8, 2019, June 18, 2020, and June 16, 2021. Solid lines indicate significant effects of water treatment ($p < 0.05$), and dashed lines indicate marginally significant results ($0.05 < p < 0.1$) as calculated from the linear mixed-model ANOVAs (Table 2.3).

We found no significant effects of precipitation reduction or grazing on percent cover of field brome or cheatgrass at either site throughout the treatment years (Figs. S2-S3, Table S3, available online at [insert URL here]).

Table 2.2. Repeated-Measures Linear Mixed-Model Analysis of Variance (F Statistics with P-Values) for Differences in Annual Bromes' Percent Green Between Precipitation Reduction Treatments and Controls without Precipitation Reduction to Each Year's Treatment Conditions at the Time of Sampling.

Site	Montana			Wyoming		
Year	df	F-Value	P-Value	df	F-Value	P-Value
2019						
Date	1, 178	0.42	0.52	1, 232	2.50	0.12
W_{19}	1, 26	25.79	**<0.001*****	1, 21	0.09	0.77
Date × W_{19}	1, 178	0.24	0.63	1, 232	1.84	0.18
2020						
Date	1, 212	0.00	1.00	1, 189	0.54	0.46
W_{20}	1, 25	6.39	**0.02****	1, 13	0.44	0.52
G_{19}	1, 5	0.06	0.82	1, 3	2.27	0.23
W_{20} × G_{19}	1, 25	0.00	0.96	1, 13	0.06	0.81
Date × W_{20}	1, 212	0.14	0.71	1, 189	0.13	0.72
Date × G_{19}	1, 212	0.09	0.76	1, 189	0.06	0.81
Date × D_{20} × G_{19}	1, 212	0.03	0.86	1, 189	0.04	0.84
2021						
Date	1, 174	0.10	0.760	1, 253	0.24	0.62
WR_{21}	1, 24	10.25	**0.004****	1, 14	3.42	**0.09***
G_{20}	2, 4	2.80	0.17	2, 3	0.64	0.59
WR_{21} × G_{20}	2, 24	1.10	0.35	2, 14	1.29	0.31
Date × WR_{21}	1, 174	0.46	0.50	1, 253	0.08	0.78
Date × G_{20}	2, 174	0.04	0.96	2, 253	0.04	0.96
Date × WR_{21} × G_{20}	2, 174	0.01	0.99	2, 253	0.02	0.98

Note. We assessed this standardized percent green response to each year's applicable precipitation reduction and grazing treatments. Data presented here were collected from summer months (May-July). W = water treatment, G = grazing treatment, WR = water treatment recovery. Numerical subscripts indicate year abbreviations for 2019-2021. Data are approximately normal, so no data transformations were necessary. Significant values are shown in boldface type, with * indicating $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$.

Table 2.3. Linear Mixed-Model Analysis of Variance (F Statistics With P-Values) for Differences in Annual Bromes' Percent Green Between Precipitation Reduction Treatments and Controls without Precipitation Reduction to Each Year's Treatment Conditions at the Time of Sampling.

Site	Montana			Wyoming		
Year	df	F-Value	P-Value	df	F-Value	P-Value
2019						
W_{19}	1, 26.00	24.56	**<0.001*** **	1, 31.60	4.81	**0.04** **
2020						
W_{20}	1, 25.00	3.78	**0.06***	1, 18.05	1.64	0.22
G_{19}	1, 25.55	0.08	0.77	1, 18.03	5.68	**0.03** **
$W_{20} \times G_{19}$	1, 25.00	0.13	0.73	1, 18.04	4.54	**0.05** **
2021						
WR_{21}	1, 28.00	18.21	**<0.001*** **	1, 30.10	0.44	0.51
G_{20}	2, 28.00	0.18	0.84	2, 5.50	0.48	0.65
$WR_{21} \times G_{20}$	2, 28.00	1.15	0.33	2, 30.11	0.65	0.53

Note. Data shown is from a single time point representing peak differences in percent green across the water treatments. Dates chosen for Montana are June 24, 2019, June 16, 2020, and June 16, 2021, and dates chosen for Wyoming are July 8, 2019, June 18, 2020, and June 16, 2021. We assessed this standardized percent green response to each year's applicable precipitation reduction and grazing treatments. W = water treatment, G = grazing treatment, WR = water treatment recovery. Numerical subscripts indicate year abbreviations for 2019-2021. Data are approximately normal, so no data transformations were necessary. Significant values are shown in boldface type, with * indicating $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$.

Discussion

The use of experimental manipulations is critical for understanding potential global change impacts; however, global change experiments are often limited in spatial and temporal scale (De Boeck et al., 2015) and rarely include recovery. Water manipulations using rain-out shelters are challenging due to the cost and difficulties of maintaining infrastructure (Svejcar et al., 1999; Yahdjian and Sala, 2002), while grazing experiments must deal with the logistical and financial challenges associated with large mammals (Bransby, 1989), making manipulated precipitation and grazing experiments rare. Those that do exist focus primarily on single-year water manipulation events, rather than multiple years of precipitation reduction. Here, we uniquely combined the impacts of two years of multi-intensity water removal treatments with summer grazing on invasive annual grasses.

We hypothesized that precipitation reduction and summer grazing would have an interactive impact on invasive annual bromes. We found evidence of this interactive effect on annual brome biomass at the Montana site only during the recovery year in 2021. Stable grazing conditions led to a decrease in annual brome biomass under precipitation reduction, while heavy grazing led to a marginal increase in annual brome production when combined with prior precipitation reduction. When water stress is severe, heavier grazing can promote annual brome abundance, possibly by reducing native plant biomass, thus reducing competition for resources (Davies et al., 2014, 2011). As these are disturbance-adapted systems, our results from summer grazing make sense given previous work on heavy or overgrazing of water-stressed systems. Grazing has been shown to maintain grassland states (Gibson, 2009), but varying intensities of grazing (e.g., moderate versus heavy) can alter the plant community (Veblen et al., 2016; Wells et al., 2022). Low to moderate grazing may have neutral or positive impacts on invasion resistance (Porensky et al., 2020) through direct negative impacts on annual bromes (Haferkamp and Karl, 1999; Stechman and Laude, 1962) and positive effects on the grazing-adapted native plant community (Collins and Barber, 1986; Patton et al., 2007). However, given that our grazing treatments occurred in the summer after annual bromes had matured (and likely dropped seeds), we did not expect to see strong main effects of our grazing treatments on annual brome performance in the next growing seasons. Spring grazing is commonly used to manage invasive annual bromes (Daubenmire, 1940; Diamond et al., 2012; Harmoney, 2007; Porensky et al., 2021), but some evidence suggests that late-season (Schmelzer et al., 2014; Stechman and Laude, 1962) or season-long (Haferkamp and Karl, 1999) grazing can decrease annual brome production. However, most evidence suggests that invasive annual bromes are not impacted by summer or end-of-season grazing conditions (Ashton et al., 2016; Bailey et al., 2019; Cook and Harris, 1952; Mosley, 1996; Mosley and Roselle, 2006; Salesman and Thomsen, 2011; Vermeire et al., 2009b), which corresponds to the timing of our grazing treatments.

Previous work on the response of invasive annual bromes to drought is mixed, and in part depends on the timing and severity of the drought (Bradley et al., 2016), and the nature of legacy effects. We hypothesized that in addition to interactive effects of precipitation reduction and grazing, we would see main effects of water reduction on annual bromes, where brome biomass and percent cover would decrease during imposed precipitation reduction years but would increase in the recovery year. Following a year-long severe natural drought, the percent cover of cheatgrass increased for three years before declining, while the dominant native species experienced declines following drought (Souther et al., 2020). Further, fall precipitation has been shown to affect annual brome biomass in the following summer (Rinella et al., 2020) and increased fall water can increase annual grass production, especially under spring drought (Vermeire and Rinella, 2020). Other evidence suggests summer drought can impact invasive annual bromes, with summer drought favoring annual brome production over native species. Generally, our hypothesis was supported for biomass responses during precipitation reduction years, though the timing and magnitude of support differed between sites and response variables. In Montana, the effects of imposed precipitation reduction treatments were stronger in the first year of precipitation reduction. Bromes decreased in biomass with precipitation reduction in 2019, and marginally decreased in 2020. In contrast, we observed no effects of imposed precipitation reduction in Wyoming during the first precipitation reduction year, and only weak effects during the second precipitation reduction year, when biomass marginally decreased with greater precipitation reduction. However, we also saw marginal lagged (legacy), negative effects of precipitation reduction from prior years on absolute annual brome biomass in 2021, with biomass still decreasing after imposed precipitation reduction.

In years of average to above-average spring/summer precipitation, native perennial species can better resist invasive annual bromes as greater water availability occurs simultaneously with periods of native plant growth, helping to compensate for moisture losses depleted by annual grasses. Alternatively, in similar systems, drought conditions during the growing season have been found to favor winter annual grasses and annual brome production since their growth periods are early in the spring when moisture inputs from snowmelt and rain are often large and evaporative losses are small (Bradford and Lauenroth, 2006; Bradley, 2009; Bradley et al., 2016; Johnston and Garbowski, 2020; Meyer et al., 1997). In our study, limiting water during the growing season (April-October) tended to reduce annual brome biomass while having no significant effects on percent cover. Only when a third year of low water (natural 2021 drought in Montana) occurred, and was combined with heavy grazing, did we see an increase in annual brome production. In all other less extreme treatment comparisons, annual brome production was unaffected or declined. This suggests that as drought periods become longer and more extreme, annual bromes may experience a competitive advantage, especially after multi-year droughts, but that the threshold by which this advantage is reached may be high. Furthermore, field experiments with rainout shelters have been shown to underestimate the response of plant biomass to drought compared to natural conditions, suggesting annual brome responses may be more extreme during natural drought (Kröel-Dulay et al., 2022).

We also hypothesized that annual bromes would senesce earlier in the season during precipitation reduction years but would delay senescence in the recovery year. In general, this hypothesis was supported. We found strong support that annual bromes senesced more quickly under imposed water treatments in 2019 at both sites and weak support for this in Montana in 2020 when assessing differences at a single time point. Further, following imposed water treatments, we found annual bromes delayed time to senescence in Montana, with weaker support for this in Wyoming. This differential response could be due to benefits of drought to annual bromes relative to native plant species or could reflect the different magnitudes of water treatment imposed and could indicate high capacity of phenological plasticity that allows varying response of annual bromes to drought. Additionally, previous year’s drought may indirectly delay senescence of annual bromes due to a release from (resource) competition with perennial grasses still weakened by prior drought (Rice et al., 1992). Invasive annual bromes, growing early in the season, can take advantage of available moisture (and nutrients) that native plants are not able to utilize (Howell et al., 2020), especially if native plants recover slowly after drought (i.e., drought legacy effects).

Our results suggest that annual bromes vary in their resistance (i.e., current-year effect) and resilience (i.e., legacy effects) to droughts by field site. We found that annual bromes were more resistant to drought in Wyoming than Montana but more resilient to drought in Montana than Wyoming. This variation by site may represent inherent vegetation differences. At the

Wyoming site, annual brome phenology overlaps less with native plant phenology, due to the greater abundance of C_4 grasses (Porensky et al., 2018). Thus, growing season precipitation reduction combined with active native plant growth in the late summer/fall could draw down resources (e.g., nitrogen, water), negatively impacting annual brome growth in the fall/winter/early spring period (Ogle et al., 2003). Whereas at the Montana site, cool-season C_3 grasses dominate, which generally grow at the same time as invasive annual bromes, leading to stronger current-year water effects (Haferkamp et al., 2005).

Alternatively, these mixed results of precipitation reduction on invasive annual bromes could be due to differences in water treatment effectiveness (Hoover et al., 2018). In our two implemented water treatment years (2019-2020), we were able to impose a significant gradient of precipitation reduction conditions at both sites (Fig. 2.1). However, the magnitude of soil moisture effect was greater in Montana. Specifically, our first year of imposed precipitation reduction (2019) was a relatively average year at the Montana site. In contrast, the Wyoming site experienced a wet year which likely minimized the effectiveness of the rainout shelters. In 2019, 99% rainfall reduction represented a 42.2% reduction in soil moisture availability in Montana, but only a 24.1% reduction in soil moisture availability in Wyoming. In 2020, which was a drought year in Wyoming, the 99% water treatment reflected only a 25.2% reduction in soil moisture availability in Wyoming but a 43.6% reduction in soil moisture availability in Montana. Overall, while still significant, our water reduction treatments (2019, 2020) were of smaller magnitude in Wyoming than Montana, which may have led to weaker and/or delayed treatment effects. Further, while 2021 was the recovery year, Montana experienced low ambient precipitation conditions. Therefore, rather than serving as a recovery year, we had a natural drought at the Montana site, which already received more severe precipitation reduction in 2019-

2020. Considering the soil moisture availability differences between sites, the decrease in biomass of annual bromes during both water treatment years in Montana makes sense, as does the more moderate responses seen in Wyoming. Further work will be needed to distinguish between these two hypotheses (which could also be acting together in our study).

Implications

Invasive annual bromes are known to decrease available high-quality forage for livestock (DiTomaso, 2000; Haferkamp et al., 1998, 1997, 1994), decrease native species diversity, and lead to broad-scale soil erosion in similar regions of the Great Basin (Knapp, 1996). Further, high annual brome abundance can decrease livestock performance by decreasing animal weight gains (Haferkamp et al., 2001). With an ever-growing human population, increased food demand, and severe consequences of climate change, it is crucial to understand how we can sustainably manage our rangeland ecosystems. Our results suggest that grazing management choices during drought can influence annual brome production, and drought can also have impacts on forage quality by affecting annual brome senescence patterns. Overall, the greater the magnitude of water reduction, the greater the reduction in annual brome biomass, but when a natural drought is combined with heavy grazing (which is common in drought years), there is potential for annual brome invasion to increase in subsequent years. In addition, in the year following reduced precipitation, legacy effects on forage quality can remain by delaying annual brome senescence. In a positive light, the threshold at which reduced precipitation and grazing stress interact to decrease rangeland sustainability may be quite high due to drought and grazing resistance of native vegetation. This highlights the need to maintain native populations of plants in these ecosystems as extreme scenarios become even more common in the future.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

SEK, KJK, LMP, KOR, KRW designed the experimental platform while MDTF designed the invasion study. All authors collected data, and MDTF, SEK, and KRW performed analyses. MDTF wrote the manuscript, and all authors edited the manuscript.

Data Availability Statement

The datasets and code [CODE AND DATA WILL BE MADE AVAILABLE TO GITHUB UPON ACCEPTANCE] for this study can be found in the [NAME OF REPOSITORY] [LINK].

CHAPTER III: INVASIVE ANNUAL GRASSES ALTER NATIVE PLANT COMMUNITY STABILITY IN A NORTHERN MIXED-GRASS PRAIRIE

Authored by: Morgan D. T. Frost, Lauren M. Porensky, Kurt O. Reinhart, Sally E. Koerner. In preparation for submission to *Ecology*

Abstract

Temporal community stability, here defined as temporal mean divided by temporal standard deviation, plays an important role in predicting certain ecosystem services. However, temporal stability can change with invasion, with greater abundances of invasive species potentially having greater impacts on native community stability. The exact consequences of invasion for temporal stability are unclear, and in part depends on the particular metric of stability measured. In rangeland ecosystems, predicable forage quality and quantity are important for livestock production but can be threatened by invasion. Therefore, using an observational field study conducted over three years in Wyoming, we assessed which metrics of plant community stability were altered by invasion and whether those effects were mediated by two environmental variables (light and soil moisture). *Bromus arvensis* and *B. tectorum* are two invasive annual weeds found across United States rangelands, including in the Northern mixed-grass prairies of Wyoming. We established plots along natural invasion gradients of *B. arvensis* and *B. tectorum* abundance and collected plant species composition data over three growing seasons from 2019-2021. We assessed associations between nine different metrics of plant community stability and invasion by *B. arvensis* and *B. tectorum*. We found that species turnover significantly increases with invasion by both species, while stability of forb (both brome species), C4 grass (*B. arvensis* only), and C3 grass (*B. tectorum* only) cover decreases with invasion. All metrics of stability associated with invasion supported the hypothesis of a destabilizing effect of invasion on the native plant community. Further, while we were unable to attribute many of these associations to mediation by light or soil moisture, we found that these environmental variables did mediate some associations between stability and invasion. Overall, our results align with previous work suggesting that invasive annual bromes can lead to decreased native plant stability, which has important implications for forage production, and thus, food security.

Keywords: *Bromus arvensis*, *Bromus tectorum*, grassland, invasion gradient, rangeland, stability

Introduction

Temporal stability, broadly defined in the literature, alters ecosystem dynamics (Ebel et al. 2022) and functioning (Tilman and Downing 1994, Loreau and Mazancourt 2013). Importantly, temporal stability can also impact provisioning of services, with temporally stable communities allowing for better prediction of certain ecosystem services (e.g., consistent pollination leading to reliable crop yield (Montoya et al. 2019)). Like most ecosystem properties, temporal community stability can be altered by invasive species (Valone and Balaban-Feld 2018). Frequently, invasion is linked to decreased species richness (Hejda et al. 2009, Mollot et al. 2017, Xu et al. 2022), evenness (Hejda et al. 2009, Xu et al. 2022), and diversity (Hejda et al. 2009, Wu et al. 2016, Xu et al. 2022). Thus, invasion should decrease stability, as high native diversity has often been shown to increase community stability (Tilman and Downing 1994, Tilman 1996, Tilman et al. 1996, 2006, 2014, Proulx et al. 2010, Cardinale et al. 2012, Wang and Loreau 2016, Hautier et al. 2020). However, previous work on the response of temporal stability to invasion is mixed and may change depending on the specific community and measure of stability (Evans et al. 2001, Pfisterer et al. 2004, Valone and Balaban-Feld 2018, Wang et al.

2019). Further, the response of native communities to invasion can be influenced by invasion abundance, where increased dominance by invasive species can lead to greater impacts on the native community (Litt and Steidl 2010, Robertson and Hickman 2012, Brummer et al. 2016).

Grasslands, covering nearly 40% of Earth's terrestrial surface (White et al. 2000, Suttie et al. 2005, Gibson 2009), are commonly used as rangeland, providing natural grazing areas for livestock and supporting the livelihoods of billions around the world (Sayre et al. 2013). However, grasslands are threatened by global change, including widespread invasive plant species (DiTomaso 2000, McCollum et al. 2017). While ecosystem heterogeneity in space and time is important for certain conservation objectives, such as wildlife habitat creation (Fuhlendorf and Engle 2001), temporal stability also supports objectives associated with other ecosystem services. Stability of key palatable forage species on rangelands is critical for ranchers and land managers who rely on predictable forage abundance each year (Tracy and Sanderson 2004, Sasaki and Lauenroth 2011, Bonin and Tracy 2012), especially under active disturbance regimes (Haughey et al. 2018).

Across the arid and semi-arid regions of North America, invasive annual grasses have significantly altered the landscape, changing portions of many ecoregions such as the Great Basin and Great Plains from perennial grass dominated communities to those dominated by invasive annual grasses (Mack 1981, D'Antonio and Vitousek 1992, Davies et al. 2021). This shift in dominance has led to changes in rangeland productivity, including increased annual variability in herbaceous forage production (Bradley and Mustard 2005, Clinton et al. 2010), as yearly abundance of invasive annual grasses more tightly depends on resource availability (Bradley et al. 2016). Invasive annuals have been shown to greatly decrease native plant abundance and diversity (Davies 2011), as invasive annuals outcompete native species (Nasri and Doescher 1995, Rafferty and Young 2002) by utilizing resources and growing rapidly earlier in the growing season (Melgoza et al. 1990, Humphrey and Schupp 2004). *Bromus arvensis* and *B. tectorum* are winter annual C_3 brome grasses that are widespread and well-established invasive species throughout North American Great Plains, especially in Northern mixed-grass prairies (Wright and Wright 1948, Hulbert 1955, Oja et al. 2003, Vermeire et al. 2009). Northern mixed-grass prairies of the Great Plains are essential for their utility as working rangeland and for their biodiversity (Samson and Knopf 1994, Martin et al. 1998, Samson et al. 2004). Though these annual brome species were introduced intentionally as forage for livestock and provide quality forage in the spring, upon flowering in ~mid-June, they become very low-quality forage (Hulbert 1955, Klemmedson and Smith 1964, Oja et al. 2003, Schachner et al. 2008, Vermeire et al. 2009) and decrease in protein percentage by ~97% after maturation (Morrow and Stahlman 1984, Chambers et al. 2007). Because of this, for long-term stability of forage usage on rangelands, and ultimately food security, it is important to understand how invasive annual bromes impact the stability of the native plant community (Ziska et al. 2011, Landmann 2017).

Using an observational field study conducted over three growing seasons, we assessed how plant community stability changes with invasion. We studied the effects of two invasive annual grasses (*B. arvensis* and *B. tectorum*) across gradients of invasion, as impacts of invasion on the native plant community vary depending on invasion abundance (Brummer et al. 2016). Further, while there are many measures and definitions of stability, such as those associated with constancy, resilience, and resistance (Grimm et al. 1992), here we assess several metrics associated with temporal stability (here described as the temporal mean divided by temporal standard deviation (Lehman and Tilman 2000)) of the plant community, as well as synchrony and species turnover, to determine which aspects of community stability change with invasion.

Specifically, we first assessed temporal stability of plant species richness, evenness, total plant cover, synchrony, and percent cover of dominant functional groups. We hypothesized that invasive bromes would decrease all metrics of plant community stability. We also hypothesized increasing brome invasion would result in higher species turnover. Invasive plants have been shown to increase turnover of native plant species by hindering reappearance of resident native species (Somodi et al. 2008), while negatively impacting community stability (Walker and Smith 1997). Second, we assessed whether patterns of community stability associated with invasion were mediated by stability of environmental factors (light transmittance to the soil surface and soil moisture). Invasive annual bromes can decrease light at the soil surface (Vinton and Goergen 2006, Bennett et al. 2014) and deplete soil moisture early in the growing season (Stark and Norton 2015, Souther et al. 2020). Thus, we explored both the direct and indirect (via light and soil moisture) effects of invasion on measures of community stability.

Methods

Site description

Northern mixed grass prairies cover 38% of grassland area in North America (Lauenroth 1979, Chimner and Welker 2011) and are important regions for biodiversity and livestock production, with up to 50% used for livestock grazing (Holechek et al. 2011, Vold 2018). We conducted our study in Converse County in northeastern Wyoming (43.30° N, -105.05° W) on private land within the Thunder Basin ecoregion, a 7000 km^2 region centered on the United States Forest Service-managed Thunder Basin National Grassland (Porensky et al. 2018). The climate in this shrubland-grassland ecotone is semi-arid (30-year MAP = 363 mm/year, with 40-50% of precipitation occurring April-June; mean temperature for 2019 = 5.9°C, with mean temperature ranges from -5°C in December to 22°C in July; elevation = 1097-1585 m above sea level) (Curtis and Grimes 2004, Connell et al. 2019, Porensky et al. 2020, NOAA National Centers for Environmental Information 2022). During this study, annual precipitation in Converse County, WY, was 390.7 mm (2019), 216.4 mm (2020), and 341.6 mm (2021) (Figure S2, NOAA National Centers for Environmental Information 2022). This area experiences moderate summer grazing, a conventional practice for this system. Common native plant species include *Artemisia tridentata* (Wyoming big sagebrush), *Bouteloua gracilis* (blue grama), *Carex filifolia* (threadleaf sedge), *Hesperostipa comata* (needle-and-thread grass), *Pascopyrum smithii* (Western wheatgrass), *Plantago patagonica* (wooly plantain), *Lepidium densiflorum* (common pepperweed), *Sphaeralcea coccinea* (scarlet globemallow), and *Opuntia polyacantha* (Plains pricklypear) (Porensky et al. 2018).

Study design

Data collection and study design was consistent across all 3 study years from 2019-2021. In July 2019, we established blocks along 10 natural invasion gradients in the Thunder Basin ecoregion. Each gradient (hereafter referred to as blocks) consisted of 5 permanent, 1 × 1 m plots with different levels of invasion (0%, 25%, 50%, 75%, and 100% relative cover) of each respective invasive species grouped together in space (Figure S1). Invasion levels represent approximate categorized aerial cover of the invasive annual brome. *B. tectorum* and *B. arvensis* each had 5 blocks, giving a total of 50 plots. Each year in June-July, we collected all data. At each plot, we measured plant species composition across the plot by visually estimating foliar cover (i.e., calibrated to estimates generated by a 100 pin-point intercept frame) for each species to the nearest percent. Additionally, we measured photosynthetically active radiation (PAR) below and above the plant canopy using an AccuPAR LP-80 Ceptometer to calculate percent transmittance of light to the soil surface. Last, we collected soil moisture (% volumetric water content [VWC]) from the center of each plot. We measured all abiotic variables (PAR and soil moisture) from all plots within a two-hour period centered around mid-day to account for daily variability.

Data analysis

To analyze relationships between stability and invasion, we used linear mixed-model regressions with invasion abundance as a fixed effect, block as a random effect, and the stability of richness, evenness, total cover, bareground cover, C_4 grass cover, C_3 grass cover, forb cover, light, and soil moisture, as well as turnover and synchrony, as response variables (lmerTest package (Kuznetsova et al. 2017). We assessed fixed effect significance using Type III analysis of variance (ANOVA) with Satterthwaite's method (Satterthwaite 1941)). We also examined how average soil moisture and light availability changed with invasion abundance using the same model structure. For each metric, we calculated stability as the temporal mean divided by temporal standard deviation across all 3 study years (2019-2021). We used the codyn package to calculate stability (of all 9 variables), synchrony, and turnover (Hallett et al. 2016). Because annual bromes are part of the plant community, we assessed how turnover, synchrony, and stability of richness, evenness, total cover, and C_3 grass cover changed in association with annual brome invasion using two methods: without (Table 3.1) and with (Table S1) brome data included (i.e., with and without *B. arvensis* data included in *B. arvensis* gradients and *B. tectorum* data included in *B. tectorum* gradients). For ease, we refer to the non-brome plant community throughout as the native plant community. However, our plant composition data also included low cover of several introduced species, all annual forbs (*Alyssum desertorum*, *Camelina microcarpa*, *Lactuca serriola*, *Logfia arvensis*, *Polygonum aviculare*, and *Tragopogon dubius*).

Following Duchardt et al. (2021), we tested for mediation of the effects of *B. arvensis* and *B. tectorum* on plant community stability by light availability and soil moisture. We used structural equation modeling using the lavaan package (Rosseel 2012) to build a model including all links and assessed whether each link was fully, partially, or not mediated by either light or soil moisture. We tested for evidence of full (A -> B -> C), partial (A -> B -> C; A -> C), and no (A -> C) mediation both by comparing path coefficients in the partial mediation models and assessing differences in Akaike Information Criterion corrected for small sample size (ΔAIC_c Burnham and Anderson 2002) between full, partial, and no mediation models. We used a ΔAIC_c cutoff of 5 in combination with strength of path coefficients to determine if we had enough support for one model over another. We conducted two separate mediation analyses – one with stability of light and soil moisture as mediators and the other with average light and soil moisture as mediators.

We conducted all calculations and analyses in R version 3.6.2 (R Core Team 2019) ($\alpha = 0.05$, but we report results with $0.05 < p < 0.1$ as marginally significant). We assessed normality of the residuals of all response variables using Shapiro-Wilk, Anderson-Darling, Cramer-von Mises, and Kolmogorov-Smirnov tests as part of the Olsrr package (Hebbali 2020). We then log-transformed data when necessary to achieve approximate normality (Tables 3.1, S1). We conducted all analyses for gradients of *B. arvensis* and *B. tectorum* separately. To ensure the gradients of invasion abundance held over time, we used repeated measures mixed-model ANOVAs. Predictors were invasion levels (categorical), year (categorical), and the interaction between invasion level and year; the response variable was the actual percent brome cover (*B. arvensis* in *B. arvensis* gradients and *B. tectorum* in *B. tectorum* gradients), and a random effect of block was included (Figure 3.1).

Table 3.1. Linear Mixed Model Analysis of Variance (F Statistics with P-Values) for the Response of Stability Metrics to Invasion by Annual Bromes.

	B. arvensis				*B. tectorum*			
Stability Metric	Log Transformation	df	F-Value	P-Value	Log Transformation	df	F-Value	P-Value
Richness Stability	Yes	1, 22.24	2.15	0.156	No	1, 20.00	7.03	**0.015****
Evenness Stability	Yes	1, 23.00	0.01	0.934	Yes	1, 23.00	3.74	**0.066***
Synchrony	No	1, 23.00	0.16	0.692	No	1, 23.00	0.66	0.425
Species Turnover	No	1, 22.97	6.25	**0.020****	No	1, 19.579	16.16	**<0.001*****
Cover Stability	Yes	1, 23.00	0.95	0.340	Yes	1, 23.00	0.13	0.726
Bareground Stability	Yes	1, 23.00	0.68	0.418	No	1, 19.547	4.72	**0.042****
C_4 Grass Stability	Yes	1, 18.22	6.01	**0.025****	Yes	1, 20.00	0.03	0.874
C_3 Grass Stability	Yes	1, 22.56	1.30	0.266	No	1, 19.62	13.84	**0.001*****
Forb Stability	Yes	1, 21.52	6.71	**0.017****	Yes	1, 16.04	3.85	**0.067***
Light Stability	Yes	1, 23.00	42.51	**<0.001*****	Yes	1, 23.00	25.75	**<0.001*****
Soil Moisture Stability	Yes	1, 20.85	0.26	0.614	No	1, 20.75	1.41	0.249

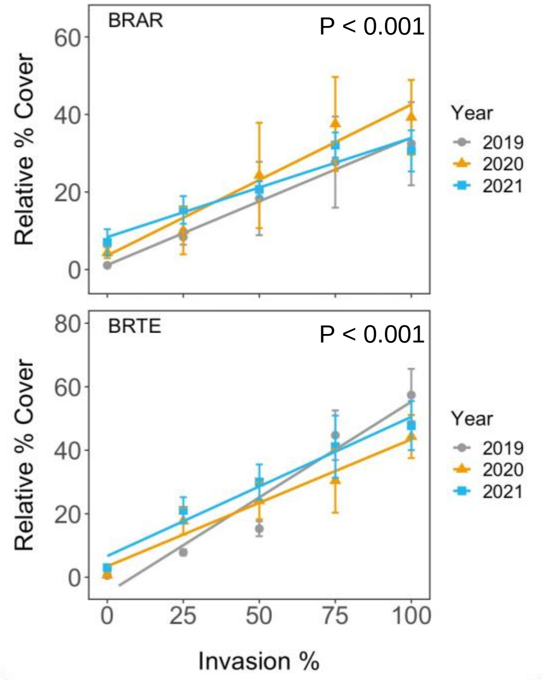
Note. Stability of richness, evenness, total cover, and C_3 grass cover, as well as turnover and synchrony, were calculated without respective brome data for each gradient type. Significant values are shown in boldface type, with * indicating $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$.

Results

Effectiveness of brome gradients

The gradients of invasion held across time for both *B. arvensis* and *B. tectorum* gradients (Figure 3.1). Percent cover of both *B. arvensis* and *B. tectorum* increased significantly with categorical invasion level throughout all three years of the study (for *B. arvensis*, invasion level $F_{1, 67} = 88.3$, $p < 0.0001$; for *B. tectorum*, invasion level $F_{1, 67} = 132.5$, $p < 0.0001$). In the *B. arvensis* gradients only, we also found a significant effect of year on percent cover of *B. arvensis* (year $F_{1, 67} = 5.5$, $p < 0.0001$, $p = 0.022$), but we found no interaction between invasion level and time (invasion level * year $F_{1, 67} = 2.3$, $p = 0.132$). In the *B. tectorum* gradients, we found no significant effect of year (year $F_{1, 67} = 0.9$, $p = 0.345$) or interaction between invasion level and year on percent cover of *B. tectorum* (invasion level * year $F_{1, 67} = 2.6$, $p = 0.113$).

Figure 3.1. Mean +/- Standard Error of Percent Cover of *B. arvensis* (BRAR) and *B. tectorum* (BRTE) across Categorized Invasion Levels from 2019-2021.

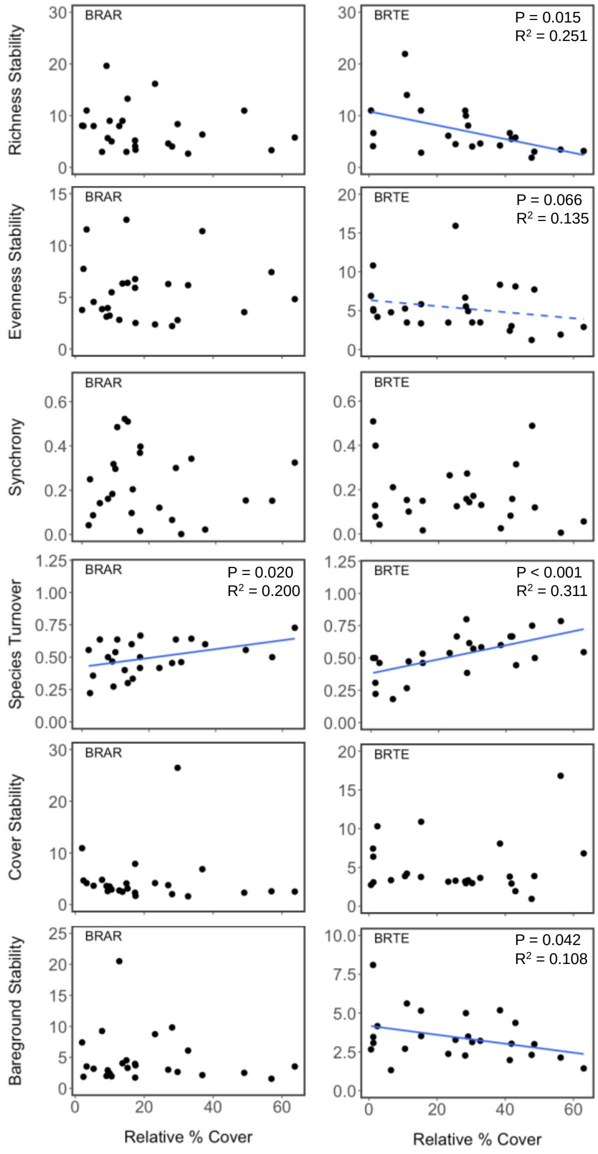


Note. Solid lines indicate significant relationships between invasion level and relative invasion cover ($p < 0.05$). P-values are for the main effect of invasion level from repeated measures mixed-model ANOVAs.

Associations between invasion and stability metrics

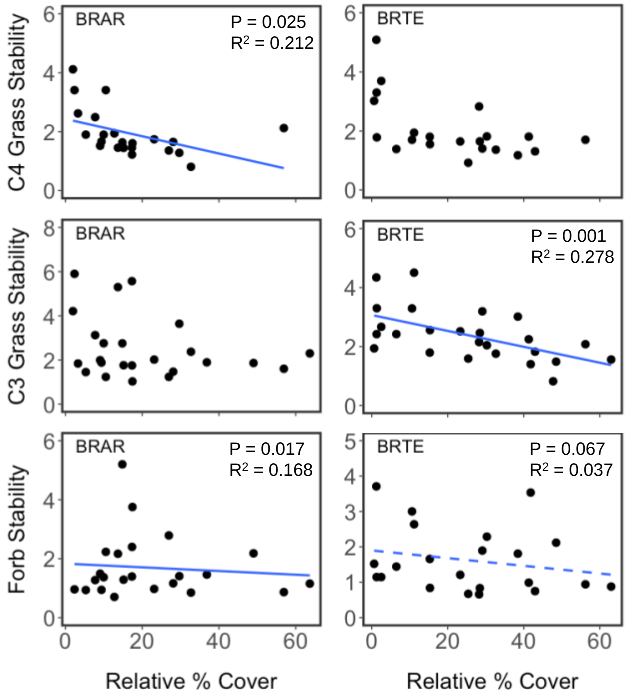
For both species of invasive brome, native plant species turnover significantly increased with invasion (Figure 3.2). In the *B. arvensis* gradients, stability of C_4 grass and forb cover significantly decreased with invasion (Figure 3.3, Table 3.1). In the *B. tectorum* gradients, native plant species richness stability, C_3 grass cover stability, and bareground cover stability significantly decreased with invasion, and native species evenness stability and forb cover stability marginally decreased with invasion (Figure 3.3, Table 3.1). We found no significant impact of either annual brome species on synchrony or total cover stability (Figure 3.2, Table 3.1). When including *B. arvensis* and *B. tectorum* data in each species' respective analyses, we again found that species turnover significantly increased with invasion and, in *B. tectorum* gradients only, richness stability significantly decreased with invasion (Table S1).

Figure 3.2. Changes in Plant Species Richness Stability, Evenness Stability, Synchrony, Species Turnover, Total Cover Stability, and Bareground Stability with Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE).



Note. Stability of richness, evenness, and total cover, as well as turnover and synchrony were calculated without respective brome data for each gradient type. P-values and marginal R^2 values for significant (solid lines) or marginally significant (dashed line) effects of invasion on stability metrics are shown according to results from mixed-model ANOVAs (Table 3.1).

Figure 3.3. Changes in Stability of C_4 Grass, C_3 Grass, and Forb Cover with Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE).



Note. Stability of C_3 grass cover was calculated without respective brome data for each gradient type. C_4 grass cover was largely dominated by one species, *Bouteloua gracilis*. P-values and marginal R^2 values for significant (solid lines) or marginally significant (dashed line) effects of invasion on stability metrics are shown according to results from mixed-model ANOVAs (Table 3.1).

Stability of light availability and average light availability significantly decreased with invasion by both annual brome species, while soil moisture stability and average soil moisture were not related to the brome invasion gradients (Figures 3.4, S3, Tables 3.1, S2).

Abiotic mediation of invasion-stability relationships

In the *B. arvensis* gradients, we found strong evidence that stability of light availability fully or partially mediated the effects of invasion on stability of C_4 grass cover, and weak evidence of this mediation on stability of forb cover. We also found weak support that soil moisture stability fully or partially mediated the effects of *B. arvensis* on stability of plant species richness. In the *B. tectorum* gradients, soil moisture stability strongly mediated the effects of invasion on stability of C_4 grass cover and weakly mediated the effects of invasion on forb cover stability (Table 3.2).

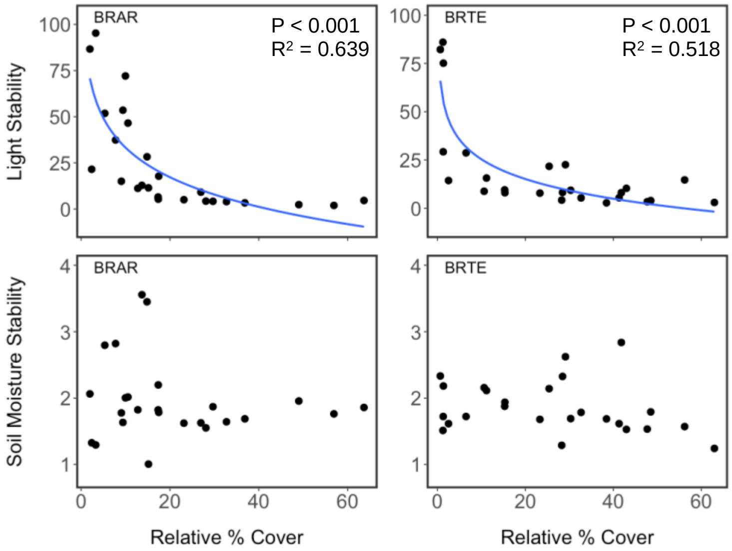
In addition, in the *B. arvensis* gradients, we found evidence that average light availability fully mediated the effects of invasion on C_4 grass stability and fully or partially mediated the effect of invasion on forb stability, though support for this was weaker. Further, we found strong support that average soil moisture fully or partially mediated the effects of invasion on richness stability. In the *B. tectorum* gradients, we found strong support that average soil moisture fully or partially mediated the effects of invasion on C_4 grass stability and forb stability (Table S3).

Table 3.2. Tests of Mediation to Assess Support for Direct and Indirect Effects of Invasive Annual Bromes on Plant Community Stability.

		Path Coefficients			△AICc			
Question	X	Mediating Variable (A -> B -> C)		Not Mediated (A -> C)	Fully mediated	Partially mediated	Not mediated	Conclusion
		Light stability	Soil moisture stability					
1. Is the effect of *B. arvensis* invasion on X mediated by abiotic variable stability (light, soil moisture)?	Richness Stab	-0.07	**-0.31***	-0.31	0	3.4	7.8	full/part mediated by SM stab
	Evenness Stab	0.19	0.023	0.17	0	4.1	8.5	no conclusion
	Synch-rony	0.05	0.056	-0.04	0	4.4	8.8	no conclusion
	Species Turnover	0.44	**0.29***	**0.81****	3.0	0	4.4	no conclusion
	Cover Stab	-0.17	0.08	-0.31	0	3.5	7.9	no conclusion
	C_4 Grass Stab	**0.73****	-0.12	0.12	0	4.9	10.4	full/part mediated by L stab
	C_3 Grass Stab	-0.44	0.21	**-0.58***	0	1.2	5.5	no conclusion
	Forb Stab	**0.55***	0.08	0.17	0	4.1	8.5	full/part mediated by L stab
2. Is the effect of *B. tectorum* invasion on X mediated by abiotic variable stability (light, soil moisture)?	Richness Stab	-0.32	0.27	**-0.67****	1.8	0	5.0	no conclusion
	Evenness Stab	0.16	0.02	-0.26	0	3.5	7.1	no conclusion
	Synch-rony	0.32	0.12	0.10	0	4.3	7.9	no conclusion
	Species Turnover	0.02	-0.03	**0.63****	2.4	0	3.6	no conclusion
	Cover Stab	0.14	-0.27	-0.045	0	4.4	8.0	no conclusion
	C_4 Grass Stab	0.28	**-0.58****	-0.07	0	5.0	9.8	full mediated by SM stab
	C_3 Grass Stab	0.08	-0.03	**-0.54****	0.5	0	3.6	no conclusion
	Forb Stab	0.03	**0.36***	-0.17	0	4.7	9.8	full/part mediated by SM stab

Note. Mediator variables here are stability of light (L) availability and soil moisture (SM). Stability (stab) of richness, evenness, total cover, and C_3 grass cover, as well as turnover and synchrony, were calculated without respective brome data for each gradient type. △AICc is change in Akaike information criterion corrected for small sample size. Significant values are shown in boldface type, with * indicating $p < 0.1$ and ** $p < 0.05$.

Figure 3.4. Changes in Stability of Light and Soil Moisture with Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE).



Note. P-values and marginal R^2 values for significant (solid lines) effects of invasion on stability metrics are shown according to results from mixed-model ANOVAs (Table 3.1).

Discussion

Overall, we saw that multiple metrics of plant community stability were associated with brome invasion. Importantly, when any stability metric was altered, invasion was associated with a destabilizing effect on the plant community. This is consistent with prior research, where greater dominance by bromes tends to produce less stable native plant productivity and cover (Germino et al. 2016). However, not all measured metrics of plant community stability were altered by annual brome invasion. Further, some results differed between species. In general, more measures of stability were associated with invasion in *B. tectorum* gradients, suggesting that this species may be more disruptive to stability. In both *B. arvensis* and *B. tectorum* gradients, species turnover was strongly related to brome abundance, demonstrating that even in the short-term, invasion can shape community structure (Leibold et al. 1997). High turnover of species can lead to deregulation of trophic structures (Leibold et al. 1997) and functional traits (Lepš et al. 2011). Decreases in C_4 grass (*B. arvensis* gradients), C_3 grass (*B. tectorum* gradients) and forb (both gradient types) cover stability with invasion could suggest possible increases in variability of forage and pollination availability, as high abundances of native grasses and forbs improve forage production and pollinator diversity on disturbance-adapted rangelands (Shaw et al. 2005, Drobney et al. 2020). In addition, in the *B. tectorum* gradients, decreases in richness stability and evenness stability indicate that invasion is associated with greater variability in biodiversity. Dominance by invasive bromes can lead to differences in plant community composition, compared to native dominated communities, causing consequences for both above and belowground properties of rangeland ecosystems (Duncan et al. 2004, Gasch et al. 2013). Further, decreases in bareground stability in *B. tectorum* gradients may indicate increased spatial heterogeneity, which can be beneficial for rare species' richness (Porensky et al. 2013), but could also be a mechanism for further invasion, as invasive species can co-occur with natives (Stotz et al. 2020) and can utilize patchy bareground cover to spread (Mealor et al. 2012, Chambers et al. 2014).

Our tests of mediation revealed that in several cases, relationships between invasion and plant community stability were mediated by abiotic factors. For example, in both brome gradients, C_4 grass cover stability and forb cover stability were mediated by light (*B. arvensis* gradients) or soil moisture (*B. tectorum* gradients). Annual bromes have been shown to alter microclimatic conditions, which in turns affects plant community composition (Ogle 2000). Success of C_4 grasses often depend on moderate-high light availability (Still et al. 2003) and can be influenced by soil moisture (Nie et al. 1992). Similarly, forb success is related to soil moisture (Fay and Schultz 2009) and light availability (Turner and Knapp 1996), so it is expected that the relationship between invasion and stability of C_4 grass cover and forb cover would be mediated by soil moisture and light. Understanding direct and indirect responses to invasion are important, as resistance and response to invasion are highly related to the environment (including climate and soil properties) (Chambers et al. 2014). Conversely, continued spread and impact of invasion on native communities are also related to these environmental factors. For instance, high summer precipitation can increase resistance to brome invasion (Chambers et al. 2007, 2016), but high variability in soil moisture with low perennial cover can contribute to further invasion (Chambers et al. 2007). Further, dominance by bromes is related to high light availability, while low irradiance hinders brome establishment (Bookman and Mack 1983, Pierson et al. 1990).

For other stability metrics, we were unable to draw conclusions about the direct or indirect effects of invasion on metrics of plant community stability. In particular, we were unable to attribute the relationship between invasion and C_3 grass stability to light or soil moisture, possibly because other, unmeasured variables may more strongly contribute to this relationship, such as soil nitrogen availability (Vasquez et al. 2008). Nevertheless, it is also notable that we did not find strong evidence of direct effects (unmediated by abiotic factors) for any metric. Because these analyses were conducted as part of this observational field study, a more controlled experimental manipulation could be useful to tease apart the direct and indirect effects of invasion on stability.

Interestingly, over this three year study, the invasion gradients held, suggesting *B. arvensis* and *B. tectorum* abundance in each plot was relatively constant. The first year of the study, 2019, was a relatively wet year, while year two, 2020, was a relatively dry year, and year three, 2021, had near average precipitation (Figure S2). Yearly brome abundance tends to be greatly associated with precipitation (Ganskopp and Bedell 1979, Bradley et al. 2016), so it is somewhat surprising that the invasion gradients held so constant given these differences in yearly precipitation. However, bromes tend to be more heavily influenced by fall/winter/spring precipitation (Bradley et al. 2016), which had less variability over the course of the study than later spring/summer precipitation (Figure S2).

Understanding how temporal stability changes with invasion has important consequences for ecosystem services like food security, and even restoration potential of invaded range. Native plant production is critical to range-fed livestock. The forage quality of invasive annual bromes is known to peak early in the growing season and to decline rapidly relative to native vegetation, which can negatively impact livestock performance and animal weight gain (Haferkamp et al. 1994, 1997, 2001, DiTomaso 2000). In addition, invasion by annual species, coupled with year to year variability in climate, can impact restoration success, as unstable native cover may lead to long-term changes in soil properties (Mahood et al. 2022). In general, we found that annual bromes were associated with destabilization of plant communities, especially metrics associated with native forage (stability of C_3 grass, C_4 grass, and forb cover). Therefore, annual brome invasion may increase the need for adaptive management to cope with increased inter-annual variability in forage quantity and quality (Monaco et al. 2016), as this may have unforeseen consequences for the livelihoods of billions of people worldwide who depend on working rangeland (Sayre et al. 2013).

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

MDTF and SEK designed the study; MDTF conducted the study and all analyses. MDTF wrote the manuscript, and all authors advised on analyses and edited the manuscript.

CHAPTER IV: PLANT, INSECT, AND SOIL MICROBIAL COMMUNITY RESPONSES TO INVASION ABUNDANCE IN NORTHERN MIXED-GRASS PRAIRIES

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Abstract

Native communities are shaped by interactions between plants, microbes, and insects. Changes in plants, in particular, have cascading effects on interactions within communities, and like all aspects of ecosystems invasion threatens native communities and the dynamic processes that shape them. The consequences of invasive species, especially plants, stretch across taxa to impact plants, insects, and soil microbial communities directly and indirectly, with consequences for ecological functioning and the delivery of ecosystem services. In northern mixed-grass prairies, invasion by two annual brome grasses, *Bromus arvensis* and *B. tectorum*, negatively impacts rangeland plants; however, the simultaneous effects for insects and soil microbes, and the implications for ecological function, has gotten less attention. Here, using observational field studies conducted at two mixed-grass prairie sites in Montana and Wyoming, we assessed the relationships between plant, insect, and soil microbial communities and a gradient of invasion by *B. arvensis* and *B. tectorum*. To do this, we established plots along natural invasion gradients of each annual brome species and collected community data from three organismal groups (plant, insect, and soil microbes). Overall, we found differences in plant and insect communities and functional groups with increasing invasion abundance for both brome species. However, we only saw associations between invasion and the soil microbial community under *B. tectorum* invasion, implying both that *B. tectorum* may have more substantial consequences for rangelands, and that management may need to differ according to brome species. While invasion by annual bromes may cause changes in certain functions, such as forage availability due to both insect herbivory pressure and competition with invasive bromes, other ecological functions, like nutrient cycling in the soil, may be less impacted, especially under *B. arvensis* invasion. This work sheds light on the unique relationships between invasion and native plants, insects, and soil microbes, demonstrating the need to explore changes in natural communities of all taxa and to all invasive species, as this could have important implications for ecosystem functioning.

Keywords: *Bromus arvensis*, *Bromus tectorum*, arthropods, herbivory, soil microbes

Introduction

Plant-microbe-insect interactions of natural ecosystems are intricately tied together and are ecologically and evolutionarily important (Biere and Bennett, 2013; Ohgushi, 2005; Van der Putten et al., 2001). Growing evidence suggests that changes in one aspect of these three way interactions can have cascading consequences for overall community structure, function, and stability (Biere and Bennett, 2013; Ohgushi, 2008). For example, soil microbes can trigger bottom-up effects on insect herbivores by altering plant abundance and overall nutritional quality (Hartley and Gange, 2009; Van der Putten et al., 2001). Changes in plants, in particular, have cascading effects on interactions with other taxa, shaping their community structure (Ohgushi, 2008, 2005; Van der Putten et al., 2001). Like all aspects of ecosystems, invasion directly and indirectly threatens native communities and the dynamic processes that shape them including plant, insect, and microbe interactions, with consequences for ecological functioning and the delivery of ecosystem services (McCary et al., 2016; Schirmel et al., 2016; Traveset and Richardson, 2014; Vilà et al., 2011).

Invasive species are present in nearly every ecosystem on the planet (Pejchar and Mooney, 2009) and are known to affect community composition and taxonomic richness across ecosystem types (Denley et al., 2019). Plant invasion can lead to loss of certain taxa, including plants (Maskell et al., 2006) and insects (Litt et al., 2014). Invasive plants outcompete native plants for limiting resources to drive down plant diversity, often by affecting typical nutrient cycling and soil water (Hejda et al., 2009; Walker and Smith, 1997). This in turn creates less habitat and food for arthropods, thus impacting insect composition (Litt et al., 2014), often by decreasing suitable oviposition habitat and available nutritious forage (Bezemer et al., 2014). However, some insect herbivores perform as well or nearly as well under plant invasion, in part depending on whether the herbivores are generalist or specialist species (Bezemer et al., 2014). Further, invasive plants can affect the structure and composition of soil microbial communities, likely through changes in soil properties, (Batten et al., 2006; Reinhart and Callaway, 2006; Wolfe and Klironomos, 2005), even after removal of the invasive species (Corbin and D'Antonio, 2012). For instance, soil microbial diversity and activity can increase under plant invasion due to changes in soil nutrients, pH, and root exudates from the invasive (Xu et al., 2022). Moreover, the feedback between soil communities and invasive plants can be positive or negative, where soil microbes can resist or facilitate invasion and invasives can in turn affect the composition of soil biota (Reinhart and Callaway, 2006). In all, complexity across food webs can predict stability of ecosystem processes, either by enhancing or hindering stability, but these connections are impacted by invasion (Landi et al., 2018).

Changes in community composition can lead to changes in functional group composition, so we can gather information about functional composition by assigning taxa to ecologically relevant functional groups. Both taxonomic and functional identifications are important for understanding ecosystem consequences from changes in species patterns (Slade et al., 2007). Functional groups used for plants can center around life form, morphology, leaf or root structure, and physiology (Korner, 1993), which gives insight into productivity, light availability, soil properties, and water/resource usage (McLaren and Turkington, 2010). Additionally, insect communities can be grouped into functional groups corresponding to feeding guilds (Novotny et al., 2010). This allows for an understanding of guild structure within insect communities, such as predator/prey relationships, as well as how those insects relate to other communities (e.g., different classifications of herbivores consume plant material differently) (Cagnolo et al., 2002). Last, ecological functions for soil microbial communities center around nutrient cycling, pathogenic behavior, and decomposition, which gives insight into resource availability and soil health (Brussaard, 1997). Because many taxa across plants, insects, and microbes can belong to the same functional group (Simberloff and Dayan, 1991), understanding functional composition is important for understanding functional redundancy.

As mentioned, changes in community composition can lead to changes in ecological function, even if richness is constant (Spaak et al., 2017). While there is some thought that distinct soil microbial communities will function the same way in identical environments, evidence suggests that soil microbes are not always functionally redundant, and function depends on specific composition (Lucas et al., 2020; Strickland et al., 2009), with large differences in function related to disturbance (Berga et al., 2012). However, invasive plants can cause changes in certain microbial taxa without altering much ecological function (Gibbons et al., 2017). In plant communities, while global change drivers can shift community composition, leading to large changes in productivity and overall ecosystem function (Avolio et al., 2014), natural variation in plant communities can also predict changes to ecosystem functioning (Kahmen et al., 2005). In diverse plant communities, loss of one plant species can be compensated by other species (Joner et al., 2011). For insects, alterations in community composition can alter functional composition, where fewer insect functional groups is associated with decreased diversity, richness, and changes in composition (Bellamy et al., 2018). Further, invasive plants can lead to decreases in insect biomass/diversity and altered function without altering overall insect abundance (Heleno et al., 2009). Changes in diversity in response to invasion can ultimately alter ecological functioning, including carbon and nitrogen cycling, pollination, and plant forage quality (Batten et al., 2006; Kaiser-Bunbury et al., 2011; Memmott and Waser, 2002; Stout and Morales, 2009).

Across the North American Great Plains, including in northern mixed-grass prairies, the invasive winter annuals, *Bromus arvensis* and *B. tectorum*, cause damage to native rangeland ecosystems by outcompeting native grasses, which are better forage species (Hulbert, 1955; Oja et al., 2003; Vermeire et al., 2009; Wright and Wright, 1948). However, how these two annual brome species impact communities simultaneously across plants, insects, and soil microbial communities, remains to be explored. Therefore, using observational field studies in the northern mixed-grass prairies of Wyoming and Montana, we simultaneously explored the associations between annual brome abundance and plant, insect, and soil microbial communities, including their diversity, community composition, and functional composition. We hypothesized that (1) richness across all three groups (plants, insects, soil microbes) would decrease with increasing levels of invasion and that (2) both community and functional composition of each group would shift gradually with increasing invasion abundance. Additionally, we predicted no differences in responses between plants, insects, and microbes (i.e., plants are not more sensitive to invasion than soil microbes) and that all three groups would relate to both species of bromes similarly.

Methods

Site description

We conducted this observational field study at two sites (in 2019 at the Wyoming site and in 2020-2022 at the Montana site) within the Northern Great Plains steppe ecoregion, an area dominated by temperate and semiarid mixed-grass prairie (Martin et al., 1998). The Northern Great Plains steppe is important for livestock grazing, with nearly 50% used to support livestock (Holechek et al., 2011; Vold, 2018). The Wyoming site (43.30° N, -105.05° W) is located on private land in a shrubland-grassland ecotone in Converse County, WY, at the southern end of the Northern Great Plains (an area known locally as the Thunder Basin ecoregion) (Porensky et al., 2018). The Montana site (46.34° N, -105.99° W) is located at the Fort Keogh Livestock and Range Research Laboratory in Custer County, MT, and is central in the Northern Great Plains steppe.

Both sites have a semi-arid climate and are moderately grazed in the summer. At the Wyoming site, mean annual precipitation (MAP) is 250-300 mm, with 40-50% falling in April-June, and mean monthly temperature ranges from -5°C in December to 22°C in July (Curtis and Grimes, 2004; Porensky et al., 2018). In Converse County, WY, annual precipitation in 2019 was 390.7 mm (NOAA National Centers for Environmental Information, 2022). For the Montana site, MAP is 342 mm, with ~50% of the precipitation falling in May-June, and mean monthly temperature ranges from -10°C in January to 24°C in July (Peterson and Reinhart, 2012; Waterman et al., 2021; Wilcox et al., 2015). In Custer County, MT, annual precipitation in 2020 was 251.0 mm, in 2021 was 257.3 mm, and in 2022 was 366.3 mm (NOAA National Centers for Environmental Information, 2022). Common plant species at both sites include *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young (Wyoming big sagebrush), *Bouteloua* *gracilis* (blue grama), *Carex filifolia* Nutt. (threadleaf sedge), *Hesperostipa comata* (needle-and-thread grass), *Pascopyrum smithii* (western wheatgrass), *Bromus tectorum* (cheatgrass), *Bromus arvensis* [*Bromus japonicus*] (field brome), *Vulpia octoflora* (Walter) Rydb. (six-week fescue), and *Plantago patagonica* Jacq. (wooly plantain) (Porensky et al., 2018; Russell et al., 2017).

Study design

Wyoming site: During the summer of 2019, we established blocks along 10 natural invasion gradients in Wyoming. Each block consisted of five, 1 m^2 plots with different levels of invasion (0%, 25%, 50%, 75%, and 100% cover) of each respective invasive species. Invasion levels represent an approximate categorized aerial cover of *B. arvensis* or *B. tectorum* compared to the rest of the plant community. *B. tectorum* and *B. arvensis* each had 5 blocks, giving a total of 50 plots.

Montana site: During the summer of 2020, we established blocks along 8 natural invasion gradients in Montana. Each block consisted of six, 1 m^2 plots across three levels of invasion abundance (low: 0-10%, medium: 45-55%, and high: 90-100%) by *B. arvensis*. Again, invasion levels represent an approximate categorized aerial percent cover of *B. arvensis* compared to the rest of the plant community. In 2020, we collected data from a total of 48 plots, but in 2021 and 2022, we only present data from half (24) of these plots.

Field data collection

Field data was collected identically from both sites across all time points. In June/July of each year, at each plot, we recorded plant species composition by visually estimating foliar cover across the entire 1 m^2 area (i.e., calibrated to estimates generated by a 100 pin-point intercept frame) for each species to the nearest percent. We also collected insects from each plot using a modified vacuum leaf blower according to the Dietrick Vacuum (D-VAC) method (Dietrick et al., 1960) between 11:00am-2:00pm at each sampling point. All insect samples were frozen after collection until processing. We took three, 10 cm deep soil cores from the outer edge of each plot to assess soil microbial (bacterial and archaeal) taxonomic diversity (in 2019 at Wyoming and 2020 at Montana only) and homogenized all three cores in the field before freezing. We collected all soil cores between 10:00am – 3:00pm at each sampling point and sterilized the soil probe and researchers' gloves between plots with 70% isopropyl alcohol to avoid cross contamination.

In 2021 (late June) and 2022 (early June) at Montana only, we collected insect herbivory data according to the Herbivory Variability Network (Pearse et al., 2021). To calibrate our visual estimates of leaf and total plant herbivory damage, we first used the LeafByte application (Getman-Pickering et al., 2020) to ensure our estimates were accurate, and the same researcher collected all herbivory measurements across both sampling periods. In each of the 24 plots, we collected estimates of insect herbivory damage on 12 individuals. Individuals were selected according to species composition data to get a representation across native and invasive species, with 6 samples corresponding to invasive bromes (either *B. arvensis* or *B. tectorum*) and 6 samples corresponding to abundant native species in the plot (native species were selected based on species composition data for each plot, so exact species selected differed between plots). We estimated both total plant herbivory damage and individual leaf damage on no more than 10 randomly selected leaves per individual.

Laboratory sample processing

We used morphological traits to identify insects to family. After, we dried insect samples at 60 ºC for 7 days before collecting total dried insect biomass for each plot.

To process the soil microbial samples (collected in 2019 (WY) and 2020 (MT) only), we sent the samples to Oregon State University's Center for Genome Research and Biocomputing.

Soil DNA was extracted using a Qiagen MagAttract PowerSoil kit and quantified. The V4 hypervariable region of the 16s rRNA gene for both bacteria and archaea was then amplified according to the Earth Microbiome Project (Gilbert et al., 2010) and cleaned with 16s amplicon PCR cleanup. Sequencing was performed with Illumina MiSeq (Caporaso et al., 2012) to generate 250-bp paired-end reads. The forward and reverse reads were merged using FLASH (Magoč and Salzberg, 2011) and the merged reads were then quality-controlled using the DADA2 pipeline (Callahan et al., 2016) in Qiime2 (Hall and Beiko, 2018). This removed chimeras and the data were filtered to further remove mitochondria, chloroplast, and unassigned sequences. We then removed any amplicon sequence variants with fewer than 10 reads and clustered sequences into operational taxonomic units (OTUs) with a 97% similarity threshold using the Silva database (Pruesse et al., 2007) for reference. We continued to follow the Qiime2 pipeline at a sampling depth of 30,000, which only excluded one plot with less than 8,000 reads.

Data analysis

We conducted all calculations and analyses in R version 3.6.2 (R Core Team, 2019) (α = 0.05, but we report results with $0.05 < p < 0.1$ as marginally significant). First, to ensure successful invasion gradients (Figure S1), we assessed the relationship between actual percent cover of brome with categorical invasion level using Type III mixed model analysis of variance (ANOVA) with a random effect of gradient included.

We assessed community level richness across plants, insects, and soil microbes in Wyoming in 2019 and Montana in 2020. For plant species and insect family richness, we used the codyn package (Hallett et al., 2016) in R. We calculated soil microbial OTU (level-7 in Qiime2) richness in Qiime2 and imported the results to R for subsequent analyses. We used Bray-Curtis dissimilarity matrices to plot the multidimensional community composition of the plant species, insect families, and microbial OTU's using non-metric multidimensional scaling (NMDS). We calculated Bray-Curtis dissimilarity for the plant and insect communities using the vegan package (Dixon, 2003) and Qiime2 for the microbial communities.

We then assessed functional level responses across plants, insects, and soil microbes in Wyoming in 2019 and Montana in 2020. For plant communities, we assigned each species to a functional group (C_3 annual grass, C_3 perennial grass, C_4 perennial grass, cactus, forb, sub-shrub/shrub). For insect communities, we assigned each family to a functional feeding guild (leaf chewing herbivore, parasitoid, pollen/nectar eating herbivore, predator, sap sucking herbivore, other herbivore) (La Pierre and Smith, 2016). For the soil microbial communities, we used the Faprotax prokaryotic environmental function database to assign each OTU to an ecological function; OTU's not matching any taxa in the database were left as unassigned. Using this method, OTU's could be assigned to multiple functional groups (Louca et al., 2016; Su et al., 2023). We used rank abundance curves to assess changes in function between the lowest (0%) and highest (100%) invasion levels in each gradient type. For plants, we did not include *B. arvensis* in *B. arvensis* gradients and *B. tectorum* in *B. tectorum* gradients in order to assess changes in non-brome functional dominance. Because there are significantly more functions associated with microbes than plants or insects, we selected the top 10 ecological functions (anerobic ammonia oxidation, aerobic chemoheterotrophy, chemoheterotrophy, manganese oxidation, nitrate reduction, nitrification, nitrogen fixation, photoautotrophy, phototrophy, ureolysis) shared across the lowest and highest invasion levels in each gradient type to analyze in our RACs (Figure 4.4); all other functions were left as other (Figure S2). We again used Bray-Curtis dissimilarity matrices to plot multidimensional functional composition of the plant, insect, and microbial functions using NMDS space. Here, we used all ecological functions associated with the microbial communities (~50 functions total).

For all analyses, we modeled each site, year, and invasive brome species separately. Because we did not collect soil microbial data in 2021 and 2022, we did not include plant or insect community data from 2021 and 2022 in subsequent community and functional level analyses. To assess how community richness and each functional group changed with invasion abundance, we used Type III mixed-model ANOVAs with a random effect of block included (lmerTest package (Kuznetsova et al., 2017), followed by Type III analysis of variance (ANOVA) with Satterthwaite's method (Satterthwaite, 1941)). We used permutational multivariate ANOVA (PERMANOVA) to assess compositional differences among invasion levels with a random effect of block included for both community and functional level analyses. For significant effects, we calculated all pairwise comparisons using the RVAideMemoire package (Hervé, 2022). For insect herbivory data from Montana in 2021 and 2022, we tested the effect of invasion level, species status (native or invasive), and their interaction on total plant herbivory using Type III ANOVA with a random effect of block included. We also tested this for leaf level herbivory damage, but the results were very similar, so we present only on total plant herbivory. Last, we used Type III mixed-model ANOVAs with a random effect of block included to assess the effect of invasion abundance on total insect biomass for all 4 study years and all gradient types.

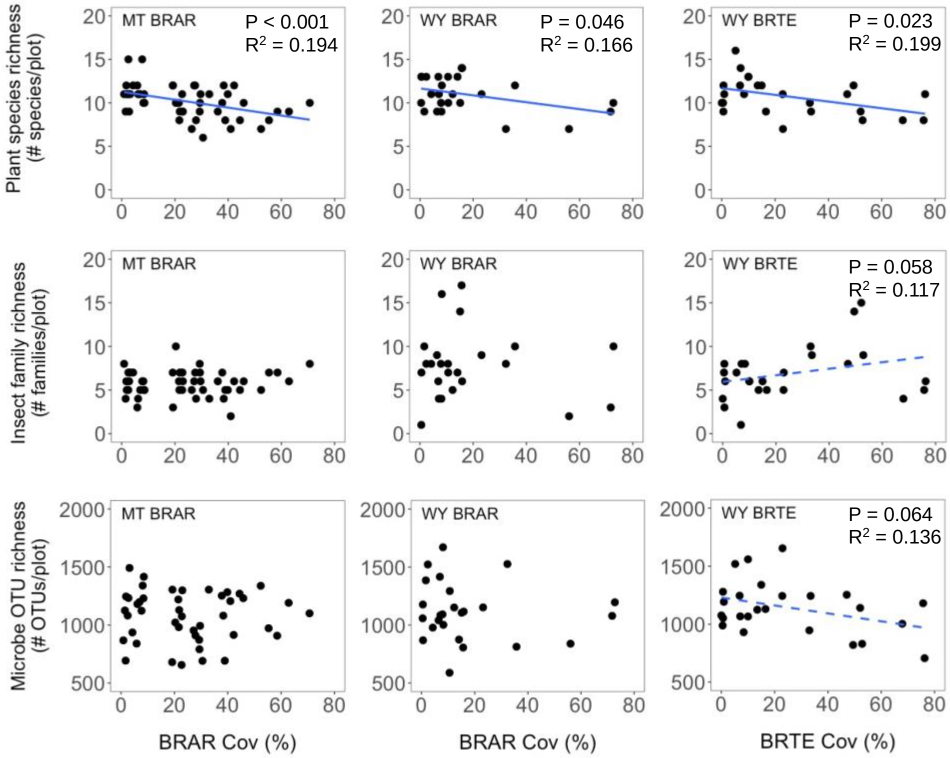
For all analyses, we assessed normality of the residuals of all response variables using Shapiro-Wilk, Anderson-Darling, Cramer-von Mises, and Kolmogorov-Smirnov tests as part of the Olsrr package (Hebbali, 2020), transforming data when necessary to achieve approximate normality.

Results

Invasion gradients

We were able to successfully impose gradients of invasion in both Montana and Wyoming for *B. arvensis* and *B. tectorum* (Figure S1). Relative percent cover of bromes significantly increased with categorized invasion level across all three gradients (Montana *B. arvensis*: $F_{2,\,38} = 72.7$, $p < 0.0001$; Wyoming *B. arvensis*: $F_{4,\,16} = 5.2$, $p = 0.007$; Wyoming *B. tectorum*: $F_{4,\,16} = 27.9$, $p < 0.0001$).

Figure 4.1. Changes in Plant Species, Insect Family, and Soil Microbial OTU Richness with Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).



Note. P-values and marginal R^2 values for significant (solid lines) or marginally significant (dashed line) effects of invasion on richness are shown according to results from mixed-model ANOVAs (Table 4.1).

Plant responses

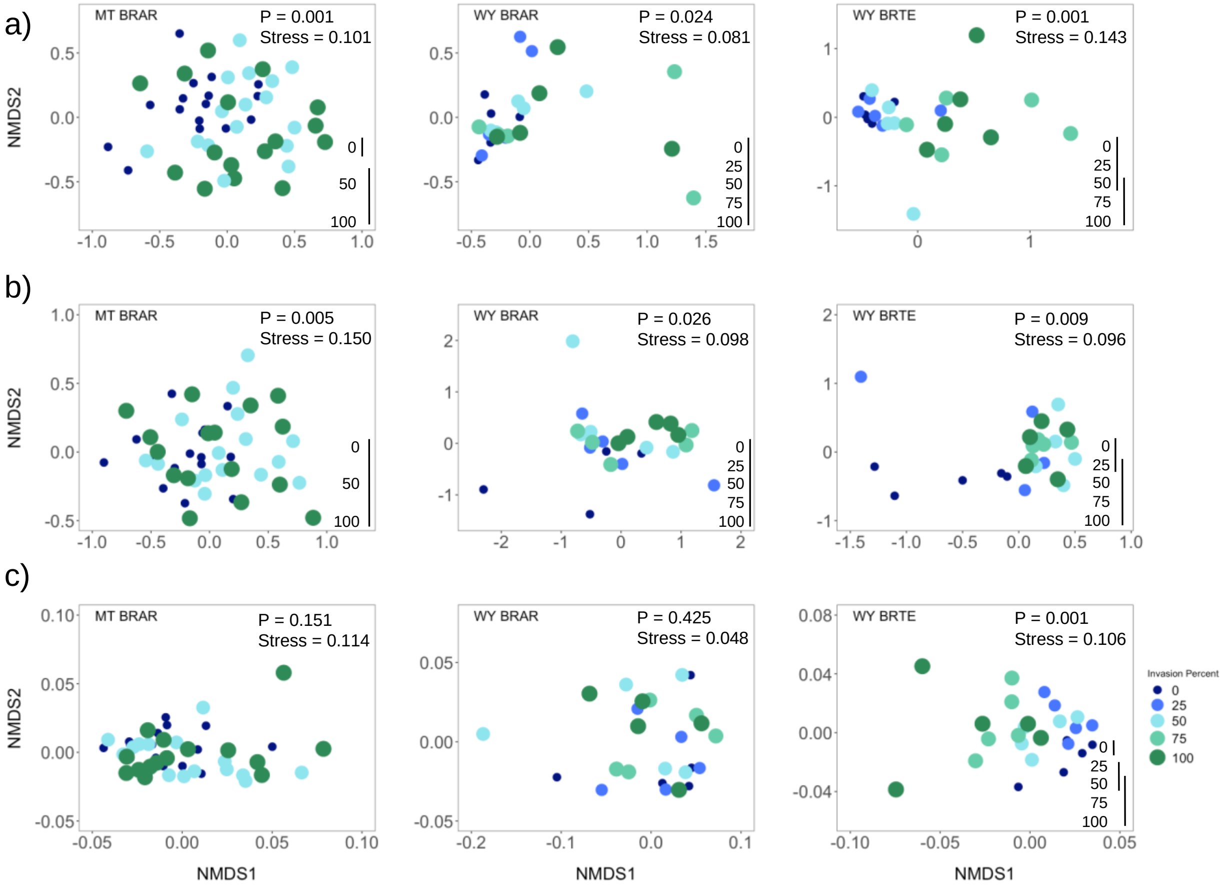
Plant species richness decreased across all three invasion gradients (Figure 4.1a, Table 4.1). Further, plant species community composition (Figure 4.2a, Table 4.2) and functional composition (Figure 4.3a, Table 4.3) differed significantly with invasion levels across all three experimental gradients. In Montana, *B. arvensis* invasion was negatively correlated with C_3 annual grass, C_3 perennial grass, C_4 perennial grass, forb, and sub-shrub/shrub cover (Figure S2a, Table S1). In Wyoming, we saw a decrease in dominance by C_4 perennial grasses from 0 to 100% invasion levels in both *B. arvensis* and *B. tectorum* gradients (Figure 4.4a), and *B. arvensis* and *B. tectorum* cover was negatively correlated with C_3 annual grass and C_4 perennial grass cover (Figure S2a, Table S1).

Table 4.1. Linear Mixed-Model Analysis of Variance (F Statistics with P-Values) for the Response of Plant Species, Insect Family, and Soil Microbial OTU Richness to Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).

	MT BRAR			WY BRAR			WY BRTE		
Group	df	F-value	P-value	df	F-value	P-value	df	F-value	P-value
Plant	1, 43.48	17.042	**<0.001**	1, 15.69	4.703	**0.046**	1, 23.00	5.953	**0.023**
Insect	1, 44.56	0.285	0.596	1, 21.83	0.313	0.582	1, 19.93	4.052	**0.058**
Soil microbe	1, 41.95	0.122	0.729	1, 23.00	0.293	0.593	1, 23.00	3.784	**0.064**

Note. Significant values are shown in boldface type.

Figure 4.2. Non-Metric Multidimensional Scaling (NMDS) of A) Plant, B) Insect, and C) Soil Microbial Community Compositions in Response to Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).



Note. P-values for significant changes in composition are shown according to the PERMANOVA results (Table 4.2). Stress values for goodness of fit are also shown. Additionally, vertical black lines indicate significant differences between invasion levels as found from pairwise comparisons.

Insect responses

Insect family richness differed marginally with invasion abundance in the *B. tectorum* gradients in Wyoming, where insect family richness slightly increased with invasion (Figure

4.1b, Table 4.1). However, insect community composition differed significantly with invasion in all three gradients (Figure 4.2b, Table 4.2). Further, insect functional composition was correlated to invasion in *B. arvensis* in Montana gradients and *B. tectorum* in Wyoming gradients (Figure 4.3b, Table 4.3). In Montana, insects classified as other herbivores decreased in abundance from 0 to 100% invasion by *B. arvensis* (Figure 4.4b) and leaf-chewing herbivores and sap-sucking herbivores were negatively correlated to *B. arvensis* invasion (Figure S2b, Table S1). In Wyoming, pollen/nectar eating herbivores greatly increased in abundance from 0 to 100% invasion by *B. arvensis* (Figure 4.4b) and parasitoid abundance was positively correlated to *B. arvensis* invasion (Figure S2b, Table S1).

Table 4.2. Permutational Analysis of Variance (F Statistics with P-Values) for the Response of Plant Species, Insect Family, and Soil Microbial OTU Community Composition to Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).

	MT BRAR			WY BRAR			WY BRTE		
Group	df	F-value	P-value	df	F-value	P-value	df	F-value	P-value
Plant	1, 46.00	6.242	**0.001**	1, 23.00	3.162	**0.024**	1, 23.00	8.498	**0.001**
Insect	1, 46.00	4.047	**0.005**	1, 22.00	2.281	**0.026**	1, 23.00	3.257	**0.009**
Soil microbe	1, 43.00	1.417	0.151	1, 23.00	0.908	0.425	1, 23.00	5.378	**0.001**

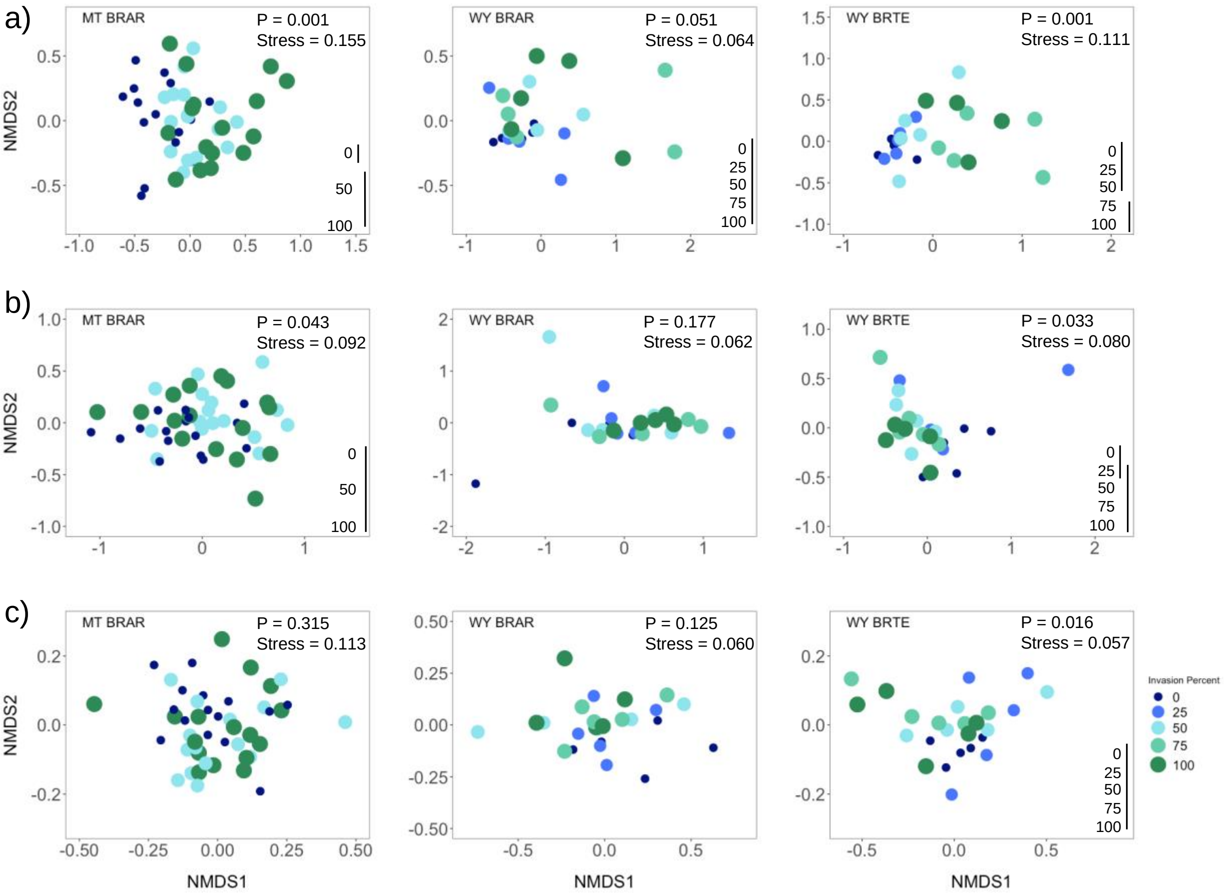
Note. Significant values are shown in boldface type.

Table 4.3. Permutational Analysis of Variance (F Statistics with P-Values) for the Response of Plant Species, Insect Family, and Soil Microbial OTU Functional Group Composition to Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).

	MT BRAR			WY BRAR			WY BRTE		
Group	df	F-value	P-value	df	F-value	P-value	df	F-value	P-value
Plant	1, 46.00	6.831	**0.001**	1, 23.00	2.962	**0.051**	1, 23.00	12.188	**0.001**
Insect	1, 46.00	3.087	**0.043**	1, 22.00	1.552	0.177	1, 23.00	3.043	**0.033**
Soil microbe	1, 44.00	1.087	0.315	1, 23.00	2.047	0.125	1, 23.00	5.151	**0.016**

Note. Significant values are shown in boldface type.

Figure 4.3. Non-Metric Multidimensional Scaling (NMDS) of A) Plant, B) Insect, and C) Soil Microbial Functional Group Compositions in Response to Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).



Note. P-values for significant changes in functional groups are shown according to the PERMANOVA results (Table 4.3). Stress values for goodness of fit are also shown. Additionally, vertical black lines indicate significant differences between invasion levels as found from pairwise comparisons.

Total insect biomass was not related to invasion across any gradient type or year studied (Figure 4.5 top; Figure S4; Table S2). However, total plant damage as a result of insect herbivory marginally or significantly differed between native and invasive plant species within every invasion level. Invasion level did not often affect average herbivory, except in 2021 when plant herbivory at the 0% invasion level was marginally lower than plant herbivory at the 100% invasion level (Figure 4.5 bottom, Table 4.4). Overall, in 2021, average total plant herbivory on invasive annual bromes was 0.84 ± 0.14 %, compared to 4.06 ± 0.78 % on native plants, and in 2022, herbivory on bromes was 1.02 ± 0.29 %, compared to 4.36 ± 0.65% on native species.

Table 4.4. Linear Mixed-Model Analysis of Variance (F Statistics with P-Values) for the Response of Total Plant Herbivory to Invasion by *B. arvensis* in Montana.

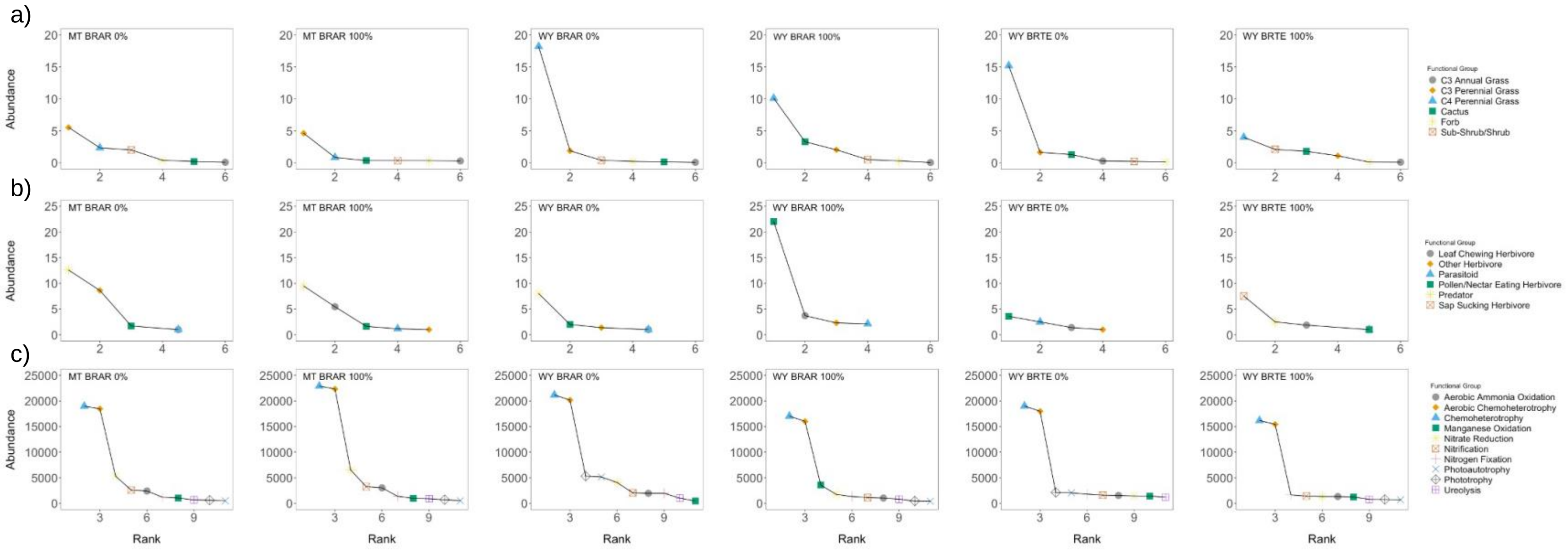
	Log transformation	df	F-value	P-value
2021				
Invasion %	Yes	2, 35.00	7.522	**0.002**
Plant status		1, 35.00	32.028	**<0.001**
Invasion % × Plant status		2, 35.00	0.177	0.839
2022				
Invasion %	Yes	2, 35.00	2.153	0.131
Plant status		1, 35.00	39.004	**<0.001**
Invasion % × Plant status		2, 35.00	0.826	0.446

Note. Significant values are shown in boldface type.

Soil microbial responses

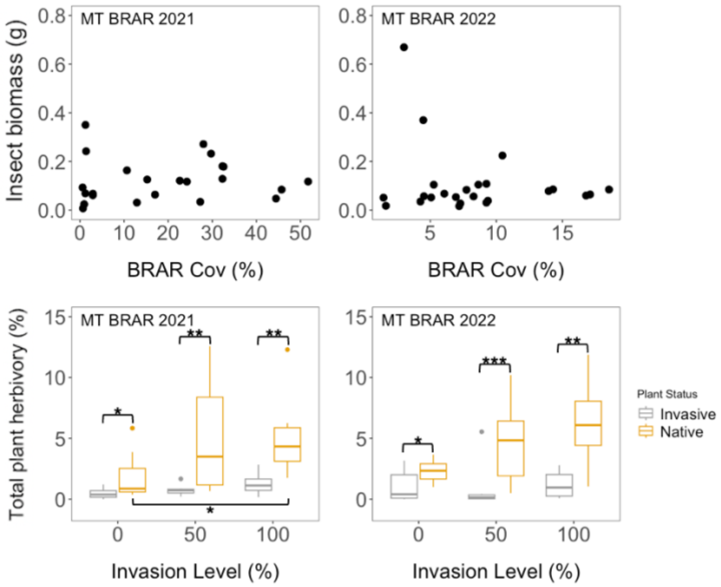
Soil microbial OTU richness was also only marginally associated with invasion in the *B. tectorum* gradients, where microbe richness slightly decreased with invasion (Figure 4.1c, Table 4.1). Likewise, microbial community composition (Figure 4.2c, Table 4.2) and functional composition (Figure 4.3c, Table 4.3) differed with invasion in *B. tectorum* gradients only. Notably, the top two microbial functions across all gradient types (chemoheterotrophy and aerobic chemoheterotrophy) remained relatively constant in abundance and dominance (Figure 4.4c). This remained consistent when including all functional groups, though functional groups classified as other (all functions not in the top ten common functions between 0 and 100% invasion levels) was the most dominant in all cases (Figure S3c). Only two soil microbial functional groups (oxygenic photoautotrophy and photosynthetic cyanobacteria) were negatively correlated with *B. arvensis* invasion in Montana, while 14 (2 positive, 12 negative) and 19 (all negative) soil microbial functional groups were correlated with *B. arvensis* and *B. tectorum* invasion in Wyoming, respectively (Figure S2c, Table S1).

Figure 4.4. Rank-Abundance Curves of A) Plant, B) Insect), and C) Soil Microbial Functional Groups Under Invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY).



Note. The first two columns compare functional group changes between low (0%) and high (100%) invasion by BRAR in MT, the middle two columns compare functional group changes between low (0%) and high (100%) invasion by BRAR in WY, and the last two columns compare functional group changes between low (0%) and high (100%) invasion by BRTE in WY.

Figure 4.5. Changes in Total Insect Biomass and Total Plant Herbivory with Invasion by *B. arvensis* (BRAR) in Montana (MT) in 2021 and 2022.



Note. Significant differences in plant herbivory from mixed-model ANOVAs (Table 4.4) are indicated by asterisks, where * means p < 0.1, ** means p < 0.05, and *** means p < 0.001.

Discussion

Our study uniquely assessed the simultaneous responses of plants, insects, and soil microbes to gradients of invasion at multiple study sites with two different invasive brome species. Overall, we found that plant communities corresponded more strongly to annual brome invasion, with negative relationships with plant diversity and shifts in both community and functional composition. Insect and particularly microbial communities appear to be more resistant to invasive effects. Additionally, we saw that the *B. tectorum* related more strongly to insects and soil microbes, suggesting *B. tectorum* and *B. arvensis* may not impact rangelands to the same degree. Our findings suggest that plants, insects, and soil microbes show differential sensitivity to invasion and that not all invasive species impact communities in the same way.

We found that plant community richness significantly decreased with brome invasion and plant community and functional composition shifted with invasion. The results for plant species richness aligns with previous work (Gasch et al., 2013; Germino et al., 2016b), as annual bromes often have a competitive advantage over native species. This is partially because *B. arvensis* and *B. tectorum* can germinate in the fall or spring depending on favorable climatic conditions, allowing them to utilize available nutrients and moisture earlier than perennial species (Harris, 1967; Hulbert, 1955; Mack and Pyke, 1984; Pellant, 1996). We specifically found declines in C_3 annual grasses and C_4 perennial grasses with invasion. C_4 perennials, growing later in the season, are highly sensitive to light availability (Still et al., 2003). As annual bromes use available moisture and decrease light availability earlier in the season, they can outcompete native C_4 species, thus reducing C_4 abundance (Chambers et al., 2007; Nie et al., 1992; Still et al., 2003). Further, our results suggest that annual bromes may outcompete one another, possibly due to slight phenological differences (Germino et al., 2016a).

While insect richness did not vary consistently with invasion, insect community composition significantly differed with invasion. As annual bromes shift plant composition, insect communities subsequently change with invasion, given the feedback between available plant species and arthropod presence (Biere and Bennett, 2013). In particular, we saw declines in leaf-chewing and sap-sucking herbivores in Montana, and an increase in parasitoids in Wyoming *B. arvensis* gradients. The declines in certain herbivores may be a reflection of less heterogenous habitat (Germino et al., 2016a) with increased invasion cover and/or a preference for native forage species (Cumberland et al., 2016). However, the increase in parasitoids suggests a preference for annual brome species; previous work shows that parasitoid species can prefer annual bromes as an oviposition site (Perez-Mendoza et al., 2006). Further, the relationships between functional composition and invasion reflected the associations of community composition with invasion, where plant functional group composition shifted with all three gradients and insect functional groups differed with *B. arvensis* invasion in Montana and *B. tectorum* invasion in Wyoming.

In our study, community functional composition generally changed with altered composition, suggesting a lack of functional redundancy in plants, insects, and soil microbes, which has potential consequences for ecosystem services of palatable forage availability, pollination, and pest control (Kaiser-Bunbury et al., 2011; Memmott and Waser, 2002; Stout and Morales, 2009). We predicted that compositional and functional changes with invasion would occur across plants, insects, and soil microbes. Brome species have been shown to negatively affect plant communities, and, albeit to a lesser extent, insect and soil microbial communities (Belnap et al., 2005; Germino et al., 2016b). However, plants, insects, and soil microbes differed in their sensitivity to annual brome invasion. Plant communities were most strongly associated with changes in annual brome abundance, as seen by variable richness, composition, and functional groups across all invasion gradients. Brome invasion has been associated with decreased native plant richness and altered composition (Gasch et al., 2013), which corresponds to our findings.

On the other hand, soil microbial communities seem the least sensitive to brome invasion, as we saw marginal changes in richness, and compositional/functional differences in *B. tectorum* gradients only. We specifically found declines in functional groups associated with phototrophy, which, given that *B. tectorum* can greatly decrease light availability and C_4 plants that rely on light availability (Bennett et al., 2014; Still et al., 2003; Vinton and Goergen, 2006), makes sense. While *B. tectorum* has previously been linked to decreased soil microbial abundance

(Gasch et al., 2013) and altered community composition (Nasto et al., 2022), potentially due to soil moisture differences (Gasch et al., 2013), our results could suggest limited impacts to microbial functional groups by *B. arvensis,* implying that the microbial communities may be resilient to even large shifts in *B. arvensis* abundance, protecting services associated with microbial communities like nutrient cycling (Batten et al., 2006). Alternatively, the limited relationships between soil microbes and invasive annual bromes could be due to other factors entirely. For instance, livestock grazing, soil chemistry, and other disturbances may play a much greater role in shaping inherent soil microbial composition (Lindsay et al., 2010; Wakelin et al., 2009). Well-established perennial species, which have a different litter composition than annual grasses, may change soil decomposition properties that then have a greater influence on soil microbes than short-lived annuals (Potthoff et al., 2006). Further, our sequencing methodology and functional groupings, while commonly used, may be limited in ability to capture rare taxa and functions, potentially overinflating functional redundancy in our study (Gasc and Peyret, 2018; Louca et al., 2016).

We also found that the plant, insect, and soil microbial communities did not relate to *B. arvensis* and *B. tectorum* invasion equally. Insect family richness and microbial OTU richness, composition, and function were associated with *B. tectorum* invasion only, suggesting *B. tectorum* may have more substantial and far reaching consequences for community structure than *B. arvensis*. Our results suggest that these species do not impact rangeland communities in the same way, requiring targeted management strategies depending on species identity (Brooks et al., 2016), and that the consequences of invasion for soil health may not be too damaging under invasion by *B. arvensis*.

During the course of the study, we observed that insect herbivory seemed less common on the invasive annual bromes than on the native species. Interestingly, across all years and study sites, invasion level was never related to total insect biomass (Figure 4.5 top, S4). Based on these observations, we measured herbivory in 2 years in Montana. We found that insect herbivores, under the context of any level of invasion abundance, preferred native forage species to invasive annual bromes. While there is some evidence that certain insect herbivores prefer native species over bromes later in the growing season, generally herbivores will consume bromes earlier in the season (Cumberland et al., 2016). However, we found that both later in the season (2021) and early in the growing season (2022), insect herbivores avoided consuming invasive bromes. This supports our previous finding of a decline in certain herbivore functional group abundance as well. Further, this, combined with the lack of response of total insect biomass to invasion, could indicate substantial added pressure to native forage species, as insect herbivores compete with livestock for forage (Branson et al., 2006; Branson and Haferkamp, 2014).

Overall, this work sheds light on the understudied consequences of annual brome invasion in mixed-grass prairies for plants, insects, and soil microbes. Interactions between plants, insects, and microbes shape ecosystem processes and function, and these dynamics are influenced by biodiversity (Thébault and Loreau, 2005) and invasion. Annual brome invasion related to plant and insect community structure and function, highlighting the potential for cascading consequences of invasion by *B. arvensis* and *B. tectorum* for rangeland ecosystems. Additionally, however, soil microbial communities appeared to be more resistant to change in relation to invasive abundance, suggesting these communities may be slightly more buffered against the negative consequences of invasive plant species. Responses to invasion vary across taxa and further studies are needed to examine cross-community change in response to invasion.

Understanding how invasion alters community composition and functional group diversity across rangeland communities is vital not only for long-term rangeland sustainability (DiTomaso, 2000), but also for advancing invasion science and management (Ricciardi et al., 2017; Simberloff et al., 2013, 2005).

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

MDTF and SEK designed the study; MDTF conducted the study and all analyses. MDTF wrote the manuscript, and all authors advised on analyses and edited the manuscript.

CHAPTER V: NATIVE SPECIES FARE BETTER IN DROUGHT COMPARED TO INTRODUCED SPECIES IN GRASSLANDS: A META-ANALYSIS

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Abstract

Drought is predicted to increase in frequency and intensity as a result of human-induced climate change, and grassland ecosystems, many of which are water limited but adapted to drought, may be hit particularly hard with these climate changes. Simultaneously, invasion threatens grasslands globally, and forecasted increases in drought occurrence are expected to alter invasion both by altering the invasibility of a system as well as by altering the competitive dynamics between already established invasive species and the native plant community. The response of invasive plant species, relative to their native counterparts, to drought is complex and individual studies have shown contradictory results. Therefore, there is a need to synthesize these results across grassland studies to determine how introduced and native plant species respond to drought so that we can begin to speculate how the competitive landscape of native and invasive species may shift in grasslands under future climate scenarios. Using a meta-analysis to synthesize results across 66 peer-reviewed journal articles with 1205 datapoints, we found that introduced species in grasslands around the world are almost always more negatively affected by drought than native species, with this pattern holding true across a variety of local climate conditions and drought intensities. Introduced woody species in particular tend to do worse than their native counterparts under drought. While competitive dynamics are complex, our findings suggest that the competitive landscape may shift to favor natives more than invasive species in grasslands experiencing drought. However, drought will not be the sole consequence of climate change for grasslands, and other global change factors will co-occur. We found that under drought, in the context of another global change factor, native and introduced plants responded equally poorly, meaning that other global change drivers can somewhat alleviate the effect of drought on introduced species, and mitigate the competitive advantage of native plants over introduced species.

Keywords: invasion, grasslands, water reduction, global change, climate change

Introduction

Increased severity of climate extremes, including drought, is expected around the world as a result of global climate change (Ades et al., 2020; Rosenzweig et al., 2001; Smith, 2011). Changes to drought regimes, including increased frequency of drought days, point to overall more severe conditions and are the result of changes to precipitation and snowfall patterns as well as increases in evapotranspiration (Satoh et al., 2022). As frequently water limited ecosystems, grasslands depend on drought to maintain their composition and structure (Gibson, 2009) and exhibit drought resilience through well-adapted, drought-tolerant species (Craine et al., 2013). However, grasslands are also expected to be one of the most responsive biomes to drought, as variability in productivity is highly coupled with precipitation (Knapp and Smith, 2001). In addition to drought, invasion dramatically impacts grasslands globally (DiTomaso, 2000; McCollum et al., 2017), but the response of invasive versus native plant species to drought lacks broad synthesis.

The relationships between drought and native and invasive species are complex and previous research is mixed. Studies show that native plant species in grasslands, having evolved to their specific ecological niches, can be well-adapted to some level of drought and can display phenotypic plasticity in water use efficiency and other drought-related characteristics (Zhang et al., 2011). Additionally, growth and reproduction of invasive species has also been shown to respond more negatively to drought than native species (Valliere et al., 2019), resulting in native species faring better under drought than invasives. Conversely, successful invaders, which can have highly adapted ecological and physiological characteristics that allow them to be drought-resistant (Pintó-Marijuan and Munné-Bosch, 2013), often exhibit rapid growth and low germination requirements compared to their native counterparts, especially under high resource availability (Baker and Stebbins, 1965; Pyšek and Richardson, 2007). Further, other work shows that drought can also lead to low intraspecific variation within native species and high interspecific variation among species, resulting in poor overall response to drought (Weißhuhn et al., 2011). These results then imply that invasive plants are expected to fare better than native plants under climate change, especially extreme variability in water availability (Dukes and Mooney, 1999; Engel et al., 2011).

Grasslands are widespread around the world, covering ~40% of Earth's land area (Gibson, 2009; Suttie et al., 2005; White et al., 2000). As such, there is considerable variation in local climate as grasslands change in thermal condition and moisture availability, ranging from arid to humid conditions (Liu et al., 2019), which could influence the response of native and invasive species to drought. Additionally, while drought is considered a marked period of below-average precipitation, the duration, magnitude, and extent of drought can be highly variable, with differential impacts to native and invasive species seen under different intensities of drought (Beguería et al., 2010; Carroll et al., 2021). For instance, intense, shorter drought can reduce function on grasslands more than longer, lower intensity drought (Carroll et al., 2021). Even within similar grassland types, local variation in rainfall patterns, like rainfall event size, can greatly determine productivity responses to drought (Cherwin and Knapp, 2012). Furthermore, the relationship between drought and native/invasive plant species in grasslands becomes even more complicated when considering drought in combination with other global change drivers. For example, under high nitrogen availability and drought, native woody species declined in abundance, while invasive annual species, which tend to favor high nitrogen availability, increased (Valliere et al., 2017). Additionally, while drought caused greater reductions in invasive forb abundance compared to natives, nutrient addition mitigated these impacts, thereby alleviating some of the competitive advantage of natives over invasives under drought (Kelso et al., 2020).

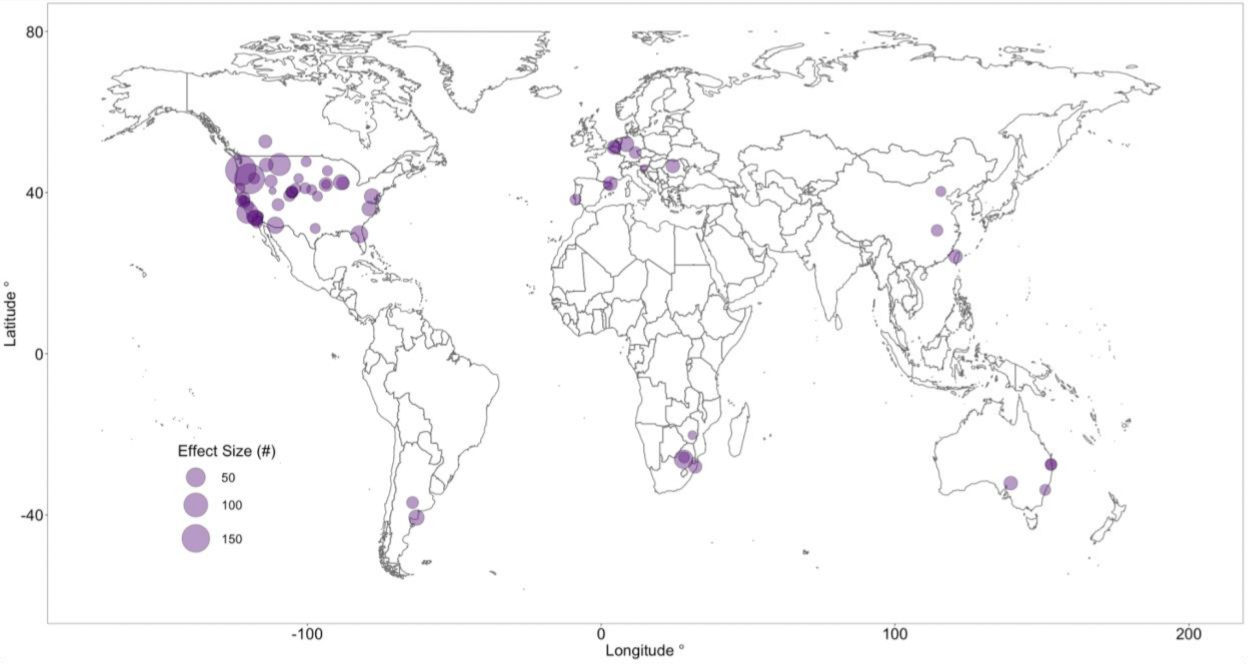
As highlighted, the relationship between drought and plant species in grasslands varies widely (Aroca, 2012). Therefore, a better understanding of the conditions in which invasive or native plants fare better under drought will allow us to predict the competitive outcomes between invasive and native species under future climate change scenarios (Sheley and James, 2014). To address this, we used a global meta-analysis to answer two key questions. First, we assessed how native and invasive plant species in grasslands respond to drought. We predicted that metrics of fitness and growth for both native and invasive species would decrease under drought compared to control conditions, but that invasive species would be more negatively impacted by drought than the natives. Second, we sought to understand if the results from our first question vary by local climate and drought intensity, plant functional group, or study type, and if additional global change drivers alter the drought-modified competitive landscape.

Methods

Literature search

To identify studies on the response of invasive plant species to drought on grasslands, we conducted a literature search for peer-reviewed publications on Environment Complete database (https://www.ebsco.com/products/research-databases/environment-complete), using the following search terms: “invasive plants”, “drought”, and “grassland”. Environment Complete automatically searches for related keywords, but we also conducted searches with related terms: “introduced plants”, “exotic plants”, “non-native plants”, “precipitation reduction”, “soil moisture reduction”, “water reduction”, “grazing lands”, and “rangelands”. We included all published records up until June 2020, giving us 1835 studies. We conducted a systematic screening process using the metagear package (Lajeunesse, 2016) in R. We included all studies based on the abstract/study title that included mention of plant species, grasslands, and either directly mentioned drought or alluded to drought being a potential factor in the study. Based on this initial screening, we narrowed our selection down to 610 studies. From there, we narrowed our search further to 81 papers by individually searching through each paper to decide if it fit our criteria based on if the study included introduced/invasive plants, drought, and was conducted in a grassland or was done on plant species from grassland ecosystems. If a paper was not included past this step, it either did not include drought, did not specifically study introduced/invasive plants, was not a study of grassland species, and/or was a review/opinion paper with no primary data. Last, we extracted relevant data from each article (means, error (standard deviation, standard error, or confidence interval), and sample size) from figures using PlotDigitizer v2.6.9 (https://plotdigitizer.sourceforge.net/), and tables, including items in supplemental documents. From this step, if any article did not actually include a true control (i.e., no comparison of drought versus no drought), we excluded the study, leaving us with 66 unique peer-reviewed published articles. These studies included data from 18 countries and 6 continents (as mapped in Figure 5.1) and included ~83 unique introduced/invasive species and ~76 unique native species. Where possible, we collected exact GPS coordinates from the studies based on where plant samples came from or where the experiment occurred. All field studies included GPS locations or city location, from which approximate GPS coordinates were obtained online. In the case of greenhouse studies, if GPS locations or relevant city location for the origin of the plant samples was not included, we found an approximate, central latitude/longitude location in the range the species is known to be native or introduced.

Figure 5.1. Global Map of Effect Size (Data Point) Locations.



Note. Opacity and size of dots represent number of effect sizes at that location.

We collected data from each study on plant responses to drought and control conditions, as well as eight categorical moderators (aridity, plant status, functional group, study type, drought implementation, percent decrease in water, drought length, response type) used in our multi-factor meta-analysis (Table 5.1). Aridity index was calculated as the average yearly precipitation divided by the average yearly evapotranspiration. Precipitation data was collected from WorldClim V2 (Fick and Hijmans, 2017) and evapotranspiration data was collected from CGIAR-CSI Geoportal (https://cgiarcsi.community/). We categorized percent decrease in water, drought length, and aridity (aridity was categorized according to the generalized climate classification scheme (Trabucco and Zomer, 2018; United Nations Environment Programme, 1997)). We also recorded information on study location and specific plant species. Last, if a study included another driver (e.g., nutrient addition (~45%), elevated temperature (~20%), and grazing/clipping (~20%)), together considered "drivers", in combination with drought, we separately analyzed how drought in addition to another driver impacted plant responses. Because it was not always possible to tell whether species were invasive or just exotic species, from this point, we consider all non-native species to be introduced and group them together as such.

Table 5.1. The Categorical Fixed-Effect Moderators Included in our Meta-Analyses.

Explanatory Variable	Levels	Description of levels
Climate class	4	<0.03 hyper-arid*; 0.03-0.2 arid; 0.2-0.5 semi-arid; 0.5-0.65 dry sub-humid; >0.65 humid *No studies included contained plants originating from hyper-arid climates, leaving 4 levels of aridity
Plant status	2	introduced or native; for ease, we refer to all non-native species as introduced
Functional group	5	forb, C3 grass, C4 grass, sub-shrub/shrub/tree, community* *community refers to plant species of multiple functional groups
Study type	3	greenhouse, field (experiment), field (observational)
Drought implementation	2	precipitation reduction or soil moisture reduction
Percent decrease in water	4	0-25%, 26-50%, 51-75%, 76-100% calculated as: ((control water level - drought water level/control water level)*100)
Drought length*	4	<2 months, 2-6 months, 6 months - 1.5 years, >1.5 years *length of either experimentally imposed or natural drought
Response type	4	growth, production, fitness, physiology

Effect size and variance calculations

We calculated an effect size for each plant response using the log response ratio (Hedges et al., 1999).

$$\ln R = \ln \left(\frac{X_t}{X_c}\right)$$

X_t and X_c are the mean values associated with each individual measure in treatment (t) and control (c) groups. Here, a negative value indicates a negative response of plants to drought, while a positive value indicates a positive response to drought. For studies including an extra driver in addition to drought, we also calculated the log response ratios of the other driver (where other driver is the treatment) and the other driver in combination with drought (whether other driver + drought is the treatment). We calculated the variance of the log ratio (Hedges, 1981) as

$$v_{lnR} = \frac{SD_c{}^2}{N_c(X_c)^2} + \frac{SD_t{}^2}{N_t(X_t)^2}$$

where N is the sample size, SD is standard deviation, and X is the mean for control (c) and treatment (t). In total, we included 1205 effect sizes in the main drought analyses and 238 effect sizes in the analyses incorporating another driver (alone and with drought).

Data analysis

We conducted all calculations and analyses in R version 3.6.2 (R Core Team, 2019) (α = 0.05, but we report results with $0.05 < p < 0.1$ as marginally significant). For all analyses, we used linear mixed-model regressions with a random effect of study ID (i.e., each unique study) (lmerTest package (Kuznetsova et al., 2017), followed by Type III analysis of variance (ANOVA) with Satterthwaite's method (Satterthwaite, 1941)). We tested the relationship between lnR and each of the eight fixed-effects moderators (Table 5.1) separately. First, we assessed the overall relationship between lnR and plant status, then we tested the relationship between lnR with plant status, each other moderator, and their interaction. We also ran models assessing the random effects of response nested within study ID (i.e., most studies included more than one relevant response), but in every case, the AIC value was lower when only including a random effect of study ID, so we present analyses with the simpler model. When interactions were significant or moderately significant, we assessed pairwise contrasts using the emmeans package (Lenth et al., 2023).

Results

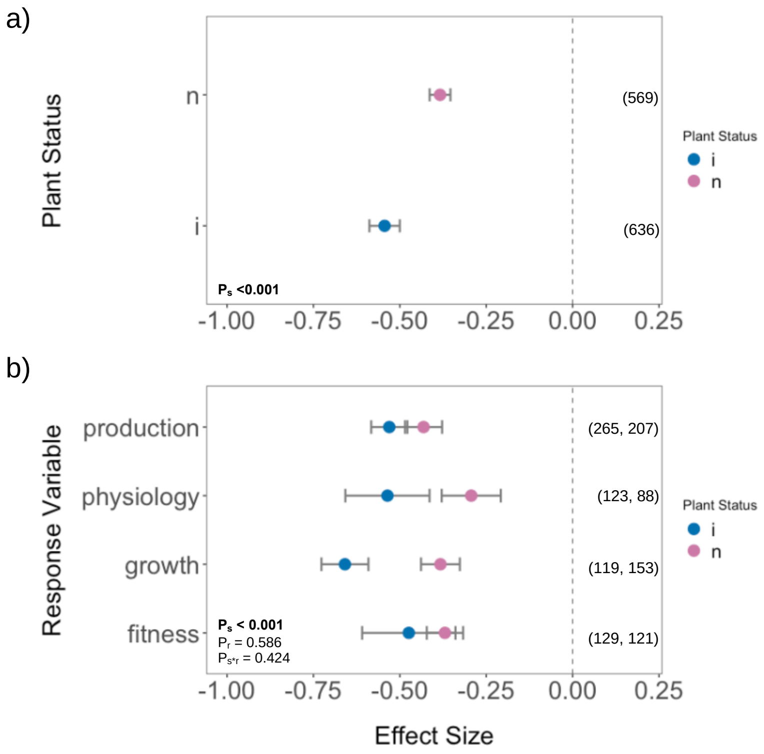
Table 5.2. Linear Mixed-Model Analysis of Variance (F Statistics with P-Values) for Responses of Plant Species to 1-9) Drought, 10) Other Global Change Driver, or 11) Drought in Combination with Another Global Change Driver.

Model	df	F-value	P-value
1. Overall - drought			
PS	1, 1056.10	13.23	**<0.001*****
2. Response type			
PS	1, 1095.65	13.64	**<0.001*****
R	3, 273.63	0.65	0.586
PS × R	3, 1188.65	0.93	0.424
3. Study type			
PS	1, 1069.56	3.52	**0.061***
R	2, 70.36	1.64	0.201
PS × R	2, 1063.34	1.81	0.165
4. Climate class			
PS	1, 568.35	0.22	0.637
R	3, 56.06	0.65	0.584
PS × R	3, 748.54	4.52	**0.004****
5. Water decrease			
PS	1, 975.31	6.14	**0.013****
R	3, 111.20	0.72	0.541
PS × R	3, 951.38	0.66	0.575
6. Drought duration			
PS	1, 714.18	5.16	**0.023****
R	3, 70.37	2.35	**0.080***
PS × R	3, 831.35	0.50	0.684
7. Drought implementation			
PS	1, 1087.03	14.09	**<0.001*****
R	1, 47.67	0.72	0.402
PS × R	1, 1090.93	2.86	**0.091***
8. Functional group			
PS	1, 1063.97	2.44	0.118
R	4, 145.53	1.27	0.286
PS × R	4, 1077.89	2.05	**0.085***
9. Overall - drought (subset)			
PS	1, 234.65	10.91	**0.001****
10. Overall - other drivers (subset)			
PS	1, 234.5	5.87	**0.016****
11. Overall - drought + drivers (subset)			
PS	1, 235.71	0.28	0.599

Note. In 1, we assessed overall how plant species under drought responded based on plant status (introduced or native; abbreviated as PS). In 2-8, we assessed how plant species under drought status responded based on PS, how the response to drought changed under other categorical moderators (see Table 5.1; abbreviated as R), and the interaction between PS and R. In 9, we assessed overall how plant species under drought responded based on PS for the subset of effect sizes that were included in 10 and 11. In 10, we assessed overall how plant species under other global change drivers responded based on PS. In 11, we assessed overall how plant species under drought in combination with other global change drivers responded based on PS.

Overall, we found that both introduced and native plants responded negatively to drought, but introduced plants were more significantly affected by drought than natives (Figure 5.2a, Table 5.2). This held true across all response variable types (Figure 5.2b, Table 5.2) and study types (Figure S1, Table 5.2). We did find an interaction between climate class and plant status, where introduced plants in humid and semi-arid climates showed stronger negative responses to drought than native species (Figure 5.3a, Table 5.2), but introduced plants across different drought magnitudes and durations responded more negatively to drought than natives (Figure 5.3b and c, Table 5.2). We also found a marginal interaction between method of drought implementation and plant status, where introduced plants exposed to a decrease in soil moisture experienced a stronger negative response to drought than native species (Figure S2, Table 5.2). Further, we found a marginal interaction between plant functional group and plant status, where introduced woody species were more negatively impacted by drought than native woody species (Figure 5.4, Table 5.2).

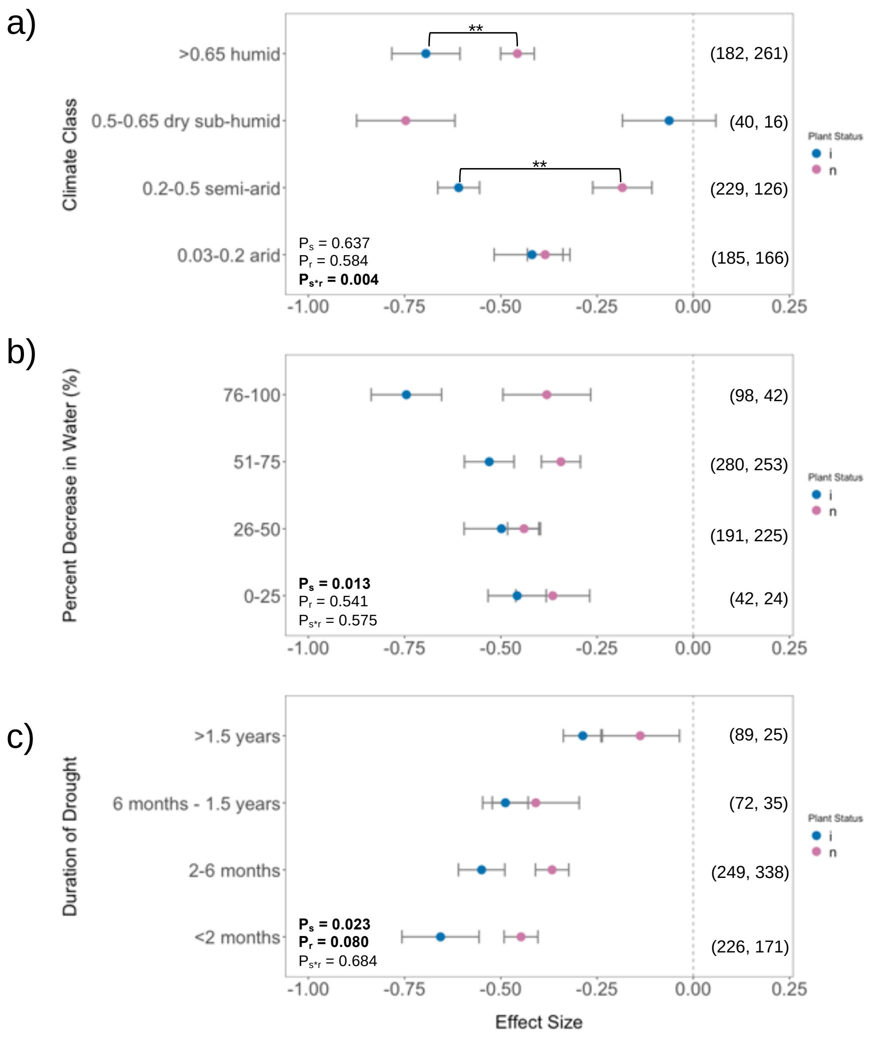
Figure 5.2. Plant Responses (Mean ± Standard Error) Under Drought A) Only and B) to Different Response Variable Types.



Note. The number of response ratios included at each level are shown in parentheses, with number for introduced (i) species first and number of native (n) species second. P-values for plant status (P_s), response variable (P_r), and the interaction between plant status and response variable ($P_{s \times r}$) are included, with boldface type indicating significant results.

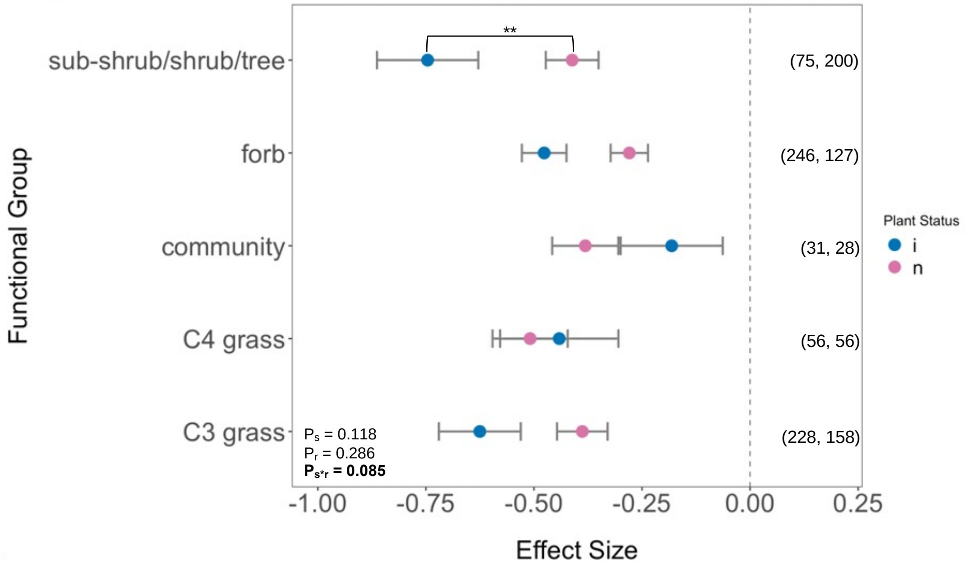
The overall pattern of response of plant status to drought held when sub-setting our data to compare across studies that included another global change driver. Here, we again found that introduced plants fare worse than native plants under drought (Figure 5.5a, Table 5.2). Alternatively, we found that under another global change driver only, introduced plants were positively impacted, while native plants were unaffected (Figure 5.5b, Table 5.2). However, while both were negatively affected by another global change driver in combination with drought, there was no significant difference between native and introduced plants (Figure 5.5c, Table 5.2).

Figure 5.3. Plant Responses (Mean ± Standard Error) Under Drought to Different A) Climate Classes, B) Magnitude of Drought, C) Drought Length.



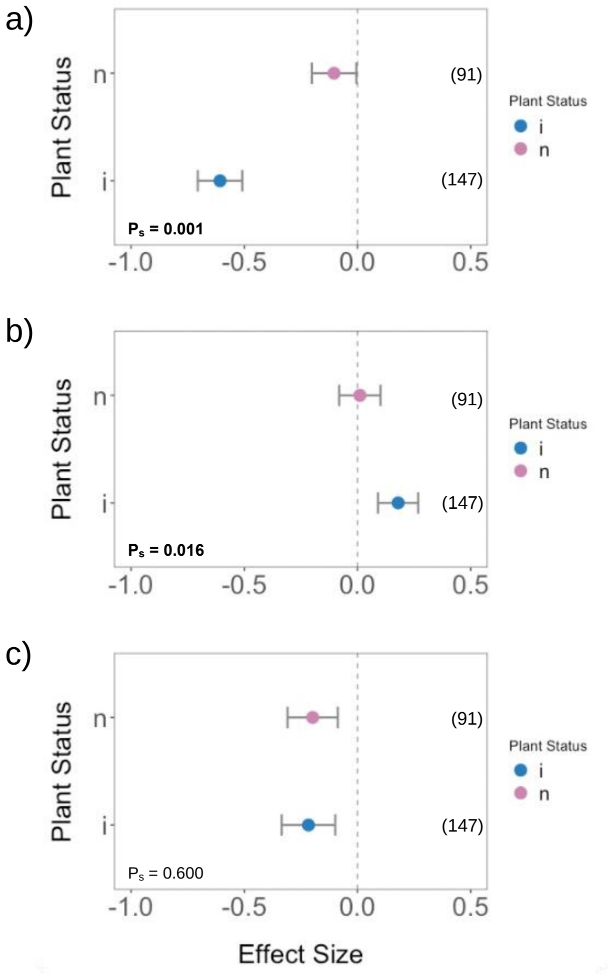
Note. The number of response ratios included at each level are shown in parentheses, with number for introduced (i) species first and number of native (n) species second. P-values for plant status (P_s), other moderator (climate class, drought magnitude, drought length) (P_r), and the interaction between plant status and other moderator ($P_{s \times r}$) are included, with boldface type indicating significant or marginally significant results.

Figure 5.4. **Plant Responses (Mean ± Standard Error) Under Drought to Different Plant Functional Groups.**



Note. The number of response ratios included at each level are shown in parentheses, with number for introduced (i) species first and number of native (n) species second. P-values for plant status (P_s), other moderator (functional group) (P_r), and the interaction between plant status and other moderator ($P_{s \times r}$) are included, with boldface type indicating marginally significant results. ** indicates significant differences within groups, where $p < 0.05$.

Figure 5.5. Plant Responses (Mean ± Standard Error) to A) Drought Only, B) Another Global Change Driver, and C) Drought in Combination with Another Global Change Driver.



Note. The number of response ratios included at each level are shown in parentheses, with number for introduced (i) species first and number of native (n) species second. P-values for plant status (P_S) are included, with boldface type indicating significant results.

Discussion

While both native and introduced plant species were negatively impacted by drought, we found that introduced grassland species fare worse under drought than their native counterparts. This was fairly universal across our included moderators, suggesting that, on average, native species may be more resistant to drought conditions than their introduced counterparts. Work from a previous meta-analysis supports this, though they found only moderately significant differences between invasive and native plants under decreased precipitation (Liu et al., 2017). Native plants, having evolved with their native ecosystems, may be better able to adapt to variable water availability by utilizing drought escape, avoidance, and tolerance strategies (Kooyers, 2015). Thus, native plants may express greater phenotypic plasticity overall compared to introduced plants, giving them a competitive advantage as grasslands respond to increasing droughts from climate change (Dickman et al., 2019; Lambrecht et al., 2020).

Interestingly, introduced and native plants from the most arid climates showed the lowest differences under drought. Vegetation from these regions, which are more naturally prone to water stress, are also considered the most drought resilient and contain high abundances of drought-adapted species (Finch et al., 2016). Because arid ecosystems have naturally lower moisture availability, they may be more inherently resistant to invasion (Zefferman et al., 2015), but those species that do successfully invade often possess high resource acquisition and conservation traits that allow them to sustain under drought comparable to native species (Funk, 2013). Further, evidence and theory predict that climate extremes, including severe drought, can promote invasion by decreasing native community resistance (Diez et al., 2012; Jiménez et al., 2011; Ravi et al., 2022). However, we did not find this to be the case; introduced species performed worse than native species across drought magnitudes and lengths. This suggests that, even though climate change predicts worsening drought severity, including longer and higher intensity droughts (Sheffield and Wood, 2008), introduced plants may still do worse than natives, which is promising for conservation of native grasslands.

We also found that, for the most part, plant functional group does not affect the response of native or introduced species to drought. However, native woody species (sub-shrubs, shrubs, trees) seem to have an advantage over introduced woody species under drought. Native woody species display high drought survival mechanisms, including the ability to access deep water (Pivovaroff et al., 2016). Previous work in individual study systems show that invasive and native woody species use different drought strategies, and seem to support an advantage of invasive over native woody species in this context (Barros et al., 2020; Lu et al., 2022; Oliveira et al., 2014). When synthesizing across grasslands, we did not find this to be the case, suggesting that invasive woody plants in general do not actually have a competitive advantage over natives during drought.

Our results seem promising for invaded grasslands in the context of climate change-induced drought. However, climate change predicts simultaneous impacts of many global change drivers (Diez et al., 2012). We found that other global change drivers alone actually benefit introduced plants. While native plants may have a competitive advantage over introduced plants under drought alone, in combination with other global change drivers, this advantage disappeared, and both introduced and native plants fared equally poorly. This aligns well with previous work that shows that multiple global change drivers can mitigate any competitive advantage of natives over invasive species (Orbán et al., 2021; Valliere et al., 2017). Even so, these responses may be context specific, as certain global change drivers can promote both the expansion and contraction of invasives (Bradley et al., 2010). Further work is needed to fully understand the complex dynamics of invasion under multifaceted global change.

In addition to multiple global change drivers, the legacy effects of drought and drought-recovery are important considerations in the dynamics of invasives and natives. After drought, when resource availability increases, there is potential for invasive species to outperform natives or rapidly take over space created when both natives and invasives are suppressed during drought

(Diez et al., 2012; Jiménez et al., 2011; Manea et al., 2016; Mojzes et al., 2020). This can be due to changes in soil biota (i.e., abundance of soil pathogens and plant symbionts) and available nitrogen that enhance invasion while suppressing native species (Meisner et al., 2013). Additionally, invasive plants can exhibit fast drought recovery with higher photosynthetic rates and lower leaf construction cost from greater energy and nitrogen use efficiency (Barros et al., 2020). When this is the case, in the long-run, invasive species may still have the ultimate competitive advantage over native species.

Our work synthesizes complicated, and in some cases contradictory, consequences of drought for introduced and native plant species in grassland ecosystems. Yet, understanding the complex interactions and how future climate scenarios may alter these interactions is imperative for preserving, and in many cases, restoring grasslands (Gaskin et al., 2021). Our results suggest an overall competitive advantage of native plants over introduced plants in grasslands, providing promise for invaded ecosystems during drought years. However, these results must be viewed in the context of multiple global change factors, which will occur simultaneously with climate change, to consider a more realistic picture of how grassland plant species will respond to global change.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

MDTF designed the study, collected all data, performed analyses, and wrote the manuscript. SEK funded the work and advised on study design and analyses. SEK and MDTF edited the manuscript.

CHAPTER VI: CONCLUSIONS

Invasive species impact nearly every ecosystem on the planet, making them one of the most pervasive problems associated with widespread global change (Pejchar and Mooney, 2009). The consequences of invasion for native ecosystems are vast, making our understanding of these impacts critical to conservation of ecosystem integrity, function, and services (Charles and Dukes, 2007; Pejchar and Mooney, 2009). Grassland ecosystems, which cover ~40% of Earth's terrestrial surface, are important for many ecosystem services, including utility as working rangeland (Gibson, 2009; Suttie et al., 2005; White et al., 2000). However, grasslands around the world are threatened by invasive plant species (DiTomaso, 2000; McCollum et al., 2017; Poland et al., 2021). My dissertation addresses how we might expect invasion to respond to global climate change, using two problematic invasive grasses in North America as a representative system.

Chapter II tested the effects of experimentally implemented multi-year, multi-intensity drought and grazing at two northern mixed-grass prairie sites invaded by annual brome grasses, *Bromus arvensis* and *B. tectorum*. In general, precipitation reduction resulted in reduced annual brome biomass and grazing alone had little effect on these species. However, in the year after implemented precipitation reduction, and during a natural drought, invasive annual brome biomass actually increased after heavy grazing at one field site. Climate changes predicts increases in extreme scenarios like this, making this a realistic outcome for the future of rangelands. Cattle management choices will impact long-term sustainability and recovery from drought.

In Chapter III, I used an observational field study to assess the response of rangeland plant community stability to gradients of invasion by *B. arvensis* and *B. tectorum*. I assessed how several metrics of temporal stability change with annual brome invasion, and whether these relationships between invasion and stability are mediated by light and soil moisture availability. Stability of several plant community metrics was associated with changes in invasion abundance, including stability of plant functional groups that are important for quality forage. Further, some stability metrics were mediated by light and soil moisture. Altogether, this project has implications for native plant community stability on rangelands and potentially, food security, as ranchers rely on dominant grass production for cattle weight gain.

In Chapter IV, I used observational field studies in two northern mixed-grass prairies to assess relationships between invasion by *B. arvensis* and *B. tectorum* and rangeland communities. I addressed how simultaneous changes in plant, insect, and soil microbial communities relate to gradients of brome invasion abundance. Increasing invasion abundance was associated with changes in plant and insect community composition and function for both invasive brome species, but soil microbe composition only changed under *B. tectorum* invasion. This suggests that while invasive bromes may have negative consequences for rangeland community and functional composition, soil health may be slightly more resilient and that management should address invasive species independently, as *B. tectorum* invasion may be worse than *B. arvensis* invasion for grasslands.

In Chapter V, I synthesized results from 66 studies on the response of introduced and native grassland plants to drought using a meta-analysis. Prior results from single studies are mixed, where sometimes invasive species perform better under drought than their native counterparts, while other studies indicate the opposite is true. While both native and introduced plants did worse under drought, we did find promising results for grassland conservation, as introduced species seem to fare worse than native species in nearly all climates and under variable drought intensities. However, because global climate change predicts that multiple drivers will impact grasslands simultaneously, these results must be considered in the context of other global change drivers as well. In this scenario, when drought is combined with another global change driver, the competitive advantage of natives over introduced species disappears.

Using a diverse suite of approaches, including experimental field work, observational field studies, and meta-analysis synthesis tools, my dissertation has important implications for invasion science and ecological theory of network structure, stability, and functioning (Frost et al., 2019), as well as for management of grassland ecosystems in a complex and human-altered world. This work furthers our understanding of (1) how invasion alters multiple trophic levels directly and through mediating resources, (2) how invasion destabilizes native communities, and (3) how global change alters the competitive dynamics between native and invasive species. As the climate continues to change and these systems are simultaneously stressed by multiple global change drivers, a complex dynamic will play out between native and invasive species. Importantly, my work also stresses that management decisions can influence the competitive outcomes between native and invasive species across the western United States. With more knowledge and a greater understanding of the multiple stressors our imperiled grasslands are facing, we may be able to turn the tide and conserve our native species.

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APPENDIX A: SUPPLEMENTARY MATERIALS

Chapter II Supplemental Materials

Table S1. Grazing treatments (destock, stable, & heavy) involved variable stocking rates (i.e., animal unit equivalent days (AUD) per ha) of beef cattle (*Bos taurus*). For each site and year, stocking rates were controlled to reach prescribed forage utilization targets (e.g., 30, 50, 70%) based on daily visual obstruction readings. Heifers are calculated as 0.7 animal equivalent unit (AUE).

			Block 1 AUD/ha			Block 2 AUD/ha			Block 3 AUD/ha		
Site	Year	Herd size and type	Destock	Stable	Heavy	Destock	Stable	Heavy	Destock	Stable	Heavy
MT	2019	11 heifers*	40.7	40.7	80.1	40.7	40.7	80.1	40.7	40.7	85.1
	2020	5 cows, 5 heifers and 4 calves	5.9	53.3	100.7	11.8	27.6	75.0	23.7	71.1	142.2
	2021	6 heifers	2.8	12.5	12.5	3.0	9.6	9.6	8.6	11.5	11.5
WY	2019	3 heifers for B1; 2 for B2 and B3	14.9	14.9	47.0	8.3	8.3	39.8	15.7	15.7	54.1
	2020	2 heifers	11.7	19.0	34.1	2.8	11.4	22.8	3.7	7.6	17.1
	2021	2 heifers	3.4	10.6	10.6	3.1	8.0	8.0	2.6	7.2	7.2

* Logistical constraints necessitated two bouts of grazing in August 2019. First, blocks were grazed by 11 heifers. Next, the heavy treatment block portions were grazed by 6 cows, 1 heifer, and 5 calves. B = Block.

Table S2. Linear mixed-model analysis of variance (F statistics with p-values) for percent cover responses of invasive annual bromes to each year's treatment conditions at the time of sampling in Wyoming (WY). We assessed percent cover response to each year's applicable precipitation reduction and grazing treatments. Here, no plots were dropped (compared to Table S3) to compare results to analyses that removed plots that never contained field brome or cheatgrass throughout the study (only occurred in WY).

	Site		Wyoming		
Species	Year	Data Transformation	df	F-Value	P-Value
B. arvensis	2019	N/A			
	W_{19}		1, 44.00	0.43	0.52
	2020	ln(data + 0.1)			
	W_{20}		1, 43.00	0.00	0.97
	G_{19}		1, 6.63	1.70	0.24
	$W_{20} \times G_{19}$		1, 43.00	0.15	0.70
	2021	ln(data + 0.1)			
	WR_{21}		1, 42.00	0.11	0.74
	G_{20}		2, 10.61	0.70	0.52
	$WR_{21} \times G_{20}$		2, 42.00	1.37	0.27
B. tectorum	2019	N/A			
	W_{19}		1, 50.00	1.35	0.25
	2020	N/A			
	W_{20}		1, 43.00	0.94	0.34
	G_{19}		1, 18.13	0.10	0.76
	$W_{20} \times G_{19}$		1, 43.00	0.54	0.47
	2021	N/A			
	WR_{21}		1, 42.00	1.11	0.30
	G_{20}		2, 11.36	1.50	0.26
	$WR_{21} \times G_{20}$		2, 42.00	1.29	0.29

W = water treatment, G = grazing treatment, WR = water treatment recovery. Numerical subscripts indicate year abbreviations for 2019-2021.

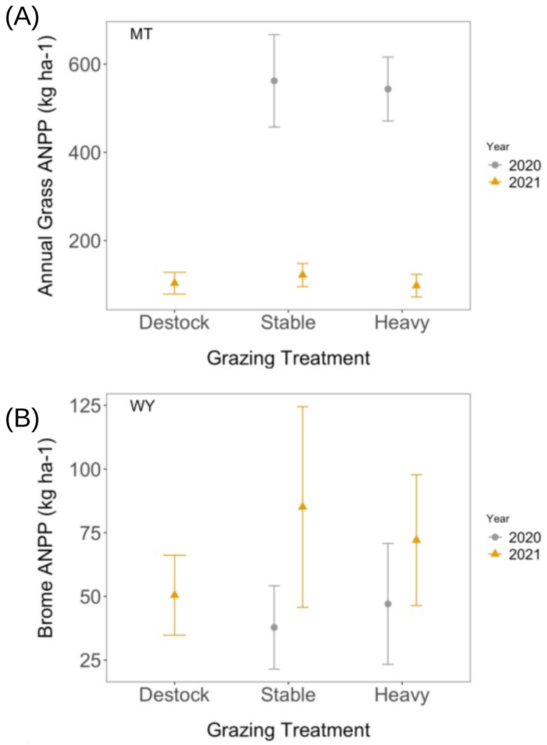

Figure S1. Mean +/- standard error of aboveground net primary production (ANPP) of a) annual grass species at Montana (MT) and b) invasive annual brome species at Wyoming (WY) across the grazing treatments through the 2 grazing years. Model fit was assessed using linear mixed-model ANOVAs (Table 2.1).

Table S3. Linear mixed-model analysis of variance (F statistics with p-values) for percent cover responses of invasive annual bromes to each year's treatment conditions at the time of sampling. We assessed percent cover response to each year's applicable precipitation reduction and grazing treatments. Two plots at Wyoming (WY) never contained field brome or cheatgrass across all 4 study years and were dropped from the analyses. Similarly, 8 additional plots at WY never contained cheatgrass across all 4 study years and were dropped from the analyses.

	Site	Montana				Wyoming			
Species	Year	Data Transformation	df	F-Value	P-Value	Data Transformation	df	F-Value	P-Value
B. arvensis	2019	N/A				N/A			
	W_{19}		1, 44.00	1.00	0.32		1, 43.26	0.59	0.45
	2020	N/A				ln(data + 0.1)			
	W_{20}		1, 43.00	0.26	0.61		1, 41.21	0.05	0.83
	G_{19}		1, 9.57	0.33	0.58		1, 6.73	1.67	0.24
	$W_{20} \times G_{19}$		1, 43.00	0.79	0.38		1, 41.21	0.40	0.53
	2021	ln(data + 0.1)				ln(data + 0.1)			
	WR_{21}		1, 46.00	0.48	0.49		1, 41.09	0.02	0.88
	G_{20}		2, 46.00	2.39	0.10		2, 11.00	0.65	0.54
	$WR_{21} \times G_{20}$		2, 46.00	0.65	0.52		2, 41.00	1.00	0.38
B. tectorum	2019	N/A				N/A			
	W_{19}		1, 44.00	0.01	0.93		1, 40.24	1.38	0.25
	2020	N/A				N/A			
	W_{20}		1, 48.00	0.13	0.72		1, 35.38	0.89	0.35
	G_{19}		1, 48.00	0.10	0.76		1, 23.90	0.01	0.92
	$W_{20} \times G_{19}$		1, 48.00	0.04	0.84		1, 35.41	0.27	0.61
	2021	N/A				N/A			
	WR_{21}		1, 46.00	0.10	0.75		1, 34.11	1.14	0.29
	G_{20}		2, 46.00	1.00	0.38		2, 12.84	1.35	0.29
	$WR_{21} \times G_{20}$		2, 46.00	0.40	0.67		2, 33.90	1.13	0.33

W = water treatment, G = grazing treatment, WR = water treatment recovery. Numerical subscripts indicate year abbreviations for 2019-2021.

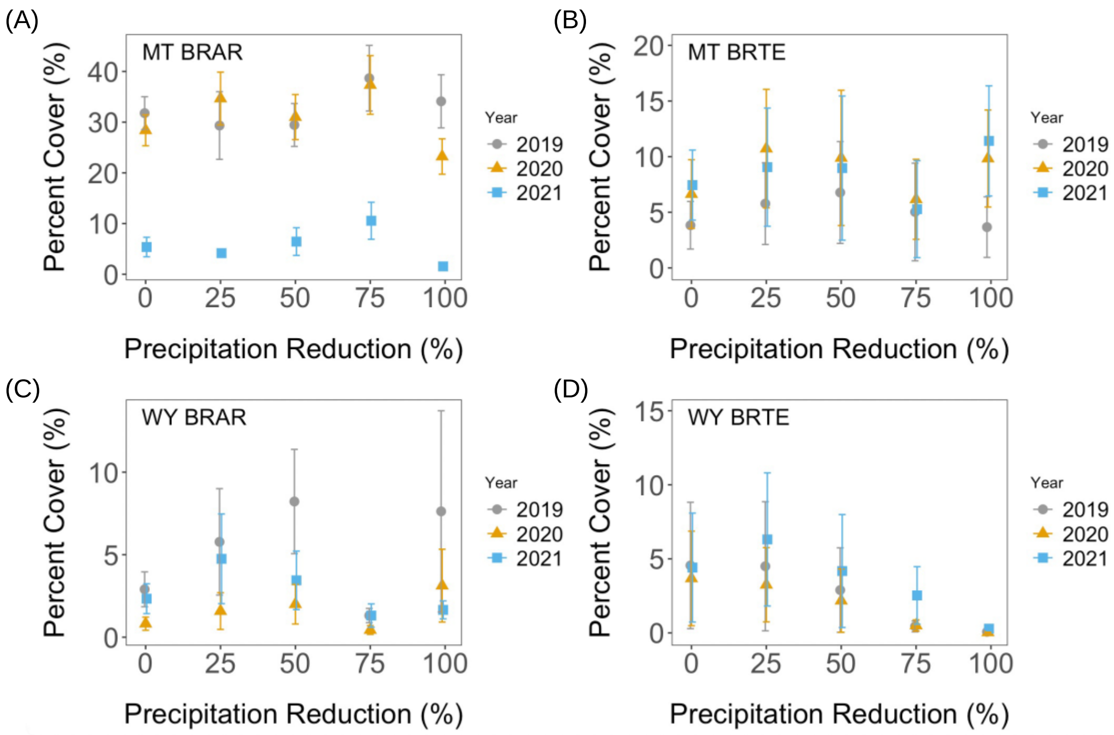

Figure S2. Mean +/- standard error of percent cover (cover) of A-B) *B. arvensis* (BRAR) and *B. tectorum* (BRTE) at Montana (MT) and C-D) BRAR and BRTE at Wyoming (WY) across the water treatments through the 3 treatment years. Model fit was assessed using linear mixed-model ANOVAs (Table S3). Two plots at WY never contained BRAR or BRTE across all 4 study years and were dropped from the analyses. Similarly, 8 additional plots at WY never contained BRTE across all 4 study years and were dropped from the BRTE analyses.

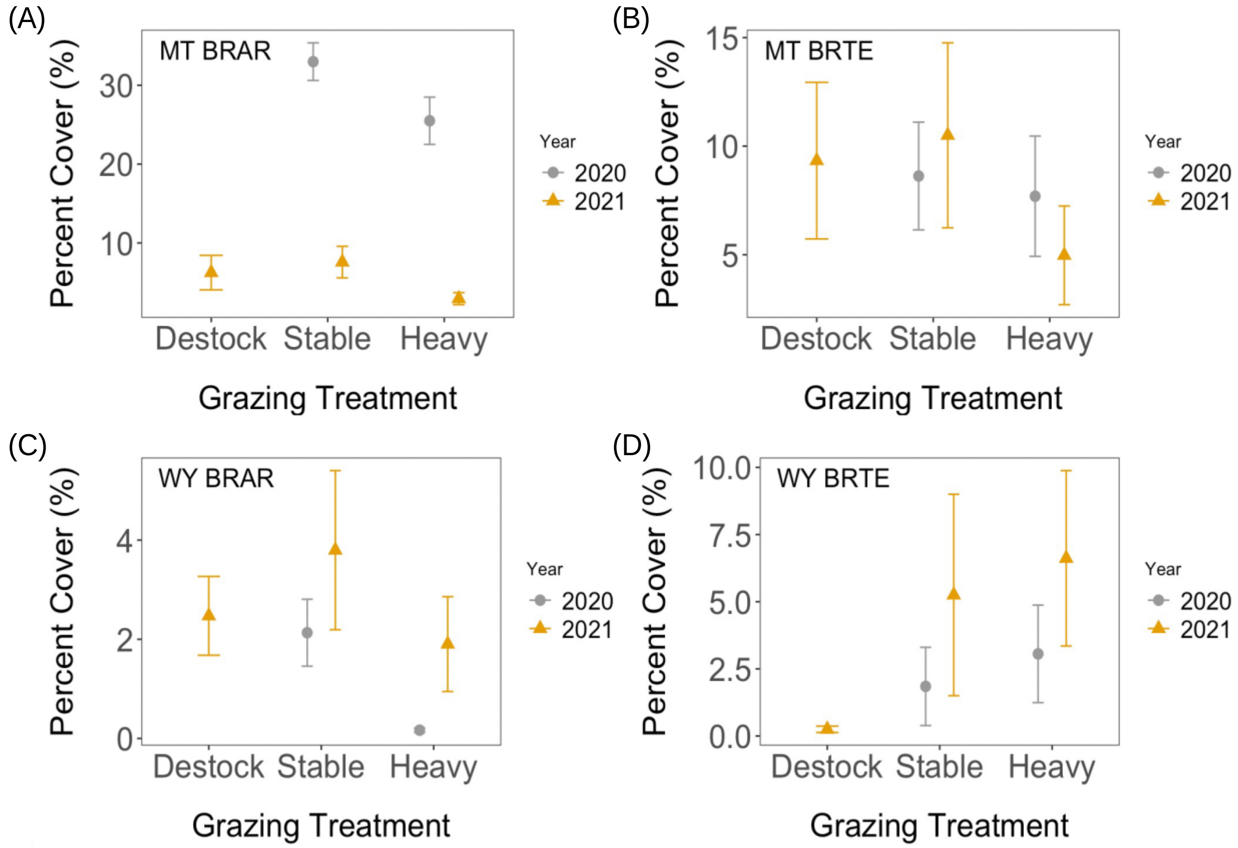

Figure S3. Mean +/- standard error of percent cover (cover) of A-B) *B. arvensis* (BRAR) and *B. tectorum* (BRTE) at Montana (MT) and C-D) BRAR and BRTE at Wyoming (WY) across the grazing treatments through the 2 grazing years. Model fit was assessed using linear mixed-model ANOVAs (Table S3). Two plots at WY never contained BRAR or BRTE across all 4 study years and were dropped from the analyses. Similarly, 8 additional plots at WY never contained BRTE across all 4 study years and were dropped from the BRTE analyses.

Chapter III Supplemental Materials

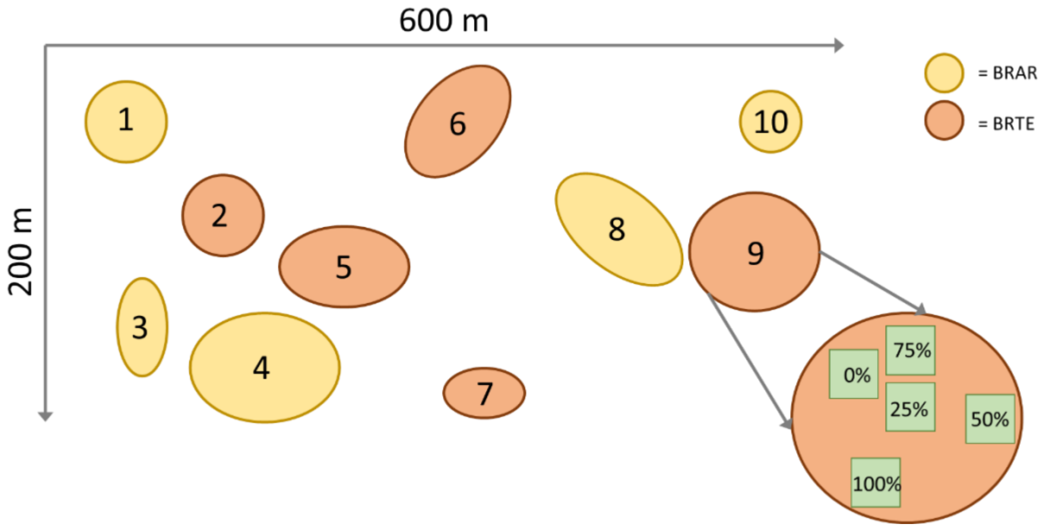

Figure S1. Cartoon drawing of approximate plot layout. Blocks were selected randomly across the landscape by identifying areas that had a high abundance of the two target invasive species. From there, 5 plots were established by selecting plots that fit into the 5 categories of invasion abundance. If a plot could not be found within 10 m of another plot in a block, that block was abandoned, and a new block established. This created blocks of varying geographic extent ranging from 200 m x 600 m.

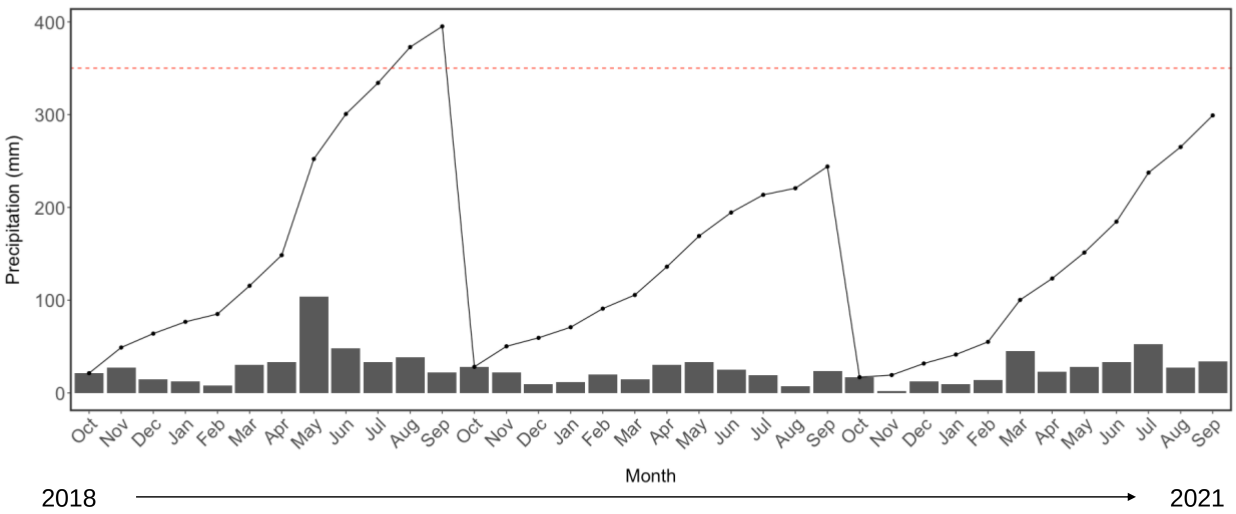

Figure S2. Monthly precipitation from Converse County throughout the 3 years of the study. Bars represent monthly precipitation, while lines correspond to cumulative precipitation. Horizontal red dashed line is the 30-year average October-September precipitation. Data retrieved from the National Oceanic and Atmospheric Administration’s National Centers for Environmental Information (NOAA National Centers for Environmental Information 2022).

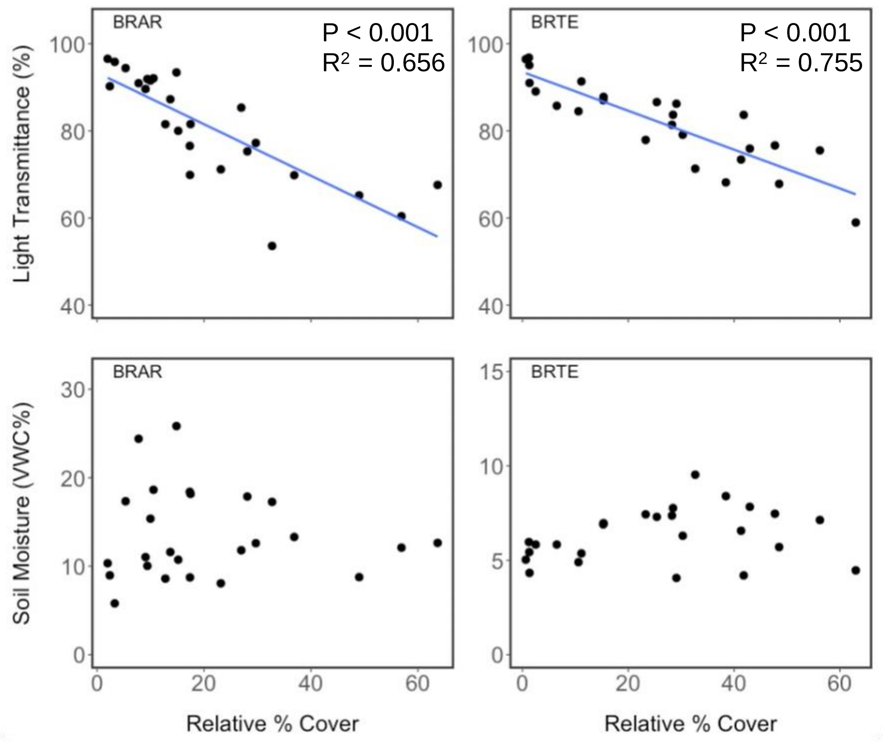

Figure S3. Changes in average light and soil moisture with invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE). P-values and marginal R^2 values for significant (solid lines) effects of invasion on stability metrics are shown according to results from mixed-model ANOVAs (Table S2).

Table S1. Linear mixed model analysis of variance (F statistics with p-values) for the response of stability metrics to invasion by annual bromes. Here, each metric was calculated with respective brome data included for each gradient type (as opposed to results in Table 3.1). Of note, we found less significant results overall when including annual brome data in analyses. Significant values are shown in boldface type, with * indicating $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$.

	B. arvensis				*B. tectorum*			
Stability Metric	Log Transformation	df	F-Value	P-Value	Log Transformation	df	F-Value	P-Value
Richness Stability	Yes	1, 22.31	1.81	0.192	No	1, 20.00	5.03	**0.036****
Evenness Stability	Yes	1, 22.36	2.21	0.151	No	1, 20.53	1.13	0.300
Synchrony	No	1, 23.00	0.92	0.348	No	1, 20.28	1.60	0.220
Species Turnover	No	1, 22.97	5.50	**0.028****	No	1, 19.54	13.18	**0.002****
Cover Stability	Yes	1, 23.00	0.18	0.679	Yes	1, 19.90	0.14	0.711
C3 Grass Stability	Yes	1, 23.00	1.21	0.283	Yes	1, 20.12	2.32	0.143

Table S2. Linear mixed model analysis of variance (F statistics with p-values) for the response of average light availability and soil moisture to invasion by annual bromes. Here, each metric was calculated with respective brome data included for each gradient type. Significant values are shown in boldface type, with *** $p < 0.001$.

		B. arvensis			*B. tectorum*	
Abiotic Variable	df	F-Value	P-Value	df	F-Value	P-Value
Average Light Availability	1, 22.14	45.32	**<0.001*** **	1, 20.88	75.34	**<0.001*** **
Average Soil Moisture	1, 20.10	1.93	0.180	1, 20.10	1.59	0.222

Table S3. Tests of mediation to assess support for direct and indirect effects of invasive annual bromes on plant community stability. Mediator variables here are average light availability and soil moisture (as opposed to stability of these variables as shown in Table 3.2). Stability of richness, evenness, total cover, and C3 grass cover, as well as turnover and synchrony, were calculated without respective brome data for each gradient type. △AICc is change in Akaike information criterion corrected for small sample size. Significant values are shown in boldface type, with * indicating $p < 0.1$ and ** $p < 0.05$.

Question	X	Path Coefficients			△AICc			Conclusion
		Mediating Variable (A -> B -> C)		Not Mediated (A -> C)	Fully mediated	Partially mediated	Not mediated	
		Light	Soil moisture					
1. Is the effect of *B. arvensis* invasion on X mediated by abiotic variables (light, soil moisture)?	Richness Stability	0.33	-0.64***	0.05	0	4.4	9.1	fully or partially mediated by soil moisture
	Evenness Stability	0.05	-0.03	0.06	0	4.4	9.2	no conclusion
	Synchrony	-0.15	0.21	-0.21	0	4.0	8.8	no conclusion
	Species Turnover	0.02	0.56***	0.44*	0	1.3	6.1	no conclusion
	Cover Stability	0.27	-0.21	0.04	0	4.4	9.2	no conclusion
	C4 Grass Stability	0.67**	-0.15	0.10	0	5.0	10.3	fully mediated by light
	C3 Grass Stability	-0.15	-0.12	-0.37	0	3.2	8.0	no conclusion
	Forb Stability	0.56*	-0.12	0.18	0	4.1	8.9	fully or partially mediated by light
2. Is the effect of *B. tectorum* invasion on X mediated by abiotic variables (light, soil	Richness Stability	-0.06	-0.16	-0.57*	0	2.4	7.7	no conclusion
	Evenness Stability	-0.12	0.12	-0.51	0	2.5	6.9	no conclusion
	Synchrony	0.36	0.00	0.15	0	4.3	8.6	no conclusion
	Species Turnover	0.69**	0.26*	1.14***	9.1	0	4.4	no conclusion
	Cover Stability	-0.33	-0.03	-0.36	0	3.6	7.9	no conclusion
	C4 Grass Stability	-0.47	-0.49**	-0.30	0	4.5	10.4	fully or partially mediated by soil moisture
	C3 Grass Stability	-0.28	-0.11	-0.81**	1.6	0	4.4	no conclusion
	Forb Stability	-0.05	-0.51**	-0.24	0	4.6	10.3	fully or partially mediated by soil moisture

Chapter IV Supplemental Materials

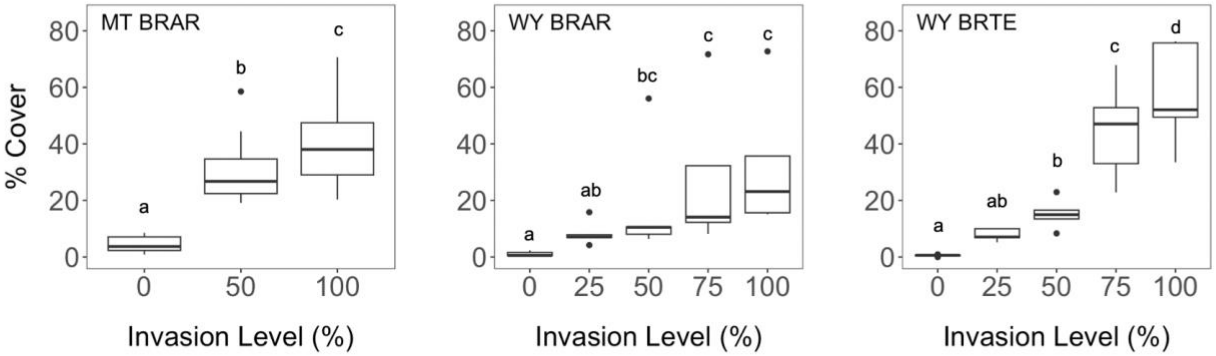

Figure S1. Relativized percent cover of *B. arvensis* (BRAR) and *B. tectorum* (BRTE) across categorized invasion levels in Montana (MT) and Wyoming (WY). Letters indicate significant differences in relativized percent invasion abundance at that invasion category.

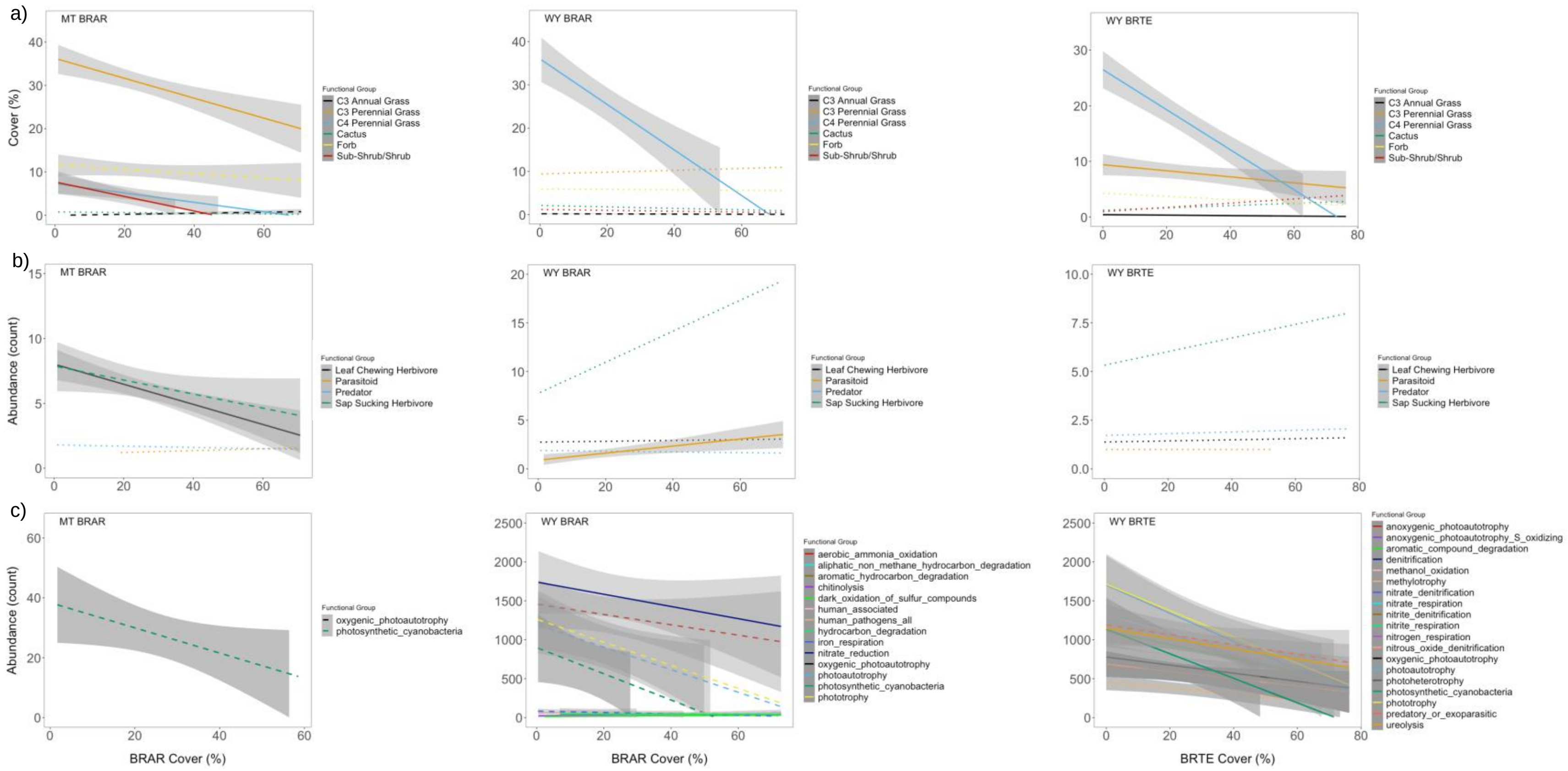

Figure S2. Changes in a) plant, b) insect, and c) soil microbial functional groups with invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY). Solid lines indicate significant relationships, dashed lines indicate marginally significant relationships, and dotted lines indicate non-significant relationships according to mixed model ANOVAs. Grey shading represents error bars for significant or marginally significant relationships. For soil microbes, only significant or marginally significant relationships are presented, excluding microbes classified as "other".

Table S1. Linear mixed model analysis of variance (F statistics with p-values) for the response of plant, insect, and soil microbial functional groups to invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY). Significant and marginally significant values are shown in boldface type. ID indicates insufficient data for regression analyses and N/A indicates that functional group was not present in that gradient type. For soil microbial functional assignments, some OTU's were assigned to multiple functional groups based on ecological function.

	MT BRAR			WY BRAR			WY BRTE		
Trophic level	df	F-value	P-value	df	F-value	P-value	df	F-value	P-value
Plant									
C3 annual grass	1, 46.00	3.641	**0.063**	1, 22.88	4.228	**0.051**	1, 20.13	4.402	**0.049**
C3 perennial prass	1, 46.00	14.643	**<0.001**	1, 23.00	0.729	0.402	1, 23.00	4.414	0.407
C4 perennial grass	1, 42.87	13.258	**0.001**	1, 18.33	30.470	**<0.001**	1, 19.85	71.739	**<0.001**
Cactus	1, 44.89	0.717	0.402	1, 18.21	0.079	0.782	1, 20.75	1.365	0.256
Forb	1, 42.84	3.055	**0.088**	1, 19.28	0.006	0.941	1, 19.84	2.150	0.158
Sub-shrub/shrub	1, 44.49	14.889	**<0.001**	1, 22.79	0.693	0.414	1, 20.83	2.320	0.143
Insect									
Detritivore	ID	ID	ID	N/A	N/A	N/A	N/A	N/A	N/A
Leaf chewing herbivore	1, 45.35	8.995	**0.004**	1, 15.06	0.047	0.832	1, 17.90	0.384	0.543
Predator	1, 39.86	0.675	0.416	1, 18.00	0.143	0.710	1, 16.80	0.337	0.570
Sap sucking herbivore	1, 44.23	3.730	**0.060**	1, 19.98	0.801	0.382	1, 22.00	1.828	0.190
Parasitoid	1, 3.00	0.000	0.997	1, 11.35	12.014	**0.005**	1, 3.00	1.110	0.370
Pollen/nectar eating herbivore	ID	ID	ID	ID	ID	ID	ID	ID	ID
Other herbivore	ID	ID	ID	ID	ID	ID	ID	ID	ID
Fungivore	N/A	N/A	N/A	ID	ID	ID	N/A	N/A	N/A
Soil Microbe									
Aerobic ammonia oxidation	1, 43.87	0.141	0.709	1, 23.00	2.976	**0.098**	1, 23.00	1.049	0.317
Aerobic chemoheterotrophy	1, 43.97	0.254	0.617	1, 23.00	0.298	0.590	1, 23.00	2.410	0.134
Aerobic nitrite oxidation	1, 41.72	0.195	0.661	1, 22.00	1.267	0.272	1, 22.00	0.000	0.994
Aliphatic non-methane hydrocarbon degradation	1, 7.00	0.005	0.947	1, 1.00	1609.400	**0.016**	1, 5.00	0.599	0.555
Animal parasites or symbionts	1, 42.00	0.825	0.369	1, 22.00	0.280	0.602	1, 22.00	1.977	0.174
Anoxygenic photoautotrophy	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.328	**0.049**
Anoxygenic photoautotrophy S oxidizing	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.328	**0.049**
Aromatic compound degradation	1, 43.00	0.704	0.406	1, 23.00	2.139	0.157	1, 20.94	9.716	**0.005**
Aromatic hydrocarbon degradation	1, 7.00	0.005	0.947	1, 1.00	1609.400	**0.016**	1, 8.00	0.134	0.724
Cellulolysis	1, 35.00	0.000	0.991	1, 16.91	0.295	0.594	1, 20.82	0.569	0.459
Chemoheterotrophy	1, 43.96	0.256	0.615	1, 23.00	0.289	0.596	1, 23.00	2.810	0.107
Chitinolysis	1, 38.63	0.040	0.843	1, 12.91	4.808	**0.047**	1, 4.00	0.004	0.956
Dark oxidation of sulfur compounds	1, 13.00	0.163	0.693	1, 4.00	9.605	**0.036**	1, 1.01	31.099	0.111
Dark thiosulfate oxidation	N/A	N/A	N/A	N/A	N/A	N/A	1, 3.00	4.629	0.121
Denitrification	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.285	**0.050**
Fermentation	1, 42.98	0.012	0.913	1, 23.00	0.045	0.834	1, 23.00	0.583	0.453
Human associated	1, 22.00	0.010	0.921	1, 14.62	7.504	**0.015**	1, 15.63	0.298	0.593
Human gut	ID	ID	ID	1, 1.80	0.892	0.454	1, 5.00	0.061	0.815
Human pathogens all	1, 21.00	0.171	0.684	1, 12.12	3.752	**0.076**	1, 12.21	0.714	0.414
Human pathogens pneumonia	N/A	N/A	N/A	N/A	N/A	N/A	1, 3.00	4.629	0.121
Human pathogens septicemia	N/A	N/A	N/A	N/A	N/A	N/A	1, 3.00	4.629	0.121
Hydrocarbon degradation	1, 7.00	0.005	0.947	1, 1.00	1609.400	**0.016**	1, 8.00	0.134	0.724
Intracellular parasites	1, 14.43	0.251	0.624	1, 9.61	0.019	0.894	1, 10.38	3.184	0.104
Iron respiration	1, 8.08	0.691	0.430	1, 8.29	4.487	**0.066**	1, 15.00	1.538	0.234
Mammal gut	ID	ID	ID	1, 1.80	0.892	0.454	1, 5.00	0.061	0.815
Manganese oxidation	1, 43.06	0.015	0.902	1, 23.00	1.573	0.222	1, 20.36	0.679	0.420
Methanol oxidation	1, 44.00	1.236	0.272	1, 17.49	2.001	0.175	1, 20.64	8.001	**0.010**
Methylotrophy	1, 44.00	1.236	0.272	1, 17.49	2.001	0.175	1, 20.64	8.001	**0.010**
Nitrate denitrification	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.285	**0.050**
Nitrate reduction	1, 43.79	0.138	0.712	1, 15.70	5.921	**0.027**	1, 23.00	1.020	0.323
Nitrate respiration	1, 43.61	0.228	0.636	1, 22.73	1.674	0.209	1, 23.00	4.330	**0.049**
Nitrification	1, 43.79	0.158	0.693	1, 23.00	2.351	0.139	1, 23.00	0.904	0.352
Nitrite denitrification	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.285	**0.050**
Nitrite respiration	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.285	**0.050**
Nitrogen fixation	1, 43.59	0.217	0.644	1, 22.35	0.402	0.533	1, 20.91	0.395	0.537
Nitrogen respiration	1, 43.61	0.228	0.636	1, 22.73	1.674	0.209	1, 23.00	4.330	**0.049**
Nitrous oxide denitrification	1, 43.63	0.240	0.627	1, 22.95	0.568	0.459	1, 23.00	4.285	**0.050**
Nonphotosynthetic cyanobacteria	1, 38.72	0.008	0.928	1, 14.56	0.738	0.404	1, 23.00	1.989	0.172
Other	1, 43.38	0.165	0.686	1, 15.58	0.560	0.465	1, 23.00	4.402	**0.047**
Oxygenic photoautotrophy	1, 31.60	3.661	**0.065**	1, 20.00	2.600	0.123	1, 20.11	12.754	**0.002**
Photoautotrophy	1, 43.75	0.033	0.857	1, 16.48	3.360	**0.085**	1, 20.12	19.194	**<0.001**
Photoheterotrophy	1, 43.76	0.213	0.647	1, 22.16	0.750	0.396	1, 21.35	4.479	**0.046**
Photosynthetic cyanobacteria	1, 31.60	3.661	**0.065**	1, 20.00	2.600	0.123	1, 20.11	12.754	**0.002**
Phototrophy	1, 43.86	0.042	0.838	1, 16.49	3.335	**0.086**	1, 20.07	20.205	**<0.001**
Plant pathogen	ID	ID	ID	ID	ID	ID	1, 3.00	4.629	0.121
Plastic degradation	N/A	N/A	N/A	N/A	N/A	N/A	1, 3.00	4.629	0.121
Predatory or exoparasitic	1, 42.25	0.002	0.969	1, 18.88	0.941	0.344	1, 23.00	3.127	**0.090**
Respiration of sulfur compounds	1, 36.32	0.020	0.888	1, 16.79	0.587	0.454	1, 17.00	0.637	0.436
Sulfate respiration	1, 36.32	0.020	0.888	1, 16.79	0.587	0.454	1, 17.00	0.637	0.436
Ureolysis	1, 43.94	0.853	0.361	1, 23.00	0.000	0.999	1, 21.24	6.697	**0.017**
Xylanolysis	ID	ID	ID	ID	ID	ID	ID	ID	ID

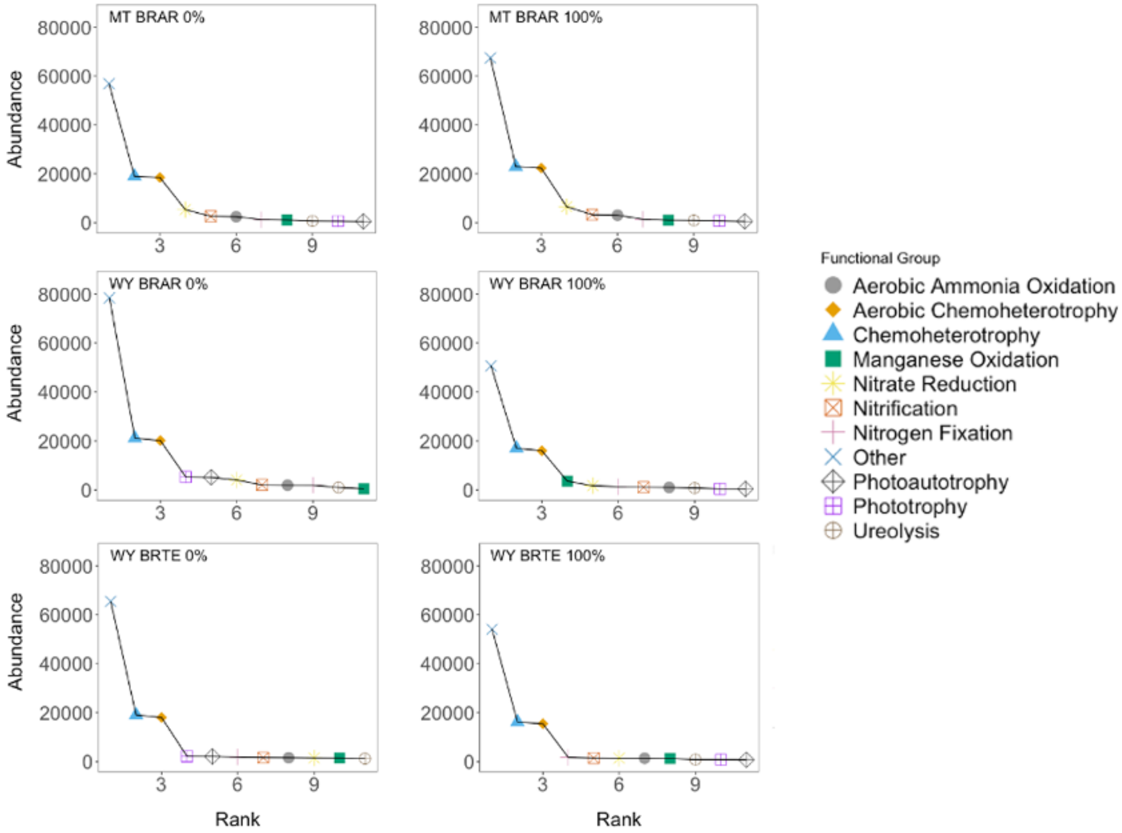

Figure S3. Rank-abundance curves (RACs) for soil microbial functional groups under invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY). Here, we included all microbial functions that were not part of the top ten common functions between invasion levels as other, as compared to Figure 4.4c. The first row compares functional group changes between low (0%) and high (100%) invasion by BRAR in MT, the middle row compares functional group changes between low (0%) and high (100%) invasion by BRAR in WY, and the bottom row compare functional group changes between low (0%) and high (100%) invasion by BRTE in WY.

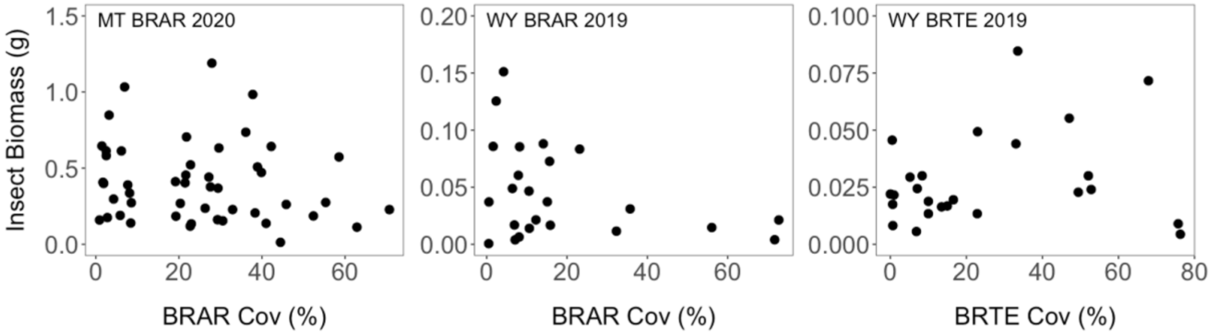

Figure S4. Changes in total insect biomass with invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY) in 2019 and 2020.

Table S2. Linear mixed model analysis of variance (F statistics with p-values) for the response of total insect biomass to invasion by *B. arvensis* (BRAR) and *B. tectorum* (BRTE) in Montana (MT) and Wyoming (WY) .

Gradient	Log transformation	df	F-value	P-value
WY BRAR 2019	No	1, 21.48	0.689	0.416
WY BRTE 2019	Yes	1, 23.00	0.018	0.894
MT BRAR 2020	Yes	1, 43.69	2.192	0.146
MT BRAR 2021	Yes	1, 17.87	1.119	0.304
MT BRAR 2022	Yes	1, 22.00	0.017	0.897

Chapter V Supplemental Materials

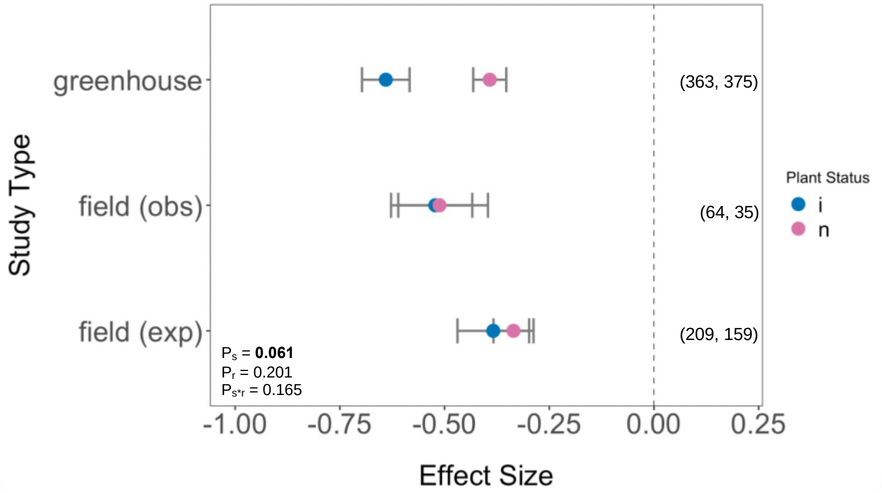

Figure S1. Plant responses (mean ± standard error) under drought to different study types – greenhouse, observational field studies (field (obs)), and experimental field studies (field (exp)). The number of response ratios included at each level are shown in parentheses, with number for introduced (i) species first and number of native (n) species second. P-values for plant status (P_s), study type (P_r), and the interaction between plant status and study type ($P_{s\ x\ r}$) are included, with boldface type indicating significant or marginally significant results.

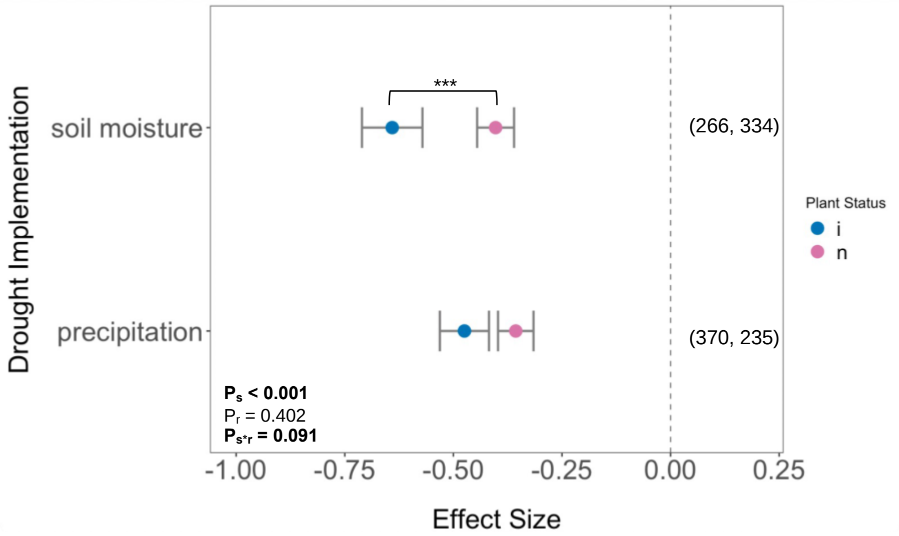

Figure S2. Plant responses (mean ± standard error) under drought to different methods of drought implementation – as measured by either a reduction in soil moisture or precipitation. The number of response ratios included at each level are shown in parentheses, with number for introduced species first and number of native species second. P-values for plant status (P_s), drought implementation (P_r), and the interaction between plant status and drought implementation ($P_{s\ x\ r}$) are included, with boldface type indicating significant or marginally significant results. *** indicates significant differences within groups, where $p < 0.001$.


Miles City, Montana

“A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.” -Aldo Leopold, A Sand County Almanac and Sketches Here and There