

PLANT COMMUNITY RESPONSE TO *BROMUS TECTORUM* MANAGEMENT IN THE
HIGH-ELEVATION SAGEBRUSH STEPPE OF SOUTHWEST MONTANA

by

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DEDICATION

I would like to dedicate this dissertation to my family. My grandparents, Bob and Mary Blotkamp, my parents, Terise and Wayne Mumford, my brother Drew Mumford, and of course Huck. Without their love and support, this would not exist.

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ABSTRACT

Bromus tectorum (cheatgrass) invasion is a management concern across the western United States. Herbicide is the most common *B. tectorum* control method, but integrated management is becoming more common. Previous research indicates that the high-elevation sagebrush steppe is resilient to *B. tectorum* invasion due to a combination of native perennial grass abundance, topography, and cooler and wetter climate. Additionally, plant-soil feedbacks, the interaction between plants and their soil microbial community, are proposed to play a role in ecosystem invasibility. We explored the response of *B. tectorum* invaded plant communities to herbicide, grazing, restoration seeding, and plant soil feedbacks (PSF).

In the high-elevation sagebrush steppe of southwest Montana, we found that herbicide reduced *B. tectorum* for three to four years. Importantly, the paired “reference” communities did not observe an increase in *B. tectorum*. The herbicide control was not associated with an increase in species richness nor perennial grass biomass. A community analysis found the sprayed communities were resilient to *B. tectorum* management. Both sprayed and reference community assemblages shifted due to slight increases in *B. tectorum* and native perennial forb cover and a reduction in native perennial grass cover. These changes were correlated with warmer and drier seasons, which could impact the future resiliency of this system.

Integrated non-native plant management is a successful alternative to singular methods. Through a combination of grazing, herbicide and restoration seeding we found that intensive fall grazing was the most effective form of *B. tectorum* management. Unexpectedly, herbicide application resulted in a nutrient pulse, possibly altering soil nutrient cycling and soil microbial communities. Indeed, our PSF study found that *B. tectorum* received a strong positive feedback that was not affected by competition; though native soil reduced the competitive effect of *B. tectorum*. We propose that PSFs are a mechanism by which plant communities confer resilience to non-native plant invasion.

This research demonstrates that where *B. tectorum* has invaded south-facing slopes of sagebrush steppe in southwest Montana, it can be controlled by herbicide though without, increased diversity or productivity, and that both invaded and uninvaded communities are resilient.

CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

Introduction

Plant ecology is the study of plant interactions with their environment and one another. Non-native plant ecology is a sub-discipline of plant ecology, and primarily focuses on *why* non-native plants behave the way they do, *how* their populations remain stable or expand, and *what* if anything can land managers do about their presence. These are not questions unique to non-native plant ecology; rather they are a specific subset of questions that arise from the foundational questions of plant succession and assemblage theory that Clements (1916), Gleason (1939), Sutherland (1974) and others have attempted to answer for decades. To date no defined set of rules explains all plant community assemblages. However, the literature is rife with theory that provide frameworks by which we can empirically test the mechanisms that might be most influential under varying environmental contexts. It is the goal of this brief literature review to provide a synthesis of the relevant topics for the following dissertation. I begin with a discussion of foundational theories as they relate to plant ecology, invasion ecology, and plant soil feedback theory. We then consider the ecology and impact of the non-native annual grass, *Bromus tectorum* L. (cheatgrass) and non-native plant management strategies as they pertain to *B. tectorum*. Finally, we conclude with a statement of need for this research and overview of the subsequent chapters.

Plant Ecology

Ecological Filtering

Alexander von Humboldt is often credited with first documenting the abiotic limits of different vegetation communities. Humboldt used elevation and latitude as proxies for one another and found that increasing elevation had a similar effect on plant distributions as latitude (variance in temperature and precipitation). Holdridge (1947) advanced Humboldt's findings to include potential evapotranspiration ratio, annual precipitation, and humidity provinces (e.g., arid, semi-arid, etc.) described as the Life Zone System, and Whittaker (1956) included topographic features such as slope and aspect. These major contributions to understanding landscape level distributions of plant communities was critical in the conceptualization of the fundamental constraints on vegetation distribution, that would later be called the fundamental niche formalized by the limnologist G.E. Hutchinson (1957). Hutchinson extended the niche beyond the abiotic factors to include biotic factors (e.g., species interaction/competition, dispersal limitation etc.) to describe what is now called the realized niche. The niche was an important theoretical step towards conceptualizing plant community composition. Based on these theories we understand the niche as having multiple dimensions, that is, it is described by a magnitude of abiotic and biotic factors. Each of these dimensions can be thought of as the conditions that each species requires to survive and reproduce. Each species is assumed to have its own niche, species with high overlap in niche space (i.e. similar requirements for survival and reproduction) will eventually displace the other, as proposed by Gause (1934). Communities are therefore composed of species which inevitably have some niche overlap, but not to the extent that exclusion occurs, i.e., co-existence (MacArthur 1958, MacArthur 1970, May and Arthur

1972). The combination of these theories make up the theoretical underpinnings of species distribution modeling; which have allowed land managers to focus conservation or non-native plant management resources more effectively. For example, Chambers et al. (2023) use climate and topography to predict areas more or less suitable for annual grass invasion in the western United States. In theory these predictions should help land managers to target high risk areas; leading to a more efficient allocation of resources.

At a finer spatial extent, vegetation communities are unique in that each member is static in its lifetime, and must adapt to changing conditions, including losses and additions of competitors. The process by which a species establishes in a new environment has been likened to passing through multiple environmental filters; at each level of ecological filtering the species must pass some kind of biotic or abiotic constraint which vary by species (Woodward and Diament 1991). These ecological filters establish the capacity of a system to support incoming species, both native and non-native. For grasslands, Seastedt and Pyšek (2011a) defined a system of filters that impact the success of invasion by non-native plants. They are split broadly into invader characteristics, as well as regional and community traits. These traits are further dissected into, climate, site, resource, and disturbance filters. Within this filtering process invaders experience both positive and negative feedbacks and must withstand the negative ones to remain on the landscape and contribute to community composition.

The theories mentioned above attempt to explain how plant communities assemble and fluctuate over time and space. However, for these theories to be tested ecologists require a quantitative metric that will allow them to track changes and make comparisons between communities.

Quantifying Biodiversity

The suite of species that make it through the ecological filtering process forms not a static community but rather a dynamic one over time. This temporal variation in community composition has led to the need for a robust quantification method. Species richness (occurrence) offers a simple form of community measure but biodiversity metrics provide more information by combining richness and abundance (Goodman 1975, Magurran and McGill 2010). Diversity can then be decomposed into richness and evenness, which is essentially the relative abundance of each species in a community and provides useful insight into plant community structure. For example, high evenness indicates equal representation of all species, whereas low evenness indicates dominance by a single species. Further, the similarity of plant community membership can be compared using beta-diversity indices. These indices vary in complexity, either accounting for only similarity in membership or accounting for both membership and abundance (Magurran and McGill 2010). One of the most commonly used indexes, Bray-Curtis, accounts for both membership and abundance (Magurran and McGill 2010).

Despite the stated simplicity here, the selection of indices based on research goals should always be considered (Morris et al. 2014). For example, Simpson's index, a measure of alpha-diversity, has perhaps the only practical interpretation, it measures the probability of recording a given species, but is less sensitive to rare species detection due to its weighting of evenness (Magurran and McGill 2010). Shannon's index, also a measure of alpha-diversity, does not have a straightforward interpretation, but is best suited for capturing rare and abundant species, and therefore more commonly implemented (Magurran and McGill 2010, Morris et al. 2014). A simple solution to the ambiguity of alpha diversity indices is rank abundance. This methodology is simply a quantification of the community data that reflects the identity of each species and

their position relative to one another based on abundance. This proves a useful tool for understanding plant community dynamics because the dominant and rare species can be identified and tracked temporally and spatially.

The Niche, Competition and Community Structure

How each species interacts is defined in part by its niche, and niche overlap largely determine whether coexistence occurs (Gause 1934). At a larger scale communities consists of a suite of niches, with each species having its own niche, both potential and realized (Hutchinson 1959). The degree to which species can be “packed” into a community has been well theorized and studied, and melds competition with community structure (MacArthur 1970, May and Arthur 1972). Defining a species’ comprehensive niche is likely un-realistic, but basic constraints and limiting factors are important first steps. This information can help build predictive models and habitat suitability maps to aid managers. For example, the niche of the relatively new invasive winter annual grass *Ventenata dubia* (Leers) Coss. (*Ventenata*/ North African grass) has been explored specifically with the above in mind (Jones et al. 2018).

Niche overlap directly influences the competitive interaction between two or more species within a community. Ultimately, the strength of these interactions dictates whether community members coexist or are competitively excluded (Hastings 1980, Tilman 1982, Tilman 2004). However, conceptualization of this idea quickly becomes complicated with the realization that niche “space” does not exist in a single dimension but is rather a multidimensional space, i.e., plants compete for a multitude of resources that fluctuate over time and space. Regardless, identifying the limiting resource for each species-niche relationship is paramount for understanding their impact on community structure and ecosystem function (MacArthur 1970,

Tilman 1985, Tilman 2004). The realized niche is constrained by abiotic factors and by competition. These competitive interactions structure the niche assemblages, and thus community assemblages. Similar to community composition, competitive effects vary both spatially, temporally, and in response to external stressors (drought, grazing, fire etc.), directly influencing co-existence and thus community structure (Chesson and Huntly 1997).

Of particular importance is the idea of temporal variation, that is species can have overlapping niches, but due to temporal differences, e.g., annual vs. perennial, differing times of resource uptake etc. These temporal differences lead to co-existence and reduced competitive interactions, though some overlap still may occur, and the competition may be indirect (reduction of soil water earlier in growing season) (Chesson and Huntly 1997). The duration over which we study these ecological components is important. Dominance, for example, can have different meanings across different time spans, a growing season, the life of a perennial grass, a shrub or tree, all experience dominance and community structure differently (Gleason 1939). Whether due to shortsightedness or lack of funding, many studies do not extend beyond a year or two, with very few monitoring beyond five years, and additionally are often spatially limited to a hectare or less (Monaco et al. 2017). This is especially problematic when trying to monitor non-native plant invasion, and restoration efforts. As a result, ecologists have attempted to create predictive models of plant community response to varying environmental stimuli (May 1971, 1972, May and Arthur 1972, Holling 1973, Holling 1996, Peterson et al. 1998, May 2019). These theoretical and predictive models have been applied with some degree of success with regard to species distribution models, e.g., Bradley et al. (2018).

Stability, Resilience, and Diversity

Ecological stability, equilibrium, and resilience were the focal points of early theoretical ecologists (Elton 1958, Hutchinson 1959, May 1971, 1972, May and Arthur 1972), many of which built on empirical competition studies to create community response predictions. By their very nature, these studies have incorporated the concept of diversity and attempt to understand the linkages between stability, resilience, and diversity.

At their core stability, resilience, and equilibrium are all descriptive terms for system behaviors and defining their meaning is axiomatic. Holling (1973) defines stability as "...the ability of a system to return to an equilibrium state after a temporary disturbance; the more rapidly it returns and the less it fluctuates the more stable it would be." and resilience as "...a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables.". Evidence for both positive and negative relationships between complexity, that is, species linkages, and stability have been produced (May 1971, 1972, May and Arthur 1972, De Angelis 1975, Pimm 1979, 1984). Additionally, Holling (1973) proposed that stability and resilience are responses of the observed systems caused by external factors (e.g., disturbance), creating an emphasis on abiotic controls for system behavior. Because stability deals with speed at which a system returns to a prior state, resilience has been suggested as a more realistic and important ecosystem trait for manipulation by land managers because of its focus on resisting/absorbing change (Holling 1973, Holling 1996, Peterson et al. 1998). Further, Peterson et al. (1998) emphasized the diversity of species present and that their interaction between one another directly influences ecosystem function and resilience. By this logic, greater species diversity increases the potential for functional redundancy, which increases the number of possible relationships that can occur

between species and maintains ecosystem function if species are lost (i.e. increased resilience). Huston's (1979) general theory of species diversity foreshadowed Peterson et al.'s (1998) connection between diversity and ecosystem function. Huston states "Diversity is determined not so much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of their interactions", emphasizing the importance of environmental conditions on competitive dynamics that ultimately shape species interactions and thus community structure which Peterson et al. (1998) relates to resilience. Empirical evidence supports the positive relationship between diversity and stability (Tilman et al. 2006) and negates it (Bezemer and Van Der Putten 2007).

From the perspective of land management, resilience, resistance and stability have been touted as key ecosystem characteristics that can reduce the impact of non-native plant invasion (Chambers et al. 2014b). Specifically, abundance and diversity of native plants, precipitation quantity and timing, temperature, and disturbance regime have all been correlated with ecosystem resilience, resistance, and stability (Folke et al. 2004, Chambers 2016, Roundy et al. 2018, Van Meerbeek et al. 2021).

Invasion Ecology

Invasion theory is a specific form of community ecology, focused on community assemblage, which has been discussed in depth in prior sections. Of the vast work that has touched on community assemblage, Connell and Slatyer (1977) exploration of the mechanisms (e.g., facilitation, tolerance, inhibition) of community assemblage acknowledges the importance of competitive interactions, resource availability, and disturbance frequency and intensity. In addition to these concepts, Lonsdale (1999) proposed that ecosystem properties (e.g., resistance

to invasion, susceptibility to invasion, disturbance), propagule pressure/dispersal rates, and invader traits were key components of invasion ecology.

Unique to the field of invasion ecology is the term “invasibility” which has been defined as the abiotic and biotic factors that characterize a systems vulnerability to non-native plant invasions (Seastedt and Pyšek 2011b). Importantly, invasibility incorporates a temporal component and is not a static attribute of plant communities but rather one that fluctuates (Davis et al. 2000) and can differ based on the ability of the invader to exploit specific ecosystem properties and establish a viable population (Levine and D’Antonio 1999). As a result, the character of both the invader and the native plant community will dictate the response of the system, often resulting in changes to community composition or structure. For example, Levine and D’ Antonio 1999 suggested that greater diversity leaves fewer niches available to support invaders. In contrast, Palmer and Maurer (1997) suggested that micro-heterogeneity caused by increased diversity also increases niche availability and the likelihood that a species which promotes coexistence with an invader will be present in the community. The latter is consistent with Lonsdale (1999), who found that native and non-native species richness are positively correlated. Both Palmer and Maurer (1997) and Lonsdale (1999) directly contradicted earlier theory by Huston (1979), who suggested that increased diversity also increased the chance of a plant community containing a species that repelled invaders, and thus increased the community’s ability to resist invasion. Because no unified relationships between community composition and invasibility have emerged, many theories exist to explain the possible mechanisms of non-native plant invasion. Only those relevant to this body of work: the “enemy release”, “intermediate disturbance”, “fluctuating resource”, and “plant soil feedback” hypotheses are discussed here.

Fluctuating Resource Hypothesis

The fluctuating resource hypothesis emphasizes that unused resources (light, water, nutrients, space) or pulses in un-used resources are correlated with the invasability of a site; the causes of this resource release can be due to loss of competitors, disturbance, or natural flux of abiotic factors (Davis et al. 2000). This hypothesis is an extension of Grime's Triangle, which states that stress and disturbance dictate the degree of competition (within a community of plants), because they both affect resource availability in different ways (Grime 1988). Neither disturbance nor stress are constant over time and space, emphasizing the importance of both Grime's Triangle and the fluctuating resource hypothesis on invasibility, within communities and across landscapes.

Intermediate Disturbance Hypothesis

The intermediate disturbance hypothesis was first conceived of by Connell 1978. Similar to the fluctuating resource hypothesis, intermediate disturbance hypothesis makes use of Grime's Triangle (Grime 1988). The intermediate disturbance hypothesis proposes that intermediate levels of disturbance allow for a greater array of species to co-exist by increasing the importance of tolerance to disturbance/stress relative to competition (Connell 1978). Huston (1979) extended the intermediate disturbance hypothesis by emphasizing that competitive interactions/exclusions are secondary to the frequency and intensity of disturbances that communities experience. These theories suggest that disturbances of intermediate frequency and intensity will promote species co-existence by providing each affected species enough time to recover, but not enough time to dominate.

Enemy Release Hypotheses

Unlike the afore-mentioned theories, the enemy release hypothesis (Elton 1958) does not consider competition or resources. Instead, the foundation of this theory rests on the assumptions that co-evolved disease, herbivores, and competitors (“enemies”) of the invader do not exist in the new system (Keane and Crawley 2002). This “release” results in a competitive advantage for the invader in the new system, where native plants are competing and defending themselves from co-evolved pathogens, herbivores, and competitors. This results in a comparative advantage to the “enemy” free invader. While first applied to plant community interactions and invasion ecology, this hypothesis has also been referenced in the field of belowground ecology and plant soil feedbacks (Agrawal et al. 2005).

Plant Soil Feedbacks and Non-Native Plant Invasion

Plant community alteration most commonly occurs by way of disturbance, which in turn is frequently followed by non-native plant invasion, likely due to increased soil nutrient availability and reduced competition for resources (Davis et al. 2000, MacDougall and Turkington 2005, Seastedt and Pyšek 2011a). Despite the frequent occurrence of non-native plant invasions, the persistence of non-native species is not well understood, however, tight linkages between resource availability and community composition, suggest that plant soil feedbacks (PSFs) may provide an explanation (Bever et al. 1997, Van Der Putten et al. 2013). Non-native plants can implement PSFs that promote their persistence on the landscape by altering soil nutrients, litter quality, and soil microbial community composition (Bever et al. 1997, Belnap and Phillips 2001, Evans et al. 2001, Van Der Putten et al. 2013). Invasion ecology and PSFs are naturally intertwined, and characterization of plant strategies and traits have revealed complex

relationships that connect soil microbial communities, plants, higher trophic levels, and nutrient cycling (Wardle et al. 2004, Van Der Putten et al. 2007, Van Der Putten et al. 2013). There is some potential for non-native plants to implement ecosystem changes via the soil microbial community. Largely this potential is driven by temporal variation in nutrient availability via litterfall timing and quality (Schimel et al. 1985, Burke 1989, Tilman and Wedin 1991, Evans et al. 2001). As a result, non-native plants could impact microbial community abundance and structure if soil microbes are sensitive to nutrient availability, timing, and quantity. Most plant-microbe partnerships occur on the basis of nutrient exchanges, and can result in heightened competitive abilities for plants due to increased resources made available by soil microbes (Wardle et al. 2004). Additionally, anti-microbial plant secondary metabolite (PSM) production and priming of plant defenses act as interactive pathways that impact the relationship between plants and soil microbes (Marschner and Dell 1994, Van Rhijn and Vanderleyden 1995, Venturi and Keel 2016).

Non-native plant invasion introduces novel traits to a community, these traits often result in temporal changes to nutrient cycling, rates, and quality (Davis et al. 2000, Ehrenfeld 2003, 2010). Grass monoculture studies have revealed how slight changes in nitrogen (N) mineralization rates, have the potential to change plant community composition and dominance (Tilman and Wedin 1991, Wedin and Pastor 1993). Temporal re-allocation of N could impact availability for native plant community and for soil microbial community response and composition, leading to changes in nutrient cycling (carbon (C) and N) rates (Hobbie 1992). For example, enhanced litter quality (higher N content) could increase decomposition rates of litter

and N cycling, conversely an increase C content of litter in the form of lignin or other complex carbon structures could increase decomposition rates and quantity of N and C inputs.

Bromus tectorum Ecology

Bromus tectorum History

To understand *B. tectorum*'s life history and physiology is to understand a great deal of its competitive ability and its proliferation across the landscape. This non-native winter annual grass is capable of germinating and emerging in the fall, followed by a period of overwintering as a seedling. Conversely, it is capable of overwintering as a seed and germinating in the spring, at which time it rapidly grows to maturity by early summer. Regardless of germination timing, *B. tectorum* typically senesces by early summer.

Bromus tectorum was likely introduced as a grain contaminant in the early 1800's, in the Pacific north-west (Mack 1981). From there it spread due to grazing, agriculture, and homesteading practices, and by the mid 1930's *B. tectorum* occurred widely (Mack 1981). By 1970 *B. tectorum* was observed in northern Idaho, near the Montana border (Daubenmire 1970), however, the earliest observation of *B. tectorum* in Montana was much earlier in 1898 (Herbaria 2021). Initially utilized as a highly nutritious early season forage for cattle, this winter annuals quick and inconsistent maturation ultimately rendered it an unreliable forage (Harris 1967).

Plasticity of Response to Environment

In general, annual species optimize growth and seed production by responding to within season variability (Stutz 1994). On the other hand, perennial species maximize growth and seed production over multiple growing seasons (Stutz 1994). Each phenology has its advantages, for

example, established mature perennial plant communities will have a competitive advantage over annual invader seedlings, but when competition occurs at the seedling stage; the competitive advantage appears to sway to annual species (Rummell 1946, Hull 1963, Harris 1967, Harris and Wilson 1970, Harris 1977, Melgoza et al. 1990, Dawn and Young 2002).

Bromus tectorum has been documented to grow in cold- down to 3°C, and wet conditions (Mccarlie et al. 2001, Monaco et al. 2005) but is ultimately, limited in its range by the extreme cold (Brummer et al. 2016). Under warmer conditions *B. tectorum* germinates at a greater rate (Thill et al. 1984), yields more biomass and produces more seeds compared to native perennial grasses (Aguirre and Johnson 1991, Nasri and Doescher 1995). However, it is necessary that these warmer conditions are coupled with sufficient soil moisture to induce germination and support growth (Bradley et al. 2016a). Not only does *B. tectorum* exhibit plasticity in response to growing season conditions, but also shows plasticity within its genetic variation, that allows for establishment in different habitat types (Rice et al. 1992). For example, arid populations of *B. tectorum* produce fewer but larger seeds and flower earlier than both wet forest and mesic populations (Rice et al. 1992). Further, culm height and spikelet production show great variation in response to soil moisture, nutrients, and light availability (Harris 1967). Additionally, *B. tectorum* had greater N absorption rates and whole-plant nitrogen uptake at lower temperatures compared to native grasses (Leffler et al. 2011a). The adaptive response of *B. tectorum* to a variety of environmental conditions including varying levels of soil moisture, temperature, and soil N likely makes *B. tectorum* a stronger competitor allowing it to produce more seed and subsequently persist on the landscape. Indeed, in some instances *B. tectorum* has been reported to produce anywhere from 13,000 to 20,000 seeds/m² (Hulbert 1955, Hempy-Mayer and Pyke

2008). The observed plasticity in growth and reproduction investment based on environmental conditions are evidence of its competitive ability compared to perennial species which also exhibit plasticity in response to changing environmental conditions, albeit, to a lesser extent (Leffler et al. 2011b).

Bromus tectorum and the Nitrogen Cycle

Bromus tectorum allocates a greater amount of N to ripe seeds compared to plant tissue because of reduced allocation to maintain perennial growth (Rickard 1985). As a result *B. tectorum* seeds store N both temporally and spatially that might otherwise be immobilized by plants and microbes, and offers an under-considered N sink (Rickard 1985). However, not all seeds become plants, and the N in seeds that do not germinate is returned to the soil. In general *B. tectorum* has a great affinity for nitrogen (N), preferentially in the form of nitrate (NO₃) but also in the form of ammonium (NH₄) (Monaco et al. 2003) and responds positively to N additions by producing more above and belowground biomass, as a result of increased growth rate (James 2008, Vasquez et al. 2008). This is counter to the response observed in native grasses, which typically do not respond to N addition to the same degree or at all when compared to *B. tectorum* (Orloff et al. 2013). At the seedling stage *B. tectorum* has a higher rate of mass specific absorption and whole plant uptake of N compared to the native perennial grasses across a wide range of temperatures (Leffler et al. 2011a). This is important from two perspectives: first *B. tectorum* has greater resource acquisition capability compared to native perennial seedlings, over a wider variety of conditions as discussed above, which has important implications for competition. Further, Morris et al. (2016) found that *B. tectorum* roots exuded twice the total amount of nitrogen compared to *Agropyron cristatum* L. Gaertn. (crested wheatgrass). In the

same greenhouse study, *B. tectorum* immobilized 30% more N and organic carbon. In the field, evidence for increasing and decreasing soil pools of N in response to *B. tectorum* invasion exists. For example, the high N content found in *B. tectorum* litter and its relatively rapid decomposition rate compared to native litter, have been proposed to increase soil N (Evans et al. 2001, Booth et al. 2003) and other studies appear to confirm these findings (Jackson et al. 1988, Stark and Norton 2015, Blank and Morgan 2016, Morris et al. 2016). Some exceptions do exist (O'connor and Prevey 2015, Mahood et al. 2022), however, and suggest that *B. tectorum* invasion might have varied results with regard to N depending on context.

Thus far I have discussed the direct effects of *B. tectorum* on nitrogen cycling, but some evidence suggests that *B. tectorum* has indirect effects via alteration of the soil microbial community. For example, microbial immobilization of N, in the field, was higher in *B. tectorum* invaded communities vs. un-invaded communities, and denitrification enzyme activity was enhanced in non-invaded communities compared to invaded communities (Evans et al. 2001). In a greenhouse study, greater microbial activity (respiration) was observed in pots that contained *B. tectorum* (Morris et al. 2016), suggesting that the presence of *B. tectorum* could be inducing changes to soil microbial cycling of nutrients.

Plant Soil Feedback Potential

Soil nutrient cycling in plant communities is largely driven by plant community composition, soil microbial community, and abiotic influences (temperature, precipitation, soil type, aspect, and slope) (Schimel et al. 1985, Hobbie 1992, Wardle et al. 2004). Litter and roots are the greatest input of “recycled” C and N at the community scale, though fixation of C as CO₂ and N from the atmosphere do occur. Plant community composition influences soil nutrient

availability through uptake, litter timing and quality, and microbial community alteration via root exudates (Callaway and Ridenour 2004) and/or symbiotic exchange for nutrients (Van Rhijn and Vanderleyden 1995). The soil microbial community to a large degree determines the rate at which these nutrients are made available to plants and other organisms, which to an extent is mediated by plant root exudates, soil moisture and temperature, and plant community composition (Hobbie 1992, Wardle et al. 2004). While all these components interact, the degree to which each component is most important likely depends on both temporal and spatial scale (Burke 1989). Furthermore, soil microbial communities provide a host of roles beyond nutrient cycling. They can, for example, act as vectors for disease, symbiosis, or have no effect at all for some or all plants in the community (Wardle et al. 2004).

I have already discussed the theory of PSFs as they relate to plant and invasion ecology, and here I provide a review of PSF literature as it pertains to *B. tectorum*. Evidence for no plant soil feedbacks (Perkins and Nowak 2012, 2013) and positive plant soil feedbacks exist (Kulmatiski et al. 2011, Blank and Morgan 2013, O'connor and Prevey 2015, Vargas and Cheng 2015, Blank et al. 2016, Blank and Morgan 2016, Kulmatiski 2019) but in a recent survey of the literature no studies provided evidence for negative PSFs. Importantly, all the studies listed above, except for Kulmatiski (2019), were conducted in a greenhouse setting.

In the instances of positive PSFs, *B. tectorum* grew better in soil that it had conditioned compared to soil conditioned by other native and non-native plants and in every instance its competitive ability was not altered based on soil conditioning. Interestingly, this was also the case in the two studies that did not find evidence for PSFs, that is, there was no difference in biomass or competitive ability of *B. tectorum* based on soil type (Perkins and Nowak 2012,

2013). Despite these findings, no mechanism has currently been proposed to explain how *B. tectorum* conditioned soils enhance biomass production. The strong evidence for positive PSFs that favor *B. tectorum* growth and abundance have been proposed to have a myriad of repercussions. Suding et al. (2013) suggested that positive PSFs, act as density dependent advantages that can promote dominance of a singular species. Other studies have found that in addition to increased growth and biomass, positive PSFs for *B. tectorum* were also related to reduced soil mineral N and increased N uptake (Blank and Morgan 2013, Blank et al. 2016) and increased abundances of soil bacterial and fungal groups (Evans et al. 2001, Gehring et al. 2016, Mcleod et al. 2016, Mcleod et al. 2021, Nasto et al. 2022). In nutrient limited systems, these impacts as the result of plant-microbe interaction, have been proposed to have great importance for structuring plant competitive dynamics (Revillini et al. 2016).

Competition

Agropyron spicatum Pursh. (bluebunch wheatgrass) and *B. tectorum* have been a common focus of competition experiments. Although other comparisons between *B. tectorum* exist involving *A. cristatum*, *Agropyron smithii* (Rydb.) A. Love (western wheatgrass), *Stipa comata* Trin. & Rupr. Barkworth (needle and thread grass) and others (Rummell 1946). Early literature emphasizes that *B. tectorum* was widely found in *A. spicatum* stands, however, dominance only occurred when associated with overgrazing, fire, plowing, fertilizer application, or trampling (Harris 1967). *Bromus tectorum* seedlings often have an overall higher growth rate compared to established perennial grasses (*A. spicatum*, *A. cristatum* and *Elymus elymoides* Raf. Swezey (squirreltail)) which has contributed to its success as an invader (Harris 1967, Harris and Wilson 1970, Harris 1977, Arredondo et al. 1998). However, some native perennial grasses such

as *Elymus multisetus* M.E. Jones (big squirreltail), compete well with *B. tectorum* (Blank 2010, Rowe and Leger 2011). Furthermore, findings from Orloff et al. (2013) suggest that *A. spicatum* suppressed *B. tectorum* to a greater extent when given a four-leaf stage growth advantage and an experimental increase in soil N in a greenhouse experiment. While encouraging, it is unlikely that this scenario occurs in nature due to the comparatively fast-growing phenology of annual vs. perennial seedlings. Further, *B. tectorum* seedlings typically germinate in the fall, whereas native perennial seedlings typically emerge in the spring. However, the fast-slow plant economic spectrum hypothesized by Reich (2014) posits that “fast” traits such as rapid/efficient soil resource uptake, only provided benefit when resources are not limited, and prove detrimental otherwise. This theory also posits that the spatial and temporal heterogeneity of resources allows a mixture of “fast” and “slow” strategies to exist simultaneously. This is apparent in the comparison of *B. tectorum* and the native sagebrush steppe plant community. For example, the historic composition of native plants has been perennial with the absence of many annuals and suggests that a “slow” perennial strategy has been favored evolutionarily until the arrival of European settlers, non-native flora, and climate change. Indeed, human-caused disturbance and changing climate are important factors for *B. tectorum* invasion (Lavin et al. 2013, Brummer et al. 2016).

Competition between *B. tectorum* and the native plant community is typically discussed within the ecosystem context of the sagebrush biome. In this biome, *B. tectorum* invasion is often correlated with a decrease in native plant cover (Anderson and Inouye 2001). Specifically, native grass cover above 25% reduces the range and probability of *B. tectorum* invasion (Brummer et al. 2016). Though native grasses are an important ecological and economic component of

rangelands, Reisner et al. (2013) suggest that the entire native plant community assemblage is equally important when assessing the resilience to *B. tectorum* invasion.

Ecological Impacts

Two distinct characteristics of *B. tectorum* drive its ability to impact ecosystems: its annual life cycle (Mack 1981) and its relationship with fire (Chambers et al. 2016). Above I have discussed the phenology of *B. tectorum*, here I focus on its relationship with fire. *Bromus tectorum* can increase fire return rates to native systems, both reducing sagebrush and native perennial grasses (Pellant 1989, Pyke et al. 2014, Pilliod et al. 2017, Bradley et al. 2018, Pyke et al. 2022). This cycle is largely driven by its invasion of shrub interspaces (Pellant 1989), resulting in a more continuous and flammable fuel (Brooks et al. 2004, Zouhar 2008, Pilliod et al. 2017), that is available earlier in the season than native vegetation (Harris 1967). As a result, this positive fire feedback cycle can increase *B. tectorum* growth, abundance, and dominance (Chambers et al. 2007a). Following fire, plant community composition is largely driven by the surviving fire tolerant members and recruitment from the seedbank (Zouhar 2008). As discussed above, *B. tectorum* is highly competitive at the seedling stage, and it is at this critical point that *B. tectorum* can enact community composition change.

When considering the fire feedback cycle, it is important to understand that disturbance such as fire do not occur in a vacuum. In reality, the plant community following fire can result from the interaction of multiple disturbances such as grazing, herbicide application, and fire (Seefeldt and McCoy 2003, Seastedt and Pyšek 2011b). Further, the degree to which fire promotes *B. tectorum* depends on climate. For example, in wetter and colder climates within the sagebrush biome, there is no response to the *B. tectorum* fire cycle (Taylor et al. 2014). In these

climates physical disturbance due to roads or grazing has been associated with a greater abundance of non-native plants compared to communities that had been burned (Lavin et al. 2013, Taylor et al. 2014, Larson et al. 2017).

Bromus tectorum Management

Non-native plant management is a costly and time intensive, estimated to cost \$34 billion dollars nationally (Pimentel et al. 2005). Within the sagebrush biome, Nevada spends an estimated \$6 to \$12 million dollars annually (Eiswerth et al. 2005). Similarly, Montana spent \$12 million dollars over the fiscal years of 2018 and 2019 (Montana Department of Agriculture Noxious Weed Program 2020). As a result, the need for lasting and cost-efficient management methods are paramount. This is especially true for, *B. tectorum* which has been well-established for over a century (Mack 1981) and is widespread throughout the Snake River Plain, North Central Basin and Range, and the Central Basin and Range (often referred to as the Great Basin) (Bradley et al. 2018), but is less abundant in the Middle Rockies. Despite the extensive efforts by managers and researchers alike, few long-term solutions to *B. tectorum* invasion exist (Mack 2011). Several studies have stated that *B. tectorum* management efforts should be focused in areas of lower abundance where successful control is more likely (Hemstrom et al. 2002, Elseroad and Rudd 2011, Kyser et al. 2013, Crist et al. 2019). Here I review three common *B. tectorum* management actions: herbicide, restoration seeding, and grazing.

Herbicide Application to Control *Bromus tectorum*

Perhaps the most common and straightforward approach to control *B. tectorum* has been the application of herbicides. Specifically, imazapic (Plateau®; BASF Corporation, 100 Park

Ave., Florham Park, NJ), is commonly used to control *B. tectorum* in rangeland settings. Imazapic is a non-selective ALS-inhibiting herbicide known to affect both monocots (grasses) and some broad leaf plants (Beste 1983). Although initially developed as a pre-emergent herbicide, recent studies in southwest Montana have found strong control of *B. tectorum* using a fall post-emergent application (Mangold et al. 2013). Fall applications increase the selectivity and efficacy of control by targeting *B. tectorum* in its post-emergent stage. At this time the native perennial component of the plant community is largely senesced, reducing non-target impacts. However, others have shown that timely pre-emergence application can selectively impact annuals over perennials (Schroeder et al. 2022). Post-application, imazapic has a soil residual period of 120 days with a primary mode of degradation due to soil microbes (Beste 1983).

Following application, length of control is varied (one to four years) and often site dependent (Elseroad and Rudd 2011, Pyke 2011, Pyke et al. 2014, Roundy et al. 2018). Conversely, long-term studies, 10 and 15 years post-treatment, show *B. tectorum* returns to prior abundances (Rinella et al. 2012, Roundy et al. 2018). Early restoration efforts following herbicide application increases the probability of restoration success (Davis et al. 2000). A review of management efforts to control *B. tectorum* has shown the most successful “long term” suppression of *B. tectorum* was herbicide application followed immediately by seeding (Monaco et al. 2017).

The incorporation of multiple control methods is referred to as integrated management. Combinations of fire, restoration seeding, herbicide, and grazing are examples of effective integrated *B. tectorum* management (Menalled et al. 2008, Calo et al. 2012, Lehnhoff et al. 2019). The combination of integrated management and early detection and response ideology,

which prioritizes the protection of non-invaded and vulnerable habitat (Hobbs and Huenneke 1992, Hobbs and Humphries 1995, Radosevich et al. 2007) has the potential to prevent widespread non-native plant establishment. Further, research also suggests that these approaches be adaptive, that is, change in response to observed success/failures spatially and temporally (Chambers et al. 2014a, Schroeder et al. 2022, Shriver 2022). As a result, it is crucial that the interaction of management methods, such as restoration seeding, grazing, and herbicide, and their response to environmental variation such as precipitation, temperature, and disturbance, are studied.

Restoration Seeding in the Sagebrush Biome

Restoration of the sagebrush biome has proven difficult due to hot and dry growing conditions which contribute to slow recovery rates, projected to exceed 100 years (Knick 1999). Most often restoration seeding follows management to reduce non-native plant populations, such as herbicide application (Owen et al. 2011, Orloff et al. 2015). Depending on the severity of disturbance or infestation land managers must decide if passive or active restoration is most appropriate. An active approach that integrates grazing, seeding, herbicide and fire, is often most effective in slowing conversion of shrublands to non-native annual grasslands (Hemstrom et al. 2002). To guide management, successional theory is often implemented, and has been used to inform restoration seeding efforts (Sheley et al. 2006, Hoelzle et al. 2012). Explicitly, restoration seeding has lasting effects on the long-term, 25 years post-seeding, trajectory of plant community assemblage (Hoelzle et al. 2012). In addition, the combination of seeding and herbicide (Rinella et al. 2012, Clements et al. 2022), precipitation timing and quantity (Kyser et al. 2013), seeding method (drill or broadcast), species traits (Clements et al. 2022), timing of seeding itself (Harvey

et al. 2020), and seeding rate (Sheley and Bates 2008) influence the establishment and composition of restoration plant communities. As a result, each restoration plan may require a unique approach that addresses the limitations of the given scenario.

Grazing's Effect on *Bromus tectorum*

Historically, *B. tectorum* was a critical spring forage across Nevada, Utah, and southern Idaho, due to its early maturation and nutrient quality (Fleming et al. 1942, Cook 1952, Klemmedson and Smith 1964). Due to its palatability, *B. tectorum* can be managed with targeted grazing (Mosley and Roselle 2006). Over the last decade, research has supported and dissuaded the use of specifically targeted fall grazing to control *B. tectorum*. For example, targeted fall grazing using cattle, in both the Great Basin and Montana, has led to reduced *B. tectorum* cover, increased bare ground, and increased perennial grass cover (Schmelzer et al. 2014, Vermeire et al. 2023b). However, a study from Montana observed an increase in *B. tectorum* abundance following targeted fall cattle grazing (Rew et al. 2023), as did a meta-analysis by Marchetto et al. (2021). Following fire, Davies et al. (2021), found fall grazing effective for managing *B. tectorum*. Additionally, intensive targeted spring grazing in the Great Basin (Diamond et al. 2012) and widespread fall grazing in southeastern Oregon show the potential of grazing to reduce the abundance of *B. tectorum* in seedbanks (Perryman et al. 2020). Importantly, all studies listed here caution that grazing be used as a tool within an integrated management plan and do not recommend intensive grazing in any season as a solution to *B. tectorum* invasion.

In Montana, the incorporation of herbicide and targeted grazing by sheep as a management strategy led to only minor reductions in *B. tectorum* abundance (Lehnhoff et al. 2019). Of note, the effects of targeted grazing using sheep appear to yield mixed results. That is,

Seefeldt and McCoy (2003) found spring and fall grazing regimes to enhance native forbs or grasses but not both, and grazing resulted in higher cover of non-natives compared to non-grazed treatments. Interestingly, a complete removal of grazing alone does not appear to promote re-establishment of native plant species (West et al. 1984), suggesting that grazing could be an important aspect of restoration in some but not all scenarios (Marchetto et al. 2021).

Bromus tectorum Control and Restoration in the
High-elevation Sagebrush Steppe of Southwest Montana

Bromus tectorum's ecosystem impacts have been well documented across the western United States. Historically, at the northern extent of its range, in the Middle Rockies ecoregion, *B. tectorum*'s impacts have received less attention and more speculation based on findings from the Columbia Basin, Snake River Plain, and the North and Central Basin and Range ecoregions. These assumptions are based on models that relate resilience and resistance to *B. tectorum* invasion on elevation, aspect, temperature and precipitation projections (Chambers et al. 2007a, Reisner et al. 2013, Chambers et al. 2016, Maestas et al. 2016, Roundy et al. 2018, Doherty et al. 2022b, Smith et al. 2022). However, over the last decade, studies from the Middle Rockies indicate that this ecoregion is less likely to support the positive fire feedback cycle that drives ecosystem change documented in other ecoregions (Taylor et al. 2014) and that disturbance is more important than fire (Lavin et al. 2013), climate (Brummer et al. 2016), or both (Larson et al. 2017). These results suggest that the threat positive fire feedbacks and *B. tectorum* to high-elevation sagebrush steppe are relatively low. Despite these studies and perhaps due to the widespread ecosystem impacts observed in other ecoregions, land managers in the Middle Rockies ecoregion, and specifically the Centennial Valley of southwestern Montana, have

expressed concern over anecdotal increases in *B. tectorum* abundance. Early detection and response methodologies and “protect the core” ideology (Doherty et al. 2022b) are the driving factors behind management in this system but management efficacy in this area lacks long-term quantification.

The goal of the following body of research is to provide public and private land managers with information on the response of plant communities, including *B. tectorum*, to management in the Middle Rockies ecoregion, and specifically southwestern Montana. In the following chapters we present the findings from four studies that address: 1) long-term local scale response of *B. tectorum* to herbicide application; 2) the long-term landscape scale resilience of high-elevation sagebrush steppe to *B. tectorum*, herbicide, and climate; 3) the interactive effects of grazing, herbicide, and seeding on restoration of high-intensity disturbance areas invaded by *B. tectorum*; and 4) the role of plant soil feedbacks on the competitive interactions between *A. spicatum* and *B. tectorum*. It is the authors hope that these findings will help inform land managers now and, in the future, as they decide how best to respond to a variety of land management goals and directives.

Literature Cited

- Agrawal, A. A., P. M. Kotanen, C. E. Mitchell, A. G. Power, W. Godsoe, and J. Klironomos. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above-and belowground enemies. *Ecology* 86:2979-2989.
- Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses.
- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological monographs* 71:531-556.
- Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *Rangeland Ecology & Management/Journal of Range Management Archives* 51:584-589.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* 11:1261-1275.
- Beste, C. 1983. *Herbicide Handbook of the Weed Science Society of America*. Weed Science Society of America.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the Soil Community into Plant Population Dynamics: The Utility of the Feedback Approach. *Journal of Ecology* 85:561-573.
- Bezemer, T. M., and W. H. van der Putten. 2007. Diversity and stability in plant communities. *Nature* 446:E6-E7.
- Blank, R., B. Mackey, and T. Morgan. 2016. Do a native and two exotic grasses respond differently in soils conditioned by native vegetation versus an exotic grass? *Rhizosphere* 2:38-47.
- Blank, R. R. 2010. Intraspecific and interspecific pair-wise seedling competition between exotic annual grasses and native perennials: plant–soil relationships. *Plant and soil* 326:331-343.
- Blank, R. R., and T. Morgan. 2013. Soil engineering facilitates downy brome (*Bromus tectorum*) growth—a case study. *Invasive Plant Science and Management* 6:391-400.
- Blank, R. R., and T. Morgan. 2016. Plant interactions with soils conditioned by different vegetation: A potential explanation of *Bromus tectorum* L. invasion into salt-deserts? *Journal of Arid Environments* 124:233-238.

- Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003. Inorganic N turnover and availability in annual-and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. *Biogeochemistry* 66:311-330.
- Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016. *Bromus* response to climate and projected changes with climate change. Pages 257-274 *Exotic brome-grasses in arid and semiarid ecosystems of the western US*. Springer.
- Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M.-N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions* 20:1493-1506.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of Invasive Alien Plants on Fire Regimes. *BioScience* 54:677-688.
- Brummer, T. J., K. T. Taylor, J. Rotella, B. D. Maxwell, L. J. Rew, and M. Lavin. 2016. Drivers of *Bromus tectorum* Abundance in the Western North American Sagebrush Steppe. *Ecosystems* 19:986-1000.
- Burke, I. C. 1989. Control of Nitrogen Mineralization a Sagebrush Steppe Landscape. *Ecology* 70:1115-1126.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2:436-443.
- Calo, A., S. Brause, and S. Jones. 2012. Integrated treatment with a prescribed burn and postemergent herbicide demonstrates initial success in managing cheatgrass in a northern Colorado natural area. *Natural Areas Journal* 32:300-304.
- Chambers, J., B. A. Roundy, R. Blank, S. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invisable by *Bromus tectorum*? *Ecol. Monogr.* 77:117-145.
- Chambers, J. C. 2016. Using resilience and resistance concepts to manage threats to sagebrush ecosystems, Gunnison sage-grouse, and greater sage-grouse in their eastern range: a strategic multi-scale approach.
- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014a. Resilience to Stress and Disturbance, and Resistance to *Bromus tectorum* L. Invasion in Cold Desert Shrublands of Western North America. *Ecosystems* 17:360-375.

- Chambers, J. C., J. L. Brown, J. B. Bradford, D. I. Board, S. B. Campbell, K. J. Clause, B. Hanberry, D. R. Schlaepfer, and A. K. Urza. 2023. New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, United States. *Frontiers in Ecology and Evolution* 10:1009268.
- Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. S. Clair. 2016. Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:275-304.
- Chambers, J. C., D. A. Pyke, J. D. Maestas, M. Pellant, C. S. Boyd, S. B. Campbell, S. Espinosa, D. W. Havlina, K. E. Mayer, and A. Wuenschel. 2014b. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. United States Department of Agriculture, Forest Service, Rocky Mountain.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150:519-553.
- Clements, C. D., D. N. Harmon, and R. R. Blank. 2022. Seed mix performance and cheatgrass suppression on arid rangelands. *Rangelands* 44:129-135.
- Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie institution of Washington.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science* 199:1302-1310.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* 111:1119-1144.
- Cook, C. W. 1952. Nutritive value of cheatgrass and crested wheatgrass on spring ranges of Utah. *Rangeland Ecology & Management/Journal of Range Management Archives* 5:331-337.
- Crist, M. R., J. C. Chambers, S. L. Phillips, K. L. Prentice, and L. A. Wiechman. 2019. Science framework for conservation and restoration of the sagebrush biome: linking the department of the Interior's Integrated Rangeland Fire Management Strategy to long-term strategic conservation actions. Part 2. Management applications. General Technical Report-Rocky Mountain Research Station, USDA Forest Service.

- Daubenmire, R. 1970. Steppe vegetation of Washington. Technical Bulletin. Washington Agricultural Experiment Station:131 pp.
- Davies, K. W., J. D. Bates, B. Perryman, and S. Arispe. 2021. Fall-winter grazing after fire in annual grass-invaded sagebrush steppe reduced annuals and increased a native bunchgrass. *Rangeland Ecology & Management* 77:1-8.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating Resources in Plant Communities: A General Theory of Invasibility. *Journal of Ecology* 88:528-534.
- Dawn, L. R., and J. A. Young. 2002. Cheatgrass Competition and Establishment of Desert Needlegrass Seedlings. *Journal of Range Management* 55:70-72.
- De Angelis, D. L. 1975. Stability and Connectance in Food Web Models. *Ecology* 56:238-243.
- Doherty, K., D. M. Theobald, J. B. Bradford, L. A. Wiechman, G. Bedrosian, C. S. Boyd, M. Cahill, P. S. Coates, M. K. Creutzburg, M. R. Crist, S. P. Finn, A. V. Kumar, C. E. Littlefield, J. D. Maestas, K. L. Prentice, B. G. Prochazka, T. E. Remington, W. D. Sparklin, J. C. Tull, Z. Wurtzebach, and K. A. Zeller. 2022. A sagebrush conservation design to proactively restore America's sagebrush biome. Report 2022-1081, Reston, VA.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503-523.
- Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 41:59-80.
- Eiswerth, M. E., T. D. Darden, W. S. Johnson, J. Agapoff, and T. R. Harris. 2005. Input–output modeling, outdoor recreation, and the economic impacts of weeds. *Weed Science* 53:130-137.
- Elseroad, A. C., and N. T. Rudd. 2011. Can Imazapic Increase Native Species Abundance in Cheatgrass (*Bromus tectorum*) Invaded Native Plant Communities? *Rangeland Ecology & Management* 64:641-648.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Boston, MA: Springer US, Boston, MA.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic Plant Invasion Alters Nitrogen Dynamics in an Arid Grassland. *Ecological Applications* 11:1301-1310.
- Fleming, C. E., M. A. Shipley, and M. R. Miller. 1942. Bronco grass on Nevada ranges. Bulletin. Agricultural Experiment Station, University of Nevada.

- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics* 35:557-581.
- Fuller, K. B., and J. Mangold. 2017. The costs of noxious weeds: what you can do about them. *Big Sky Small Acres*:8-9.
- Gause, G. 1934. *The struggle for existence* Williams and Wilkins. Baltimore, Maryland.
- Gehring, C. A., M. Hayer, L. Flores-Rentería, A. F. Krohn, E. Schwartz, and P. Dijkstra. 2016. Cheatgrass invasion alters the abundance and composition of dark septate fungal communities in sagebrush steppe. *Botany* 94:481-491.
- Gleason, H. A. 1939. The individualistic concept of the plant association. *American Midland Naturalist* 21:92-110.
- Goodman, D. 1975. The Theory of Diversity-Stability Relationships in Ecology. *The Quarterly Review of Biology* 50:237-266.
- Grime, J. P. 1988. The CSR model of primary plant strategies—origins, implications and tests. Pages 371-393 *Plant evolutionary biology*. Springer.
- Harris, G. A. 1967. Some Competitive Relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.
- Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. *Rangeland Ecology & Management/Journal of Range Management Archives* 30:172-177.
- Harris, G. A., and A. Wilson. 1970. Competition for Moisture among Seedlings of Annual and Perennial Grasses as Influenced by Root Elongation at Low Temperature. *Ecology*:530-534.
- Harvey, A. J., S. C. Simanonok, L. J. Rew, T. S. Prather, and J. M. Mangold. 2020. Effect of *Pseudoroegneria spicata* (bluebunch wheatgrass) Seeding Date on Establishment and Resistance to Invasion by *Bromus tectorum* (cheatgrass). *Ecological Restoration* 38:145-152.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical population biology* 18:363-373.
- Hempy-Mayer, K., and D. A. Pyke. 2008. Defoliation Effects On *Bromus tectorum* Seed Production: Implications For Grazing. *Rangeland Ecology & Management* 61:116-123.

- Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-Steppe Vegetation Dynamics and Restoration Potential in the Interior Columbia Basin, U.S.A. *Conservation Biology* 16:1243-1255.
- Herbaria, C. o. P. N. 2021. Consortium of Pacific Northwest Herbaria. Page <https://www.pnwherbaria.org/resources.php>.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* 7:336-339.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-337.
- Hobbs, R. J., and S. E. Humphries. 1995. An Integrated Approach to the Ecology and Management of Plant Invasions. *Conservation Biology* 9:761-770.
- Hoelzle, T. B., J. L. Jonas, and M. W. Paschke. 2012. Twenty-five years of sagebrush steppe plant community development following seed addition. *Journal of Applied Ecology* 49:911-918.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual review of ecology and systematics* 4:1-23.
- Holling, C. S. 1996. Engineering resilience versus ecological resilience. *Engineering within ecological constraints* 31:32.
- Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual brome grasses. *Ecological monographs* 25:181-213.
- Hull, A. 1963. Competition and water requirements of cheatgrass and wheatgrass in the greenhouse. *Rangeland Ecology & Management/Journal of Range Management Archives* 16:199-204.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113:81-101.
- Hutchinson, G. E. 1957. *A treatise on limnology*. New York : Wiley, New York.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93:145-159.

- Jackson, L., R. Strauss, M. Firestone, and J. Bartolome. 1988. Plant and soil nitrogen dynamics in California annual grassland. *Plant and soil* 110:9-17.
- James, J. 2008. Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. *Journal of Arid Environments* 72:1775-1784.
- Jones, L. C., N. Norton, and T. S. Prather. 2018. Indicators of ventenata (*Ventenata dubia*) invasion in sagebrush steppe rangelands. *Invasive Plant Science and Management* 11:1-9.
- Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). *The Botanical Review* 30:226-262.
- Knick, S. T. 1999. Requiem for a sagebrush ecosystem? *Northwest science*. 73:53-57.
- Kulmatiski, A. 2019. Plant-Soil Feedbacks Predict Native but Not Non-native Plant Community Composition: A 7-Year Common-Garden Experiment. *Frontiers in Ecology and Evolution* 7.
- Kulmatiski, A., J. Heavilin, and K. H. Beard. 2011. Testing predictions of a three-species plant-soil feedback model. *Journal of Ecology* 99:542-550.
- Kyser, G. B., R. G. Wilson, J. Zhang, and J. M. DiTomaso. 2013. Herbicide-Assisted Restoration of Great Basin Sagebrush Steppe Infested With Medusahead and Downy Brome. *Rangeland Ecology and Management* 66:588-596, 589.
- Larson, C. D., E. A. Lehnhoff, and L. J. Rew. 2017. A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. *Oecologia* 185:763-774.
- Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern Idaho, U.S.A. *Ecology and Evolution* 3:1626-1641.
- Leffler, A., T. Monaco, and J. James. 2011a. Nitrogen acquisition by annual and perennial grass seedlings: testing the roles of performance and plasticity to explain plant invasion. *Plant Ecology* 212:1601-1611.
- Leffler, A., T. A. Monaco, and J. James. 2011b. Nitrogen acquisition by annual and perennial grass seedlings: testing the roles of performance and plasticity to explain plant invasion. *Plant Ecol.* 212:1601-1611.
- Lehnhoff, E. A., L. J. Rew, J. M. Mangold, T. Seipel, and D. Ragen. 2019. Integrated management of cheatgrass (*Bromus tectorum*) with sheep grazing and herbicide. *Agronomy* 9:315.

- Levine, J. M., and C. M. D'Antonio. 1999. Elton Revisited: A Review of Evidence Linking Diversity and Invasibility. *Oikos* 87:15-26.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522-1536.
- MacArthur, R. 1970. Species packing and competitive equilibrium for many species. *Theoretical population biology* 1:1-11.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42-55.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: An ecological chronicle. *Agro-Ecosystems* 7:145-165.
- Mack, R. N. 2011. Fifty years of 'waging war on cheatgrass': research advances, while meaningful control languishes. Fifty years of invasion ecology: the legacy of Charles Elton. Oxford, UK: Wiley-Blackwell:253-265.
- Maestas, J. D., S. B. Campbell, J. C. Chambers, M. Pellant, and R. F. Miller. 2016. Tapping Soil Survey Information for Rapid Assessment of Sagebrush Ecosystem Resilience and Resistance. *Rangelands* 38:120-128.
- Magurran, A. E., and B. J. McGill. 2010. Biological diversity: frontiers in measurement and assessment. OUP Oxford.
- Mahood, A. L., R. O. Jones, D. I. Board, J. K. Balch, and J. C. Chambers. 2022. Interannual climate variability mediates changes in carbon and nitrogen pools caused by annual grass invasion in a semiarid shrubland. *Global change biology* 28:267-284.
- Mangold, J., H. Parkinson, C. Duncan, P. Rice, E. Davis, and F. Menalled. 2013. Downy brome (*Bromus tectorum*) control with imazapic on Montana grasslands. *Invasive Plant Science and Management* 6:554-558.
- Marchetto, K. M., T. M. Wolf, and D. J. Larkin. 2021. The effectiveness of using targeted grazing for vegetation management: a meta-analysis. *Restoration Ecology* 29:e13422.
- Marschner, H., and B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant and soil* 159:89-102.

- May, R. M. 1971. Stability in multispecies community models. *Mathematical Biosciences* 12:59-79.
- May, R. M. 1972. Will a large complex system be stable? *Nature* 238:413-414.
- May, R. M. 2019. *Stability and complexity in model ecosystems*. Princeton university press.
- May, R. M., and R. H. M. Arthur. 1972. Niche Overlap as a Function of Environmental Variability. *Proceedings of the National Academy of Sciences* 69:1109-1113.
- McCarlie, V. W., L. D. Hansen, and B. N. Smith. 2001. Respiratory and physiological characteristics in subpopulations of Great Basin Cheatgrass. and DJ Fairbanks, compilers. *Proc. Shrubland ecosystem genetics and biodiversity*, Provo, UT. Ogden, UT: USDA-Forest Service Rocky Mountain Research Station, RMRS-P-21:271-275.
- McLeod, M. L., L. Bullington, C. C. Cleveland, J. Rousk, and Y. Lekberg. 2021. Invasive plant-derived dissolved organic matter alters microbial communities and carbon cycling in soils. *Soil Biology and Biochemistry* 156:108191.
- McLeod, M. L., C. C. Cleveland, Y. Lekberg, J. L. Maron, L. Philippot, D. Bru, and R. M. Callaway. 2016. Exotic invasive plants increase productivity, abundance of ammonia-oxidizing bacteria and nitrogen availability in intermountain grasslands. *Journal of Ecology* 104:994-1002.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13.
- Menalled, F., J. Mangold, and E. Davis. 2008. *Cheatgrass: identification, biology and integrated management*. Bozeman, MT, USA: Montana State University Publication.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *Rangeland Ecology & Management/Journal of Range Management Archives* 56:282-290.
- Monaco, T. A., J. M. Mangold, B. A. Meador, R. D. Meador, and C. S. Brown. 2017. Downy brome control and impacts on perennial grass abundance: a systematic review spanning 64 years. *Rangeland Ecology & Management* 70:396-404.
- Monaco, T. A., S. B. Monsen, B. Smith, and L. Hansen. 2005. Temperature-dependent physiology of *Poa secunda*, a cool season grass native to the Great Basin, United States. *Russ. J. Plant Physiol.* 52:653-658.
- Montana Invasive Species Advisory Council. 2016. *Management Assessment of Invasive Species*.

- Morris, E. K., T. Caruso, F. Buscot, M. Fischer, C. Hancock, T. S. Maier, T. Meiners, C. Müller, E. Obermaier, and D. Prati. 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and evolution* 4:3514-3524.
- Morris, K. A., J. M. Stark, B. Bugbee, and J. M. Norton. 2016. The invasive annual cheatgrass releases more nitrogen than crested wheatgrass through root exudation and senescence. *Oecologia* 181:971-983.
- Mosley, J. C., and L. Roselle. 2006. Targeted livestock grazing to suppress invasive annual grasses. *Targeted grazing: A natural approach to vegetation management and landscape enhancement*:67-76.
- Nasri, M., and P. S. Doescher. 1995. Effect of temperature on growth of cheatgrass and Idaho fescue. *Rangeland Ecology & Management/Journal of Range Management Archives* 48:406-409.
- Nasto, M. K., M. L. McLeod, L. Bullington, Y. Lekberg, and J. M. Stark. 2022. The effect of plant invasion on soil microbial carbon-use efficiency in semi-arid grasslands of the Rocky Mountain West. *Journal of Ecology* 110:479-493.
- O'Connor, J. J., and J. S. Prevey. 2015. Effects of short-term soil conditioning by cheatgrass and western wheatgrass.
- Orloff, L. N., J. M. Mangold, and F. D. Menalled. 2013. Role of size and nitrogen in competition between annual and perennial grasses. *Invasive Plant Science and Management* 6:87-98.
- Orloff, L. N., J. M. Mangold, and F. D. Menalled. 2015. Site-Specific Effects of Exotic Annual Grass Control Integrated with Revegetation. *Ecological Restoration* 33:147-155.
- Owen, S. M., C. H. Sieg, and C. A. Gehring. 2011. Rehabilitating Downy Brome (*Bromus tectorum*)–Invaded Shrublands Using Imazapic and Seeding with Native Shrubs. *Invasive Plant Science and Management* 4:223-233.
- Palmer, M. W., and T. A. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. *Journal of vegetation science* 8:235-240.
- Pellant, M. 1989. The cheatgrass-wildfire cycle-are there any solutions?
- Perkins, L. B., and R. S. Nowak. 2012. Soil conditioning and plant–soil feedbacks affect competitive relationships between native and invasive grasses. *Plant Ecology* 213:1337-1344.

- Perkins, L. B., and R. S. Nowak. 2013. Native and non-native grasses generate common types of plant–soil feedbacks by altering soil nutrients and microbial communities. *Oikos* 122:199-208.
- Perryman, B. L., B. W. Schultz, M. Burrows, T. Shenkoru, and J. Wilker. 2020. Fall-grazing and grazing-exclusion effects on cheatgrass (*Bromus tectorum*) seed bank assays in Nevada, United States. *Rangeland Ecology & Management* 73:343-347.
- Peter Chesson, and Nancy Huntly. 1997. The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities. *The American Naturalist* 150:519-553.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7:8126-8151.
- Pimm, S. L. 1979. The structure of food webs. *Theoretical population biology* 16:144-158.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321-326.
- Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. *Studies in avian biology* 38:531-548.
- Pyke, D. A., S. E. Shaff, J. C. Chambers, E. W. Schupp, B. A. Newingham, M. L. Gray, and L. M. Ellsworth. 2022. Ten-year ecological responses to fuel treatments within semiarid Wyoming big sagebrush ecosystems. *Ecosphere* 13:e4176.
- Pyke, D. A., S. E. Shaff, A. I. Lindgren, E. W. Schupp, P. S. Doescher, J. C. Chambers, J. S. Burnham, and M. M. Huso. 2014. Region-Wide Ecological Responses of Arid Wyoming Big Sagebrush Communities to Fuel Treatments. *Rangeland Ecology & Management* 67:455-467.
- Radosevich, S. R., J. S. Holt, and C. M. Ghera. 2007. *Ecology of weeds and invasive plants: relationship to agriculture and natural resource management*. John Wiley & Sons.
- Reich, P. B. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102:275-301.
- Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* 50:1039-1049.

- Revillini, D., C. A. Gehring, and N. C. Johnson. 2016. The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. *Functional Ecology* 30:1086-1098.
- Rew, L. J., B. F. Sowell, and K. A. Cutting. 2023. Evaluating integrated control practices for cheatgrass at high-elevation sagebrush sites. Society of Range Management Meeting.
- Rice, K. J., R. A. Black, G. Rademaker, and R. D. Evans. 1992. Photosynthesis, Growth, and Biomass Allocation in Habitat Ecotypes of Cheatgrass (*Bromus tectorum*). *Functional Ecology* 6:32-40.
- Rickard, W. 1985. Shoot production and mineral nutrient assimilation in cheatgrass communities.
- Rinella, M. J., J. M. Mangold, E. K. Espeland, R. L. Sheley, and J. S. Jacobs. 2012. Long-term population dynamics of seeded plants in invaded grasslands. *Ecological Applications* 22:1320-1329.
- Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* 19:155-162.
- Roundy, B. A., J. C. Chambers, D. A. Pyke, R. F. Miller, R. J. Tausch, E. W. Schupp, B. Rau, and T. Gruell. 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. *Ecosphere* 9:e02417.
- Rowe, C. L. J., and E. A. Leger. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications* 4:485-498.
- Rummell, R. S. 1946. Some Effects of Competition from Cheatgrass *Brome* on Crested Wheatgrass and Bluestem Wheatgrass. *Ecology* 27:159-167.
- Schimel, D., M. A. Stillwell, and R. G. Woodmansee. 1985. Biogeochemistry of C, N, and P in a Soil Catena of the Shortgrass Steppe. *Ecology* 66:276-282.
- Schmelzer, L., B. Perryman, B. Bruce, B. Schultz, K. McAdoo, G. McCuin, S. Swanson, J. Wilker, and K. Conley. 2014. Case Study: Reducing cheatgrass (*Bromus tectorum* L.) fuel loads using fall cattle grazing. *The Professional Animal Scientist* 30:270-278.
- Schroeder, V. M., D. D. Johnson, R. C. O'Connor, C. G. Crouch, W. J. Dragt, H. E. Quicke, L. F. Silva, and D. J. Wood. 2022. Managing invasive annual grasses, annually: A case for more case studies. *Rangelands* 44:210-217.
- Seastedt, T., and P. Pyšek. 2011a. Mechanisms of plant invasions of North American and European grasslands. *Annual Review of Ecology, Evolution, and Systematics* 42.

- Seastedt, T. R., and P. Pyšek. 2011b. Mechanisms of Plant Invasions of North American and European Grasslands. *Annual Review of Ecology, Evolution, and Systematics* 42:133-153.
- Seefeldt, S. S., and S. D. McCoy. 2003. Measuring plant diversity in the tall threetip sagebrush steppe: influence of previous grazing management practices. *Environmental Management* 32:234-245.
- Sheley, R. L., and J. D. Bates. 2008. Restoring western juniper-(*Juniperus occidentalis*) infested rangeland after prescribed fire. *Weed Science* 56:469-476.
- Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. *Ecological monographs* 76:365-379.
- Shriver, L. C. 2022. Restoration and evolution in the Great Basin: non-target herbicide effects and potential for adaptive responses to fire.
- Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, M. O. Jones, A. R. Kleinhesselink, J. D. Maestas, S. L. Morford, and D. E. Naugle. 2022. The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA. *Diversity and Distributions* 28:83-96.
- Stark, J. M., and J. M. Norton. 2015. The invasive annual cheatgrass increases nitrogen availability in 24-year-old replicated field plots. *Oecologia* 177:799-809.
- Stutz, H. C. 1994. Evolution of weedy annuals. General Technical Report INT.:9.
- Suding, K. N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and W. H. van der Putten. 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology* 101:298-308.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *The American Naturalist* 108:859-873.
- Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* Response to Fire Varies with Climate Conditions. *Ecosystems* 17:960-973.
- Thill, D. C., K. G. Beck, and R. H. Callihan. 1984. The biology of downy brome (*Bromus tectorum*). *Weed Science* 32:7-12.
- Tilman, D. 1982. Resource competition and community structure. Princeton university press.

- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist* 125:827-852.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U. S. A.* 101:10854-10861.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629-632.
- Tilman, D., and D. Wedin. 1991. Plant Traits and Resource Reduction For Five Grasses Growing on a Nitrogen Gradient. *Ecology* 72:685-700.
- van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol, J. N. Klironomos, A. Kulmatiski, and J. A. Schweitzer. 2013. Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology* 101:265-276.
- van der Putten, W. H., J. N. Klironomos, and D. A. Wardle. 2007. Microbial ecology of biological invasions. *The ISME journal* 1:28-37.
- Van Meerbeek, K., T. Jucker, and J.-C. Svenning. 2021. Unifying the concepts of stability and resilience in ecology. *Journal of Ecology* 109:3114-3132.
- van Rhijn, P., and J. Vanderleyden. 1995. The Rhizobium-plant symbiosis. *Microbiological Reviews* 59:124.
- Vargas, T., and W. Cheng. 2015. Rhizosphere-mediated effects of the invasive grass *Bromus tectorum* L. and native *Elymus elymoides* on nitrogen cycling in Great Basin Desert soils. *Plant and soil* 393:245-257.
- Vasquez, E., R. Sheley, and T. Svejcar. 2008. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Science and Management* 1:287-295.
- Venturi, V., and C. Keel. 2016. Signaling in the rhizosphere. *Trends in plant science* 21:187-198.
- Vermeire, L. T., R. C. Waterman, K. O. Reinhart, and M. J. Rinella. 2023. Grazing Intensity and Seasonality Manipulate Invasive Annual Grasses and Native Vegetation. *Rangeland Ecology & Management* 90:308-313.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological Linkages Between Aboveground and Belowground Biota. *Science* 304:1629.

- Wedin, D. A., and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia* 96:186-192.
- West, N. E., F. D. Provenza, P. S. Johnson, and M. K. Owens. 1984. Vegetation change after 13 years of live-stock grazing exclusion on sagebrush semidesert in west central Utah. *Rangeland Ecology & Management/Journal of Range Management Archives* 37:262-264.
- Whittaker, R. H. 1956. Vegetation of the great smoky mountains. *Ecological monographs* 26:2-80.
- Woodward, F., and A. Diament. 1991. Functional approaches to predicting the ecological effects of global change. *Functional Ecology*:202-212.
- Zouhar, K. 2008. Wildland fire in ecosystems: fire and nonnative invasive plants. Forest Service.

CHAPTER TWO

LONG-TERM LOCAL SCALE RESPONSE OF *BROMUS TECTORUM* TO HERBICIDE
APPLICATIONIntroduction

Non-native plant management frameworks emphasize proactive mitigation of initial invasions to reduce ecosystem scale impacts (Crist et al. 2019, Doherty et al. 2022a). Herbicide application is one of the oldest, most common, and accessible methods of non-native plant control. By applying herbicide, managers attempt to address the issue of propagule pressure, one of the three major tenants of invasion ecology proposed by Lonsdale (1999). This methodology has the potential to reduce the number of individuals, through direct mortality, to a degree that the plant population cannot expand or is competitively restricted by other vegetative components, or both. Additionally, removal of mature individuals, before seed production, reduces seedbank stores directly through mortality and indirectly by inhibiting seedbank replenishment. However, herbicide use can come with the risk of removal or reduction of native non-target plants (Rinella et al. 2009, Shriver 2022) and reductions in soil microbial diversity and abundance (Beaumelle et al. 2023). Careful attention to herbicide application rate, timing, and mode of action can reduce these effects (Radosevich et al. 2007) and herbicide should help to reduce the spread and distribution of established invaders. This is important because non-native plant management is costly, estimated to cost \$34 billion dollars nationally, representing a top concern for land managers (Pimentel et al. 2005, Fuller and Mangold 2017). At the state level, Eiswerth et al. (2005) estimated that economic loss stemming from non-native plant

invasion is between \$6 and \$12 million per year in Nevada, and \$12 million in Montana (Montana Department of Agriculture Noxious Weed Program 2020).

One of the most widespread non-native species is the winter annual grass *Bromus tectorum* L. (cheatgrass). This species has been present for nearly two centuries in the western United States (Mack 1981) and its effects are most commonly documented in three major level III ecoregions; the Snake River Plain, North Central Basin and Range, and the Central Basin and Range (often referred to as the Great Basin) (Omernik 1987, Corvallis Environmental Research Laboratory and Omernik 1995, U.S. Environmental Protection Agency 2013) (Supplemental Figure 1). *Bromus tectorum* is extremely tolerant of disturbance due to its winter-annual life cycle (Mack 1981, Mack and Pyke 1983, Young et al. 1987), and this species is often correlated with disturbance, typically in the form of intensive grazing or landscape development (Seefeldt and McCoy 2003, Lavin et al. 2013). *Bromus tectorum* invasions are frequently associated with increased fire frequency (Brooks et al. 2004, Balch et al. 2013, Pilliod et al. 2017) resulting in reduced perennial grass abundance that is important for wildlife and cattle forage (Reisner et al. 2013). A historic combination of intensive grazing by livestock, human development, positive wildfire feedbacks and changing climate have contributed to the continued expansion and persistence of *B. tectorum* across the sagebrush biome (Brooks et al. 2004, Lavin et al. 2013, Chambers et al. 2014a, Chambers et al. 2016, Bradley et al. 2018).

Since 1990 *B. tectorum* has expanded rapidly at a rate of $>2,300\text{km}^2/\text{year}$ in the Great Basin region and at a rate of $430\text{ km}^2/\text{year}$ in the Snake River Plain (Smith et al. 2022). Expansion observed in the Great Basin is tightly correlated with positive fire feedback cycles, however this has not been documented in the upper Snake River Plains (northern Idaho) and

southwest Montana (Lavin et al. 2013, Taylor et al. 2014, Brummer et al. 2016). Southwest Montana lies east of the Snake River Plains in the Missouri River basin (Figure C1). As a result, findings from other ecoregions, especially the Great Basin, may not be applicable to southwest Montana due to its colder and wetter climate. As a result of a colder and wetter climate, southwest Montana is hypothesized to have greater resistance and resilience, i.e., the ability to maintain ecosystem structure and function, to *B. tectorum* invasion, compared to the North Central and Central Basin and Range (Chambers et al. 2014a, Chambers et al. 2019, Chambers et al. 2023). Private and public land managers have raised concern over an increase in *B. tectorum* abundance and occurrence in the last decade. In southwestern Montana this has been most notable on south-facing hillsides that were not historically invaded. South-facing hillsides in this region provide crucial food resources that impact the offspring production of *Centrocercus urophasianus* (Greater sage-grouse), a sagebrush obligate (Cutting et al. 2021). Recent spatial analysis of invasive annual grass expansion in the Snake River Plain ecoregions confirms that non-native annual grasses, including *B. tectorum*, are establishing at higher elevations especially on steep south-facing hillsides (Smith et al. 2022), which agrees with prior species distribution models that account for changing climate (Bradley et al. 2016a) and aspect (north-south) (Brakeholder 2021). These increases across elevations and aspects are likely an interaction between topography and shifting climate, which is an important factor in predicting *B. tectorum*'s range in the Snake River Plain (Taylor et al. 2014).

If *B. tectorum*'s range continues to expand, it is imperative that land managers, both private and public, understand the efficacy of herbicide as a control option and the resultant impact on the vegetation community. To provide this information, our study assessed the long-

term ability of herbicide (imazapic) to reduce *B. tectorum* abundance and secondly, the impact of *B. tectorum* reduction by herbicide on the plant community composition, in the high-elevation sagebrush steppe of southwestern Montana, USA.

Imazapic is an acetolactate synthase (ALS) enzyme inhibitor which disrupts the production of branched-chain amino acids (Beste 1983). As a result its selectivity is limited, many broadleaves and grasses are susceptible (Beste 1983, Ditomaso et al. 2013). Non-target effects can be limited by using a fall post-emergent application, which has proven to be the most effective timing for reducing *B. tectorum* in Montana (Mangold et al. 2013). Despite its initial effectiveness, control lasting more than two years is infrequent (Orloff et al. 2015).

Therefore, we hypothesized that herbicide would result in a short-term reduction of *B. tectorum* abundance and reduce its probability of occurrence, but that *B. tectorum* would return to prior abundances and probability of occurrence after one or two growing seasons. Additionally, we hypothesized that a reduction in *B. tectorum* abundance would result in increased species richness, proportion of native vegetation and perennial grass productivity.

Methods

Study Area

This study was conducted in southwestern Montana, USA, in the Centennial Valley, a 65,000-ha high-elevation (2,000-2,500m asl) sagebrush steppe valley, typified by cold winters and short, cool summers. The Centennial Valley has been utilized for cattle grazing since the 1870's (Vivion 1968). Average stocking rate varies from 1.2-2.0 ha per adult cow (453 kg weight) (Kyle Cutting, personal communication). Two regions characterized by distinct soils and dominant vegetation exist within the valley's foothills. The Antelope Peak (AP) region is

comprised of primarily clay/loam soil while the Eastern Sandhills (ES), are composed of mostly sandy soil (Table 3.1). The flora of the AP region is dominated by a mixture of sagebrush and shrub types; *Artemesia tridentata* Nutt. (big sagebrush), *Artemesia tripartite* Rydb. (three-tip sagebrush), *Artemesia frigida* Wild. (fringed sagebrush) and *Chrysothamnus nauseosus* Nutt. (rabbit brush) (Culver 1994) and by our observation native perennial bunchgrasses. The ES region is dominated by *Agropyron dasystachyum* Scribn. & J.G. Sm. (thickspike wheatgrass), *Phacelia hastata* Douglas ex Lehm. (silver leaf phacelia), *A. tridentata*, *A. tripartite*, and *Festuca idahoensis* Elmer (Idaho Fescue) (Culver 1994). Across both regions and nearby mountains approximately 487 plant species (~21% of Montana's native flora) have been identified including regional endemic species and those occurring at their range extents (Culver 1994). Twelve steep, south-facing hillslopes, averaging 4 hectares each, were selected as sites. Four of these sites are in the ES and the remaining eight in the AP area. Each site consisted of an area that was infested (~15% average cover) by *B. tectorum*.

Experimental Treatment

In early October of 2017 and 2018, after *B. tectorum* had emerged, the herbicide imazapic (Plateau®; BASF Corporation, 100 Park Ave., Florham Park, NJ) was aerially broadcasted at 0.17 active ingredient (a.i.) kg/ha with a carrier rate of 11.35L of water per acre, 25 PSI pressure, and an aerial speed of 65-70 kmph by helicopter after *B. tectorum* had emerged. Within the infested and sprayed area, paired plots were established. Each plot was 10m² and was sprayed or not sprayed. The non-sprayed control was achieved by placing a plastic tarp on the ground before herbicide application in both years. The sprayed plot was directly adjacent to the non-sprayed

plot and separated by one meter. This paired plot design allowed direct comparison between non-sprayed and sprayed areas.

Vegetation Canopy Cover Sampling: Each year from 2019 through 2022, all plant species canopy cover along with bare ground, rock and litter were estimated to the nearest 1% using a Daubenmire frame (20cmx50cm; 0.1m²) (Daubenmire 1959). Total cover was allowed to exceed 100% for the frame to account for overlapping species. Frames were randomly placed within each sprayed and non-sprayed area. Each year monitoring was initiated in mid-June and concluded around July 1st. Five evenly spaced Daubenmire frames were placed within each of the 10m² sprayed and non-sprayed areas.

Perennial Grass Biomass Collection: In 2022, native perennial grass biomass was estimated by destructively harvesting the five most abundant species, as identified by observed cover estimates, in the study: *Stipa comata* Trin. & Rupr. (needle and thread grass), *A. dasystachum*, *Agropyron spicatum* Pursh. (bluebunch wheatgrass), *Poa secunda* J. Presl. (sandberg bluegrass) and *F. idahoensis*. These species represented the four dominant native perennial grass genera. Each species was sought out in the field and its cover estimated within a Daubenmire frame. Four cover classes per species were used, 10%, 20%, 30%, and 40%, and for each cover class four replicates were harvested (n=80). Each species was clipped at ground level and transported to the Montana State University (MSU) (Bozeman, MT, USA) for drying and weighing. Biomass was dried for 72hrs at 49 °C and weighed to the nearest tenth of a gram.

Statistical Analysis

All statistical analyses were conducted in the software R (Version 4.2.2) (R Core Team 2022). We used linear mixed effects models and a hurdle model to analyze differences in *B.*

tectorum abundance, plant species richness, and proportion of plant functional group abundance. All models were assessed for adherence to the assumptions of equal variance and normality when applicable, using Pearson's Residuals and QQ-plots, and no violations to these assumptions were present. For the hurdle model, dispersion was measured and found to be minimal. All figures were constructed using the package "ggplot2" (Hadley 2016).

Bromus tectorum abundance: *Bromus tectorum* abundance was zero-inflated (53% zeroes). To address zero-inflation the "pscl" package (Zeileis et al. 2008) using a linear zero-altered negative binomial (ZANB) model with a "logit" link function, was used. The ZANB method utilizes a hurdle methodology described by Zuur and Ieno (2016). Following this method, the data are split into two components and modeled separately and then recombined to create the final ZANB model estimate. First, the non-zero portion of *B. tectorum* abundance is modeled assuming a negative-binomial distribution, next the *B. tectorum* presence, including zeroes, is modeled using a binomial distribution to estimate the probability of occurrence. Lastly, the two model estimates are multiplied to create the final ZANB model estimate, similar to logistic regression. This method captures the biological zero-generating process in the final model estimation. In this study, we assume this zero-generating process to be the application of herbicide. Therefore, use of the hurdle model methodology is appropriate. The "pscl" package does not allow for the use of random/mixed effects in its modeling structure, therefore the nested design and temporal replication could not be accounted for. The dispersion parameter was calculated using the equation suggested by Zuur and Ieno (2016) (pgs. 172 & 173) and found to be minimal (0.999). Final model estimates were compared using the "emmeans" package (Lenth 2022).

The final model was:

$$\text{BRTE} \sim \text{herbicide} * \text{year} * \text{region}$$

where BRTE is *B. tectorum* abundance, herbicide is a two-level factor (sprayed/non-sprayed), year is four-level factor (2019, 2020, 2021, 2022), and region is a two-level factor (Antelope Peak/Eastern Sandhills). Lastly, we compared the mean abundance of *B. tectorum* in 2017, pre-herbicide application, in plots that were subsequently sprayed, to the mean abundance of *B. tectorum* in 2022, to determine the long-term efficacy of herbicide using a Dunnett's post-hoc test.

Our goal was to analyze the response of the two communities after management, therefore we used a subset of the vegetation data, which ranged from 2019 to 2022. This subset was used for comparing differences in *B. tectorum* abundance between treatments, over time, and between regions. We felt that including pre-herbicide (2017) data and one year after herbicide (2018) data would reduce our ability to detect meaningful responses due to treatment. However, because we were interested in understanding whether *B. tectorum* management was long lasting, we conducted a Dunnett's post-hoc test using the "emmeans" package (Lenth 2022). The Dunnett's test allowed us to analyze whether post-management (2018, 2019, 2020, 2021, 2022) *B. tectorum* abundance differed from pre-herbicide (2017) management levels in both the sprayed and reference communities.

Plant Community Response: Species richness response to the independent variables, herbicide, year and region, were assessed using the packages "vegan" (Oksanen et al. 2022), and "bioDiversityR" (Kindt and Coe 2005) was used to assess the relative rank abundances of each species. The linear mixed effects model (Pinheiro et al. 2022) incorporated site and frame as

nested random effects and assumed a Poisson distribution. *Bromus tectorum* was omitted from the species richness analysis because it was a target species for removal, i.e., inclusion of *B. tectorum* could artificially create differences between sprayed and non-sprayed treatments. The proportion of the vegetative cover for each functional group --annual forb non-native (AFI), annual forb native (AFN), annual grass non-native (AGI), perennial forb non-native (PFI), perennial forb native (PFN), and perennial grass native (PGN)-- was calculated by summing the cover of each functional group and then dividing it by the total cover, which included all vegetative and non-vegetative cover (litter, rock and bare ground). Additionally, the proportion of non-vegetative cover components were analyzed following the same procedure. The proportion of each functional group over time, between treatments (sprayed/non-sprayed) and between regions (Antelope Peak/Eastern Sandhills) was calculated. The model included random effects to account for experimental design structure, i.e., frames nested within site. Specifically, the “glmmTMB” package (Brooks et al. 2017) was used to conduct a generalized linear mixed effects model assuming a beta distribution to test for mean differences in proportional abundance. A critical assumption of the beta distribution is that observations lie between two distinct bounds, in this case 0 and 1. Our observations included zeros and ones which required the following transformation to be conducted:

$$(Y_i \times (N - 1) + 0.5) / N$$

where Y_i are the observed proportions and N is the sample size. This transformation constricts observations into a range from 0.005 to 0.995 following the suggestions of Zuur and Ieno (2016) (pg. 359) and the methodology of Smithson and Verkuilen (2006). The model was tested for dispersion using the standard deviation of residuals fitted vs. simulated using the “DHARMA”

package and methodology (Hartig 2022). Dispersion was not a concern for this model and was calculated to be 1.0093; a value of 1 indicates no dispersion.

Native Perennial Grass Biomass Estimation: A linear model was fit for each native perennial grass species to predict biomass based on observed cover. We found strong evidence for a positive correlation between cover and dry biomass for each of the species, though these relationships differed in strength (Table S1). These linear models were then used to predict the biomass of each genus (*Festuca*, *Agropyron*, *Poa*, *Stipa*) based on the prior year's cover observations. The predicted biomass was then analyzed using a linear mixed effects model from the "nlme" package (Pinheiro et al. 2022), and the estimated marginal means between genus and year were compared using a Tukey's post-hoc pairwise test via the "emmean" package (Lenth 2022).

Results

Bromus tectorum Abundance

Bromus tectorum abundance responded differently depending on year, region, and herbicide treatment (Chi-Sq: 8.33, df: 3, p: 0.039). In the Antelope Peak region, mean *B. tectorum* abundance ranged from 5-20% in the non-sprayed treatment over four years (2019-2022). The sprayed treatment remained lower in abundance than the non-sprayed until the fourth year (2022), at which time there was no difference between the two (Figure 3.1). *Bromus tectorum* mean abundance in the non-sprayed treatment declined from years one to three (2021), ranging from <1% to 12%, before increasing again in the fourth year in the Antelope Peak Region (Figure 3.1). In the Eastern Sandhills region, *B. tectorum* abundance in the sprayed treatment remained lower than in the non-sprayed treatment for the duration of the study (Figure

3.1), and the mean ranged from <1% to 1.4%. The non-sprayed plots showed a slight decline in *B. tectorum* abundance in the second (2020) and third years compared to the first year after herbicide application (Figure 3.1). By the final year of the study, *B. tectorum* abundance returned to a similar level as the first year after herbicide application (Figure 3.1). Mean *B. tectorum* cover in the non-sprayed plots ranged from 3-6% over four years. Ultimately, there were no differences between the 2017 pre-herbicide abundances of *B. tectorum* and four years after herbicide application for both regions in the sprayed and non-sprayed plots ($t=1$, $df: 118$, $p: 0.318$).

Probability of *B. tectorum* Occurrence

Probability of *B. tectorum* occurrence varied depending on region, treatment, and year (Chi-Sq: 8.33, $df: 3$, $p: 0.039$). Probability of occurrence was on average 56% higher in the non-sprayed treatment in the Antelope Peak ($t: 9.43$, $df: 447$, $p: <0.0001$) and 55% greater in the non-sprayed treatment for the Eastern Sandhills region ($t: 6.81$, $df: 447$, $p: <0.0001$), despite the similarity in abundance by the fourth year (Figure 3.1). There was an exception in year three in the Eastern Sandhills where both treatments had statistically similar probabilities of occurrence (Figure 3.2).

Plant Richness and Rank Abundance

We observed 148 native and non-native plant species over the course of this study. Mean richness increased over the course of the study by 1.28 species/0.1m² ($t: 6.12$, $df: 403$, $p: <0.0001$) (Figure 3.3) (Table 3.3), and there were no differences between regions or treatments. We observed a mean species richness of 3.4 in the first year and 4.7 in the fourth year. Additionally, the proportional abundance of the top five species was compared graphically to

track whether *B. tectorum* returned as a dominant species in terms of community composition. Indeed, we found that *B. tectorum* returned as dominant member of the plant community by the fourth year in the Antelope Peak region but not in the Eastern Sandhills region (Figure 3.4) (Table 3.S2). In both regions, the top five species in the sprayed treatments were composed of mostly desirable native species, compared to the adjacent non-sprayed community (Figure 3.4).

Herbicide Effect on the Proportion of Vegetative and Non-vegetative Cover

The proportion of total cover (vegetative and non-vegetative) was explained by the three-way interaction of functional group, treatment, and year (Chi-Sq: 55.52, df: 27, p: <0.001). Because we expect natural variation in cover over time due to environmental variation, for the sake of clarity and brevity, we report only the differences between the sprayed and non-sprayed communities within each year.

We found that of the 10 functional groups that made up the total cover in each Daubenmire frame, only three of seven vegetative and two of three non-vegetative functional groups fluctuated between treatments over the course of the study (Figure 3.5). Two non-native functional groups and one native functional group differed over the course of the study. The non-native annual grasses comprised a greater proportion of the non-sprayed plant community in the first (2019) post-herbicide (t:5.36, df: 4716, p: <0.0001), second (2020) (t: 3.37, df:4716, p: 0.001), and fourth years (t: 3.11, df: 4716, p: 0.002) (Table 3.5). There were no differences in the proportion of non-native annual grasses between the two plant communities in the third season. The non-native annual forbs comprised a greater proportion of the non-sprayed plant community in only the second year after herbicide application (t: 2.18, df: 4167, p: 0.029), after which there were no differences between the two communities (Table 3.5). The native perennial forbs

constituted a greater proportion of the sprayed community in the first (t: 2.48, df:4716, p: 0.013) and second year post herbicide application (t: 2.75, df: 4716, p: 0.006). Of the non-vegetative groups, the proportion of bare ground was greater in the sprayed community in all four years following herbicide application, but to differing extents depending on year (Table 3.5). In the first year following herbicide application the sprayed community had a greater proportion of litter (t: 2.23, df: 4716, p: 0.026), but in the second (t: 3.71, df: 4716, p: <0.0001) and third (t: 3.33, df: 4716, p: 0.001) years there was a greater proportion of litter in the non-sprayed community. By the fourth year after herbicide application there was no difference in the proportion of litter (Table 3.5).

Perennial Grass Biomass

We observed differences in perennial grass biomass production by year (f: 2.86, df: 3, 244, p: 0.037) and genus (F:14.25, df:4, 244, p:<0.0001) but not between treatments or regions. The four year mean *Festuca* biomass was 39.3 kg/ha, mean *Agropyron* biomass was 36 kg/ha, mean *Stipa* biomass was 104 kg/ha, and mean *Poa* biomass was 91.6 kg/ha. *Festuca* and *Agropyron* did not differ statistically from one another. *Stipa* and *Poa* did not differ statistically, either. Mean combined perennial grass biomass from the first to fourth year (2019-2022) post herbicide application was: 78.7 kg/ha (SE: 12.9), 54.9 kg/ha (SE:12.1), 71.5 kg/ha (SE: 11.2), and 88.6 kg/ha (SE:13.2) respectively. Statistically only the second and fourth year differed from one another (t: 2.8, df: 244, p: 0.027).

Discussion

Bromus tectorum Abundance and Occurrence

Early detection and management of non-native plant populations is critical for preventing a loss of ecosystem service and function (Radosevich et al. 2007, Vilà et al. 2011, Monaco et al. 2017). Herbicide application is a common management action used to control non-native plants, but it can be costly. Ideally, these costs are justified with an improvement in ecosystem service or function, often quantified by increases in plant richness, desirable forage grasses (i.e., native perennial grasses), and a greater proportion of native flora. We found that two successive applications of imazapic, a common herbicide used in rangelands to control annual grass invasions, resulted in three years of reduced *B. tectorum* abundance in the Antelope Peak region and four years of suppression in the Eastern Sandhills region. Ultimately, *B. tectorum* returned to pre-herbicide levels four years after application in the Antelope Peak region. This response is similar to the three year suppression observed by Pyke et al. (2014) across the Columbia Plateau, Northern and Central Basin and Range and by Elseroad and Rudd (2011) in the Columbia Plateau (north-central Oregon).

Despite similar abundances between sprayed and non-sprayed communities, the probability of *B. tectorum* occurrence remained lower in the sprayed community. This indicates that although cover was similar between sprayed and non-sprayed plots, there were fewer instances of *B. tectorum* per frame on average. This could be explained by complete eradication in locations that had a lower density population when herbicide was initially applied while heavily infested areas increased due to a more abundant seedbank. The initial reductions in *B. tectorum* abundance in the two years following herbicide applications were the result of direct

mortality of exposed individuals which reduced that year's contribution to the seedbank. The continued suppression in the second and third years were likely due to reduced recruitment as the result of drier than average springs in the first, second-, and third-years post-herbicide application and below average precipitation in the fall of the second year (Table 6 and 7). It should be noted, however, that in the first- and third-years post-herbicide, the fall was warmer and wetter than average, which should favor *B. tectorum*. As a winter annual, spring and fall precipitation and temperature are crucial factors determining *B. tectorum* survival (Mack 1981, Vermeire and Rinella 2020). From a management perspective, our results represent a best-case scenario, as herbicide application was followed by reduced recruitment and poor growing seasons for *B. tectorum*, as shown by the natural reductions in *B. tectorum* abundance in years two and three (Figure 1). As a result, these same conditions likely contributed to the extended control of *B. tectorum* in the sprayed treatment beyond the typical one- to two-year post-application period.

Plant Community Response

Reduced species richness is often correlated with non-native plant invasion if invaders alter ecosystem function, e.g., increased fire frequency (Kennedy et al. 2002, Ehrenfeld 2010, Davies 2011). It is unclear whether the patterns between ecosystem function and invasion are causal, symptomatic, or both (MacDougall and Turkington 2005, Davis 2009). Interestingly, despite reductions in *B. tectorum* abundance and probability of occurrence early in the study, we did not observe differences in species richness between the sprayed and the non-sprayed communities across all four years of the study. It is important to note that *B. tectorum* was not included in the species richness analysis. It does not appear that *B. tectorum* abundance is

correlated with a reduction in species richness in this system, unlike other studies (Anderson and Inouye 2001, Larson et al. 2017, Wood and Meador 2022). However, species richness is an absolute count of membership, and it does not define the assemblage or structure of a plant community. By using the rank abundance to analyze the composition of the top five most dominant species, we found that while richness did not differ between the sprayed and non-sprayed communities, species composition did. Perhaps allowing for a temporary alteration of the competitive dynamics for the top species in the sprayed communities, regardless, community composition did not enhance the resistance of the sprayed community to *B. tectorum* as a dominant in the Antelope Peaks region. Another important signal from the rank abundance analysis is the low representation of native perennial bunchgrasses. One of the five most dominant species was always a bunchgrass in the Antelope Peak region, but it was never the same bunchgrass, and in the fourth year its ‘place’ was taken by *B. tectorum*. This was not the case for the Eastern Sandhills, which was dominated by bunchgrasses in both the sprayed and non-sprayed communities. In the face of these regional differences in community composition, we did not find any evidence that the biomass production of native perennial bunchgrasses differed by region or treatment, only annually, which is expected given annual environmental fluctuation.

As an extension of species richness and species rank abundance, the proportion of each vegetative functional group and non-vegetative cover type provided a holistic view of the vegetative community composition between treatments within each year after herbicide application. Of the vegetative component, non-native annual grass (i.e., *B. tectorum*), non-native forbs, and native perennial forbs were the only functional groups to respond differently between

treatments within years over the duration of the study. *Bromus tectorum* abundance, when analyzed alone, was sensitive to regional differences in response to herbicide, while proportional analysis of functional groups was not.

A common management goal is to increase the productivity of rangelands for cattle/wildlife by releasing native perennial grasses from the competitive effects of non-native annuals via herbicide. In this study, despite initial reductions in *B. tectorum* abundance, and lower proportions of non-native annual grass, we did not observe any differences in the proportion of native perennial grasses between the sprayed and non-sprayed communities, similar to Elseroad and Rudd (2011) in the Columbia Basin ecoregion. However, a recent study by Wood and Meador (2022) found that native perennial bunchgrasses received little benefit from the reduction of *B. tectorum* when pre-herbicide application cover of *B. tectorum* was below 25-30%. Over the course of the study the proportion of native perennial forbs increased in both sprayed and non-sprayed communities. The increase in the proportion of the native perennial forbs in the sprayed treatment was a surprising result as other work found that imazapic reduced native forb abundance (Owen et al. 2011). The authors of this study applied imazapic at a similar rate a.i. 0.132kg/ha (compared to our a.i. 0.17 kg/ha) and at a similar time (November). We hypothesize that the increase in native perennial forbs was driven by a shift in timing and quantity of precipitation that favored this functional group over the others. In the sagebrush ecosystem, the diet of cattle is comprised of mostly grass (88%) (Beck and Peek 2005) making native perennial forbs less desired by cattle but important for wildlife, pollinators, and forbs typically contribute to a large portion of native plant diversity in these systems (Pokorny et al. 2004).

We observed changes in two important non-vegetative cover types over the course of the study, bare ground and litter. Together these cover types can provide insights about fuel loading and connectivity between vegetation (Brooks et al. 2004, Reisner et al. 2013). Increased proportions of litter could be associated with heightened risk of fire and greater connectivity between vegetation. While bare ground could reduce connectivity between vegetation, it is also the most susceptible to non-native plant invasion. The proportion of litter was greater in the sprayed community in the first-year post-herbicide application. In the second- and third-years post-application there was a shift from less litter in the sprayed community to more litter in the non-sprayed community. However, by the fourth year we found that the proportion of litter was the same between both communities. This pattern in litter proportion between the two communities over time is likely driven by initial mortality of any standing crop of *B. tectorum* at the time of herbicide application. Once herbicide application stopped, this litter likely degraded quickly, due to chemical and mechanical breakdown (cattle trampling), or was removed due to wind. This subsequent loss of litter appears to have resulted in an increased proportion of bare ground, more so in the sprayed than the non-sprayed community, and not an increase in vegetative cover until the fourth year after herbicide application.

Conclusion

There is an extensive body of literature warning of the negative impacts of *B. tectorum*, which are largely driven by the increased frequency of wildfire, and subsequent conversion of shrublands to grasslands (Brooks et al. 2004, Germino et al. 2016). Herbicide provides a straightforward management option but only targets one of three major components of invasion ecology proposed by Lonsdale (1999), propagule pressure, by directly reducing populations via

standing crop and indirectly by reducing contribution of that crop to the seedbank. We see the embodiment of this in our study. Herbicide effectively reduced *B. tectorum* abundance, probability of occurrence and its proportion of the plant community. The effects of imazapic lasted longer than expected given a prior study in central Montana (Orloff et al. 2015), but resembled control length observed across the Columbia Plateau and North and Central Basin and Range (Elseroad and Rudd 2011, Pyke et al. 2014). The control we observed could be due in part to poor growing conditions for *B. tectorum* and the slow degradation of imazapic which could have reduced *B. tectorum* seedling survival in the subsequent springs after application (Ehlert et al. 2015). Despite the reduction in *B. tectorum*, we did not observe a correlated increase in native perennial grasses or differences in species richness between sprayed and non-sprayed communities. These findings contrast the findings of others who observed an increase in native perennial grass abundance following reductions in *B. tectorum* (Davies and Sheley 2011, Kyser et al. 2013, Orloff et al. 2015) and others who have observed a correlation between increasing annual grass cover, including *B. tectorum*, and decreasing native plant richness (Gasch et al. 2013, Bansal and Sheley 2016). We observed an early increase in native perennial forbs that could have benefits for *Centrocercus urophasianus* (Greater sage-grouse), other wildlife and pollinators, but this response occurred in both sprayed and non-sprayed communities.

From the standpoint of wildfire risk, applying herbicide initially increased litter in the first year after application, posing a temporary increase in risk compared to the non-sprayed alternative. However, in the second and third years after herbicide application we did observe considerable reductions in litter and an increased proportion of bare ground which could potentially reduce the risk of fire if bare ground is correlated with increased gaps between

vegetation (Zouhar 2008, Reisner et al. 2013). These possible benefits of reduced fire risk are only important if a positive fire-feedback cycle is likely to occur, which has not been the case in the northern Snake River Plain or southwest Montana (Lavin et al. 2013, Taylor et al. 2014, Larson et al. 2017). The potential risk of a greater proportion of bare ground in this situation is the increased risk of re-invasion and higher albedo, which increases soil temperature, in turn creating favorable growing conditions for *B. tectorum* (Maxwell et al. 2023). Bare ground represents an empty niche space within which *B. tectorum* or other non-natives could establish. Despite imazapic's effectiveness to control *B. tectorum*, we did not observe compositional changes in the plant community resultant of these reductions, which questions the benefit of *B. tectorum* management. Early detection and control are crucial for managing the potential impacts of non-native plant invasions. However, operating under this management framework requires that managers make choices based on the potential impacts of the invader in other systems. The decision to manage *B. tectorum* in the context of this study, is founded on two critical assumptions. The first is that the high-elevation sagebrush steppe, in southwest Montana, will respond similarly to the sagebrush communities of the arid Northern and Central Basin and Range, upon invasion by *B. tectorum*, but little evidence suggest that it does (Lavin et al. 2013, Taylor et al. 2014, Brummer et al. 2016, Larson et al. 2017, Larson et al. 2018). Secondly, and perhaps most critically, is the assumption that *B. tectorum* presence alone warrants management action. It is possible that *B. tectorum* is invading a small niche created by a subtle combination of suitable climate and disturbance in an otherwise high functioning and diverse sagebrush community. We observed no increase in species richness nor native perennial grass biomass productivity – of most importance to cattle and wildlife, as a result of management. Indeed, our

study provides little evidence that reducing *B. tectorum* created any long-lasting or differential changes to the vegetation community, i.e., proportions of all functional groups behaved similarly regardless of whether herbicide was applied. This suggests that *B. tectorum* removal alone has little impact on the structure and function of high elevation sagebrush steppe communities, that have been invaded, in southwestern Montana. We therefore hypothesize that *B. tectorum* is a “passenger” or symptom of changing climatic suitability coupled with disturbance, following MacDougall and Turkington (2005)’s discussion.

Aerial herbicide application via helicopter is effective but costly and potentially unwarranted unless used within a greater restoration framework that addresses disturbance and stress to existing vegetation. If managers wish to alter existing community assemblages with the goal of disfavoring *B. tectorum* we suggest an integrated management plan including a comprehensive revegetation component and various ecological processes (Sheley et al. 1996, Monaco et al. 2017), e.g., account for climate, disturbance, soil characteristics, existing vegetation and selecting plant species most suitable for the site conditions (Krautzer et al. 2006, Pyke et al. 2014, Orloff et al. 2015). Further, an integrated approach targets the two ecological components of Lonsdale (1999)’s invasion theory -- ecosystem properties and invader properties -- not addressed by herbicide alone.

Tables

Table 3.1: Site locations and soil texture descriptions for each site in the Antelope Peak (AP) and Eastern Sandhills (ES) regions of the Centennial Valley, MT, USA. A soil ribbon test was conducted to approximate the soil texture in the field.

Region	Site	Latitude	Longitude	Elevation (meter/feet)	Soil Texture
AP	16	44.65958603	-111.9954618	2089/6853	Sandy Clay Loam
AP	15	44.66054363	-112.0015361	2135/7004	Gravelly Sand Loam
AP	14	44.65813905	-112.0055019	2131/6991	Silty Clay
AP	11	44.65858126	-112.0165624	2176/7139	Silty Clay
AP	3	44.65876424	-112.0404955	2168/7112	Gravelly Silt Loam
AP	2	44.66065154	-112.044243	2176/7139	Silty Clay Loam
AP	21	44.65637509	-112.0095762	2293/7522	Silty Loam
AP	22	44.67905552	-112.0189539	2381/7811	Silty Loam
ES	1	44.68076541	-111.6899827	2137/7011	Sand
ES	2	44.67944641	-111.6886901	2101/6893	Sand
ES	5	44.69461276	-111.7088441	2169/7116	Sand
ES	6	44.65939491	-111.6707083	2057/6748	Sand

Table 3.2: Fixed effects used in the zero-altered negative binomial hurdle model of *B. tectorum* abundance in the Centennial Valley, MT, USA. An analysis of deviance table was constructed using a Type II Wald chi-square test. Bold lettering indicates effects that are statistically significant using an alpha level of <0.05.

Fixed Effects	χ^2	df	p
Region	18.34	1	<0.0001
Herbicide	12.50	1	0.001
Year	21.91	3	<0.0001
Region*Herbicide	0.01	1	0.890
Region*Year	15.05	3	0.001
Herbicide*Year	14.33	3	0.002
Herbicide*Year*Region	8.33	3	0.030

Table 3.3: Fixed effects used in the linear mixed effects model of species richness in the Centennial Valley, MT, USA. An analysis of variance was conducted to interpret which fixed effects were important. Statistically significant fixed effects based on an alpha level of <0.05 are in bold.

Fixed Effects	numerator df	denominator df	F	p
Richness (intercept)	1	413	176.59	<0.0001
Year	3	413	17.99	<0.0001
Herbicide	1	413	7.75	0.006
Region	1	10	0.53	0.483

Table 3.4: Fixed effects used in the negative binomial mixed effects model of functional group proportion in the Centennial Valley, MT, USA. An analysis of deviance table was constructed using a Type II Wald chi-square test. Bold lettering indicates effects that are statistically significant using an alpha level of <0.05.

Fixed Effects	χ^2	df	p
Functional Group (Intercept)	2050.20	9	<0.0001
Herbicide	0.04	1	0.843
Year	3.20	3	0.362
Region	0.01	1	0.942
Functional Group*Herbicide	145.73	9	<0.0001
Functional Group*Year	203.48	27	<0.0001
Herbicide*Year	1.47	3	0.689
Functional Group*Herbicide*Year	55.53	27	0.001

Table 3.5: The difference in functional group proportion between the sprayed and non-sprayed treatments in each of the four years post-herbicide application. Herbicide was applied fall 2017 and 2018. Negative values indicate greater proportions in the non-sprayed community and positive values indicate greater proportions in the sprayed community. Bold values indicate statistically significant estimates (alpha= 0.05). The functional groups are AGI=annual non-native grass, AFI= annual non-native forb, PFI= perennial invasive forb, AFN= annual native forb, PFN= perennial native forb, PGN= perennial native grass, SN= shrub, BG= bare ground, LIT= litter, and Rck= rock.

Year 1 (2019)					
Functional Group	Estimate	SE	df	t	p
AFI	-0.73	0.83	4716	-0.88	0.381
AGI	-8.07	1.50	4716	-5.36	<0.0001
PFI	-0.72	0.87	4716	-0.82	0.411
AFN	0.06	0.71	4716	0.08	0.933
PFN	3.67	1.48	4716	2.48	0.013
PGN	1.74	1.31	4716	1.33	0.183
SN	0.63	0.85	4716	0.74	0.461
BG	4.54	2.23	4716	2.04	0.042
LIT	9.30	4.17	4716	2.23	0.026
Rck	2.64	1.69	4716	1.57	0.117
Year 2 (2020)					
AFI	-2.15	0.98	4716	-2.18	0.029
AGI	-4.05	1.20	4716	-3.37	0.001
PFI	-0.76	0.90	4716	-0.84	0.399
AFN	-0.31	0.82	4716	-0.37	0.708
PFN	5.02	1.82	4716	2.75	0.006
PGN	1.21	1.47	4716	0.82	0.410
SN	-0.03	0.80	4716	-0.03	0.973
BG	16.58	2.72	4716	6.10	<0.0001
LIT	-14.85	4.00	4716	-3.71	<0.0001
Rck	2.00	1.66	4716	1.20	0.229
Year 3 (2021)					
AFI	-1.51	0.94	4716	-1.60	0.110
AGI	-1.44	0.93	4716	-1.55	0.121
PFI	-0.38	0.90	4716	-0.42	0.677
AFN	0.13	0.71	4716	0.18	0.857
PFN	2.18	1.48	4716	1.48	0.139
PGN	-0.17	1.81	4716	-0.10	0.924
SN	1.50	0.91	4716	1.64	0.101
BG	9.74	2.82	4716	3.46	0.001
LIT	-13.09	3.93	4716	-3.33	0.001
Rck	1.50	1.78	4716	0.84	0.399

Table 3.5: Continued

	Year 4 (2022)				
AFI	-1.01	1.05	4716	-0.96	0.339
AGI	-4.67	1.50	4716	-3.11	0.002
PFI	-1.39	0.95	4716	-1.47	0.142
AFN	0.38	0.95	4716	0.40	0.690
PFN	0.62	2.31	4716	0.27	0.787
PGN	1.33	1.13	4716	1.17	0.241
SN	0.17	0.72	4716	0.23	0.816
BG	6.60	2.72	4716	2.43	0.015
LIT	-2.66	2.56	4716	-1.04	0.299
Rck	-0.33	1.49	4716	-0.22	0.823

Table 3.6: Average seasonal temperatures for the Antelope Peak (AP) and Eastern Sandhills (ES) regions of the Centennial Valley, MT, USA. Bold text indicates the departure from the 30-year average (bottom). Positive values indicate above average temperature and negative values below average. Data were downloaded from the PRISM climate group (<https://prism.oregonstate.edu/explorer/>).

Antelope Peak												
	Minimum Temp (°C)				Average (Mean) Temperature (°C)				Max Temperature (°C)			
Year	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
2019	-5.7	5.5	-5.1	-13.3	1.0	14.0	1.5	-8.3	7.7	22.5	8.0	-3.4
	0.8	0.0	1.7	-0.4	0.6	0.0	1.9	0.0	0.4	0.0	1.9	0.4
2020	-5.0	5.9	-3.7	-13.7	1.7	14.2	3.9	-8.2	8.5	22.6	11.5	-2.7
	0.1	-0.4	0.3	0.1	-0.1	-0.3	-0.6	-0.1	-0.3	-0.1	-1.6	-0.3
2021	-5.0	7.8	-0.7	-12.7	1.8	16.2	5.2	-7.8	8.7	24.6	11.1	-3.0
	0.1	-2.3	-2.6	-1.0	-0.2	-2.2	-1.9	-0.5	-0.5	-2.1	-1.2	0.0
2022	-5.6				0.5				6.7			
	0.7				1.1				1.4			
Eastern Sandhills												
	Minimum Temp (°C)				Average (Mean) Temperature (°C)				Max Temperature (°C)			
Year	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
2019	-6.1	5.2	-5.7	-14.0	0.9	13.9	1.2	-8.7	7.9	22.7	8.1	-3.3
	0.7	-0.4	1.7	-0.4	0.6	-0.2	1.8	-0.1	0.4	-0.1	1.9	0.3
2020	-5.2	5.7	-4.1	-14.5	1.7	14.2	3.8	-8.6	8.6	22.7	11.7	-2.7
	-0.2	-0.9	0.2	0.1	-0.3	-0.5	-0.7	-0.2	-0.3	-0.1	-1.6	-0.4
2021	-5.7	7.0	-1.3	-13.5	1.5	15.8	5.0	-8.4	8.8	24.7	11.2	-3.2
	0.3	-2.2	-2.6	-0.9	-0.1	-2.1	-1.9	-0.3	-0.5	-2.1	-1.2	0.2
2022	-6.1				0.4				6.8			
	0.7				1.1				1.4			
30-year Average												
	Minimum Temp (°C)				Average (Mean) Temperature (°C)				Max Temperature (°C)			
Region	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
AP	-5.0	5.5	-3.3	-13.7	1.6	14.0	3.3	-8.3	8.1	22.5	9.9	-3.0
ES	-5.4	4.8	-3.9	-14.4	1.4	13.7	3.1	-8.7	8.3	22.6	10.0	-3.1

Table 3.7: Average seasonal precipitation for the Antelope Peak and Eastern Sandhills (ES) regions of the Centennial Valley, MT, USA. Non-bold text indicates the average precipitation, bold text indicates the departure from the 30-year average (bottom). Positive values indicate above average precipitation and negative values below average precipitation. Data were downloaded from the PRISM climate group (<https://prism.oregonstate.edu/explorer/>).

Antelope Peak				
Precipitation (mm)				
Year	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
2019	37.5	35.8	47.6	68.7
	18.8	4.1	-6.6	-24.4
2020	43.3	42.6	23.3	42.8
	12.9	-2.7	17.7	1.4
2021	40.3	28.7	53.4	57.7
	15.9	11.2	-12.4	-13.4
2022	62.4			
	-6.2			
Eastern Sandhill				
Precipitation (mm)				
Year	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
2019	41.9	36.0	56.6	67.8
	16.9	3.8	-12.7	-19.7
2020	50.8	44.4	25.4	49.6
	7.9	-4.6	18.5	-1.5
2021	46.2	31.8	58.1	65.5
	12.6	8.0	-14.3	-17.4
2022	70.3			
	-11.5			
30-year Average				
Precipitation (mm)				
Region	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
AP	56.3	39.9	41.0	44.3
ES	58.7	39.8	43.9	48.1

Figures

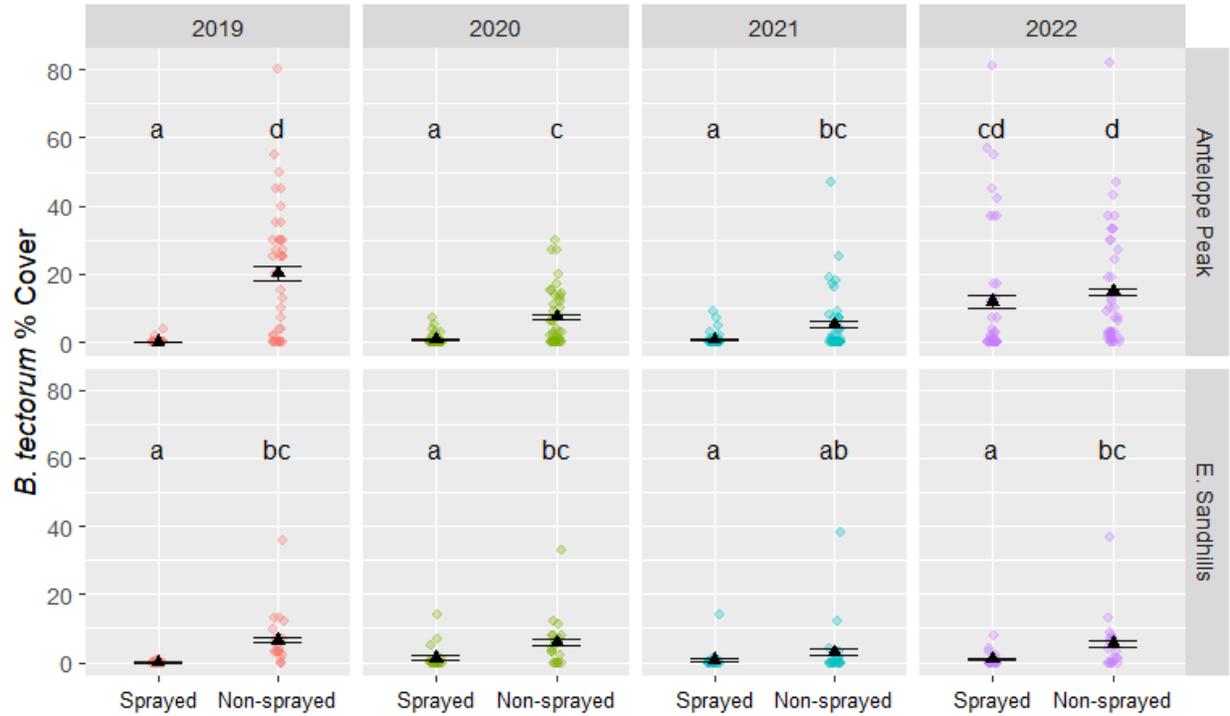


Figure 3.1: Estimated *Bromus tectorum* abundance four years post herbicide application (fall 2017 & 2018) for the sprayed and non-sprayed treatments in the Antelope Peak (AP) and Eastern Sandhills (ES) regions of the Centennial Valley, MT, USA. Groups that share a letter(s) are statistically similar at an alpha level of <0.05 . Black triangles are the means, error bars are constructed using standard errors and the points are the jittered observed abundances.

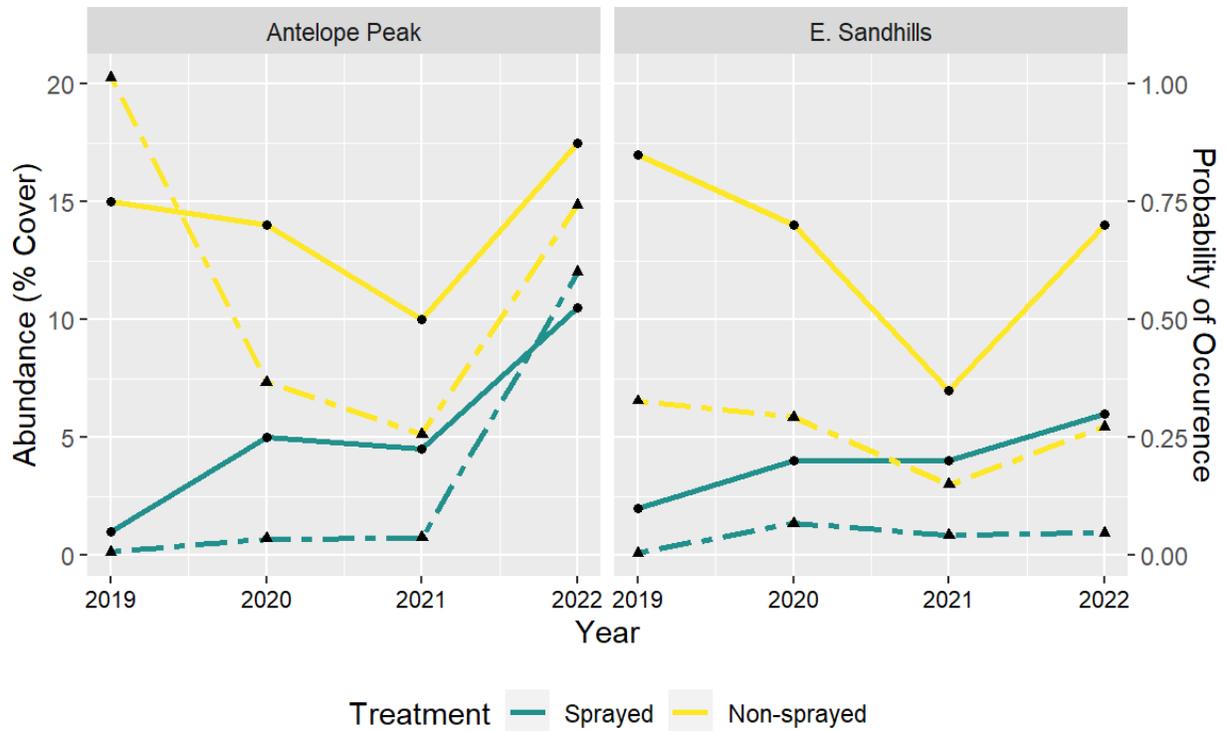


Figure 3.2: Estimated probability of occurrence (solid line) and abundance (dashed line) of *B. tectorum* four years post herbicide application for the sprayed and non-sprayed treatments in the Antelope Peak and Eastern (E.) Sandhills regions of the Centennial Valley, MT, USA. Black triangles represent the mean abundance estimates and the black circles represent the mean probability of occurrence.

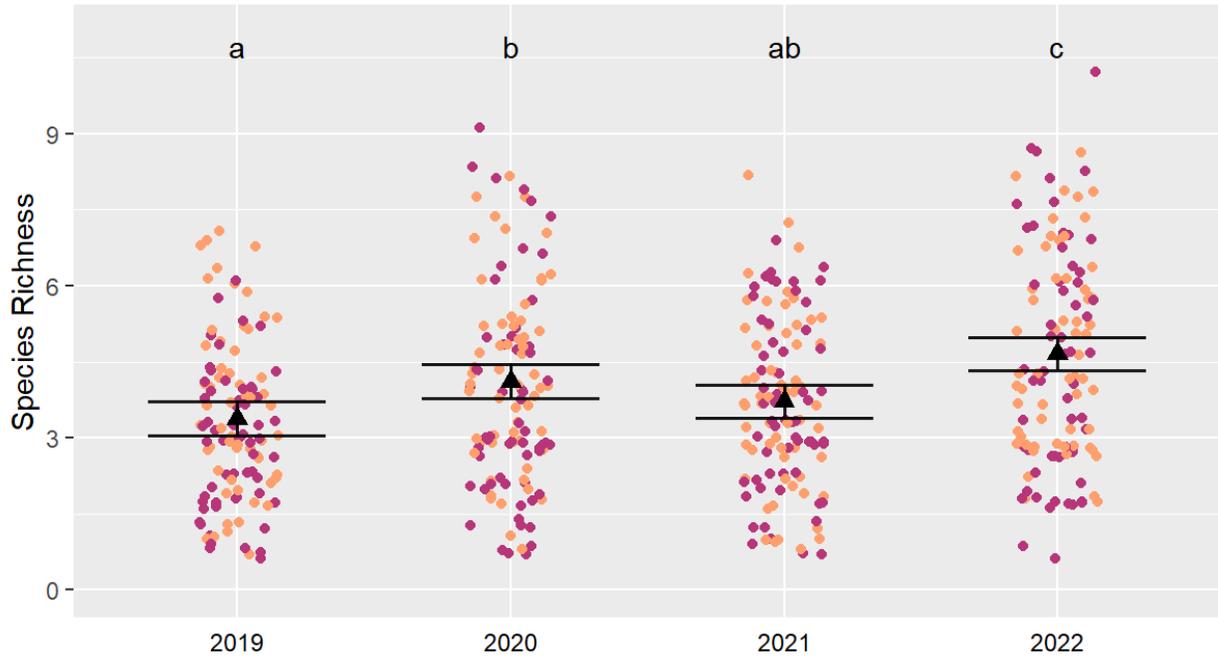


Figure 3.3: Estimated mean species richness (0.1m²) for the four years post-herbicide application in the Centennial Valley, MT, USA. Mean species richness fluctuated by year but not by region or treatment. Note that *B. tectorum* is omitted from this analysis. The observations are plotted as jittered points, which differ by treatment in color: orange is the sprayed treatment and purple is the non-sprayed treatment. Black triangles are the means, error bars are constructed using standard error of the mean. Groups that share a letter(s) are statistically similar at an alpha level of <0.05.

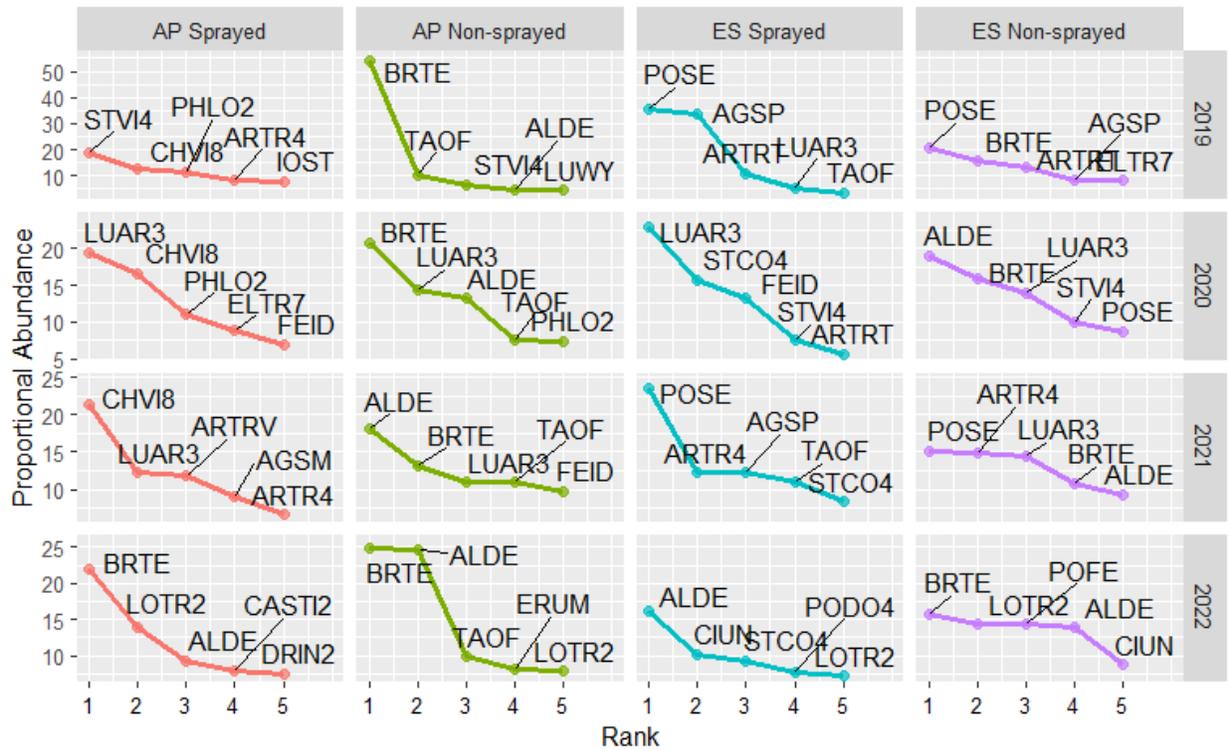


Figure 3.4: Proportional abundance of the top five species in each plant community over the four years post-herbicide application in the Centennial Valley, MT, USA. The regions, Antelope Peak (AP) and Eastern Sandhills (ES), are combined with their respective herbicide treatment (sprayed/non-sprayed). Note that steeper lines indicate less even distribution of abundance among the top five species. Species are represented by their four letter USDA Plant Database code as follows: AGSM: *Agropyron smithii*, AGSP: *Agropyron spicatum*, ALDE: *Alyssum desertorum*, ARTR4: *Artemesia tridentata*, ARTRV: *Artemesia tridentata* var. *vaseyena*, BRTE: *Bromus tectorum*, CASTI2: *Castilleja flava*, CHVI8: *Chrysthosanthmus visidiflorus*, CIUN: *Cirisium undulatum*, DRIN2: *Draba incerta*, ELTR7: *Elymus trachycaulus*, ERUM: *Eriogonum umbellatum*, FEID: *Festuca idahoensis*, LOTR2: *Lomatium triternatum*, LUAR3: *Lupinus argentiis*, LUWY: *Lupinus wyethii*, PHLO2: *Phlox longifolia*, PODO4: *Polygonum douglasii*, POSE: *Poa secunda*, STCO4: *Stipa comata*, STVI4: *Stipa viridula*, TAOF: *Taraxicum officinale*.

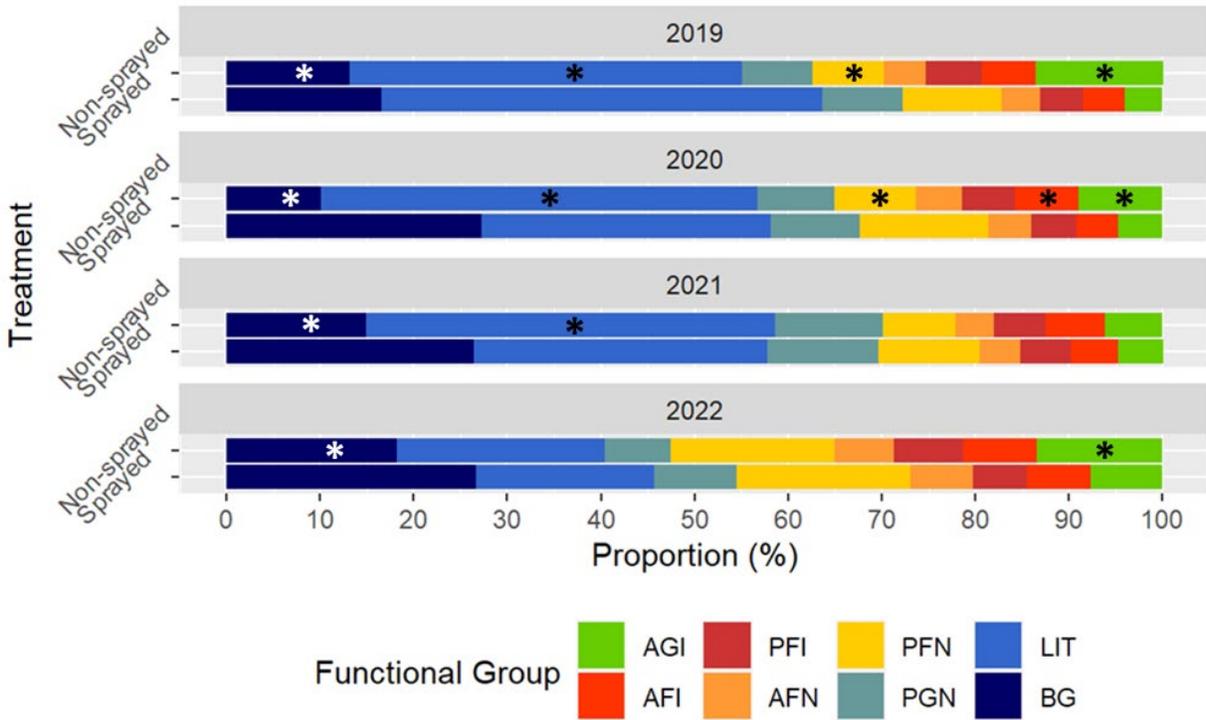


Figure 3.5: Mean proportional change in functional group cover over time between the sprayed and non-sprayed treatments. Asterisks denote statistical differences between functional groups within a single year using an alpha level of 0.05. The functional groups are as follows: AGI=annual non-native grass, AFI= annual non-native forb, PFI= perennial invasive forb, AFN= annual native forb, PFN= perennial native forb, PGN= perennial native grass, LIT= litter, and BG= bare ground. Bar widths represent the relative mean proportion of each functional group. This figure omits the shrub functional group and rock cover type for clarity of display, neither differed in their proportion over time or between treatments.

Literature Cited

- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological monographs* 71:531-556.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global change biology* 19:173-183.
- Beaumelle, L., L. Tison, N. Eisenhauer, J. Hines, S. Malladi, C. Pelosi, L. Thouvenot, and H. R. Phillips. 2023. Pesticide effects on soil fauna communities—A meta-analysis. *Journal of Applied Ecology*.
- Beck, J. L., and J. M. Peek. 2005. Diet Composition, Forage Selection, and Potential for Forage Competition Among Elk, Deer, and Livestock on Aspen–Sagebrush Summer Range. *Rangeland Ecology & Management* 58:135-147.
- Beste, C. 1983. *Herbicide Handbook of the Weed Science Society of America*. Weed Science Society of America.
- Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016. *Bromus* response to climate and projected changes with climate change. Pages 257-274 *Exotic brome-grasses in arid and semiarid ecosystems of the western US*. Springer.
- Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M.-N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions* 20:1493-1506.
- Brakeholder, B. 2021. *Bromus tectorum* (Cheatgrass) predicted suitable habitat model created on February 22, 2021.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Boker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9(2):378-400.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677-688.

- Brummer, T. J., K. T. Taylor, J. Rotella, B. D. Maxwell, L. J. Rew, and M. Lavin. 2016. Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. *Ecosystems* 19:986-1000.
- Chambers, J. C., C. R. Allen, and S. A. Cushman. 2019. Operationalizing ecological resilience concepts for managing species and ecosystems at risk. *Frontiers in Ecology and Evolution* 7:241.
- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegee, R. F. Miller, and D. A. Pyke. 2014. Resilience to Stress and Disturbance, and Resistance to *Bromus tectorum* L. Invasion in Cold Desert Shrublands of Western North America. *Ecosystems* 17:360-375.
- Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. S. Clair. 2016. Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:275-304.
- Corvallis Environmental Research Laboratory, and J. M. Omernik. 1995. Level III ecoregions of the continental United States. Corvallis Environmental Research Laboratory, US Environmental Protection Agency.
- Crist, M. R., J. C. Chambers, S. L. Phillips, K. L. Prentice, and L. A. Wiechman. 2019. Science framework for conservation and restoration of the sagebrush biome: linking the department of the Interior's Integrated Rangeland Fire Management Strategy to long-term strategic conservation actions. Part 2. Management applications. General Technical Report-Rocky Mountain Research Station, USDA Forest Service.
- Culver, D. R. 1994. Floristic analysis of the Centennial Region, Montana. Montana State University-Bozeman, College of Letters & Science.
- Cutting, K. A., J. J. Rotella, J. A. Waxe, A. O'Harra, S. R. Schroff, L. Berkeley, M. Szczypinski, A. R. Litt, and B. F. Sowell. 2021. Resource allocation effects on the timing of reproduction in an avian habitat specialist. *Ecosphere* 12:e03700.
- Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43-64.
- Davies, K. W. 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia* 167:481-491.
- Davis, M. A. 2009. *Invasion biology*. Oxford University Press on Demand.

- DiTomaso, J. M., G. B. Kyser, S. R. Oneto, R. G. Wilson, S. B. Orloff, L. W. Anderson, S. D. Wright, J. A. Roncoroni, T. L. Miller, and T. S. Prather. 2013. Weed control in natural areas in the western United States. Weed Research and Information Center, University of California 544.
- Doherty, K., D. M. Theobald, J. B. Bradford, L. A. Wiechman, G. Bedrosian, C. S. Boyd, M. Cahill, P. S. Coates, M. K. Creutzburg, and M. R. Crist. 2022. A sagebrush conservation design to proactively restore America's sagebrush biome. 2331-1258, US Geological Survey.
- Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 41:59-80.
- Eiswerth, M. E., T. D. Darden, W. S. Johnson, J. Agapoff, and T. R. Harris. 2005. Input-output modeling, outdoor recreation, and the economic impacts of weeds. *Weed Science* 53:130-137.
- Elseroad, A. C., and N. T. Rudd. 2011. Can Imazapic Increase Native Species Abundance in Cheatgrass (*Bromus tectorum*) Invaded Native Plant Communities? *Rangeland Ecology & Management* 64:641-648.
- Fuller, K. B., and J. Mangold. 2017. The costs of noxious weeds: what you can do about them. *Big Sky Small Acres*:8-9.
- Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus *Bromus*. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications:61-95.
- Hadley, W. 2016. *Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Hartig, F. 2022. *_DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models_*.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636-638.
- Kindt, R., and R. Coe. 2005. *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*.
- Krautzer, B., W. Graiss, and C. Partl. 2006. Composition and use of seed mixtures in the high altitudes of the Alps. Pages 27-28 *in* Proceedings of the Conference Grassland-part of mountain agriculture and landscape.

- Larson, C. D., E. A. Lehnhoff, C. Noffsinger, and L. J. Rew. 2018. Competition between cheatgrass and bluebunch wheatgrass is altered by temperature, resource availability, and atmospheric CO₂ concentration. *Oecologia* 186:855-868.
- Larson, C. D., E. A. Lehnhoff, and L. J. Rew. 2017. A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. *Oecologia* 185:763-774.
- Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern Idaho, U.S.A. *Ecology and Evolution* 3:1626-1641.
- Lenth, R. 2022. `_emmeans`: Estimated Marginal Means, aka Least-Squares Means_.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522-1536.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42-55.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-ecosystems* 7:145-165.
- Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. *The Journal of Ecology*:69-93.
- Mangold, J., H. Parkinson, C. Duncan, P. Rice, E. Davis, and F. Menalled. 2013. Downy brome (*Bromus tectorum*) control with imazapic on Montana grasslands. *Invasive Plant Science and Management* 6:554-558.
- Maxwell, T. M., M. J. Germino, S. Romero, L. M. Porensky, D. M. Blumenthal, C. S. Brown, and P. B. Adler. 2023. Experimental manipulation of soil-surface albedo alters phenology and growth of *Bromus tectorum* (cheatgrass). *Plant and soil*:1-15.
- Monaco, T. A., J. M. Mangold, B. A. Meador, R. D. Meador, and C. S. Brown. 2017. Downy Brome Control and Impacts on Perennial Grass Abundance: A Systematic Review Spanning 64 Years. *Rangeland Ecology & Management* 70:396-404.
- Montana Invasive Species Advisory Council. 2016. Management Assessment of Invasive Species.

- Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlinn, M. Ouellette, C. E. Ribeiro, S. A. Smith T, B. C. Ter, and J. Weedon. 2022. `_vegan: Community Ecology Package_`.
- Omernik, J. M. 1987. Ecoregions of the Conterminous United States. *Annals of the Association of American Geographers* 77:118-125.
- Orloff, L. N., J. M. Mangold, and F. D. Menalled. 2015. Site-Specific Effects of Exotic Annual Grass Control Integrated with Revegetation. *Ecological Restoration* 33:147-155.
- Owen, S. M., C. H. Sieg, and C. A. Gehring. 2011. Rehabilitating Downy Brome (*Bromus tectorum*)–Invaded Shrublands Using Imazapic and Seeding with Native Shrubs. *Invasive Plant Science and Management* 4:223-233.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7:8126-8151.
- Pinheiro, J., D. Bates, and R Core Team. 2022. `_nlme: Linear and Nonlinear Mixed Effects Models_`.
- Pokorny, M. L., R. L. Sheley, T. J. Svejcar, and R. E. Engel. 2004. Plant species diversity in a grassland plant community: evidence for forbs as a critical management consideration. *Western North American Naturalist*:219-230.
- Pyke, D. A., S. E. Shaff, A. I. Lindgren, E. W. Schupp, P. S. Doescher, J. C. Chambers, J. S. Burnham, and M. M. Huso. 2014. Region-Wide Ecological Responses of Arid Wyoming Big Sagebrush Communities to Fuel Treatments. *Rangeland Ecology & Management* 67:455-467.
- R Core Team. 2022. R: A language and environment for statistical computing Vienna, Austria.
- Radosevich, S. R., J. S. Holt, and C. M. Ghera. 2007. Ecology of weeds and invasive plants: relationship to agriculture and natural resource management. John Wiley & Sons.
- Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* 50:1039-1049.
- Rice, P. M. 2003. Invaders database system. University of Montana, Missoula, MT.
- Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* 19:155-162.

- Seefeldt, S. S., and S. D. McCoy. 2003. Measuring plant diversity in the tall threetip sagebrush steppe: influence of previous grazing management practices. *Environmental Management* 32:234-245.
- Sheley, R. L., T. J. Svejcar, and B. D. Maxwell. 1996. A Theoretical Framework for Developing Successional Weed Management Strategies on Rangeland. *Weed Technology* 10:766-773.
- Shriver, L. C. 2022. Restoration and evolution in the Great Basin: non-target herbicide effects and potential for adaptive responses to fire.
- Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, M. O. Jones, A. R. Kleinhesselink, J. D. Maestas, S. L. Morford, and D. E. Naugle. 2022. The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA. *Diversity and Distributions* 28:83-96.
- Smithson, M., and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological methods* 11:54.
- Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* Response to Fire Varies with Climate Conditions. *Ecosystems* 17:960-973.
- U.S. Environmental Protection Agency. 2013. Level III ecoregions of the continental United States: Corvallis, Oregon. *in* U. S. E.-N. H. a. E. E. R. Laboratory, editor.
- Vermeire, L. T., and M. J. Rinella. 2020. Fall Water Effects on Growing Season Soil Water Content and Plant Productivity. *Rangeland Ecology & Management* 73:252-258.
- Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702-708.
- Wood, C. W., and B. A. Meador. 2022. Identifying Structural Thresholds in Annual Grass–Invaded Rangelands. *Rangeland Ecology & Management* 83:1-9.
- Young, J. A., R. A. Evans, R. E. Eckert, and B. L. J. R. A. Kay. 1987. Cheatgrass. 9:266-270.
- Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression Models for Count Data in R. *Journal of Statistical Software* 27(8).
- Zouhar, K. 2008. Wildland fire in ecosystems: fire and nonnative invasive plants. Forest Service.
- Zuur, A. F., and E. N. Ieno. 2016. Beginner's guide to zero-inflated models with R. Highland Statistics Limited United Kingdom.

CHAPTER THREE

LONG-TERM LANDSCAPE SCALE RESILIENCE OF HIGH-ELEVATION SAGEBRUSH
STEPPE TO *BROMUS TECTORUM*, HERBICIDE AND CLIMATEIntroduction

The sagebrush biome encompasses 651,316 square kilometers (km²) of North America, representing about half of its pre-European extent (Homer et al. 2015) and its floral richness is often understated. For example, southeast Idaho, USA, a relatively small component of the sagebrush biome, has been found to contain nearly 700 species (Lavin personal communication). However, this biome's diversity extends beyond its flora, including 27 wildlife species, of which 14 are mammals, five are reptiles and amphibians, and eight are birds, including *Centrocercus urophasianus* (Greater sage-grouse) and *Centrocercus minimus* (Gunnison sage-grouse), typically associated with sagebrush biome conservation (Remington et al. 2021). The biome encompasses multi-use systems comprising federal, state, and private lands, all with varying management objectives (Remington et al. 2021, Doherty et al. 2022b). These systems provide major ecosystem services, such as livestock forage and recreation (hunting, camping, off-highway vehicle (OHV) use, etc.), and have both practical and cultural significance for many Native American Tribes across the West (Moerman 1998). With a world population slated to reach 9 billion people by 2050, and conjunctly ruminant meat consumption projected to increase by 88% in the next 30 years (Searchinger et al. 2014), recreation and grazing demands will only increase. This system is also under threat due to non-native annual grass fire feedback cycles, climate

adaptation, conifer expansion, land use and development, and interactions between them (Remington et al. 2021).

Recently, *Bromus tectorum*, has begun to establish at higher elevations, especially on steep south- and north-facing slopes across the biome; this is in contrast to historical observations in the Great Basin and Snake River Plain (Smith et al. 2022). This expansion is likely occurring due to factors that influence the expansion and persistence of *B. tectorum* on the landscape: intensive grazing, human development, and positive wildfire feedbacks (Seefeldt and McCoy 2003, Lavin et al. 2013, Reisner et al. 2013, Pilliod et al. 2017). In Montana *B. tectorum* has been present since 1898 (CPNWH 2017) and has been documented in every county (Rice 2003), indicating a historic statewide suitable niche for *B. tectorum*, whether from disturbance, climate, or both. Anecdotally, future climate projections appear to be more favorable for *B. tectorum* across the state but especially in southwest Montana, as indicated by projected warmer and wetter springs and falls (Whitlock et al. 2017). These changes could result in an increased abundance and distribution of *B. tectorum*. Historically, the climate of southwest Montana has been cooler and wetter, disfavoring widespread *B. tectorum* dominance when compared with the Columbia Basin, North, and Central Basin and Range (Chambers et al. 2014a, Maestas et al. 2016). For example, in southwest Montana the average (1981-2010) spring mean temperature was 2.9 °C with 18cm of precipitation, and the mean fall temperature was 4.1 °C with 11.7cm of precipitation (Whitlock et al. 2017). In comparison, Nevada, the central U.S. state in the Northern Basin and Range, has a historic (1981-2010) spring temperature of 9 °C with 7.5cm of precipitation and a fall temperature of 10.5 °C and 5.4cm of precipitation (Noaa National Centers for Environmental Information 2023).

Resiliency to non-native plant invasion can be influenced by a combination of abiotic and biotic factors, such as climate, competition, and resource availability (D'Antonio et al. 2001, D'Antonio and Thomsen 2004, Chambers et al. 2014a, Chambers et al. 2014b). Holling (1973) first proposed managing systems for ecological resilience, an idea that has been further expounded upon in recent years (Chambers et al. 2014a, Chambers et al. 2014b, Chambers 2016, Chambers et al. 2016, Roundy et al. 2018, Chambers et al. 2019). For example, a recent framework emphasizes the need for integration of pattern and process across spatial extents relevant for management, largely focusing on the maintenance of key ecological process (structure and function) and identification of key ecosystem characteristics that drive resilience and its limits (Chambers et al. 2019). In the context of *B. tectorum* management, this framework uses climate and topography to predict ecological resilience across the biome (Chambers et al. 2023). However, this research has relied almost entirely on empirical studies from the Columbia Basin, Northern and Central Basin and Range, to predict resilience in other regions of the biome. Regardless, the term resilience, in an ecological context, has not always been clearly defined (Grimm and Wissel 1997). We chose to follow the definition of resilience stated by Holling (1973); "...a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables." In this definition, Holling (1973) incorporates resistance, "...persistence of systems...", as a component of resilience. Resilience then can be measured as a probability of persistence (high resilience) or extinction (low resilience) of species linkages (Holling 1973). Resilience is often invoked to describe a system's behavior after perturbation, such as disturbance or non-native plant invasion, making it inherently linked to temporal and spatial scope and evolutionary history

(Grimm and Wissel 1997). These “behaviors” encompass many different ecological processes that exist on a spectrum of biotic and abiotic factors (Davis et al. 2000); it follows that resilience will exhibit a range of expressions depending on the unique factors of each system. Indeed, the resilience of a system to *B. tectorum* invasion has been characterized by a large number of studies conducted in the Columbia Basin and the North and Central Basin and Range (Chambers et al. 2007b, Chambers et al. 2014a, Bradley et al. 2016b, Chambers et al. 2016, Roundy et al. 2018, Smith et al. 2022). These studies utilize elevational and topographical gradients to evaluate resilience over a climatic gradient, i.e., higher elevation and northern aspects representing cooler and wetter climates. High-elevation sagebrush steppe, which includes southwest Montana, should be more resilient to *B. tectorum* invasion, because of its relatively cooler and wetter climate. However, this assumption has not been adequately quantified for high-elevation sagebrush steppe in the Northern Snake River Plain/southern Middle Rockies, which includes southwest Montana, which is projected to be highly resilient to *B. tectorum* invasion (Chambers et al. 2023). Currently, there is little evidence that suggests *B. tectorum* will impart the same effect at the northern edge of its distribution as it does in its southern distributions, largely due to the lack of observed and predicted positive fire-feedback (Lavin et al. 2013, Taylor et al. 2014, Brummer et al. 2016, Larson et al. 2017, Larson et al. 2018). Despite this research, private and public land managers have raised concern over increases in *B. tectorum* abundance. There is growing concern that these populations may impart the same negative effects observed in the Columbia Basin and the North and Central Basin and Range. Specifically, land managers are observing increases in *B. tectorum* abundance on steep south-facing hillsides that have historically not been infested, calling into question this area’s resilience.

In response to these observations, increasingly suitable climate projections for *B. tectorum* (Whitlock et al. 2017), and spatial analysis of *B. tectorum* expansion (Bradley et al. 2016b, Bradley et al. 2018), we sought to evaluate the impact of herbicide application on *B. tectorum* abundance and the native plant community. To assess this goal, we quantified the response of high-elevation sagebrush steppe to management and *B. tectorum* by analyzing assemblages of herbicide treated and non-treated reference plant communities using species richness, nestedness, alpha diversity, and beta diversity. We then characterized the response of the treated plant community to herbicide application by comparing it to the non-treated reference community using resilience theory, terminology, and management concepts (Holling 1973, Chambers et al. 2014b, Chambers 2016, Chambers et al. 2019).

Methods

Study Area

This study was conducted in southwest Montana, USA, in the Centennial Valley, a 65,000-ha high-elevation (2,000-2,500m asl) sagebrush steppe valley, typified by cold winters and short, cool summers. Two areas characterized by distinct soils and dominant vegetation exist within the valley's foothills: Antelope Peak has primarily clay/loam soil, whereas the Eastern Sandhills have mostly sandy soil (Table 1.1). The flora of the Antelope Peak area is dominated by a mixture of sagebrush and other shrub types; *Artemisia tridentata* Nutt. (big sagebrush), *A. tripartita* Rydb. (three-tip sagebrush), *A. frigida* Wild. (fringed sagebrush) and *Chrysothamnus nauseosus* Nutt. (rabbit brush) (Culver 1994) and, by our observation, native perennial bunchgrasses. The Eastern Sandhills area is dominated by *A. tridentata*, *A. tripartita*, *Agropyron dasystachyum* Scribn. & J.G. Sm. (thickspike wheatgrass), *Festuca idahoensis* Elmer (Idaho

Fescue) and *Phacelia hastata* Douglas ex Lehm. (silver leaf phacelia) (Culver 1994). The Centennial Valley, including both Antelope Peak and the Eastern Sandhills, and nearby mountains provide habitat for approximately 487 plant species (representing ~21% of Montana's native flora), some of which are regionally endemic or species occurring at their range extents (Culver 1994).

Twelve steep, south-facing hillslopes, averaging 8 hectares each, were selected as sites. Four of these sites were in the Eastern Sandhills and the remaining eight near Antelope Peak. Each site consisted of an area that was infested (9% mean cover) by *B. tectorum* and an adjacent area with no or low invasion of *B. tectorum* that was considered the non-treated "reference" site.

Experimental Design

In early October 2017 and 2018, the herbicide imazapic (Plateau®; BASF Corporation, 100 Park Ave., Florham Park, NJ) was aerially broadcasted at 0.17 active ingredient (a.i.) kg/ha with a carrier rate of 11.35L of water per hectare and at a pressure of 25 PSI. Herbicide was applied at an aerial speed of 65-70 kmph by helicopter. *Bromus tectorum* was targeted post-emergence at the infested areas of each site (hereafter "sprayed" treatment). Vegetation was monitored at the entire hillside scale (~8ha): Three 50-meter transects were randomly placed within the infested and sprayed area and the adjacent reference area. Transects ran parallel with the slope of the hill to encompass any gradients. Each transect consisted of five Daubenmire frames (20cmx50cm; 0.1m²) (Daubenmire 1959) evenly spaced along the transect.

Vegetation Canopy Cover Sampling: *Bromus tectorum* foliar cover was monitored every year from 2017 (prior to herbicide application) until 2022. Vegetation crews only monitored *B. tectorum* cover in 2017 and 2018, and no other species were recorded. From 2019 until 2022 an

ocular assessment of each plant specie's foliar cover along with bare ground, rock and litter was estimated to the nearest 1% using a Daubenmire frame (Daubenmire 1959). Cover was allowed to exceed 100% total for the frame to account for overlapping species' canopy. Each year monitoring was initiated in mid-June and concluded around July 1st. For the multivariate analysis, species abundances were combined by life form (grass, forb, shrub) and origin (native, non-native) to create the functional groups: non-native annual grass, non-native perennial forb, native perennial forb, native annual fob, native perennial grass, and native shrub.

Climate variables, including monthly temperature (minimum, maximum, mean) and precipitation data were downloaded from the PRISM Climate Group's (Oregon State University) website (<https://prism.oregonstate.edu/explorer/>) using 4km² grid cells that were interpolated for each site location using inverse-distance squared weighting. Precipitation and temperature were aggregated into seasonal (spring, summer, fall, winter) quarterly-groups. Spring is defined as March, April, and May, summer as June, July, and August, fall as September, October, and November, and winter as December, January, and February. We considered the beginning of the growing season to be fall, due to the winter annual phenology of *B. tectorum*, which can result in fall germination. Therefore, fall and the first month of winter were from the preceding calendar year.

Statistical Analysis

Bromus tectorum abundance: *Bromus tectorum* abundance was zero-inflated (78% zeros). To address zero-inflation, a linear zero-altered negative binomial (ZANB) model with a "logit" link function was used from the "pscl" package (Zeileis et al. 2008). The ZANB method utilizes a hurdle methodology described by Zuur and Ieno (2016). Following this method, the data are

split into two components and modeled separately and then recombined to create the final ZANB model estimate. First, the non-zero portion of *B. tectorum* abundance are modeled assuming a negative-binomial distribution, next the *B. tectorum* presence, including zeros, are modeled using a binomial distribution to estimate the probability of occurrence; lastly, the two model estimates are multiplied to create the final ZANB model estimate, similar to logistic regression. This method captures the biological zero-generating process in the final model estimation. In this study, we assume this zero-generating process to be the application of herbicide, therefore, use of the hurdle model methodology is appropriate. Further, we report both the final ZANB model estimates for *B. tectorum* abundance and the probability of occurrence. The “pscl” package does not allow for the use of random/mixed effects in its modeling structure, therefore the nested design and temporal replication could not be accounted for. The dispersion parameter was calculated using the equation suggested by Zuur and Ieno (2016) (pgs. 172 &173) and found to be minimal (0.999). Final model estimates were compared using the “emmeans” package (Lenth 2022). The final models were:

$$\text{BRTE} \sim \text{herbicide} * \text{year} + \text{area}$$

where BRTE was *B. tectorum* abundance, and herbicide (sprayed/reference), year (2017, 2018, 2019, 2020, 2021, 2022), and area (Antelope Peak/Eastern Sandhills) were all categorical factors.

Our goal was to analyze the response of the two communities using two time periods; from before to after management (2017-2022) and the four years (2019-2022) directly after two fall applications of herbicide (2017 and 2018). We conducted a Dunnett’s post-hoc test using the “emmeans” package (Lenth 2022) to assess changes over time for these models. Our first model

allowed us to analyze whether post-management (2018, 2019, 2020, 2021, 2022) *B. tectorum* abundance differed from pre-herbicide (2017) management levels in both the sprayed and reference communities. This allowed us to assess the level of control that was achieved after the first (2018) and second (2019) applications of herbicide. Our second model compared differences in *B. tectorum* abundance for the four years after treatment, and between areas. We felt that including pre-herbicide (2017) data and one year after herbicide (2018) data would reduce our ability to detect meaningful responses to the two fall herbicide treatments.

Plant Community Response: Species richness, Shannon's diversity index (H) (alpha diversity) (Pielou 1974), Bray-Curtis index (Bray and Curtis 1957) (beta diversity), and rank abundance were calculated using the packages "vegan" (Oksanen et al. 2022) and "bioDiversityR" (Kindt and Coe 2005). The variables, herbicide, year (2019-2022) and area were used as explanatory fixed effect variables in a linear mixed effects model ("nlme" (Pinheiro et al. 2022)) that incorporated site, transect and frame as nested variables. *Bromus tectorum* was omitted from the species richness analysis because it was a target species for removal, i.e., inclusion of *B. tectorum* could artificially create differences between sprayed and non-treated/reference treatments. *Bromus tectorum* was included in all other diversity measures.

Multivariate Analysis and Ordination: We used the Bray-Curtis index (Bray and Curtis 1957) to assess beta diversity, and it was used for the multivariate analysis and non-metric multi-dimensional scaling (NMDS) ordination. The Bray-Curtis index maximizes the association between known ecological distances and simulated gradients, making it most suitable for ordination methods such as NMDS (Faith et al. 1987). We used a non-parametric analysis of variance (PERMANOVA) test to identify how herbicide, treatment, year, area, climate,

environmental (bare ground, litter) and biotic variables explained beta-diversity. Biotic variables included *B. tectorum* abundance and individual functional group cover. The vegetation data were averaged to the treatment level (frame and transect, combined) for community analysis and to the site level (frame, transect, and treatment combined) to match the spatial resolution of the climate data. An alpha level cutoff of 0.05 was used to determine which variables were important in the PERMANOVA test. Following variable selection, we plotted the NMDS ordination with environmental gradients applied using ggplot (Hadley 2016). Explicitly, the NMDS ordination was un-constrained and environmental variables were applied post-hoc. We are making an assumption that vegetation and environmental variables are related; as a result we cannot be sure that the environmental variables applied here constrain the community assemblages (Roberts 2020).

After plotting the seasonal minimum, maximum, and mean temperature strata as vectors on the NMDS ordination, we found that spring, summer, fall, and winter minimum and maximum temperatures, while all significant in our PERMANOVA test, appeared to be highly correlated, i.e., vectors were tightly spaced and indicated the same direction. To confirm this speculation, we conducted a Pearson's correlation test and observed a >80% correlation between the seasonal minimum, maximum, and the mean temperatures, as might be expected because the calculation of a mean incorporates both maximum and minimum temperatures, so they inherently share information. This correlation is not problematic for the PERMANOVA test. However, for the sake of visual clarity we removed the seasonal minimum and maximum temperatures, from the ordination plots, leaving the mean temperature to represent the impact of seasonal temperature differences.

Results

Bromus tectorum response

The Antelope Peak and Eastern Sandhills areas did not differ in their response to herbicide application, however, there was a yearly difference (Chi-sq: 124.19, df: 5, p:<0.0001). Following the first herbicide application, *B. tectorum* abundance was 7-8% lower from 2018-2021 (Table 2.2). However, *B. tectorum* abundance increased to 5% in the fourth year (2022), 4% less than the abundance seen before herbicide application (2017) (9%) (Table 2.2 and 2.3). The abundance of *B. tectorum* did not change in the reference community from pre-herbicide to the fourth year (1%) (Table 2.2 and 2.3).

There were no differences in *B. tectorum*'s abundance in the four years post herbicide application for either sprayed or reference communities between the Antelope Peak and the Eastern Sandhills. The first summer (2019) after the two fall herbicide applications there was no difference between the sprayed and reference communities' *B. tectorum* abundance; however, in the second (2020) and third (2021) years, the sprayed community had 1% greater abundance, compared to the reference (Table 2.3 and 2.4). It is worth noting that these differences, while statistically significant, might not represent biologically meaningful differences in abundance. By the fourth year there was 4% more *B. tectorum* in the sprayed community (5%) compared to the reference (1%) (Table 2.3 and 2.4) (Figure 2.1).

Bromus tectorum Probability of Occurrence

There were no differences in the probability of occurrence of *B. tectorum* between Antelope Peak and the Eastern Sandhills. Before herbicide was applied the probability of occurrence for the invaded community was 87%, and after a single fall application (2018) the

probability of occurrence dropped to 57% (Figure 2.3, Table 2.5 and 2.6). Following the second herbicide application (2019) there were no differences in the probability of occurrence between the sprayed and the reference communities (Table 2.5). In the following three years (2020-2022), the probability of occurrence was greater in the sprayed compared to the reference community, and the greatest difference occurred in the fourth year (2022) (Figure 2.3; Table 2.5 and 2.6). The probability of occurrence in the fourth year for the sprayed community was 41%, 38% lower than it was pre-herbicide (Table 2.5).

Plant Richness

In total 147 species of native and non-native flora were observed, and species richness ranged from zero to 12 species/0.1m². Species richness differed depending on area and herbicide application (f-stat: 4.93, df:1,1208, p: 0.026) (Figure 2.4). In the Antelope Peak area, we observed 4.8 species/0.1m² in the reference community and 3.7 species/0.1m² in the sprayed community (t: 10.12, df: 1208, p: <0.0001). In the Eastern Sandhills area there were 4.8 species/0.1m² observed in the reference community and 4.1 species/0.1m² in the sprayed community (t:4.45, df: 1208, p: 0.0001).

Community Nestedness Over Time

The reference community always had greater absolute species richness than the sprayed community and shared many of the same species, increasing from 62% shared species to 84% over the four years post treatment (Table 2.7). The reference community had a range of 8 to 27 more species over the course of the study (Table 2.7) and a range of 16 to 30 unique species, that is, species that were not shared with the sprayed community (Table 2.7). Comparatively, the

sprayed community had a range of 3 to 9 unique species over the duration of the study (Table 2.7).

Alpha Diversity

Plant alpha diversity, unlike richness, varied depending on area, herbicide, and year (f-stat: 2.40, df: 3, 1208, p: 0.065). We acknowledge that 0.05 is the typical alpha level cutoff, but in this instance the strong evidence for two of the three lower order interactions, year*area (f: 13.92, df: 3,1208, p: <0.0001) and year*herbicide (f-stat: 13.35, df: 3, 1208, p: <0.0001), prompts a more succinct discussion of the ecological patterns by discussing the behavior of the three-way interaction among area, herbicide, and year. Diversity was greater in the reference compared to the sprayed community in the Antelope Peak and Eastern Sandhill areas only in year one (Figure 2.5), but in years two to four the communities did not differ from one another. Overall, plant diversity increased from one to four years after herbicide application in the Antelope Peak area for both sprayed and reference communities. However, diversity remained the same from year one to four in the reference and sprayed community in the Eastern Sandhills (Figure 2.5).

Beta Diversity/Dissimilarity

Using a type III permutational multivariate analysis of variance (PERMANOVA) test, we found that year (23.4%), site (16.8%), and treatment (3%) explained a combined ~43% of the observed variance (Table 2.8). We found the mean pairwise Bray-Curtis dissimilarity indices to indicate high within and between community dissimilarity for both the sprayed and reference communities (Tables 2.9-11). The within community composition of the sprayed and reference treatments became more similar overtime, i.e., became less dissimilar (Tables 2.9 and 2.10). The

community dissimilarity between the sprayed and reference communities fluctuated slightly over the course of the study (Table 2.9) but was only different by 0.05 by the final year (Table 2.11). A visualization of these relationships using a non-metric multi-dimensional scale (NMDS) ordination confirmed that the sprayed and reference communities were similar following herbicide application, and that over time, both communities moved across the ordination space following a similar pattern (Figures 2.6 and 2.7).

We attempted to identify potential drivers for the yearly change in both community's composition by plotting seasonal temperature, precipitation, plant functional group cover, and litter cover. We found that seasonal precipitation and temperature were important for explaining the variation observed in the ordination, as were the cover of litter and plant functional group. Specifically, we found that spring, summer, fall and winter precipitation had R^2 values of 0.66, 0.43, 0.45, and 0.34, respectively (Table 2.8). Seasonal mean temperature in spring, summer, and fall had R^2 values of 0.66, 0.48, and 0.49, respectively (Table 2.8). We found that litter had an R^2 value of 0.46, while the perennial native grasses (PGN), perennial native forbs (PFN), and non-native annual grasses (AGI) plant functional groups had R^2 values of 0.37, 0.41, and 0.28, respectively (Table 2.8). The shift in community assemblages from the first to fourth year followed a trend of increasing fall, spring, and summer precipitation, and decreasing winter precipitation (Figure 2.8). Additionally, this shift was associated with warmer fall and summer mean temperatures and cooler spring mean temperature (Figure 2.9). From a canopy cover perspective, the yearly trend was associated with an increase in AGI, PFN, and litter cover (Figure 2.10) and decreasing PGN cover (Figure 2.10).

Rank Abundance

The proportional abundance of the top five species was compared graphically to track whether *B. tectorum* returned as a dominant species (Figure 2.11). *Bromus tectorum* was the third most dominant plant at Antelope Peak and the most dominant species at Eastern Sandhill areas sprayed communities by the fourth year. It was not in the top five species in any other year. *Bromus tectorum* was absent from the top five in both Antelope Peak and Eastern Sandhill areas reference community (Figure 2.11).

By the fourth year of the study, the dominant members of both plant communities comprised eight perennial native forbs, *Eriogonum umbellatum* Torr. (sulphur-flower buckwheat), *Lomatium triternatum* (Pursh) J.M. Coult. & Rose (nineleaf biscuitroot), *Erigeron compositus* Pursh. (cutleaf daisy), *Erigeron corymbosus* Nutt. (longleaf fleabane) and *Castilleja* sp. Mutis ex L. f. (Indian paintbrush), *Phlox hoodii* Richardson (spiny phlox), *Cirsium undulatum* (Nutt.) Spreng. (wavyleaf thistle), *Psoraleidum lanceolatum* (Pursh) Rydb. (lemon scurfpea); two native perennial grasses, *Stipa comata* Trin. & Rupr. (needle and thread) and *Agropyron dasystachyum* (Hook.) Scribn. & J.G. Sm. (thickspike wheatgrass); one native shrub, *Artemisia* L. sp. (sagebrush); and one non-native forb, *Alyssum desertorum* Stapf. (desert alyssum). This represented the transition from mostly native perennial grass dominated communities to a composition of mostly native perennial forbs.

Discussion

Bromus tectorum Response to Herbicide Application

Two consecutive fall post-emergent applications of imazapic successfully reduced *B. tectorum* abundance and probability of occurrence for three years following application,

independent of area, compared to pre-treatment levels. Despite this suppression, *B. tectorum* returned as the third most abundant member of the Antelope Peak sprayed community and the most dominant member of the Eastern Sandhills sprayed community four years post-application. Interestingly, even though *B. tectorum* abundance remained low (4.9%), the probability of occurrence increased to 42% in the final year. This indicates that while these populations were low in abundance, the area remains suitable for invasion. Overall, the length of *B. tectorum* control observed in this study was similar to the findings of others, (Pyke et al. 2014) (Elseroad and Rudd 2011). We attribute the longevity of control in part to an interaction between application timing and drier than average springs in the first three years and a drier than average fall in the second year, which are reflected in departures of our site precipitation and moisture from the 30-year mean (Table 11). The resurgence of *B. tectorum* in the fourth year following herbicide application correlates with a warmer and wetter than average spring and fall (Table 12 and 13). Fall precipitation has been positively correlated with increased *B. tectorum* germination and spring precipitation with biomass and survival (Vermeire and Rinella 2020). It is also plausible that imazapic remained active in the soil into the subsequent springs following fall application as observed by Ehlert et al. (2015). This extended soil residual time could have impacted both fall germinating and spring germinating *B. tectorum*, leading to further seedbank depletion.

Plant Community Resilience

Resilience is an ecosystem behavior (Holling 1973, Levine and D'Antonio 1999, D'Antonio and Thomsen 2004) that can vary along both biotic and abiotic gradients (D'Antonio and Thomsen 2004). Our ability to quantify this behavior relies on access to either an un-

changed analogue or a sufficient temporal history that encompasses natural variation for reference. Here we discuss the resiliency of an invaded and then herbicide-treated plant community relative to a minimally invaded and non-treated reference community; these areas are adjacent to each other and consequently have been managed similarly over the last century, to the best of our knowledge. We found the sprayed community to be an increasingly nested version of the reference community over the duration of the study, indicating that it had a similar but reduced species membership. These two measures, richness and nestedness, represent the potential number of species-linkages or interactions possible for each community, if one considers that all species have equal opportunity to interact. However, all species interactions are not equally important from a functional standpoint. Using alpha (Shannon's), beta (Bray-Curtis) indices of diversity, and rank abundance we observed that communities distinguished themselves more than might be expected by comparing the percentage of absolute species shared. This provides evidence that the rank abundance, not a lack of shared species, is the driving factor in differentiating these communities.

Over time the sprayed and reference communities became more similar, despite *B. tectorum* abundance being lower in the reference compared to the sprayed. We propose that *B. tectorum*'s presence/abundance alone may not be an ecologically important feature in defining the assemblages of these two communities in this part of the sagebrush biome, at the observed abundances, and despite an increase in probability of occurrence. Because this high-elevation sagebrush steppe ecosystem appears to be unresponsive to the reduction followed by possible recovery of just one species, *B. tectorum*, we characterize it as resilient within the scope of this study. Further evidence for this resiliency lies in this ecosystem's evolutionary history; historic

conditions that include high seasonal variability in temperature and precipitation have selected against a substantial annual grass component in favor of perennial grasses and forbs, as evidenced by the lack of dominant native annual grasses. As a result, it seems reasonable that the fluctuations of a non-native annual grass might have little impact on a community already well adapted to its absence. In stark contrast, the Columbia Basin and the North and Central Basin and Range have experienced ecosystem-wide conversion of shrubland to annual grassland as the result of widespread annual grass invasion, drastically changing plant community assemblages, however, these changes are in theory reliant on the occurrence of positive fire-feedback cycles (D'Antonio and Vitousek 1992, Brooks et al. 2004, Balch et al. 2013, Germino et al. 2016, Bradley et al. 2018). This is not to say that invasion of the Columbia Basin and the North and Central Basin and Range do not occur without fire (Lavin et al. 2013, Brummer et al. 2016, Smith et al. 2023).

Our study provides evidence that without a concurrent positive fire-feedback cycle, high-elevation sagebrush steppe in southwest Montana is resilient to changes in plant community structure when *B. tectorum* is managed at low abundances. However, it does not appear that management reduces the probability of occurrence where *B. tectorum* has previously invaded, indicating that a suitable niche for *B. tectorum* still remains and further restoration action is warranted. The observed persistence of *B. tectorum* in our study could be contributed in part to plant-induced soil legacy effects, which have been shown to have long-term consequences for plant community productivity (Kulmatiski and Beard 2011) and soil microbial ecology (Eisenhauer et al. 2010). Indeed, *B. tectorum* has been documented to impart such effects, by creating a self-promoting soil legacy (positive plant-soil feedback), that results in greater

competitive ability and biomass production (Blank and Morgan 2013, O'connor and Prevey 2015, Blank and Morgan 2016).

Both the sprayed and reference communities were similar in assemblage within each year over the course of the study. However, between years we observed both communities becoming increasingly dissimilar from year to year. For both communities this trend was driven by an increasing native perennial forb, non-native annual grass, and litter component and a decreasing native perennial grass component. Our analysis indicates that these vegetative shifts are correlated with increasingly warmer falls and summers and cooler springs coupled with wetter falls, springs, and summers and drier winters when compared to 30-year means (Figure 2.8 and 2.9; Table 2.12 and 2.13). Patterns of precipitation and temperature along with their timing are important factors in structuring plant communities (Hawkins et al. 2003, Keeley et al. 2005, Rahbek et al. 2019). Within the context of this study, we do not have a historical analog with which to compare these changes in community structure. Therefore, it is difficult to characterize the resilience of these communities in response to shifts in temperature and precipitation patterns. We speculate, however, that the observed dissimilarity arises from a shift in the existing community assemblages' relative abundance to one another and not its membership; as suggested by the increase in non-native annual grass and native perennial forb cover over time, coupled with the decrease in native perennial grass, without a loss of absolute species richness. Further evidence for this line of reasoning exists in the rank abundance analysis, where we observed a transition from native perennial grass to native perennial forbs species over the course of the study. This indicates that the linkages between species are maintained, i.e., species did not become locally extinct, and maintained their relationships with one another but not their relative

position as dominants. This response to shifts in precipitation and temperature pattern, as detailed above, is evidence for high resiliency to climate in these systems.

The structural shifts in both plant communities observed in this study should not be taken as an indicator of no-change. Here we observe only a small portion of the plant community's trajectory and speculate that it is driven by precipitation and temperature shifts. This trajectory, depending on which ecological theory is applied (Westoby et al. 1989, Holling 1996, Kuehn 2011, May 2019), could be toward or away from "equilibrium, stable-state, or transition threshold", and calls attention to the need for threshold identification (Folke et al. 2004, Scheffer et al. 2012). For example, do ecosystems transition from perennial grass- and shrub-dominated to perennial forb- and shrub-dominated before they transition to annual grass dominated systems? Or, as observed by Anderson and Inouye (2001), do these communities transition away from a dominant annual grass component, and shift toward a diverse (alpha and beta) native community? Identifying thresholds for each of these scenarios could help managers to change the trajectory of their systems, further investigation is warranted.

Conclusion

This study illustrates the importance of long-term plant monitoring following management to assess outcomes, which is crucial for adaptive management and experiments (Rinella et al. 2012, Chambers et al. 2019). This study emphasizes the power of using a reference community to evaluate the impacts of an annual grass invader and herbicide management. We used alpha and beta diversity indices to characterize the plant community's response to management and environment. We urge further research to follow suit by investigating a wider array of metrics to quantify the response of plant communities to management. For example, by

comparing alpha diversity, beta diversity, species richness and rank abundance we were able to gather more refined information on plant community response. As a result, we observed changes in community structure over time to changing seasonal temperature and precipitation, all of which influence ecosystem resilience (Peterson et al. 1998, Chambers et al. 2014a, Chambers 2016, Chambers et al. 2016, Levine et al. 2016, Roundy et al. 2018). Further, we found that if herbicide is used as a management tool, it is effective at reducing *B. tectorum* in this ecosystem and that reduction of *B. tectorum* resulted in a compositionally similar, but less species rich community compared to the reference community.

We do not know the species composition of the sprayed community prior to *B. tectorum* invasion; however, we assume that our reference community provides a sufficient analog from which to extrapolate this information. Indeed, the invaded and sprayed community appears to be a nested version of the reference. As a result, we hypothesize that the species unique to the reference community may be important indicators or contributors to the reference communities' resilience to *B. tectorum* invasion. Specifically, we found the following species to be unique to the reference community in at least three of the four years during our study: *Agoseris glauca* (Pursh) Raf. Var. *dasycephala* (Torr. & A. Gray) Jeps. (pale agoseris), *Agoseris* spp. Raf. (agoseris), *Allium textile* A. Nelson & J.F. Macbr. (textile onion), *Eriogonum ovalifolium* Nutt. (cushion buckwheat), *Erigeron speciosus* (Lindl.) DC. (aspen fleabane), *Eriogonum umbellatum* Torr. (sulphur-flower buckwheat), *Linum lewisii* Pursh (Lewis flax), and *Sedum lanceolatum* Torr. (spearleaf stonecrop). Further, we hypothesize that the absence of these species could be responsible for the higher probability of *B. tectorum* occurrence despite management, as their absence represents the potential for reduced niche space and competition for resources. Equally,

the recent establishment of *B. tectorum* may have led to a decline in species richness, but this is purely speculative. This hypothesis represents the frequent paradox of invasion ecology often referred to as “drivers or passengers”, which questions whether invaders are a symptom or driver of observed change (e.g., plant community composition, ecosystem function) (MacDougall and Turkington 2005).

Though these communities appear to be resilient to *B. tectorum* management, the climate driven shift from perennial grass to an annual grass and native forb dominated community could lead to reduced resilience in the future. For example, many studies correlate a cooler and wetter climate, north facing slopes, high-elevation, and native perennial grasses with greater resilience to *B. tectorum* invasion (Chambers et al. 2007b, Davies 2011, Chambers et al. 2014a, Davies and Johnson 2017, Roundy et al. 2018). As a result, continued research is needed to assess whether the shifts in community structure we observed, will continue to favor perennial native forbs and non-native annual grasses and disfavor native perennial grasses as climate changes, thereby potentially decreasing resiliency. Further monitoring would also provide better resolution of this study within the context of historic natural variation. As suggested by Anderson and Inouye (2001) this system may fluctuate widely within a historical context.

Tables

Table 2.1: Site locations and soil texture descriptions for each site in the Antelope Peak (AP) and Eastern Sandhills (ES) areas of the Centennial Valley, MT, USA.

Area	Site	Latitude	Longitude	Elevation (meter(feet))	Soil Texture
AP	16	44.65958603	-111.9954618	2089(6853)	Sandy Clay Loam
AP	15	44.66054363	-112.0015361	2135(7004)	Gravelly Sand Loam
AP	14	44.65813905	-112.0055019	2131(6991)	Silty Clay
AP	11	44.65858126	-112.0165624	2176(7139)	Silty Clay
AP	3	44.65876424	-112.0404955	2168(7112)	Gravelly Silt Loam
AP	2	44.66065154	-112.044243	2176(7139)	Silty Clay Loam
AP	21	44.65637509	-112.0095762	2293(7522)	Silty Loam
AP	22	44.67905552	-112.0189539	2381(811)	Silty Loam
ES	1	44.68076541	-111.6899827	2137(7011)	Sand
ES	2	44.67944641	-111.6886901	2101(6893)	Sand
ES	6	44.69461276	-111.7088441	2169(7116)	Sand
ES	6	44.65939491	-111.6707083	2057(6748)	Sand

Table 2.2: Estimated difference between pre-herbicide (2017) *Bromus tectorum* cover (%) and each year following, within the reference (top) and the sprayed (bottom) communities in the Centennial Valley, MT, USA. There were no differences in the reference community when compared to 2017 abundances. The sprayed community had consistently lower abundances compared to the 2017 abundances. Positive values indicate cover (%) greater than the 2017 mean and negative values indicate cover (%) lower than the 2017 mean. Bold text indicates statistical differences using an alpha level of 0.05. Estimates are rounded up to the nearest whole number.

Reference					
Year	Estimate	SE	df	t	p
2018	1	3.75	1044	0.01	0.995
2019	1	3.75	1044	0.06	0.955
2020	1	3.75	1044	0.02	0.980
2021	-1	19.91	1044	-0.0002	0.999
2022	1	3.75	1044	0.16	0.873
Sprayed					
2018	-7	0.48	1060	-14.97	<0.0001
2019	-9	0.40	1060	-22.50	<0.0001
2020	-8	0.44	1060	-18.32	<0.0001
2021	-9	0.42	1060	-20.14	<0.0001
2022	-4	0.61	1060	-6.83	<0.0001

Table 2.3: The estimated mean *Bromus tectorum* abundance, percent cover, pre-herbicide (2017), post- first application (2018), post- second application (2019), and for each year thereafter in the Centennial Valley, MT, USA. Estimates are rounded up to the nearest whole number.

Treatment	Year	estimate	SE	df	lower CI	upper CI
Pre-herbicide	2017	9	0.39	2107	8.298	9.821
Reference	2017	1	0.01	2107	-13.573	13.594
Reference	2018	1	0.03	2107	-0.021	0.085
Reference	2019	1	0.07	2107	0.052	0.342
Reference	2020	1	0.05	2107	-0.005	0.185
Reference	2021	1	0.01	2107	-89.287	89.298
Reference	2022	1	0.23	2107	0.078	0.961
Sprayed	2018	2	0.20	2107	1.487	2.253
Sprayed	2019	1	0.04	2107	-0.002	0.172
Sprayed	2020	1	0.15	2107	0.703	1.298
Sprayed	2021	1	0.11	2107	0.306	0.741
Sprayed	2022	5	0.52	2107	3.878	5.917

Table 2.4: Estimated difference in *Bromus tectorum* abundance (% cover) between the sprayed and the reference communities for the four years post-herbicide application in the Centennial Valley, MT, USA. Positive values indicate a greater abundance in the sprayed community. The estimated differences between the two communities were statistically significant in 2021 and 2022, but these differences may not represent biologically meaningful differences. Bold text indicates statistically significant differences using an alpha level of 0.05. Estimates are rounded up to the nearest whole number.

Year	Estimate	SE	df	t	p
2019	-1	0.09	1395	-1.35	0.177
2020	1	0.16	1395	6.95	<0.0001
2021	1	0.75	1395	0.72	<0.0001
2022	5	0.57	1395	7.93	<0.0001

Table 2.5: Estimated difference in the probability of *Bromus tectorum* occurrence between the sprayed and the reference communities for all six years of the study in the Centennial Valley, MT, USA. Negative values indicate a greater probability of occurrence in the sprayed community. Despite having small differences in mean abundance between the two communities (Table 2) the sprayed community retained a higher probability of occurrence compared to the reference in all years but 2019. Bold text indicates years in which differences were statistically significant using an alpha level of 0.05.

Year	Diff.	SE	df	t	p
2017	-0.86	0.03	2107	-32.64	<0.0001
2018	-0.56	0.04	2107	-14.47	<0.0001
2019	0.01	0.02	2107	0.26	0.792
2020	-0.25	0.04	2107	-6.96	<0.0001
2021	-0.19	0.03	2107	-6.31	<0.0001
2022	-0.38	0.04	2107	-9.47	<0.0001

Table 2.6: Estimated probability of *Bromus tectorum* occurrence (Prob. Occu.) in the sprayed and reference communities for all years in the Centennial Valley, MT, USA. Despite having small differences in mean abundance between the two communities (Table 2) the sprayed community retained a higher probability of occurrence compared to the reference in all years but 2019.

Treatment	Year	Prob. Occu.	SE
Reference	2017	1%	1%
Reference	2018	2%	1%
Reference	2019	4%	1%
Reference	2020	3%	1%
Reference	2021	1%	1%
Reference	2022	4%	1%
Sprayed	2017	87%	3%
Sprayed	2018	57%	4%
Sprayed	2019	4%	1%
Sprayed	2020	27%	3%
Sprayed	2021	19%	3%
Sprayed	2022	42%	4%

Table 2.7: The total and shared number of species for each community in each year following herbicide application in the Centennial Valley, MT, USA. The first two rows represent the total species richness for each community and year. The additional reference (Ref.) row is the total number of unique and additional species found in the reference (total unique number of reference species minus the number of unique sprayed community species). Note that in all cases the reference community has a greater number of species and that the number of shared species is nearly that of the sprayed, indicating high nestedness of the two communities.

Community	2019	2020	2021	2022
Reference	81	73	80	78
Sprayed	54	65	67	66
Shared	51	57	67	57
Additional				
Ref.	27	8	13	12
% Shared	62%	78%	83%	84%

Table 2.8: The variation (R^2) and statistical significance (p) of each climate variable with the non-metric multidimensional scaling (NMDS) ordination axis used to plot the vegetation community dissimilarity (Bray-Curtis) data in the Centennial Valley, MT, USA. Bold text indicates statistically significant variables at an alpha level of 0.05. Note that the minimum and maximum seasonal temperatures were not plotted in the ordination because of their high correlation with the mean temperature but are reported here for reference.

Climate Variable	R^2	p	Functional Group	R^2	p
Spring Precip.	0.66	0.001	Annual Non-native Forbs	0.05	0.28
Summer Precip.	0.43	0.001	Annual Native Forbs	0.05	0.352
Fall Precip.	0.45	0.001	Annual/Perennial Native Forbs	0.14	0.032
Winter Precip.	0.34	0.001	Perennial Non-native Forbs	0.05	0.347
Spring Min. Temp.	0.23	0.001	Perennial Native Forbs	0.41	0.001
Summer Min. Temp.	0.44	0.001	Annual Non-native Grass	0.28	0.001
Fall Min. Temp.	0.64	0.001	Perennial Native Grass	0.37	0.001
Winter Min. Tem.	0.05	0.339	Native Shrubs	0.10	0.082
Spring Mean Temp.	0.66	0.001	Bare Ground	0.07	0.17
Summer Mean Temp.	0.48	0.001	Litter	0.46	0.001
Fall Mean Temp.	0.49	0.001			
Winter Mean Temp.	0.00	0.91			
Spring Max Temp.	0.50	0.001			
Summer Max Temp.	0.45	0.001			
Fall Max Temp.	0.29	0.002			
Winter Max Temp.	0.33	0.001			

Table 2.9: Mean Bray-Curtis pairwise dissimilarities within the sprayed community for the four years post herbicide treatment, in the Centennial Valley, MT, USA. The range of possible values are from zero to one, with a value of one indicating no shared species between the community assemblages. The diagonal hi-lighted in green indicates the dissimilarity within the sprayed community in the same year. Column one indicates the increasing difference in community composition of the sprayed community over the duration of the study.

Year.Treatment	2019.Sprayed	2020.Sprayed	2021.Sprayed	2022.Sprayed
2019.Sprayed	0.74			
2020.Sprayed	0.77	0.67		
2021.Sprayed	0.86	0.83	0.78	
2022.Sprayed	0.91	0.87	0.90	0.63

Table 2.10: Mean Bray-Curtis pairwise dissimilarities within the reference community over the course of the four years in the Centennial Valley, MT, USA. The range of possible values are from zero to one, with a value of one indicating no shared species between the community assemblages. The diagonal hi-lighted in orange indicates the dissimilarity within the reference community in the same year. Column one indicates the increasing difference in community composition of the reference community over the duration of the study.

Year.Treatment	2019.Reference	2020.Reference	2021.Reference	2022.Reference
2019.Reference	0.72			
2020.Reference	0.71	0.67		
2021.Reference	0.84	0.85	0.81	
2022.Reference	0.90	0.93	0.93	0.67

Table 2.11: Mean Bray-Curtis pairwise dissimilarities between sprayed and reference communities over the four years post treatment, in the Centennial Valley, MT, USA. The range of possible values are from zero to one, with a value of one indicating no shared species between the community assemblages. The blue hi-lighted diagonal indicates the dissimilarity between the two communities within each year.

Year.Treatment	2019.Sprayed	2020.Sprayed	2021.Sprayed	2022.Sprayed
2019.Reference	0.76	0.80	0.88	0.90
2020.Reference	0.80	0.73	0.87	0.92
2021.Reference	0.87	0.88	0.81	0.92
2022.Reference	0.92	0.92	0.93	0.71

Table 2.12: Mean seasonal temperatures for each vegetative year in the Antelope peak (AP) and Eastern Sandhills (ES) areas of the Centennial Valley, MT, USA. Bold text indicates the departure from the 30-year mean (bottom). Positive values indicate above mean temperature and negative values below mean. Data is from PRISM (<https://prism.oregonstate.edu/explorer/>).

Antelope Peak												
	Minimum Temp (C°)				Mean Temperature (C°)				Max Temperature (C°)			
Year	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
2019	-6.7	6.6	-6.1	-13.3	1.0	14.0	1.6	-8.3	7.7	22.6	8.0	-3.4
	-0.8	0.0	-1.7	0.4	-0.6	0.0	-1.9	0.0	-0.4	0.0	-1.9	-0.4
2020	-6.0	6.9	-3.7	-13.7	1.7	14.2	3.9	-8.2	8.6	22.6	11.6	-2.7
	-0.1	0.4	-0.3	0.1	0.1	0.3	0.6	0.1	0.3	0.1	1.6	0.3
2021	-6.0	7.8	-0.7	-12.7	1.8	16.2	6.2	-7.8	8.7	24.6	11.1	-3.0
	-0.1	2.3	2.6	1.0	0.2	2.2	1.9	0.6	0.6	2.1	1.2	0.0
2022	-6.6				0.6				6.7			
	-0.7				-1.1				-1.4			
Eastern Sandhills												
	Minimum Temp (C°)				Mean Temperature (C°)				Max Temperature (C°)			
Year	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
2019	-6.1	6.2	-6.7	-14.0	0.9	13.9	1.2	-8.7	7.9	22.7	8.1	-3.3
	-0.7	0.4	-1.7	0.4	-0.6	0.2	-1.8	0.1	-0.4	0.1	-1.9	-0.3
2020	-6.2	6.7	-4.1	-14.6	1.7	14.2	3.8	-8.6	8.6	22.7	11.7	-2.7
	0.2	0.9	-0.2	-0.1	0.3	0.6	0.7	0.2	0.3	0.1	1.6	0.4
2021	-6.7	7.0	-1.3	-13.6	1.6	15.8	6.0	-8.4	8.8	24.7	11.2	-3.2
	-0.3	2.2	2.6	0.9	0.1	2.1	1.9	0.3	0.6	2.1	1.2	-0.2
2022	-6.1				0.4				6.8			
	0.7				1.1				1.4			
30-year Mean												
	Minimum Temp (C°)				Mean Temperature (C°)				Max Temperature (C°)			
Area	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
AP	-6.0	6.6	-3.3	-13.7	1.6	14.0	3.3	-8.3	8.1	22.6	9.9	-3.0
ES	-6.4	4.8	-3.9	-14.4	1.4	13.7	3.1	-8.7	8.3	22.6	10.0	-3.1

Table 2.13: Mean seasonal precipitation for each vegetative year in the Antelope peak (AP) and Eastern Sandhills (ES) areas of the Centennial Valley, MT, USA. Non-bold text indicates the mean precipitation, bold text indicates the departure from the 30-year mean (bottom). Positive values indicate above mean precipitation and negative values below mean. Data were downloaded from the PRISM climate group (<https://prism.oregonstate.edu/explorer/>).

Antelope Peak				
Precipitation (mm)				
Year	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
2019	37.5	35.8	47.6	68.7
	-18.8	-4.1	6.6	24.4
2020	43.3	42.6	23.3	42.8
	-12.9	2.7	-17.7	-1.4
2021	40.3	28.7	53.4	57.7
	-15.9	-11.2	12.4	13.4
2022	62.4			
	6.2			
Eastern Sandhill				
Precipitation (mm)				
Year	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
2019	41.9	36.0	56.6	67.8
	-16.9	-3.8	12.7	19.7
2020	50.8	44.4	25.4	49.6
	-7.9	4.6	-18.5	1.5
2021	46.2	31.8	58.1	65.5
	-12.6	-8.0	14.3	17.4
2022	70.3			
	11.5			
30-year Mean				
Precipitation (mm)				
Area	<u>Spring</u>	<u>Summer</u>	<u>Fall</u>	<u>Winter</u>
AP	56.3	39.9	41.0	44.3
ES	58.7	39.8	43.9	48.1

Figures

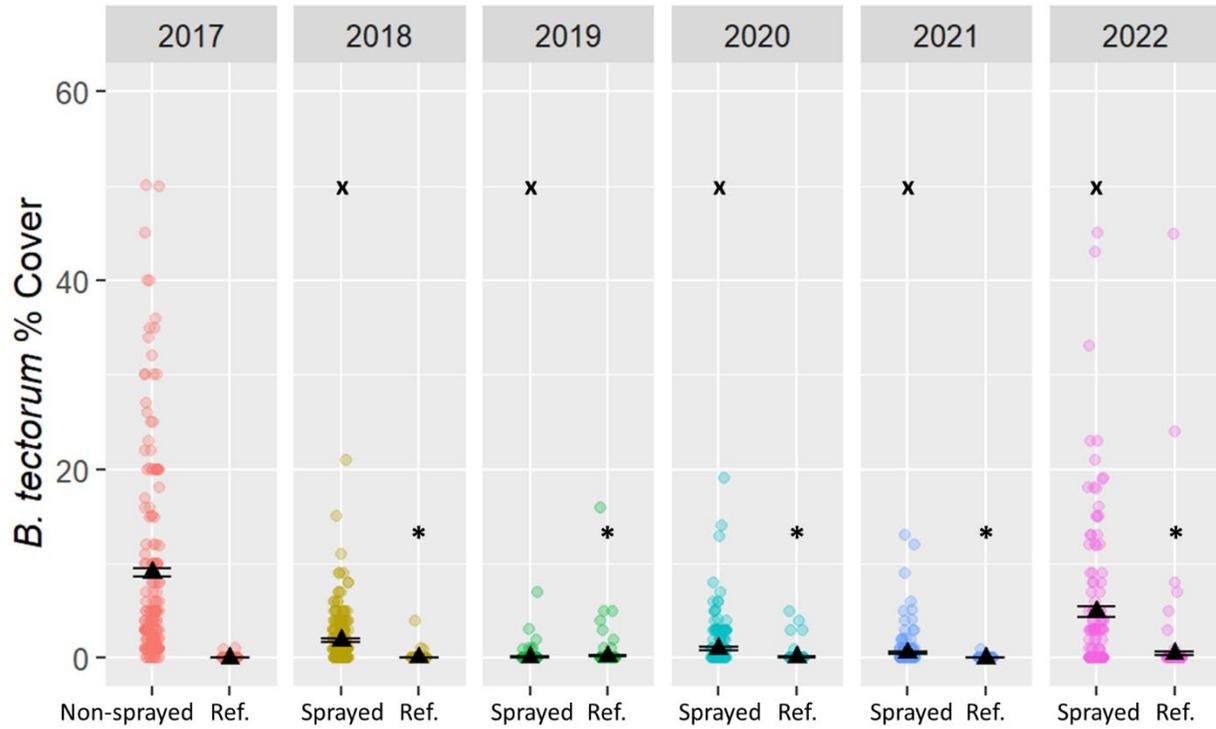


Figure 2.1: *Bromus tectorum* mean cover from the year before (2017) herbicide application (fall 2017-2018) until four years post application in the sprayed and reference communities in the Centennial Valley, MT, USA. Black triangles represent means, error bars are constructed using standard errors and observations are plotted as points. “X”s and “*”s indicate years that were statistically different from 2017 using a Dunnett’s test and alpha level of 0.05, for the sprayed and reference communities, respectively.

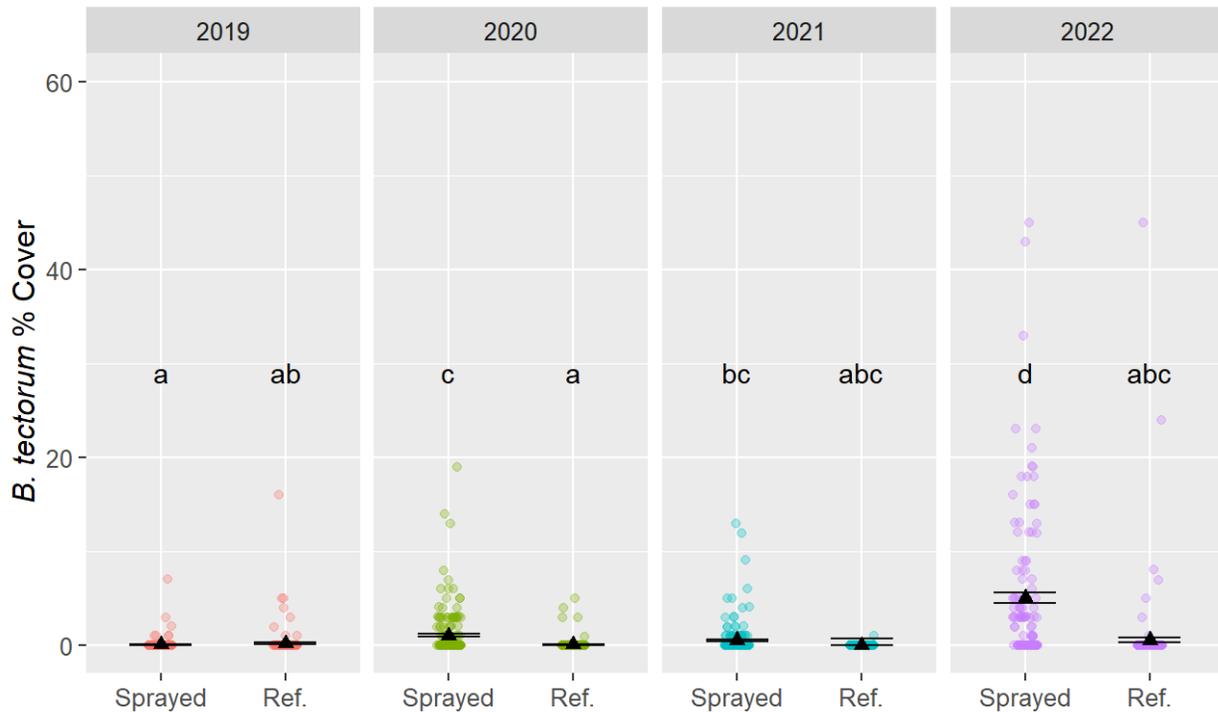


Figure 2.2: *Bromus tectorum* mean cover for the four years post-herbicide application for the sprayed and reference (Ref.) communities in the Centennial Valley, MT, USA. Two fall applications (2017 and 2018) of imazapic reduced *B. tectorum* abundance to nearly that of the reference for three years post application. Note that while groups that share the same letter are considered statistically similar based on an alpha level of 0.05, the differences between the sprayed and reference are minimal for 2019-2021 (Table 2) and are, likely, not biologically meaningful

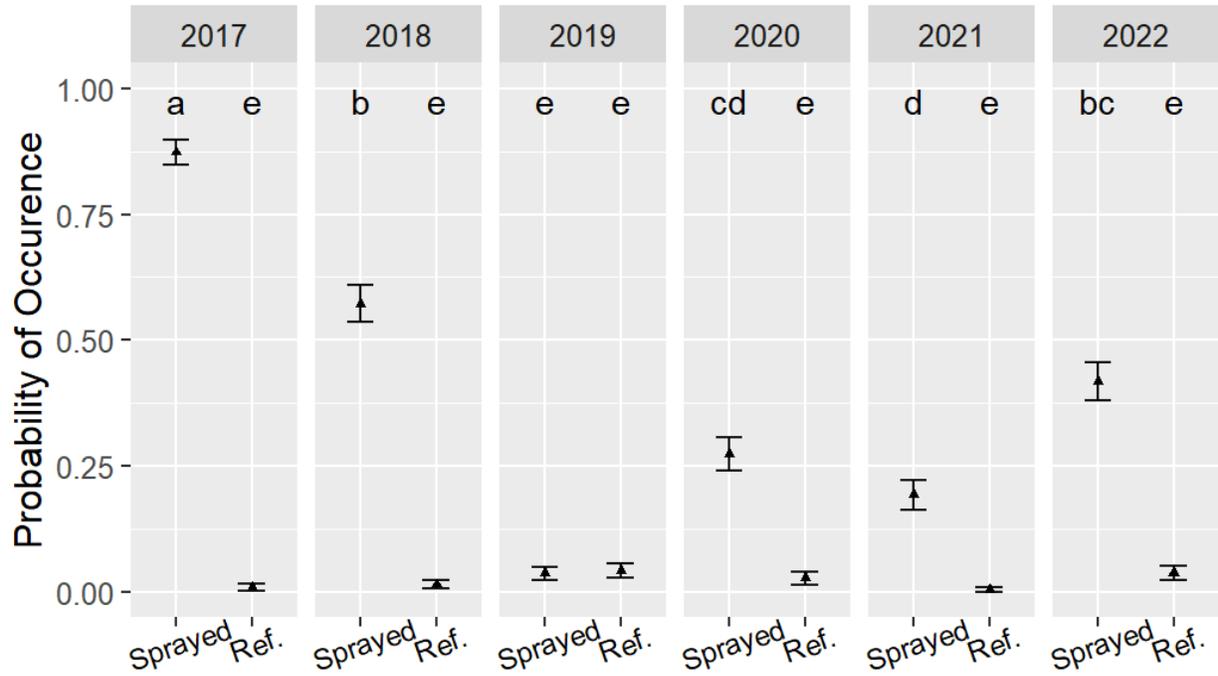


Figure 2.3: Probability of *Bromus tectorum* occurrence for the sprayed and reference (Ref.) communities over the duration of the study. 2019 represents the first year after the second herbicide application. Despite the similarity in abundances between the sprayed and reference communities, there was still a greater probability of *B. tectorum* occurring in the sprayed community. Black triangles are estimated probability of occurrence, error bars are constructed using standard errors. Groups that share the same letter(s) are statistically similar.

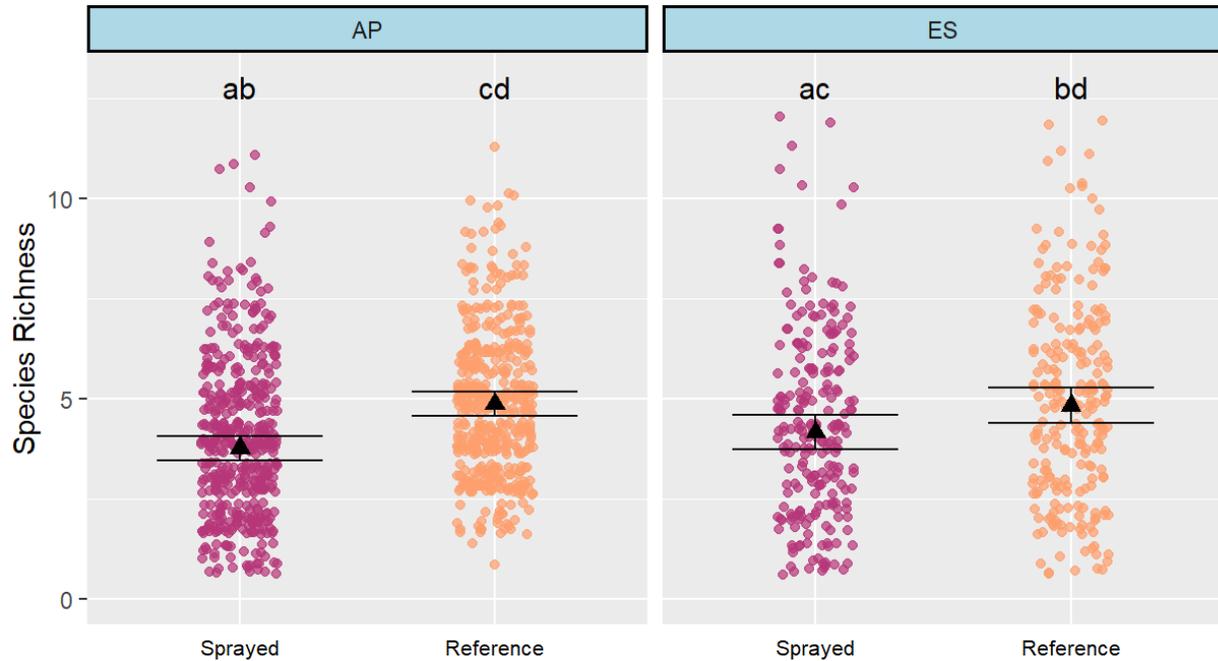


Figure 2.4: Species richness for sprayed and reference communities in the Antelope Peak (AP) and Eastern Sandhill (ES) areas within the Centennial Valley, MT, USA. Sprayed communities in both areas had similar species richness, as did reference communities. Within both areas the reference community always had greater species richness. Groups that share letters are statistically similar given an alpha level of 0.05. Black triangles represent means, error bars are constructed using standard errors and observations are plotted as jittered points. *Bromus tectorum* was omitted from this analysis.

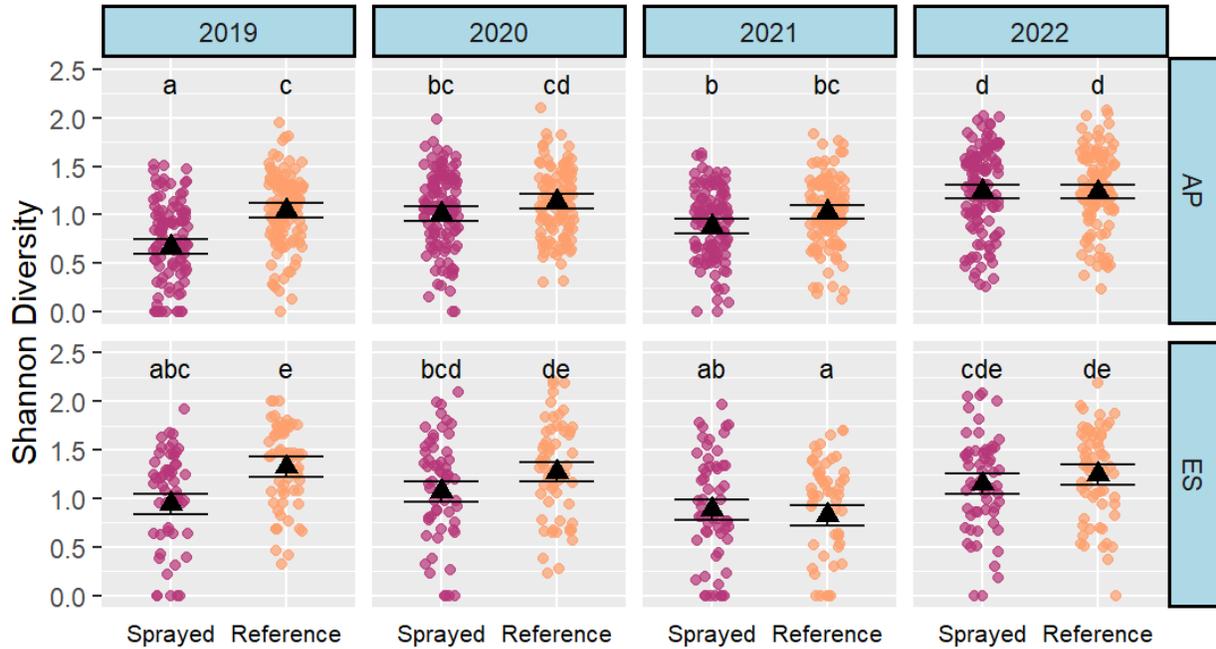


Figure 2.5: Landscape scale plant diversity for the Antelope Peak (AP) and Eastern Sandhill (ES) areas over the four years post-herbicide application within the Centennial Valley, MT, USA. This figure displays statistical differences between treatments and across years within each area, i.e., there were no area differences. Groups sharing the same letters within each area are statistically similar given an alpha level of 0.05. Black triangles represent means, error bars are constructed using standard errors and observations are plotted as jittered points.

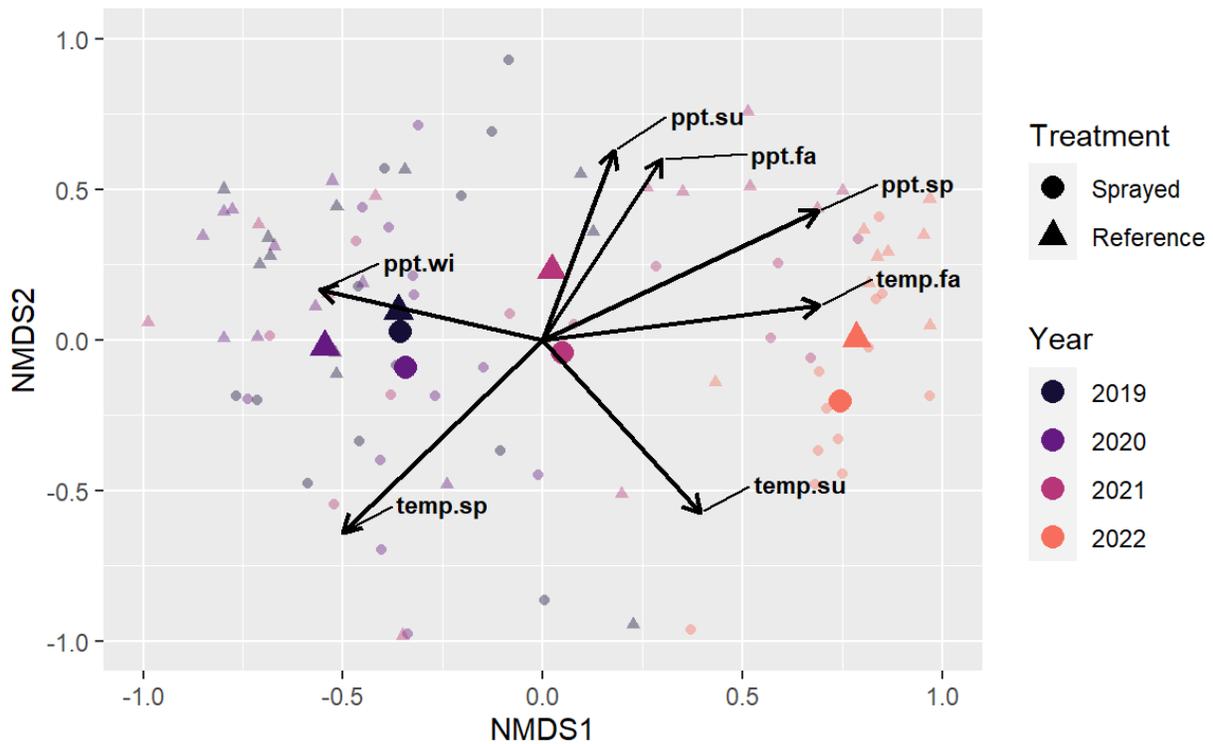


Figure 2.6: Bray-Curtis beta dissimilarities plotted using non-metric multi-dimensional scale (NMDS) ordination for the sprayed and reference communities over the four years post-herbicide application in the Centennial Valley, MT, USA. There is a small amount of dissimilarity between the sprayed (large circles) and the reference (large triangles) communities within each year and over the four years of the study. There is overlap between the sprayed site centroids (small circles) and the reference site centroids (small triangles) within each year, representing similar amounts of variation. Mean precipitation (ppt) and temperature (temp) are plotted as vectors and their lengths are proportional to their strength of relation with the community data. Seasonality is represented as spring (sp), summer (su), winter (wi), and fall (fa).

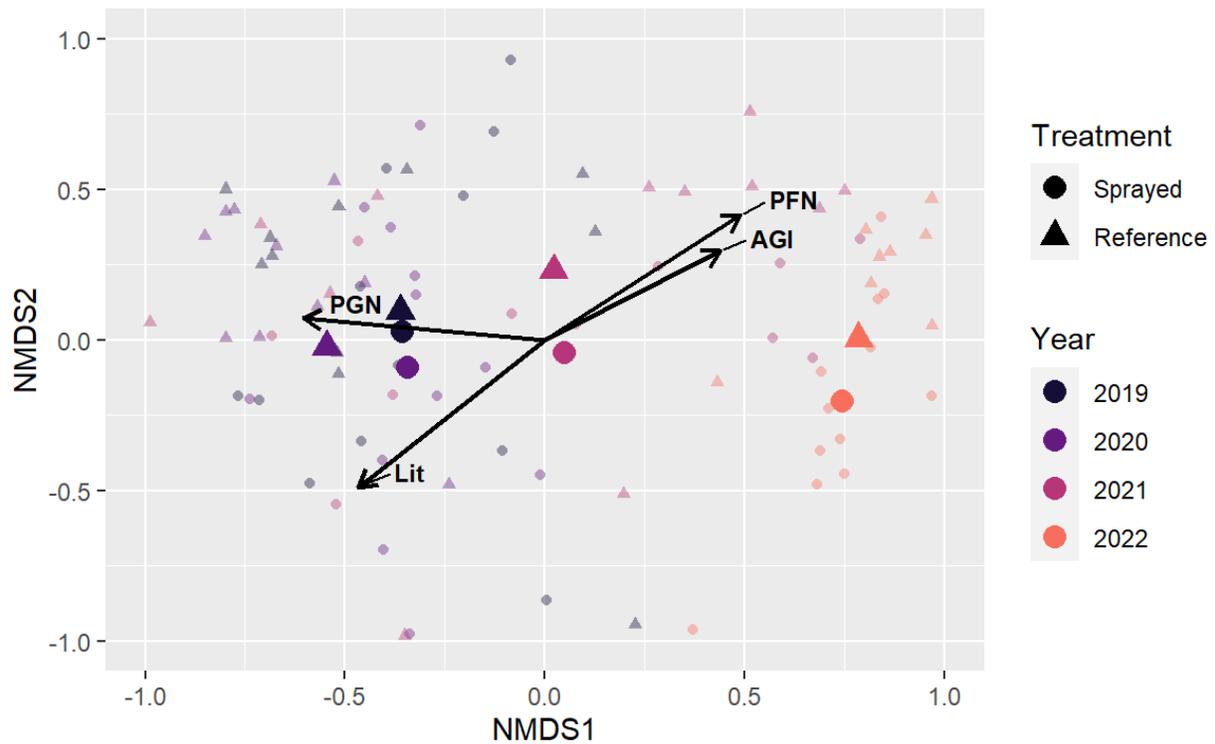


Figure 2.7: Bray-Curtis beta dissimilarities plotted using non-metric multi-dimensional scale (NMDS) ordination for the sprayed and reference communities over the four years post-herbicide application in the Centennial Valley, MT, USA. There is a small amount of dissimilarity between the sprayed (large circles) and the reference (large triangles) communities within each year and over the four years of the study. There is overlap between the sprayed site centroids (small circles) and the reference site centroids (small triangles) within each year, representing similar amounts of variation. Mean cover for the native perennial grasses (PGN), native perennial forbs (PFN), non-native annual grasses (AGI), and litter (Lit) groups are plotted as vectors with their relative lengths proportional to their strength of association with the ordination.

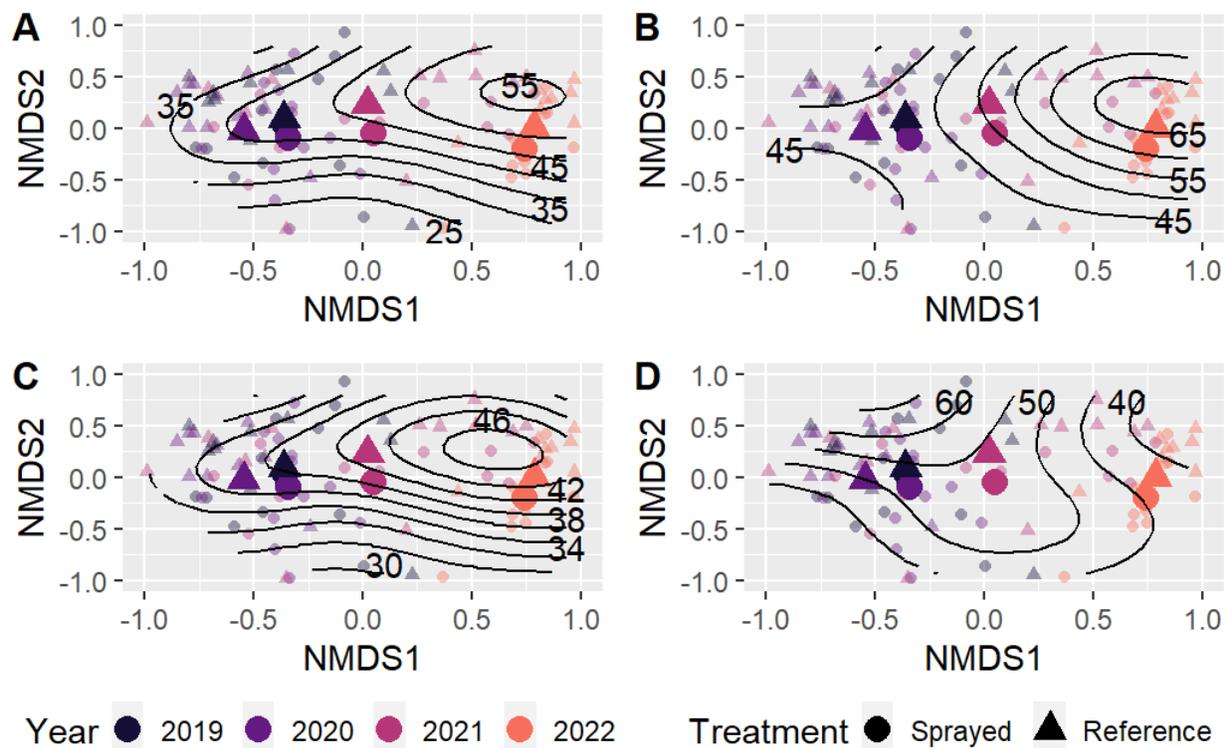


Figure 2.8: The mean fall (A), spring (B), summer (C), and winter (D) precipitation (mm) plotted as gradients across the non-metric multi-dimensional scaling (NMDS) ordination. Note the fall precipitation is the year prior as that is considered part of the growing season. The ordination displays the observed dissimilarity over time of sprayed (circles) and reference (triangles) communities in the Centennial Valley, MT, USA. The years are represented by the colors black (2019), dark purple (2020), light purple (2021), and orange (2022).

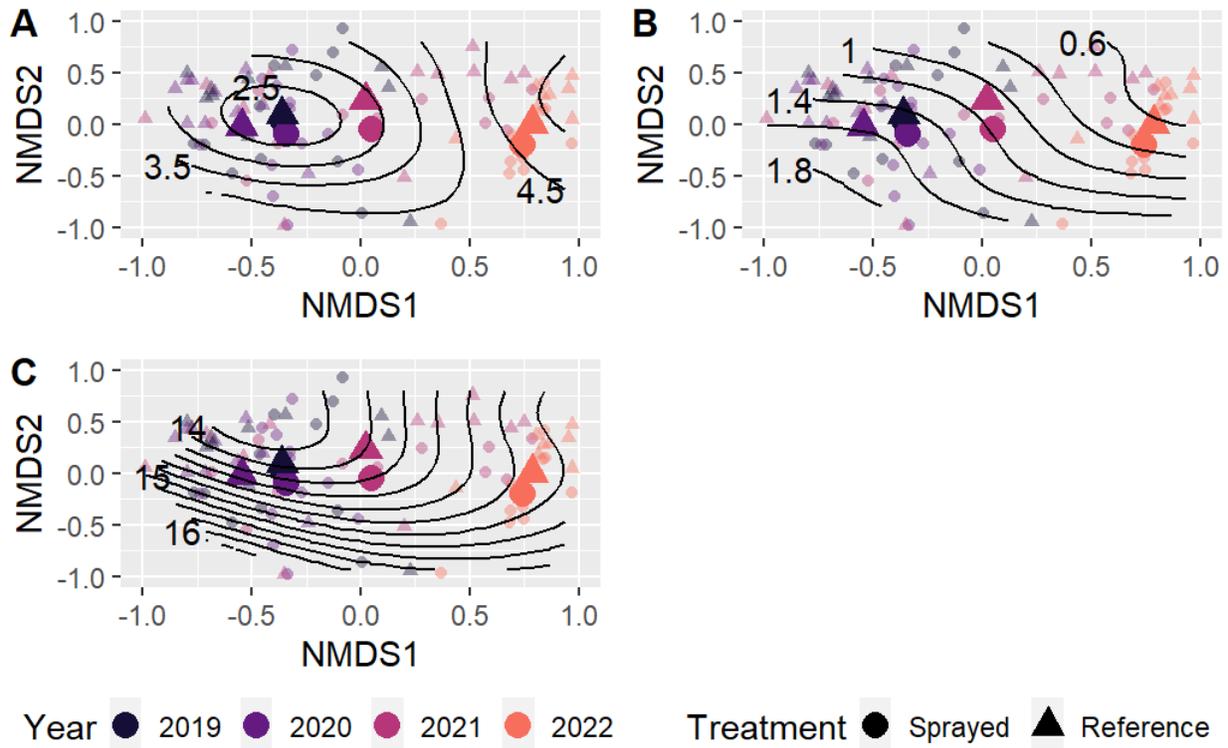


Figure 2.9: The mean temperatures (°C) for the seasons, fall (A), spring (B), and summer (C), plotted as gradients across the non-metric multi-dimensional scaling (NMDS) ordination. The ordination displays the observed dissimilarity over time of sprayed (circles) and reference (triangles) communities in the Centennial Valley, MT, USA. The years are represented by the colors black (2019), dark purple (2020), light purple (2021), and orange (2022).

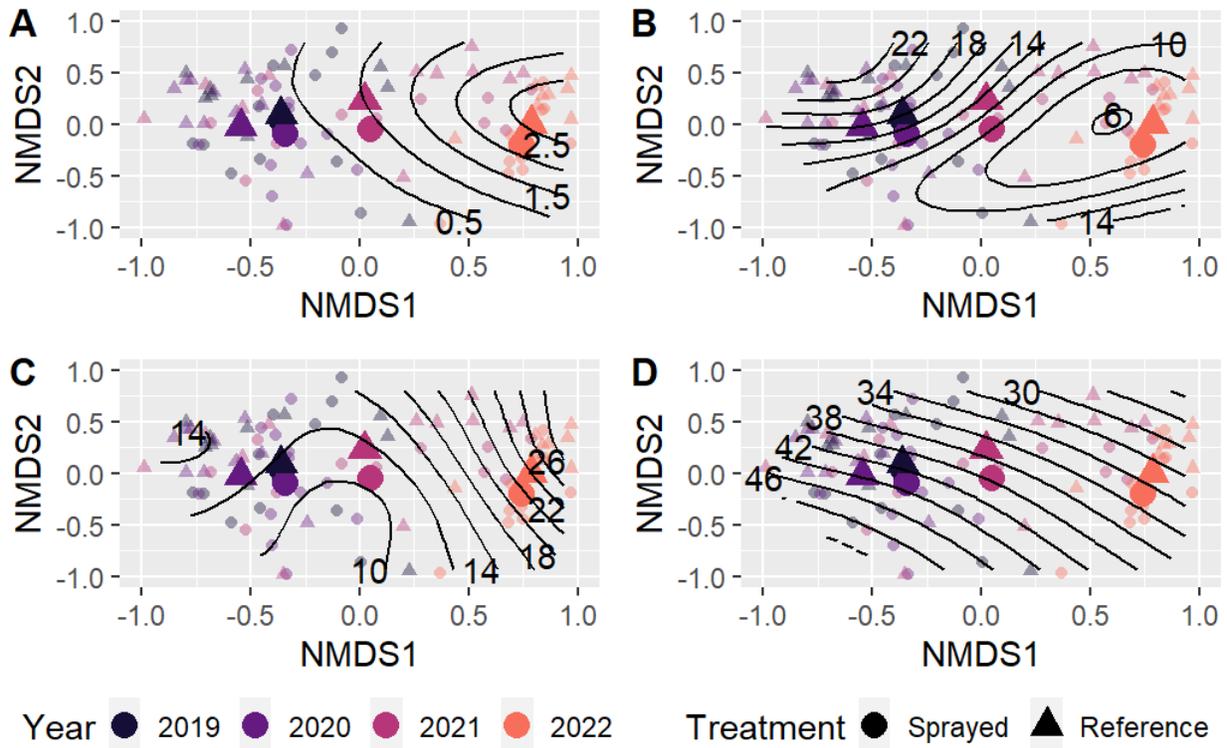


Figure 2.10: The non-native annual grass (A), native perennial grass (B), native perennial forb (C) and litter (D) cover (%) groups plotted as gradients across the non-metric multi-dimensional scaling (NMDS) ordination. The ordination displays the observed dissimilarity over time of sprayed (circles) and reference (triangles) communities in the Centennial Valley, MT, USA. The years are represented by the colors black (2019), dark purple (2020), light purple (2021), and orange (2022).

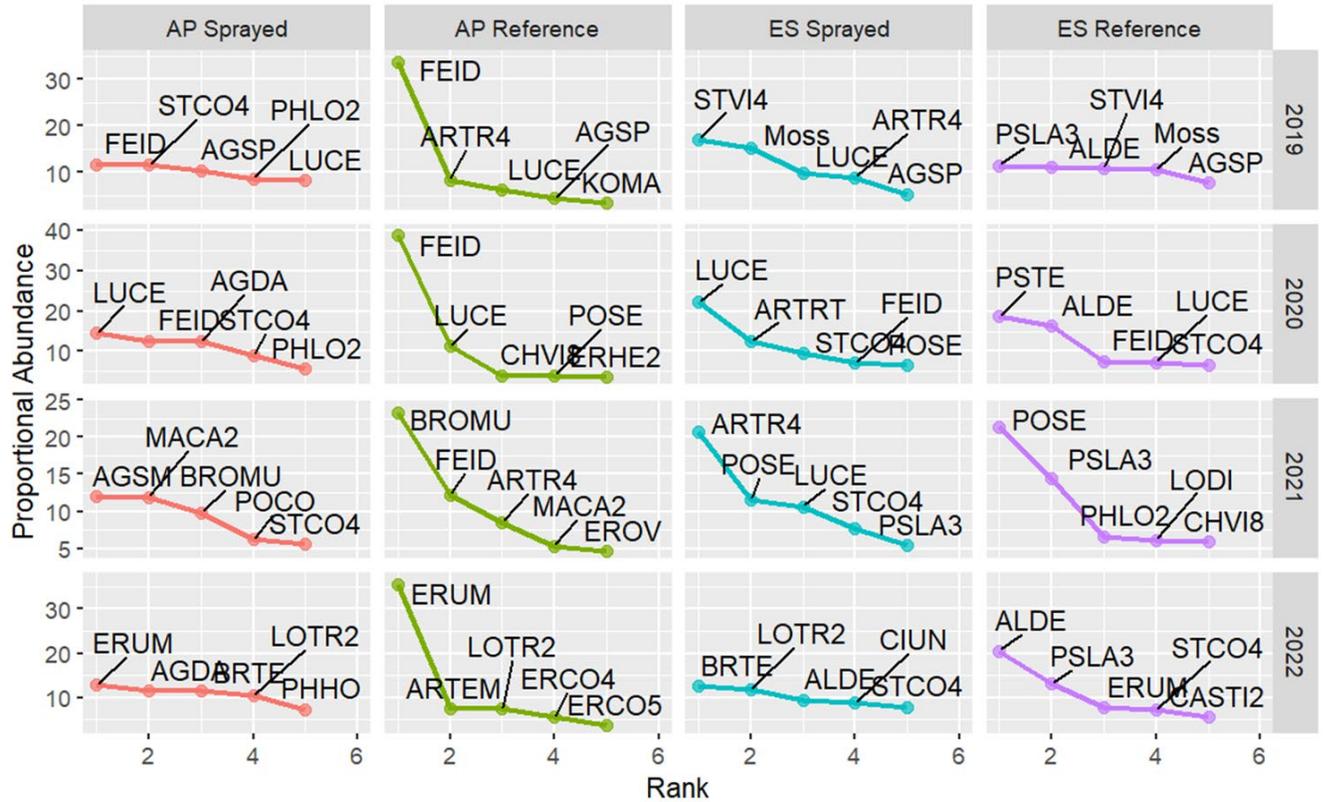


Figure 2.11: Landscape scale proportional abundance of the top five ranked species in each area, Antelope Peak (AP) and Eastern Sandhills (ES), and treatment over the four years following herbicide application. The top five species were chosen because that was the mean number of species observed in a frame. Species are listed by their four letter USDA plant codes as follows: *Agropyron spicatum* (AGSP), *Agropyron dasystachium* (AGDA), *Agropyron smithii* (AGSM), *Artemisia tripartita* (ARTR4), *Artemisia* spp. (ARTEM), *Artemisia tridentata* ssp. *tridentata* (ARTRT), *Alyssum desertorum* (ALDE), *Bromus riparius* (BROMU), *Bromus tectorum* (BRTE), *Chrysothamnus viscidiflorus* (CHVI8), *Cirisum undulatum* (CIUN), *Castilleja* sp. (CASTI2), *Eriogonum umbellatum* (ERUM), *Erigeron compositus* (ERCO4), *Erigeron corymbosus* (ERCO5), *Eriogonum ovalifolium* (EROV), *Festuca idahoensis* (FEID), *Koeleria macrantha* (KOMA), *Lupinus wyethi* (LUCE), *Lomatium triternatum* (LOTR2), *Lomatium dissectum* (LODI), *Machaeranthera canescens* (MACA2), *Phlox longifolia* (PHLO2), *Poa compressa* (POCO), *Phlox hoodii* (PHHO), *Poa secunda* (POSE), *Psoralidium lanceolatum* (PSLA3), *Psilocarphus tenellus* (PSTE), *Stipa comata* (STCO4), and *Stipa viridula* (STVI4).

Literature Cited

- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological monographs* 71:531-556.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global change biology* 19:173-183.
- Blank, R. R., and T. Morgan. 2013. Soil engineering facilitates downy brome (*Bromus tectorum*) growth—a case study. *Invasive Plant Science and Management* 6:391-400.
- Blank, R. R., and T. Morgan. 2016. Plant interactions with soils conditioned by different vegetation: A potential explanation of *Bromus tectorum* L. invasion into salt-deserts? *Journal of Arid Environments* 124:233-238.
- Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016. *Bromus* response to climate and projected changes with climate change. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications:257-274.
- Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M.-N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions* 20:1493-1506.
- Bray, J. R., and J. T. Curtis. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological monographs* 27:326-349.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677-688.
- Brummer, T. J., K. T. Taylor, J. Rotella, B. D. Maxwell, L. J. Rew, and M. Lavin. 2016. Drivers of *Bromus tectorum* Abundance in the Western North American Sagebrush Steppe. *Ecosystems* 19:986-1000.
- Chambers, J. C. 2016. Using resilience and resistance concepts to manage threats to sagebrush ecosystems, Gunnison sage-grouse, and greater sage-grouse in their eastern range: a strategic multi-scale approach.

- Chambers, J. C., C. R. Allen, and S. A. Cushman. 2019. Operationalizing ecological resilience concepts for managing species and ecosystems at risk. *Frontiers in Ecology and Evolution* 7:241.
- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014a. Resilience to Stress and Disturbance, and Resistance to *Bromus tectorum* L. Invasion in Cold Desert Shrublands of Western North America. *Ecosystems* 17:360-375.
- Chambers, J. C., J. L. Brown, J. B. Bradford, D. I. Board, S. B. Campbell, K. J. Clause, B. Hanberry, D. R. Schlaepfer, and A. K. Urza. 2023. New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, United States. *Frontiers in Ecology and Evolution* 10:1009268.
- Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. S. Clair. 2016. Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications:275-304.
- Chambers, J. C., D. A. Pyke, J. D. Maestas, M. Pellant, C. S. Boyd, S. B. Campbell, S. Espinosa, D. W. Havlina, K. E. Mayer, and A. Wuenschel. 2014b. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. United States Department of Agriculture, Forest Service, Rocky Mountain .
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological monographs* 77:117-145.
- CPNWH. 2017. Consortium of Pacific Northwest Herbaria Specimen Database.
- Culver, D. R. 1994. Floristic analysis of the Centennial Region, Montana. Montana State University-Bozeman, College of Letters & Science.
- D'Antonio, C. M., and M. Thomsen. 2004. Ecological Resistance in Theory and Practice1. *Weed Technology* 18:1572-1577.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics* 23:63-87.
- D Antonio, C., J. Levine, and M. Thomsen. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology* 2:233-246.

- Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43-64.
- Davies, K. W. 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia* 167:481-491.
- Davies, K. W., and D. D. Johnson. 2017. Established Perennial Vegetation Provides High Resistance to Reinvansion by Exotic Annual Grasses. *Rangeland Ecology & Management* 70:748-754.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528-534.
- Doherty, K., D. M. Theobald, J. B. Bradford, L. A. Wiechman, G. Bedrosian, C. S. Boyd, M. Cahill, P. S. Coates, M. K. Creutzburg, M. R. Crist, S. P. Finn, A. V. Kumar, C. E. Littlefield, J. D. Maestas, K. L. Prentice, B. G. Prochazka, T. E. Remington, W. D. Sparklin, J. C. Tull, Z. Wurtzebach, and K. A. Zeller. 2022. A sagebrush conservation design to proactively restore America's sagebrush biome. Report 2022-1081, Reston, VA.
- Eisenhauer, N., H. BEßLER, C. Engels, G. Gleixner, M. Habekost, A. Milcu, S. Partsch, A. C. Sabais, C. Scherber, and S. Steinbeiss. 2010. Plant diversity effects on soil microorganisms support the singular hypothesis. *Ecology* 91:485-496.
- Elseroad, A. C., and N. T. Rudd. 2011. Can Imazapic Increase Native Species Abundance in Cheatgrass (*Bromus tectorum*) Invaded Native Plant Communities? *Rangeland Ecology & Management* 64:641-648.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57-68.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics* 35:557-581.
- Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus *Bromus*. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications:61-95.
- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323-334.
- Hadley, W. 2016. *Elegant Graphics for Data Analysis*. Springer-Verlag New York.

- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003. Energy, Water, and Broad-scale Geographic Patterns of Species Richness. *Ecology* 84:3105-3117.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual review of ecology and systematics* 4:1-23.
- Holling, C. S. 1996. Engineering resilience versus ecological resilience. *Engineering within ecological constraints* 31:32.
- Homer, C. G., G. Xian, C. L. Aldridge, D. K. Meyer, T. R. Loveland, and M. S. O'Donnell. 2015. Forecasting sagebrush ecosystem components and greater sage-grouse habitat for 2050: Learning from past climate patterns and Landsat imagery to predict the future. *Ecological Indicators* 55:131-145.
- Keeley, J. E., C. J. Fotheringham, and M. Baer-Keeley. 2005. Determinants of Postfire Recovery and Succession in Mediterranean-climate Shrublands of California. *Ecological Applications* 15:1515-1534.
- Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies.
- Kuehn, C. 2011. A mathematical framework for critical transitions: Bifurcations, fast-slow systems and stochastic dynamics. *Physica D: Nonlinear Phenomena* 240:1020-1035.
- Kulmatiski, A., and K. H. Beard. 2011. Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure. *Soil Biology and Biochemistry* 43:823-830.
- Larson, C. D., E. A. Lehnhoff, C. Noffsinger, and L. J. Rew. 2018. Competition between cheatgrass and bluebunch wheatgrass is altered by temperature, resource availability, and atmospheric CO₂ concentration. *Oecologia* 186:855-868.
- Larson, C. D., E. A. Lehnhoff, and L. J. Rew. 2017. A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. *Oecologia* 185:763-774.
- Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern Idaho, U.S.A. *Ecology and Evolution* 3:1626-1641.
- Lenth, R. 2022. `_emmeans: Estimated Marginal Means, aka Least-Squares Means_`.

- Levine, J. M., and C. M. D'Antonio. 1999. Elton Revisited: A Review of Evidence Linking Diversity and Invasibility. *Oikos* 87:15-26.
- Levine, N. M., K. Zhang, M. Longo, A. Baccini, O. L. Phillips, S. L. Lewis, E. Alvarez-Dávila, A. C. Segalin de Andrade, R. J. W. Brienen, T. L. Erwin, T. R. Feldpausch, A. L. Monteagudo Mendoza, P. Nuñez Vargas, A. Prieto, J. E. Silva-Espejo, Y. Malhi, and P. R. Moorcroft. 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proceedings of the National Academy of Sciences* 113:793-797.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42-55.
- Maestas, J. D., S. B. Campbell, J. C. Chambers, M. Pellant, and R. F. Miller. 2016. Tapping Soil Survey Information for Rapid Assessment of Sagebrush Ecosystem Resilience and Resistance. *Rangelands* 38:120-128.
- May, R. M. 2019. *Stability and complexity in model ecosystems*. Princeton university press.
- Moerman, D. E. 1998. *Native american ethnobotany*. Timber press.
- NOAA National Centers for Environmental Information. 2023. *Climate at a Glance: Statewide Time Series*.
- O'Connor, J. J., and J. S. Prevey. 2015. Effects of short-term soil conditioning by cheatgrass and western wheatgrass.
- Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlenn, M. Ouellette, C. E. Ribeiro, S. A. Smith T, B. C. Ter, and J. Weedon. 2022. *_vegan: Community Ecology Package_*.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Pielou, E. C. 1974. *Population and community ecology: principles and methods*. CRC Press.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7:8126-8151.
- Pinheiro, J., D. Bates, and R Core Team. 2022. *_nlme: Linear and Nonlinear Mixed Effects Models_*.

- Pyke, D. A., S. E. Shaff, A. I. Lindgren, E. W. Schupp, P. S. Doescher, J. C. Chambers, J. S. Burnham, and M. M. Huso. 2014. Region-Wide Ecological Responses of Arid Wyoming Big Sagebrush Communities to Fuel Treatments. *Rangeland Ecology & Management* 67:455-467.
- Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-Holme, D. Nogues-Bravo, R. J. Whittaker, and J. Fjelds . 2019. Humboldt’s enigma: What causes global patterns of mountain biodiversity? *Science* 365:1108-1113.
- Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* 50:1039-1049.
- Remington, T. E., P. A. Deibert, S. E. Hanser, D. M. Davis, L. A. Robb, and J. L. Welty. 2021. Sagebrush conservation strategy—Challenges to sagebrush conservation. Report 2020-1125, Reston, VA.
- Rice, P. M. 2003. Invaders database system. University of Montana, Missoula, MT.
- Rinella, M. J., J. M. Mangold, E. K. Espeland, R. L. Sheley, and J. S. Jacobs. 2012. Long-term population dynamics of seeded plants in invaded grasslands. *Ecological Applications* 22:1320-1329.
- Roberts, D. W. 2020. Comparison of distance-based and model-based ordinations. *Ecology* 101:e02908.
- Roundy, B. A., J. C. Chambers, D. A. Pyke, R. F. Miller, R. J. Tausch, E. W. Schupp, B. Rau, and T. Gruell. 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. *Ecosphere* 9:e02417.
- Scheffer, M., S. R. Carpenter, T. M. Lenton, J. Bascompte, W. Brock, V. Dakos, J. van de Koppel, I. A. van de Leemput, S. A. Levin, E. H. van Nes, M. Pascual, and J. Vandermeer. 2012. Anticipating Critical Transitions. *Science* 338:344-348.
- Searchinger, T., C. Hanson, J. Ranganathan, B. Lipinski, R. Waite, R. Winterbottom, A. Dinshaw, R. Heimlich, M. Boval, and P. Chemineau. 2014. Creating a sustainable food future. A menu of solutions to sustainably feed more than 9 billion people by 2050. World resources report 2013-14: interim findings. Creating a sustainable food future. A menu of solutions to sustainably feed more than 9 billion people by 2050. World resources report 2013-14: interim findings, World Resources Institute (2014).
- Seefeldt, S. S., and S. D. McCoy. 2003. Measuring plant diversity in the tall threetip sagebrush steppe: influence of previous grazing management practices. *Environmental Management* 32:234-245.

- Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, M. O. Jones, A. R. Kleinhesselink, J. D. Maestas, S. L. Morford, and D. E. Naugle. 2022. The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA. *Diversity and Distributions* 28:83-96.
- Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* Response to Fire Varies with Climate Conditions. *Ecosystems* 17:960-973.
- Vermeire, L. T., and M. J. Rinella. 2020. Fall Water Effects on Growing Season Soil Water Content and Plant Productivity. *Rangeland Ecology & Management* 73:252-258.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic Management for Rangelands Not at Equilibrium. *Journal of Range Management* 42:266-274.
- Whitlock, C., W. F. Cross, B. D. Maxwell, N. Silverman, and A. A. Wade. 2017. 2017 Montana Climate Assessment: Stakeholder driven, science informed. Montana Institute on Ecosystems.
- Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression Models for Count Data in R. *Journal of Statistical Software* 27(8).
- Zuur, A. F., and E. N. Ieno. 2016. *Beginner's guide to zero-inflated models with R*. Highland Statistics Limited United Kingdom.

CHAPTER FOUR

BROMUS TECTORUM RESTORATION: THE INTERACTION BETWEEN GRAZING,
HERBICIDE, AND SEEDINGIntroduction

One of the great challenges for land managers is the assessment of risk posed by non-native plant introductions in their early stages (Hobbs and Huenneke 1992, Radosевич et al. 2007). *Bromus tectorum* L. (cheatgrass), a non-native winter annual grass, has effectively demonstrated its potential to shape ecosystems across North America (Mack 1981, Mack and Pyke 1983, Weber 2015, Monaco et al. 2017, Maxwell and Germino 2022). The primary mechanism by which *B. tectorum* promotes ecosystem level change is by its reduction of fire return intervals, which result in the transition of shrublands to grasslands dominated primarily by non-native annual grasses (Knapp 1996, Brooks et al. 2004, Balch et al. 2013, Germino et al. 2016, Pilliod et al. 2017, Bradley et al. 2018). Conversion from shrubland to grassland can result in a loss of floral diversity and habitat structure (Germino et al. 2016) which have rippling effects; insect communities are compositionally changed as a result (Rohde et al. 2019) but habitat loss is most impactful for sagebrush obligate species such as the Brewer's Sparrow (*Spizella breweri*) (Earnst and Holmes 2012), a native song bird, and the Greater Sage-Grouse (*Centrocercus urophasianus*) (Schroeder et al. 2004). Further, changes in plant community composition that disfavor native perennial grasses of high-forage quality have direct effects on cattle and native ungulates that rely on these grasses for sustenance. This evidence has left little

wonder in the minds of most land managers, across North America, that the presence of *B. tectorum* warrants management action.

The Middle Rockies ecoregion is the epitome of high-elevation sagebrush steppe; the most resilient and resistant sagebrush ecotype to *B. tectorum* invasion due to its relatively cooler and wetter climate than the other sagebrush ecoregions (e.g. Cold Deserts of the North and Central Basin and Range) (Chambers et al. 2007b, Chambers et al. 2014a, Chambers et al. 2016, Chambers et al. 2023). Importantly, the Middle Rockies have not historically supported the non-native annual grass positive-fire feedback cycle observed in other ecoregions (Lavin et al. 2013, Taylor et al. 2014, Brummer et al. 2016, Larson et al. 2017). Furthermore, relative to other ecoregions, *B. tectorum* populations in the Middle Rockies are moderate in size and warrant management now to mitigate ecosystem level alterations (Rowland et al. 2010, Sheley and Smith 2012, Meador et al. 2013, Chambers et al. 2023). Early detection and control is a critical first step for an effective non-native management strategy and follows the theory that non-native plant management should focus on protecting areas of high-value and high potential for invasion (Hobbs and Humphries 1995, Radosевич et al. 2007). However, a long-term strategy calls for an integrated approach, which includes not only reduction of the target species (population spread) but also a revegetation (ecosystem characteristic) component and re-evaluation of land use practices (human activities) (Hobbs and Humphries 1995).

Imazapic, a common herbicide used to control *B. tectorum*, provides effective annual grass control but the duration of control varies, often not exceeding three years (Kyser et al. 2007, Elseroad and Rudd 2011, Owen et al. 2011, Mangold et al. 2013, Pyke et al. 2022, Wood and Meador 2022). Prior research, from the Central Basin and Range ecoregions, suggests that

restoration seeding following herbicide treatment by imazapic has a strong potential for success compared to seeding alone or herbicide application alone, if favorable precipitation follows seeding (Kyser et al. 2013). Restoration seeding can be further enhanced by the correct selection of species that exhibit traits tolerant of the restoration site conditions and seeding methodology, i.e., broadcast vs. drill (Clements et al. 2022).

In this study we assessed the success of an integrated weed management strategy with the goal of reducing *B. tectorum* and restoring native plant communities in a high disturbance environment within the Middle Rockies ecoregion. The study addressed the four components of Hobbs and Humphries (1995) non-native plant invasion framework: invasive plant characteristics, propagule pressure, ecosystem characteristics (revegetation), and human activities (management, recreation, grazing practices) by: 1) assessing the efficacy of the herbicide imazapic to control *B. tectorum*; 2) developing a disturbance tolerant restoration seed mix and testing its performance against a native perennial grass mix in the greenhouse and in the field; 3) testing the interactive effect of grazing with herbicide and restoration seeding; and 4) assessing the impacts of herbicide, grazing, and restoration seeding on plant available soil nutrients. We performed this study in the cooler and wetter northeastern ecoregion of the sagebrush biome, referred to as the Middle Rockies.

Methods

Experimental Design

Three greenhouse experiments were conducted to assess the competitive ability of two grass seed mixes (native and ruderal) with *B. tectorum*. The native seed mix contained three bunch grasses: *Agropyron spicatum* Pursh. (bluebunch wheatgrass), *Koeleria macrantha*

(Ledeb.) Shult. (prairie junegrass), and *Stipa viridula* Trin. (green needlegrass). The ruderal mix included two rhizomatous species: *Agropyron intermedium* (Host.) P. Beauv. (intermediate wheatgrass) and *Agropyron dasystachium* (Cribn. & J.G. Sm.) Gould (thickspike wheatgrass), and the sterile *xTriticosecale* Wittm. Ex A. Camus [Secale x Triticum] (triticale) (Triticale). *xTriticale* is a second-generation sterile hybrid between wheat (*Triticum*) and rye (*Secale*), hereafter *Triticosecale*.

Each seed mix was subjected to three competition experiments: experiment 1) each species grown alone (intra-specific) to analyze individual species biomass production (6 species*4 replications, 2 trials, n=56); experiment 2) each species of the same mixture grown together (inter-specific, with species sown in equal ratios) to assess competition within the mix and total mix biomass production (2 mixes, 4 replications, 2 trials, n=16); and experiment 3) each seed mixture grown with *B. tectorum* at three densities, high (18:6), equal (12:12), and low (6:18) to assess the competitive ability of each mix with *B. tectorum* at different densities (2 mixes, 3 densities, 4 replications, 2 trials, n=48). For example, 18 *B. tectorum*, 2 *A. spicatum*, 2 *S. viridula*, and 2 *K. macrantha* were sown in the high *B. tectorum* density treatment. Plants were grown at a density of 24 plants per pot (19 cm diameter) for each experiment, and all trials. The greenhouse temperature range of ~22°C [16-27°C] during the day and ~18°C [10-24°C] at night, and 16:8 hour light:dark photoperiod. Each experiment was conducted for 30 days in the Montana State University, Plant Growth Center (Bozeman, MT, USA) after which above ground biomass was cut at soil level, air dried for 72 hours at 49° C, and weighed. Above ground biomass was used to quantify the competitive effects of all experiments.

Plants were grown in a 50:50 (by volume) mix of sunshine mix #1 and Montana State University (MSU) Mix, from the MSU Plant Growth Center, for all experiments. The sunshine mix #1 is a soil-less mix of Canadian Sphagnum peat moss and Perlite, buffered with dolomitic lime, and containing a starter fertilizer and wetting agent. The pH was 5.8. The MSU Mix is a mix of mineral soil, Canadian Sphagnum peat moss, and washed concrete sand that is blended at a 1:1:1 by volume ratio. This soil contains Aqua-Gro 2000G as a wetting agent to increase soil moisture retention, at the rate of one pound per meter, to increase soil moisture retention, and is steam pasteurized. The 50:50 mix had pH of 7.4, closely matching our field soils (pH 7.3, Table 4.1). Plants were watered every two days to ensure adequate soil moisture.

Response of *Bromus tectorum*, plant community, and soil nutrients to grazing, herbicide, and seed mix experimental design

The effect of herbicide (imazapic/Plateau®), grazing, and seed mixes on *B. tectorum* abundance, plant community diversity, and plant available soil nutrients was assessed at four high-use livestock water tanks in the Centennial Valley, MT, USA (44.680750, -111.790583). Sites were selected based on similarity of disturbance determined by the amount of bare ground, abundance of *B. tectorum* and site characteristics (elevation, aspect, proximity to one another, etc.).

The field experiment consisted of a split-split block design (grazing/herbicide/seeding) at each site. The blocking treatment was grazing (grazed/non-grazed, 40.5m²/treatment), the first split within each grazing block was herbicide treatment (sprayed/non-sprayed) and the second split was seeding (native, ruderal, no seeding). This was replicated three times (2-grazing X 2-herbicide X 3-seeding X 3-replications (n=36) at four sites (n=144). Cattle were present each fall

from late August to mid-September 2021 and 2022, as allowed by grazing permit. A pre-emergent application of the herbicide, imazapic (0.17kg/ha/ai) occurred in October of 2020 using a backpack sprayer and a carrier rate of 201L/ha. For the seeding treatment, seed was broadcast at a rate of 20.17kg/ha of each seed mix (native, ruderal, or no seed) in October 2020 after herbicide application. Each species was represented equally within each mix. Vegetation was sampled in early July in both year one (2021) and two (2022), using three 1m² frames within each treatment plot. Ocular cover estimates were recorded for each species, bare ground, rock, and litter. Total cover was allowed to exceed 100% for a single frame to allow for overlapping species cover.

Field soils were classified as predominately sand (91%, 5%, 4%; sand, silt, clay respectively: Agvise, Benson, MN, USA) (Table 4.1). Each of the four sites received a soil temperature and moisture logger. Soil temperature (°C) and soil moisture (m³/m³) were measured in the plant rooting zone (5cm depth) using Onset® (Onset Computer Corporation Bourne, MA, USA) HOBO® USB Micro Station Data Logger (H21-USB) stations equipped with EC5 Soil Moisture Smart Sensors (S-SMx-M005) and 12-Bit Temperature Smart Sensors (S-TMB-M002), from October 2020 to October 2022. The HOBOWare® software interface was used to retrieve data from the logging stations and for export of data to Excel (Microsoft®). Soil moisture and temperature were recorded every ten minutes and aggregated to create a monthly mean which was then analyzed in the statistical software R (R Core Team 2022).

One of the four field sites was chosen at random for the plant available soil nutrient analysis. Fifteen nutrients were evaluated in the rooting zone, i.e., the top 10cm: ammonium (NH₄⁺), nitrate (NO₃⁻), zinc (Zn), boron (B), lead (Pb), aluminum (Al), iron (Fe), copper (Cu),

magnesium (Mg), manganese (Mn), cadmium (Cd), sulfur (S), potassium (K), phosphorous (P), and calcium (Ca) using Plant Root Simulator (PRS®, Western AG Innovations (Saskatoon, Canada)) probes. Probes adsorb available nutrients in the rooting zone of plants, in two treatments within the non-grazed block. The two treatments were: sprayed and seeded with the native seed mix, and non-sprayed and non-seeded. Each treatment combination was replicated three times. Within each of these three replicates, four pairs of cation and anion PRS® probes were deployed. Western AG Innovations' laboratory analysis collates four pairs as a single composite value. Three, 30-day burial periods were conducted and referred to by season (Mid-May to mid-June=spring, mid-June to mid-July=summer, September first to October first=fall) in 2021 and 2022. The late summer burial period (mid-July to mid-August) was added in the second year, to create greater temporal resolution of nutrient availability over the course of the growing season.

Statistical Analysis

All statistical analyses were conducted in the software R (R Core Team 2022). Linear mixed effect models (nlme package) (Pinheiro et al. 2022), general linear mixed effect models (lme4 package) (Douglas et al. 2015) and a post-hoc, Tukey's Honestly Significantly Different (HSD) (multcomp package) (Hothorn et al. 2008) or estimated marginal mean contrasts using the emmeans package (Lenth 2022) were conducted to analyze differences between treatments for both the greenhouse and field experiment. Assumptions of equal variance and normality were checked by assessing Pearson's residuals and quantile (QQ)-plots, respectively, and no extreme violations were present. Statistical analyses unique to each experiment are described below.

Seed Mix Performance Analysis

Each model incorporated trial and pot as random effects in the model structure to account for the nested structure of the greenhouse experimental design. This modeling approach was used to compare the mean aboveground biomass production of each species in greenhouse experiment one and of each species mix in greenhouse experiment two. For greenhouse experiment three, competitive effects of each seed mix on *B. tectorum* were quantified using a relative interaction index (Rii) (Armas et al. 2004) and mean pot biomass comparisons. Relative interaction index values greater than zero indicate a positive interaction/facultative effect, values less than zero indicate a negative interaction/competitive effect, and values of zero indicate no interaction. The following is an example of the equation used to calculate the Rii for the competitive response of *B. tectorum*.

$$\begin{aligned} & \text{Competitive Response of } B. \text{ tectorum} \\ & = (B_{\text{Comp. with mix}} - B_{\text{Monoculture}}) / (B_{\text{Comp. with mix}} + B_{\text{Monoculture}}) \end{aligned}$$

The $B_{\text{Comp. with mix}}$ is the aboveground biomass of *B. tectorum* when grown in competition with one of the seed mixes, and $B_{\text{Monoculture}}$ represents the aboveground biomass when grown alone. Two-tailed single sample t-tests were conducted to assess if the mean Rii was different from zero for each treatment group. For all greenhouse experiments, the goal density of plants (24 plants/pot) was not always achieved, as a result the mean individual aboveground biomass (cumulative biomass/number of individuals) were used for Rii calculations.

Response of *Bromus tectorum* and Plant Community to Grazing, Herbicide and Seed Mix Analysis

Data collected from all sites were compiled. Linear mixed effects models were used to analyze differences between the grazing, herbicide and seeding treatments for *B. tectorum* abundance, plant species richness, and Shannon's diversity index (H) and plant available nutrients. At the single site selected for plant available soil nutrients linear mixed effects models, were also used to analyze the treatment effects of herbicide and seeding on: *B. tectorum* abundance, plant species richness, Shannon's diversity index (H), and plant available nutrients. Both analysis used the packages "vegan" (Oksanen et al. 2022) and "bioDiversityR" (Kindt and Coe 2005) for analysis of plant diversity. *Bromus tectorum* was omitted from the species richness analysis because it was a target species for removal, i.e., inclusion of *B. tectorum* could artificially create differences between sprayed and non-sprayed treatments. *Bromus tectorum* was included in the Shannon's alpha diversity index which incorporates both species richness and abundance.

Bromus tectorum abundance data was zero inflated (35% zeros), as a result several zero-inflated/alterred models were attempted (Supplemental Table 4.1) and ultimately, a zero-altered linear mixed effects model assuming a negative binomial distribution was used. Dispersion was assessed using the equation suggested by Zuur and Ieno (2016) (pgs 172 & 173) (Supplemental Table 4.2). Models of plant richness, alpha diversity, and *B. tectorum* abundance included grazing, herbicide, and seed mix as fixed effects and site and replication as random effects. Plant richness was modeled assuming a Poisson distribution. Plant diversity and *B. tectorum* abundance models assumed a Gaussian/normal distribution.

Field Soil Temperature, Moisture, and Nutrient Analysis

Mean monthly soil temperature and moisture means were compared between years using a post-hoc pairwise t-test. Data from all four sites were combined to create a mean and standard error for the entire study area. Negative values for soil moisture were omitted from the analysis, because they represent periods where soil moisture was below detection levels (i.e. zero), and their removal did not impact the overall trends observed. Soil moisture and temperature data were subset by year and two-sided t-tests were used to make pairwise comparisons by year.

The response of soil nutrient availability due to *B. tectorum* management, changes in vegetation cover, and seasonality were recorded over two field seasons. In our analysis we assumed that plant nutrients would have natural fluctuations within seasons and that those seasonal fluctuations would differ between years. For example, we would expect nutrient availability to be higher, in general, in the spring and decrease over the course of the growing season. Further the degree to which this occurs likely will vary from year to year. Therefore, an interaction between year and season was not tested for. Instead, the analysis was conducted using the mean soil nutrient availability from the sprayed and non-sprayed plots. To account for the variation contributed by year and season these predictors were included as additive effects. A separate model was conducted for each of the 15 soil nutrients collected and included replication as a random effect. The assumption of equal variance and normality was checked visually using Pearson's residual and QQ plots, respectively, and no major departures were identified.

Results

Experiment 1: Individual Species Biomass Production

Species differed in their individual production of biomass (Table 4.2). *Triticale* produced the most biomass (0.13g) per plant. *Bromus tectorum* produced the second most biomass (0.09g) and was similar to *A. dasystachum* (0.07g) ($z:2.15$, SE: 0.01, $p: 0.319$). *Agropyron dasystachyum* biomass (0.07g) did not differ from *A. intermedium* ($z:0.98$, SE:0.01, $p:0.957$), *Stipa viridula* ($z: 1.33$, SE:0.01, $p:0.834$), or *A. spicatum* ($z: 2.17$, SE:0.01, $p:0.31$). *Koelaria macrantha* (0.02g) and *A. spicatum* (0.04g) produced the least biomass.

Experiment 2: Within Seed Mix Competition and Seed Mix Biomass Production

Species within their respective seed mix produced differing amounts of biomass leading to differences in total seed mix biomass (Table 4.3). The ruderal mix had greater overall mean biomass (0.25g) than the native (0.16g; $p: 0.026$; Figure 4.1). The biomass of the ruderal mix was highly influenced by *Triticale* which was 0.21g greater than *A. dasystachum* ($p: <0.0001$) and 0.20g greater than *A. intermedium* ($p: <0.0001$) when grown as a mixture (Figure 4.1). In the native mix, *S. viridula* produced 0.07g more biomass than *K. macrantha* ($t: -3.96$, $df: 35$, $p: 0.004$), which produced the least amount of biomass in the native mix (0.02g). *Agropyron spicatum*'s biomass (0.05g) was not statistically different than *K. macrantha* nor *S. viridula*.

Experiment 3: Seed Mix Competition with *Bromus tectorum* Biomass Production

Species differed in their aboveground biomass production when grown in competition with *B. tectorum* but there was no effect of *B. tectorum* density on biomass production (Table 4.4). The ruderal and native seed mixes differed in their total biomass production but did not differ across densities of *B. tectorum* (Table 4.4). When the ruderal mix was grown in competition with *B. tectorum*, *Triticale* still produced more biomass than the other two species in the ruderal mix and *B. tectorum* (Table 4.5) but there was no difference in biomass between any of the other species, including *B. tectorum* (Table 4.5). The native mix showed a different pattern in species biomass. *Bromus tectorum* and *A. spicatum* produced 0.03g more biomass than *K. macrantha* ($t:3.93$, $df=83$, $p: 0.001$ and $t:3.78$, $df=83$, $p:0.002$). *Stipa viridula* biomass did not differ from the other two species in the native mix (Table 4.5).

Competitive Effects: The ruderal mix had a consistent negative effect on *B. tectorum* with a relative interaction index (Rii) of -0.6, -0.6, and -0.64 at the low, equal, and high densities, respectively (Figure 4.2 and Table 4.6). The native mix elicited a negative Rii response in *B. tectorum* in the high (-0.38) and equal (-0.5) densities but not at the low density (-0.15) which was not statistically different from zero (Figure 4.2 and Table 4.6). Conversely, *B. tectorum* had a similar negative impact on both mixes; independent of density (Figure 4.3 and Table 4.6).

Seed Mix Field Establishment

The native and ruderal seed mixes were applied at four field sites. Few individuals of triticale ($n=18$) established and grew to maturity in all the seeded split-treatments, in both years. It was the only species from either seed mix to establish. The low number of triticale seedlings combined with the lack of establishment of any other seeded species in the field rendered a

comparison between the two mixes futile. As a result, the seeding treatment had no statistical significance when we attempted to model *B. tectorum* abundance, species richness, and alpha diversity, so we removed it as a fixed effect to increase our degrees of freedom.

Bromus tectorum Abundance

We found strong evidence for a three-way interaction between grazing, herbicide, and year (Table 4.7) (Figure 4.4). In the first year *B. tectorum* abundance ranged from 2.4% to 0.1% cover across all treatment combinations, but none were statistically different from one another. In the second year, *B. tectorum* abundance increased in all treatments and ranged from 55% to 21% (Table 4.8). From year one to two, there was no difference between the sprayed and non-sprayed treatments within each of the grazing treatments; between the grazing treatments, there was greater *B. tectorum* abundance in the non-grazed treatment compared to the grazed treatment (Figure 4.4 and Table 4.9).

Further, at the single site analyzed for plant available soil nutrients, we found no evidence that suggested a difference in *B. tectorum* abundance between sprayed and non-sprayed treatments ($f:0.90$, $df: 30$, $p: 0.349$). However, there was an increase in *B. tectorum* from the first (0%) to second year (36%) of 36% cover ($t: 6.92$, $df:30$, $p: <0.0001$), and total vegetative cover, including *B. tectorum*, increased from year one (25%) to year two (86%) by 61% cover ($t:15.18$, $df:30$, $p: <0.0001$). Conversely, we observed a decrease in litter cover from year one (74%) to year two (25%) of 49% cover ($t:14.13$, $df: 30$, $p: <0.0001$). There was no statistical evidence for a change in the cover of bare ground.

Plant Community Response

Species richness was best explained by herbicide (f: 3.52, df:240, p:0.06) and year (f:141.30, df: 240, p:<0.0001), grazing had no effect, and there were no interactions (Table 4.10). There were 0.4 more species/m² in the non-sprayed than in the sprayed treatments (t:2.65, df: 240, p:0.008) and 1.8 more species/m² were found in the second year than the first (t:-11.88,df: 240,p:<0.0001).

Herbicide and year were important for explaining plant alpha diversity, but grazing was not (Table 4.10). Shannon's diversity increased from the first year to the second year by 0.44 units (t-stat: -8.54, df= 245, p: <0.0001) and was 0.15 units greater in the non-sprayed compared to the sprayed (t-stat: 2.89, df=245, p: 0.004).

At the site randomly selected for the plant available soil nutrient study we found that species richness depended on year (f: 93.75, df:31, p: <0.0001) and herbicide (f: 9.60, df: 31, p: 0.004). On average there were 0.9 more species in the non-sprayed (4.9) than the sprayed (4) treatment (t: 3.09, df: 31, p:0.004) and 2.7 more species in the second year (5.8) than the first (3.1) (t: 9.68, df: 31, p: <0.0001). Similarly, herbicide (f: 4.47, df: 31, p: 0.042) and year (f: 13.39, df: 31, p: 0.001) were important for explaining alpha diversity at this site. There was an increase of 0.38 units of diversity from the first (0.86) to the second (1.24) year (t:3.66, df: 31, p: 0.001) and the non-sprayed treatment (1.16) had 0.22 units greater diversity than the sprayed treatment (0.94) (t: 2.11, df: 31, p: 0.042).

Treatment Effect on Plant Available Soil Nutrients

At a single site, plant available nutrients were collected within the non-grazed treatment. Within this treatment the sprayed and non-sprayed treatments were sampled. Of the fifteen

nutrients tested only nitrate (NO₃) (t:-2.36, df:34, p:0.023) and sulfur (S) (t:-1.99, df:34, p: 0.054) showed differences, 57.40 µg/10cm²/30-days and 4.01 µg/10cm²/30-days respectively, between sprayed and non-sprayed treatments, both were greater in the sprayed than non-sprayed treatment (Table 4.11).

Soil Moisture and Temperature

The soil temperature and moisture were different between the two-years (Table 4.13 and 14). In general, we observed cooler and wetter soil conditions in the spring of the second year and a warmer and drier fall (Table 4.13 and 14). The summer (June, July, August) was drier in the second year compared to the first (Table 4.13). We observed a cooler start to the summer (June and July) that ended with hotter soil temperatures than the preceding year in August (Table 4.14).

Discussion

Reducing non-native annual grass abundance is a critical first step towards restoration of invaded areas but it is the remaining native species that confer resistance to further invasion (Davies and Johnson 2017). In the case of highly degraded systems lacking remnant native species, restoration seeding is essential. Therefore, selecting a suite of species and species' traits most suitable for the restoration goal and environment is paramount (Pyke 2011, Clements et al. 2022). In this study we implemented restoration in the form of a series of experiments. In the design of our ruderal restoration seed mix, we considered the intensity and frequency of disturbance, the local species pool, and the properties of the non-native invader, *B. tectorum*. Further, we compared the suppressive effects of this disturbance tolerant mix on *B. tectorum* with

that of a native grass seed mix. We found the ruderal seed mix, in particular its member species *Triticale*, more successful than the native seed mix in competing with *B. tectorum* in a controlled environment. Often implemented as a sterile forage/fodder species, *Triticale* matches *B. tectorum*'s annual phenology, and its genetics enhance its ability to produce biomass quickly. Our findings support the anecdotal evidence from farmers in the Pacific Northwest who planted *Triticale* to directly compete with *B. tectorum* (Herdrich 2001) and suggestions that *Triticale* is an effective “place holder” until native plants are established (Hoffert-Hay 2002, Sheley 2008). As a complete seed mix, the ruderal mix reduced *B. tectorum*'s biomass across all densities, which was not the case for the native seed mix. The native mix only increased in biomass production when released from *B. tectorum* competition. Given the two suites of species in the ruderal or native seed mix, our ruderal mix was the best candidate as a restoration seed mix high-intensity disturbance scenarios where *B. tectorum* is present. This is congruent with prior research that found early successional species to compete better with *B. tectorum* than climax species (Uselman et al. 2015). Additionally, seed mixes utilizing a mix of native annuals and perennials was successful in reducing *B. tectorum* abundance (Herron et al. 2013). Further, Ott et al. (2019), found that rhizomatous grasses were a strong component of restoration seed mix success due to their ability to reproduce during drought. Despite its promise, the ruderal seed mix did not establish well under field conditions. Only *Triticale* established, but weakly, with only 18 individuals observed to grow to maturity across the entire study area (24-1m² plots). Warmer and drier conditions in the fall and spring of our first year likely limited the success of our herbicide application and seeding treatment. For example, Vermeire and Rinella (2020) found that annual

grass germination is most influenced by fall precipitation and its survival and biomass by spring precipitation.

A pre-emergent fall herbicide application had no effect on *B. tectorum* abundance, further re-enforcing findings by Mangold et al. (2013) who found post-emergent applications were more effective than pre-emergent applications in reducing *B. tectorum* (Mangold et al. 2013). Our application was conducted in mid-October a time that typically targets *B. tectorum* seedlings in the one-two leaf stage (early post-emergence), however, a lack of fall precipitation did not stimulate fall germination of *B. tectorum*, forcing us to apply the herbicide as a pre-emergent. Due to lack of herbicide control and cooler and wetter soil conditions in the second year we observed an increase in *B. tectorum* abundance across all treatments from year one to year two. As a result, herbicide did not play a major role in reducing propagule pressure, i.e., return of seed to the seedbank, which is a crucial step in non-native plant management (Hobbs and Humphries 1995). However, this occurred to a lesser extent in the grazed treatment compared to the non-grazed treatment. This is in agreeance with Vermeire et al. (2023a), who found that intensive-isolated fall grazing reduced non-native annual grasses, but in contrast to Souther et al. (2019) who found that high intensity summer grazing led to a greater annual and non-native plant abundance, and Stohlgren et al. (1999) who found richness and cover of non-native species was greater in grazed vs. non-grazed areas for Grand Teton National Park, WY,USA. Despite the lack of *B. tectorum* control in the sprayed treatment, we observed a reduced species richness and diversity in the sprayed compared to non-sprayed plots over both years of the study, implying that herbicide had non-target impacts on the plant community. This was not true for the grazing

treatment, which did not differ in richness or diversity, corroborating the findings of Rinella et al. (2009), who found that grazing mitigated non-target effects of herbicide.

The impact of reduced species richness and diversity in the sprayed treatment manifested itself in the form of increased plant available soil NO₃ and S. We did not observe differences in total vegetation cover, which included *B. tectorum*, litter, or bare ground between the sprayed and non-sprayed treatments that were not grazed at the site where soil nutrients were evaluated. If we had observed reduced total vegetation in the sprayed treatment, we might have expected a concurrent reduction in plant uptake, especially of NO₃, which would have led to increased availability in the soil. This was not the case. We might also have expected to see increased nutrient availability if there was an increase in bare ground in the sprayed treatment, which also would have indicated a reduction in soil nutrient immobilization; this was also not observed in our study. Lastly, if litter was reduced in the sprayed treatment, which it was not, it could have been correlated with a reduction in decomposition of organic matter and thus reduced nutrient availability in the soil. We therefore hypothesize that nutrient availability increased as a result of differences in plant community nutrient requirements between the sprayed and non-sprayed treatment due to reductions in richness and diversity. We also hypothesize that in conjunction with the former mechanism the decomposition of imazapic by soil microbes, its primary method of degradation (Beste 1983), led to an increase in NO₃ and S. A recent meta-analysis supports this hypothesis, suggesting that herbicides are affecting soil microbial diversity (Beaumelle et al. 2023). It is plausible then that imazapic may have played a role in decoupling plant and microbial immobilization or mineralization of NO₃ and S.

This study, conducted in the cooler and wetter part of the sagebrush biome known as the Middle Rockies ecoregion, clearly illustrates the complexities that arise as the result of an interaction between an integrated management strategy and natural variation. We hypothesize that if management is to occur during continued use of an area, as in this instance, intensive cattle trampling and grazing may be another tool for reducing the target species. However, this benefit must be carefully weighed against the expense of potentially reduced seedling establishment by restoration seed mixes, although trampling during restoration seeding could enhance seedling establishment. We also emphasize the need to consider the non-target effects of herbicide on plant community richness, diversity, and soil nutrient availability, which could have implications for the future trajectory of the plant community or subsequent success of restoration. This may be the first study that has observed increased nutrients following herbicide application without controlling *B. tectorum*. As a result, future long-term non-native plant management and restoration strategies should incorporate this knowledge into their integrated strategy, as suggested by Hobbs and Humphries (1995), because it pertains directly to the capacity for target species propagule pressure (increased nutrient availability/lack of control), ecosystem character (nutrient cycling/plant community), and future land use practices (grazing intensity/land abandonment).

Tables

Table 4.1: pH and soil texture classification for each site in the Centennial valley, MT, USA.

Site	1:1 Soil pH	pH	% Sand	% Silt	% Clay	Texture
Tank 19	6.4	6.7	91	5	4	Sand
Tank 32	7.4	7.2	91	5	4	Sand
Tank 82	7.7	7.2	90	5	5	Sand
Tank 22	7.6	7.2	93	6	1	Sand

Table 4.2: The relative biomass of the six individual species differed when grown in monoculture in a greenhouse experiment. Statistical analysis was conducted using a linear mixed effect model and the importance of the predictor was assessed with an analysis of variance test.

Response	Predictor	numerator df	denominator df	F	p
Relative Biomass		1	42	469.73	<0.0001
	Species	5	42	25.55	<0.0001

Table 4.3: The relative mean biomass of the six individual species and the seed mixes themselves when grown in equal density in a greenhouse experiment. Statistical analysis was conducted using a linear mixed effect model and the importance of the predictor was assessed with an analysis of variance test.

Response	Predictor	numerator df	denominator df	F	p
Relative Biomass		1	35	51.64	<0.0001
	Species	5	35	42.61	<0.0001
Mix Biomass		1	7	37.52	0.001
	Mix	1	7	9.36	0.018

Table 4.4: Analysis of variance of the relative biomass of each species when grown in high, equal, and low densities of *Bromus tectorum* (BRTE Density) and total mix biomass produced when grown in high, equal, and low densities of *B. tectorum*. Bold text indicates predictor variables that are statistically significant at $\alpha < 0.05$.

Response	Predictor	numerator df	denominator df	F	p
Relative Biomass		1	159	186.19	<0.0001
	BRTE Density	2	159	1.01	0.364
	Species	6	159	64	<0.0001
	BRTE Density*Species	12	159	0.58	0.854
Total Mix Biomass		1	174	64.82	<0.0001
	BRTE Density	2	174	0.35	0.702
	Seed Mix	1	174	12.39	0.001
	BRTE Density*Seed				
	Mix	2	174	0.26	0.764

Table 4.5: Tukey's Honestly Significant Difference pairwise test results for ruderal and native seed mix biomass when grown in competition with *Bromus tectorum* in a greenhouse experiment. Bold text indicates predictor variables that were statistically significant using $\alpha < 0.05$.

Comparison	estimate	SE	df	t	p
Ruderal Seed Mix					
<i>A. dasystachyum</i> - <i>A. intermedium</i>	-0.008	0.01	82	-0.40	0.977
<i>A. dasystachyum</i> - <i>B. tectorum</i>	-0.005	0.01	82	-0.25	0.994
<i>A. dasystachyum</i>-<i>Triticale</i>	-0.25	0.01	82	-12.47	<0.0001
<i>A. intermedium</i> - <i>B. tectorum</i>	0.003	0.02	82	0.15	0.999
<i>A. intermedium</i>-<i>Triticale</i>	-0.24	0.02	82	-11.94	<0.0001
<i>B. tectorum</i>-<i>Triticale</i>	-0.24	0.02	82	-12.09	<0.0001
Native Seed Mix					
<i>A. spicatum</i> - <i>B. tectorum</i>	-0.001	0.009	83	-0.15	0.999
<i>A. spicatum</i>-<i>K. macrantha</i>	0.03	0.009	83	3.78	0.002
<i>A. spicatum</i> - <i>S. viridula</i>	0.01	0.009	83	1.56	0.403
<i>B. tectorum</i>-<i>K. macrantha</i>	0.03	0.009	83	3.93	0.001
<i>B. tectorum</i> - <i>S. viridula</i>	0.01	0.009	83	1.72	0.319
<i>K. macrantha</i> - <i>S. viridula</i>	-0.02	0.009	83	-2.24	0.118

Table 4.6: Seed mix relative interaction index (R_{ii}) estimates are reflective of the competitive effect of *Bromus tectorum* on each seed mix at varying densities of *B. tectorum*, in the top half of the table. In the bottom half of the table, the R_{ii} values indicate the competitive effect of each seed mix on *B. tectorum*. Negative estimates indicate competitive effects that resulted in reduced biomass compared to monoculture. Positive values indicate synergistic/mutualistic, increased biomass in response to competition. Values of zero indicate no competitive interaction, i.e., no difference in biomass between monoculture and competition treatments. one-sample two-tailed t-test results. Bold values indicate R_{ii} estimates that were statistically different from zero, that is their 95% confidence interval did not include zero.

<i>Bromus tectorum</i> Density	Seed Mix	Estimate (Seed mix)	df	CI Low	CI High	t	p
Low	Native	-0.24	23	-0.40	-0.08	-3.16	0.004
Equal	Native	-0.30	23	-0.44	-0.16	-4.46	0.0002
High	Native	-0.30	21	-0.48	-0.13	-3.56	0.001
Low	Ruderal	-0.37	23	-0.58	-0.16	-3.68	0.001
Equal	Ruderal	-0.35	23	-0.54	-0.15	-3.58	0.001
High	Ruderal	-0.24	21	-0.42	-0.06	-2.72	0.012
(<i>Bromus tectorum</i>)							
Low	Native	-0.15	7	-1.28	-0.44	0.13	0.24
Equal	Native	-0.50	7	-4.10	-0.78	-0.21	0.004
High	Native	-0.38	7	-3.78	-0.61	-0.14	0.006
Low	Ruderal	-0.60	6	-9.41	-0.75	-0.44	0.0001
Equal	Ruderal	-0.60	7	-7.68	-0.79	-0.42	0.0001
High	Ruderal	-0.64	7	-8.28	-0.82	-0.46	0.0001

Table 4.7: Importance of grazing and herbicide over two years on *Bromus tectorum* abundance, at four sites in the Centennial Valley, MT, USA. Bold text indicates predictor variables that were statistically significant at $\alpha < 0.05$ using an analysis of variance.

Response	Predictor	Chi-square	df	p
<i>B. tectorum</i> abundance	Year	351.67	1	<0.0001
	Grazing	12.13	1	<0.0001
	Herbicide	13.69	1	<0.0001
	Year*Grazing	7.39	1	0.006
	Year*Herbicide	41.1	1	<0.0001
	Grazing*Herbicide	0.3	1	0.581
	Year*Grazing*Herbicide	4.71	1	0.029

Table 4.8: Estimated average abundance of *Bromus tectorum* for each year and treatment. Estimates are reported as percent cover and therefore rounded to the nearest whole number, unless doing so would result in a zero value, in which instance rounding was to the nearest tenth.

Year	Treatment		Est.	SE	df	lower CI	upper CI
2021	Grazed	Non-sprayed	2	0.8	Inf	0.8	4.0
2022	Grazed	Non-sprayed	17	5.4	Inf	6.8	28.0
2021	Non-grazed	Non-sprayed	2	0.7	Inf	0.7	3.5
2022	Non-grazed	Non-sprayed	55	17.0	Inf	21.9	88.5
2021	Grazed	Sprayed	0.1	0.1	Inf	0.0	0.3
2022	Grazed	Sprayed	21	6.6	Inf	8.3	34.3
2021	Non-grazed	Sprayed	0.3	0.1	Inf	0.1	0.6
2022	Non-grazed	Sprayed	43	13.2	Inf	16.6	68.5

Table 4.9: Difference in the estimated mean *Bromus tectorum* abundance between year one (2021) and two (2022). Estimates are reported as cover (%) and therefore rounded to the nearest whole number, as were the standard errors. Bold text indicates statistical significance based on an $\alpha < 0.05$.

Contrast	Treatment		Estimate	SE	z	p
2021-2022	Grazed	Non-sprayed	+15	5	-3.02	0.003
2021-2022	Non-grazed	Non-sprayed	+53	17	-3.20	0.001
2021-2022	Grazed	Sprayed	+21	7	-3.20	0.001
2021-2022	Non-grazed	Sprayed	+42	13	-3.20	0.001

Table 4.10: The importance of herbicide, year, and grazing for explaining species richness and Shannon's diversity indices from four sites in the Centennial Valley, MT, USA. Analysis was conducted using an analysis of variance. Bold text indicates predictor variables deemed statistically significant at $\alpha < 0.05$.

Response	Predictor	numerator df	denominator df	F	p
Richness		1	239	155.03	<0.0001
	Herbicide	1	239	3.52	0.02
	Year	1	239	141.5	<0.0001
Diversity	Grazing	1	239	1.28	0.219
		1	244	109.34	<0.0001
	Herbicide	1	244	5.48	0.02
	Year	1	244	73.19	<0.0001
	Grazing	1	244	1.51	0.219

Table 4.11: Evidence for the importance of herbicide in explaining plant available soil nutrients, nitrate, and sulfur, at one site, over the two-year study, in the Centennial Valley, MT, USA. Bold text indicates statistical significance based on an $\alpha < 0.05$.

Response	Predictor	numerator df	denominator df	F	p
Nitrate (NO ₃)		1	34	54.36	<0.0001
	Herbicide	1	34	5.61	0.023
Sulfur (S)		1	34	82.95	<0.0001
	Herbicide	1	34	3.96	0.054

Table 4.12: Differences in nutrient availability between the sprayed and non-sprayed herbicide treatment at one site in the Centennial Valley, MT, USA. Nutrient units are $\mu\text{g}/10\text{cm}^2/30$ days. Bold text indicates statistical significance based on an $\alpha < 0.05$.

Nutrient	Contrast	Estimate	df	SE	t	p
NO ₃	Spray-(No-Spray)	57.40	20	18.28	-3.13	0.005
S	Spray-(No-Spray)	4.01	20	1.44	-2.78	0.011

Table 4.13: Estimated mean monthly differences in soil moisture (m^3/m^3) between the first and second study years across all four sites in the Centennial Valley, MT, USA. The second year was wetter from January to May and drier from June to October. Analysis was conducted using a two-sided t-test. Values with a “+” indicate an increase and values with a “-” indicate a decrease from year one to two.

Month	Estimate	t	p	lower CI	upper CI
January	+0.02	-469.78	<0.0001	-0.02	-0.02
February	+0.02	-311.55	<0.0001	-0.02	-0.02
March	+0.02	-39.549	<0.0001	-0.02	-0.02
April	+0.01	-25.82	5.2E-143	-0.01	-0.01
May	+0.01	-40.01	<0.0001	-0.01	-0.01
June	-0.01	32.17	1.3E-217	0.01	0.01
July	-0.05	75.85	<0.0001	0.04	0.05
August	-0.07	63.31	<0.0001	0.07	0.08
September	-0.06	62.50	<0.0001	0.06	0.06
October	-0.07	66.80	<0.0001	0.07	0.07

Table 4.14: Estimated mean monthly differences in soil temperature ($^{\circ}\text{C}$) between the first and second years across all four sites in the Centennial Valley, MT, USA. January through March and August through September were warmer, in the second year, while April through July were cooler. Analysis was conducted using a two-sided t-test. Values with a “+” indicate an increase and values with a “-” indicate a decrease from year one to two.

Month	Estimate	t	p	lower CI	upper CI
January	+2.3	-77.04	<0.0001	-2.4	-2.2
February	+0.3	-10.89	<0.0001	-0.3	-0.2
March	+0.6	-25.58	<0.0001	-0.6	-0.5
April	-1.9	47.58	<0.0001	1.8	2.0
May	-2.8	55.46	<0.0001	2.6	2.9
June	-6.1	108.66	<0.0001	6.0	6.3
July	-0.8	12.10	<0.0001	0.6	0.9
August	+3.2	-42.72	<0.0001	-3.4	-3.0
September	+1.7	-21.50	<0.0001	-1.9	-1.5
October	+1.5	-19.97	<0.0001	-1.7	-1.3

Figures

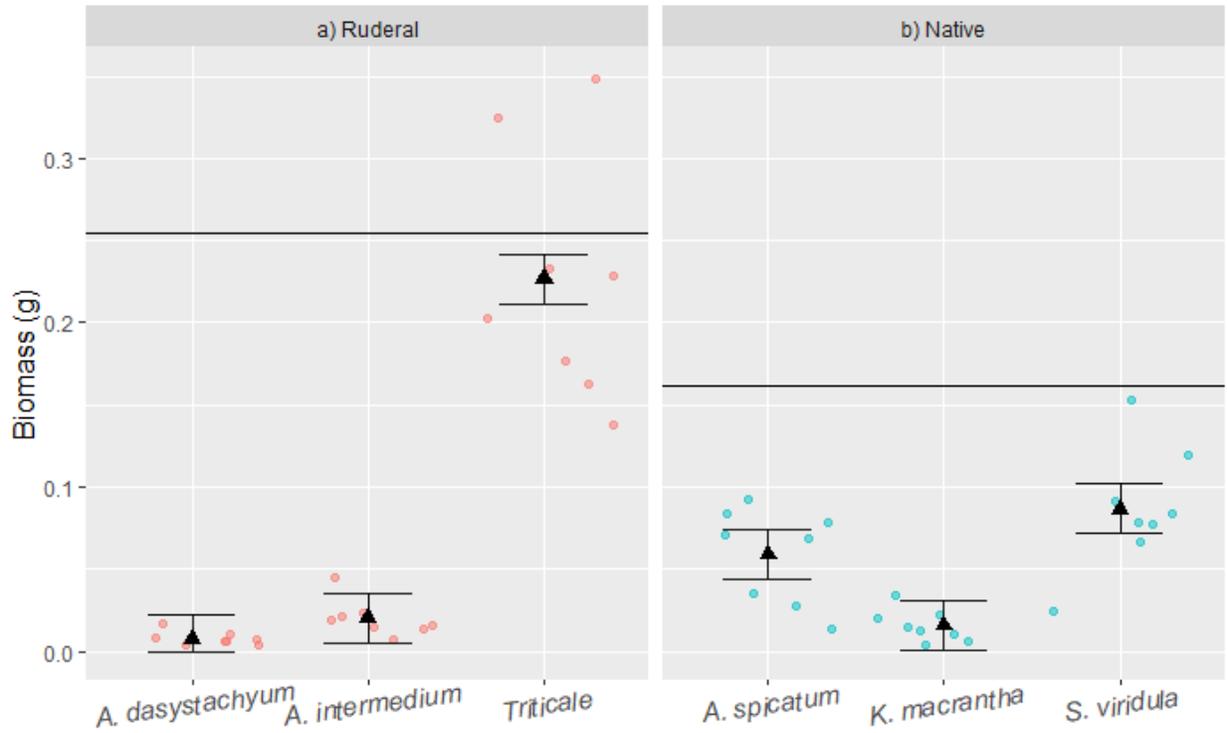


Figure 4.1: Mean species biomass per pot when grown in competition with other species of the same seed mix, a) ruderal or b) native, under controlled conditions. Triangles are estimated means, bars are standard errors and points are horizontally jittered data points. The horizontal line represents the mean biomass for each mix.

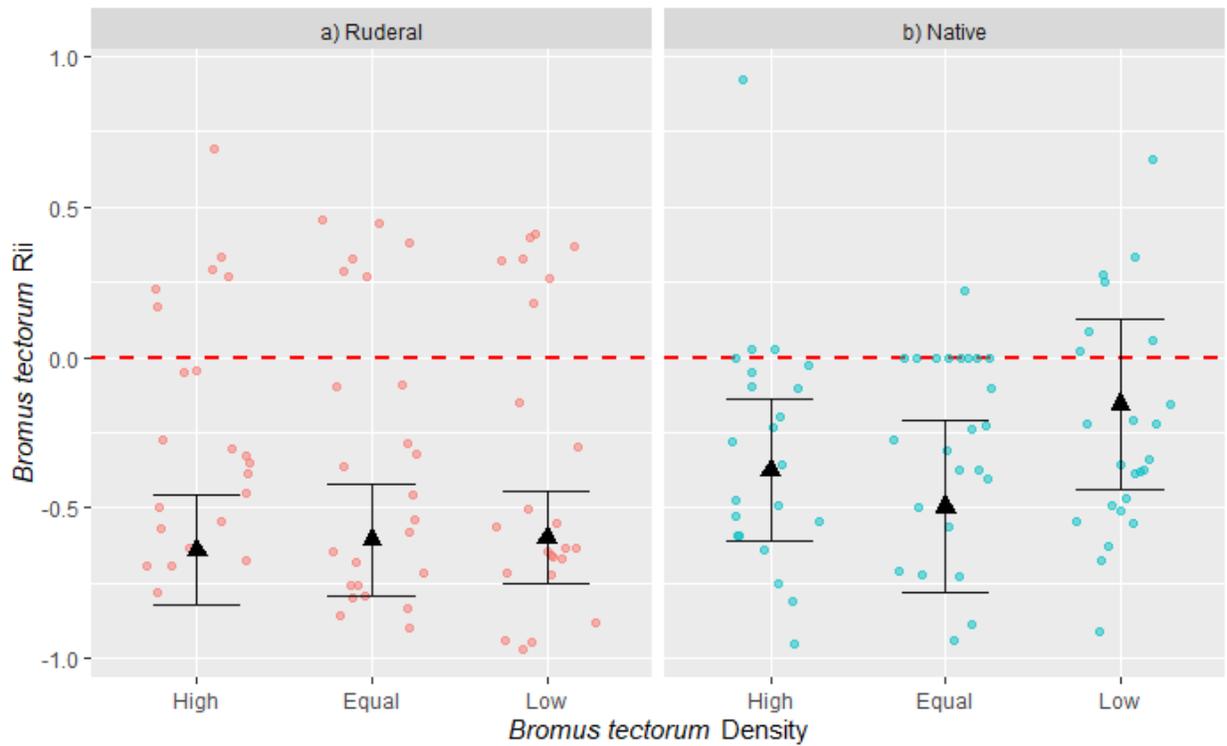


Figure 4.2: Relative interaction index (Rii) values for *Bromus tectorum* when in competition with the a) ruderal and b) native seed mixes at three densities, under controlled conditions. Values of zero included in the 95% confidence interval indicate no competitive effect, positive values signal improved growth under competition, and negative values indicate the presence of competitive effects/reduced growth. Black triangles are the estimated means, bars are 95% confidence intervals, and points are the jittered raw data.

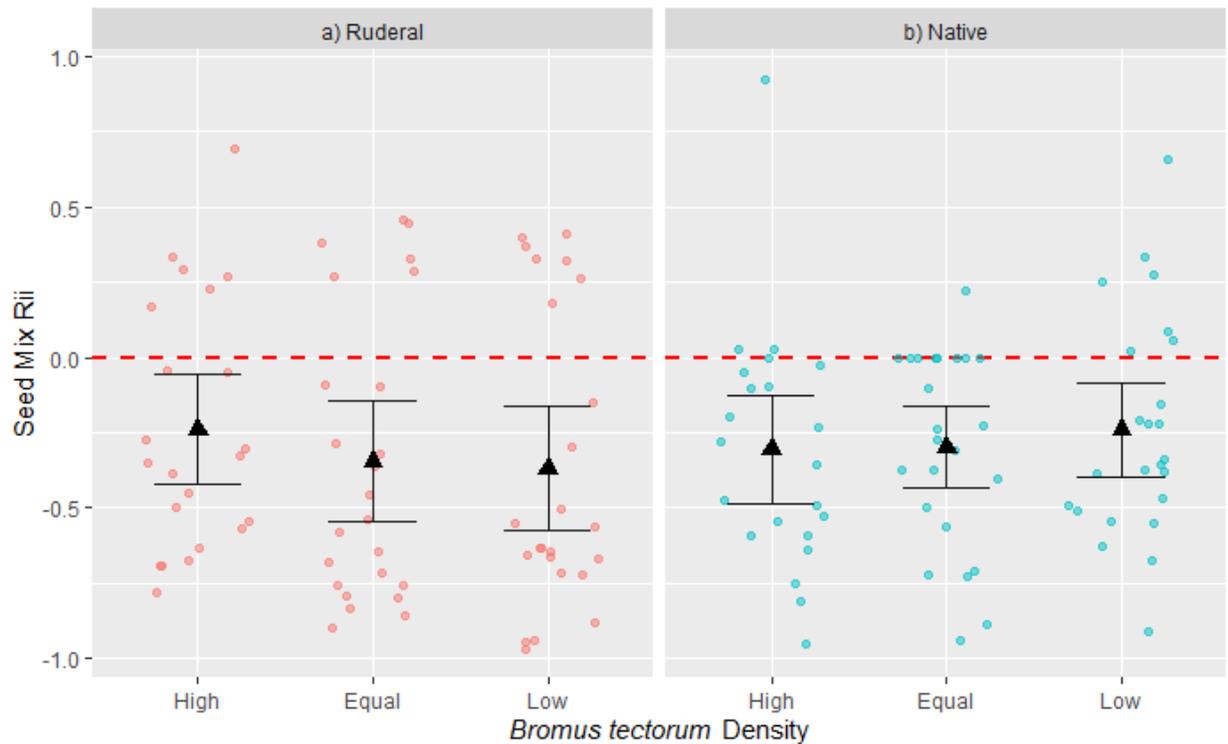


Figure 4.3: Relative interaction index (Rii) values for the a) ruderal and b) native seed mixes at three densities of *Bromus tectorum* under controlled conditions. Relative interaction index (Rii) values of zero indicate no competitive effect, positive values signal improved growth under competition, and negative values indicate the presence of competitive effects. Note that both mixes responded similarly across all densities. Black triangles are the estimated means, bars are 95% confidence intervals, and points are the jittered raw data.

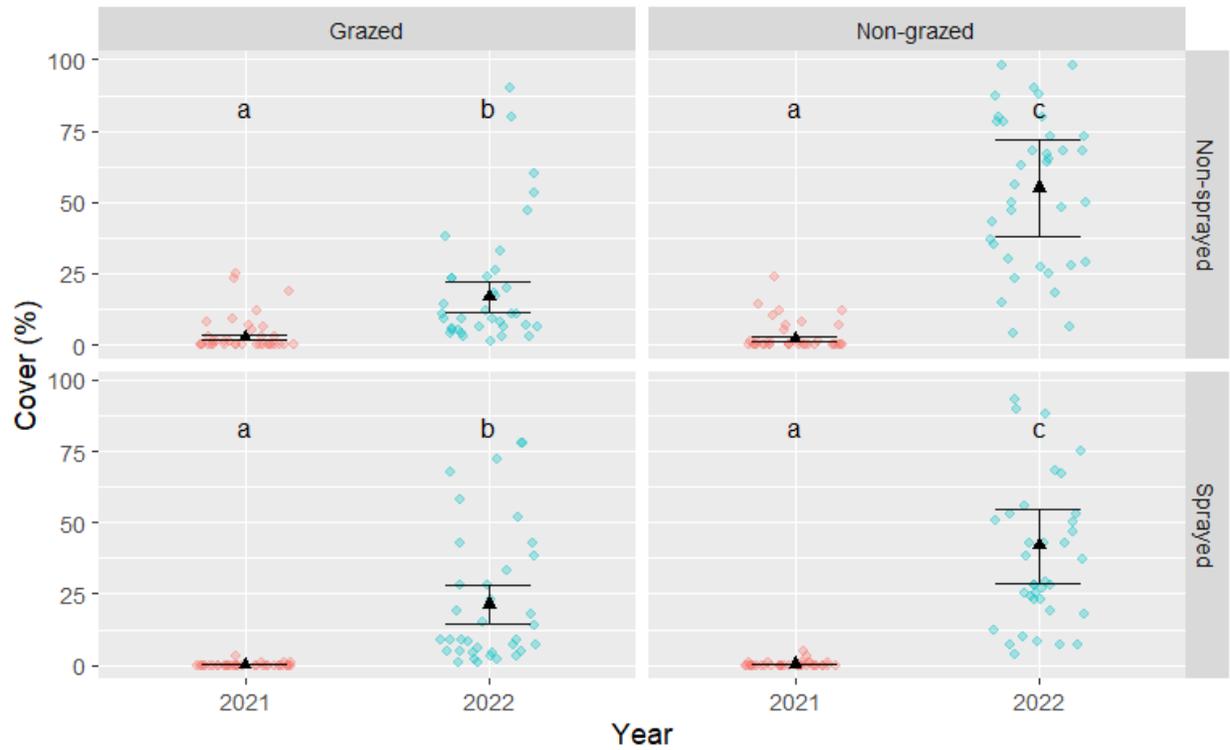


Figure 4.4: *Bromus tectorum* cover (%) illustrating the three-way interaction between herbicide (non-sprayed, sprayed), grazing (grazed, non-grazed) and year (2021,2022) at four water tanks in the Centennial Valley, MT, USA. Triangles are estimated mean abundance, bars are constructed using standard errors. Raw data points are plotted and jittered to depict the distribution of the observations.

Literature Cited

- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global change biology* 19:173-183.
- Beaumelle, L., L. Tison, N. Eisenhauer, J. Hines, S. Malladi, C. Pelosi, L. Thouvenot, and H. R. Phillips. 2023. Pesticide effects on soil fauna communities—a meta-analysis. *Journal of Applied Ecology*.
- Beste, C. 1983. *Herbicide handbook of the weed science society of america*. Weed Science Society of America.
- Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M.-N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain western united states and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions* 20:1493-1506.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677-688.
- Brummer, T. J., K. T. Taylor, J. Rotella, B. D. Maxwell, L. J. Rew, and M. Lavin. 2016. Drivers of *Bromus tectorum* abundance in the western north american sagebrush steppe. *Ecosystems* 19:986-1000.
- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* l. Invasion in cold desert shrublands of western north america. *Ecosystems* 17:360-375.
- Chambers, J. C., J. L. Brown, J. B. Bradford, D. I. Board, S. B. Campbell, K. J. Clause, B. Hanberry, D. R. Schlaepfer, and A. K. Urza. 2023. New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, united states. *Frontiers in Ecology and Evolution* 10:1009268.
- Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. S. Clair. 2016. Plant community resistance to invasion by *Bromus* species: The roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:275-304.

- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes great basin sagebrush ecosystems invisable by *Bromus tectorum*? Ecological monographs 77:117-145.
- Clements, C. D., D. N. Harmon, and R. R. Blank. 2022. Seed mix performance and cheatgrass suppression on arid rangelands. Rangelands 44:129-135.
- Davies, K. W., and D. D. Johnson. 2017. Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. Rangeland Ecology & Management 70:748-754.
- Douglas, B., M. Martin, B. Ben, and W. Steve. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1-48.
- Earnst, S. L., and A. L. Holmes. 2012. Bird—habitat relationships in interior columbia basin shrubsteppe. The Condor 114:15-29.
- Elseroad, A. C., and N. T. Rudd. 2011. Can imazapic increase native species abundance in cheatgrass (*Bromus tectorum*) invaded native plant communities? Rangeland Ecology & Management 64:641-648.
- Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus *Bromus*. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications:61-95.
- Herdrich, N. 2001. Grower experiences with alternate cereal crops in eastern washington 1997-2000 (alternate crop series).
- Herron, C. M., J. L. Jonas, P. J. Meiman, and M. W. Paschke. 2013. Using native annual plants to restore post-fire habitats in western north america. International Journal of Wildland Fire 22:815-821.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. Conservation Biology 6:324-337.
- Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology 9:761-770.
- Hoffert-Hay, D. 2002. Pine creek ranch watershed restoration plan.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346--363.

- Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the great basin desert: History, persistence, and influences to human activities. *Global Environmental Change* 6:37-52.
- Kyser, G. B., J. M. DiTomaso, M. P. Doran, S. B. Orloff, R. G. Wilson, D. L. Lancaster, D. F. Lile, and M. L. Porath. 2007. Control of medusahead (*taeniatherum caput-medusae*) and other annual grasses with imazapic. *Weed Technology* 21:66-75.
- Kyser, G. B., R. G. Wilson, J. Zhang, and J. M. DiTomaso. 2013. Herbicide-assisted restoration of great basin sagebrush steppe infested with medusahead and downy brome. *Rangeland Ecology and Management* 66:588-596, 589.
- Larson, C. D., E. A. Lehnhoff, and L. J. Rew. 2017. A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. *Oecologia* 185:763-774.
- Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern idaho, u.S.A. *Ecology and Evolution* 3:1626-1641.
- Lenth, R. 2022. `_emmeans`: Estimated marginal means, aka least-squares means_.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western north america: An ecological chronicle. *Agro-ecosystems* 7:145-165.
- Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: Variation in time and space. *The Journal of Ecology*:69-93.
- Mangold, J., H. Parkinson, C. Duncan, P. Rice, E. Davis, and F. Menalled. 2013. Downy brome (*Bromus tectorum*) control with imazapic on montana grasslands. *Invasive Plant Science and Management* 6:554-558.
- Maxwell, T. M., and M. J. Germino. 2022. The effects of cheatgrass invasion on us great basin carbon storage depend on interactions between plant community composition, precipitation seasonality, and soil climate regime. *Journal of Applied Ecology* 59:2863-2873.
- Mealor, B. A., R. D. Mealor, W. K. Kelley, D. L. Bergman, S. A. Burnett, T. W. Decker, B. Fowers, M. E. Herget, C. E. Noseworthy, and J. L. Richards. 2013. Cheatgrass management handbook: Managing an invasive annual grass in the rocky mountain region. B (Laramie, Wyo.); no. 1246.

- Monaco, T. A., J. M. Mangold, B. A. Meador, R. D. Meador, and C. S. Brown. 2017. Downy brome control and impacts on perennial grass abundance: A systematic review spanning 64 years. *Rangeland Ecology & Management* 70:396-404.
- Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlinn, M. Ouellette, C. E. Ribeiro, S. A. Smith T, B. C. Ter, and J. Weedon. 2022. `_vegan`: Community ecology package_.
- Ott, J. E., F. F. Kilkenny, D. D. Summers, and T. W. Thompson. 2019. Long-term vegetation recovery and invasive annual suppression in native and introduced postfire seeding treatments. *Rangeland Ecology & Management* 72:640-653.
- Owen, S. M., C. H. Sieg, and C. A. Gehring. 2011. Rehabilitating downy brome (*Bromus tectorum*)–invaded shrublands using imazapic and seeding with native shrubs. *Invasive Plant Science and Management* 4:223-233.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the great basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7:8126-8151.
- Pinheiro, J., D. Bates, and R Core Team. 2022. `_nlme`: Linear and nonlinear mixed effects models_.
- Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. *Studies in avian biology* 38:531-548.
- Pyke, D. A., S. E. Shaff, J. C. Chambers, E. W. Schupp, B. A. Newingham, M. L. Gray, and L. M. Ellsworth. 2022. Ten-year ecological responses to fuel treatments within semiarid wyoming big sagebrush ecosystems. *Ecosphere* 13:e4176.
- R Core Team. 2022. R: A language and environment for statistical computing Vienna, Austria.
- Radosevich, S. R., J. S. Holt, and C. M. Ghera. 2007. Ecology of weeds and invasive plants: Relationship to agriculture and natural resource management. John Wiley & Sons.
- Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* 19:155-162.
- Rohde, A. T., D. S. Pilliod, and S. J. Novak. 2019. Insect communities in big sagebrush habitat are altered by wildfire and post-fire restoration seeding. *Insect Conservation and Diversity* 12:216-230.

- Rowland, M. M., L. H. Suring, M. J. Wisdom, J. Pye, H. Rauscher, Y. Sands, D. Lee, and J. Beatty. 2010. Assessment of habitat threats to shrublands in the great basin: A case study. Advances in threat assessment and their application to forest and rangeland management. PNW-GTR-802. USDA Forest Service, Pacific Northwest and Southern Research Stations, Portland, Oregon, USA:673-685.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in north america. *The Condor* 106:363-376.
- Sheley, R. L. 2008. Revegetation guidelines for the great basin: Considering invasive weeds. USDA, Agricultural Research Service.
- Sheley, R. L., and B. S. Smith. 2012. Prioritizing invasive plant management strategies. *Rangelands* 34:11-14, 14.
- Souther, S., M. Loeser, T. E. Crews, and T. Sisk. 2019. Complex response of vegetation to grazing suggests need for coordinated, landscape-level approaches to grazing management. *Global Ecology and Conservation* 20:e00770.
- Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* 9:45-64.
- Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* response to fire varies with climate conditions. *Ecosystems* 17:960-973.
- Uselman, S. M., K. A. Snyder, E. A. Leger, and S. E. Duke. 2015. Emergence and early survival of early versus late seral species in great basin restoration in two different soil types. *Applied Vegetation Science* 18:624-636.
- Vermeire, L. T., and M. J. Rinella. 2020. Fall water effects on growing season soil water content and plant productivity. *Rangeland Ecology & Management* 73:252-258.
- Vermeire, L. T., R. C. Waterman, K. O. Reinhart, and M. J. Rinella. 2023. Grazing intensity and seasonality manipulate invasive annual grasses and native vegetation. *Rangeland Ecology & Management*.
- Weber, C. F. 2015. Reduced vertical stratification of soil bacterial community structure and composition is associated with *Bromus tectorum* invasion of sagebrush steppe. *Journal of Arid Environments* 115:90-99.

Wood, C. W., and B. A. Meador. 2022. Identifying structural thresholds in annual grass-invaded rangelands. *Rangeland Ecology & Management* 83:1-9.

Zuur, A. F., and E. N. Ieno. 2016. *Beginner's guide to zero-inflated models with r*. Highland Statistics Limited United Kingdom.

CHAPTER FIVE

THE INFLUENCE OF PLANT SOIL FEEDBACKS ON COMPETITION BETWEEN
BROMUS TECTORUM AND *AGROPYRON SPICATUM*Introduction

Plant-soil interactions are the essential link between above and belowground processes, many of which are essential for ecosystem structure and function (Wardle et al. 2004, Lambers et al. 2008). Primarily these linkages drive the cycling of nutrients; plants provide organic matter for decomposition, which is subsequently mineralized by soil microbes into inorganic, plant available forms. In addition to nutrient cycling, entire soil food webs have been shown to change with plant community alterations (Porazinska et al. 2022). As a result, the specific interaction between plants and their associated soil microbial communities can play an important role in the assemblages of native plant communities and their invaders (Kulmatiski 2018).

Early ecologists recognized that the order in which plants colonized had implications for the trajectory of succession, that is, plant community assemblage (Belyea and Lancaster 1999, Körner et al. 2008). One of the earliest examples is the study at Glacier Bay, which showed the effects of early colonizing nitrogen fixers on the subsequent community trajectory (Crocker and Major 1955). As a result, these alterations became known as priority effects, a term that broadly refers to the impacts of initial colonizers on the soil system and the impact of those changes on the establishment and success of subsequent propagules. Both restoration and invasion ecology have adopted the ideology of priority effects, and emphasized their consideration for the management of invaders and subsequent site restoration (Young et al. 2005, Hess et al. 2019). If

priority effects represent a broad ecological concept, then plant-soil feedbacks (PSFs) (Bever et al. 1997) provide a mechanism by which priority effects operate. Plant-soil feedback theory dictates that for a PSF to occur plants must alter soil microbial community structure, and in turn that change must result in a modification of plant performance (Bever et al. 1997). In their simplest form, PSFs, are a direct interaction between plants and the soil microbial community; the resultant alteration to performance being directly positive (self-promoting) or negative (self-regulating) (Bever et al. 1997). When two plant species are added to this concept, indirect PSF influences can occur. For example, the effects of plant A on the soil microbial community can impact neighboring plant B either positively or negatively (Bever et al. 1997). As a result, PSFs have been proposed to play a role in the maintenance or disruption of diversity, i.e., positive PSFs may promote monodominance and negative PSFs greater diversity (Bever 1999, Bever 2003). Further, these feedbacks have been proposed to play a role in the success of non-native plant invasion and persistence (Reinhart and Callaway 2006). For example, meta-analysis suggests that, in general, native plants more commonly experience a negative PSF (Kulmatiski et al. 2008) and non-natives a positive PSF (Suding et al. 2013).

One of the most dominant non-native plants in the western United States is *Bromus tectorum* L. (cheatgrass) which can create near monocultures in the sagebrush biome via its positive fire-feedback cycle (Pellant 1996, Germino et al. 2016). Following fire or disturbance, *B. tectorum* often establishes a persistent population that is difficult to control or restore back to native rangeland. This is largely due to the strong competitive ability against native perennial grasses at the seedling stage (Hull 1963, Aguirre and Johnson 1991, Dawn and Young 2002, Larson et al. 2018) and harsh growing conditions in rangelands (Kyser et al. 2013, Crist et al.

2019, Kainrath et al. 2022). Historically, *B. tectorum*'s competitive ability has largely been attributed to its winter annual phenology, high relative growth rate, and ability to capture soil nutrients and water more efficiently than native perennial seedlings (Hull 1963, Harris 1977, Melgoza et al. 1990, Aguirre and Johnson 1991, Dawn and Young 2002, Craine 2006, Orloff et al. 2013). However, it has been shown that *B. tectorum* commonly generates a positive PSF greenhouse studies (Blank 2005, Blank and Morgan 2013, O'connor and Prevey 2015, Blank et al. 2016, Blank and Morgan 2016) and alters nitrogen cycling (Rimer and Evans 2006, Leffler et al. 2011a, Schaeffer et al. 2012, Orloff et al. 2013, Reitstetter et al. 2022). As a result, PSFs may provide evidence for previously unconsidered mechanisms of competition, which may be an important aspect of *B. tectorum* invasion ecology.

We propose that PSFs and alterations of nutrient availability are two important mechanisms by which *B. tectorum* imparts priority effects, and that these effects are an important consideration for land managers (Hess et al. 2019). Specifically, we believe that a greater understanding of how PSFs, nutrient availability and competition interact on the landscape could help land managers to leverage soil-based mechanisms to enhance the success of restoration. As a result, our study sought to identify the presence of a PSF for *B. tectorum* and a well-studied native perennial grass *Agropyron spicatum* Pursh. (bluebunch wheatgrass), and if present to determine the direction (positive/negative), strength, and influence of PSFs on the species' competitive performance and soil nutrient availability. To achieve this, we quantified the difference in the above ground biomass production and soil nutrient availability for each species grown in invaded and native soils, in competition and monoculture.

Methods

Field Soil Collection

This study used two field collected soils, *B. tectorum* invaded, and native plant dominated, to serve as soil microbial inoculum. A third sterile soil from the Montana State University (MSU) Plant Growth Center (PGC) was used to serve as a neutral. We refer to these soils as: invaded, native, and neutral, respectively. Two field soils were collected from the Centennial Valley, MT, USA (44.680750, -111.790583) and were classified as a sandy soil (91% sand, 5% silt, 4% clay, hydrometer method) with a pH of 7.6 (1:1 water) by Agvise, Benson, MN, USA. Invaded soil was collected under dense stands (~20-30% cover) of *B. tectorum*, while the native soil was collected from under a variety of native plants; the neutral soil was a pasteurized (70°C for 60 minutes) soil produced by the MSU PGC. Both field soils were collected in the top 8cm (rooting zone) of the soil profile over an area of 5m² for each soil to reduce spatial heterogeneity of the microbial community and reduce the likelihood of capturing a beneficial microbe purely due to chance (Reinhart and Rinella 2016, Rinella and Reinhart 2018, 2019). The soil corer was sterilized between each sample collection by flaming after rinsing with isopropyl alcohol, to eliminate cross-contamination of microbial communities. Field soils were transported in plastic zip-loc bags in a cooler from the field to MSU, where soils were refrigerated for seven days. After refrigeration but before use in the PSF experiment each field soil was homogenized to equally distribute microbes throughout the inoculum.

The neutral soil is a 50:50, by volume, mix of sunshine mix #1 and Montana State University Mix. The sunshine mix #1 is a soil-less mix of Canadian Sphagnum peat moss and Perlite, buffered with dolomitic lime, and containing a starter fertilizer and wetting agent. The

pH was 5.8. The MSU Mix is a mix of mineral soil, Canadian Sphagnum peat moss, and washed concrete sand that is blended at a 1:1:1 by volume ratio. This soil contains Aqua-Gro 2000G as a wetting agent to enhance moisture retention, at the rate of one pound per meter, to increase soil moisture retention, and is steam pasteurized. The 50:50 mix had pH of 7.4, closely matching our field soils.

Experimental Design

This study utilized a two-phase soil conditioning design as suggested by Pernilla Brinkman et al. (2010), in which plants were grown for 30 days in each phase. It is assumed that in the first phase, also referred to as the conditioning phase, seedlings establish a representative soil microbial community. In the second stage, the PSF effects of the microbial community are then quantified by assessing the above ground biomass of the second generation of plants.

At the inception of the conditioning phase, pots (10cm diameter x 23cm ht, 1,806cm³) were filled within three cm of the top with neutral soil; the remaining three centimeters (236cm³) were filled with a layer of field soil to act as an inoculum, or more neutral soil for the third soil treatment. The seeds of *B. tectorum* and *A. spicatum* were sown directly into the top three centimeters of the field soil layer to ensure seedlings and microbes interacted. Similarly, seeds were sewn into the top three centimeters in pots containing only neutral soil. Seedlings were allowed to grow for 30 days. Both species were grown in monoculture and competition in invaded, native, and neutral soil (Table 5.1), which yielded 12 total treatment combinations. *Bromus tectorum* and *A. spicatum* were planted together in equal density (10 plants/species) in each soil type. Similarly, each species was planted in monoculture for each soil type at a density of 10 plants/species to serve as a baseline for assessing competition and PSF effects. In both

phases, two trials were conducted that consisted of four replications per treatment for a sample size of 96 per phase (12 soil-competition combinations x four replications x two trials). Pot locations were randomized and moved periodically during each trial and phase to avoid any patterns arising from environmental variation in the greenhouse. Plants were grown at ~20°C (16-27°C) during the day and ~16°C (10-24°C) at night, with a mean photoperiod of 16 hours. No additional field soil or fertilization was added over the duration of the study. Pots were watered every two days to prevent desiccation. At the end of the first phase, the above ground biomass was clipped at soil level. Below ground biomass, i.e., roots, were not removed. Following aboveground biomass clipping, pots were not watered for 10 days to ensure mortality of the existing plants. At the inception of phase two, seeds were sown in the same combinations, into existing pots, mimicking phase one. Plants were grown again for 30 days in phase two, after which above ground biomass was cut at soil level, air dried for 72 hours at 49 °C, and weighed. Above ground biomass was used to quantify the PSF and competitive effects of each soil and plant combination.

Select Soil Nutrient Availability

During the second phase of the greenhouse study, the following fifteen nutrients were evaluated: ammonium (NH_4^+), nitrate (NO_3^-), zinc (Zn), boron (B), lead (Pb), aluminum (Al), iron (Fe), copper (Cu), magnesium (Mg), manganese (Mn), cadmium (Cd), sulfur (S), potassium (K), phosphorous (P), and calcium (Ca). Plant Root Simulator (PRS®, Western AG Innovations (Saskatoon, Canada)) probes were used to adsorb available nutrients in pots containing, *A. spicatum* in native soil, *B. tectorum* in native soil, *B. tectorum* in *B. tectorum* soil, *B. tectorum* and *A. spicatum* in native soil, and *B. tectorum* and *A. spicatum* in *B. tectorum* soil. Upon

termination of the second phase of the study probes were removed and shipped to Western AG Innovations for analysis, where nutrients were extracted with 0.5N HCl and analyzed colourimetrically with an autoanalyzer. Nutrient availability is reported as micrograms adsorbed per 10cm² over 30 days (µg/10cm²/30 days).

Biomass calculation and Relative Interaction Index

The total number of plants that emerged in each pot was not consistent. As a result the total biomass for each species/pot was divided by the number of surviving plants in that pot to calculate the mean individual biomass per individual per pot which was used for all analysis. We used a relative interaction index (R_{ii}) (Armas et al. 2004), following the similar analysis of Perkins and Nowak (2012), to assess the effects of soil type and competition. The R_{ii} values allow for a standardized comparison of aboveground productivity of the plants grown in different soil types and competitive combinations. Explicitly, the response is bound between negative and positive one, allowing for direct comparison of response strength. To assess the effects of each soil type on the above ground biomass of each species we used the mean aboveground biomass of each species grown in monoculture in each soil type. For example, to calculate the R_{ii} value for *B. tectorum*, we used the following equation:

$$R_{ii} \text{ of } B. \text{ tectorum in Response to Native Soil} = \frac{(B_{\text{Invaded soil}} - B_{\text{Native soil}})}{(B_{\text{Invaded soil}} + B_{\text{Native soil}})}$$

The above ground biomass of the target species, *B. tectorum*, is represented by “B” and the subscript identifies the soil type. It is important to note which soil is listed first in the numerator because it dictates the direction (positive/negative) of the PSF. Similarly, the competition equation:

$$R_{ij} \text{ of } B. \textit{tectorum} \text{ in Response to Competition} = \frac{(B_{\text{Comp. in Invaded soil}} - B_{\text{Mono. in Invaded soil}})}{(B_{\text{Comp. in Invaded soil}} + B_{\text{Mono. in Invaded soil}})}$$

The competition response isolates the effect of the competition from the PSF effect by comparing the aboveground biomass grown in competition and in monoculture within the same soil types. Conversely, by changing the soil type in the equation we assessed the impact of soil on competition. Relative interaction index values greater than zero indicate a positive PSF/facultative effect of competition or soil, values less than zero indicate a negative PSF/competitive effect, and values of zero indicate no PSF/competitive effect.

Statistical Analysis

All statistical analysis was conducted using the software R (R Core Team 2022). Linear mixed effect models (nlme package) (Pinheiro et al. 2022), general linear mixed effect models (lme4 package) (Douglas et al. 2015) and a post-hoc contrast using the emmeans package (Lenth 2022) were conducted to test for differences in R_{ij} and aboveground biomass between each plant-soil combination for each species independently. Similarly, plant available soil nutrients were analyzed using linear mixed effects models and treatment means compared using the emmeans package. An alpha level of 0.05 was used to deem differences in estimated means statistically significant. However, we disregarded any difference in means that were not greater than 10 $\mu\text{g}/10\text{cm}^2/30$ days based on recommendations from Western AG Innovations. Mixed effects models included trial and pot as random effects to account for the nested structure of the experimental design. Assumptions of equal variance and normality were checked by assessing Pearson's Residuals plots and quantile (QQ)-plots, respectively, no extreme violations were present.

To quantify the direction (positive, negative, none) of the plant soil feedback and competitive response we used a two-sided, single sample, t-test to test the null hypothesis that the true mean R_{ii} was equal to zero. Rejection of the null hypothesis indicated that the 95% confidence interval did not include zero, and we took this result to indicate the presence of a positive or negative effect depending on the estimate of the mean. If we did not reject the null hypothesis, i.e., the 95% confidence interval included zero, we presumed that there was no PSF effect.

Results

Aboveground Biomass Production

Our model provided evidence that biomass production was affected by two separate interactions: between species and soil (f: 13.71, df: 2, 83, p: <0.0001), and species and competition type (f: 4.39, df:1,83, p: 0.039). Subsequently, species, competition, and soil type (invaded, native, neutral) were all significantly lower order terms in our analysis of variance (Table 5.2).

Agropyron spicatum produced the same amount of biomass in all soil types when grown in monoculture (0.23-0.36g, SE= 0.10g) (Table 5.3) (Figure 5.1). While *B. tectorum* grew best in the invaded soil (0.62g), compared to native soil (0.31g) and neutral soil (0.11g) (Table 5.3) (Figure 5.1). Comparatively, the two species grown in monoculture produced the same amount of biomass in the neutral and native conditioned soil (Table 5.3) (Figure 5.1) and *B. tectorum* produced more biomass than *A. spicatum* when grown in invaded soil (Table 5.3) (Figure 5.1). When grown in competition, *A. spicatum* and *B. tectorum* produced the same amount of biomass

in all soil types except for invaded soil, where *B. tectorum* produced more biomass (0.46g total) (Table 5.3) (Figure 5.1).

Plant Soil Feedback Response and Competition

We found evidence that PSF relative interaction index (R_{ii}) values differed by soil type (F: 9.94, df: 2,43, p: <0.0001) and by species (F: 88.92, df: 1, 43, p: <0.0001) (Figure 5.2A). We found evidence for a strong positive plant soil feedback for *B. tectorum* (0.39 R_{ii}) when grown in monoculture in invaded soil (Table 5.4) (Figure 5.2A). Conversely, we found no evidence of a plant soil feedback effect for *A. spicatum* when grown in monoculture (-0.15 R_{ii}) (Table 5.4) (Figure 5.2A). When the two species' competitive responses were compared across soil type, we observed a similar pattern. *Bromus tectorum* maintained a positive PSF (0.31 R_{ii}) and *A. spicatum* received no PSF benefit (0.02 R_{ii}) (Figure 5.2B) (Table 5.5).

We observed little evidence for differences in competitive R_{ii} values across soil types, when monoculture and competition responses for each species within each soil type were compared (F: 0.70, df: 2, 42, p: 0.497) (Figure 5.2B). Explicitly, *A. spicatum* had a negligible competitive effect on *B. tectorum*, regardless of soil type (Table 5.6) (Figure 5.3). In contrast, we found that *B. tectorum* had a strong negative competitive effect on *A. spicatum* in both invaded and neutral soil (Table 5.6) (Figure 5.3). There was no competitive effect imposed by *B. tectorum* on *A. spicatum* when *A. spicatum* was grown in the native soil (Table 5.6) (Figure 5.3).

Nutrient Availability

Of the fifteen nutrients tested, only NO_3 differed among treatments (Table 5.5). When *A. spicatum* was grown in monoculture in the native soil, we observed more NO_3 (76 $\mu\text{g}/10\text{cm}^2$) compared to *B. tectorum* monocultures grown in native soil over the 30-day study (Table 5.5).

Similarly, we observed more NO₃ (61.58 µg/10cm²) in pots containing *A. spicatum* monocultures grown in native soil compared to *B. tectorum* monocultures grown in invaded soils (Table 5.5).

Discussion

Our study clearly demonstrates the complexities of the relationship between plants and soil microbial communities and their importance for consideration within the context of plant community assemblage. We confirmed that *B. tectorum* receives a positive plant soil feedback (PSF) when grown in invaded soil, both in monoculture and in competition, which resulted in a greater competitive effect on *A. spicatum*. This is in congruence with other studies that found *B. tectorum* cultivated a positive PSF in the form of increased above ground biomass (Blank and Morgan 2013, 2016). Further our study re-affirms the hypothesis that positive PSFs could be a mechanism for reinforcing monodominance (Reynolds et al. 2003). Interestingly, we found that *A. spicatum* did not exhibit a PSF based on soil type. Making quantitative comparisons between studies is difficult because soil handling, experimental methods, and statistical analysis are not standardized across studies (Rinella and Reinhart 2018, Crawford et al. 2019, Gundale et al. 2019, Rinella and Reinhart 2019). Further, there are few PSF studies that include *A. spicatum* specifically, and fewer comparing *A. spicatum* and *B. tectorum* competition within the context of PSFs. For the few examples that do exist, very few report the actual PSF response values. We found the lack of PSF displayed by *A. spicatum* to be counter to the observed negative PSF for native plants (dominated by *A. spicatum*) in one field study (Kulmatiski et al. 2004) and a positive PSF for *A. spicatum* specifically, in another (Kulmatiski et al. 2017).

Given our findings, we might have expected *B. tectorum* to reduce *A. spicatum* performance with both its strong positive PSF and competitive ability; we did not. Instead, we

found that when grown together in competition, native soil mitigated the competitive effects of *B. tectorum* on *A. spicatum*. This result is counter to the research of Perkins and Nowak (2012) who found soil conditioning did not affect the competitive performance of *A. spicatum* grown in competition with *B. tectorum*. The response observed in this study could promote a greater resilience and resistance to *B. tectorum* invasion in the field and is in accordance with a meta-analysis by Lekberg et al. (2018), who found that PSFs have the ability to moderate the effect of competition.

Partitioning the effects of competition for resources and PSF on plant performance is difficult; soil nutrients and their availability play an important role in competition (Tilman 1982). However, we did not observe differences in nutrient levels that would lead us to believe that competition for soil nutrients were driving the observed differences in plant performance. For example, when *A. spicatum* was grown alone in its own soil did, we observe a greater (~60 $\mu\text{g}/10\text{cm}^2/30$ days) amount of NO_3 , and this difference was not associated with an increase in aboveground biomass production. This agrees with Vasquez et al. (2008), who found that neither *A. spicatum* nor *B. tectorum* produced more biomass in response to increased NO_3 when levels were experimentally increased from 60 $\mu\text{g}/10\text{cm}^2/30$ days to 130 $\mu\text{g}/10\text{cm}^2/30$ days, indicating that changes in NO_3 observed in our study were not of the magnitude necessary to cause competitive differences. Indeed, there is little evidence to suggest that altering soil nitrogen (N) levels impacts the competitive dynamic between these two species (Monaco et al. 2003, James et al. 2011, Leffler et al. 2011a, Orloff et al. 2013). However, we acknowledge that these findings are within the context of a controlled greenhouse environment, and that other environmental

factors such as disturbance frequency and herbivory may change the reliance of these species on nutrient availability.

Like other studies we have explored the impact of PSFs on plant performance and demonstrated its existence for two plant species. However, it remains a limitation of this field that no specific mechanisms are identifiable for PSF responses. This limitation was the exact problem that Bever et al. (1997) identified decades ago and was the impetus for his suggestion of the PSF approach, which acknowledges that the soil microbial community structure and function is a “black box”. This is largely due to the lack of resolution of soil microbial community structure and function as it relates to plant-microbe interactions, in spite of recent advancements in the field of microbiology, such as the use of metabolomics, metatranscriptomics, quorum-sensing (QS), and quantitative stable isotope probing (qSIP) (Revillini et al. 2016, Venturi and Keel 2016).

In this study we attempted to eliminate ambiguity surrounding the role of PSFs in plant performance by accounting for nutrient availability and competition. Bever et al. (2010) suggest three broad mechanisms by which soil microbes can alter plant performance: soil microbes alter resource uptake by plants, plant-microbe mutualisms enhance plant performance, and changes in soil microbial diversity. In our study we did not observe a change in resources that would suggest soil microbes were affecting resource levels in a way that affected plant performance. However, changes in mutualists and soil microbial diversity remain plausible mechanisms for the results we observed. There is some evidence that plant species cultivate unique soil microbial communities (Hannula et al. 2019) and *B. tectorum* has been shown to favor a greater microbial fraction of bacteria vs fungi, when compared to native grasses (Belnap and Phillips 2001).

Specifically, *B. tectorum* does not appear to favor dark septate fungal communities in rangelands and reduces native grass root fungal colonization (Hawkes et al. 2006). Further, a reduction in arbuscular mycorrhizal fungi has been proposed to favor *B. tectorum* and disfavor native grass performance (Owen et al. 2013). This, however, does not provide an explanation for why the native soil, in our study, reduced the competitive effects of *B. tectorum* on *A. spicatum*. Because there is a paucity of research on the soil microbial community of *A. spicatum*, we propose two plausible mechanisms. First, it is possible that native soils contained pathogens that were perpetuated by and tolerable to *A. spicatum* and detrimental to the performance of *B. tectorum*. This mechanism has been proposed as an important consideration for PSF research (Franci 2001, Van Der Putten et al. 2016). Secondly, we hypothesize that *B. tectorum* was not able to utilize or disrupt a mutualistic relationship between *A. spicatum* and the native soil, as suggested by others (Hawkes et al. 2006, Owen et al. 2013). We find some small evidence for this hypothesis within our study, where we observed similar competitive response from *A. spicatum* in both invaded and neutral soils, indicating that the reduced performance of *A. spicatum* was due to the competitive ability of *B. tectorum* and not the soil microbial communities associated with the invaded and neutral soils.

Our findings provide evidence for the consideration of PSFs when assessing the competitive interactions between native and non-native plant species. Our findings suggest that these interactions could have implications for the resistance and resilience of native dominated or non-native dominated sites to invasion or restoration, respectively. For example, Kulmatiski et al. (2017), found that plant abundance and PSF strength were positively correlated for a number of native and non-native plant species, including *A. spicatum* and *B. tectorum*. This finding along

with our study, suggests that species identity, competitive interaction, and relative abundance are important dynamics for consideration when assessing the potential resilience or resistance of a community to invasion. For example, PSF direction appears to be related to both rarity (Klironomos 2002) and origin (Kulmatiski 2019), and we speculate that the combination of positive and negative PSFs within a community could negate any benefit to one individual species, thereby promoting greater diversity (Bever et al. 1997). On the other hand, the density dependent nature of PSFs proposed by Kulmatiski et al. (2017) could reinforce patterns of reduced diversity and dominance by a single species; which has been suggested elsewhere by Suding et al. (2013). Specifically, we envision areas where high-disturbance or frequent fire has reduced diversity and increased the dominance of *B. tectorum*. In this situation it seems plausible that *B. tectorum*'s positive PSF could contribute to its dominance. Similarly, if intact native plant communities are dominated by *A. spicatum*, they could mitigate the competitive effects of *B. tectorum* and thereby its establishment. If true, this would further emphasize the need for managers to mitigate processes that reduce diversity and invasion potential, e.g. disturbance (Lavin et al. 2013).

Resilience and resistance to *B. tectorum* invasion in the sagebrush biome has been attributed to climate, topography, and native plant diversity, especially perennial grasses (Chambers et al. 2014a, Hirsch-Schantz et al. 2014, Chambers et al. 2023). However, the contribution of native perennial bunchgrasses, including *A. spicatum*, to resilience and resistance appear to be highly correlated with unsuitable climate and topography for *B. tectorum* (Chambers et al. 2007b, Reisner et al. 2013, Rodhouse et al. 2014) and mature *A. spicatum* stands are often referred to as resistant to *B. tectorum* invasion (Davies et al. 2015, Davies and Johnson 2017). In

contrast, most greenhouse studies find *A. spicatum* to be competitively inferior to *B. tectorum* at the seedling stage (Perkins and Nowak 2012, Orloff et al. 2013, Larson et al. 2018, Harvey et al. 2020). We propose, based on the findings of our study, that PSFs could provide a previously unconsidered mechanism by which native plants, especially perennial bunchgrasses, help promote the observed resilience and resistance patterns of other studies. Future research will need to expand this hypothesis to a field setting and include a further variety of plant species-soil combinations.

Tables

Table 5.1: The plant-soil feedback experimental design indicating the field soil type (invaded, native, and neutral), which species conditioned each soil (*Bromus tectorum*, *Agropyron spicatum*), and the competition and monocultures of each plant-soil combination.

Plant-soil Feedback Experimental Design		
Conditioning		
Field Soil	Species	
Invaded Soil	<i>B. tectorum</i>	Monoculture: <i>B. tectorum/A. spicatum</i>
		Competition: <i>B. tectorum + A. spicatum</i>
Native Soil	<i>A. spicatum</i>	Monoculture: <i>B. tectorum/A. spicatum</i>
		Competition: <i>B. tectorum + A. spicatum</i>
Neutral Soil	None	Monoculture: <i>B. tectorum/A. spicatum</i>
		Competition: <i>B. tectorum + A. spicatum</i>

Table 5.2: Importance of model variables explanation of biomass production in second phase of a plant soil feedback study. Analysis of variance confirmed the statistical importance of each variable given an alpha level of 0.05. Variables with p-values below the alpha level are listed in bold.

Fixed Effects	df	df	F-value	pue
	1	83	7.13	0.009
Species	1	83	20.82	<0.0001
Competition	1	83	28.25	<0.0001
Soil	2	83	30.41	<0.0001
Species*Competition	1	83	4.40	0.039
Species*Soil	2	83	13.72	<0.0001
Competition*Soil	2	83	1.70	0.189
Species*Competition*Soil	2	83	0.45	0.641

Table 5.3: Estimated individual biomass of each species when grown in competition (comp.) or monoculture (mono.) for each of the soils (Native, Invaded, Neutral). Treatments that are statistically similar, based on an alpha level of 0.05, share the same letter in the compact letter display (CLD) column.

Soil	Species	Competition	Estimate (g)	SE	df	CIL	CIU	CLD
Neutral	<i>A. spicatum</i>	comp.	0.06	0.10	1.00	-1.25	1.36	a
Native	<i>A. spicatum</i>	comp.	0.09	0.10	1.00	-1.21	1.40	a
Invaded	<i>A. spicatum</i>	comp.	0.10	0.10	1.00	-1.21	1.40	a
Neutral	<i>B. tectorum</i>	comp.	0.12	0.10	1.00	-1.19	1.42	a
Native	<i>B. tectorum</i>	comp.	0.21	0.10	1.00	-1.10	1.51	a
Invaded	<i>B. tectorum</i>	comp.	0.47	0.10	1.00	-0.84	1.77	b
Neutral	<i>B. tectorum</i>	mono.	0.12	0.10	1.00	-1.18	1.42	a
Neutral	<i>A. spicatum</i>	mono.	0.24	0.10	1.00	-1.07	1.54	ab
Native	<i>A. spicatum</i>	mono.	0.25	0.10	1.00	-1.05	1.55	ab
Native	<i>B. tectorum</i>	mono.	0.31	0.10	1.00	-0.99	1.62	ab
Invaded	<i>A. spicatum</i>	mono.	0.37	0.10	1.00	-0.94	1.67	b
Invaded	<i>B. tectorum</i>	mono.	0.63	0.10	1.00	-0.68	1.93	c

Table 5.4: The estimated mean relative interaction index (R_{ii}) values for the plant soil feedback (PSF) experiment when both species were grown in monoculture. *Agropyron spicatum* received no PSF benefit, while *B. tectorum* received a positive PSF. Confidence intervals, upper (CIU) and lower (CIL), that contain zero indicate a lack of PSF. Bold values indicate results that are statistically significant given an alpha level of 0.05. Pues indicate the strength of evidence for the inclusion of zero in a 95% confidence interval.

Plant Soil Feedback						
<i>Agropyron spicatum</i>						
Soil	R_{ii}	CIL	CIU	t	df	p
Native	-0.15	-0.34	0.03	1.94	7	0.092
<i>Bromus tectorum</i>						
BRTE	0.39	0.29	0.48	10.15	7	<0.0001

Table 5.5: Two-sided t-test results for the effect of soil type on competition. *Bromus tectorum* was more competitive when competition occurred in the invaded compared to native soil. Conversely, *A. spicatum*'s competitive ability was not altered in the native compared to invaded soil. Confidence intervals, upper (CIU) and lower (CIL), that contain zero indicate a lack of PSF. Bold values indicate results that are statistically significant given an alpha level of 0.05. Pues indicate the strength of evidence for the inclusion of zero in a 95% confidence interval.

Plant Soil Feedback and Competition						
<i>Agropyron spicatum</i>						
Soil	R _{ii}	CIL	CIU	t	df	p
Native	0.02	-0.29	0.33	0.16	7	0.8715
<i>Bromus tectorum</i>						
Invaded	0.31	0.09	0.53	3.5	7	0.012

Table 5.6: Two-sided t-test results for the effect of competition while holding soil type constant, that is, the comparison of species grown in competition compared to when grown in monoculture in each soil type. *Bromus tectorum* was not impacted by *Agropyron spicatum* competition. In neutral and invaded soil, *A. spicatum* was negatively impacted by competition. However, in the native soil *A. spicatum* was not affected. Confidence intervals, upper (CIU) and lower (CIL), that contain zero indicate a lack of PSF. Bold values indicate results that are statistically significant given an alpha level of 0.05. Pues indicate the strength of evidence for the inclusion of zero in a 95% confidence interval (CI).

Competition						
<i>A. spicatum</i>						
Soil Type	R _{ii}	CIL	CIU	t	df	p
Invaded	-0.41	-0.55	-0.27	7.15	7	0.0001
Native	-0.027	-0.57	0.02	2.19	7	0.064
Neutral	-0.58	-0.74	-0.42	8.71	7	<0.0001
<i>B. tectorum</i>						
Invaded	-0.11	-0.39	0.15	1.02	7	0.339
Native	-0.03	-0.38	0.31	0.24	7	0.812
Neutral	0.02	-0.22	0.27	0.22	7	0.831

Table 5.7: The plant available nitrate (NO₃) differed by competition type. Two competition types were analyzed: *Bromus tectorum* (BRTE) and *Agropyron spicatum* (AGSP) grown in monoculture or in competition (BRTE+AGSP). Statistical differences in the estimated mean are represented by differing letters in the compact letter display (CLD) column. Differences that were deemed significant by using an alpha value of 0.05 are in bold. Any groups that share a letter are statistically similar.

Competition	Soil	Mean Availability (µg/10cm²/30 days)	SE	df	CIL	CIU	CLD
BRTE+AGSP	Invaded	11.92	6.35	1	-68.71	92.55	a
BRTE+AGSP	Native	17.2	6.35	1	-63.43	97.83	a
BRTE	Invaded	26.08	6.35	1	-54.55	106.71	a
BRTE	Native	11.64	6.35	1	-68.99	92.27	a
AGSP	Native	87.66	6.35	1	7.03	168.29	b

Figures

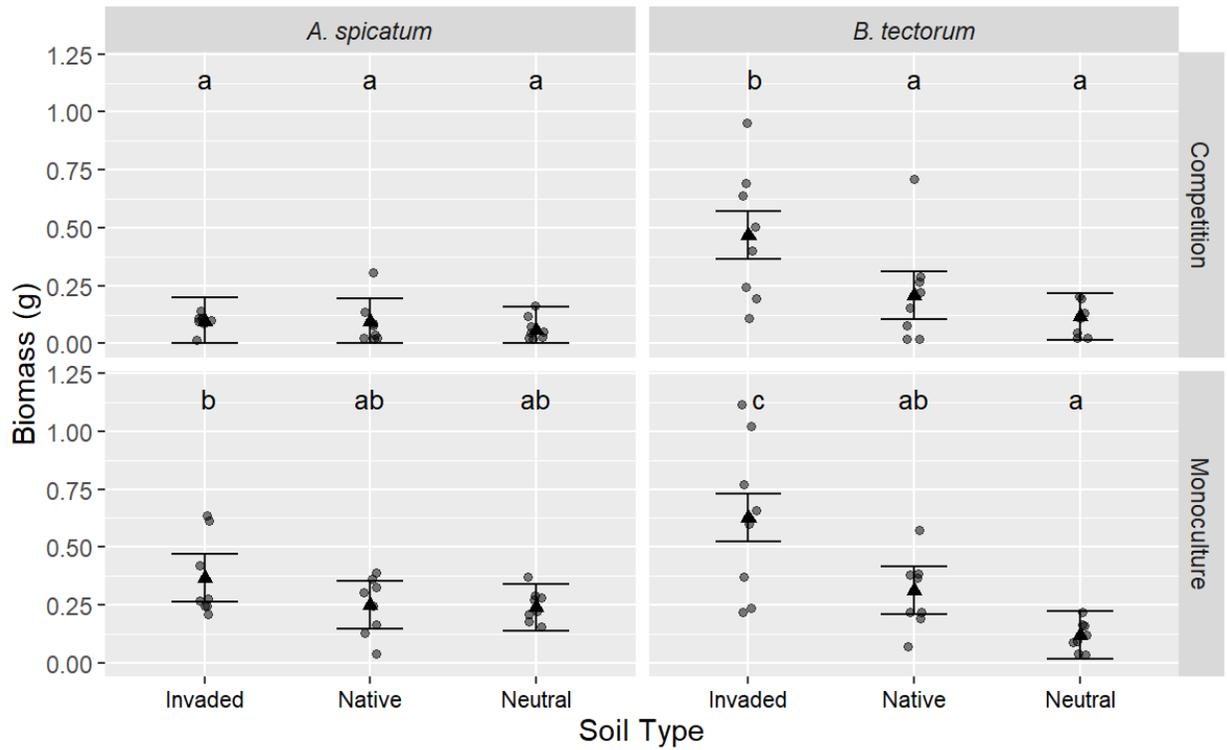


Figure 5.1: Mean individual biomass of *Agropyron spicatum* and *Bromus tectorum* when grown in competition or in monoculture in each soil type. Points are jittered to avoid overlap. Means are represented by black triangles, and the error bars are constructed using the standard errors. Groups that share the same letter are statistically similar based on an alpha level of 0.05.

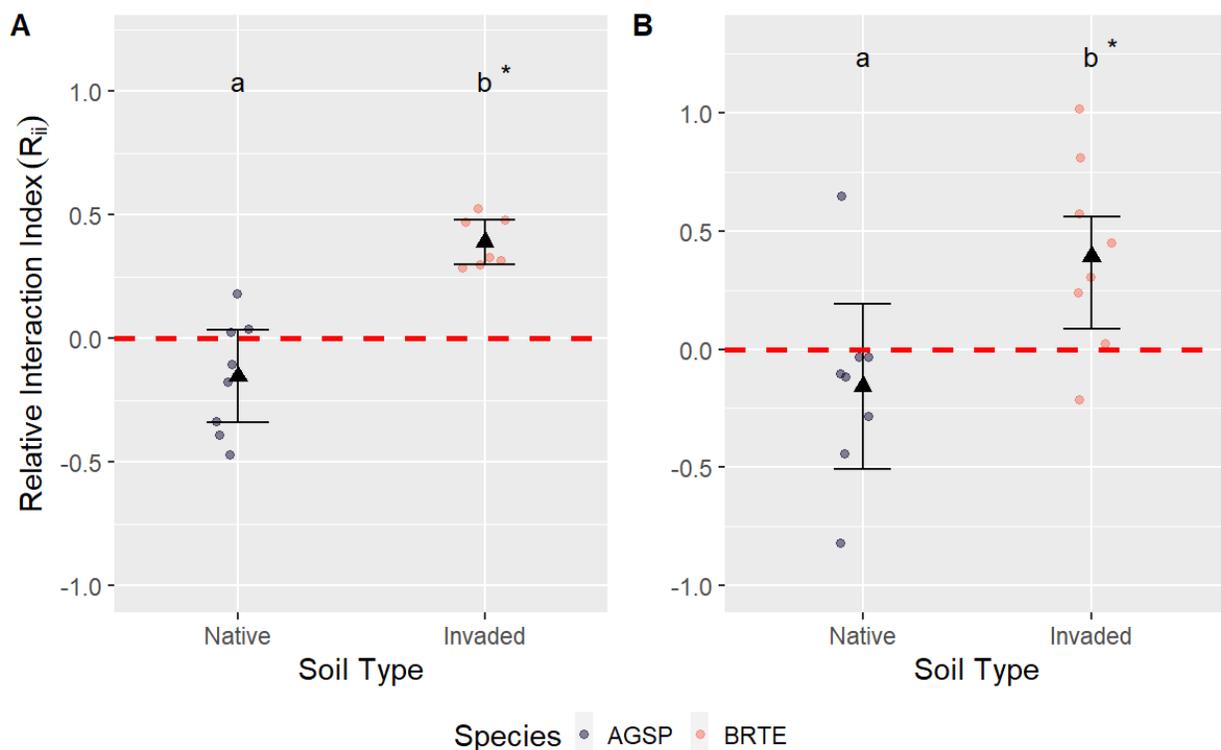


Figure 5.2: The relative response (R_{ii}) of *Agropyron spicatum* (AGSP) and *Bromus tectorum* (BRTE), when grown in their own soil compared to the competitors soil; in monoculture (A) and competition (B). *Agropyron spicatum* performs the same in native compared to invaded when grown in monoculture (A) and competition (B). Conversely, *B tectorum* receives a performance benefit from growing in invaded soil compared to native soil in both monoculture and competition. Points are jittered and represent the observed mean individual R_{ii} for each species-soil combination. Black triangles are the estimated mean R_{ii} bracketed by the 95% confidence intervals (CI). Treatments that share the same letters represent soil combinations that were statistically similar based on an alpha level of 0.05. Letters with an asterisk indicate a 95% CI that does not include zero.

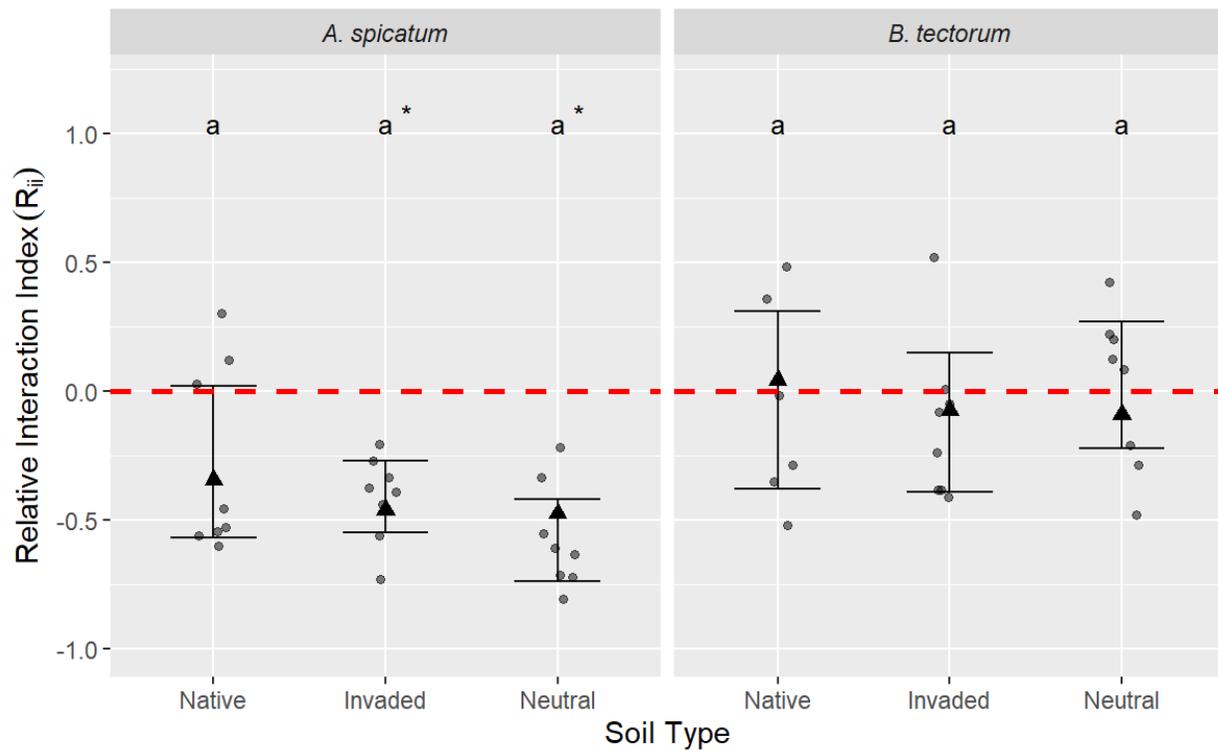


Figure 5.3: The relative interaction index (R_{ij}) of *Agropyron spicatum* and *Bromus tectorum* when grown in monoculture compared to competition in native, invaded, and neutral soils. Soil type did not affect the performance of *B. tectorum*. *Agropyron spicatum* was not affected by competition in native soil but was negatively affected in the invaded and neutral soils. Points are jittered and represent individual R_{ij} values for each soil type. Black triangles are the estimated mean R_{ij} bracketed by the 95% confidence intervals (CI). Treatments that have shared letters represent plant-soil combinations that were statistically similar within species, but not between, based on an alpha level of 0.05. Letters with an asterisk indicate 95% CIs that did not contain zero.

Literature Cited

- Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses.
- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: A new comparative index. *Ecology* 85:2682-2686.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* 11:1261-1275.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402-416.
- Bever, J. 1999. Dynamics within mutualism and the maintenance of diversity: Inference from a model of interguild frequency dependence. *Ecology Letters* 2:52-61.
- Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytologist* 157:465-473.
- Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D. Stock, M. Tibbett, and M. Zobel. 2010. Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution* 25:468-478.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology* 85:561-573.
- Blank, R., B. Mackey, and T. Morgan. 2016. Do a native and two exotic grasses respond differently in soils conditioned by native vegetation versus an exotic grass? *Rhizosphere* 2:38-47.
- Blank, R. R. 2005. Plant-soil relationships of *Bromus tectorum*: Monitoring an invasion for five years. *in* Abstracts, Annual Meeting of the Soil Science Society of America, Salt Lake City, Utah.
- Blank, R. R., and T. Morgan. 2013. Soil engineering facilitates downy brome (*Bromus tectorum*) growth—a case study. *Invasive Plant Science and Management* 6:391-400.
- Blank, R. R., and T. Morgan. 2016. Plant interactions with soils conditioned by different vegetation: A potential explanation of *Bromus tectorum* l. Invasion into salt-deserts? *Journal of Arid Environments* 124:233-238.

- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* l. Invasion in cold desert shrublands of western north america. *Ecosystems* 17:360-375.
- Chambers, J. C., J. L. Brown, J. B. Bradford, D. I. Board, S. B. Campbell, K. J. Clause, B. Hanberry, D. R. Schlaepfer, and A. K. Urza. 2023. New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, united states. *Frontiers in Ecology and Evolution* 10:1009268.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes great basin sagebrush ecosystems invisable by *Bromus tectorum*? *Ecological monographs* 77:117-145.
- Craine, J. M. 2006. Competition for nutrients and optimal root allocation. *Plant and soil* 285:171-185.
- Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, A. E. Strand, K. N. Suding, and J. Umbanhowar. 2019. When and where plant-soil feedback may promote plant coexistence: A meta-analysis. *Ecology Letters* 22:1274-1284.
- Crist, M. R., J. C. Chambers, S. L. Phillips, K. L. Prentice, and L. A. Wiechman. 2019. Science framework for conservation and restoration of the sagebrush biome: Linking the department of the interior's integrated rangeland fire management strategy to long-term strategic conservation actions. Part 2. Management applications. General Technical Report-Rocky Mountain Research Station, USDA Forest Service.
- Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at glacier bay, alaska. *Journal of Ecology* 43:427-448.
- Davies, K. W., C. S. Boyd, D. D. Johnson, A. M. Nafus, and M. D. Madsen. 2015. Success of seeding native compared with introduced perennial vegetation for revegetating medusahead-invaded sagebrush rangeland. *Rangeland Ecology & Management* 68:224-230.
- Davies, K. W., and D. D. Johnson. 2017. Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. *Rangeland Ecology & Management* 70:748-754.
- Dawn, L. R., and J. A. Young. 2002. Cheatgrass competition and establishment of desert needlegrass seedlings. *Journal of Range Management* 55:70-72.

- Douglas, B., M. Martin, B. Ben, and W. Steve. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1):1-48.
- Francl, L. J. 2001. The disease triangle: A plant pathological paradigm revisited. *The Plant Health Instructor* 10.
- Gehring, C. A., M. Hayer, L. Flores-Rentería, A. F. Krohn, E. Schwartz, and P. Dijkstra. 2016. Cheatgrass invasion alters the abundance and composition of dark septate fungal communities in sagebrush steppe. *Botany* 94:481-491.
- Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus *bromus*. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:61-95.
- Gundale, M. J., D. A. Wardle, P. Kardol, and M. C. Nilsson. 2019. Comparison of plant–soil feedback experimental approaches for testing soil biotic interactions among ecosystems. *New Phytologist* 221:577-587.
- Hannula, S. E., A. M. Kielak, K. Steinauer, M. Huberty, R. Jongen, J. R. De Long, R. Heinen, and T. M. Bezemer. 2019. Time after time: Temporal variation in the effects of grass and forb species on soil bacterial and fungal communities. *MBio* 10:e02635-02619.
- Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. *Rangeland Ecology & Management/Journal of Range Management Archives* 30:172-177.
- Harvey, A. J., S. C. Simanonok, L. J. Rew, T. S. Prather, and J. M. Mangold. 2020. Effect of *pseudoroegneria spicata* (bluebunch wheatgrass) seeding date on establishment and resistance to invasion by *Bromus tectorum* (cheatgrass). *Ecological Restoration* 38:145-152.
- Hawkes, C. V., J. Belnap, C. D’Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and soil* 281:369-380.
- Hess, M. C., F. Mesléard, and E. Buisson. 2019. Priority effects: Emerging principles for invasive plant species management. *Ecological Engineering* 127:48-57.
- Hirsch-Schantz, M. C., T. A. Monaco, C. A. Call, and R. L. Sheley. 2014. Large-scale downy brome treatments alter plant-soil relationships and promote perennial grasses in salt desert shrublands. *Rangeland Ecology & Management* 67:255-265.
- Hull, A. 1963. Competition and water requirements of cheatgrass and wheatgrass in the greenhouse. *Rangeland Ecology & Management/Journal of Range Management Archives* 16:199-204.

- James, J., R. Drenovsky, T. Monaco, and M. Rinella. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: Effective strategy or incomplete framework? *Ecological Applications* 21:490-502.
- Kainrath, N. B., P. Dijkstra, C. A. Gehring, C. Updike, and K. C. Grady. 2022. Water as the key to sagebrush restoration success in cheatgrass-invaded ecosystems. *Restoration Ecology* 30:e13473.
- Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67-70.
- Körner, C., J. Stöcklin, L. Reuther-Thiébaud, and S. Pelaez-Riedl. 2008. Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist* 177:698-705.
- Kulmatiski, A. 2018. Community-level plant–soil feedbacks explain landscape distribution of native and non-native plants. *Ecology and Evolution* 8:2041-2049.
- Kulmatiski, A. 2019. Plant-soil feedbacks predict native but not non-native plant community composition: A 7-year common-garden experiment. *Frontiers in Ecology and Evolution* 7.
- Kulmatiski, A., K. H. Beard, J. M. Norton, J. E. Heavilin, L. E. Forero, and J. Grenzer. 2017. Live long and prosper: Plant–soil feedback, lifespan, and landscape abundance covary. *Ecology* 98:3063-3073.
- Kulmatiski, A., K. H. Beard, and J. M. Stark. 2004. Finding endemic soil-based controls for weed growth. *Weed Technology* 18:1353-1358, 1356.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant–soil feedbacks: A meta-analytical review. *Ecology Letters* 11:980-992.
- Kyser, G. B., R. G. Wilson, J. Zhang, and J. M. DiTomaso. 2013. Herbicide-assisted restoration of great basin sagebrush steppe infested with medusahead and downy brome. *Rangeland Ecology and Management* 66:588-596, 589.
- Lambers, H., F. S. Chapin, and T. L. Pons. 2008. *Plant physiological ecology*. Springer.
- Larson, C. D., E. A. Lehnhoff, C. Noffsinger, and L. J. Rew. 2018. Competition between cheatgrass and bluebunch wheatgrass is altered by temperature, resource availability, and atmospheric co2 concentration. *Oecologia* 186:855-868.
- Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern idaho, u.S.A. *Ecology and Evolution* 3:1626-1641.

- Leffler, A., T. Monaco, and J. James. 2011. Nitrogen acquisition by annual and perennial grass seedlings: Testing the roles of performance and plasticity to explain plant invasion. *Plant Ecology* 212:1601-1611.
- Lekberg, Y., J. D. Bever, R. A. Bunn, R. M. Callaway, M. M. Hart, S. N. Kivlin, J. Klironomos, B. G. Larkin, J. L. Maron, and K. O. Reinhart. 2018. Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. *Ecology Letters* 21:1268-1281.
- Lenth, R. 2022. `_emmeans`: Estimated marginal means, aka least-squares means_.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: Competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Rangeland Ecology & Management/Journal of Range Management Archives* 56:282-290.
- O'Connor, J. J., and J. S. Prevey. 2015. Effects of short-term soil conditioning by cheatgrass and western wheatgrass.
- Orloff, L. N., J. M. Mangold, and F. D. Menalled. 2013. Role of size and nitrogen in competition between annual and perennial grasses. *Invasive Plant Science and Management* 6:87-98.
- Owen, S. M., C. H. Sieg, N. C. Johnson, and C. A. Gehring. 2013. Exotic cheatgrass and loss of soil biota decrease the performance of a native grass. *Biological Invasions* 15:2503-2517.
- Pellant, M. 1996. Cheatgrass: The invader that won the west. US Department of the Interior, Bureau of Land Management.
- Perkins, L. B., and R. S. Nowak. 2012. Soil conditioning and plant–soil feedbacks affect competitive relationships between native and invasive grasses. *Plant Ecology* 213:1337-1344.
- Pernilla Brinkman, E., W. H. Van der Putten, E.-J. Bakker, and K. J. F. Verhoeven. 2010. Plant–soil feedback: Experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology* 98:1063-1073.
- Pinheiro, J., D. Bates, and R Core Team. 2022. `_nlme`: Linear and nonlinear mixed effects models_.

- Porazinska, D. L., T. R. Seastedt, E. M. Gendron, and S. K. Schmidt. 2022. Invasive annual cheatgrass enhances the abundance of native microbial and microinvertebrate eukaryotes but reduces invasive earthworms. *Plant and soil* 473:591-604.
- R Core Team. 2022. R: A language and environment for statistical computing Vienna, Austria.
- Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. *New Phytologist* 170:445-457.
- Reinhart, K. O., and M. J. Rinella. 2016. A common soil handling technique can generate incorrect estimates of soil biota effects on plants. *New Phytologist* 210:786-789.
- Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* 50:1039-1049.
- Reitstetter, R., B. Yang, A. D. Tews, and A. Barberán. 2022. Soil microbial communities and nitrogen associated with cheatgrass invasion in a sagebrush shrubland. *Plant and soil*.
- Revillini, D., C. A. Gehring, and N. C. Johnson. 2016. The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. *Functional Ecology* 30:1086-1098.
- Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. Grassroots ecology: Plant–microbe–soil interactions as drivers of plant community structure and dynamics. *Ecology* 84:2281-2291.
- Rimer, R., and R. Evans. 2006. Invasion of downy brome (*Bromus tectorum* l.) causes rapid changes in the nitrogen cycle. *The American midland naturalist* 156:252-258.
- Rinella, M. J., and K. O. Reinhart. 2018. Toward more robust plant-soil feedback research. *Ecology* 99:550-556.
- Rinella, M. J., and K. O. Reinhart. 2019. Toward more robust plant-soil feedback research: Reply. *Ecology* 100:e02810.
- Rodhouse, T. J., K. M. Irvine, R. L. Sheley, B. S. Smith, S. Hoh, D. M. Esposito, and R. Mata-Gonzalez. 2014. Predicting foundation bunchgrass species abundances: Model-assisted decision-making in protected-area sagebrush steppe. *Ecosphere* 5:art108.
- Schaeffer, S. M., S. E. Ziegler, J. Belnap, and R. Evans. 2012. Effects of *Bromus tectorum* invasion on microbial carbon and nitrogen cycling in two adjacent undisturbed arid grassland communities. *Biogeochemistry* 111:427-441.

- Suding, K. N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and W. H. van der Putten. 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology* 101:298-308.
- Tilman, D. 1982. Resource competition and community structure. Princeton university press.
- van der Putten, W. H., M. A. Bradford, E. Pernilla Brinkman, T. F. van de Voorde, and G. Veen. 2016. Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology* 30:1109-1121.
- Vasquez, E., R. Sheley, and T. Svejcar. 2008. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Science and Management* 1:287-295.
- Venturi, V., and C. Keel. 2016. Signaling in the rhizosphere. *Trends in plant science* 21:187-198.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304:1629.
- Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecology Letters* 8:662-673.

CHAPTER SIX

CONCLUSIONS AND FUTURE RESEARCH

Our series of studies suggest that *Bromus tectorum* L. (cheatgrass) management in the Middle Rockies ecoregion is achievable, similar to the findings of (Mangold et al. 2013). However, reductions in *B. tectorum* abundance did not result in an increase of species diversity, richness, or native perennial grass biomass, an important consideration for land managers. Further, we found that *B. tectorum* did begin to recover post-herbicide, albeit not completely over the four years of our study. Surprisingly, *B. tectorum* abundance did not increase in the reference area where small abundances of *B. tectorum* occurred. We interpreted this finding as evidence for the hypothesized resilience of this system to *B. tectorum* invasion and speculate that there is some unconsidered factor differentiating sprayed and reference communities, perhaps site-specific disturbance, because all sites were on steep, south-facing slopes. On a broader scale, our study suggests that this system's resiliency could be shifting. Prior research suggests that cooler and wetter climate and native perennial grass abundance are major factors determining the resilience and resistance of ecosystems to *B. tectorum* invasion (Folke et al. 2004, Chambers et al. 2014a, Roundy et al. 2018, Chambers et al. 2023). We observed a departure in precipitation and temperature from 30-year averages, and these drier and warmer conditions were correlated with a greater community component of *B. tectorum* and native perennial forbs, and a reduced native perennial grass component. However, it is also possible that fluctuations of this kind are common occurrence and well within the range of natural variation for this system (Anderson and Inouye 2001), emphasizing the need for long-term vegetation monitoring.

In areas where disturbance is the obvious driver of *B. tectorum* invasion, e.g., rangeland water tanks, multiple methods of management action may be needed. Interestingly, we found that intense fall grazing and trampling, by cattle, at water tanks reduced the abundance of *B. tectorum* without the aid of herbicide. We speculate that if herbicide application had been applied post-emergence that the combination of grazing and herbicide together would have led to an even greater reduction in *B. tectorum* abundance. This approach may be necessary for multiple seasons to exhaust the non-native seedbank. Unexpectedly, we found that herbicide application, though unsuccessful in reducing *B. tectorum* abundance, resulted in an increase of nitrate and sulfur in plots that were not grazed. We speculate that this pulse in nutrients, especially nitrate, could have consequences for the competitive dynamics of some species if nitrate is limiting in this system. From a restoration perspective, we observed limited establishment of our seeded species, including plots where we observed a nitrate and sulfur pulse. It does not appear that a nutrient pulse favored the establishment of our seeded species, but this pulse was an unintended consequence of herbicide application. We propose that once the non-native seedbank is reduced, restoration seeding should follow. To maximize the establishment potential of the restoration species, ideally, seeding should occur concomitantly with favorable precipitation, no herbicide, and no grazing. Though our seed mixes failed to establish with vigor in the field, our greenhouse study suggests that a native ruderal grass species mix with the addition of *Triticale* will provide the best competition with *B. tectorum*. This suggestion is largely supported by the observation that *Triticale* had the greatest competitive effect on *B. tectorum* in our greenhouse study and was the only species to establish in both grazed and non-grazed field settings.

Ultimately the establishment of species and subsequent community composition and trajectory are dictated by the interaction of species. That is, their interaction with one another, competitively, and with their environment. We investigated the role of plant-soil feedbacks (PSF) in competition between *B. tectorum* and *Agropyron spicatum* Pursh. (bluebunch wheatgrass). In doing so, we found that *B. tectorum* produces a positive PSF that is not affected by competition. Interestingly, this was not the case for *A. spicatum*, which did not have a PSF response. Surprisingly though, *A. spicatum* was not affected by *B. tectorum* competition when it was grown in native soil. This suggests that soils conditioned by native plants could play a role in the resilience and resistance to *B. tectorum* invasion. Conversely, the strong PSF observed for *B. tectorum* could promote its dominance once established. Both findings support the hypothesis that PSFs have the potential to contribute to shifts in plant community assemblage (Bever 2003, Wardle et al. 2004, Crawford et al. 2019).

This research has expanded our understanding of *B. tectorum* and native plant ecology in the high-elevation sagebrush steppe of southwest Montana and the Middle Rockies ecoregion. Exciting venues of research await. Namely, the investigation of nutrient pulses following herbicide application, which could alter nutrient cycling, soil microbial community composition and restoration seeding success. Additionally, further exploration of the potential role of PSFs in resilience and resistance of non-native plant invasion seems prudent. At a landscape scale, a wider investigation of resiliency to *B. tectorum* invasion and management that encompasses a greater diversity of environmental gradients, e.g., differing aspects, slope angles, and elevations is needed. For example, we assessed the resiliency of plant communities to *B. tectorum* and management across a narrow window of environmental gradients, that is, steep south facing

slopes. Expanding future research by comparing the community response and assemblages across elevation, aspects, and slope would allow for a more accurate depiction of this ecosystem's resilience to changes in temperature, moisture, and management. At a microsite level, the mechanisms that allow persistence of *B. tectorum* on some but not all of the steep south facing slopes in this study would be another intriguing avenue of research. Lastly, it has been a common trend in many studies to promote long-term monitoring of plant communities, and we unsurprisingly support this.

Literature Cited

- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological monographs* 71:531-556.
- Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytologist* 157:465-473.
- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegee, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* l. Invasion in cold desert shrublands of western north america. *Ecosystems* 17:360-375.
- Chambers, J. C., J. L. Brown, J. B. Bradford, D. I. Board, S. B. Campbell, K. J. Clause, B. Hanberry, D. R. Schlaepfer, and A. K. Urza. 2023. New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, united states. *Frontiers in Ecology and Evolution* 10:1009268.
- Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, A. E. Strand, K. N. Suding, and J. Umbanhowar. 2019. When and where plant-soil feedback may promote plant coexistence: A meta-analysis. *Ecology Letters* 22:1274-1284.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557-581.
- Mangold, J., H. Parkinson, C. Duncan, P. Rice, E. Davis, and F. Menalled. 2013. Downy brome (*Bromus tectorum*) control with imazapic on montana grasslands. *Invasive Plant Science and Management* 6:554-558.
- Roundy, B. A., J. C. Chambers, D. A. Pyke, R. F. Miller, R. J. Tausch, E. W. Schupp, B. Rau, and T. Gruell. 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. *Ecosphere* 9:e02417.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304:1629.

LITERATURE CITED

- Agrawal, A. A., P. M. Kotanen, C. E. Mitchell, A. G. Power, W. Godsoe, and J. Klironomos. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above-and belowground enemies. *Ecology* **86**:2979-2989.
- Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses.
- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological monographs* **71**:531-556.
- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: A new comparative index. *Ecology* **85**:2682-2686.
- Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of intermountain perennial and weedy annual grasses. *Rangeland Ecology & Management/Journal of Range Management Archives* **51**:584-589.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global change biology* **19**:173-183.
- Bansal, S., and R. L. Sheley. 2016. Annual grass invasion in sagebrush steppe: The relative importance of climate, soil properties and biotic interactions. *Oecologia* **181**:543-557.
- Beaumelle, L., L. Tison, N. Eisenhauer, J. Hines, S. Malladi, C. Pelosi, L. Thouvenot, and H. R. Phillips. 2023. Pesticide effects on soil fauna communities—a meta-analysis. *Journal of Applied Ecology*.
- Beck, J. L., and J. M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen–sagebrush summer range. *Rangeland Ecology & Management* **58**:135-147.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: Response to annual grass (*bromus tectorum*) invasion. *Ecological Applications* **11**:1261-1275.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* **86**:402-416.
- Beste, C. 1983. *Herbicide handbook of the weed science society of america*. Weed Science Society of America.
- Bever, J. 1999. Dynamics within mutualism and the maintenance of diversity: Inference from a model of interguild frequency dependence. *Ecology Letters* **2**:52-61.

- Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytologist* **157**:465-473.
- Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D. Stock, M. Tibbett, and M. Zobel. 2010. Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution* **25**:468-478.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology* **85**:561-573.
- Bezemer, T. M., and W. H. van der Putten. 2007. Diversity and stability in plant communities. *Nature* **446**:E6-E7.
- Blank, R., B. Mackey, and T. Morgan. 2016. Do a native and two exotic grasses respond differently in soils conditioned by native vegetation versus an exotic grass? *Rhizosphere* **2**:38-47.
- Blank, R. R. 2005. Plant-soil relationships of *bromus tectorum*: Monitoring an invasion for five years. *in* Abstracts, Annual Meeting of the Soil Science Society of America, Salt Lake City, Utah.
- Blank, R. R. 2010. Intraspecific and interspecific pair-wise seedling competition between exotic annual grasses and native perennials: Plant–soil relationships. *Plant and soil* **326**:331-343.
- Blank, R. R., and T. Morgan. 2013. Soil engineering facilitates downy brome (*bromus tectorum*) growth—a case study. *Invasive Plant Science and Management* **6**:391-400.
- Blank, R. R., and T. Morgan. 2016. Plant interactions with soils conditioned by different vegetation: A potential explanation of *bromus tectorum* l. Invasion into salt-deserts? *Journal of Arid Environments* **124**:233-238.
- Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003. Inorganic n turnover and availability in annual-and perennial-dominated soils in a northern utah shrub-steppe ecosystem. *Biogeochemistry* **66**:311-330.
- Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016a. *Bromus* response to climate and projected changes with climate change. Pages 257-274 *Exotic brome-grasses in arid and semiarid ecosystems of the western us*. Springer.
- Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016b. *Bromus* response to climate and projected changes with climate change. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:257-274.

- Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M.-N. Tuanmu. 2018. Cheatgrass (*bromus tectorum*) distribution in the intermountain western united states and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions* **20**:1493-1506.
- Brakeholder, B. 2021. *Bromus tectorum* (cheatgrass) predicted suitable habitat model created on february 22, 2021.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern wisconsin. *Ecological monographs* **27**:326-349.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Boker. 2017. Glimtmb balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9(2)**:378-400.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* **54**:677-688.
- Brummer, T. J., K. T. Taylor, J. Rotella, B. D. Maxwell, L. J. Rew, and M. Lavin. 2016. Drivers of *bromus tectorum* abundance in the western north american sagebrush steppe. *Ecosystems* **19**:986-1000.
- Burke, I. C. 1989. Control of nitrogen mineralization a sagebrush steppe landscape. *Ecology* **70**:1115-1126.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* **2**:436-443.
- Calo, A., S. Brause, and S. Jones. 2012. Integrated treatment with a prescribed burn and postemergent herbicide demonstrates initial success in managing cheatgrass in a northern colorado natural area. *Natural Areas Journal* **32**:300-304.
- Chambers, J., B. A. Roundy, R. Blank, S. Meyer, and A. Whittaker. 2007a. What makes great basin sagebrush ecosystems invasible by *bromus tectorum*? *Ecol. Monogr.* **77**:117-145.
- Chambers, J. C. 2016. Using resilience and resistance concepts to manage threats to sagebrush ecosystems, gunnison sage-grouse, and greater sage-grouse in their eastern range: A strategic multi-scale approach.
- Chambers, J. C., C. R. Allen, and S. A. Cushman. 2019. Operationalizing ecological resilience concepts for managing species and ecosystems at risk. *Frontiers in Ecology and Evolution* **7**:241.

- Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegee, R. F. Miller, and D. A. Pyke. 2014a. Resilience to stress and disturbance, and resistance to *bromus tectorum* l. Invasion in cold desert shrublands of western north america. *Ecosystems* **17**:360-375.
- Chambers, J. C., J. L. Brown, J. B. Bradford, D. I. Board, S. B. Campbell, K. J. Clause, B. Hanberry, D. R. Schlaepfer, and A. K. Urza. 2023. New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, united states. *Frontiers in Ecology and Evolution* **10**:1009268.
- Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. S. Clair. 2016. Plant community resistance to invasion by *bromus* species: The roles of community attributes, *bromus* interactions with plant communities, and *bromus* traits. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:275-304.
- Chambers, J. C., D. A. Pyke, J. D. Maestas, M. Pellant, C. S. Boyd, S. B. Campbell, S. Espinosa, D. W. Havlina, K. E. Mayer, and A. Wuenschel. 2014b. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: A strategic multi-scale approach. United States Department of Agriculture, Forest Service, Rocky Mountain .
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007b. What makes great basin sagebrush ecosystems invisable by *bromus tectorum*? *Ecological monographs* **77**:117-145.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* **150**:519-553.
- Clements, C. D., D. N. Harmon, and R. R. Blank. 2022. Seed mix performance and cheatgrass suppression on arid rangelands. *Rangelands* **44**:129-135.
- Clements, F. E. 1916. *Plant succession: An analysis of the development of vegetation*. Carnegie institution of Washington.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science* **199**:1302-1310.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**:1119-1144.
- Cook, C. W. 1952. Nutritive value of cheatgrass and crested wheatgrass on spring ranges of utah. *Rangeland Ecology & Management/Journal of Range Management Archives* **5**:331-337.

- Corvallis Environmental Research Laboratory, and J. M. Omernik. 1995. Level iii ecoregions of the continental united states. Corvallis Environmental Research Laboratory, US Environmental Protection Agency.
- CPNWH. 2017. Consortium of Pacific Northwest Herbaria Specimen Database.
- Craine, J. M. 2006. Competition for nutrients and optimal root allocation. *Plant and soil* **285**:171-185.
- Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, A. E. Strand, K. N. Suding, and J. Umbanhowar. 2019. When and where plant-soil feedback may promote plant coexistence: A meta-analysis. *Ecology Letters* **22**:1274-1284.
- Crist, M. R., J. C. Chambers, S. L. Phillips, K. L. Prentice, and L. A. Wiechman. 2019. Science framework for conservation and restoration of the sagebrush biome: Linking the department of the interior's integrated rangeland fire management strategy to long-term strategic conservation actions. Part 2. Management applications. General Technical Report-Rocky Mountain Research Station, USDA Forest Service.
- Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at glacier bay, alaska. *Journal of Ecology* **43**:427-448.
- Culver, D. R. 1994. Floristic analysis of the centennial region, montana. Montana State University-Bozeman, College of Letters & Science.
- Cutting, K. A., J. J. Rotella, J. A. Waxe, A. O'Harra, S. R. Schroff, L. Berkeley, M. Szczypinski, A. R. Litt, and B. F. Sowell. 2021. Resource allocation effects on the timing of reproduction in an avian habitat specialist. *Ecosphere* **12**:e03700.
- D'Antonio, C., J. Levine, and M. Thomsen. 2001. Ecosystem resistance to invasion and the role of propagule supply: A california perspective. *Journal of Mediterranean Ecology* **2**:233-246.
- D'Antonio, C. M., and M. Thomsen. 2004. Ecological resistance in theory and practice1. *Weed Technology* **18**:1572-1577.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics* **23**:63-87.
- Daubenmire, R. 1970. Steppe vegetation of washington. Technical Bulletin. Washington Agricultural Experiment Station:131 pp.
- Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* **33**:43-64.

- Davies, K. W. 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia* **167**:481-491.
- Davies, K. W., J. D. Bates, B. Perryman, and S. Arispe. 2021. Fall-winter grazing after fire in annual grass-invaded sagebrush steppe reduced annuals and increased a native bunchgrass. *Rangeland Ecology & Management* **77**:1-8.
- Davies, K. W., C. S. Boyd, D. D. Johnson, A. M. Nafus, and M. D. Madsen. 2015. Success of seeding native compared with introduced perennial vegetation for revegetating medusahead-invaded sagebrush rangeland. *Rangeland Ecology & Management* **68**:224-230.
- Davies, K. W., and D. D. Johnson. 2017. Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. *Rangeland Ecology & Management* **70**:748-754.
- Davies, K. W., and R. L. Sheley. 2011. Promoting native vegetation and diversity in exotic annual grass infestations. *Restoration Ecology* **19**:159-165.
- Davis, M. A. 2009. *Invasion biology*. Oxford University Press on Demand.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* **88**:528-534.
- Dawn, L. R., and J. A. Young. 2002. Cheatgrass competition and establishment of desert needlegrass seedlings. *Journal of Range Management* **55**:70-72.
- De Angelis, D. L. 1975. Stability and connectance in food web models. *Ecology* **56**:238-243.
- Diamond, J. M., C. A. Call, and N. Devoe. 2012. Effects of targeted grazing and prescribed burning on community and seed dynamics of a downy brome (*bromus tectorum*)–dominated landscape. *Invasive Plant Science and Management* **5**:259-269.
- DiTomaso, J. M., G. B. Kyser, S. R. Oneto, R. G. Wilson, S. B. Orloff, L. W. Anderson, S. D. Wright, J. A. Roncoroni, T. L. Miller, and T. S. Prather. 2013. Weed control in natural areas in the western united states. Weed Research and Information Center, University of California **544**.
- Doherty, K., D. M. Theobald, J. B. Bradford, L. A. Wiechman, G. Bedrosian, C. S. Boyd, M. Cahill, P. S. Coates, M. K. Creutzburg, and M. R. Crist. 2022a. A sagebrush conservation design to proactively restore america's sagebrush biome. 2331-1258, US Geological Survey.

- Doherty, K., D. M. Theobald, J. B. Bradford, L. A. Wiechman, G. Bedrosian, C. S. Boyd, M. Cahill, P. S. Coates, M. K. Creutzburg, M. R. Crist, S. P. Finn, A. V. Kumar, C. E. Littlefield, J. D. Maestas, K. L. Prentice, B. G. Prochazka, T. E. Remington, W. D. Sparklin, J. C. Tull, Z. Wurtzebach, and K. A. Zeller. 2022b. A sagebrush conservation design to proactively restore america's sagebrush biome. Report 2022-1081, Reston, VA.
- Douglas, B., M. Martin, B. Ben, and W. Steve. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**(1):1-48.
- Earnst, S. L., and A. L. Holmes. 2012. Bird—habitat relationships in interior columbia basin shrubsteppe. *The Condor* **114**:15-29.
- Ehlert, K. A., R. E. Engel, and J. M. Mangold. 2015. Imazapic activity in a semiarid climate in downy brome (*bromus tectorum*)—infested rangeland and crp sites. *Weed Technology* **29**:472-479.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**:503-523.
- Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* **41**:59-80.
- Eisenhauer, N., H. BEBLER, C. Engels, G. Gleixner, M. Habekost, A. Milcu, S. Partsch, A. C. Sabais, C. Scherber, and S. Steinbeiss. 2010. Plant diversity effects on soil microorganisms support the singular hypothesis. *Ecology* **91**:485-496.
- Eiswerth, M. E., T. D. Darden, W. S. Johnson, J. Agapoff, and T. R. Harris. 2005. Input–output modeling, outdoor recreation, and the economic impacts of weeds. *Weed Science* **53**:130-137.
- Elseroad, A. C., and N. T. Rudd. 2011. Can imazapic increase native species abundance in cheatgrass (*bromus tectorum*) invaded native plant communities? *Rangeland Ecology & Management* **64**:641-648.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Boston, MA: Springer US, Boston, MA.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* **11**:1301-1310.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57-68.
- Fleming, C. E., M. A. Shipley, and M. R. Miller. 1942. Bronco grass on nevada ranges. *Bulletin. Agricultural Experiment Station, University of Nevada*.

- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* **35**:557-581.
- Francl, L. J. 2001. The disease triangle: A plant pathological paradigm revisited. *The Plant Health Instructor* **10**.
- Fuller, K. B., and J. Mangold. 2017. The costs of noxious weeds: What you can do about them. *Big Sky Small Acres*:8-9.
- Gasch, C. K., S. F. Enloe, P. D. Stahl, and S. E. Williams. 2013. An aboveground–belowground assessment of ecosystem properties associated with exotic annual brome invasion. *Biology and Fertility of Soils* **49**:919-928.
- Gause, G. 1934. *The struggle for existence williams and wilkins*. Baltimore, Maryland.
- Gehring, C. A., M. Hayer, L. Flores-Rentería, A. F. Krohn, E. Schwartz, and P. Dijkstra. 2016. Cheatgrass invasion alters the abundance and composition of dark septate fungal communities in sagebrush steppe. *Botany* **94**:481-491.
- Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus *bromus*. *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications*:61-95.
- Gleason, H. A. 1939. The individualistic concept of the plant association. *American Midland Naturalist* **21**:92-110.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. *The Quarterly Review of Biology* **50**:237-266.
- Grime, J. P. 1988. The csr model of primary plant strategies—origins, implications and tests. Pages 371-393 *Plant evolutionary biology*. Springer.
- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* **109**:323-334.
- Gundale, M. J., D. A. Wardle, P. Kardol, and M. C. Nilsson. 2019. Comparison of plant–soil feedback experimental approaches for testing soil biotic interactions among ecosystems. *New Phytologist* **221**:577-587.
- Hadley, W. 2016. *Elegant graphics for data analysis*. Springer-Verlag New York.
- Hannula, S. E., A. M. Kielak, K. Steinauer, M. Huberty, R. Jongen, J. R. De Long, R. Heinen, and T. M. Bezemer. 2019. Time after time: Temporal variation in the effects of grass and forb species on soil bacterial and fungal communities. *MBio* **10**:e02635-02619.

- Harris, G. A. 1967. Some competitive relationships between *agropyron spicatum* and *bromus tectorum*. *Ecological Monographs* **37**:89-111.
- Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. *Rangeland Ecology & Management/Journal of Range Management Archives* **30**:172-177.
- Harris, G. A., and A. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology*:530-534.
- Hartig, F. 2022. *_dharma*: Residual diagnostics for hierarchical (multi-level/mixed) regression models_.
- Harvey, A. J., S. C. Simanonok, L. J. Rew, T. S. Prather, and J. M. Mangold. 2020. Effect of *pseudoroegneria spicata* (bluebunch wheatgrass) seeding date on establishment and resistance to invasion by *bromus tectorum* (cheatgrass). *Ecological Restoration* **38**:145-152.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical population biology* **18**:363-373.
- Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and soil* **281**:369-380.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**:3105-3117.
- Hempy-Mayer, K., and D. A. Pyke. 2008. Defoliation effects on *bromus tectorum* seed production: Implications for grazing. *Rangeland Ecology & Management* **61**:116-123.
- Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior columbia basin, u.S.A. *Conservation Biology* **16**:1243-1255.
- Herbaria, C. o. P. N. 2021. Consortium of pacific northwest herbaria. Page <https://www.pnwherbaria.org/resources.php>.
- Herdrich, N. 2001. Grower experiences with alternate cereal crops in eastern washington 1997-2000 (alternate crop series).
- Herron, C. M., J. L. Jonas, P. J. Meiman, and M. W. Paschke. 2013. Using native annual plants to restore post-fire habitats in western north america. *International Journal of Wildland Fire* **22**:815-821.

- Hess, M. C., F. Mesléard, and E. Buisson. 2019. Priority effects: Emerging principles for invasive plant species management. *Ecological Engineering* **127**:48-57.
- Hirsch-Schantz, M. C., T. A. Monaco, C. A. Call, and R. L. Sheley. 2014. Large-scale downy brome treatments alter plant-soil relationships and promote perennial grasses in salt desert shrublands. *Rangeland Ecology & Management* **67**:255-265.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* **7**:336-339.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* **6**:324-337.
- Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* **9**:761-770.
- Hoelzle, T. B., J. L. Jonas, and M. W. Paschke. 2012. Twenty-five years of sagebrush steppe plant community development following seed addition. *Journal of Applied Ecology* **49**:911-918.
- Hoffert-Hay, D. 2002. Pine creek ranch watershed restoration plan.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* **105**:367-368.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual review of ecology and systematics* **4**:1-23.
- Holling, C. S. 1996. Engineering resilience versus ecological resilience. *Engineering within ecological constraints* **31**:32.
- Homer, C. G., G. Xian, C. L. Aldridge, D. K. Meyer, T. R. Loveland, and M. S. O'Donnell. 2015. Forecasting sagebrush ecosystem components and greater sage-grouse habitat for 2050: Learning from past climate patterns and landsat imagery to predict the future. *Ecological Indicators* **55**:131-145.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* **50**:346--363.
- Hulbert, L. C. 1955. Ecological studies of *bromus tectorum* and other annual brome grasses. *Ecological monographs* **25**:181-213.
- Hull, A. 1963. Competition and water requirements of cheatgrass and wheatgrass in the greenhouse. *Rangeland Ecology & Management/Journal of Range Management Archives* **16**:199-204.

- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* **113**:81-101.
- Hutchinson, G. E. 1957. *A treatise on limnology*. New York : Wiley, New York.
- Hutchinson, G. E. 1959. Homage to santa rosalia or why are there so many kinds of animals? *The American Naturalist* **93**:145-159.
- Jackson, L., R. Strauss, M. Firestone, and J. Bartolome. 1988. Plant and soil nitrogen dynamics in california annual grassland. *Plant and soil* **110**:9-17.
- James, J. 2008. Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. *Journal of Arid Environments* **72**:1775-1784.
- James, J., R. Drenovsky, T. Monaco, and M. Rinella. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: Effective strategy or incomplete framework? *Ecological Applications* **21**:490-502.
- Jones, L. C., N. Norton, and T. S. Prather. 2018. Indicators of ventenata (*ventenata dubia*) invasion in sagebrush steppe rangelands. *Invasive Plant Science and Management* **11**:1-9.
- Kainrath, N. B., P. Dijkstra, C. A. Gehring, C. Updike, and K. C. Grady. 2022. Water as the key to sagebrush restoration success in cheatgrass-invaded ecosystems. *Restoration Ecology* **30**:e13473.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* **17**:164-170.
- Keeley, J. E., C. J. Fotheringham, and M. Baer-Keeley. 2005. Determinants of postfire recovery and succession in mediterranean-climate shrublands of california. *Ecological Applications* **15**:1515-1534.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**:636-638.
- Kindt, R., and R. Coe. 2005. *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*.
- Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*bromus tectorum* l.). *The Botanical Review* **30**:226-262.
- Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* **417**:67-70.
- Knapp, P. A. 1996. Cheatgrass (*bromus tectorum* l) dominance in the great basin desert: History, persistence, and influences to human activities. *Global Environmental Change* **6**:37-52.

- Knick, S. T. 1999. Requiem for a sagebrush ecosystem? *Northwest science*. **73**:53-57.
- Körner, C., J. Stöcklin, L. Reuther-Thiébaud, and S. Pelaez-Riedl. 2008. Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist* **177**:698-705.
- Krautzer, B., W. Graiss, and C. Partl. 2006. Composition and use of seed mixtures in the high altitudes of the alps. Pages 27-28 *in* Proceedings of the Conference Grassland-part of mountain agriculture and landscape.
- Kuehn, C. 2011. A mathematical framework for critical transitions: Bifurcations, fast–slow systems and stochastic dynamics. *Physica D: Nonlinear Phenomena* **240**:1020-1035.
- Kulmatiski, A. 2018. Community-level plant–soil feedbacks explain landscape distribution of native and non-native plants. *Ecology and Evolution* **8**:2041-2049.
- Kulmatiski, A. 2019. Plant-soil feedbacks predict native but not non-native plant community composition: A 7-year common-garden experiment. *Frontiers in Ecology and Evolution* **7**.
- Kulmatiski, A., and K. H. Beard. 2011. Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure. *Soil Biology and Biochemistry* **43**:823-830.
- Kulmatiski, A., K. H. Beard, J. M. Norton, J. E. Heavilin, L. E. Forero, and J. Grenzer. 2017. Live long and prosper: Plant–soil feedback, lifespan, and landscape abundance covary. *Ecology* **98**:3063-3073.
- Kulmatiski, A., K. H. Beard, and J. M. Stark. 2004. Finding endemic soil-based controls for weed growth. *Weed Technology* **18**:1353-1358, 1356.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant–soil feedbacks: A meta-analytical review. *Ecology Letters* **11**:980-992.
- Kulmatiski, A., J. Heavilin, and K. H. Beard. 2011. Testing predictions of a three-species plant–soil feedback model. *Journal of Ecology* **99**:542-550.
- Kyser, G. B., J. M. DiTomaso, M. P. Doran, S. B. Orloff, R. G. Wilson, D. L. Lancaster, D. F. Lile, and M. L. Porath. 2007. Control of medusahead (*taeniatherum caput-medusae*) and other annual grasses with imazapic. *Weed Technology* **21**:66-75.
- Kyser, G. B., R. G. Wilson, J. Zhang, and J. M. DiTomaso. 2013. Herbicide-assisted restoration of great basin sagebrush steppe infested with medusahead and downy brome. *Rangeland Ecology and Management* **66**:588-596, 589.
- Lambers, H., F. S. Chapin, and T. L. Pons. 2008. *Plant physiological ecology*. Springer.

- Larson, C. D., E. A. Lehnhoff, C. Noffsinger, and L. J. Rew. 2018. Competition between cheatgrass and bluebunch wheatgrass is altered by temperature, resource availability, and atmospheric CO₂ concentration. *Oecologia* **186**:855-868.
- Larson, C. D., E. A. Lehnhoff, and L. J. Rew. 2017. A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. *Oecologia* **185**:763-774.
- Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern Idaho, U.S.A. *Ecology and Evolution* **3**:1626-1641.
- Leffler, A., T. Monaco, and J. James. 2011a. Nitrogen acquisition by annual and perennial grass seedlings: Testing the roles of performance and plasticity to explain plant invasion. *Plant Ecology* **212**:1601-1611.
- Leffler, A., T. A. Monaco, and J. James. 2011b. Nitrogen acquisition by annual and perennial grass seedlings: Testing the roles of performance and plasticity to explain plant invasion. *Plant Ecol.* **212**:1601-1611.
- Lehnhoff, E. A., L. J. Rew, J. M. Mangold, T. Seipel, and D. Ragen. 2019. Integrated management of cheatgrass (*Bromus tectorum*) with sheep grazing and herbicide. *Agronomy* **9**:315.
- Lekberg, Y., J. D. Bever, R. A. Bunn, R. M. Callaway, M. M. Hart, S. N. Kivlin, J. Klironomos, B. G. Larkin, J. L. Maron, and K. O. Reinhart. 2018. Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. *Ecology Letters* **21**:1268-1281.
- Lenth, R. 2022. `_emmeans`: Estimated marginal means, aka least-squares means.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* **87**:15-26.
- Levine, N. M., K. Zhang, M. Longo, A. Baccini, O. L. Phillips, S. L. Lewis, E. Alvarez-Dávila, A. C. Segalin de Andrade, R. J. W. Brienen, T. L. Erwin, T. R. Feldpausch, A. L. Monteagudo Mendoza, P. Nuñez Vargas, A. Prieto, J. E. Silva-Espejo, Y. Malhi, and P. R. Moorcroft. 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proceedings of the National Academy of Sciences* **113**:793-797.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- MacArthur, R. 1970. Species packing and competitive equilibrium for many species. *Theoretical population biology* **1**:1-11.

- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:599-619.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**:42-55.
- Mack, R. N. 1981. Invasion of *bromus tectorum* l. Into western north america: An ecological chronicle. *Agro-ecosystems* **7**:145-165.
- Mack, R. N. 2011. Fifty years of 'waging war on cheatgrass': Research advances, while meaningful control languishes. Fifty years of invasion ecology: the legacy of Charles Elton. Oxford, UK: Wiley-Blackwell:253-265.
- Mack, R. N., and D. A. Pyke. 1983. The demography of *bromus tectorum*: Variation in time and space. *The Journal of Ecology*:69-93.
- Maestas, J. D., S. B. Campbell, J. C. Chambers, M. Pellant, and R. F. Miller. 2016. Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. *Rangelands* **38**:120-128.
- Magurran, A. E., and B. J. McGill. 2010. Biological diversity: Frontiers in measurement and assessment. OUP Oxford.
- Mahood, A. L., R. O. Jones, D. I. Board, J. K. Balch, and J. C. Chambers. 2022. Interannual climate variability mediates changes in carbon and nitrogen pools caused by annual grass invasion in a semiarid shrubland. *Global change biology* **28**:267-284.
- Mangold, J., H. Parkinson, C. Duncan, P. Rice, E. Davis, and F. Menalled. 2013. Downy brome (*bromus tectorum*) control with imazapic on montana grasslands. *Invasive Plant Science and Management* **6**:554-558.
- Marchetto, K. M., T. M. Wolf, and D. J. Larkin. 2021. The effectiveness of using targeted grazing for vegetation management: A meta-analysis. *Restoration Ecology* **29**:e13422.
- Marschner, H., and B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant and soil* **159**:89-102.
- Maxwell, T. M., and M. J. Germino. 2022. The effects of cheatgrass invasion on us great basin carbon storage depend on interactions between plant community composition, precipitation seasonality, and soil climate regime. *Journal of Applied Ecology* **59**:2863-2873.
- Maxwell, T. M., M. J. Germino, S. Romero, L. M. Porensky, D. M. Blumenthal, C. S. Brown, and P. B. Adler. 2023. Experimental manipulation of soil-surface albedo alters phenology and growth of *bromus tectorum* (cheatgrass). *Plant and soil*:1-15.

- May, R. M. 1971. Stability in multispecies community models. *Mathematical Biosciences* **12**:59-79.
- May, R. M. 1972. Will a large complex system be stable? *Nature* **238**:413-414.
- May, R. M. 2019. *Stability and complexity in model ecosystems*. Princeton university press.
- May, R. M., and R. H. M. Arthur. 1972. Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences* **69**:1109-1113.
- McCarlie, V. W., L. D. Hansen, and B. N. Smith. 2001. Respiratory and physiological characteristics in subpopulations of great basin cheatgrass. and DJ Fairbanks, compilers. *Proc. Shrubland ecosystem genetics and biodiversity*, Provo, UT. Ogden, UT: USDA-Forest Service Rocky Mountain Research Station, RMRS-P-21:271-275.
- McLeod, M. L., L. Bullington, C. C. Cleveland, J. Rousk, and Y. Lekberg. 2021. Invasive plant-derived dissolved organic matter alters microbial communities and carbon cycling in soils. *Soil Biology and Biochemistry* **156**:108191.
- McLeod, M. L., C. C. Cleveland, Y. Lekberg, J. L. Maron, L. Philippot, D. Bru, and R. M. Callaway. 2016. Exotic invasive plants increase productivity, abundance of ammonia-oxidizing bacteria and nitrogen availability in intermountain grasslands. *Journal of Ecology* **104**:994-1002.
- Mealor, B. A., R. D. Mealor, W. K. Kelley, D. L. Bergman, S. A. Burnett, T. W. Decker, B. Fowers, M. E. Herget, C. E. Noseworthy, and J. L. Richards. 2013. *Cheatgrass management handbook: Managing an invasive annual grass in the rocky mountain region*. B (Laramie, Wyo.); no. 1246.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: Competition between *bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**:7-13.
- Menalled, F., J. Mangold, and E. Davis. 2008. *Cheatgrass: Identification, biology and integrated management*. Bozeman, MT, USA: Montana State University Publication.
- Moerman, D. E. 1998. *Native american ethnobotany*. Timber press.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Rangeland Ecology & Management/Journal of Range Management Archives* **56**:282-290.
- Monaco, T. A., J. M. Mangold, B. A. Mealor, R. D. Mealor, and C. S. Brown. 2017. Downy brome control and impacts on perennial grass abundance: A systematic review spanning 64 years. *Rangeland Ecology & Management* **70**:396-404.

- Monaco, T. A., S. B. Monsen, B. Smith, and L. Hansen. 2005. Temperature-dependent physiology of *poa secunda*, a cool season grass native to the great basin, united states. *Russ. J. Plant Physiol.* **52**:653-658.
- Montana Department of Agriculture Noxious Weed Program. 2020. State agency and county weed district biennial noxious weed report.
- Morris, E. K., T. Caruso, F. Buscot, M. Fischer, C. Hancock, T. S. Maier, T. Meiners, C. Müller, E. Obermaier, and D. Prati. 2014. Choosing and using diversity indices: Insights for ecological applications from the german biodiversity exploratories. *Ecology and evolution* **4**:3514-3524.
- Morris, K. A., J. M. Stark, B. Bugbee, and J. M. Norton. 2016. The invasive annual cheatgrass releases more nitrogen than crested wheatgrass through root exudation and senescence. *Oecologia* **181**:971-983.
- Mosley, J. C., and L. Roselle. 2006. Targeted livestock grazing to suppress invasive annual grasses. *Targeted grazing: A natural approach to vegetation management and landscape enhancement*:67-76.
- Nasri, M., and P. S. Doescher. 1995. Effect of temperature on growth of cheatgrass and idaho fescue. *Rangeland Ecology & Management/Journal of Range Management Archives* **48**:406-409.
- Nasto, M. K., M. L. McLeod, L. Bullington, Y. Lekberg, and J. M. Stark. 2022. The effect of plant invasion on soil microbial carbon-use efficiency in semi-arid grasslands of the rocky mountain west. *Journal of Ecology* **110**:479-493.
- NOAA National Centers for Environmental Information. 2023. *Climate at a Glance: Statewide Time Series*.
- O'Connor, J. J., and J. S. Prevey. 2015. Effects of short-term soil conditioning by cheatgrass and western wheatgrass.
- Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlinn, M. Ouellette, C. E. Ribeiro, S. A. Smith T, B. C. Ter, and J. Weedon. 2022. *_vegan: Community ecology package_*.
- Omernik, J. M. 1987. Ecoregions of the conterminous united states. *Annals of the Association of American Geographers* **77**:118-125.
- Orloff, L. N., J. M. Mangold, and F. D. Menalled. 2013. Role of size and nitrogen in competition between annual and perennial grasses. *Invasive Plant Science and Management* **6**:87-98.

- Orloff, L. N., J. M. Mangold, and F. D. Menalled. 2015. Site-specific effects of exotic annual grass control integrated with revegetation. *Ecological Restoration* **33**:147-155.
- Ott, J. E., F. F. Kilkenny, D. D. Summers, and T. W. Thompson. 2019. Long-term vegetation recovery and invasive annual suppression in native and introduced postfire seeding treatments. *Rangeland Ecology & Management* **72**:640-653.
- Owen, S. M., C. H. Sieg, and C. A. Gehring. 2011. Rehabilitating downy brome (*bromus tectorum*)–invaded shrublands using imazapic and seeding with native shrubs. *Invasive Plant Science and Management* **4**:223-233.
- Owen, S. M., C. H. Sieg, N. C. Johnson, and C. A. Gehring. 2013. Exotic cheatgrass and loss of soil biota decrease the performance of a native grass. *Biological Invasions* **15**:2503-2517.
- Palmer, M. W., and T. A. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. *Journal of vegetation science* **8**:235-240.
- Pellant, M. 1989. The cheatgrass-wildfire cycle—are there any solutions?
- Pellant, M. 1996. Cheatgrass: The invader that won the west. US Department of the Interior, Bureau of Land Management.
- Perkins, L. B., and R. S. Nowak. 2012. Soil conditioning and plant–soil feedbacks affect competitive relationships between native and invasive grasses. *Plant Ecology* **213**:1337-1344.
- Perkins, L. B., and R. S. Nowak. 2013. Native and non-native grasses generate common types of plant–soil feedbacks by altering soil nutrients and microbial communities. *Oikos* **122**:199-208.
- Pernilla Brinkman, E., W. H. van der Putten, E.-J. Bakker, and K. J. F. Verhoeven. 2010. Plant–soil feedback: Experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology* **98**:1063-1073.
- Perryman, B. L., B. W. Schultz, M. Burrows, T. Shenkoru, and J. Wilker. 2020. Fall-grazing and grazing-exclusion effects on cheatgrass (*bromus tectorum*) seed bank assays in nevada, united states. *Rangeland Ecology & Management* **73**:343-347.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* **1**:6-18.
- Pielou, E. C. 1974. Population and community ecology: Principles and methods. CRC Press.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the great basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* **7**:8126-8151.

- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the united states. *Ecological economics* **52**:273-288.
- Pimm, S. L. 1979. The structure of food webs. *Theoretical population biology* **16**:144-158.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* **307**:321-326.
- Pinheiro, J., D. Bates, and R Core Team. 2022. `_nlme: Linear and nonlinear mixed effects models_`.
- Pokorny, M. L., R. L. Sheley, T. J. Svejcar, and R. E. Engel. 2004. Plant species diversity in a grassland plant community: Evidence for forbs as a critical management consideration. *Western North American Naturalist*:219-230.
- Porazinska, D. L., T. R. Seastedt, E. M. Gendron, and S. K. Schmidt. 2022. Invasive annual cheatgrass enhances the abundance of native microbial and microinvertebrate eukaryotes but reduces invasive earthworms. *Plant and soil* **473**:591-604.
- Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. *Studies in avian biology* **38**:531-548.
- Pyke, D. A., S. E. Shaff, J. C. Chambers, E. W. Schupp, B. A. Newingham, M. L. Gray, and L. M. Ellsworth. 2022. Ten-year ecological responses to fuel treatments within semiarid wyoming big sagebrush ecosystems. *Ecosphere* **13**:e4176.
- Pyke, D. A., S. E. Shaff, A. I. Lindgren, E. W. Schupp, P. S. Doescher, J. C. Chambers, J. S. Burnham, and M. M. Huso. 2014. Region-wide ecological responses of arid wyoming big sagebrush communities to fuel treatments. *Rangeland Ecology & Management* **67**:455-467.
- R Core Team. 2022. *R: A language and environment for statistical computing* Vienna, Austria.
- Radosevich, S. R., J. S. Holt, and C. M. Ghera. 2007. *Ecology of weeds and invasive plants: Relationship to agriculture and natural resource management*. John Wiley & Sons.
- Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-Holme, D. Nogues-Bravo, R. J. Whittaker, and J. Fjeldså. 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* **365**:1108-1113.
- Reich, P. B. 2014. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology* **102**:275-301.
- Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. *New Phytologist* **170**:445-457.

- Reinhart, K. O., and M. J. Rinella. 2016. A common soil handling technique can generate incorrect estimates of soil biota effects on plants. *New Phytologist* **210**:786-789.
- Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* **50**:1039-1049.
- Reitstetter, R., B. Yang, A. D. Tews, and A. Barberán. 2022. Soil microbial communities and nitrogen associated with cheatgrass invasion in a sagebrush shrubland. *Plant and soil*.
- Remington, T. E., P. A. Deibert, S. E. Hanser, D. M. Davis, L. A. Robb, and J. L. Welty. 2021. Sagebrush conservation strategy—challenges to sagebrush conservation. Report 2020-1125, Reston, VA.
- Revillini, D., C. A. Gehring, and N. C. Johnson. 2016. The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. *Functional Ecology* **30**:1086-1098.
- Rew, L. J., B. F. Sowell, and K. A. Cutting. 2023. Evaluating integrated control practices for cheatgrass at high-elevation sagebrush sites. Society of Range Management Meeting.
- Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. Grassroots ecology: Plant–microbe–soil interactions as drivers of plant community structure and dynamics. *Ecology* **84**:2281-2291.
- Rice, K. J., R. A. Black, G. Rademaker, and R. D. Evans. 1992. Photosynthesis, growth, and biomass allocation in habitat ecotypes of cheatgrass (*bromus tectorum*). *Functional Ecology* **6**:32-40.
- Rice, P. M. 2003. Invaders database system. University of Montana, Missoula, MT.
- Rickard, W. 1985. Shoot production and mineral nutrient assimilation in cheatgrass communities.
- Rimer, R., and R. Evans. 2006. Invasion of downy brome (*bromus tectorum* l.) causes rapid changes in the nitrogen cycle. *The American midland naturalist* **156**:252-258.
- Rinella, M. J., J. M. Mangold, E. K. Espeland, R. L. Sheley, and J. S. Jacobs. 2012. Long-term population dynamics of seeded plants in invaded grasslands. *Ecological Applications* **22**:1320-1329.
- Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* **19**:155-162.
- Rinella, M. J., and K. O. Reinhart. 2018. Toward more robust plant-soil feedback research. *Ecology* **99**:550-556.

- Rinella, M. J., and K. O. Reinhart. 2019. Toward more robust plant-soil feedback research: Reply. *Ecology* **100**:e02810.
- Roberts, D. W. 2020. Comparison of distance-based and model-based ordinations. *Ecology* **101**:e02908.
- Rodhouse, T. J., K. M. Irvine, R. L. Sheley, B. S. Smith, S. Hoh, D. M. Esposito, and R. Mata-Gonzalez. 2014. Predicting foundation bunchgrass species abundances: Model-assisted decision-making in protected-area sagebrush steppe. *Ecosphere* **5**:art108.
- Rohde, A. T., D. S. Pilliod, and S. J. Novak. 2019. Insect communities in big sagebrush habitat are altered by wildfire and post-fire restoration seeding. *Insect Conservation and Diversity* **12**:216-230.
- Roundy, B. A., J. C. Chambers, D. A. Pyke, R. F. Miller, R. J. Tausch, E. W. Schupp, B. Rau, and T. Gruell. 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. *Ecosphere* **9**:e02417.
- Rowe, C. L. J., and E. A. Leger. 2011. Competitive seedlings and inherited traits: A test of rapid evolution of *elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications* **4**:485-498.
- Rowland, M. M., L. H. Suring, M. J. Wisdom, J. Pye, H. Rauscher, Y. Sands, D. Lee, and J. Beatty. 2010. Assessment of habitat threats to shrublands in the great basin: A case study. Advances in threat assessment and their application to forest and rangeland management. PNW-GTR-802. USDA Forest Service, Pacific Northwest and Southern Research Stations, Portland, Oregon, USA:673-685.
- Rummell, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. *Ecology* **27**:159-167.
- Schaeffer, S. M., S. E. Ziegler, J. Belnap, and R. Evans. 2012. Effects of *bromus tectorum* invasion on microbial carbon and nitrogen cycling in two adjacent undisturbed arid grassland communities. *Biogeochemistry* **111**:427-441.
- Scheffer, M., S. R. Carpenter, T. M. Lenton, J. Bascompte, W. Brock, V. Dakos, J. van de Koppel, I. A. van de Leemput, S. A. Levin, E. H. van Nes, M. Pascual, and J. Vandermeer. 2012. Anticipating critical transitions. *Science* **338**:344-348.
- Schimel, D., M. A. Stillwell, and R. G. Woodmansee. 1985. Biogeochemistry of c, n, and p in a soil catena of the shortgrass steppe. *Ecology* **66**:276-282.
- Schmelzer, L., B. Perryman, B. Bruce, B. Schultz, K. McAdoo, G. McCuin, S. Swanson, J. Wilker, and K. Conley. 2014. Case study: Reducing cheatgrass (*bromus tectorum* l.) fuel loads using fall cattle grazing. *The Professional Animal Scientist* **30**:270-278.

- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in north america. *The Condor* **106**:363-376.
- Schroeder, V. M., D. D. Johnson, R. C. O'Connor, C. G. Crouch, W. J. Dragt, H. E. Quicke, L. F. Silva, and D. J. Wood. 2022. Managing invasive annual grasses, annually: A case for more case studies. *Rangelands* **44**:210-217.
- Searchinger, T., C. Hanson, J. Ranganathan, B. Lipinski, R. Waite, R. Winterbottom, A. Dinshaw, R. Heimlich, M. Boval, and P. Chemineau. 2014. Creating a sustainable food future. A menu of solutions to sustainably feed more than 9 billion people by 2050. World resources report 2013-14: Interim findings. Creating a sustainable food future. A menu of solutions to sustainably feed more than 9 billion people by 2050. World resources report 2013-14: interim findings, World Resources Institute (2014).
- Seastedt, T., and P. Pyšek. 2011a. Mechanisms of plant invasions of north american and european grasslands. *Annual Review of Ecology, Evolution, and Systematics* **42**.
- Seastedt, T. R., and P. Pyšek. 2011b. Mechanisms of plant invasions of north american and european grasslands. *Annual Review of Ecology, Evolution, and Systematics* **42**:133-153.
- Seefeldt, S. S., and S. D. McCoy. 2003. Measuring plant diversity in the tall threetip sagebrush steppe: Influence of previous grazing management practices. *Environmental Management* **32**:234-245.
- Sheley, R. L. 2008. Revegetation guidelines for the great basin: Considering invasive weeds. USDA, Agricultural Research Service.
- Sheley, R. L., and J. D. Bates. 2008. Restoring western juniper-(*juniperus occidentalis*) infested rangeland after prescribed fire. *Weed Science* **56**:469-476.
- Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. *Ecological monographs* **76**:365-379.
- Sheley, R. L., and B. S. Smith. 2012. Prioritizing invasive plant management strategies. *Rangelands* **34**:11-14, 14.
- Sheley, R. L., T. J. Svejcar, and B. D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* **10**:766-773.
- Shriver, L. C. 2022. Restoration and evolution in the great basin: Non-target herbicide effects and potential for adaptive responses to fire.

- Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, M. O. Jones, A. R. Kleinhesselink, J. D. Maestas, S. L. Morford, and D. E. Naugle. 2022. The elevational ascent and spread of exotic annual grass dominance in the great basin, USA. *Diversity and Distributions* **28**:83-96.
- Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, A. R. Kleinhesselink, S. L. Morford, and D. E. Naugle. 2023. Fire needs annual grasses more than annual grasses need fire. *Biological Conservation* **286**:110299.
- Smithson, M., and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological methods* **11**:54.
- Souther, S., M. Loeser, T. E. Crews, and T. Sisk. 2019. Complex response of vegetation to grazing suggests need for coordinated, landscape-level approaches to grazing management. *Global Ecology and Conservation* **20**:e00770.
- Stark, J. M., and J. M. Norton. 2015. The invasive annual cheatgrass increases nitrogen availability in 24-year-old replicated field plots. *Oecologia* **177**:799-809.
- Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* **9**:45-64.
- Stutz, H. C. 1994. Evolution of weedy annuals. General Technical Report INT.:9.
- Suding, K. N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and W. H. van der Putten. 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology* **101**:298-308.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *The American Naturalist* **108**:859-873.
- Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* response to fire varies with climate conditions. *Ecosystems* **17**:960-973.
- Thill, D. C., K. G. Beck, and R. H. Callihan. 1984. The biology of downy brome (*bromus tectorum*). *Weed Science* **32**:7-12.
- Tilman, D. 1982. Resource competition and community structure. Princeton university press.
- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist* **125**:827-852.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U. S. A.* **101**:10854-10861.

- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**:629-632.
- Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* **72**:685-700.
- U.S. Environmental Protection Agency. 2013. Level iii ecoregions of the continental united states: Corvallis, oregon.*in* U. S. E.-N. H. a. E. E. R. Labratory, editor.
- Uselman, S. M., K. A. Snyder, E. A. Leger, and S. E. Duke. 2015. Emergence and early survival of early versus late seral species in great basin restoration in two different soil types. *Applied Vegetation Science* **18**:624-636.
- van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol, J. N. Klironomos, A. Kulmatiski, and J. A. Schweitzer. 2013. Plant–soil feedbacks: The past, the present and future challenges. *Journal of Ecology* **101**:265-276.
- van der Putten, W. H., M. A. Bradford, E. Pernilla Brinkman, T. F. van de Voorde, and G. Veen. 2016. Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology* **30**:1109-1121.
- van der Putten, W. H., J. N. Klironomos, and D. A. Wardle. 2007. Microbial ecology of biological invasions. *The ISME journal* **1**:28-37.
- Van Meerbeek, K., T. Jucker, and J.-C. Svenning. 2021. Unifying the concepts of stability and resilience in ecology. *Journal of Ecology* **109**:3114-3132.
- van Rhijn, P., and J. Vanderleyden. 1995. The rhizobium-plant symbiosis. *Microbiological Reviews* **59**:124.
- Vargas, T., and W. Cheng. 2015. Rhizosphere-mediated effects of the invasive grass *bromus tectorum* l. And native *elymus elymoides* on nitrogen cycling in great basin desert soils. *Plant and soil* **393**:245-257.
- Vasquez, E., R. Sheley, and T. Svejcar. 2008. Nitrogen enhances the competitive ability of cheatgrass (*bromus tectorum*) relative to native grasses. *Invasive Plant Science and Management* **1**:287-295.
- Venturi, V., and C. Keel. 2016. Signaling in the rhizosphere. *Trends in plant science* **21**:187-198.
- Vermeire, L. T., and M. J. Rinella. 2020. Fall water effects on growing season soil water content and plant productivity. *Rangeland Ecology & Management* **73**:252-258.
- Vermeire, L. T., R. C. Waterman, K. O. Reinhart, and M. J. Rinella. 2023a. Grazing intensity and seasonality manipulate invasive annual grasses and native vegetation. *Rangeland Ecology & Management*.

- Vermeire, L. T., R. C. Waterman, K. O. Reinhart, and M. J. Rinella. 2023b. Grazing intensity and seasonality manipulate invasive annual grasses and native vegetation. *Rangeland Ecology & Management* **90**:308-313.
- Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* **14**:702-708.
- Vivion, O. H. 1968. Red rock lakes range management plan. U.S. Fish & Wildlife Service:Page 6.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**:1629.
- Weber, C. F. 2015. Reduced vertical stratification of soil bacterial community structure and composition is associated with *bromus tectorum* invasion of sagebrush steppe. *Journal of Arid Environments* **115**:90-99.
- Wedin, D. A., and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia* **96**:186-192.
- West, N. E., F. D. Provenza, P. S. Johnson, and M. K. Owens. 1984. Vegetation change after 13 years of live-stock grazing exclusion on sagebrush semidesert in west central utah. *Rangeland Ecology & Management/Journal of Range Management Archives* **37**:262-264.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**:266-274.
- Whitlock, C., W. F. Cross, B. D. Maxwell, N. Silverman, and A. A. Wade. 2017. 2017 montana climate assessment: Stakeholder driven, science informed. Montana Institute on Ecosystems.
- Whittaker, R. H. 1956. Vegetation of the great smoky mountains. *Ecological monographs* **26**:2-80.
- Wood, C. W., and B. A. Meador. 2022. Identifying structural thresholds in annual grass-invaded rangelands. *Rangeland Ecology & Management* **83**:1-9.
- Woodward, F., and A. Diament. 1991. Functional approaches to predicting the ecological effects of global change. *Functional Ecology*:202-212.
- Young, J. A., R. A. Evans, R. E. Eckert, and B. L. J. R. A. Kay. 1987. Cheatgrass. **9**:266-270.
- Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecology Letters* **8**:662-673.

Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count data in r. *Journal of Statistical Software* **27(8)**.

Zouhar, K. 2008. Wildland fire in ecosystems: Fire and nonnative invasive plants. Forest Service.

Zuur, A. F., and E. N. Ieno. 2016. *Beginner's guide to zero-inflated models with r*. Highland Statistics Limited United Kingdom.

APPENDICES

APPENDIX A

Chapter Two Supplemental Tables and Study Location

Table A1: Dispersion estimates for the three zero-altered negative binomial models used to model *B. tectorum* abundance in the Centennial Valley, MT, USA. Dispersion values of 1 indicate perfect agreement between the assumed distribution and the model residuals. Values less than 1 indicate under-dispersion and values greater than 1 indicate over-dispersion.

Data Range	Treatment	Model Structure	Dispersion Estimate
2019-2022	Sprayed+Ref.	BRTE~Herbicide*Year+Region	1.04
2017-2022	Sprayed	BRTE~Year+Region	1.11
2017-2022	Reference	BRTE~Year+Region	0.93

Table A2: Analysis of variance for the zero-altered negative binomial models of *B. tectorum* abundance used to conduct a Dunnett's post-hoc test for the reference (top) and sprayed (bottom) communities in the Centennial Valley, MT, USA.

Reference			
Fixed Effects	Chisq	df	p
Region	0.29	1	0.588
Year	9.98	5	0.075
Spray			
Region	0.02	1	0.882
Year	124.19	5	<0.0001

Table A3: Analysis of deviance for the zero-altered negative binomial model of *B. tectorum* abundance for the four years following the final herbicide application (2018). Note that while only year is statistically significant in the analysis of deviance, there was a statistically significant difference in the abundance of *B. tectorum* between the sprayed and reference communities. Bold lettering indicates statistically significant fixed effects using an alpha level of 0.05.

Fixed Effects	Chisq	df	p
Region	0.38	1	0.539
Herbicide	0.55	1	0.457
Year	65.45	3	<0.0001
Herbicide*Year	1.78	3	0.620

Table A4: Estimated probability of *B. tectorum* occurrence in the sprayed and reference communities in the Centennial Valley, MT, USA. Estimates are expressed as proportions not percentages.

Year	Treatment	Estimate	SE	df	lower CL	upper CL
2017	Sprayed	0.87	0.03	2107	0.08	0.18
2017	Reference	0.01	0.01	2107	0.97	1.00
2018	Sprayed	0.57	0.04	2107	0.35	0.50
2018	Reference	0.02	0.01	2107	0.97	1.00
2019	Sprayed	0.04	0.01	2107	0.94	0.99
2019	Reference	0.04	0.01	2107	0.93	0.99
2020	Sprayed	0.27	0.03	2107	0.66	0.79
2020	Reference	0.03	0.01	2107	0.95	1.00
2021	Sprayed	0.19	0.03	2107	0.75	0.86
2021	Reference	0.01	0.01	2107	0.98	1.01
2022	Sprayed	0.42	0.04	2107	0.51	0.65
2022	Reference	0.04	0.01	2107	0.93	0.99

Table A5: Analysis of variance for the linear mixed effects model of plant diversity in the Cenennial Valley, MT, USA. Note that we report the three-way interaction of year, herbicide, and region instead of discussing the two lower-order interactions for ease of explanation. Bold text indicates terms that are significant given an alpha level of 0.05.

Fixed Effects	numerator df	denominator df	f	p
(Intercept)	1	1208	378.44	<0.0001
Year	3	1208	44.58	<0.0001
Herbicide	1	1208	58.57	<0.0001
Region	1	10	0.26	0.619
Year*Herbicide	3	1208	13.35	<0.0001
Year*Region	3	1208	13.92	<0.0001
Herbicide*Region	1	1208	0.01	0.926
Year*Herbicide*Region	3	1208	2.41	0.066

Table A6: Estimated difference in Shannon's Diversity between the sprayed and the reference community for both the Antelope Peak and Eastern Sandhills regions in the Centennial Valley, MT, USA. Negative estimates indicate greater diversity in the reference community and positive values indicate greater diversity in the sprayed community. Bold lettering indicates statistically significant differences based on an alpha level of 0.05.

Antelope Peak					
Year	estimate	SE	df	t	p
2019	-0.37	0.05	1208	-7.35	<0.0001
2020	-0.12	0.05	1208	-2.36	0.018
2021	-0.15	0.05	1208	-2.88	0.004
2022	0.001	0.05	1208	0.03	0.974
Eastern Sandhills					
Year	estimate	SE	df	t	p
2019	-0.38	0.07	1208	-5.30	<0.0001
2020	-0.20	0.07	1208	-2.79	0.005
2021	0.06	0.07	1208	0.78	0.438
2022	-0.10	0.07	1208	-1.34	0.179

Table A7: Species rank abundance for the sprayed community in the first year post herbicide application (2019), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover. Frequency (Freq.) is the accumulation frequency. Prop. Is the proportion of the plant community based on abundance.

Sprayed Community Rank Abundance (2019)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
FEID	1	494	8.5	8.5	CIUN	34	23	0.4	96.5
LUAR3	2	489	8.4	16.8	CRAC2	35	22	0.4	96.9
AGSP	3	483	8.3	25.1	FECA	36	21	0.4	97.2
STCO4	4	466	8	33.1	ANPA4	37	20	0.3	97.6
STVI4	5	352	6	39.1	BRTE	38	16	0.3	97.8
PHLO2	6	339	5.8	44.9	CAPU	39	16	0.3	98.1
AGSpp	7	331	5.7	50.6	ASMI9	40	15	0.3	98.4
Moss	8	288	4.9	55.6	CAREX	41	15	0.3	98.6
ARTR4	9	262	4.5	60	PHHO	42	15	0.3	98.9
ERCO5	10	253	4.3	64.4	ARFR4	43	12	0.2	99.1
TAOF	11	217	3.7	68.1	COLI	44	9	0.2	99.2
CHVI8	12	208	3.6	71.7	POSE	45	9	0.2	99.4
POFE	13	188	3.2	74.9	MACA2	46	6	0.1	99.5
BASA3	14	162	2.8	77.7	BRMA4	47	5	0.1	99.6
LUWY	15	130	2.2	79.9	ARDR4	48	5	0.1	99.7
IOST	16	118	2	81.9	LEPU	49	5	0.1	99.8
ACOC3	17	97	1.7	83.6	AGPA14	50	4	0.1	99.8
COUM	18	82	1.4	85	ERPU2	51	4	0.1	99.9
PSLA3	19	76	1.3	86.3	ASTRA	52	2	0	99.9
OPPO	20	75	1.3	87.6	DRABA	53	2	0	100
ERHE2	21	65	1.1	88.7	LILE3	54	2	0	100
TRDU	22	54	0.9	89.6					
ACMI2	23	50	0.9	90.5					
AGGLG	24	43	0.7	91.2					
ERIGE2	25	41	0.7	91.9					
OPFR	26	40	0.7	92.6					
TECA2	27	39	0.7	93.2					
ARTRV	28	30	0.5	93.8					
HEUN	29	29	0.5	94.3					
MEBU	30	28	0.5	94.7					
ELTR7	31	27	0.5	95.2					
KOMA	32	27	0.5	95.7					
ERCO4	33	25	0.4	96.1					

Table A8: Species rank abundance for the sprayed community in the second-year post herbicide application (2020), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover. Frequency (Freq.) is the accumulation frequency. Prop. Is the proportion of the plant community based on abundance.

Sprayed Community Rank Abundance (2020)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
LUAR3	1	1070	15.2	15.2	ALDE	30	42	0.6	93
FEID	2	673	9.5	24.7	ARFR4	31	42	0.6	93.5
AGDA	3	598	8.5	33.2	AGSP	32	36	0.5	94.1
STCO4	4	578	8.2	41.4	SELAG	33	32	0.5	94.5
TAOF	5	443	6.3	47.7	BRMA4	34	30	0.4	94.9
ARTRT	6	338	4.8	52.5	ASTRA	35	30	0.4	95.4
CHVI8	7	286	4.1	56.5	LEPU	36	29	0.4	95.8
STVI4	8	271	3.8	60.4	LUWY	37	29	0.4	96.2
PHLO2	9	258	3.7	64	ASMI9	38	28	0.4	96.6
VIOLA	10	206	2.9	67	ARSO2	39	26	0.4	97
BRTE	11	185	2.6	69.6	LASQ	40	24	0.3	97.3
POSE	12	171	2.4	72	DRABA	41	22	0.3	97.6
ELTR7	13	156	2.2	74.2	MEBU	42	21	0.3	97.9
ERCO5	14	129	1.8	76	CIUN	43	19	0.3	98.2
ERIGE2	15	126	1.8	77.8	MACA2	44	18	0.3	98.4
PSTE	16	113	1.6	79.4	TRDU	45	15	0.2	98.6
COUM	17	112	1.6	81	AGPA14	46	13	0.2	98.8
COPA3	18	96	1.4	82.4	ARDR4	47	8	0.1	98.9
AGSpp	19	92	1.3	83.7	ERPU2	48	8	0.1	99
ACMI2	20	77	1.1	84.8	LIRU4	49	8	0.1	99.2
ARTR4	21	77	1.1	85.9	MYST2	50	8	0.1	99.3
ERHE2	22	75	1.1	86.9	POFE	51	7	0.1	99.4
KOMA	23	71	1	87.9	ERUM	52	6	0.1	99.5
TECA2	24	59	0.8	88.8	AGHE2	53	5	0.1	99.5
AGOSE	25	51	0.7	89.5	ANUM2	54	5	0.1	99.6
BASA3	26	51	0.7	90.2	CRAC2	55	5	0.1	99.7
OPFR	27	51	0.7	91	AGSM	56	4	0.1	99.7
OPPO	28	50	0.7	91.7	CAREX	57	4	0.1	99.8
AGAL	29	49	0.7	92.4	PEAR	58	4	0.1	99.8
					ARCO5	59	2	0	99.9
					COLI	60	2	0	99.9
					PHHA	61	2	0	99.9
					PHMU3	62	2	0	100
					ASNE6	63	1	0	100

Table A8: Continued

HAMI	64	1	0	100
LOMA3	65	1	0	100

Table A9: Species rank abundance for the sprayed community in the third-year post herbicide application (2021), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover. Frequency (Freq.) is the accumulation frequency. Prop. Is the proportion of the plant community based on abundance.

Sprayed Community Rank Abundance (2021)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
AGSM	1	437	8.5	8.5	CRAC2	35	29	0.6	92.9
ARTR4	2	405	7.9	16.4	BASA3	36	28	0.5	93.4
MACA2	3	394	7.7	24.1	Moss	37	23	0.4	93.8
BRI7	4	318	6.2	30.3	PHHA	38	20	0.4	94.2
TAOF	5	308	6	36.3	LASQ	39	19	0.4	94.6
POSE	6	298	5.8	42.1	ALDE	40	18	0.4	95
STCO4	7	284	5.5	47.6	AGDA	41	17	0.3	95.3
LUAR3	8	233	4.5	52.1	AGOSE	42	16	0.3	95.6
POCO	9	214	4.2	56.3	AGPA14	43	16	0.3	95.9
TECA2	10	198	3.9	60.2	MEBU	44	16	0.3	96.2
CHVI8	11	183	3.6	63.7	MATA2	45	15	0.3	96.5
CIUN	12	116	2.3	66	EROV	46	14	0.3	96.8
ERCO4	13	104	2	68	LUAR3	47	13	0.3	97
BRTE	14	97	1.9	69.9	STAC	48	12	0.2	97.3
ERIGE2	15	97	1.9	71.8	MYOSO	49	11	0.2	97.5
OPPO	16	95	1.9	73.6	ROWO	50	11	0.2	97.7
ERHE2	17	84	1.6	75.3	ASTRA	51	10	0.2	97.9
ARTR2	18	80	1.6	76.8	KOMA	52	10	0.2	98.1
PSLA3	19	77	1.5	78.3	LEPU	53	10	0.2	98.3
AGSP	20	76	1.5	79.8	LIRU4	54	10	0.2	98.5
FEID	21	69	1.3	81.1	AGGLG	55	9	0.2	98.7
CAPU	22	68	1.3	82.5	ARFR4	56	8	0.2	98.8
DEBI	23	65	1.3	83.7	TRDU	57	8	0.2	99
COUM	24	62	1.2	84.9	ANPA4	58	6	0.1	99.1
ELTR7	25	55	1.1	86	CAREX	59	6	0.1	99.2
ERCO5	26	42	0.8	86.8	COPA3	60	6	0.1	99.3
ARSP	27	40	0.8	87.6	LERE7	61	6	0.1	99.4
PHLO2	28	40	0.8	88.4	LIPU11	62	6	0.1	99.6

Table A9: Continued

ACMI2	29	38	0.7	89.1	LODI	63	6	0.1	99.7
SELAG	30	36	0.7	89.8	Un.Gr.1	64	6	0.1	99.8
PODO4	31	33	0.6	90.5	CAFL7	65	5	0.1	99.9
VIOLA	32	32	0.6	91.1	ANUM2	66	4	0.1	100
OPFR	33	31	0.6	91.7	PHHO	67	2	0	100
ARENA	34	30	0.6	92.3					

Table A10: Species rank abundance for the sprayed community in the fourth-year post herbicide application (2022), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover. Frequency (Freq.) is the accumulation frequency. Prop. Is the proportion of the plant community based on abundance.

Sprayed Community Rank Abundance (2022)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
BRTE	1	874	10.7	10.7	LASQ	36	24	0.3	97
LOTR2	2	802	9.8	20.4	ARENA	37	21	0.3	97.2
ERUM	3	772	9.4	29.9	OPFR	38	20	0.2	97.5
AGDA	4	605	7.4	37.2	PEAR	39	19	0.2	97.7
CIUN	5	446	5.4	42.7	CAFL7	40	16	0.2	97.9
PHHO	6	414	5.1	47.7	DEBI	41	16	0.2	98.1
STCO4	7	405	4.9	52.7	AGGLG	42	15	0.2	98.3
Unk.frb.2	8	398	4.9	57.5	ASMI9	43	13	0.2	98.5
ARTEM	9	294	3.6	61.1	CHDOD	44	13	0.2	98.6
TAOF	10	292	3.6	64.7	ERAS2	45	13	0.2	98.8
ALDE	11	257	3.1	67.8	POSE	46	13	0.2	98.9
AGSP	12	212	2.6	70.4	STAC	47	11	0.1	99.1
ERCO5	13	210	2.6	73	ELTR7	48	10	0.1	99.2
POFE	14	192	2.3	75.3	ERIGE2	49	9	0.1	99.3
STVI4	15	190	2.3	77.6	ERIN7	50	8	0.1	99.4
CASTI2	16	169	2.1	79.7	ARCA6	51	6	0.1	99.5
DRIN2	17	160	2	81.6	ARCO5	52	6	0.1	99.5
PSLA3	18	112	1.4	83	AGSM	53	5	0.1	99.6
ARSP	19	106	1.3	84.3	ANPA4	54	5	0.1	99.7
DELO	20	106	1.3	85.6	FECA	55	5	0.1	99.7
MACA2	21	106	1.3	86.9	AGOSE	56	4	0	99.8
COPA3	22	83	1	87.9	ARTRV	57	3	0	99.8
BRI7	23	79	1	88.9	ASDR3	58	3	0	99.8
CHVI8	24	71	0.9	89.7	CRAC2	59	3	0	99.9

Table A10: Continued

ASNE6	25	70	0.9	90.6	MEBU	60	3	0	99.9
COLI	26	70	0.9	91.4	LOMA3	61	2	0	99.9
TECA2	27	70	0.9	92.3	ERHE2	62	1	0	100
IOAL	28	68	0.8	93.1	LEPU	63	1	0	100
ACMI2	29	61	0.7	93.9	SILO3	64	1	0	100
ERCO4	30	46	0.6	94.4	Unk.frb.1	65	1	0	100
MYST2	31	46	0.6	95	VINU2	66	1	0	100
ARFR4	32	43	0.5	95.5					
TRDU	33	36	0.4	95.9					
IOST	34	33	0.4	96.4					
COUM	35	28	0.3	96.7					

Table A11: Species rank abundance for the reference community in the first-year post herbicide application (2019), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover. Frequency (Freq.) is the accumulation frequency. Prop. Is the proportion of the plant community based on abundance.

Reference Community Rank Abundance (2019)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
FEID	1	2311	24.1	24.1	TRDU	41	44	0.5	94.3
ARTR4	2	543	5.7	29.8	PHHA	42	40	0.4	94.7
AGSP	3	472	4.9	34.7	BRTE	43	37	0.4	95.1
LUAR3	4	459	4.8	39.5	ARFR4	44	35	0.4	95.5
STVI4	5	350	3.7	43.1	EROV	45	35	0.4	95.9
TAOF	6	343	3.6	46.7	PHMU3	46	35	0.4	96.2
POFE	7	321	3.3	50.1	DRABA	47	32	0.3	96.6
PSLA3	8	281	2.9	53	ERIGE2	48	30	0.3	96.9
ALDE	9	279	2.9	55.9	ERSP4	49	27	0.3	97.2
ELTR7	10	261	2.7	58.6	LEPU	50	25	0.3	97.4
KOMA	11	261	2.7	61.3	AGGLD	51	21	0.2	97.6
Moss	12	260	2.7	64.1	ALTE	52	21	0.2	97.9
CHVI8	13	247	2.6	66.6	ERPU2	53	19	0.2	98
PHHO	14	233	2.4	69.1	AGAL	54	18	0.2	98.2
POSE	15	219	2.3	71.4	ASMI9	55	17	0.2	98.4
AGSpp	16	215	2.2	73.6	LOTR2	56	15	0.2	98.6
FECA	17	143	1.5	75.1	ARNI	57	13	0.1	98.7
IOST	18	138	1.4	76.5	ASNE6	58	13	0.1	98.8
BASA3	19	136	1.4	77.9	OPFR	59	13	0.1	99

Table A11: Continued

ERHE2	20	125	1.3	79.3	ROWO	60	12	0.1	99.1
STCO4	21	109	1.1	80.4	ASTRA	61	10	0.1	99.2
STAC	22	108	1.1	81.5	COPA3	62	9	0.1	99.3
ERCO5	23	97	1	82.5	ARDR4	63	8	0.1	99.4
ACMI2	24	95	1	83.5	MACA2	64	8	0.1	99.5
HEUN	25	93	1	84.5	SELA	65	8	0.1	99.6
SENEC	26	93	1	85.5	ARCA13	66	5	0.1	99.6
ANUM2	27	81	0.8	86.3	CRAC2	67	5	0.1	99.7
COUM	28	72	0.8	87.1	ACOC3	68	4	0	99.7
ERUM	29	69	0.7	87.8	DESCU	69	4	0	99.7
TECA2	30	63	0.7	88.4	LILE3	70	4	0	99.8
LIRU4	31	59	0.6	89	AGHE2	71	3	0	99.8
AGGLG	32	57	0.6	89.6	CHDOD	72	3	0	99.8
CAPU	33	57	0.6	90.2	OPPO	73	3	0	99.9
PHLO2	34	55	0.6	90.8	AGOSE	74	2	0	99.9
MEBU	35	53	0.6	91.4	AGPA14	75	2	0	99.9
ERCO4	36	52	0.5	91.9	CAREX	76	2	0	99.9
COLI	37	49	0.5	92.4	DEBI	77	2	0	100
LUWY	38	48	0.5	92.9	CAFL7	78	1	0	100
POCO	39	47	0.5	93.4	LERE7	79	1	0	100
ANPA4	40	44	0.5	93.9	LOMA3	80	1	0	100
					PODO4	81	1	0	100

Table A12: Species rank abundance for the reference community in the second-year post herbicide application (2020), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover.

Reference Community Rank Abundance (2020)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
FEID	1	2199	27.2	27.2	PHHA	36	36	0.4	94.3
LUAR3	2	747	9.2	36.5	STVI4	37	34	0.4	94.7
PSTE	3	402	5	41.5	MEBU	38	33	0.4	95.1
ALDE	4	356	4.4	45.9	LASQ	39	31	0.4	95.5
POSE	5	319	3.9	49.8	ARDR4	40	27	0.3	95.9
CHVI8	6	306	3.8	53.6	COPA3	41	27	0.3	96.2
ELTR7	7	258	3.2	56.8	Unk.1	42	27	0.3	96.5
TAOF	8	227	2.8	59.6	POFE	43	24	0.3	96.8
ARTRT	9	218	2.7	62.3	TRDU	44	19	0.2	97.1
ERHE2	10	195	2.4	64.7	POCO	45	18	0.2	97.3
ARFR4	11	192	2.4	67.1	PHHO	46	17	0.2	97.5
STCO4	12	165	2	69.1	BRTE	47	16	0.2	97.7
KOMA	13	161	2	71.1	ASTRA	48	16	0.2	97.9
BASA3	14	155	1.9	73.1	PHMU3	49	16	0.2	98.1
AGDA	15	145	1.8	74.9	AGGLG	50	12	0.1	98.2
ERCO5	16	128	1.6	76.4	ALTE	51	12	0.1	98.4
LEPU	17	125	1.5	78	LOMA3	52	12	0.1	98.5
VIOLA	18	119	1.5	79.5	ASNE6	53	11	0.1	98.7
AGSP	19	107	1.3	80.8	COLI	54	11	0.1	98.8
TECA2	20	95	1.2	82	DRABA	55	11	0.1	98.9
LIRU4	21	92	1.1	83.1	SELA	56	11	0.1	99.1
COUM	22	91	1.1	84.2	ARCO5	57	10	0.1	99.2
ARTR4	23	88	1.1	85.3	LUWY	58	10	0.1	99.3
ERIGE2	24	83	1	86.3	ASMI9	59	9	0.1	99.4
AGSpp	25	74	0.9	87.3	ERNA10	60	7	0.1	99.5
ANUM2	26	72	0.9	88.2	Moss	61	7	0.1	99.6
ACMI2	27	62	0.8	88.9	ERPU2	62	6	0.1	99.7
AGAL	28	61	0.8	89.7	OPFR	63	5	0.1	99.8
ERUM	29	54	0.7	90.3	CIUN	64	4	0	99.8
AGOSE	30	53	0.7	91	DRNE	65	4	0	99.9
STAC	31	50	0.6	91.6	LILE3	66	3	0	99.9
ARSO2	32	49	0.6	92.2	OPPO	67	3	0	99.9
PHLO2	33	48	0.6	92.8	BRI7	68	1	0	99.9
ROWO	34	46	0.6	93.4	AGSM	69	1	0	100
ERCO4	35	39	0.5	93.9	BRMA4	70	1	0	100

Table A12: Continued

CASTI2	71	1	0	100
IOST	72	1	0	100
MYST2	73	1	0	100

Table A13: Species rank abundance for the reference community in the third-year post herbicide application (2021), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover.

Reference Community Rank Abundance (2021)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
BRI7	1	1082	17.5	17.5	STCO4	43	25	0.4	95.1
FEID	2	560	9.1	26.6	ALTE	44	22	0.4	95.4
ARTR4	3	390	6.3	32.9	ARDR4	45	22	0.4	95.8
POSE	4	379	6.1	39	ASDR3	46	22	0.4	96.1
MACA2	5	250	4	43	MYOSO	47	19	0.3	96.4
CAPU	6	218	3.5	46.6	ACMI2	48	17	0.3	96.7
PSLA3	7	213	3.4	50	ASTRA	49	16	0.3	97
EROV	8	212	3.4	53.4	LEPU	50	16	0.3	97.2
AGSP	9	191	3.1	56.5	LOTR2	51	16	0.3	97.5
CHVI8	10	183	3	59.5	ASNE6	52	15	0.2	97.7
ERHE2	11	172	2.8	62.3	AGDA	53	13	0.2	97.9
AGSM	12	149	2.4	64.7	ARFR4	54	11	0.2	98.1
PHLO2	13	134	2.2	66.9	STAC	55	11	0.2	98.3
CIUN	14	132	2.1	69	DEBI	56	10	0.2	98.4
TAOF	15	127	2.1	71	LIPU11	57	9	0.1	98.6
ERCO4	16	99	1.6	72.6	OPPO	58	8	0.1	98.7
TECA2	17	98	1.6	74.2	PHHA	59	8	0.1	98.9
ARTRV	18	85	1.4	75.6	SELAG	60	8	0.1	99
LODI	19	82	1.3	76.9	ARCA13	61	7	0.1	99.1
ANUM2	20	74	1.2	78.1	OPFR	62	6	0.1	99.2
STVI4	21	74	1.2	79.3	POFE	63	6	0.1	99.3
LASQ	22	69	1.1	80.4	VIOLA	64	6	0.1	99.4
LUWY	23	67	1.1	81.5	ASMI9	65	5	0.1	99.5
LUAR3	24	65	1.1	82.6	BRMA4	66	4	0.1	99.5
POCO	25	65	1.1	83.6	AGOSE	67	3	0	99.6
COUM	26	61	1	84.6	CHDOD	68	3	0	99.6
AGGLG	27	59	1	85.6	LILE3	69	3	0	99.7
ARSP	28	52	0.8	86.4	MATA2	70	3	0	99.7
TRDU	29	50	0.8	87.2	MYST2	71	3	0	99.8

Table A13: Continued

ARENA	30	49	0.8	88	BASA3	72	2	0	99.8
ERIGE2	31	45	0.7	88.7	CAREX	73	2	0	99.8
ALDE	32	44	0.7	89.5	COPA3	74	2	0	99.9
MEBU	33	39	0.6	90.1	ERPU2	75	2	0	99.9
CRAC2	34	35	0.6	90.7	LIRU4	76	2	0	99.9
Moss	35	35	0.6	91.2	BRTE	77	1	0	100
ELTR7	36	34	0.5	91.8	DRABA	78	1	0	100
CAFL7	37	33	0.5	92.3	LOMA3	79	1	0	100
ERCO5	38	33	0.5	92.8	Un.Gr.1	80	1	0	100
PHHO	39	31	0.5	93.3					
PODO4	40	29	0.5	93.8					
AGPA14	41	26	0.4	94.2					
KOMA	42	26	0.4	94.6					

Table A14: Species rank abundance for the reference community in the fourth-year post herbicide application (2022), in the Centennial Valley, MT, USA. Species are identified using their United States Department of Agriculture (USDA) four letter codes. Abundance is given in cumulative percent cover.

Reference Community Rank Abundance (2022)									
Species	Rank	Abun.	Prop.	Freq.	Species	Rank	Abun.	Prop.	Freq.
ERUM	1	2251	26.1	26.1	LOSI2	37	45	0.5	94.4
LOTR2	2	468	5.4	31.6	HAPE2	38	42	0.5	94.9
ALDE	3	464	5.4	36.9	ARTRT	39	37	0.4	95.3
ARTEM	4	440	5.1	42.1	ACMI2	40	34	0.4	95.7
ERCO4	5	345	4	46.1	COPA3	41	28	0.3	96
PSLA3	6	292	3.4	49.4	AGGLG	42	27	0.3	96.3
Unk.frb.1	7	292	3.4	52.8	COUM	43	22	0.3	96.6
CASTI2	8	285	3.3	56.1	ALTE	44	21	0.2	96.8
POFE	9	278	3.2	59.4	ASMI9	45	19	0.2	97.1
AGSP	10	224	2.6	62	ERAS2	46	16	0.2	97.2
ERCO5	11	224	2.6	64.6	CHVI8	47	15	0.2	97.4
PHHO	12	182	2.1	66.7	LIPU11	48	15	0.2	97.6
IOST	13	179	2.1	68.8	MYST2	49	15	0.2	97.8
STCO4	14	175	2	70.8	POSE	50	14	0.2	97.9
TAOF	15	163	1.9	72.7	ASDR3	51	13	0.2	98.1
AGDA	16	156	1.8	74.5	ERSP4	52	13	0.2	98.2
CIUN	17	142	1.6	76.1	ARENA	53	11	0.1	98.4
PHHA	18	115	1.3	77.5	ROWO	54	11	0.1	98.5
DRIN2	19	113	1.3	78.8	CAPU	55	10	0.1	98.6
MACA2	20	108	1.3	80	DEBI	56	10	0.1	98.7
ASNE6	21	97	1.1	81.2	ELTR7	57	10	0.1	98.8
BRTE	22	93	1.1	82.3	SELA	58	10	0.1	99
COLI	23	92	1.1	83.3	LEPU	59	9	0.1	99.1
ARFR4	24	88	1	84.3	PODO4	60	9	0.1	99.2
DELO	25	87	1	85.4	ARCAC6	61	8	0.1	99.3
ANPA4	26	86	1	86.3	LIRU4	62	8	0.1	99.3
STAC	27	86	1	87.3	ARTRV	63	6	0.1	99.4
LASQ	28	76	0.9	88.2	ERIGE2	64	6	0.1	99.5
BRI7	29	74	0.9	89.1	TRDU	65	6	0.1	99.6
LIPA5	30	71	0.8	89.9	AGSM	66	4	0	99.6
TECA2	31	71	0.8	90.7	DEPI	67	4	0	99.7
STVI4	32	69	0.8	91.5	PEAR	68	4	0	99.7
AGOSE	33	53	0.6	92.2	Unk.frb.1	69	4	0	99.7
CAFL7	34	53	0.6	92.8	ERHE2	70	3	0	99.8
AGGLD	35	50	0.6	93.3	IOAL	71	3	0	99.8

Table A14: Continued

LILE3	36	45	0.5	93.9	OPFR	72	3	0	99.8
					SECR	73	3	0	99.9
					VIOLA	74	3	0	99.9
					HAMI	75	2	0	99.9
					LOMA3	76	2	0	100
					LOMAT	77	2	0	100
					LERE7	78	1	0	100

Table A15: The species shared between the sprayed and reference communities when communities were combined across all years (2019-2022). Species are represented by their United States Department of Agriculture (USDA) four letter plant codes.

Shared/Nested Species				
ACMI2	ARTRV	ERCO5	LUAR3	TAOF
ACOC3	ASDR3	ERHE2	MACA2	TECA2
AGAL	ASMI9	ERIGE2	MATA2	TRDU
AGDA	ASNE6	ERIN7	MEBU	Un.Gr.1
AGGLD	ASTRA	ERNA10	MINUA	Unk.1
AGGLG	BASA3	EROV	Moss	Unk.frb.1
AGHE2	BRMA4	ERPU2	MYOSO	Unk.frb.2
AGOSE	BRI7	ERSP4	MYST2	VINU2
AGPA14	CAFL7	ERUM	OPFR	VIOLA
AGSM	CAPU	FECA	OPPO	ZIVEV
AGSP	CAREX	FEID	PEAR	
AGSpp	CASTI2	HAMI	PHHA	
ALDE	CHDOD	HEUN	PHHO	
ALTE	CHVI8	HAPE2	PHLO2	
AMRE	CIUN	IOST	PHMU3	
ANPA4	COLI	IOAL	POCO	
ANUM2	COPA3	KOMA	PODO4	
ARCA13	COUM	LASQ	POFE	
ARCAC6	CRAC2	LEPU	POSE	
ARCO5	CRYPT	LERE7	PSLA3	
ARDR4	DEBI	LILE3	PSTE	
ARENA	DESCU	LIPA5	ROWO	
ARFR4	DELO	LIPU11	SECR	
ARNI	DEPI	LIRU4	SELA	
ARSO2	DRABA	LODI	SELAG	
ARSP	DRIN2	LOMA3	SENEC	
ARTEM	DRNE	LOMAT	SILO3	

Table A15: Continued

ARTR2	ELTR7	LOSI2	STAC
ARTR4	ERAS2	LOTR2	STCO4
ARTRT	ERCO4	LUWY	STVI4

Table A16: The list of species that were unique to the sprayed community in each year following herbicide treatment in the Centennial Valley, MT, USA. Species are represented by their four-letter United States Department of Agriculture (USDA) plant codes. The total number of species is listed at the bottom of each column.

Unique Species to the Sprayed Community			
2019	2020	2021	2022
ARTRV	AGHE2	ANPA4	ARCO5
BRMA4	AGPA14	ARTR2	ARSP
CIUN	CAREX	LERE7	CHDOD
	CRAC2	ROWO	CRAC2
	HAMI		ERIN7
	MACA2		FECA
	PEAR		MEBU
	SELAG		SILO3
			VINU2
3	8	4	9

Table A17: The list of species that were unique to the reference community in each year following herbicide treatment in the Centennial Valley, MT, USA. Species are represented by their four-letter United States Department of Agriculture (USDA) plant codes. The total number of species is listed at the bottom of each column. Asterisks denote non-native species.

Unique Species to the Reference Community			
2019	2020	2021	2022
AGAL	AGGLG	ALTE	AGGLD
AGGLD	ALTE	ARCA13	ALTE
AGHE2	BRI7*	ARDR4	ARTRT
AGOSE	CASTI2	ARTRV	CAPU
ALDE*	DRNE	ASDR3	DEPI
ALTE	ERCO4	ASMI9	ERSP4
ANUM2	ERNA10	ASNE6	HAMI
ARCA13	IOST	BRMA4	HAPE2
ARNI	LILE3	CHDOD	LERE7
ASNE6	Moss	DRABA	LILE3
CAFL7	PHHO	ERPU2	LIPA5
CHDOD	POCO*	LILE3	LIPU11
COPA3	ROWO	LOMA3	LIRU4
DEBI	SELA	LOTR2	LOMAT
DESCU*	STAC	MYST2	LOSI2
EROV	Unk.1	POFE	PHHA
ERSP4		STVI4	PODO4
ERUM			ROWO
LERE7			SECR
LIRU4			SELA
LOMA3			VIOLA
LOTR2			
PHHA			
PHMU3			
POCO*			
PODO4			
ROWO			
SELA			
SENEC			
STAC			
30	16	17	21

Table A18: The contributions of nestedness and turnover to Jaccard beta diversity between the sprayed and reference communities in the Centennial Valley, MT, USA. Groups with shared letters are statistically similar within index and across years using an alpha level of 0.05. Note that smaller values indicate a smaller contribution of the relative index to the overall observed Jaccard beta diversity/dissimilarity.

Index	2019	2020	2021	2022
Jaccard Nestedness	0.07a	0.07b	0.07ab	0.14b
Jaccard Turnover	0.41a	0.52a	0.52a	0.54a
Jaccard Beta	0.57a	0.59a	0.59a	0.6a

Table A19: List of observed species with their United States Department of Agriculture (USDA) plant code symbols, family, phenology, and native (N) or non-native (I) status.

Forbs				
Symbol	Scientific Name	Family	Phenology	Status
ACMI2	<i>Achillea millefolium</i>	Asteraceae	Perennial	N
AGGLD	<i>Agoseris glauca</i> var. <i>dasycephala</i>	Asteraceae	Perennial	N
AGGLG	<i>Agoseris glauca</i> var. <i>glauca</i>	Asteraceae	Perennial	N
AGHE2	<i>Agoseris heterophylla</i>	Asteraceae	Annual	N
AGOSE	<i>Agoseris</i> spp.	Asteraceae	—	N
AGPA14	<i>Agoseris parviflora</i>	Asteraceae	Perennial	N
ALDE	<i>Alyssum desertorum</i>	Brassicaceae	Annual	I
ALTE	<i>Allium textile</i>	Liliaceae	Perennial	N
AMAL	<i>Amaranthus albus</i> L.	Amaranthaceae	Annual	I
AMRE	<i>Amaranthus retroflexus</i> L.	Amaranthaceae	Annual	N
ANPA4	<i>Antennaria parvifolia</i>	Asteraceae	Perennial	N
ANUM2	<i>Antennaria umbellata</i>	Asteraceae	Perennial	N
ARCO5	<i>Arenaria congesta</i>	Caryophyllaceae	Perennial	N
ARENA	<i>Arenaria</i> spp.	Caryophyllaceae	—	—
ARNI	<i>Arnica</i> spp.	Asteraceae	—	—
ARSO2	<i>Arnica sororia</i>	Asteraceae	Perennial	N
ARSP	<i>Arabis sparsiflora</i> Nutt.	Brassicaceae	Perennial	N
ASDR3	<i>Astragalus drummondii</i>	Fabaceae	Perennial	N
ASMI9	<i>Astragalus miser</i>	Fabaceae	Perennial	N
ASNE6	<i>Astragalus newberryi</i>	Fabaceae	Perennial	N
ASTRA	<i>Astragalus</i> spp.	Fabaceae	—	—
BASA3	<i>Balsamorhiza sagittata</i>	Asteraceae	Perennial	N
CAFL7	<i>Castilleja flava</i>	Scrophulariaceae	Perennial	N
CASTI2	<i>Castilleja</i> spp.	Orobanchaceae	—	—
CHDOD	<i>Chaenactis douglasii</i>	Asteraceae	Perennial	N
CIUN	<i>Cirsium undulatum</i>	Asteraceae	Perennial	N
COLI	<i>Collinsia linearis</i>	Scrophulariaceae	Annual	N
COPA3	<i>Collinsia parviflora</i>	Scrophulariaceae	Annual	N
COUM	<i>Comandra umbellata</i>	Santalaceae	Perennial	N
CRAC2	<i>Crepis acuminata</i>	Asteraceae	Perennial	N
CRAM3	<i>Crypthantha ambigua</i>	Boraginaceae	Annual	N
CRAN11	<i>Crucianella angustifolia</i> L.	Rubiaceae	Annual	I
DEBI	<i>Delphinium bicolor</i>	Ranunculaceae	Perennial	N
DESCU	<i>Descurainia</i> spp.	Brassicaceae	—	—

Table A19: Continued

DRABA	<i>Draba spp.</i>	Brassicaceae	—	—
DRNE	<i>Draba nemorosa</i> L.	Brassicaceae	Annual	N
ELCI	<i>Elsholtzia ciliata</i> (Thunb.) Hyl.	Lamiaceae	Annual	—
ERCO4	<i>Erigeron compositus</i>	Asteraceae	Perennial	N
ERCO5	<i>Erigeron corymbosus</i>	Asteraceae	Perennial	N
ERHE2	<i>Erigonum heracleoides</i>	Polygonaceae	Perennial	N
ERIGE2	<i>Erigeron spp.</i>	Asteraceae	—	—
EROV	<i>Eriogonum ovalifolium</i>	Polygonaceae	Perennial	N
ERPU2	<i>Erigeron pumilus</i>	Asteraceae	Perennial	N
ERSP4	<i>Erigeron speciosus</i>	Asteraceae	Perennial	N
ERUM	<i>Eriogonum umbellatum</i>	Polygonaceae	Perennial	N
HEUN	<i>Helianthella uniflora</i>	Asteraceae	Perennial	N
IOST	<i>Ionactis stenomeres</i>	Asteraceae	Perennial	N
LASQ	<i>Lappula squarrosa</i>	Boraginaceae	Annual	I
LEPU	<i>Leptodactylon pungens</i>	Polemoniaceae	Perennial	N
LERE7	<i>Lewisia rediviva</i>	Portulacaceae	Perennial	N
LILE3	<i>Linum lewisii</i>	Linaceae	Perennial	N
LIPU11	<i>Linanthus pungens</i>	Polemoniaceae	Perennial	N
LIRU4	<i>Lithospermum ruderales</i>	Boraginaceae	Perennial	N
LODI	<i>Lomatium dissectum</i>	Apiaceae	Perennial	N
LOMA3	<i>Lomatium macrocarpum</i>	Apiaceae	Perennial	N
LOMAT	<i>Lomatium</i> Raf.	Apiaceae	Perennial	N
LOTR2	<i>Lomatium triternatum</i>	Apiaceae	Perennial	N
LUAR3	<i>Lupinus argenteus</i>	Fabaceae	Perennial	N
LUWY	<i>Lupinus wyethii</i>	Fabaceae	Perennial	N
MACA2	<i>Machaeranthera canescens</i>	Asteraceae	Perennial	N
MATA2	<i>Machaeranthera tanacetifolia</i>	Asteraceae	Annual	N
MINUA	<i>Minuartia</i> L.	Caryophyllaceae	—	N
MYOSO	<i>Myosotis</i> L.	Boraginaceae	—	—
MYST2	<i>Myosotis stricta</i>	Boraginaceae	Annual	N
PEAR	<i>Penstemon arenicola</i>	Scrophulariaceae	Perennial	N
PHHA	<i>Phacelia hastata</i>	Hydrophyllaceae	Perennial	N
PHHO	<i>Phlox hoodii</i>	Polemoniaceae	Perennial	N
PHLO2	<i>Phlox longifolia</i>	Polemoniaceae	Perennial	N
PHMU3	<i>Phlox multiflora</i>	Polemoniaceae	Perennial	N
PODO4	<i>Polygonum douglasii</i>	Polygonaceae	Annual	N

Table A19: Continued

PSLA3	<i>Psoralidium lanceolatum</i>	Fabaceae	Perennial	N
PSTE	<i>Psilocarphus tenellus</i>	Asteraceae	Annual	N
SELA	<i>Sedum lanceolatum</i>	Crassulaceae	Perennial	N
SELAG	<i>Selaginella P. Beauv.</i>	Selaginellaceae	Perennial	—
SENEC	<i>Senecio spp.</i>	Asteraceae	—	—
SECR	<i>Senecio crassulus</i>	Asteraceae	Perennial	N
STAC	<i>Stenotus acaulis</i>	Asteraceae	Perennial	N
TAOF	<i>Taraxacum officinale</i>	Asteraceae	Perennial	I
TRDU	<i>Tragopogon dubius</i>	Asteraceae	Annual	I
VINU2	<i>Viola nuttallii</i>	Violaceae	Perennial	N
VIOLA	<i>Viola spp.</i>	Violaceae	—	—
Shrubs/Subshrubs				
Symbol	Scientific Name	Family	Duration	N/I
ARCA13	<i>Artemisia cana</i>	Asteraceae	Perennial	N
ARDR4	<i>Artemisia dracunculus</i>	Asteraceae	Perennial	N
ARFR4	<i>Artemisia frigida</i>	Asteraceae	Perennial	N
ARTEM	<i>Artemisia spp.</i>	Asteraceae	—	—
ARTR2	<i>Artemisia tridentata Nutt.</i>	Asteraceae	Perennial	N
ARTR4	<i>Artemisia tripartita</i>	Asteraceae	Perennial	N
ARTRT	<i>Artemisia tridentata</i>	Asteraceae	Perennial	N
ARTRV	<i>Artemisia tridentata ssp. vaseyana</i>	Asteraceae	Perennial	N
CHVI8	<i>Chrysothamnus viscidiflorus</i>	Asteraceae	Perennial	N
ERNA10	<i>Ericameria nauseosa</i>	Asteraceae	Perennial	N
OPFR	<i>Opuntia fragilis</i>	Cactaceae	Perennial	N
OPPO	<i>Opuntia polyacantha</i>	Cactaceae	Perennial	N
ROWO	<i>Rosa woodsii</i>	Rosaceae	Perennial	N
TECA2	<i>Teradymia canescens</i>	Asteraceae	Perennial	N
Graminoids				
Symbol	Scientific Name	Family	Duration	N/I
ACOC3	<i>Achnatherum occidentale</i>	Poaceae	Perennial	N
AGAL	<i>Agropyron albicans</i>	Poaceae	Perennial	N
AGDA	<i>Agropyron dasystachyum</i>	Poaceae	Perennial	N
AGSM	<i>Agropyron smithii</i>	Poaceae	Perennial	N
AGSP	<i>Agropyron spicatum</i>	Poaceae	Perennial	N
AGSpp	<i>Agropyron spp.</i>	Poaceae	Perennial	N
BRMA4	<i>Bromus marginatus</i>	Poaceae	Perennial	N

Table A19: Continued

BRI7	<i>Bromus riparius</i>	Poaceae	Perennial	I
BRTE	<i>Bromus tectorum</i>	Poaceae	Annual	I
CAPU	<i>Calamagrostis purpurascens</i>	Poaceae	Perennial	N
CAREX	<i>Carex spp.</i>	Cyperaceae	—	—
ELSpp	<i>Elymus spp.</i>	Poaceae	Perennial	N
ELTR7	<i>Elymus trachycaulus</i>	Poaceae	Perennial	N
FECA	<i>Festuca campestris</i>	Poaceae	Perennial	N
FEID	<i>Festuca idahoensis</i>	Poaceae	Perennial	N
HOJU	<i>Hordeum jubatum</i> L.	Poaceae	Perennial	N
KOMA	<i>Koeleria macrantha</i>	Poaceae	Perennial	N
LECI4	<i>Leymus cinereus</i>	Poaceae	Perennial	N
MEBU	<i>Melica bulbosa</i>	Poaceae	Perennial	N
POCO	<i>Poa compressa</i>	Poaceae	Perennial	I
POFE	<i>Poa fendleriana</i>	Poaceae	Perennial	N
POSE	<i>Poa secunda</i>	Poaceae	Perennial	N
STCO4	<i>Stipa comata</i>	Poaceae	Perennial	N
STVI4	<i>Stipa viridula</i>	Poaceae	Perennial	N

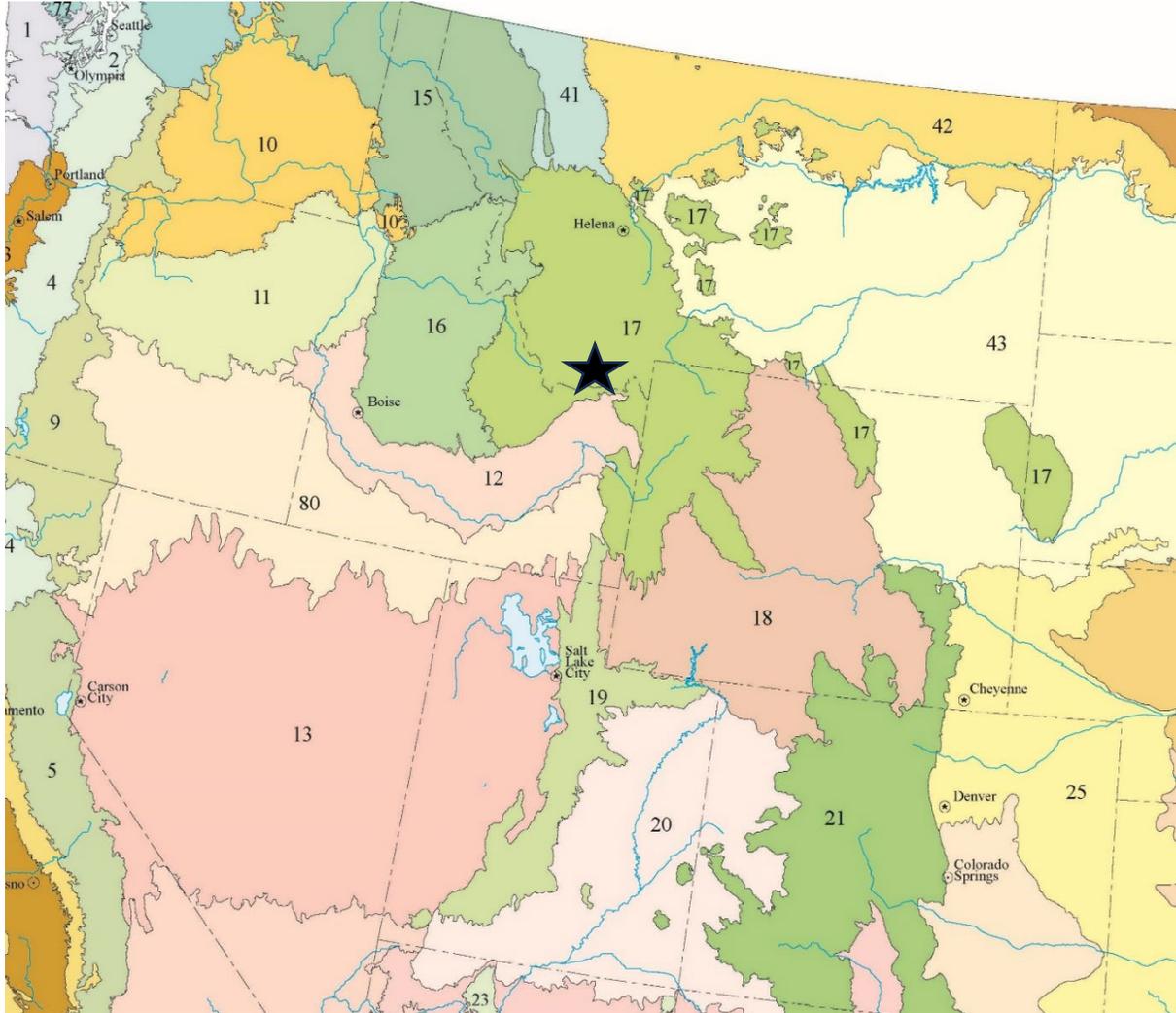


Figure A1: The sub-section of the sagebrush biome that was the focus of this and related studies mapped as level III Ecoregions of the Continental United States. (Adapted from: Omernik (1987), Corvallis Environmental Research Laboratory and Omernik (1995), U.S. Environmental Protection Agency (2013)). Each number denotes an ecoregion. Ecoregion 10 is the Columbia Plateau, 17 is the Middle Rockies, 12 is the Snake River Plain, 80 is the Northern Basin and Range, 13 is the Central Basin and Range, and 18 is the Wyoming Basin. The black star indicates the approximate study location.

APPENDIX C

Chapter Three Supplemental Tables (Species Rank Abundance)

Table B1: Adjusted R^2 values for the relationship between percent cover and dry biomass for each of the five most common native perennial bunchgrasses in the Centennial Valley, MT, USA. As percent cover increased so did dry biomass, these relationships were strong and positive in direction. Degrees of freedom (df) are expressed as; (numerator, denominator).

Species	f	df	R²
<i>A. intermedium</i>	93.73	1,18	0.83
<i>A. spicatum</i>	119.7	1,11	0.9
<i>P. secunda</i>	140.3	1,18	0.88
<i>S. comata</i>	133.7	1,18	0.87
<i>F. idahoensis</i>	157.4	1,18	0.89

Table B2: Top five species by rank abundance in each plant community for the sprayed and non-sprayed treatments in the Antelope Peak (AP) and Eastern Sandhills (ES) region for each year of the study in the Centennial Valley, MT, USA. Grey shading indicates non-native species.

2019							
Year	Region	Treatment	Species	Rank	Abundance	Proportion	Frequency
2019	AP	Sprayed	STVI4	1	196	19	19
2019	AP	Sprayed	CHVI8	2	128	12.4	31.5
2019	AP	Sprayed	PHLO2	3	118	11.5	42.9
2019	AP	Sprayed	ARTR4	4	87	8.4	51.4
2019	AP	Sprayed	IOST	5	81	7.9	59.2
2019	ES	Sprayed	POSE	1	181	35.3	35.3
2019	ES	Sprayed	AGSP	2	174	33.9	69.2
2019	ES	Sprayed	ARTRT	3	57	11.1	80.3
2019	ES	Sprayed	LUCE	4	28	5.5	85.8
2019	ES	Sprayed	TAOF	5	18	3.5	89.3
2019	AP	Non-sprayed	BRTE	1	811	54	54
2019	AP	Non-sprayed	TAOF	2	157	10.5	64.4
2019	AP	Non-sprayed	STVI4	3	101	6.7	71.2
2019	AP	Non-sprayed	ALDE	4	72	4.8	76
2019	AP	Non-sprayed	LUAR3	5	67	4.5	80.4
2019	ES	Non-sprayed	POSE	1	175	20.8	20.8
2019	ES	Non-sprayed	BRTE	2	131	15.6	36.3
2019	ES	Non-sprayed	ARTRT	3	114	13.5	49.9
2019	ES	Non-sprayed	AGSP	4	72	8.6	58.4
2019	ES	Non-sprayed	ELTR7	5	68	8.1	66.5
2020							
Year	Region	Treatment	Species	Rank	Abundance	Proportion	Frequency
2020	AP	Sprayed	LUCE	1	226	19.4	19.4
2020	AP	Sprayed	CHVI8	2	194	16.6	36
2020	AP	Sprayed	PHLO2	3	129	11.1	47.1
2020	AP	Sprayed	ELTR7	4	104	8.9	56
2020	AP	Sprayed	FEID	5	82	7	63
2020	ES	Sprayed	LUCE	1	128	22.9	22.9
2020	ES	Sprayed	STCO4	2	87	15.6	38.5
2020	ES	Sprayed	FEID	3	74	13.2	51.7
2020	ES	Sprayed	STVI4	4	42	7.5	59.2
2020	ES	Sprayed	ARTRT	5	32	5.7	64.9
2020	AP	Non-sprayed	BRTE	1	294	20.7	20.7
2020	AP	Non-sprayed	LUCE	2	202	14.3	35
2020	AP	Non-sprayed	ALDE	3	187	13.2	48.2
2020	AP	Non-sprayed	TAOF	4	106	7.5	55.7

Table B2: Continued

2020	AP	Non-sprayed	PHLO2	5	105	7.4	63.1
2020	ES	Non-sprayed	ALDE	1	140	19	19
2020	ES	Non-sprayed	BRTE	2	117	15.9	34.8
2020	ES	Non-sprayed	LUCE	3	103	14	48.8
2020	ES	Non-sprayed	STVI4	4	74	10	58.8
2020	ES	Non-sprayed	POSE	5	64	8.7	67.5
2021							
Year	Region	Treatment	Species	Rank	Abundance	Proportion	Frequency
2021	AP	Sprayed	CHVI8	1	331	21.3	21.3
2021	AP	Sprayed	LUCE	2	189	12.2	33.5
2021	AP	Sprayed	ARTRV	3	184	11.8	45.3
2021	AP	Sprayed	AGSM	4	139	9	54.3
2021	AP	Sprayed	ARTR4	5	102	6.6	60.8
2021	ES	Sprayed	POSE	1	127	23.6	23.6
2021	ES	Sprayed	ARTR4	2	66	12.3	35.9
2021	ES	Sprayed	AGSP	3	66	12.3	48.1
2021	ES	Sprayed	TAOF	4	59	11	59.1
2021	ES	Sprayed	STCO4	5	45	8.4	67.5
2021	AP	Non-sprayed	ALDE	1	282	18.1	18.1
2021	AP	Non-sprayed	BRTE	2	206	13.2	31.3
2021	AP	Non-sprayed	LUCE	3	172	11	42.4
2021	AP	Non-sprayed	TAOF	4	169	10.9	53.2
2021	AP	Non-sprayed	FEID	5	152	9.8	63
2021	ES	Non-sprayed	POSE	1	85	15.2	15.2
2021	ES	Non-sprayed	ARTR4	2	83	14.8	29.9
2021	ES	Non-sprayed	LUCE	3	81	14.4	44.4
2021	ES	Non-sprayed	BRTE	4	60	10.7	55.1
2021	ES	Non-sprayed	ALDE	5	52	9.3	64.3
2022							
Year	Region	Treatment	Species	Rank	Abundance	Proportion	Frequency
2022	AP	Sprayed	BRTE	1	480	21.9	21.9
2022	AP	Sprayed	LOTR2	2	304	13.9	35.8
2022	AP	Sprayed	ALDE	3	204	9.3	45.2
2022	AP	Sprayed	CASTI2	4	173	7.9	53.1
2022	AP	Sprayed	DRIN2	5	164	7.5	60.6
2022	ES	Sprayed	ALDE	1	92	16.2	16.2
2022	ES	Sprayed	CIUN	2	58	10.2	26.5
2022	ES	Sprayed	STCO4	3	53	9.3	35.8
2022	ES	Sprayed	PODO4	4	43	7.6	43.4

Table B2: Continued

2022	ES	Sprayed	LOTR2	5	41	7.2	50.6
2022	AP	Non-sprayed	BRTE	1	595	24.8	24.8
2022	AP	Non-sprayed	ALDE	2	594	24.7	49.5
2022	AP	Non-sprayed	TAOF	3	238	9.9	59.4
2022	AP	Non-sprayed	ERUM	4	196	8.2	67.5
2022	AP	Non-sprayed	LOTR2	5	190	7.9	75.4
2022	ES	Non-sprayed	BRTE	1	109	15.7	15.7
2022	ES	Non-sprayed	LOTR2	2	100	14.4	30.2
2022	ES	Non-sprayed	POFE	3	99	14.3	44.4
2022	ES	Non-sprayed	ALDE	4	96	13.9	58.3
2022	ES	Non-sprayed	CIUN	5	60	8.7	67

APPENDIX D

Chapter Four Supplemental Tables

Table C1: Model Akaike Information Criterion (AIC) values and structure. Note that the ZAP hurdle model contains two components, the zero-truncated Poisson and the presence component, as suggested by Zuur and Ieno (2016), the AIC for ZAP model is the sum of its components.

Model	AIC	Model Structure
GLM Poisson	3303	glmer(BRTE~ grazed*Herbicide*Year+(1 Tank/Rep),family = poisson)
ZIP	3780	zeroinfl(formula = BRTE ~ grazed * Herbicide*Year grazed * Herbicide*Year)
ZAP (zero-truncated model)	2844	glmmadmb(BRTE~ grazed*Herbicide*Year+(1 Tank/Rep),family='truncpoiss')
ZAP (presence component)	130	glmer(BRTE.1~Herbicide+Year+(1 Tank/Rep),family = binomial)
ZAP	2974	
Negative Binomial	1691	glmer.nb(BRTE~ grazed*Herbicide*Year+(1 Tank/Rep),verbose = F)

Table C2: General linear model assuming a Poisson distribution (GLM Poisson), Zero-inflated Poisson (ZIP), Zero-altered Poisson (ZAP), and negative binomial model performance. Correlation estimate is the Pearson's product-moment correlation value.

Model	Dispersion Statistic	Correlation estimate	df	t	p	lower CI	upper CI
GLM Poisson	9.95	0.82	286	24.476	<2.2e-16	0.78	0.86
ZIP	10.98	0.74	286	18.375	<2.2e-16	0.68	0.78
ZAP	69.46	0.46	286	8.6886	2.89E-16	0.36	0.54
Negative Binomial	1.06	0.69	286	16.175	< 2.2e-16	0.63	0.75

Table C3: Estimated monthly differences in soil temperature (°C) between 2021 and 2022 in the Centennial Valley, MT, USA, using a two-sided t-test. Values are expressed as 2021-2022, i.e., negative values indicate increased soil temperature in 2022.

Month	Estimate	t	p	lower CI	upper CI
January	-2.3	-77.04	<0.0001	-2.4	-2.2
February	-0.3	-10.89	<0.0001	-0.3	-0.2
March	-0.6	-25.58	<0.0001	-0.6	-0.5
April	1.9	47.58	<0.0001	1.8	2.0
May	2.8	55.46	<0.0001	2.6	2.9
June	6.1	108.61	<0.0001	6.0	6.3
July	0.8	12.10	<0.0001	0.6	0.9
August	-3.2	-42.72	<0.0001	-3.4	-3.0
September	-1.7	-21.50	<0.0001	-1.9	-1.5
October	-1.5	-19.97	<0.0001	-1.7	-1.3

Table C4: Mean monthly soil temperature and moisture for the duration of the study in the Centennial Valley, MT, USA.

Year	Month	Mean Soil Temperature	
		(°C)	Mean Soil Moisture (m ³ /m ³)
2020	December	-7.0	0.113
2020	October	0.3	0.085
2020	November	-2.3	0.115
2021	December	-1.9	0.149
2021	January	-5.8	0.119
2021	February	-4.2	0.124
2021	March	-2.6	0.171
2021	April	2.8	0.191
2021	May	9.7	0.192
2021	June	18.9	0.157
2021	July	20.6	0.140
2021	August	17.1	0.179
2021	September	12.9	0.167
2021	October	5.1	0.219
2021	November	0.3	0.175
2022	January	-3.4	0.146
2022	February	-3.9	0.147
2022	March	-2.0	0.198
2022	April	0.9	0.203
2022	May	7.0	0.208
2022	June	12.8	0.168
2022	July	19.8	0.142
2022	August	20.3	0.159
2022	September	14.6	0.161
2022	October	7.1	0.163
2022	November	3.2	0.184

Table C5: Estimated monthly differences in soil moisture (m³/m³) between 2021 and 2022, in the Centennial Valley, MT, USA. Estimates are the result of 2021-2022, i.e., negative values indicate an increase in soil moisture in 2022.

Month	Estimate	t	p	lower CI	upper CI
January	-0.027	-469.784	<0.0001	-0.027	-0.027
February	-0.023	-311.553	<0.0001	-0.023	-0.023
March	-0.027	-39.5497	<0.0001	-0.029	-0.025
April	-0.011	-25.8249	5.2E-143	-0.012	-0.010
May	-0.016	-40.0142	<0.0001	-0.017	-0.015
June	0.017	32.1788	1.3E-217	0.016	0.018
July	0.050	75.85965	<0.0001	0.049	0.052
August	0.079	63.31937	<0.0001	0.076	0.082
September	0.066	62.50057	<0.0001	0.063	0.069
October	0.073	66.80628	<0.0001	0.071	0.076

Table C6: Estimated monthly differences in soil temperature (°C) between 2021 and 2022 in the Centennial Valley, MT, USA. Values are expressed as 2021-2022, i.e., negative values indicate increased soil temperature in 2022.

Month	Estimate	t	p	lower CI	upper CI
January	-2.3	-77.0479	<0.0001	-2.4	-2.2
February	-0.3	-10.8949	<0.0001	-0.3	-0.2
March	-0.6	-25.5814	<0.0001	-0.6	-0.5
April	1.9	47.58775	<0.0001	1.8	2.0
May	2.8	55.46034	<0.0001	2.6	2.9
June	6.1	108.6661	<0.0001	6.0	6.3
July	0.8	12.10209	<0.0001	0.6	0.9
August	-3.2	-42.7247	<0.0001	-3.4	-3.0
September	-1.7	-21.5089	<0.0001	-1.9	-1.5
October	-1.5	-19.9762	<0.0001	-1.7	-1.3