

**Evidence for and Mechanisms of Ecosystem Transformation in the Great Basin of
the Western United States**

by

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Ecosystem transformations are very difficult to reverse and are likely to become more common with accelerating global change. The novel systems that often result are maintained by stabilizing feedbacks that are composed of forcing mechanisms that can be either external or internal to the system. Increasing our understanding of these feedback components and how they relate to each other is crucial to know when they can be reversed and the original ecosystem restored. Here, we studied the sagebrush biome in the western United States, where annual grass invasion and fire are converting vast areas of shrublands into annual grasslands, and these are thought to be two alternative species assemblages. In four separate studies, we aimed to understand the components of positive feedback mechanisms that maintain these two assemblages, and the impacts that conversion from shrubland to grassland has on ecosystem function.

In chapter one we found that the spatial connectivity of fuel influences the burn severity of fire, which then favors the occurrence of fire-tolerant annuals in the seedbank. In chapter two we investigated how invasion and the loss of shrubs and perennial grasses by fire influenced soil nutrient cycling, and found that the annual grass dominance in the post-fire state converted the system from a source to a sink of soil C and N. In chapter three, we constructed a fire history atlas to isolate the effect of time since fire and remove the effect of repeated fires. We found that there was very little evidence of recovery towards the pre-fire state even after 30 years. Rather, we found that livestock grazing and annual grass abundance interact to maintain the post-fire, grass-dominated state. Finally, in chapter four we created an allometric equation to calculate biomass from cover estimates.

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Introduction

Abrupt ecological changes are an emerging theme of great importance in ecological research (Andersen et al. 2009; Ratajczak et al. 2018). Global increases in temperatures and aridity, along with changing precipitation patterns, mean that in many places on Earth organisms may be experiencing climatic conditions that they are not adapted to. Changing climate is also altering patterns of disturbances, in particular wildfires (Abatzoglou and Williams 2016), hurricanes, and insect outbreaks (Kyle C. Rodman et al. 2021). Accelerating human activity is increasing the amount of disturbance due to fire (Jennifer K. Balch et al. 2017; Cattau et al. 2020), land use/land cover change and the introduction of non-indigenous propagules. The variety of new patterns can lead to multiple new processes which may interact with each other, and with already existing processes. If these processes all have positive relationships with one another, new self-reinforcing cycles can emerge (Figure 1). These new cycles can maintain new species assemblages that bear little resemblance to that which was there before, which often exist side-by-side with the native system.

So-called alternative stable states are thought to be fairly common, and not necessarily a result of recent global change. For example, there is strong evidence that in the tropics forests, savannas and grasslands represent 3 alternative stable states (Hirota et al. 2011; Staver, Archibald, and Levin 2011). They are, however, difficult to experimentally demonstrate (Petalis and Latham 1999; Schröder, Persson, and De Roos 2005), and observational studies are often the only realistic option at a scale that matters for conservation and management (Pausas and Bond 2020). In the following dissertation, we studied ecosystem transformation in the sagebrush biome, which is the largest biome of the western United States. In this system, a novel grassland has replaced almost half of the shrublands that previously existed (K. W. Davies et al. 2011). We used an observational approach where we combined remote sensing images with field observations to understand how changing patterns can influence ecological processes and lead to long-term ecosystem transformation.

Background

The sagebrush biome in the western United States began experiencing novel anthropogenic disturbances and invasions in the 19th century (R. N. Mack 1981). In pre-colonial times the

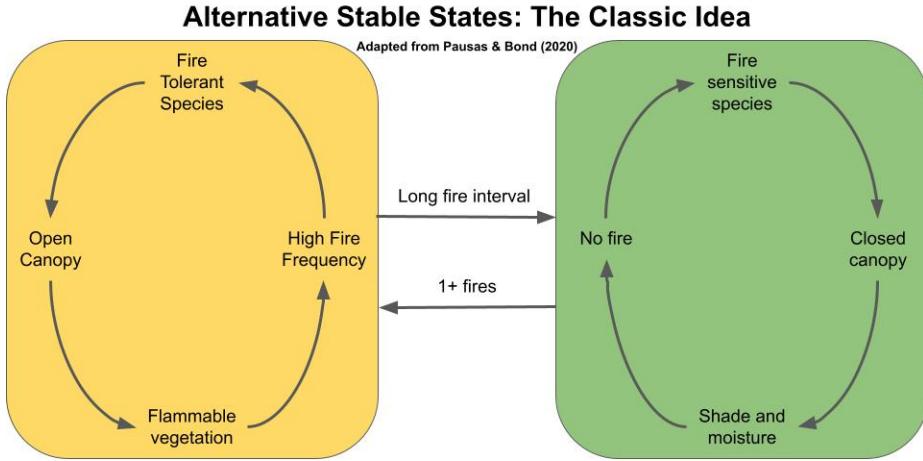


Figure 1: A typical idea of how fire and vegetation interact to form self-reinforcing feedbacks that maintain alternative stable states.

ecosystem was characterized by shrubs interspersed with perennial bunchgrasses and forbs. It typically experienced infrequent, patchy fires (Baker 2006; Bukowski and Baker 2013). Many of the plant species, including *Artemisia* spp L., are seed obligates that rely on the spatial discontinuity of disturbance to recolonize burned patches by reseeding from adjacent unburned areas (Daniel R. Schlaepfer, Lauenroth, and Bradford 2014). After European colonization livestock grazing was introduced and was initially poorly managed at best (R. N. Mack 1981). Overgrazing during this period appears to have depleted perennial grass and forb cover while increasing shrub cover. Much of the land management in the 20th century centered around trying to restore perennial grass cover for grazing utilization while attempting to deplete shrub cover. Cheatgrass (*Bromus tectorum* L.) was introduced in the late 19th century (R. N. Mack 1981), and it was during this period of management that cheatgrass appears to have spread steadily throughout the region. It was not until the early 1990s that researchers started to document that cheatgrass was changing the fire regime in some areas (Whisenant 1990; Knapp 1996) and was a likely case of a grass-fire cycle (D'Antonio and Vitousek 1992; Brooks et al. 2004). A possible explanation for the lack of fire associated with early invasion is that the mid-20th century was a relatively cool period with reduced fire activity (Littell et al. 2009), and it was not until the latter decades when fire activity started to increase noticeably across the wider western U.S (Westerling et al. 2006; Dennison et al. 2014). The transformation of sagebrush ecosystems into annual grasslands is an instructive case study to

understand the mechanisms that underlie abrupt vegetation changes, because it may be a harbinger of things to come for many of the world's ecosystems.

There are many ways ecological systems can change abruptly (Ratajczak et al. 2018). There can be different relationships between the exogenous environmental drivers and the ecological property of interest, often a structural characteristic like tree cover or the abundance of a key species (Andersen et al. 2009; Ratajczak et al. 2018). Different driver-response relationships combined with temporal variability of the driver can lead to a plethora of possible explanations for the observed temporal trends of the state variable of interest (Ratajczak et al. 2018). This complexity makes it difficult to use observational data to demonstrate clearly when an abrupt shift is an alternative stable state, a collapsing ecosystem, or a system experiencing a disturbance from which it will eventually recover. Thus experimental manipulation of the system to tease out the mechanisms of stabilizing feedbacks is seen as the gold standard (Petraitis and Latham 1999). However, actually demonstrating alternative stable states through experimental perturbation is rare (Schröder, Persson, and De Roos 2005), and often unfeasible in systems with long-lived keystone species. Furthermore, experimental manipulations rely on simplified representations of systems that in nature may harbor hundreds of plant and animal species. These simplified systems may not have inference at a broad enough scale that matters for biodiversity conservation and other management objectives. With this in mind, we will explore five pieces of observational evidence posited by Pausas and Bond (2020) which together would be strong evidence to consider two vegetation types in a landscape to be alternative states: 1) differing in the dominant growth form; 2) co-occurring in the same environment; 3) differing in their species composition; 4) having abrupt boundaries between the two states; and 5) stability over generations, which is maintained by self-reinforcing feedback mechanisms.

The sagebrush biome has two widespread species assemblages, which are the native sagebrush and the post-fire state that is dominated by introduced annual grasses. Prior work has shown that the species composition is qualitatively different, even at locations where the two states occur very close together (Mahood and Balch 2019, Figure 2a). The measurements by Mahood and Balch (2019) were made at locations where places with different fire frequencies had occurred close enough together that one could reasonably assume identical climate and very similar, pre-fire

compositions. Abrupt boundaries between the two states are one of the more remarkable features that are commonly observed in this landscape (Figure 2b). The final requirement is stability over generations, maintained by self-reinforcing feedbacks. This is the most difficult requirement to assess, and therefore the subject of most of the following dissertation.

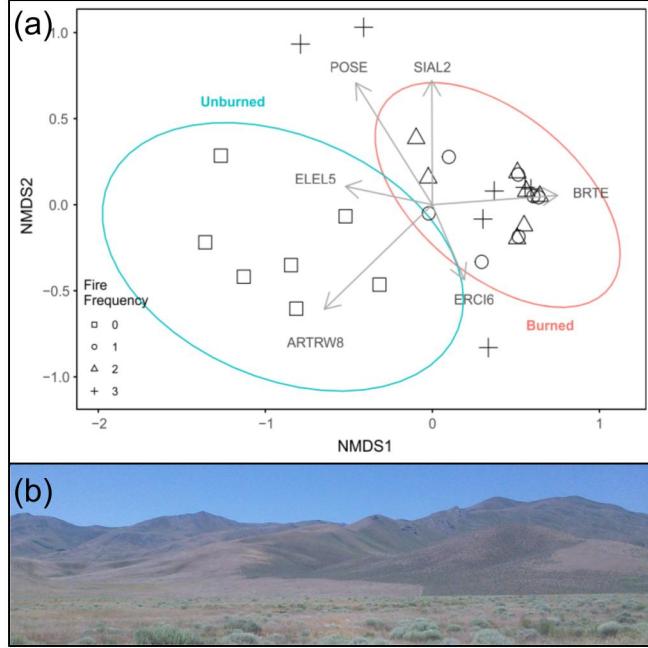


Figure 2: (a) Non-metric multidimensional scaling (NMDS) ordination showing burned and unburned plant communities from Mahood & Balch (2019). Ellipses are 95% confidence interval ellipses. (b) Abrupt boundaries between shrublands and annual grasslands which correspond to fire history are commonly observed (Photo credit: Adam Mahood). ARTRW8 = Artemisia tridentata, POSE = Poa secunda, SIAL2 = Sisymbrium altissimum, BRTE = Bromus tectorum, ERCI6 = Erodium cicutarium, ELEL5 = Elymus elymoides

Research questions

This research was driven by two questions. First, is the annual grassland that has replaced so much of the sagebrush ecosystem an alternative stable state? Second, what are the impacts that the conversion to this novel system has on ecosystem function? The primary approach we used to investigate these questions was to identify and measure the components of potential self-reinforcing feedback mechanisms (e.g Figure 1).

We focused on methodologies where remote sensing observations complimented or were used to guide field observations. Satellite remote sensing has emerged as an indispensable resource in the

study of disturbances, including wildfire (Andrus et al. 2016; Kyle C. Rodman et al. 2019). It is especially useful for fire history studies, since government records tend to become less reliable further in the past. The Landsat suite of satellites, in particular, has continuous multi-spectral coverage that is able to accurately map fire occurrence and severity starting in 1984. Landsat products are well-suited for investigating alternative stable states of vegetation, since the primary characteristic one is trying to characterize are broad structural characteristics of the system (e.g. tree cover). This approach has been successfully utilized to characterize alternative vegetative states in the tropics, for example (Hirota et al. 2011). A time series of just over 30 years may not be useful for systems that experience very infrequent fires, and have long recovery times after fire. In contrast, for the sagebrush biome it is perfect. Sagebrush typically can return to full prefire cover or at least show detectable signs of recovery after fire within 15-30 years (Harniss and Murray 1973; Shriver et al. 2019), and the invasion of annual grasses has accelerated fire activity to the point where the fire rotation (the time required for an area equal to the entire area of interest to burn) is in the range of 30 years in many areas.

How do fuel connectivity and burn severity interact to affect species composition of the seed bank?

In chapter one we tried to uncover an important missing link in the positive feedback loop that is thought to operate in *Artemisia* shrublands invaded by *B. tectorum*. This feedback loop starts with invasion of annual grasses increasing fuel connectivity (Figure 3), which increases the probability of fire (K. W. Davies and Nafus 2013). The post-fire landscape is often *B. tectorum* monocultures, which has even higher fuel connectivity and fire probability (Jennifer K. Balch et al. 2013). But what is missing is the mechanism by which fire occurrence leads to increased fuel connectivity. The loss of native propagules due to repeated fires is likely to be one mechanism by which the post-fire herbaceous ecosystem remains dominant (Bond and Midgley 1995). We hypothesized that the fuel connectivity would increase burn severity, which would then affect the composition of the soil seed bank, such that there would be more introduced annuals and fewer perennial natives. The altered seedbank composition should then lead to higher fuel connectivity.



Figure 3: Fuel connectivity is a key spatial property that is changed after invasion by *Bromus tectorum*. The filling in of shrub interspaces with straw-colored grasses (*B. tectorum*) is clearly seen. The black mountain in the background is sixmile hill, days after the Hot Pot Fire was extinguished.

How does invasion interact with interannual climate variability to affect soil carbon and nitrogen?

One of the primary ideas about alternative stable states is that the changes in ecosystem function that result from altered ecosystem structure are the drivers of the self-reinforcing feedbacks that maintain the altered structure. The grass-fire cycle is a classic example wherein invasion changes fuel structure, and that altered fuel structure changes the ecosystem function of flammability (Pausas, Keeley, and Schwilk 2017). Flammability then influences the disturbance regime, which affects ecosystem structure. But other mechanisms that are less obvious may also exist. For example, *B. tectorum* invasion alters the spatial and temporal pools and fluxes of soil nutrients. Changes in the availability of soil nutrients can influence the ability of native perennial plants to germinate, establish and persist. This is complicated further by interannual climate variability, which directly influences both plant cover (David S. Pliod, Welty, and Arkle 2017) and soil nutrient cycling (A. T. Austin et al. 2004). In chapter 2, we sampled soil nutrients and plant community composition at two points in time: first, after two abnormally dry years and second, after two years with average precipitation. We then used path models to disentangle the effects of ecosystem structure and interannual climate variability on soil nutrients.

We found that the loss of shrubs and deep-rooted perennial plants from fire has important consequences that have not previously been reported. For sites that still had shrubs and deep-rooted plants, the most important pathway for soil nutrients was perennial grasses, which responded to high moisture availability by increasing soil C and N. For sites that had lost their shrubs and native perennials were dominated by invasive annuals, the most important pathway for soil N and C was annual grasses, which responded to high moisture availability by decreasing soil C and N. Furthermore, high water availability had a direct negative effect on soil total C and N, so this effect was neutralized by the plant community in the uninvaded sites, while it was amplified in the degraded sites. This may lead to long-term depletion of soil N and C, making restoration more difficult.

If we remove the effect of repeated fires will the system recover, or will we find evidence of stabilizing feedbacks?

In chapter three, we aimed to remove the effect of repeated fire and try to understand if there are other mechanisms that maintain the annual grass-dominated assemblage. We used two satellite-based fire occurrence products to identify locations that burned only once since 1984. In these locations we attempted to detect the recovery of native shrubs and perennial herbaceous plants. The seed-obligate sagebrush can recover to pre-fire abundances after 30 years (Harniss and Murray 1973; Shinneman and McIlroy 2016), but often takes much longer. In a recent demographic modeling study, Shriver et al. (2019) showed that during the first 5-10 years, even post-fire sagebrush populations that are recovering can have a flat or even negative growth rate because the population is composed almost exclusively of high-mortality, low-fertility individuals. Once enough individuals grow and their survival and fecundity increases around 15 years post-fire. Since the satellite record covers just over 30 years, it stands to reason that while the probability of encountering sites with native plants fully returned to their pre-fire cover, the recovery of native shrubs and perennials should be at least detectable.

We found that without the effect of repeated fires, there was still little evidence of recovery to the prefire state. This adds to the available evidence that points to a system with alternative stable states by showing evidence of stability over a generation. Fire occurrence had a negative effect on native plants and a positive effect on many introduced annual plants. After fire the occurrence of many native species decreased as time since fire increased. Grazing had strong positive effects on introduced annuals, and positive effects on many short-statured perennial native forbs and resprouting shrubs, while *B. tectorum* cover had negative effects on the occurrence of *A. tridentata*.

Can we use cover estimates to model cheatgrass biomass?

One of the most important impacts of the conversion from woody plant dominance to an annual grass dominance is the impact on the carbon cycle. The loss of sagebrush in the western U.S. has already resulted in a loss of 8 Tg of aboveground biomass carbon, with perhaps 50 Tg more to come (Bradley et al. 2006; Fusco et al. 2019). These estimates are primarily derived from the aboveground biomass that is sequestered in woody plants, and do not account for the

annual productivity of herbaceous plants. In chapter four we examined how well ground-based cover estimates of cheatgrass correlate with biomass measurements, with the aim of finding an allometric equation to convert cover to biomass. Often, allometric equations are developed to be site-specific, and require intensive measurements on the ground at every site (Chai et al. 2019). Here, we sought to develop an equation using only cover, which is rapid and non-destructive, and can be estimated with satellite remote sensing data (Boyte, Wylie, and Major 2019; M. O. Jones et al. 2018). Several groups are developing models of *B. tectorum* cover (Boyte, Wylie, and Major 2019) or functional group cover (M. O. Jones et al. 2018). The ultimate goal is for future researchers to be able to estimate biomass from regional-scale cover estimates derived from satellite images.

We found the slope of the relationship to be slightly variable between years but it was linear and the relationship was quite strong. However, we also found that the slope of the relationship changes drastically as the growing season progresses, because the seeds fall from the main body of the plant and the shoot material desiccates. In addition, there is still uncertainty about how the relationship holds up at higher cover values. For the practical purpose of using biomass to estimate fire risk, the higher ends of the cover range are likely to be less important. First, it is simply not very common to have cover values higher than 70%, and second the important range of cover values within which fire risk is most affected is in the lower percentages, where fuel becomes less contiguous.

Chapter 1. High fuel connectivity from annual grass invasion increases burn severity, which alters seedbank composition to favor annual grass invasion.

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Abstract

Alternative stable states are an important topic in the context of global change in which internal positive feedbacks are required to maintain two qualitatively different types of plant communities under the same climatic conditions. In *Artemesia tridentata* communities in the western United States, annual grass invasion changes the fuel connectivity, which increases the size and spatial contiguity of fires. This results in post-fire systems that are dominated by introduced annual grasses. But it is unclear exactly how fire directly benefits the introduced annual grasses. There are many possible mechanisms by which altered fuel properties influence fire properties, and how fire itself influences the post-fire biotic community and abiotic conditions. One mechanism by which fire can influence plant communities that is rarely directly studied is the alteration of the species composition of the seed bank. Here, we collected seed bank samples across a range of burn severities immediately after a large fire was extinguished, and examined the how burn severity affected the species composition.

We focused on a positive feedback loop where fuel connectivity increases burn severity, and burn severity alters the seed bank composition such that it has a higher proportion of introduced annual plants. First, we used total vegetation cover as a proxy for fuel connectivity (TVC) and examined how it affected burn severity (H1), and then used a joint species distribution model to examine how burn severity affected the proportion of introduced annual plants in the seed bank (H2). We then tested if post-fire seed bank composition affected post-fire TVC (H3). We found that pre-fire fuel connectivity and burn severity were positively related (H1). For H2, higher burn severity had mostly positive or neutral effects on the occurrence of non-native species, and mostly negative or

neutral relationships with native species. For H3, we found that the abundance of annual grass seeds in the seedbank immediately post-fire had a positive effect on the fuel connectivity 3 years later. This is the first study that we are aware of in the *Artemisia tridentata* ssp. *wyomingensis* ecosystem that shows how burn severity influences seed bank species composition, as well as examining the full feedback loop with fuel connectivity.

1. Introduction

One of the consequences of global change in the 21st century that is most difficult to reverse is when ecosystems abruptly shift from one stable species assemblage to another (Ratajczak et al. 2018). In tropical ecosystems, three alternative stable states have been identified along a gradient of precipitation: forests, savannas and grasslands (Hirota et al. 2011; Staver, Archibald, and Levin 2011). These three states cluster around values of tree cover (approximately 80, 30 and 0 percent) that occur among overlapping levels of precipitation, and so it is thought that they exhibit states of hysteresis in which internal, self-reinforcing mechanisms maintain alternate states (Andersen et al. 2009). In the forested state there is a self-reinforcing positive feedback between evapotranspiration and tree cover (Staal et al. 2020). In the grassland and savanna states, there are feedbacks between grass flammability and fire occurrence (Staver, Archibald, and Levin 2011; D'Antonio and Vitousek 1992).

A classic example of hysteresis in a semi-arid, temperate system is the invasion of *Bromus tectorum* L. and other introduced annual grasses in the Great Basin of the western United States. Here, over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems have been degraded, fragmented or lost completely (K. W. Davies et al. 2011). This has been attributed to a host of causes, including wildfire (Jennifer K. Balch et al. 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of annual grasses. In this open shrubland, the space between shrubs is primarily composed of bare ground covered in biological soil crust, dotted with perennial bunch grasses. The lack of fuel connectivity is believed to have limited fire spread, with a fire regime of infrequent, patchy fires (Keeley and Pausas 2019). Annual grass invasion increases fuel connectivity while decreasing fuel moisture (K. W. Davies and Nafus 2013), leading to increased fire size and frequency (Whisenant 1990; Knapp 1996; Jennifer K. Balch

et al. 2013). After fire, the landscape is often dominated by introduced annual grasses and forbs. This causes a >50% loss of aboveground carbon storage (Bradley et al. 2006; Nagy et al. 2021). But in order to understand how the grassland state persists, the mechanisms by which fire benefits the introduced annual grass must be understood. Petraitis and Latham (1999) posited that the maintenance of alternate species assemblages requires first a disturbance that removes the species from the initial assemblage and second the arrival of the species of the alternate assemblage. One understudied mechanism that may explain both is the interaction between burn severity and the species composition of the soil seed bank.

Studies that directly examine the relationship between the species composition of the seed bank and fire severity and/or intensity are uncommon, but increasing attention has been given to the subject recently. In boreal forests, the depth of the burn may be more important more than the temperature of the fire, with species-specific effects on recovery depending on whether the species recovers via resprouting or from the seed bank (Morgan and Neuenschwander 1988; Schimmel and Granström 1996). In a wetland study in Japan, high severity fire was found to increase seedbank diversity, and the similarity between the seedbank composition and aboveground composition was higher in places burned at high severity (Kimura and Tsuyuzaki 2011). There have been a handful of studies in temperate, semi-arid regions. Lipoma, Funes, and Díaz (2018) found that in shrubland high-severity fire reduced the overall number of seeds in the seedbank but did not change the floristic or functional composition. Maia et al. (2012) found intraspecific differences in post-fire seedbank densities that were explained by burn severity in a pine plantation in Portugal. Palmer, Denham, and Ooi (2018) found that the residual seedbank after fire varied with severity between two *Acacia* species in Australia. Wright, Latz, and Zuur (2016) found that Australian mulga (*Acacia aneura*) had higher regeneration after higher fire temperatures. In Iran, Heydari et al. (2017) found that low-severity fire increased diversity in the soil seed bank, but high-severity fire led to losses. These studies show that the effects of fire severity on the seed bank are ecosystem- and species-specific. High severity fire can benefit species that use the seedbank (Kimura and Tsuyuzaki 2011), be seedbank-neutral (Lipoma, Funes, and Díaz 2018), or have a negative effect (Heydari et al. 2017). Furthermore, the effects of burn severity go beyond seed mortality. Fire temperature can alter physical seed dormancy thresholds (Liyanage and Ooi 2017). In different systems, individual

species have adapted strategies to cope with fires that may be tailored to different severities.

Because *B. tectorum* is annual, in order for it to benefit from fire, which it clearly does (Jennifer K. Balch et al. 2013; Mahood and Balch 2019), it would have to have enough seeds in the post-fire landscape to achieve a fitness benefit and become well-represented in the post-fire plant assemblage (Bond and Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal, and *B. tectorum* seeds have been shown to have increased dispersal distances after fire (Monty, Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. There is strong evidence that *B. tectorum* builds a well-stocked pool of seeds in the soil and litter, even when it is not well represented in the above-ground plant assemblage (Young and Evans 1975; Hassan and West 1986; Boudell, Link, and Johansen 2002). If the increase in fuel connectivity caused by *B. tectorum* increases the severity of fire, it stands to reason that burn severity would influence the community composition of the post-fire seed bank in a way that facilitates the post-fire dominance of *B. tectorum*. To our knowledge, despite several studies on the relationship between fire and the seed bank in this system (Young and Evans 1975; Hassan and West 1986; Humphrey and Schupp 2001; Boudell, Link, and Johansen 2002; Barga and Leger 2018), no studies to date have examined this potential effect of burn severity on the seed bank.

There is strong evidence that *B. tectorum* invasion alters the physical properties of fire, including fire temperature (R. O. Jones et al. 2015; Brooks et al. 2004) and burn severity (the proportion of biomass burned (Keeley 2009; J. D. Miller et al. 2009)). Direct measurements have shown low temperature (Beckstead et al. 2011; Germino, Chambers, and Brown 2016), and lower fire temperatures can be inferred from the commonly observed phenomenon that *B. tectorum*-fueled fires burn fast. Fire duration is inversely related to soil heating and therefore affects the response of vegetation to fire (Gagnon et al. 2015), including the capacity of the seeds of *B. tectorum* to remain viable after fire (Humphrey and Schupp 2001). Because *B. tectorum* increases horizontal fuel connectivity (K. W. Davies and Nafus 2013), this leads to more contiguously burned areas with fewer unburned plants, and therefore higher burn severity—even with lower fire temperatures. The fire featured in this study is a perfect example. It burned about 50,000 hectares in less than a week.

If increased burn severity is a mechanism by which *B. tectorum* excludes native plants in sagebrush shrublands, then an area with high burn severity may have a lower occurrence of viable

seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced annual plants. This would lead to the dominance of introduced annual grasses and forbs would result in higher fuel connectivity, closing the positive feedback loop. Prior work has demonstrated that *A. tridentata* communities have historically had long fire rotations (>150 years) (Baker 2006; Bukowski and Baker 2013). Plants that are adapted to infrequent fire would be unlikely to produce seeds that are adapted to surviving fire, or dispersal mechanisms to take advantage of the resources available immediately after fire (Davis et al. 2000; Keeley et al. 2011). *A. tridentata* relies on successfully tolerating drought and opportunistically devoting its resources to producing big seed crops in wet years (Meyer 1994; Perryman et al. 2001). When it burns it burns with high intensity, individual plants do not survive or resprout vegetatively, and the remaining unburned neighbors seed the area (*sensu* Schwilk and Kerr 2002). The seeds have a short dispersal distance, the vast majority falling within a few meters of the parent plant (Meyer 1994; Daniel R. Schlaepfer, Lauenroth, and Bradford 2014). They typically lose their viability after one growing season if they remain on the soil surface or under litter, but can retain some viability for at least 24 months if they are buried under a few inches of soil (Wijayratne and Pyke 2009).

The Great Basin has not escaped the recent warming and drying trend that the western U.S. has experienced (Bradford et al. 2020). This is expected to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly by causing the plants to produce lighter seeds (Daniel R. Schlaepfer, Lauenroth, and Bradford 2014). With this in mind, there is another potential self-reinforcing mechanism that could serve to maintain the high fuel connectivity state without fire. That is that the post-fire state with high fuel connectivity is associated with two mechanisms for competitive exclusion of natives. First, it reduces soil moisture which is unfavorable for *Artemisia* seedlings (Turnbull et al. 2012; Wilcox et al. 2012), and second the dominant plant, *B. tectorum*, can out-compete native plants for early spring moisture (Meyer 1994; Jeanne C. Chambers et al. 2007).

Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July 2016. Because it burned a large area in only three days, we could sample a broad area while being reasonably certain that the climatic conditions during the fire were the same at all sites. Because we collected

our samples immediately after the fire was extinguished, we felt confident that the seed bank samples did not contain seeds deposited by post-fire dispersal. We put the samples in cold storage and germinated the seeds from those cores in a greenhouse the following spring. In spring 2017 and fall 2019 we collected information on vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel connectivity would be positively related to burn severity; (H2) burn severity would increase the occurrence probability of introduced annual species in the seed bank and reduce the occurrence probability of native species; (H2a) increased fuel connectivity brought on by the invasion of annual grasses already depleted the diversity of the soil seed bank before the fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related to post-fire fuel connectivity. In addition, because in our study system sites with high fuel connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high post-fire fuel connectivity of those near-monocultures would result in lower aboveground species diversity due to competitive pressure.

2. Methods

2.1 Study Area

The study was conducted in north-central Nevada the day after a large fire (the Hot Pot Fire) was extinguished (Figure 4). The Hot Pot Fire burned just over 50,000 hectares in less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big sagebrush plant communities. The fire occurred after the early season plants, including *B. tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone to seed, and before the late season species, including Wyoming big sagebrush, had produced flowers. Thus we were able to isolate the effect of the fire without any confounding effects of post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged from 1397 to 1607 meters in elevation.

2.2 Seed Bank Sampling

In early July 2016, we collected samples of the soil seed bank at fourteen locations immediately after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites were mature

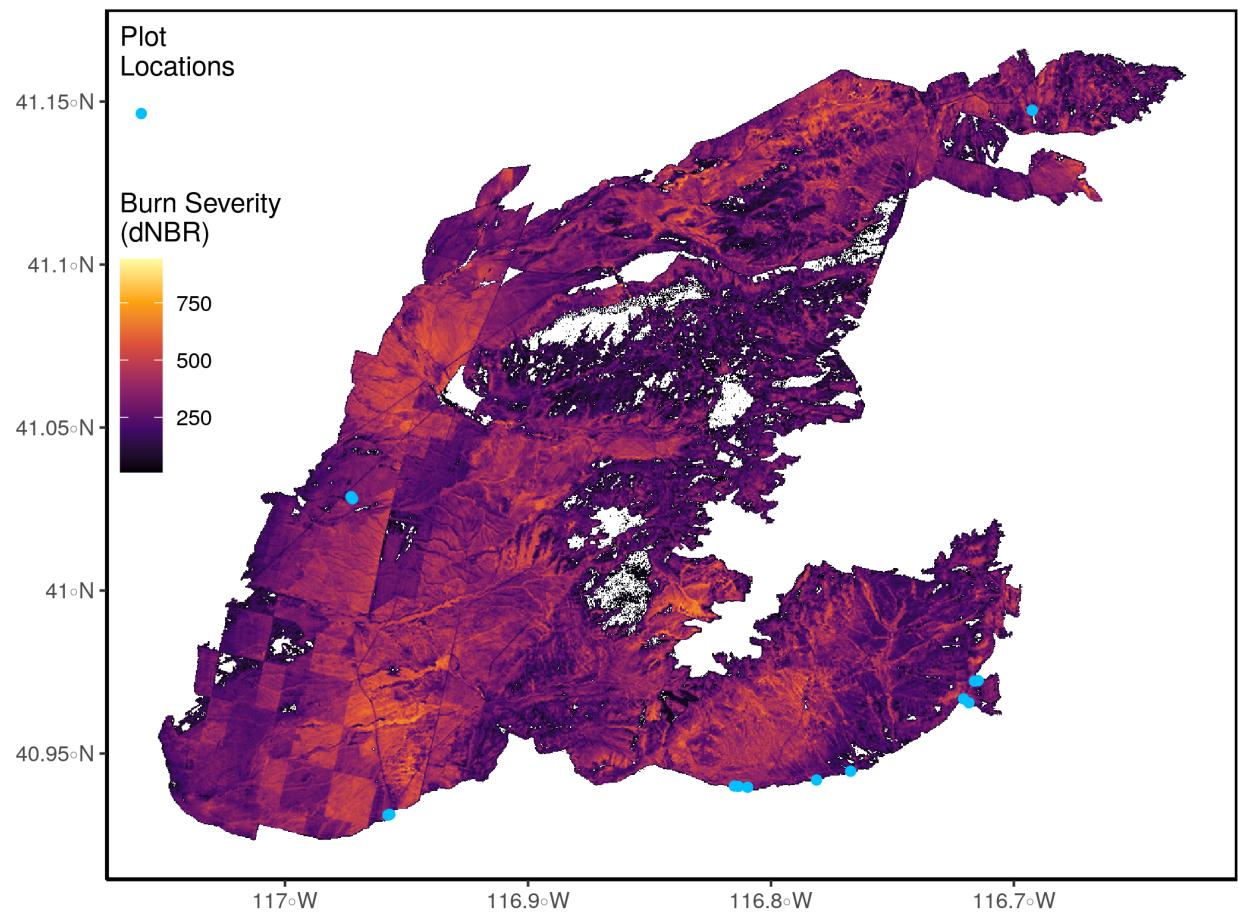


Figure 4: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

sagebrush communities with no history of fire since at least 1984. Three plots had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS) fire history (Eidenshink et al. 2007) and had high cover of *B. tectorum*, but still had scattered sagebrush cover. We used a metal stake to mark paired burned and unburned sampling locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the perimeter. Within 3 m of each marker, we extracted 12, 6 cm deep, 5 cm diameter, soil cores. Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system (Shinneman and McIlroy 2016), and so they are not uniformly distributed (Boudell, Link, and Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemesia* have different germination rates based on the micro-site they find themselves in [i.e. under a shrub or in the bare ground between shrubs (Eckert et al. 1986)]. To account for these potentially confounding effects, we placed half of the core locations under shrubs, and half in shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even when they were completely incinerated, their imprint remained on the soil surface (Bechtold and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples. Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and Mcarthur 2013).

At all sites, to be sure that we were at a site where sagebrush germination could occur we checked for first year germinants (we found them at all sites), and to ensure that there were no confounding effects of post-fire seed dispersal, we determined whether or not the sagebrush were flowering (they were not flowering at all sites), and recorded species occupancy for all plant species.

2.3 Greenhouse Germination

We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots. These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were watered as needed to stay at field capacity. Every week emerging germinants were identified, counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks we ended the germination assay.

2.4 Post-Fire Vegetation Sampling

In order to understand how the seed bank composition compares to the realized vegetative composition, we sampled the vegetative occupancy and cover in May 2017, the growing season immediately after the fire and again in September 2019. In 2017, at each location, we established 50m transects starting at the boundary of the burned and unburned sides of the perimeter, running perpendicular to the fire perimeter, and marked the transect ends with rebar. We measured the occupancy and abundance of all plant species by measuring cover of every species in 0.1 m^2 quadrats spaced every 5 m along each transect. We used the line intercept method to measure shrub cover and herbaceous plant cover along the transect. Both live and dead plants were included in these measurements. Total vegetation cover (TVC) was defined as the sum of herbaceous plant cover and shrub cover. In order to assess if sites had the potential for sagebrush regeneration immediately post-fire, we counted all first-year germinants within 50 cm of the transect, which we defined as any sagebrush individual less than 20 cm in height. In September 2019 we resampled the burned transects for occupancy and abundance of all plant species, as well as shrub and fine fuel cover.

2.5 Estimating Burn Severity with Landsat 8 OLI

We downloaded the “fire bundle” of the Hot Pot fire from <http://www.mtbs.gov>. This included cloud-free Landsat 8 scenes collected before the Hot Pot fire, and already calculated layers of the Differenced Normalized Burn Ratio (dNBR) (J. D. Miller et al. 2009). Because our sites were generally within 10 meters of the burn perimeter, The pixels directly intersecting the plot locations had the potential to be mixed pixels (i.e. containing burned and unburned ground). To minimize this effect, we extracted all the dNBR values within a 120 meter buffer for pixels whose centroids fell inside of the fire perimeter and calculated the mean.

2.6 Statistical Analysis

Our statistical analysis centered around trying to understand each component of the positive feedback loop posited by the 4 hypotheses described previously. In order to understand how pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC) from two separate data sources as a proxy for fuel connectivity, and created separate linear models with TVC

as the predictor variable and burn severity (dNBR) as the response variable. With the field data we collected, we created an ordinary least squares (OLS) linear model with burn severity (dNBR) as the dependent variable and TVC (defined as shrub cover plus herbaceous plant cover from the unburned side of the paired plots), elevation and aspect as independent variables. As a supplement, we examined the relationship using Landsat Thematic Mapper data and TVC from the Bureau of Land Management's Assessment, Inventory and Monitoring dataset (AIM) to represent fuel connectivity (U.S. Department of Interior 2018). The AIM dataset contained 813 sampling locations within the Central Basin and Range ecoregion (Commission for Environmental Cooperation 2006) that were visited by BLM field crews between 2011 and 2015. They were mostly sampled once but there were some repeats, for 1,117 total measurements. For each of these points, we extracted the values of each Landsat band for the sampling year near peak biomass using a cloud-free scene from May or early June. Then, we used those band values to calculate various vegetation indexes, including the Green Normalized Differenced Vegetation Index (Green NDVI, Equation 1), and Normalized Differenced Senesced Vegetation Index (NDSVI, Equation 2). We used these indexes to create a beta regression model of TVC, starting with the largest possible model and used backwards selection following the methodology of Zuur et al. (2009). We used this model to create a layer of predicted TVC for the study area for the pre-fire scene, and extracted both our predictions of TVC and dNBR of the fire from 1000 regularly-spaced points within the fire perimeter. Finally, to quantify the effect of TVC on burn severity, we created an OLS linear model with our modeled TVC and its second-order polynomial as predictor variables and burn severity as the response variable.

$$\text{Equation 1: } \text{Green NDVI} = \frac{\text{NIR}-\text{Green}}{\text{NIR}+\text{Green}}$$

$$\text{Equation 2: } \text{NDSVI} = \frac{\text{SWIR}_1-\text{Red}}{\text{SWIR}_1+\text{Red}}$$

To examine how burn severity affected the community composition of the seed bank (H2), we created a joint species distribution model (JSDM) in a Bayesian framework (Tikhonov, Ovaskainen, et al. 2020) for the occurrence of all species germinated from the seed bank that were found at more than one location. We created four Markov Chain Monte Carlo (MCMC) chains, each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain and then recorded every 100th for a total of 1,000 posterior samples per chain, and 4,000 total. We assessed model convergence using the effective sample size and the potential scale reduction factor (Gelman, Rubin,

and others 1992). We used the model to predict the probability of occurrence of germinable seeds of a given species along a gradient of burn severity. We included burn severity, elevation, aspect, pre-fire seedbank diversity and soil depth as independent variables.

To account for the possibility of H2a as a confounding factor, we included the Shannon-Weaver diversity index (Shannon and Weaver 1949; Hill 1973) in the paired, unburned seed bank samples as one of the predictor variables in our JSDM. We also created OLS models with the unburned species richness and Shannon-Weaver diversity index predicted by prefire fuel connectivity, with the expectation that pre-fire fuel connectivity would have had a negative effect on the prefire seedbank diversity.

To examine how community composition and burn severity then affected subsequent fuel connectivity (H3), we created OLS models with fuel connectivity three years post-fire as the dependent variable, and burn severity, seed counts for *B. tectorum*, *P. secunda* and other species, elevation, aspect, depth, and alpha diversity as independent variables.

To examine how the resulting fuel connectivity was related to biodiversity (H4), we used the diversity data and connectivity data that we collected in 2019 to create a Poisson GLM with number of species encountered aboveground at each plot location as the dependent variable, as well as an OLS linear model with the Shannon-Weaver index (Shannon and Weaver 1949; Hill 1973) as a dependent variable. We used fuel connectivity, elevation, and aspect as independent variables.

For all linear and generalized linear models, we used backwards selection to find the most parsimonious model. We fitting the largest possible model first, and removed variables that did not improve the model fit according to Akaike's Information Criterion (AIC), following the methodology of Zuur et al. (2009).

All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis is freely available on GitHub (https://www.github.com/admahood/seed_bank).

3. Results

We found support for each hypothesized component of the positive feedback loop. For H1, the most parsimonious model for our *in situ* observations had only TVC as the predictor, which

had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$, Figure 5a). For our remotely sensed analysis, our most parsimonious model of TVC explained 34% of the variation and had Green NDVI, NDSVI and their interaction as predictors. Our model of dNBR using the predicted TVC within the fire perimeter as a predictor of dNBR explained 41% of the variation and the relationship between TVC and burn severity was positive and significant ($p \ll 0.01$, Figure 5a).

The vast majority of seeds that germinated in the greenhouse were the two most common grass species, *P. secunda* and *B. tectorum*. Eight forb species were found in more than one location, and these 10 prevalent species are those that were used in our JSDM. Burned plots had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14 in the bottom 4 cm. Unburned plots had an average of 299 ± 170 in the top 2 cm and 59 ± 29 in the bottom 4 cm. For H2, the JSDM converged well (Gelman diagnostics all very close to 1 and the effective sample size centered on 4,000, Figure 6a). Elevation had the most significant effects on individual species (Figure 6b) and explained the most variance on average (36% Figure 6c). Burn severity explained 23% of the variance on average and was supported at the 95% level for 5 species (Figure 6b). For the introduced species, the predictions along a gradient of burn severity were positive for *B. tectorum*, *Sisymbrium altissimum* L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala testiculata* and *Alyssum desertorum* Stapf (Figure 5b). For native species, the effect of burn severity on occurrence was positive for *A. tridentata*, neutral for *P. secunda* and negative for the remaining species (Figure 5b). Testing H2a revealed a positive relationship between pre-fire aboveground species diversity and pre-fire fuel connectivity, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a confounding factor for H2.

For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the postfire seedbank was positively associated with the fuel connectivity in 2019 ($\beta = 0.54$, $p = 0.01$, Adj $R^2 = 0.74$, Figure 5c).

For H4 the most parsimonious model (Adj $R^2 = 0.89$) had elevation, aspect, fuel connectivity and an interaction between elevation and fuel connectivity as predictors of aboveground Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated with Shannon-Weaver diversity ($\beta = -0.28$, $p=0.004$, Figure 5d).

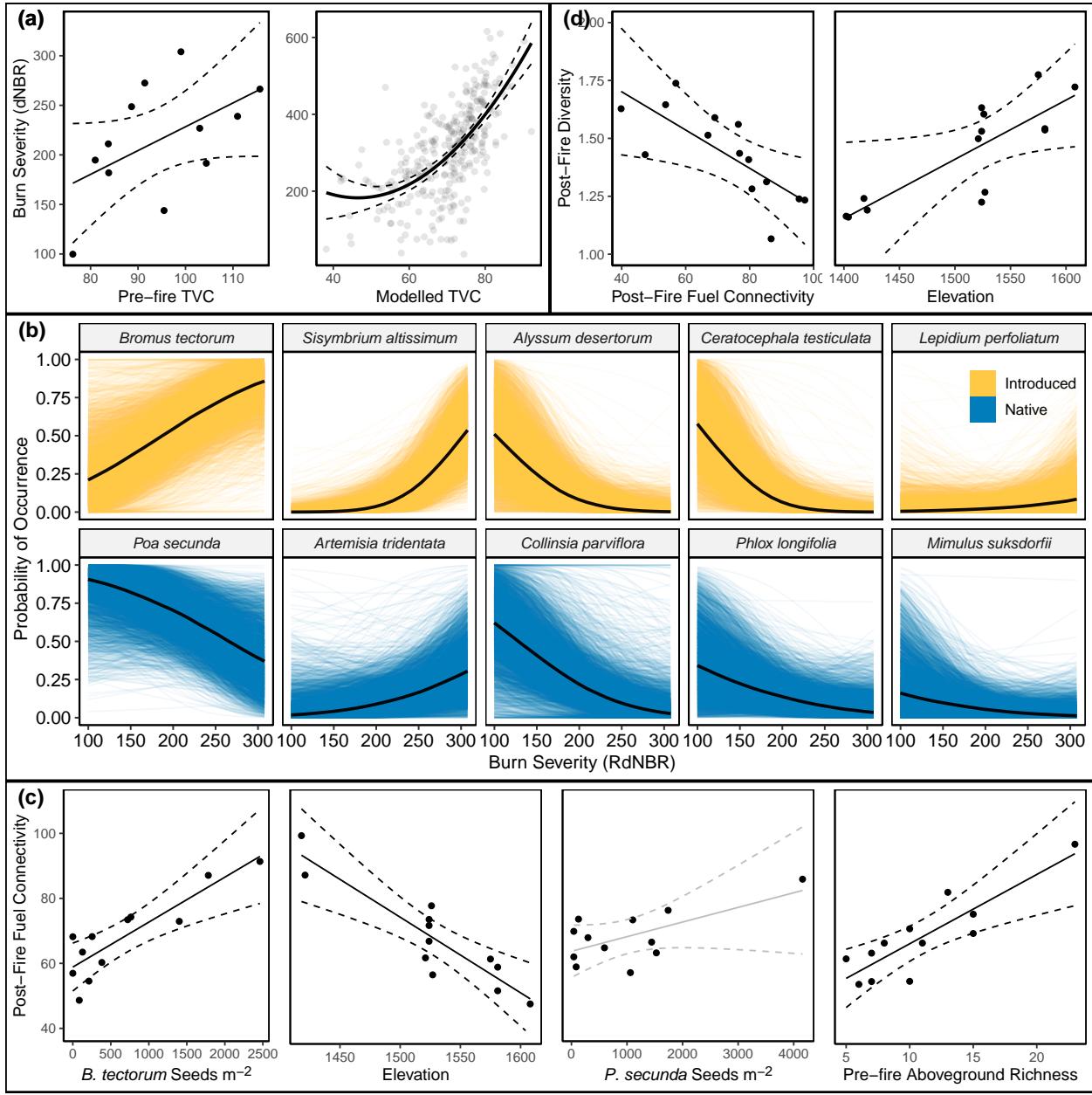


Figure 5: a) Hypothesis 1. On the left, burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Dotted lines are the 95% confidence intervals. b) Hypothesis 2. Modelled occurrence of germinable seeds for all species found at more than one location along a gradient of burn severity, after accounting for soil depth, aspect, elevation and pre-fire diversity. Black line is the mean prediction, each colored line represents one posterior sample. c) Hypothesis 3. Fuel connectivity three years post-fire as modelled by seedbank composition, elevation and pre-fire aboveground species richness. d) Hypothesis 4. Shannon-Weaver diversity index of the aboveground, post-fire community composition, was negatively affected by fuel connectivity after accounting for elevation. For a, c and d, lines are the fitted partial effects (in the case of multiple predictors), points are the partial residuals, dotted lines are the 95% confidence intervals.

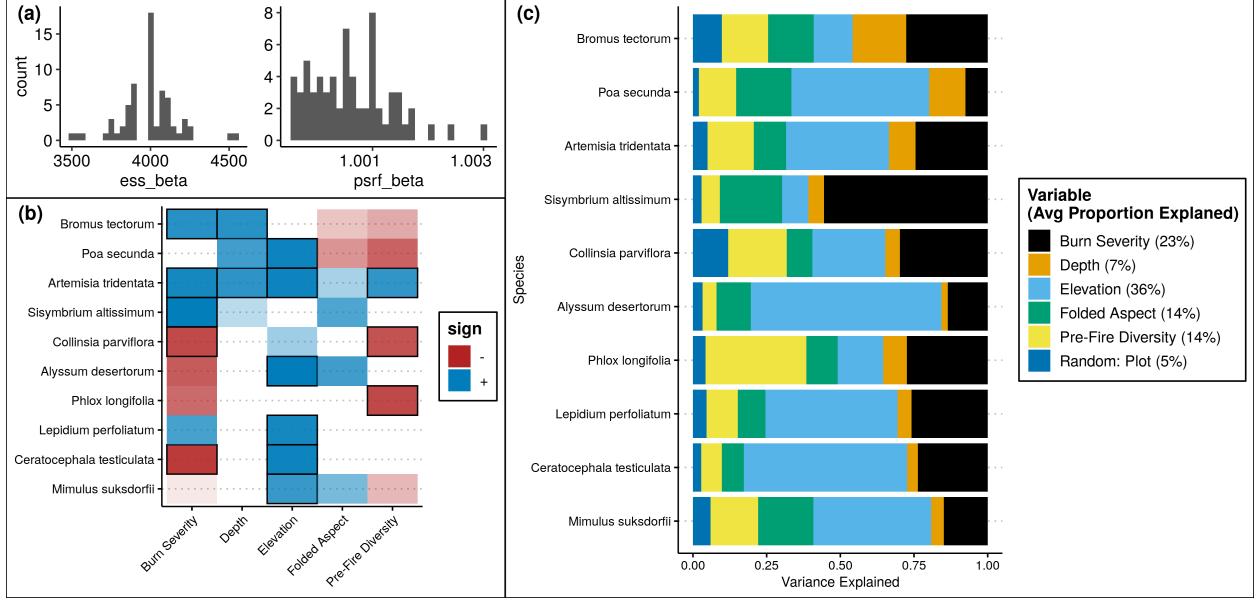


Figure 6: a) Model convergence diagnostics. On the left is the effective sample size after adjusting for autocorrelation (ideally 4,000), and on the right is the Gelman diagnostic, ideally 1. b) Predictor variables that had at least 80% support. Variables with 95% support are outlined in black. The level of transparency corresponds to the level of support. c) Variance partitioning by species. Average across all species per variable is given in the legend. Species are ordered by prevalence.

4. Discussion

In order to truly consider an annual grass-fire cycle to be maintained by self-reinforcing feedbacks, the mechanisms by which fire occurrence is linked to higher post-fire flammability must be understood. In this study we found evidence that interaction between burn severity and seed bank composition may explain that link. Prior work has shown that annual grass invasion increases fuel connectivity in western US sagebrush ecosystems by filling in shrub interspaces with a contiguous bed of fine fuels (K. W. Davies and Nafus 2013). This change in the spatial distribution of fine fuels has been associated with larger and more frequent fires (Jennifer K. Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) increases burn severity (H1, Figure 5a). Higher burn severity was associated with an increased occurrence of introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure 5b). Higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher post-fire fuel connectivity (H3, Figure 5c). In addition, we found evidence that high post-fire fuel connectivity was associated with lower aboveground diversity (H4, Figure 5d). This suggests that during inter-fire intervals, there are additional mechanisms

maintaining the post-fire species assemblage that is dominated by annual introduced plants.

The difference in species composition before and after fire explains an apparent contradiction in results between H2a (positive relationship between pre-fire fuel connectivity and diversity) and H4 (negative relationship between post-fire fuel connectivity and diversity). Most (11 out of 14) plot locations had mature canopies of native shrubs and with the inter-shrub space occupied mostly by native bunchgrasses and forbs, with fire history since 1984. The three plots with recent fire history burned in 1984 and were invaded by *B. tectorum*, but they still had significant cover of *A. tridentata*. Even in locations with high annual grass cover between shrubs, shrubs provide ecosystem structural heterogeneity and islands of fertility (Doescher, Miller, and Winward 1984; Bechtold and Inouye 2007), and perennial natives that may have been established before invasion have deep roots established that allow for the avoidance of competition for water with shallow-rooted annuals (Gibbens and Lenz 2001; Ottaviani et al. 2020). This may provide enough niche compartmentalization to allow native plants to persist. Three years after the Hot Pot fire, almost all of the plots were dominated by introduced annuals, and lacked any structural heterogeneity. Thus native plants may have been able to persist via niche compartmentalization after the initial invasion, but fire burns away most of the seeds and removes all of the structural benefits that shrub cover provides. In this clean slate post-fire environment, the altered species composition of the seedbank and superior post-fire dispersal of *B. tectorum* (Monty, Brown, and Johnston 2013) allows the process of interspecific competition to be dominant (Daniel R. Schlaepfer, Lauenroth, and Bradford 2014).

Global impacts

The grass-fire cycle in the western US is reinforced through providing fitness benefits to the introduced annual grasses and forbs via at least 4 redundant processes: i) changing the composition of the seedbank, ii) competitive exclusion of native plants, iii) CO₂ enrichment which may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of annual grass species (Nagel et al. 2004; Smith et al. 2000), strengthening the fuel connectivity to burn severity to seed composition feedback loop, and iv) ecohydrological feedbacks that create a warmer, drier microclimate (Turnbull et al. 2012; Wilcox et al. 2012). It is likely that some of these feedbacks are idiosyncratic to the

system being studied, while others may reflect the fundamental properties of ecosystem function that change when a system is converted from being dominated by woody plants to being dominated by herbaceous plants (Kitzberger et al. 2016). Understanding the mechanisms of hysteresis, and in particular how multiple redundant mechanisms act in concert, will provide important insights for ecosystem change on a global scale. At least 13 grass species initiate self-reinforcing feedbacks with fire in the U.S. (Fusco et al. 2019; Tortorelli, Krawchuk, and Kerns 2020), and many more worldwide, including Australia (G. Miller et al. 2010; Setterfield et al. 2010), Brazil (Rossi et al. 2014) and South Africa (Milton 2004). While the conversion of temperate forests and shrublands to grasslands may have a less per-hectare impact on carbon sequestration than tropical forests, the consequences are still relevant to the global carbon cycle, especially when forests (rather than the shrublands studied here) are replaced by herbaceous ecosystems (Kerns et al. 2020).

Potential limitations

We found fewer species and lower diversity in our seedbank germination assays than we did in the aboveground sampling. This result may be influenced by the methodological limitations inherent to greenhouse germination trials (Vandvik et al. 2016). In particular our results may be understating the occurrence of native species in the seedbank. Habitat specialists have been shown to emerge more in *in situ* germination assays than in greenhouse germination assays, while the opposite has been found for ruderal species (Plue et al. 2017). Nevertheless, for those species that were prevalent in our germination studies, we still found consistent relationships between their abundance and occurrence by biogeographic origin, and those species that were prevalent in the postfire seedbank germination assays were also those most common in the aboveground community postfire.

Burn severity metrics like dNBR were conceived of in the context of forested ecosystems (J. D. Miller et al. 2009), and calibrated using the composite burn index (Key and Benson 1999), tree mortality, and percent change in tree canopy cover. These do not apply in shrubland systems. Here we estimated burn severity using dNBR and understand it to be a proxy for the amount of biomass that was burned in the fire. We recorded qualitative observations of burn severity while we were sampling, mainly to ensure that we sampled a range of severities, and the dNBR we used appears

to be a good proxy for our observations. However, we note that the manual severity classification provided by MTBS had exclusively low and medium severity, but our observations of essentially complete consumption of plant and litter tissues and very few unburned patches suggested that these should have been mostly medium and high severity. This was not unexpected (Kolden, Smith, and Abatzoglou 2015). The Hot Pot fire took place during a high wind event, burning 50,000 ha in only 3 days, so the scale of weather-driven fire spread overtook any possibility of fuel disconnectivity on the scale of a few meters stopping the spread of the fire. In areas where the space between shrubs was well-connected by fine fuels (Figure 7a-c) the dNBR was higher, and the shrubs had completely burned throughout the root system, leaving only a hole in the ground filled with ashes as evidence of their prior presence. In these areas the entirety of the soil surface—underneath shrub canopy and in canopy interspaces—was consumed by fire, and there was little evidence of remaining litter or biological soil crust. In areas with lower fuel connectivity (Figure 7d-f), and lower dNBR, shrubs were usually consumed only to the stumps, and sometimes were left standing and charred, destined for mortality. In these areas the soil surface often still had biological soil crust, partially consumed litter (R. O. Jones et al. 2015) and unconsumed annual and perennial grass bases.

Management implications

Greenhouse or *in situ* germination assays are time-consuming and require botanical expertise, and are very important. One potential avenue for future research may be linking remote sensing data with retrospective meta-analyses of prior studies. There are many studies that only study fire occurrence as it relates to the seed bank. Fire history, including burn severity, is now possible to calculate for anywhere on earth at a 30 meter resolution from 1984 to present with Landsat images (Parks et al. 2018). Teasing out these mechanisms will increase our understanding of how generalizable these phenomena are, and this will allow us to know how best to manage these ecosystems and where and when it is possible to reverse the process.

This work shows that this is a clear example of a system where the degraded state represents an alternative species assemblage from that of the restoration target, where the propagules of the original assemblage are no longer present, and thus methods that rely on natural succession may

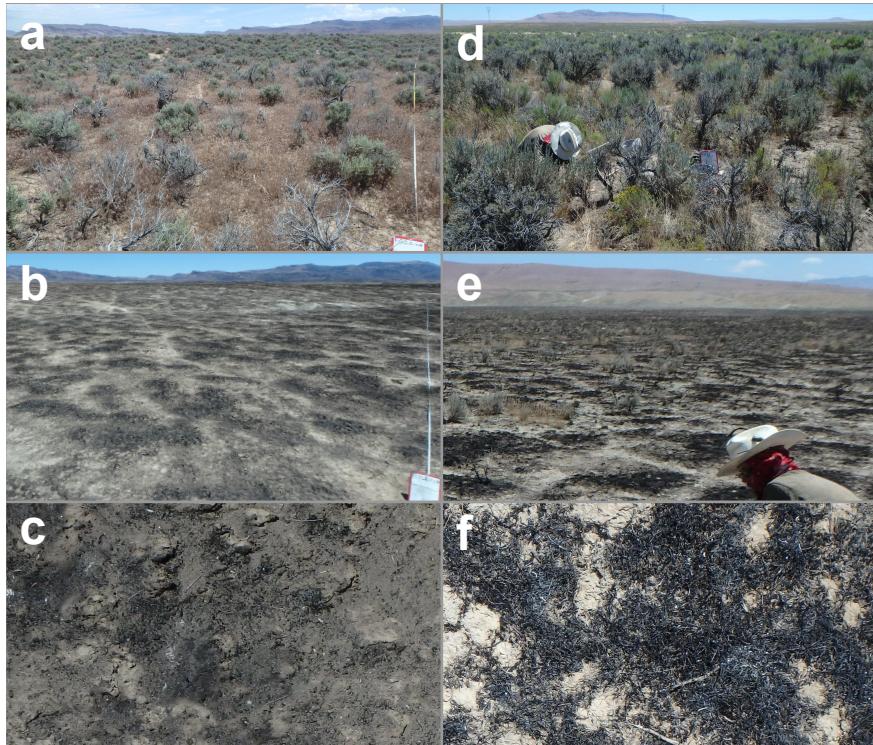


Figure 7: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space being highly invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, and approximately all of the biomass was consumed by the fire. Panel C is a closeup of the soil surface, showing in more detail how the litter was also almost completely consumed by the fire. On the right, the photos in panels d and e were on opposite sides of a fire line in an area that had minimal annual grass invasion over a broad area, and thus lower fuel connectivity. Note the remaining plants and stumps in panel e and the presence of only partially consumed litter in panel f.

not be sufficient (Suding, Gross, and Houseman 2004). Our results highlight the importance of prioritizing the preservation of native shrub cover and in particular policies that encourage land managers to maximize the preservation of unburned patches during the suppression of wildfires in this system (Steenvoorden et al. 2019). Commonly encountered native plants and the keystone shrub species *A. tridentata* depend on post-fire seed dispersal from surviving individuals in unburned patches (Daniel R. Schlaepfer, Lauenroth, and Bradford 2014). Once the system achieves a canopy dominated by annual grasses and forbs, the competitive pressure from the annual grass monoculture makes it more difficult if not impossible for perennial native forbs and shrubs to establish from the depleted seedbank. Post-fire seeding efforts may restore native propagules, but if there is dense cover of annuals further effort may be required to reduce fuel connectivity in order to reduce both fire risk and competitive pressure from annuals.

Livestock grazing can reduce fuel connectivity in uninvaded sagebrush (K. W. Davies et al. 2010). At the same time, grazing can also decrease the resistance to invasion by *B. tectorum* via negative effects on biological soil crust (BSC) (Condon and Pyke 2018), and can reduce the survival of *Artemisia* seedlings that are not protected by shrub canopies (Owens and Norton 1992). In wet years, targeted grazing at already invaded sagebrush sites may reduce fuel connectivity and alleviate fire risk. Plant community composition in the years immediately after fire may be highly variable spatially and from year to year. Post-fire grazing may help reduce *B. tectorum* cover, but it would more likely exacerbate the problem by introducing cheatgrass in uninvaded sites (Williamson et al. 2019) or increasing the already superior postfire dispersal of *B. tectorum* seeds (Monty, Brown, and Johnston 2013). We suggest management approaches that are specifically tailored each year to the conditions of a given site, and targeting grazing only in already invaded areas to reduce *B. tectorum* cover where it may aid in native plant restoration.

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Chapter 2. Interannual climate variability mediates changes in carbon and nitrogen pools caused by annual grass invasion in a semi-arid shrubland

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Abstract

Exotic plant invasions alter ecosystem properties and threaten ecosystem functions globally. Interannual climatic variability (ICV) influences plant invasions and subsequent plant community and soil properties and may interact with these properties to influence N and C pools. We asked how ICV and nonnative annual grass invasion covary to influence soil and plant N and C in a semi-arid shrubland undergoing widespread ecosystem transformation due to invasions and altered fire regimes. We sampled four progressive stages of annual grass invasion at 20 sites across a large landscape for plant community composition, soil total N and C, other soil nutrients, and plant tissue N and C in 2013 and 2016, following two years of dry and wet conditions, respectively.

The year representing higher water availability had greater herbaceous cover, particularly annual invasive grasses, generally lower soil C and N, and higher plant C:N ratios. The change in C and N pools was greater between years in later invasion stages and path analyses showed this was caused by differences in plant functional groups and their interactions with climatic variables (AET, T_{min}, P_{ant}, and σ_{CWD}). In invasion stages I and II, AET was positively related to perennial native grasses cover, which was positively related to total soil C and N. In stages III and IV, P_{ant} was strongly positively related to annual invasive grass cover, which was negatively related to total soil C and N. In addition, soil total C and C:N ratio were more homogenous in stages III and IV

as indicated by within-site standard deviations. Annual grass invasion coupled with loss of shrubs may lead to long-term declines in soil N and C, which may hamper restoration efforts. Post-fire restoration efforts to sequester C should focus on restoring shrubs and deep-rooted perennial plants before annual grasses become dominant.

1. Introduction

Exotic plant invasions threaten biological diversity and ecosystem function (Lonsdale 1999; Buckley and Catford 2016) and have long-term ecological consequences (R. N. Mack et al. 2000). Plants modify the soil physical and chemical environment in ways that feed back to vegetation community composition and structure, and non-native invasive plant species may alter soil properties in ways that differ from native plants (David S. Schimel et al. 1991; David S. Schimel et al. 1994; D'Antonio et al. 2009; Sardans et al. 2017). There is increasing recognition that “year effects” have been generally overlooked in ecological studies (Werner et al. 2020), and that Interannual climatic variability can lead to “boom and bust” cycles of invasive plant establishment, plant growth, and soil nutrient cycling (Hallett et al. 2019; Potts et al. 2019; Purity et al. 2019). Understanding the differential effects of native and invasive plant species on soil and plant nitrogen and carbon and how these effects interact with interannual climatic variability may help explain the success of invasive species (J. G. Ehrenfeld, Kourtev, and Huang 2001).

In the western United States, sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young [Asteraceae]) ecosystems are being invaded by a non-native annual grass, *Bromus tectorum* L. (Poaceae) (Germino, Chambers, and Brown 2016). In areas where native perennial grasses and forbs have been displaced, *B. tectorum* can become the dominant understory component of the *A. tridentata* community (Jeanne C. Chambers et al. 2007; Jeanne C. Chambers et al. 2016). This dominance can modify the pools and fluxes of soil carbon (C) and nitrogen (N) (Hooker et al. 2008; Joshua Leffler et al. 2016), as well as increase fire probability by increasing the abundance and spatial continuity of fine fuels (K. W. Davies and Nafus 2013; Bradley et al. 2018; Jeanne C. Chambers et al. 2019). After a fire occurs, plant community composition often experiences several years of instability after which *B. tectorum* can dominate (R. N. Mack 1981; K. W. Davies et al. 2011; Bradford et al. 2014; Mahood and Balch 2019). Domination after a period of system

instability implies a process of niche modification (Fukami 2015; Grman and Suding 2010) in which the invader alters the soil's physical and chemical environment in ways that facilitate its persistence. This self-reinforcing feedback is also likely to be influenced by external drivers like climate (Maestre et al. 2016).

Interannual climatic variability is the primary control on soil water availability in dryland systems (Maestre et al. 2016). Declines in the mean or large increases in the variability of water availability may lead to nonlinear top-down responses in ecosystem structure and function (McCluney et al. 2012; Belnap et al. 2016). These responses include increased invasion potential during periods when soil water and nutrient availability exceed the uptake capacity of the native community (Davis et al. 2000). Years with increased aridity can result in decreased concentrations of C and N due to reduced inputs from litter decomposition (Delgado-Baquerizo et al. 2013; Crowther et al. 2016), lower biomass production and soil inputs (Schwalm et al. 2010), and reduced cover of biological soil crusts (Elbert et al. 2012; Ferrenberg, Reed, and Belnap 2015; Weber, Budel, and Belnap 2016). Annual herbaceous plants are highly responsive to changes in temperature and moisture availability (Bansal and Sheley 2016; Jeanne C. Chambers et al. 2007). This makes them well-suited to take advantage of episodic pulses of resource availability and their abundance can have profound effects on soil chemistry.

Soil nutrient cycling can differ between invaded and native ecosystems, in particular cycling of C and N (Wilsey et al. 2020; Nagy et al. 2021). Many invasive species have high growth rates and nutrient concentrations that can result in increased rates of litter decomposition, mineralization, and nitrification (J. G. Ehrenfeld, Kourtev, and Huang 2001; Allison and Vitousek 2005; Liao et al. 2008; Sardans et al. 2017). Additionally, soil texture interacts with precipitation to influence the rate of nutrient cycling and productivity (A. T. Austin et al. 2004). In systems with annual precipitation below 370 mm, coarse-textured soils are more productive than finer textured soils due to the difference in water-holding capacity (Noy-Meir 1973; Sala et al. 1988). Failing to account for soil texture when studying nutrient cycling could lead to spurious results.

In *A. tridentata* ecosystems, higher N mineralization in invaded soils could lead to the depletion of long-term N storage because the increased cycling also leads to increased gaseous losses and losses through vertical and horizontal movement of labile N that is not utilized by plants (A. T.

Austin et al. 2004). Pools of inorganic and total N are often higher in *B. tectorum*-invaded sites compared to uninvaded sites (Booth, Stark, and Caldwell 2003; J. B. Norton et al. 2004; Hooker et al. 2008; Gasch et al. 2013; Johnson et al. 2011; Stark and Norton 2015; but see Rau et al. 2011). This is attributed to greater biomass turnover, faster rates of soil N cycling, and redistribution of inorganic N in surface soils (Hooker et al. 2008). In years with low, but highly variable soil moisture, the transformation of N by microbes and uptake of N by plants can be asynchronous. This is because microbes respond faster to smaller amounts of moisture than plants (Dijkstra et al. 2012). Furthermore, higher evaporation and soil temperatures in annual grass monocultures (Turnbull et al. 2012) decreases the capacity of plants to activate and uptake labile N following small moisture pulses. Thus, inorganic N can accumulate in dry years due to production of inorganic N by microbes coupled with a lack of plant uptake (R. D. Evans et al. 2001; Hanan, Tague, and Schimel 2017; U. Norton et al. 2008). This unused, labile N may leave the system via leaching or nitrification (A. T. Austin et al. 2004; Hanan, Tague, and Schimel 2017). When a system composed of deep-rooted perennial plants is converted to shallow-rooted herbaceous annuals, the depth that labile N must travel before it can no longer be accessed by the plant community decreases (Rau et al. 2011; Kulmatiski, Adler, and Foley 2020).

In semi-arid shrubland systems of the western U.S., invasion by herbaceous species can interact with drought to reduce an ecosystem's capacity to sequester C (Esch, Lipson, and Cleland 2019). *A. tridentata* communities are a C sink during the growing season and this is amplified with increased summer precipitation (Germino, Chambers, and Brown 2016; Huber et al. 2019). However, they may become a source with increases in dormant season precipitation through the asynchrony of resource availability and uptake. Accelerated microbial C mineralization triggered by precipitation occurs when plants are dormant, and so the inorganic C generated is susceptible to loss via leaching or other means (Huber et al. 2019). *B. tectorum* monocultures sequester about half the C of sagebrush communities (Germino, Chambers, and Brown 2016), and can become a net source of C to the atmosphere with increasing summer drought (Prater et al. 2006; Germino, Chambers, and Brown 2016). As with labile N, any labile C produced by episodic moisture pulses in the summer may be susceptible to leaching or atmospheric losses (J. B. Norton et al. 2004).

In *Artemisia* shrublands, soil beneath shrubs and bunch grasses has higher total C and N

than soil in shrub interspaces (Schlesinger and M. Pilmanis 1998; Jeanne C. Chambers 2001; Joan G. Ehrenfeld, Ravit, and Elgersma 2005; Bechtold and Inouye 2007), and this may be altered with progressive invasion. Environmental heterogeneity creates niche diversity, which facilitates both invasion and coexistence between competitors via niche partitioning (Shea and Chesson 2002; Tilman 2004; Melbourne et al. 2007; Lundholm 2009; Stein, Gerstner, and Kreft 2014). The loss of shrubs from fire and subsequent invasion of annual grasses yields a homogenous vegetation structure. The persistence of this simplified structure may lead to a more homogeneous distribution of soil nutrients. Soil nutrients are lost in the deeper layers and concentrated near the surface (Nagy et al. 2021), where they are being cycled by shallow, annual roots, and over time may become more evenly distributed rather than being concentrated around shrubs. In order to establish in such an environment, native propagules dispersed from adjacent unburned patches or through anthropogenic restoration efforts must compete directly with annual grasses for nutrients (Cheng et al. 2004).

Local variability in the abundance and chemical composition of plants may mediate the effect of climatic forces, but the idiosyncratic ways in which species respond to environmental change is not always linearly related to the effect they have on ecosystem processes (Suding et al. 2008; Felton, Zavislan-Pullaro, and Smith 2018). Climatic conditions affect plant tissue C:N ratios, which influence flammability, decomposition rates (Grootemaat et al. 2015) and soil inputs of C and N (J. B. Norton et al. 2004). In dry years, plants may allocate resources towards root or seed production at the expense of above-ground growth (Grime 1977; Franklin et al. 2016). This leads to higher quality litter (lower C:N), which allows for faster N cycling in the ensuing years. In wet years more above-ground growth may lead to higher C:N ratios, lower quality litter, and slower N cycling in the ensuing years. However, the relative abundance of forbs to grasses increases with growing season precipitation (Felton, Zavislan-Pullaro, and Smith 2018; Hallett et al. 2019). This increases litter quality and decomposition rates because forbs have higher leaf N content (“Plant species traits are the predominant control on litter decomposition rates within biomes worldwide” 2008). Thus, while increased water availability may increase plant C:N ratios by species, the increased abundance of forbs may cause a decrease in community mean C:N ratios. The resulting lagged effect of climate on litter quality (R. D. Evans et al. 2001; David S. Pilliod, Welty, and Arkle 2017) feeds back to soil C and N cycles (Yelenik and Levine 2010).

This broad-scale, observational study was designed to evaluate how progressive stages of *B. tectorum* invasion alter soil and plant nutrients in *A. tridentata* ssp. *wyomingensis* ecosystems in the context of interannual climatic variability. In previous studies examining the mechanisms by which *B. tectorum* influences soil nutrient cycling, soil samples were typically collected from vegetation patches within single sites that were either invaded or not invaded by *B. tectorum* (R. D. Evans et al. 2001; Rimer and Evans 2006; Sperry, Belnap, and Evans 2006; Robert R. Blank 2008). Studies that sampled several locations (J. B. Norton et al. 2004) included a range of soil types. The only climatic context given was usually 30 year normals. To our knowledge, no published studies have examined how progressive *B. tectorum* invasion influences soil and plant C and nutrients at the plant community or landscape scale. We examined four stages of invasion (I. intact sagebrush, II. sagebrush with a *B. tectorum* and native plant understory, III. cheatgrass-dominated, and IV. cheatgrass die-off) at multiple independent locations in an *A. tridentata* ssp. *wyomingensis* ecosystem. At each location, we collected soil and litter samples in spring when soil was moist, and plant cover and tissue samples in early summer at peak production. We sampled each site in 2013, a year which was the second of two dry years, and again in 2016 after two years of precipitation close to 30-year normals. We expected that both invasion and interannual climate variability would affect soil and plant C and nutrients. We had three hypotheses: (1) Loss of Artemesia shrubs and increases in *B. tectorum* cover reduces soil total C and N pools and homogenizes soil total C and N and other soil nutrients. (2) Higher water availability results in increased plant cover, greater plant tissue C:N ratios, and decreased soil total N, total C, and C:N ratios. (3) The primary drivers of soil and plant C and N differ for invasion stages with Artemesia shrubs and those dominated by *B. tectorum*.

2. Methods

2.1 Study Area

The study area encompassed 25,000 km² in the north-central part of the state of Nevada in the western U.S. Twenty sites with the same soil type were selected for study after reviewing Bureau of Land Management (BLM) fire and soil maps and consulting with land managers from the BLM Winnemucca Field Office. All sites had similar slopes (0-5%) and elevations (1297-1607 m) and

were located at least 1.5 km apart to ensure statistical independence. Mean temperatures ranged from 19°C in July to -1°C in January. Precipitation ranged from 254-304 mm with most arriving as snow in fall and winter. All sites had similar soil textures and minimal, if any carbonate content (Table S1) (O'Geen, Walkinshaw, and Beaudette 2017), and represented the same ecological site type: Loamy 10-12 precipitation zone/ *A. tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) and *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass). All sites had the same grazing regime, which was grazing from summer through fall.

The sites had four stages of *B. tectorum* invasion: (1) six sites with a mature sagebrush canopy, 0-5% aerial cover of *B. tectorum*, and no fires within the last 30 years (I. intact sagebrush), (2) five sagebrush sites with 5-20% *B. tectorum* cover and no recent fires (II. invaded sagebrush), (3) five cheatgrass-dominated sites with recent (< 5 years before 2013) fires (III. cheatgrass-dominated), and (4) four cheatgrass die-off sites, where *B. tectorum* failed to emerge, establish, or reproduce in areas that supported dense *B. tectorum* stands in previous years (Baughman and Meyer 2013) (IV. cheatgrass die-off). These later sites were a year or two post-die-off in 2013, had some *B. tectorum* plants (~ 5% cover), and were generally dominated by nonnative annual forbs such as *Erodium cicutarium* (L.) L'Hér. ex Aiton (Geraniaceae), *Sisymbrium altissimum* L. (Brassicaceae) and *Lepidium perfoliatum* L. (Brassicaceae). Five sites (3 cheatgrass-dominated, 2 intact sagebrush) that were sampled in 2013 were not re-sampled in 2016.

2.2 Field data collection

At each site, we established six, 50 m transects that were parallel and spaced 20 m apart. Transects were measured in adjacent pairs, yielding 3 replicates per site. We measured shrub cover and collected composite samples of soils and litter biomass along these transect pairs before active growth began in early-mid April 2013 and in late March 2016. The transect pairs were re-sampled during peak production in early-mid June 2013 and in mid-late June 2016. During the second visit, we estimated cover of all plant species and ground cover and collected composite samples of herbaceous vegetation for nutrient analysis. A list of all species encountered is in the supplementary material (Table S2)

We measured cover of all shrub species at each site using the line-intercept method in 2013

(Elzinga, Salzer, and Willoughby 1998). The length of each shrub that intercepted the transect line was measured and then the lengths were summed to calculate total shrub distance. Percent shrub cover was determined by dividing the total shrub distance by the total transect distance.

In April 2013 and March 2016, litter and soil samples were collected systematically every 5m along each transect for a total of 11 samples per transect ($n = 22$ per transect pair, $n = 66$ per site). Litter biomass was removed from a 15x15 cm patch at each sampling location along the transect, and then soil samples were collected from the same locations with a punch auger to a depth of 0-10 cm. Soil samples from each transect pair were placed in a bucket and homogenized, returned to the lab, and sieved to <2 mm. Soil samples ($n = 3$ sub-samples per site) were air-dried and sent to the Soil, Water and Forage Analytical Laboratory (SWFAL) at Oklahoma State University where they were analyzed for percent total C and total N using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA), and NO_3^- -N and NH_4^+ -N using KCl extraction and quantification with a Lachat® autoanalyzer. Soil Mg and Ca were measured using Mehlich 3 extraction and quantification with a Spectro ICP, and SO_4^{2-} -S using calcium phosphate monobasic extraction and quantification with a Spectro ICP. One bulk density sample was collected systematically at each transect pair, for a total of three samples per plot, with a 6 cm tall x 5 cm diameter metal cylinder. Samples were returned to the lab, dried at 105 degrees Celsius and weighed after the mass stabilized. Samples were then sieved to <2 mm. The weight and volume of any gravel removed was subtracted from the raw bulk density measurements. We used the mean of the three adjusted bulk density measurements at each plot to convert concentrations measured in the lab to area-based content. Litter biomass was oven dried at 60° C, ground in a Udy mill, and then sent to SWFAL where it was analyzed for total C and N using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA).

In June, a 0.1m² quadrat was placed along the transect adjacent to the litter and soil sampling location and used to visually estimate basal and aerial cover of all species, litter, bare ground, rocks, cryptograms, and dung. Standard protocols were used and frequent calibrations among estimators were conducted (Elzinga, Salzer, and Willoughby 1998). We used these estimates to summarize species cover by functional groups: native shrubs (SH), perennial native grasses (PNG), perennial native forbs (PNF), annual native forbs (ANF), annual invasive grasses (AIG), and annual invasive forbs (AIF). After cover was estimated, aboveground biomass of *B. tectorum*, *Poa secunda* J. Presl

(Poaceae), and all other herbaceous plants were harvested from the same quadrats. Samples were homogenized for the three different categories for every transect pair ($n = 3$ sub-samples per site) as was done for litter and soils. If either *B. tectorum* or *P. secunda* were not collected from within the quadrats, an additional sample was taken nearby from within the site. Homogenized vegetation sub-samples were returned to the lab where they were oven dried at 60°C, ground, and weighed. Vegetation sub-samples were then sent to SWFAL for analysis of total C and N using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA).

2.3 Climate data

We used minimum temperature (T_{\min}), actual evapotranspiration (AET), precipitation, and climatic water deficit (CWD) derived from gridMET (Abatzoglou 2013) (Figure 8) to evaluate how climatic variability interacted with plant-soil relationships. We chose these variables because they closely reflect physical conditions important for plant growth and survival. Minimum temperature is important because of the effects of freezing, while AET and CWD represent the supply and demand components of atmospheric water balance (Dobrowski et al. 2013). We calculated precipitation for the water year preceding sampling because of the effects of antecedent precipitation on annual grass biomass and cover (David S. Pilliod, Welty, and Arkle 2017).

2.4 Analyzing changes in community composition

Because vegetation biomass and cover can fluctuate in years with different moisture inputs, we examined the observed differences in the understory plant communities from 2013 to 2016 using ordinations. We grouped species cover data in two ways: (1) origin and life form (AIG, AIF, PNG, ANF, and PNG); and (2) life form (annuals, perennials, grasses, and forbs). We then created an ordination with non-metric multidimensional scaling (NMS) using the origin and life form groupings (Minchin 1987). We used the plant functional group cover values as arguments for the ‘envfit’ function in the vegan library (Oksanen et al. 2019). This function calculates how each variable relates to the two NMS ordination axes and was analogous to a regression model with the response variable being predicted by the two axes. The strength (R^2) and significance of the relationship was calculated using a permutation test with 9,999 replications. To examine how interannual climate, soil, litter and plant nutrients correlated with the ordination axes, we used these variables as

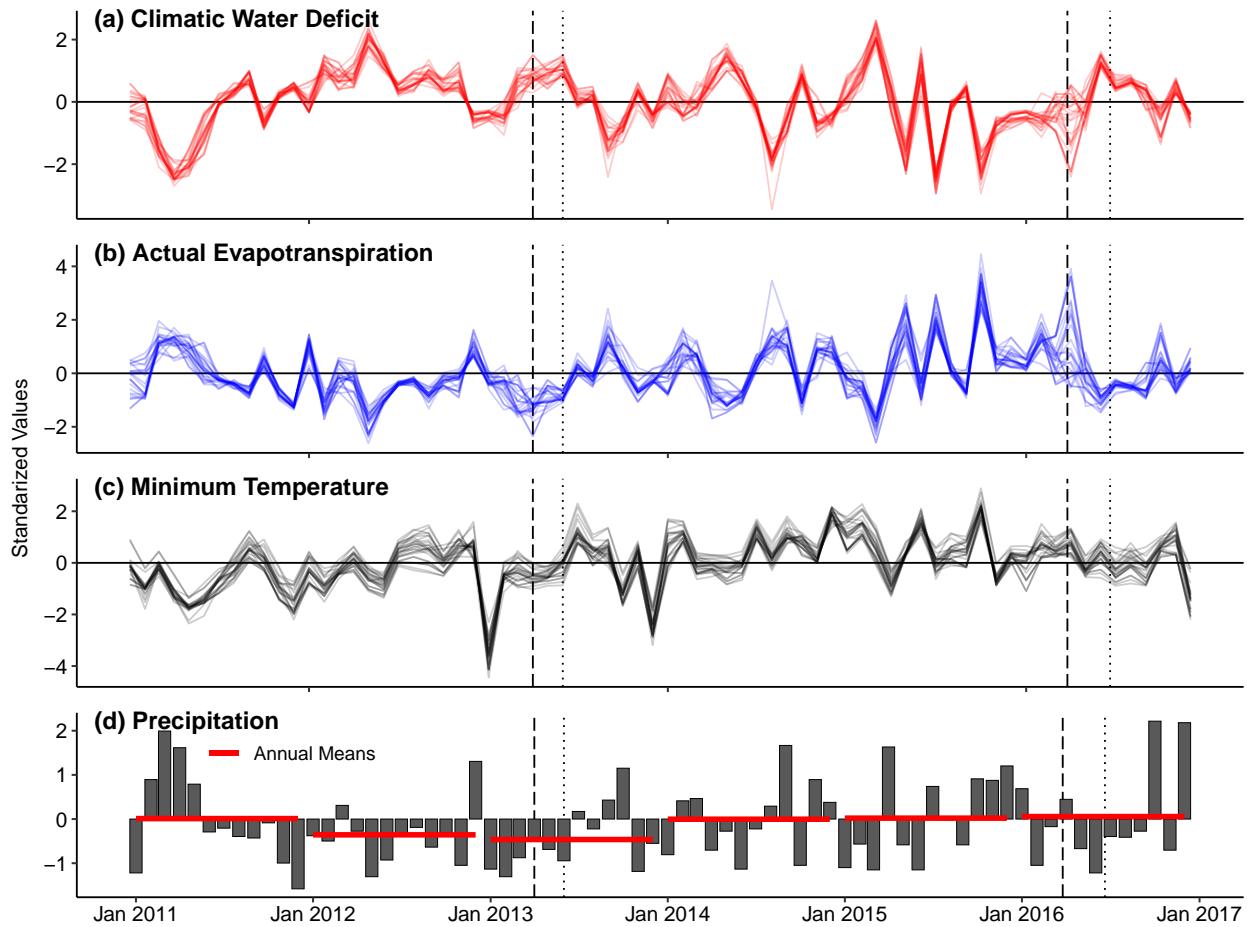


Figure 8: Climatic conditions from January 2011 to January 2017 at the study sites. Dashed vertical lines are the dates of soil and litter sampling, dotted vertical lines are the dates of vegetation cover and biomass sampling. a-c show the monthly anomaly from 30-year normals of actual evapotranspiration, climatic water deficit, and minimum temperature, with each line representing one study site. In d, bars show the monthly precipitation anomaly at the Winnemucca, Nevada airport. The red lines represent yearly averages.

arguments to the ‘envfit’ function. To examine how the composition at the different invasion stages changed between the two sample years, we calculated the yearly means of the first two ordination axes for each invasion stage.

2.5 Analyzing variation in soil, litter and plant tissue characteristics between invasion stages and year of sampling

We used linear mixed models in the R package ‘lmer’ (D. Bates et al. 2015) to determine if soil and plant nutrients differed based on year of sampling and stage of invasion. Invasion stage, year, and the interaction between the two were fixed effects and site (containing three replicated transects) was a random effect. Significance of the fixed effects was determined using a type 3 ANOVA with a Kenward-Roger approximation for degrees of freedom. Mean comparisons were performed using Tukey’s honest significant difference tests for multiple comparisons and considered significant at the 95% confidence level ($p < 0.05$).

To determine if *B. tectorum* invasion or interannual climatic variability influenced the plot-scale heterogeneity of soil resources, we calculated the standard deviation of each soil characteristic for the three transect pairs for each site. We conducted separate Kruskal-Wallis tests on the standard deviations using: (1) all four invasion stages; (2) the two sampling years; and (3) the shrub dominant invasion stages (I and II) versus the herbaceous-dominated invasion stages (III and IV). We evaluated invasion stages with different levels of shrub dominance based on the hypothesis that loss of shrub cover would correspond with loss of islands of fertility. We used a Bonferroni adjustment when necessary.

2.6 Analyzing interactions between functional group cover and interannual climate

To gain an understanding of how interannual climatic variability interacted with plant functional group cover to affect soil and plant nutrients, we built path models using the R package ‘lavaan’ (Rosseel 2012). We structured our path models such that climatic variables would affect soil and plant tissue nutrients both directly and indirectly through their effects on plant functional group cover. We built two path models with soil total N and C as response variables. One model was for the shrub-dominated invasion stages (I and II) and the other was for the herbaceous-dominated

stages (III and IV). We also built models for all sites with the C:N ratios of *B. tectorum*, *P. secunda*, and other plants as the response variables. We explored splitting the models between invasion stages as we did for soil C and N, but sample sizes were too low to achieve good model performance. We also explored models of plant N and C concentrations, but they generally mirrored the C:N ratio models, so we present results only for C:N models. We did not find enough strong relationships for litter C:N ratios to justify a path model.

We used two groups of exogenous variables and one group of endogenous variables in the path models. Exogenous variables can predict both the endogenous and response variables, but are not predicted by other variables in the model. The first group of exogenous variables accounted for interannual climate variability. We used mean T_{min} and AET, the standard deviation of CWD (σ_{CWD}) for the 180 days preceding sampling, and antecedent precipitation (P_{ant}), calculated as the sum of precipitation for the water year that ended the year prior to sampling. The second group of exogenous variables accounted for site-level characteristics that are relatively static from year to year. These were biological soil crust (BSC) cover and shrub cover. Endogenous variables predict the response and are predicted by the exogenous variables. These accounted for site-level characteristics that vary from year to year, likely as a result of climatic variability. These were the cover of the different plant functional groups and litter.

We built our models bottom-up, beginning with simple, exploratory path models, and then increased complexity. We used a modification index function from the 'lavaan' package to check for paths that could be added to the model and improve fit. We removed statistically insignificant variables unless their removal resulted in residual correlations rising above 0.1. We bootstrapped the coefficients of the standardized solution for each model with 5000 random draws and considered the coefficients significant if the 95% confidence intervals did not cross zero. Models were built to maximize (> 0.9) two measures of good fit, the Comparative Fit Index (CFI) and Tucker-Lewis Index (TLI), and to minimize (< 0.1) two measures of error, the Root Mean Square Error of Approximation (RMSEA) and Standardized Root Mean Square Residual (SRMR).

It is possible that an exogenous climate variable may not have a significant direct effect on the response variable, but may have a direct effect on an endogenous functional group predictor, which then has an indirect effect on the response variable. To examine this phenomenon, we calculated

the indirect and total effects of the exogenous climate variables on the response variables for each path model. Indirect effects were the effects of the exogenous predictors on the endogenous plant functional group cover predictors, and then on the response variables (soil total N and C, plant tissue C:N). Total effects were the indirect effects plus the direct effects of the exogenous predictors on the final response variables

All statistical analyses were done in R (R Core Team 2020). Data and code are publicly available on Github (www.github.com/admahood/invasion_climate_soil).

3. Results

3.1 Changes in community composition

The NMDS ordination that evaluated community composition fit well (stress = 0.108; non-metric fit = 0.988; linear fit = 0.946), and sites were clustered according to invasion stage (Figure 9a). The NMDS axes represented gradients of perennial to annual cover and forb to grass cover (Figure 9b). NMDS axis 1 was positively correlated with annual plant cover and negatively correlated with perennial plant cover ($R^2 = 0.95$, Table S3). Axis 2 was positively correlated with forbs and negatively correlated with grasses ($R^2 = 0.87$, Table S3). Interannual compositional change was greater for invasion stages III and IV than stages I and II and followed the AIG vector (Figure 9a). This reflected greater herbaceous cover, particularly AIG cover, in the wet year at most sites. Total soil C and N were positively related to NMDS axis 2 (corresponding to forb cover) and negatively correlated with axis 1, which corresponded to perennial cover (Figure 9c). *B. tectorum*, *P. secunda* and other plant C, litter N and *P. secunda* C:N ratio were positively correlated with axis 1, which corresponded to annual versus perennial cover, and negatively correlated with axis 2, which corresponded to grass versus forb cover (Figure 9c). Litter C and other plant N concentrations were positively correlated with axes 1 and 2, corresponding to annual forb cover (Figure 9c).

3.2 Soil and litter characteristics

Soil C, N, C:N ratios, and secondary soil nutrients were all lower in 2016 than in 2013 (Table 1). Few meaningful patterns existed among invasion stages for the soil variables (Table 1), but there were several variables with significant interactions between the years and invasion stages. In the

Table 1: Type III ANOVA results for soil total C and N, soil C:N ratio, soil nutrients, and litter and plant %C, %N, and C to N ratios. ANOVAs are based on mixed models with year and invasion stage as fixed effects, and site as the random effect. Denominator degrees of freedom (not shown) and F-statistics were calculated using the Kenward-Roger method

	Year		Invasion Stage		Year x Invasion Stage	
	F	P(>F)	F	P(>F)	F	P(>F)
Soil Total N	274.5	<0.001	3.8	0.026	6.4	0.001
Soil Total C	191.0	<0.001	1.5	0.248	3.0	0.039
Soil C:N	638.2	<0.001	0.6	0.594	0.5	0.716
Soil NO ₃	427.2	<0.001	1.5	0.256	4.5	0.006
Soil NH ₄	85.2	<0.001	1.9	0.172	2.3	0.090
Soil NH ₄ + NO ₃	239.3	<0.001	1.8	0.183	2.3	0.090
Soil SO ₄	77.0	<0.001	0.6	0.624	3.0	0.039
Soil Mg	296.7	<0.001	0.6	0.653	1.2	0.328
Soil Ca	78.3	<0.001	1.1	0.356	2.4	0.079
Litter N	245.8	<0.001	0.8	0.520	6.6	0.001
Litter C	625.5	<0.001	4.5	0.015	2.5	0.071
Litter C:N	169.1	<0.001	2.3	0.104	5.4	0.002
<i>Bromus</i> C	16352.8	<0.001	7.4	0.002	4.9	0.004
<i>Bromus</i> C:N	167.6	<0.001	0.7	0.563	2.1	0.107
<i>Bromus</i> N	185.9	<0.001	1.4	0.264	3.3	0.026
<i>Poa</i> C	7051.2	<0.001	0.6	0.629	0.4	0.728
<i>Poa</i> C:N	189.5	<0.001	1.6	0.242	1.7	0.184
<i>Poa</i> N	240.0	<0.001	3.7	0.037	11.7	<0.001
Other C	2427.8	<0.001	5.6	0.006	4.4	0.007
Other C:N	129.5	<0.001	6.1	0.004	2.2	0.096
Other N	62.1	<0.001	5.9	0.004	3.0	0.039

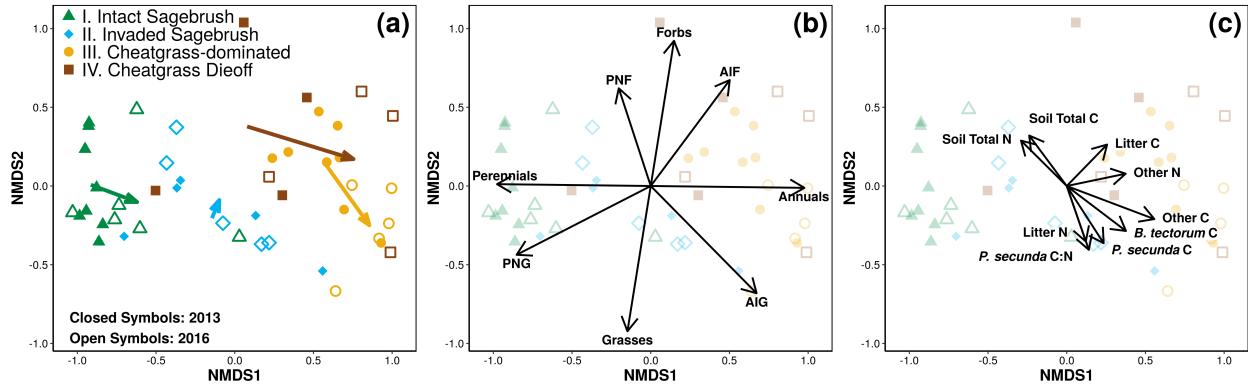


Figure 9: Non-metric multidimensional scaling ordination illustrating the differences in understory composition, and soil, plant and litter N and C between 2013 and 2016. Graphs illustrate (a), the mean change from 2013 to 2016 by invasion stage; (b), significant correlations ($p < 0.05$) of plant functional group cover with the ordination; and (c), significant correlations of soil, plant and litter nutrient concentrations with the ordination. The arrows in (a) represent the direction and magnitude of change. The length of each arrow in (b) and (c) corresponds to the R^2 of the correlation. AIG = annual invasive grass cover; AIF = annual invasive forb cover; PNF = perennial native forb cover; PNG = perennial native grass cover.

intact sagebrush stage (I) total N content was similar in 2013 and 2016 but in the other stages total N content was higher in 2013 than 2016 (Figure 10a). A similar but weaker pattern occurred for soil total C ($p=0.039$; Figure 10b). Soil SO₄ was lower for all invasion stages in 2016 except in stage IV, where it was similar for both years. (Figure 10d). Soil Ca was lower for all invasion stages in 2016 except in stage I, where it was similar for both years (Figure 10e). Litter N was higher in 2016 than in 2013 for stages I, II, and IV but did not differ in stage III (Figure 10g). Litter C and C:N were lower in 2016 than 2013 for stages I and II, but did not differ in stage III, while in stage IV C:N was lower in 2016 and C was similar in the two years (Tables 1, Figure 10h-i).

Analyses of standard deviations of soil total C and N, litter %C, %N, and C:N ratios and of soil SO₄, Ca, Mg showed differences among invasion stage and year. When sites were grouped into the four invasion stages, within-site standard deviations differed only between stages I and IV for soil total C (Table S4). However, when sites were grouped by amount of *A. tridentata* cover (stages I and II versus III and IV), within-site standard deviations in soil total C, soil C:N ratio and Ca were lower for stages III and IV than for stages I and II (Table 2). When the data were grouped by year, standard deviations of soil total N, Ca, and Mg were higher in 2013, the dry year, while

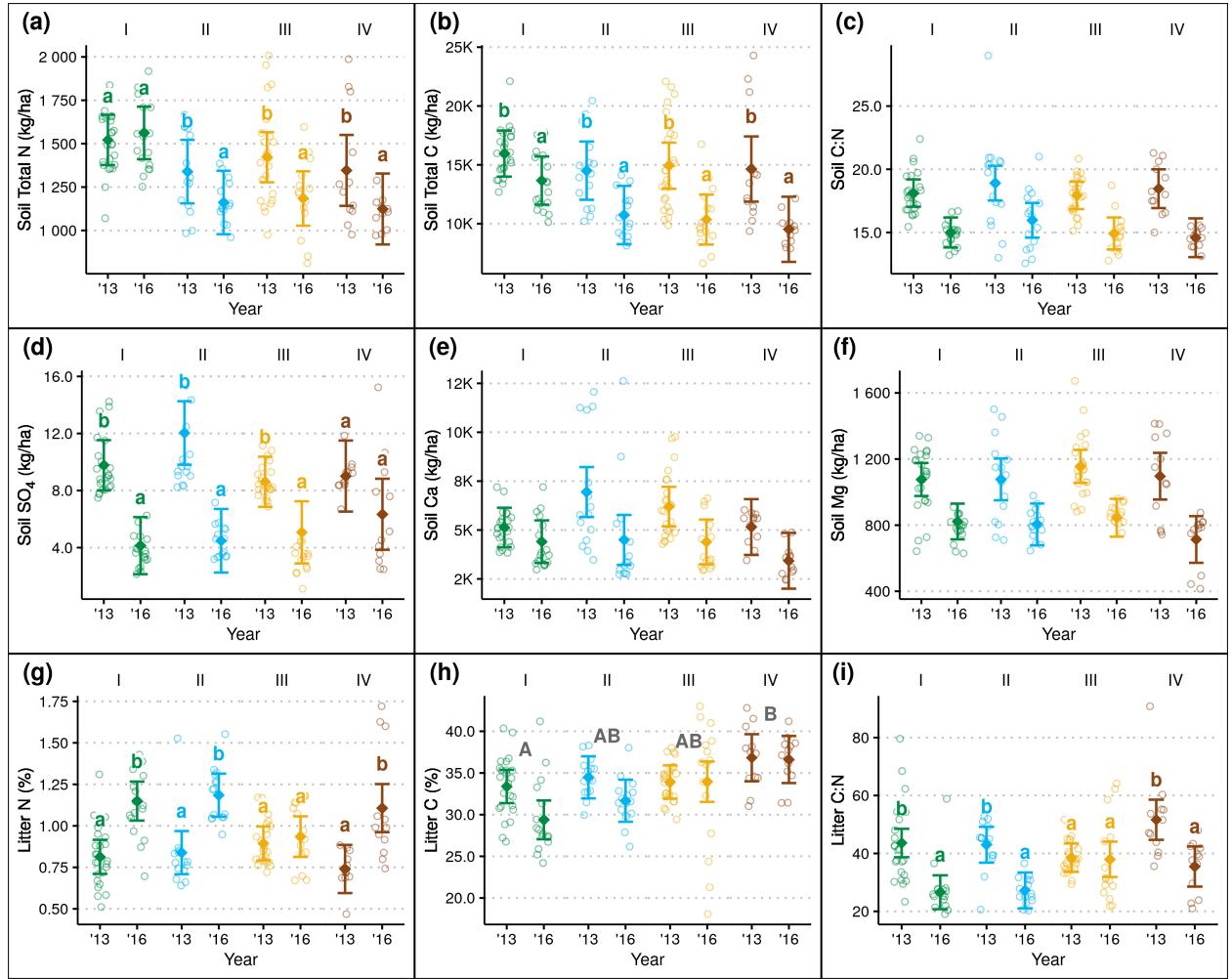


Figure 10: Effects of year and invasion stage on soil total C and N, soil C:N ratio, soil nutrients, and litter and plant %C, %N, and C:N ratios. Open circles represent individual measurements. Diamonds and error bars represent the marginal means and 95% confidence intervals estimated from the linear mixed models. Year was always significant. When the interaction between invasion stage and year is significant, colored lowercase letters above the bars illustrate differences between years within each invasion stage based on the Tukey Honest Significant Differences post-hoc test. Black capital letters illustrate significant differences among invasion stages when the interaction was not significant.

Table 2: Comparisons of stages I-II and stages III-IV and of the wet (2016) and dry (2013) years based on standard deviations calculated from three replicate samples for the sites within each category. Letters indicate significant differences between grouped stages and years based on Kruskal-Wallis tests.

	Stages I-II		Stages III-IV		2016 (Wet)	2013 (Dry)
Soil Total N (kg/ha)	96.2		85.4		59.7	b
Soil Total C (kg/ha)	1275.2	a	847.3	b	939.8	
Soil C:N	1.3	a	0.7	b	0.9	
Soil SO ₄ (kg/ha)	1.4		1.6		1.7	
Soil Ca (kg/ha)	923.5	a	396.3	b	473.4	b
Soil Mg (kg/ha)	77.8		58.1		37.3	b
Litter N (%)	0.1		0.1		0.1	a
Litter C (%)	2.8		2.5		3.2	
Litter C:N	5.9		6.6		6.7	

variation in litter N was higher in 2016, the wet year (Table 2).

3.3 Plant tissue characteristics

Carbon concentrations of *P. secunda*, *B. tectorum* and other plants were higher in the wet year (2016) than the dry year (2013), and nitrogen concentrations were lower in the wet year. Because N concentrations were lower in the wet year, C:N ratios were higher (Figure 11, Table 1). *B. tectorum* had lower C concentrations in stage I than all other stages in the dry year (2013) (Figure 11). *P. secunda* had higher N concentrations in stage III than II in 2013, but N concentrations did not vary by invasion stage in 2016. Both species had higher C concentration in stage III than stages I and II and higher N concentrations in stage IV than in stages I and II. As a result, C:N ratios were lower in stage IV than in stages I and II. The contrast in nutrient concentrations for other plants between the shrub-dominated versus herbaceous-dominated invasion stages is likely due to the difference in species composition. The other plant species present in stages I and II were generally annual and perennial native forbs, while those in stages III and IV were mostly annual invasive forbs (Table S5).

3.4 Path models for soil total nitrogen and carbon

Path models fit well with values approaching 1 for measures of fit (CFI, TLI) and values approaching 0 for measures of error (RMSEA, SRMR, Table S6). Covariance matrices for each path model are in the supplemental material in Tables S7-S11. The models for soil total C and

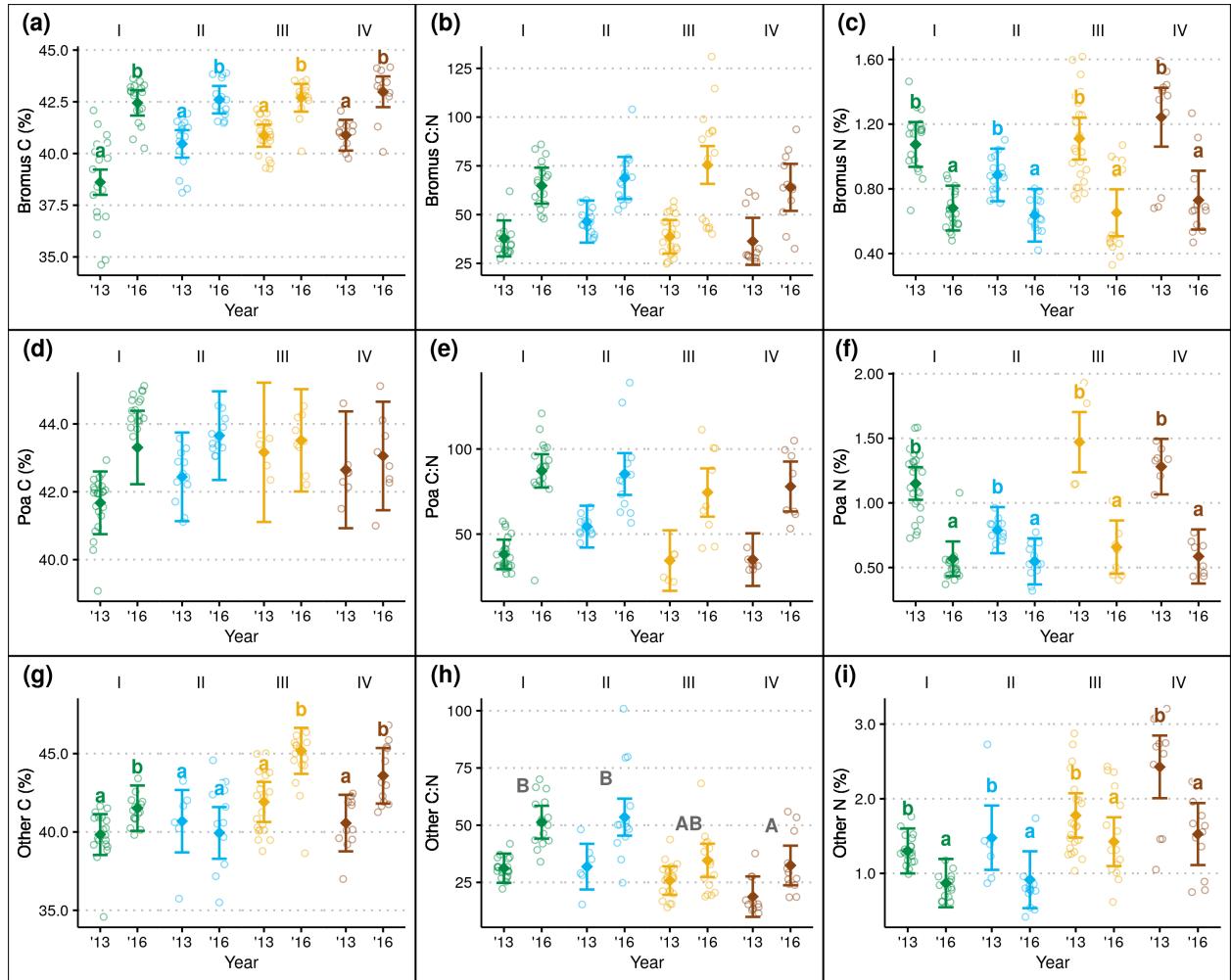


Figure 11: Effects of year and invasion stage on plant tissue C and N concentrations. Open circles represent individual measurements. Diamonds and error bars represent the marginal means and 95% confidence intervals estimated from the linear mixed models. Year was always significant. When the interaction between invasion stage and year is significant, colored lowercase letters above the bars illustrate differences between years within each invasion stage based on the Tukey Honest Significant Differences post-hoc test. Black capital letters illustrate significant differences among invasion stages when the interaction was not significant.

N were quite different when split between the shrub-dominated invasion stages (I & II) and those dominated by invasive annuals (III & IV). The model for stages I & II had many direct climate effects on soil total C and N, with indirect effects through the litter C:N ratio and perennial native grass cover. In contrast, in the model for the later invasion stages soil total C and N were strongly influenced by annual invasive grass cover.

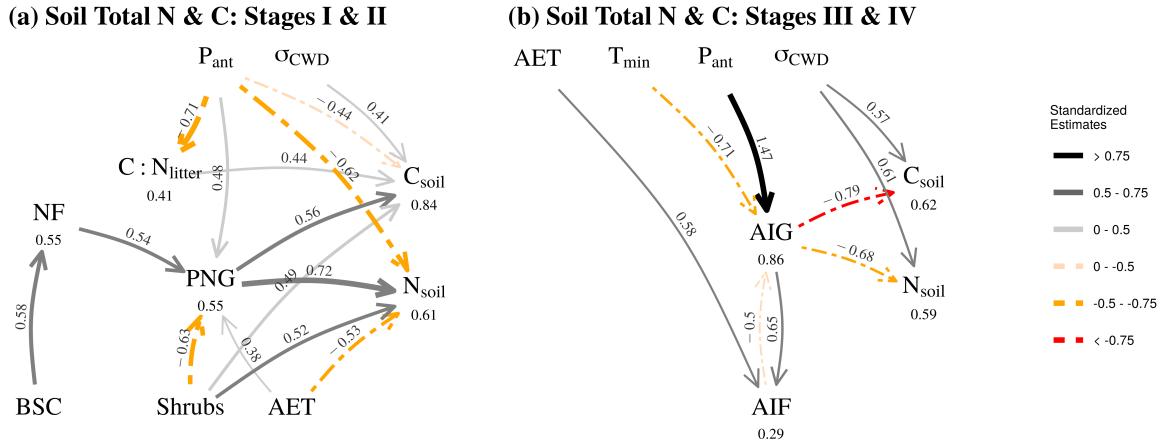


Figure 12: Path models predicting soil total carbon and nitrogen for (a) invasion stages I & II, and (b) invasion stages III & IV. Paths are based on bootstrapped standardized solutions ($R=5000$); those with bootstrapped confidence intervals crossing zero have been omitted. The numbers along each path are the median standardized coefficients, which also correspond to the line widths. The numbers below each endogenous or response variable are the median bootstrapped R^2 values. Gray and black lines indicate positive relationships; orange and red lines indicate negative relationships. AET = actual evapotranspiration; T_{min} = minimum temperature; P_{ant} = antecedent precipitation; σ_{CWD} = standard deviation of climatic water deficit; AIF = annual invasive forb cover; Litter = litter cover; NF = native forb cover; AIG = annual invasive grass cover; PNG = perennial native grass cover; Shrubs = shrub cover; BSC = biological soil crust cover; N_{soil} = soil total nitrogen; C_{soil} = soil total carbon.

The model for invasion stages I and II explained 84% of the variation for soil total C and 61% for soil total N (Figure 12a). Litter C:N, PNG, shrub cover, and σ_{CWD} were positively related to soil total C. P_{ant} was negatively related to soil total C, but positively influenced PNG and negatively influenced litter C:N. The indirect and total effects of P_{ant} on soil total C mediated through litter C:N were negative, while the effects of P_{ant} mediated through PNG were neutral (Table 3). Shrub cover and PNG had positive effects on soil total N, while P_{ant} and AET had negative effects. The indirect effects of P_{ant} and AET mediated through PNG were both neutral.

Table 3: Indirect and total effects of climatic variables on soil total nitrogen and carbon for stages III and IV. Values are the median of the bootstrapped ($n=5000$) coefficients, and stars indicate that the 95 percent confidence intervals did not cross zero. Median coefficients for the direct effects are displayed in Figure 12b.

	Mediator(s)	Soil C	Soil N	Invasion Stages
Actual Evapotranspiration				
Indirect (single pathway)	PNG	0.19	0.25	I and II
Total	PNG	-0.06	-0.26	I and II
Antecedent Precipitation				
Indirect (single pathway)	LCN	-0.30	*	I and II
Indirect (single pathway)	PNG	0.26	0.34	I and II
Total	LCN	-0.74	*	I and II
Total	PNG	-0.17	-0.27	I and II
Actual Evapotranspiration				
Indirect (multiple pathways)	AIF AIG	-0.10	-0.08	III and IV
Indirect (single pathway)	AIG	-0.31	-0.27	III and IV
Total	AIF AIG	-0.17	-0.14	III and IV
Total	AIG	0.08	0.13	III and IV
Antecedent Precipitation				
Indirect (single pathway)	AIG	-1.20	*	III and IV
Total	AIG	-0.70	*	III and IV
Minimum Temperature				
Indirect (single pathway)	AIG	0.55	*	III and IV
Total	AIG	0.54	*	III and IV

The model for invasion stages III & IV explained 62% of the variation for soil total C and 59% of the variation for soil total N (Figure 12b). Both soil total C and soil total N were positively influenced by σ_{CWD} and negatively influenced by AIG. The indirect and total effects of P_{ant} mediated through AIG were negative for total soil C and neutral for soil total N. The indirect effects of T_{min} mediated through AIG were positive for soil total C and neutral for soil total N (Table 4). The total effect of T_{min} mediated through AIG was positive.

3.5 Path models for *B. tectorum*, *P. secunda* , and other plants C:N ratios

In general, the path models showed that AET, P_{ant} and σ_{CWD} had positive direct effects on C:N ratios, PNG, AIG or AIF, while T_{min} had negative effects, when those effects were significant. Shrub cover was negatively related to AIG, AIF or Litter, when significant.

The path model for *B. tectorum*'s C:N ratio explained 70% of the variation. The strongest direct predictors of *B. tectorum*'s C:N ratio were AIF and P_{ant} , which were both positive. After taking into account all of the indirect effects, shrub cover, P_{ant} and AET were the most important exogenous predictors through their effects on AIF. The overall effects of both P_{ant} and AET were

positive, while the effect of shrub cover was negative (Table 5, Figure 13a). Indirect effects of AET and P_{ant} through AIF were positive (Table 5).

The path model for *P. secunda* explained 66% of the variation, with AET, T_{min} , P_{ant} , and PNG having significant direct effects on *P. secunda*'s C:N ratio. The total effects of T_{min} , P_{ant} and AET, were negative, positive and insignificant, respectively, after accounting for indirect effects (Table 4, Figure 13b). Shrub cover, after accounting for its effects on AIG, Litter, and PNG, had a total positive effect on *P. secunda*'s C:N ratio (Table 4).

The path model for other plants explained 58% of the variation, with AIG and all 4 climatic variables having significant direct effects on other plants C:N ratio (Table 4, Figure 13c). The direct effects of AET, P_{ant} and σ_{CWD} on other plants' C:N ratio were positive, while the indirect effects through AIG were negative. In contrast, the direct effect of T_{min} on other plants C:N ratio was negative, while the indirect effect of T_{min} through AIG was positive. The indirect effect of shrub cover through its association with lower AIG was positive. After accounting for all of the indirect effects, the total effects of P_{ant} and σ_{CWD} were positive, and the total effects of AET and T_{min} were not significant (Table 5).

The only statistically significant relationships we found between our covariates and litter's C:N ratio were with native forb cover, BSC, and P_{ant} . A linear model explained 23% of the variation. Native forb cover was positively related to litter C:N ratio ($\beta = 0.11$), while P_{ant} and BSC cover were negatively related to litter C:N ratio ($\beta = -0.32$, and $\beta = -0.09$, respectively).

4. Discussion

Here we demonstrate that the well-documented sensitivity of herbaceous cover to inter-annual climatic variability (Witwicki, Munson, and Thoma 2016; David S. Pilliod, Welty, and Arkle 2017; Hallett et al. 2019) mediates the effects of progressive invasion of exotic annual grasses and changes in plant functional group composition on soil total C, soil total N, and plant C:N ratios. Our NMS ordination indicated that differences in community composition were affecting soil total N and soil total C pools, while our linear mixed models indicated that year effects were a primary driver. Using path models to incorporate the effects of interannual climatic variability, we showed that different variables were determining soil total C and soil total N in the different invasion stages. Furthermore,

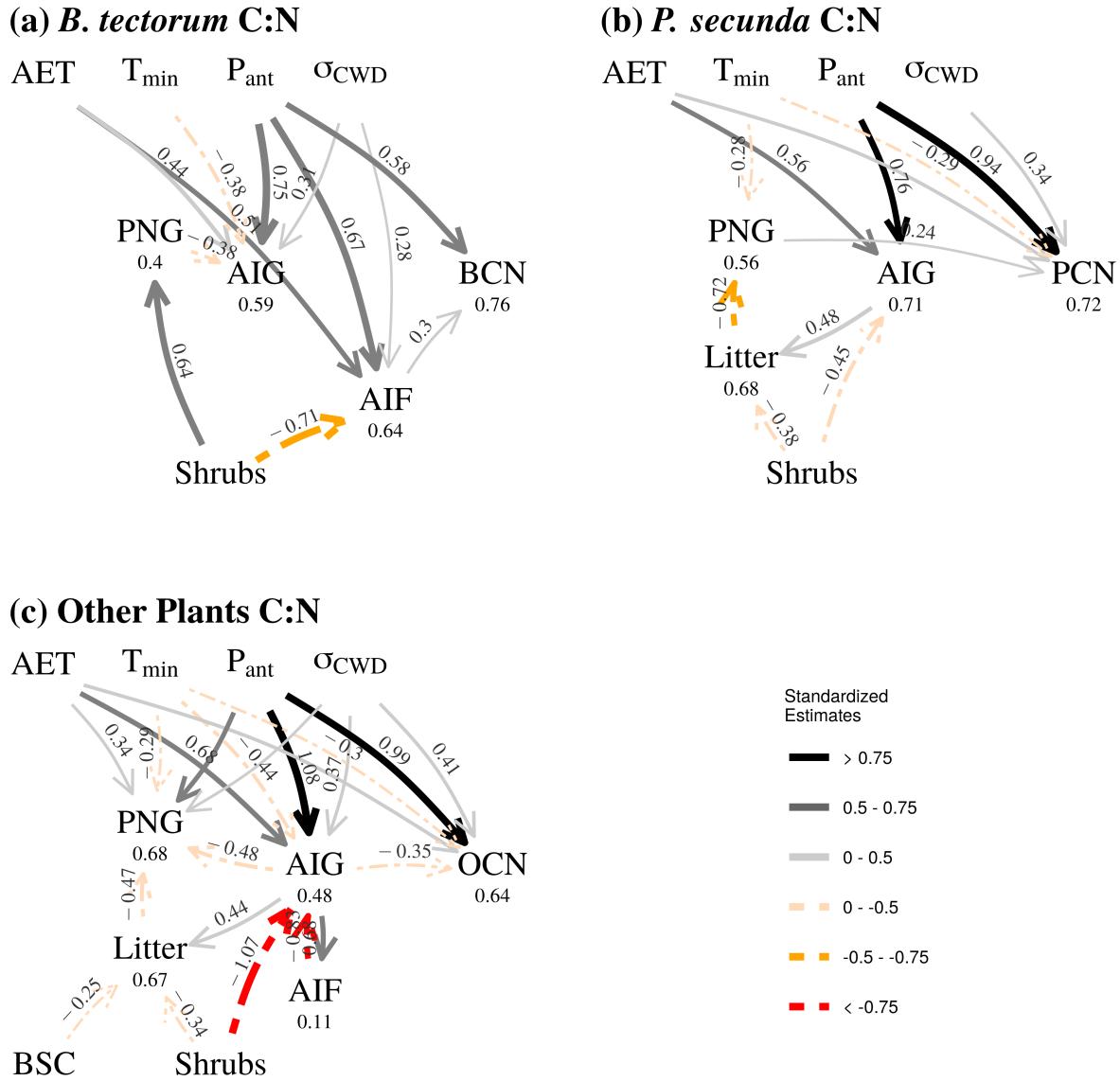


Figure 13: Bootstrapped standardized solutions ($n=5000$) for path models predicting aboveground C:N ratios for (a) *Bromus tectorum*, (b) *Poa secunda* and (c) other plants. Paths with bootstrapped confidence intervals crossing zero have been omitted. The numbers along each path are median standardized coefficients. The numbers below each endogenous or response variable are the median bootstrapped R^2 values. Line width corresponds to the effect size. Gray and black lines indicate positive relationships; yellow and red lines indicate negative relationships. AET = actual evapotranspiration; T_{min} = minimum temperature; P_{ant} = antecedent precipitation; σ_{CWD} = standard deviation of climatic water deficit; AIF = annual invasive forb cover; Litter = litter cover; AIG = annual invasive grass cover; PNG = perennial native grass cover; Shrubs = shrub cover; BSC = biological soil crust cover; BCN = *Bromus tectorum* C:N; PCN = *Poa secunda* C:N; OCN = other plants C:N.

Table 4: Indirect and total effects on the C to N ratios of *Bromus tectorum*, *Poa secunda* and other plants. Values are the median of the bootstrapped ($n=5000$) coefficients, and stars indicate that the 95 percent confidence intervals did not cross zero. Median coefficients for the direct effects are displayed in Figure 13.

Exogenous variable	Path	<i>B. tectorum</i>	<i>P. secunda</i>	Other Plants
σ Climatic Water Deficit	→ AIF →	0.08	*	
Actual Evapotranspiration		0.15	*	
Antecedent Precipitation		0.20	*	
Shrub Cover		-0.21	*	
σ Climatic Water Deficit	→ AIG →	0.08		-0.12
Actual Evapotranspiration		0.11		-0.23 *
Antecedent Precipitation		0.19		-0.38 *
Minimum Temperature		-0.09		0.15 *
Shrub Cover		-0.05		0.38 *
Shrub Cover	→ AIG → LIT → PNG →		0.10 *	
σ Climatic Water Deficit			-0.03	
Actual Evapotranspiration			-0.04	
Antecedent Precipitation			-0.06 *	
σ Climatic Water Deficit	→ All Mediators →		0.31	0.28 *
Actual Evapotranspiration		0.40 *	0.33	0.19
Antecedent Precipitation		0.98 *	0.89 *	0.62 *
Minimum Temperature		-0.23 *	-0.36 *	-0.16

climate-driven differences in herbaceous plant cover drove soil total C and soil total N in different directions depending on the composition of the herbaceous vegetation, with annual invaders resulting in losses of soil total C and soil total N, and native perennials resulting in increases (Figure 12).

To our knowledge, this is the first study in this system where multiple sites were sampled across a broad geographic extent, and both the stage of invasion and interannual climatic variability were taken into account. Prior studies on the relationship between *B. tectorum* invasion and soil total N and C pools are conflicting, with reports of both higher (Booth, Stark, and Caldwell 2003; Hooker et al. 2008; Gasch et al. 2013) and lower (Rau et al. 2011; Stark and Norton 2015) levels after invasion.. Failure to adequately account for spatial and interannual climate variability within an ecosystem is a common shortcoming in ecological research (Werner et al. 2020) and helps explain the discrepancies in prior studies.

4.1 Annual grass invasion and loss of shrubs reduce and homogenize soil total N and C

The path model for invasion stages III and IV indicated direct positive relationships between climatic variables and AIG cover, and direct negative relationships between AIG cover and soil total N and soil total C (Figure 12b). It is likely that the observed interactions between invasion stage and year effects (Table 1) are the result of climate amplifying the negative effect of annual grass productivity on soil total N and soil total C in stages III and IV. Our finding that increased annual grass cover was the driver of soil N and soil total C losses in invasion stages III and IV is consistent with an emerging consensus that the rate of nutrient cycling is likely higher in *B. tectorum*-invaded environments, and this is amplified in higher moisture years. One mechanism for faster nutrient cycling under *B. tectorum* in favorable years may be increased root exudation of N into the soil by *B. tectorum* (Morris et al. 2016), which initiates a self-reinforcing feedback that facilitates *B. tectorum* growth (O’Conner, Prevéy, and Seastedt 2015; R. R. Blank, Mackey, and Morgan 2016). Increased nutrient cycling can lead to labile N and C removal from near surface soil layers via percolation, respiration, denitrification, and runoff (A. T. Austin et al. 2004; J. B. Norton et al. 2004). In drier years, water from smaller precipitation events that does not provide sufficient moisture for plants to activate is still used by soil microbes to mineralize N and C (Dijkstra et al. 2012; S. E. Evans and

Burke 2013).

The loss of biological soil crust (BSC) further reduces the capacity of invaded sites to retain soil N and C. At our study sites, BSC cover was lower at the invaded sagebrush stage (II), and essentially absent at cheatgrass-dominated (III) and cheatgrass die-off (IV) stages (Table S7). In addition to providing N input (Condon and Pyke 2018; Belnap et al. 2016; Weber, Budel, and Belnap 2016), BSC reduces the rate of soil drying, and thus gives plants more time to activate and uptake newly available resources (A. T. Austin et al. 2004). The loss of BSC as a source of N input, combined with increased nutrient cycling leading to N and C exiting the system, may add up to significant yearly losses in near-surface soils (A. T. Austin et al. 2004; Urszula Norton et al. 2012).

The lack of shrub cover and uniform distribution of annual herbaceous plants at our sites in invasion stages III and IV is common post-fire and leads to the loss of “islands of fertility” (Doescher, Miller, and Winward 1984; R. D. Evans et al. 2001; A. T. Austin et al. 2004; Germino et al. 2018; Bechtold and Inouye 2007). We found statistically lower within-site variability of soil total C and soil C:N ratios in invasion stages that had lost shrub cover (Table 2). Lower resource heterogeneity reduces the availability and diversity of niches that species can occupy, making it harder for native species to reestablish (Tilman 2004; Melbourne et al. 2007). The reduction in within-site variability we observed here suggests that homogenization of soil total C may be a mechanism for the continued long-term dominance of invasive annual plants.

4.2 Plant tissue and litter C and N concentrations are strongly influenced by interannual climate variability

Interannual climate variability affected every variable we measured: soil total C, soil total N, and the C:N ratios of litter, soil, and the tissues of *P. secunda*, *B. tectorum*, and other plants (Table 1, Figures 3-6). The large interannual differences in soil total C (Figure 10b) were unexpected, because soil organic C is usually considered to be fairly stable. In sagebrush ecosystems, soil water content is the primary driver of soil C mineralization (Urszula Norton et al. 2012). When soil is wet, C cycling rates can be an order of magnitude greater than when soil is dry (Saetre and Stark 2005). Increased litter inputs associated with *B. tectorum* invasion are associated with higher labile C in the top 10 cm and higher C mineralization rates (Urszula Norton et al. 2012). In addition to losses

from higher rates of soil respiration, this increased nutrient cycling may be leading to significant C losses through vertical movement of labile C from the top 0-10 cm sampled here to deeper soil depths (Nagy et al. 2021).

After accounting for indirect effects, the cover and tissue nutrient content of the herbaceous plants were more strongly influenced by interannual climatic variability than by plant functional group composition (Figure 12). The effect of interannual climate variability on litter chemistry may have regional scale consequences for fire risk and nutrient cycling. The biomass from plants with C:N ratios in dry periods becomes litter with low C:N ratios (S. E. Evans and Burke 2013), which persists for 2-3 years (David S. Pilliod, Welty, and Arkle 2017). This can lead to increased rates of nutrient cycling, and loss of mineralized N through leaching and gaseous loss of CO₂ and NO₃, and volatilization of NH₄ when soil moisture is available (A. T. Austin et al. 2004; S. E. Evans and Burke 2013). In contrast, years with more moisture availability have litter with higher C:N ratios. In the wet period, in invasion stages III and IV, litter C:N was higher, *B. tectorum* and *P. secunda* C:N ratios were universally higher, and other plant C:N ratio was higher. The layer of dead and cured fine fuel created by the pulse of growth in a wet year will potentially persist longer than the fuel produced in a dry year, since plant and litter tissue with higher C:N ratios may decompose more slowly (Pausas, Keeley, and Schwilk 2017; Grootemaat et al. 2015). Consequently, in wet years there is not only an increase in fine fuel biomass, but those fine fuels may be more flammable and take longer to decompose.

4.3. Drivers of soil C and N differ with invasion stage

Simplification of ecosystem structure to a single herbaceous cover layer, and the alteration of the species composition in that cover, results in different pathways through which C and N travel. In all stages, the strongest direct predictors of C and N were abundance of the dominant grass type, i.e., PNG in stages I and II, and AIG in stages III and IV (Figure 12). In stages I and II, PNG had positive relationships with soil total N and soil total C, and the negative effect of higher water availability on soil total N and C was dampened by its positive influence on PNG cover. In these stages sites with higher cover of shrubs, BSC, NF, and PNG were all associated with higher soil total N and C. This agrees with prior work indicating that sagebrush communities sequester C

(Prater et al. 2006), but that their ability to sequester C declines as the cover of key ecosystem components declines. In stages III and IV, the simplified species composition yielded a simple path model centered around a single pathway through AIG. In these sites, P_{ant} led to higher AIG which led to lower soil total N and soil total C. In contrast to Artemisia-dominated stages I and II, the negative effect of higher water availability on soil total N and soil total C was amplified by its effect on the abundance of AIG, agreeing with Prater et al. (2006) who found *B. tectorum* monocultures to be a net C source.

Litter chemistry and abundance is known to change after invasion with important consequences for soil nutrient cycling (Joan G. Ehrenfeld 2003; Sperry, Belnap, and Evans 2006; U. Norton et al. 2008). Here, litter C:N ratio operated differently between the soil total C and soil total N path models. In stages I and II litter C:N ratio was positively related to soil total C. P_{ant} drove decreases in both soil total C, and litter C:N ratios, and higher litter C:N ratios amplified the effect of P_{ant} on soil total C (Table 4). Huber et al. (2019) also found that increases in winter rainfall can turn soil under sagebrush plants into a net C source. In stages III and IV, litter C:N ratio was not a significant part of the model, perhaps because the litter layer was composed mainly *B. tectorum* detritus, and the C:N ratio did not differ between years.

4.4 Implications for management

Loss of native perennial shrubs and grasses and conversion to invasive annual grass dominance may decrease an ecosystem's ability to retain soil resources and sequester carbon in the face of interannual climatic variability. Restoration of diverse plant communities has the potential to reverse these trends (Lange et al. 2015; Yang et al. 2019). However, in *A. tridentata* ecosystems invaded by *B. tectorum*, restoration efforts have had mixed success (Knutson et al. 2014; Jeanne C. Chambers et al. 2017). Progressive homogenization and depletion of soil nutrient pools (Davis et al. 2000) may reduce resource availability and decrease niche availability (Fukami 2015; Melbourne et al. 2007) negatively affecting establishment processes and making restoration more difficult.

No single management action will likely be sufficient to restore invaded *A. tridentata* ecosystems. Fire suppression efforts designed to maximize unburned patches within fire perimeters may minimize loss of ecological function associated with *A. tridentata* fertility islands (Steenvoorden et al. 2019).

In the first 1-3 years after fire, *B. tectorum* typically has relatively low density and cover (Jeanne C. Chambers, Miller, et al. 2014; Urza et al. 2017, 2019) providing a critical window of opportunity for perennial plants to establish with less competition from annual invasive grasses. Restoring diverse communities that include the dominant plant functional groups can increase the spatial and temporal capacity to maximize resource use and more effectively compete with *B. tectorum* (Yang et al. 2019). Seasonal weather forecasts that account for interannual variability (Bradford et al. 2018; Hardegree et al. 2018) can help ensure that seeding is implemented in years when conditions are favorable for plant establishment. In addition, repeated seeding in several successive years may improve restoration success by increasing the odds that seed availability coincides with favorable conditions for establishment (Wilson et al. 2004; K. W. Davies, Bates, and Boyd 2019; Shriver et al. 2018).

Shrubs are particularly important for regaining ecohydrological function (Turnbull et al. 2012; Wilcox et al. 2012), reducing the loss of soil N, and sequestering soil C. Shrubs sequester C in their woody tissues and in their deep root systems and have higher soil moisture, higher soil nutrient concentrations, and lower soil temperatures below their canopies (A. T. Austin et al. 2004). Because *A. tridentata* often takes a decade or more to achieve full canopy cover and can be difficult to establish (Shriver et al. 2019), species mixes should include both *A. tridentata* and resprouting shrubs that are known to establish more quickly and are more likely to survive repeated fires (e.g. *Chrysothamnus* spp. and *Ericameria* spp.), as well as a diverse complement of perennial herbaceous plants (Booth, Stark, and Caldwell 2003; Huber-Sannwald and Pyke 2005; Goergen, Leger, and Espeland 2011; Wainwright et al. 2020; Pyke et al. 2018).

4.5 Implications for future research

Future research should investigate the effects of annual grass invasion on ecosystem function in different stages of invasion at wider spatial extents and with enough repeated measurements to capture long-term trends in the context of interannual variability (Cusser et al. 2021). Functional components include stocks of above- and belowground biomass, soil total C and N storage, albedo and soil water storage. Annual or subannual data collected at temporal extents long enough to capture the full range of variability are necessary to disentangle long-term trends of these functional

components from the confounding effects of interannual variability (Werner et al. 2020), time since invasion, time since disturbance and soil characteristics (Noy-Meir 1973; A. T. Austin et al. 2004). Some prior studies had well defined invasion stages (Rau et al. 2011), or a well-defined time of introduction (Stark and Norton 2015), but no study that we are aware of has adequately captured the range of interannual variability in this system. Time since initial introduction may not always be feasible to ascertain, but annual grass invasions initiated during the satellite record may be detected from seasonal differences in NDVI (Bradley et al. 2006; Boyte, Wylie, and Major 2019). Time since the loss of woody plant cover may be ascertained from satellite-derived datasets of fire occurrence (Hawbaker et al. 2017; Jennifer K. Balch et al. 2020) and functional group fractional cover (M. O. Jones et al. 2018). Understanding the inter- and intra-annual variability in each component of above- and below-ground C and N pools and fluxes over decadal temporal extents will allow for the determination of rates of change at each site, rather than relying on space for time substitutions.

5. Conclusion

Episodic differences in temperature and water availability have predictable effects on *B. tectorum* invasion and soil nutrients, but have seldom been adequately analyzed. Our results indicate that annual grass invasion changes mechanisms and pathways of nutrient cycling and carbon storage, especially after the loss of shrubs. Other studies found that soil water content is perhaps the single most important factor in nutrient cycling in arid ecosystems (A. T. Austin et al. 2004; Urszula Norton et al. 2012). We found weak direct effects of temperature and water availability on soil nutrients, but strong indirect effects on soil C and N through their effects on herbaceous plant cover. The changes in mechanisms and pathways of nutrient cycling and carbon storage will likely lead to the long-term depletion of soil resources and a decline in resource heterogeneity.

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Chapter 3. One & done: Annual grass invasion and grazing maintain an alternative species assemblage initiated by fire in a semi-arid shrubland

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Abstract

Invasion by introduced plants and changing fire regimes are two of the more difficult ecological challenges we face today. In the western U.S., the initiation of a novel grass-fire cycle has transformed vast areas of a semi-arid shrublands into grasslands dominated by non-native annuals. Although repeated fire is likely the primary mechanism that excludes native species, it may obscure other self-reinforcing processes that maintain the annual grassland. Here we aimed to eliminate this confounding effect by creating a regional scale chronosequence for areas that burned only once since 1984. We hypothesized that if fire was the only driver maintaining the grassland state, native diversity and shrub cover would increase as time since fire (TSF) increased. If fire was not the only driver, native diversity and shrub cover would be unrelated to TSF, and instead be driven by grazing and annual grass cover. We also explored how fire year climate affected species composition. We built a 32-year fire history atlas of northern Nevada with two Landsat-derived burned area products to identify pixels that had burned only once from 1984-2017. We collected species composition data at 35 plots within these pixels that represented a gradient of 4-32 years since fire. We used indirect gradient analysis (IGA) and a joint species distribution model (JSDM) to examine how the community composition was related to time since fire, long-term grazing pressure, cheatgrass abundance, topography, diversity indexes and fire year climate.

We found that without repeated fire, alternative assemblages were maintained by additional positive feedbacks. Diversity and evenness were unrelated to time since fire, but had strong negative relationships with cheatgrass cover. Both the IGA and JSDM analyses suggested longer time since fire was associated with degraded sites dominated by introduced plants, whereas more recently

burned sites had more natives. Fire occurrence had negative impacts on native species, with the exception of a resprouting shrub, while positively impacting one highly prevalent non-native forb. Cheatgrass cover negatively impacted sagebrush occurrence. Grazing intensity had a negative impact on an important perennial competitor and benefited introduced annuals, a native resprouting shrub and several native short-statured forb species. This suggests that even with successful fire suppression, in already burned sites the combination of grazing and cheatgrass competition will maintain the post-fire herbaceous-dominated plant community. Reseeding with resprouting shrubs and shorter-statured forbs could be a foot-in-the-door approach to restoring ecosystem structure following fire. Land managers may be able to use pre-fire climate to prepare species mixtures for post-fire restoration applications.

1. Introduction

Invasions by introduced plants are one of the more difficult ecological challenges facing land managers today (Buckley and Catford 2016). They can alter ecosystem structure and functioning in myriad ways, affecting biogeochemical cycling (Hooker et al. 2008; Van der Putten et al. 2013) and fire regimes (Brooks et al. 2004; D'Antonio and Vitousek 1992), and this can lead to permanent ecosystem transformation (Brooks et al. 2004). In the sagebrush (*Artemesia* L.) ecosystems of the western United States, such a change is likely occurring. Here, the invasion of the annual grass *Bromus tectorum* L. has increased the connectivity and flammability of fuels (K. W. Davies and Nafus 2013). This has led to larger, more frequent and more spatially contiguous fires (Jennifer K. Balch et al. 2013; Keeley and Pausas 2019), resulting in the loss or degradation of sagebrush for over half of its original extent (R. N. Mack 1981; K. W. Davies et al. 2011). Sagebrush restoration efforts thus far have been met with limited success, especially at lower elevations (Knutson et al. 2014). One reason why restoration is so challenging is that the post-fire assemblage is likely to be an alternative stable state that is maintained by self-reinforcing feedback mechanisms. In order to restore such a system to its pre-fire condition, passive restoration approaches that rely on succession may not be effective (Suding, Gross, and Houseman 2004). Rather, feedbacks that maintain the post-fire assemblage must be identified and action must be taken to reverse them. In highly flammable systems, the effects of repeated fire may be so pervasive (G. M. Davies et al. 2012; Mahood and Balch 2019) that they may mask the effects of other processes. Here, we constructed a 32 year,

satellite-derived fire history atlas to guide field surveys in order to examine if the system recovered towards the pre-fire assemblage without repeated fires, and if not, there were additional feedback mechanisms maintaining the post-fire species assemblage.

Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle & Young) is the most widespread *Artemisia* taxa in the U.S. It is a slow-growing shrub that grows on dry, upland sites across much of the arid portions of the western US. It tolerates periods of drought and then sporadically recruits new members into the population in years with high moisture availability (Meyer 1994; Daniel R. Schlaepfer, Lauenroth, and Bradford 2014). Pre-colonial fire regimes in sagebrush were likely characterized by infrequent, small, and patchy fires (Baker 2006; Bukowski and Baker 2013; Keeley and Pausas 2019). As a seed obligate *A. t. wyomingensis* relies on recolonization from unburned individuals for regeneration (K. W. Davies et al. 2011; R. F. Miller et al. 2013; Jeanne C. Chambers, Bradley, et al. 2014). When it does recover, the first individuals to colonized the burned area typically establish within 5 years of the fire and reach a mature size class in as few as 15 years (Shinneman and McIlroy 2016), with a return to pre-fire cover after 30-50 years or longer (Harniss and Murray 1973; Mata-González et al. 2007; Daniel R. Schlaepfer, Lauenroth, and Bradford 2014; Shriver et al. 2019; J. D. Bates, Boyd, and Davies 2020). Often *B. tectorum* still initially dominates, but is overtaken by native species after 15 years (Mata-González et al. 2007; K. Taylor et al. 2014; Moffet, Taylor, and Booth 2015; Shinneman and McIlroy 2016; Ellsworth et al. 2016). Studies documenting successful recovery have mostly been conducted at higher elevation sites with higher soil water availability and less severe summer drought. As elevation declines, the ability of *A. t. wyomingensis* to recover after fire declines (Jeanne C. Chambers, Bradley, et al. 2014), while the ability of *B. tectorum* to grow and reproduce increases (Jeanne C. Chambers et al. 2007). But even slow recovery still appears to be detectable (e.g. 5% canopy recovery) within the 32 year satellite fire record (Lesica, Cooper, and Kudray 2007). From these examples, we can glean two key components of detecting recovery: a decline in the cover of introduced annual grasses and forbs, and a rise in the cover of perennial native grasses and forbs and native shrubs, be they sagebrush or other species.

Long-term grazing pressure and annual grass dominance are two key processes that both are likely to act and even interact to maintain the annual grass dominated assemblage in the absence of

fire. Grazing favors annual over perennial species in general (Díaz et al. 2007), and in this system is associated with increased presence of *B. tectorum* in particular (Williamson et al. 2019). This may be driven by a superior tolerance to grazing by *B. tectorum* coupled with negative impacts of grazing on competitors (Beckstead and Augspurger 2004). Perennial grasses with a tussock architecture are known to be negatively impacted by grazing (Díaz et al. 2007), and these include some of the most important competitors against *B. tectorum* (e.g. *Elymus elymoides* L.) (Booth, Stark, and Caldwell 2003; Reisner et al. 2013). Biological soil crust, which inhibits *B. tectorum* germination, is also damaged by grazing (Ponzetti, Mccune, and Pyke 2007). *B. tectorum* is highly palatable, especially in the spring when grazing is most damaging to native perennials (D. D. Austin et al. 1994; Strand et al. 2014), and so native species that persist at low abundances at sites dominated by *B. tectorum* may be more vulnerable to local extirpation via grazing. Annual grass dominance can also suppress native perennial bunchgrasses (Jeanne C. Chambers et al. 2007; Reisner et al. 2013) via competition for light which reduces their growth and reproduction (Dyer and Rice 1999). *B. tectorum* is able to uptake spring moisture before most native perennials (Jeanne C. Chambers et al. 2007), and is superior competitor for soil nitrogen (James et al. 2011). The litter of *B. tectorum* is also important, as it can increase the emergence of *B. tectorum* (Young and Evans 1975) while inhibiting emergence of native species (Jeanne C. Chambers 2000).

A critical window of opportunity for post-fire establishment and recovery is the growing season in which the fire occurs. The climatic conditions preceding the fire heavily influence the severity, intensity and extent of fire (Abatzoglou 2013) as well as the growth and reproduction of the species present (R. Mack and Pyke 1983). The remainder of the growing season after fire occurrence is when resource availability is highest and uptake is lowest (Davis et al. 2000). It is during this time when plants have the opportunity to colonize newly available niche space via resprouting, seedbank reserves or dispersal from adjacent unburned areas. The introduced annuals that now dominate so many areas tend to have higher growth rates than native perennials and a superior ability to quickly take advantage of episodic moisture availability (Jeanne C. Chambers et al. 2016; David S. Pilliod, Welty, and Arkle 2017). Mature perennial plants can coexist with *B. tectorum* due to deeper root systems (Gibbens and Lenz 2001; Ottaviani et al. 2020). However, After a fire competition with *B. tectorum* for water and sunlight can result in increased seedling mortality (Dyer and Rice 1999;

Daniel R. Schlaepfer, Lauenroth, and Bradford 2014). Resprouting plants may need to deplete their belowground carbon reserves in order to re-establish aboveground tissues, thus making them more susceptible to competition from shallow-rooted annuals. The results of these interactions may have lasting legacies on species composition, especially in areas with no adjacent source of native seed dispersal (Buckley and Catford 2016; Fukami 2015). The establishment of both *B. tectorum* (Klemmendson and Smith 1964) and sagebrush (Daniel R. Schlaepfer, Lauenroth, and Bradford 2014) are sensitive to precipitation and temperature. *A. t. wyomingensis* is an obligate seeder, and relies on spring soil moisture (Meyer 1994), but *B. tectorum* is competitively superior for moisture during the period in early spring after snowmelt, and can exclude sagebrush and other seedlings. Precipitation in the two water years before fire occurrence has lasting impacts on post-fire community composition in this system (Mahood and Balch 2019). Drier conditions have direct negative effects on germination and seedling survival of Wyoming big sagebrush (Daniel R. Schlaepfer, Lauenroth, and Bradford 2014), with sufficient winter precipitation being vital to pulses in recruitment (Maier et al. 2001). After fire, cheatgrass responds positively in years with higher temperatures and higher winter precipitation (Jeanne C. Chambers et al. 2007; K. Taylor et al. 2014; Jeanne C. Chambers, Bradley, et al. 2014). *A. t. wyomingensis* is more resilient after fire at sites that experienced both lower burn severity (i.e. some mature adults survive) and more precipitation during the winter immediately following fire at sites (Shinneman and McIlroy 2016). The ecological legacies that these fire year climatic forces leave, and how they manifest to affect the long-term persistence of plant communities is understudied.

Here, we used a space for time substitution to explore how plant communities persisted after fire occurrence, without the added effect of repeated fires. We sampled plant species composition at 35 sites encompassing a gradient of 4-32 years since fire occurrence over 36,000 km². We hypothesized that (H1₀) if repeated fires were the only driver that maintains the annual grass assemblage, we would see higher shrub cover, perennial grass cover and native plant diversity as time since fire increased. If there are other self-reinforcing processes maintaining the annual grass assemblage, (H1_a) there would be no relationship between time since fire and community composition and diversity. If H1_a was true, we hypothesized that (H2) long-term grazing pressure and annual grass abundance would have a positive relationship with the occurrence of non-native annual plants and

a negative relationship with native perennial grasses and forbs. We also explored how fire year climate variables were predictive of species composition, with an eye towards trying to understand how post-fire restoration strategies might be designed to account for fire year climate.

2. Methods

2.1 Study area

The study was conducted across a 36,000 km² area in northern Nevada (Figure 17). Soils were generally clay loams. The region has hot, dry summers and cold, wet winters. Annual precipitation averages 266 ± 46 mm, falling mostly from November to May. Mean annual temperatures are 9.4 ± 0.5 degrees Celsius, with seasonal peaks of 22 ± 0.5 in July and -1 ± 0.5 in December (PRISM Climate Group 2018). The region consists of mountain ranges that run north-south, and the sagebrush ecosystems generally lie on the lower slopes of the mountains. Our sites ranged from 1275 to 1631 m in elevation (mean 1460). Study sites were located 10 km apart on average to ensure statistical independence.

2.2 Fire History Atlas

To design our sampling scheme we created a fire history atlas, from which we selected plot locations along a gradient of time since fire. Since fire frequency has been shown to influence community composition and diversity (G. M. Davies et al. 2012; Mahood and Balch 2019), we sought to avoid these confounding affects by keeping fire frequency constant. Thus, when we created the fire history atlas we used two landsat-based products to exclude all burned pixels except those where the two products agreed that they had only burned once between 1984 and 2015. The first product we used was the yearly burn severity mosaics from the Monitoring Trends in Burn Severity database (Eidenshink et al. 2007). We extracted low to high burn severity classifications from this product, effectively removing potential unburned pixels from fire perimeters. We converted the resulting raster file from each year to a binary grid, summed all years to get a fire frequency grid, and then excluded pixels that were not equal to one. Then, we converted the MTBS Burned Areas Boundaries dataset to a fire frequency layer and extracted only those pixels where the two datasets had matching frequencies of one. The second dataset was the USGS Burned Area Essential Climate

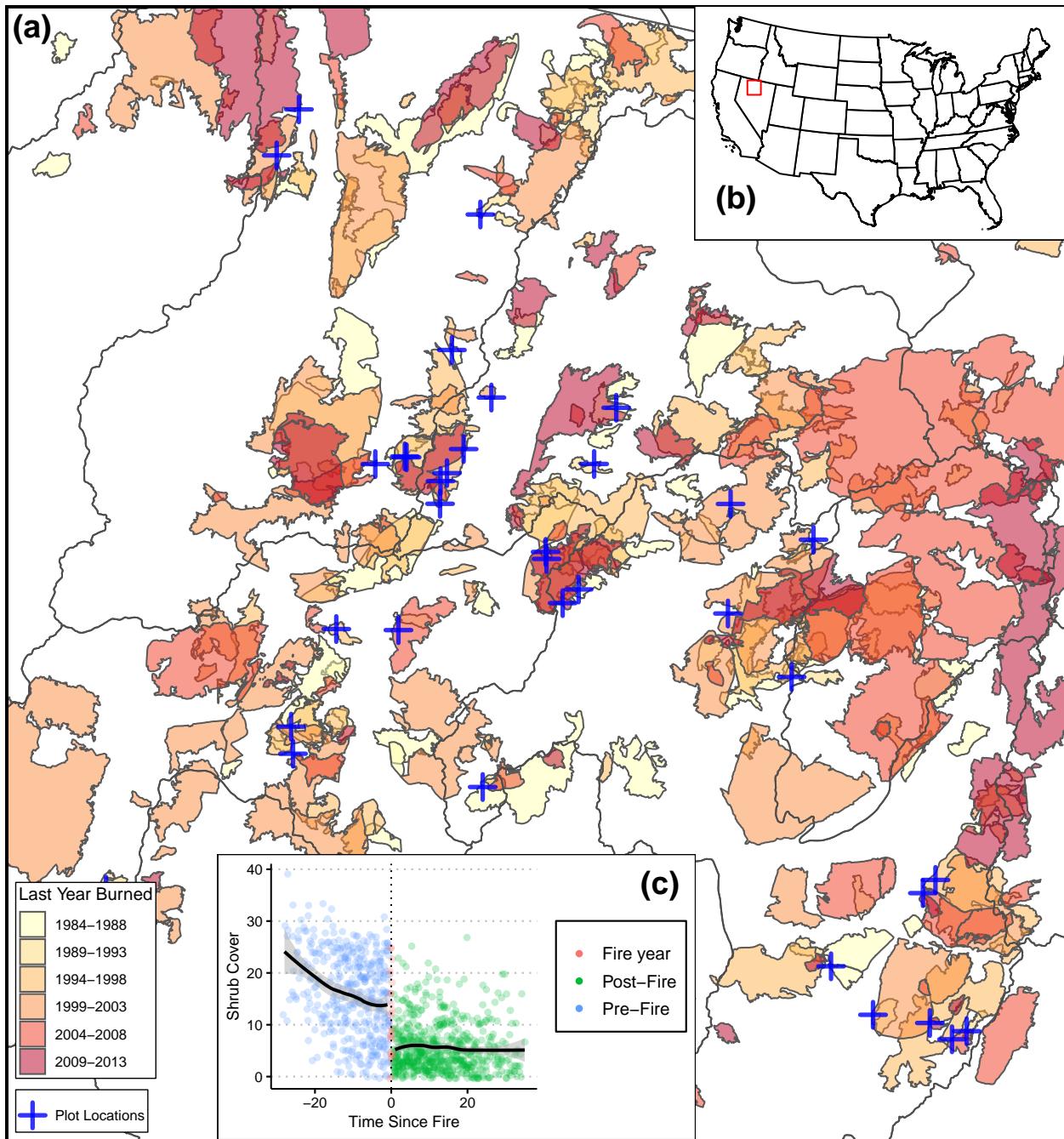


Figure 14: In (a), polygons show fire history in the study area from the Monitoring Trends in Burn Severity fire perimeters. Blue crosses represent sampling locations and dark grey outlines represent USGS 250k watersheds which we used as study blocks. (b) is a locator box. We also provide evidence that sampling locations had mature shrub canopies before they burned. In (c), shrub cover estimations from 1984–2019 for each sampling location were extracted from <https://rangeland.app>, and are centered on the year that each site burned. Lines are loess smoothers, shaded areas are the standard error

Variable (BAECV) (Hawbaker et al. 2017). With this data we similarly converted each year to a binary grid and summed all of the layers. Finally, we extracted only those pixels where both the BAECV and our MTBS-derived layer equaled one. The result is a fire history layer where we could be reasonably certain that those areas on the map had burned only once since 1984. After the filtering process was complete, we converted the values of the remaining burned pixels to the year of the last fire.

To keep other potentially confounding factors constant, we masked away all land not managed by the Bureau of Land management, all land that was more than 2km from roads, and all land where the environmental site potential was not of the Great Basin Big Sagebrush Shrubland vegetation alliance as defined by LANDFIRE (Rollins 2009). We used the Land Treatment Digital Library (David S. Pilliod and Welty 2013) to exclude any areas that had undergone successful ecosystem restoration. We confined the study to the Central Basin and Range ecoregion (Commission for Environmental Cooperation 2006) to keep climate consistent. We also used the shrub cover layer produced by <http://rangelands.app> (M. O. Jones et al. 2018) to ensure that sites had shrub canopies at the beginning of the time series.

2.3 Sampling design

We stratified the sampling space spatially and temporally. Spatially, we divided the region into study blocks using 1:250,000-scale hydrologic units (Steeves and Nebert 1994). Temporally, we divided the last year burned into six, five-year bins, from 1984-2013 (Figure 14). We sampled 4 hydrologic units (hereafter, watersheds), splitting one large watershed into two study blocks. We sampled one plot from each temporal bin plus an unburned plot, yielding 7 plots per watershed, for 35 plots total. If one of the 5 year time periods could not be sampled in a watershed, we sampled an extra plot from an adjacent time period if possible. We generated spatially balanced random points (Theobald et al. 2007) within each spatiotemporal bin to select the exact sampling locations, selecting plots that were at least 50 meters from the edge of a given burned patch to avoid any uncertainty associated with mixed pixels at the edges.

2.4 Field sampling

At each sampling location, we delineated a 50 m x 50 m plot with nine, randomly located 1m² subplots within. We estimated cover of every species in each subplot then did a systematic gridded plant walk to catch any species that were not in the subplots. Because this method tends to underestimate shrubs, we used the point-centered quarter method (PQ) to estimate shrub cover if shrubs were present (David S. Pilliod and Arkle 2013). PQ is a plotless method where for each of four quadrants around a central point, the distance to the nearest shrub and its canopy cover is measured. We did this at 4 points for each plot. This method is known to yield biased cover estimates for species that are not randomly distributed spatially. Many of plot locations we visited had very low, sporadic shrub cover, often with just a few individuals, and PQ works well for capturing rare individuals (David S. Pilliod and Arkle 2013). We were willing to accept that areas with high shrub cover would have less precise estimates, in exchange for consistently capturing sporadic individuals along with the rapid implementation of the PQ method.

2.5 Climate and grazing data

To assess the influence of fire year climatic conditions on subsequent vegetative composition we extracted climatic information at each sampling location from gridded monthly data on actual evapotranspiration (AET), climatic water deficit (CWD) and minimum temperature (T_{min}) from gridMET (Abatzoglou 2013). For all of these climate variables, we calculated z-scores based on 30-year medians and median absolute deviations, and capped the outliers to absolute values of 3. For each variable, we extracted the minimum, maximum and median z-scores preceding (January - the month before the fire) and following (month after fire - December) the fire, as well as the month in which the fire occurred.

In this system, cattle grazing is ubiquitous. In order to account for the influence of cattle grazing, we acquired data for animal unit months (AUMs) for each grazing allotment in our study from the Bureau of Land Management's Rangeland Administration System for 13 years during the middle of the study period (1990-2002). We divided AUMs by the area of the allotment to get an approximation of grazing intensity. Because grazing intensity is not homogeneous within a given grazing allotment, this information is a coarse estimate. However, because our study sites were very

widely distributed, almost every site was within its own unique allotment. In addition, billed AUMs do not change much from year to year. Thus, we felt confident that this was an appropriate metric of long-term grazing pressure for our particular application.

2.6 Statistical analysis

Linear mixed models We created linear mixed models to examine the relationship between time since fire and the cover of each plant functional group, with the watershed as a random intercept. We also created two sets of models to examine Shannon-weaver alpha diversity and Pielou's evenness as response variables. The first set had time since fire as the predictor variable, and the watershed as a random effect. The second set was the same, except with cheatgrass cover as the predictor variable.

Indirect gradient analysis To analyze community composition we used indirect gradient analysis [IGA; Walker (2015)]. This is a Bayesian method that uses Markov-chain Monte Carlo simulations on presence/absence data to detect a latent variable of the probability of occurrence. This latent variable is similar to that of a principle components analysis axis, in that its meaning can be inferred by correlating it against environmental variables (Walker 2015). We set prior means to zero, such that the prior distribution can be thought of as a null model (Walker 2015). The prior variance for the gradient were set to one, and prior variances of the species parameters were set to 0.2. These parameters are thought to be an appropriate compromise between over- and under-fitting (Walker 2015).

Because it uses occurrence data, both rare species (those that occur at only one site), and species that occurred at every site, were removed from the analysis because they add no information. Thus, *B. tectorum* was removed because it occurred at every site, along with several uncommon species that only occurred at one site, and the IGA was performed on 34 species. The exclusion of cheatgrass from the IGA was beneficial to the analysis since we were then able to test how it influenced the gradient that was estimated, and thus assess the effect of the abundance of cheatgrass on the occurrence of other common species. We used two methods for model diagnostics. First, we used the Gelman–Rubin convergence diagnostic (Plummer et al. 2006) to assess whether the model converged well. Second, we used posterior predictive checks to visually examine how well the

predicted values from the model lined up with the observations.

To examine how fire year climate, grazing intensity and time since fire were related to community composition, we estimated the posterior density of the Pearson correlation coefficients between the estimated gradient and the observed environmental variables at each plot. We used the quantile function in R to compute 89% credible intervals for the correlations for the slope parameters for each species, the gradient position parameters for each site, and the correlations between the environmental parameters and the gradient.

We performed IGA twice. One analysis was on all of the plots, and the other was on the burned plots only. Running IGA on the burned plots only allowed us to analyse the effect of climate around the time of the fire, as well as time since fire, on community composition. Pearson correlation coefficients were used to assess how environmental and climate variables were related to the gradients. Because we created two versions of the IGA model and because the gradient that is outputted from the model is a unitless index, we ended up with two very similar gradient analyses that arbitrarily went in opposite directions. Because the direction of the gradient is essentially meaningless, we multiplied the results of one of the models by -1 to avoid confusion in the interpretation of the results.

Joint species distribution modeling In order better understand how individual species responded to environmental variables and time since fire, we created two joint species distribution models (JSDMs) of species occurrence using the R package *Hmsc* (Tikhonov, Opedal, et al. 2020). One JSDM was created for the burned plots only to explore the effect time since fire, ignition month, and three fire year climate variables that were found to be correlated with the IGA gradient on each species' occurrence probability. The other JSDM modeled the species at all plots in order to examine the effects of fire occurrence and *B. tectorum* cover. For both models we used the same environmental predictor variables: elevation, folded aspect, grazing intensity, and plot coordinates as a spatial random effect. We also included three qualitative traits in each model: origin (introduced or native), duration (annual, perennial, woody or cactus), and cotyledons (monocot vs dicot).

We used the default priors provided by the *Hmsc* package (Tikhonov et al. 2019). We ran four MCMC chains for 150,000 iterations. The first 50,000 iterations were removed as burn-in and 1

out of every 100 remaining iteration was sampled, resulting in 1,000 posterior samples per chain (4,000 total). To validate the model convergence and chain mixing we used the Gelman–Rubin convergence diagnostic and effective sample size. To evaluate the explanatory power of the model we used the coefficient of discrimination (Tjur R^2).

To look for evidence of environmental filtering, we calculated the posterior mean and support for each species response to the environmental covariates we used in the models. We considered anything with a support over 89% to be strong evidence of environmental filtering. To better understand and visualize the effect sizes, we generated posterior predictions along gradients of time since fire, *B. tectorum* cover, grazing intensity, and fire occurrence with all other predictor variables held constant for both JSDMs.

Code and data to reproduce the analysis and figures is given in the supplementary material, and is also available at <https://github.com/admahood/lyb>.

3. Results

We found no effect of time since fire on functional group cover (Figure 15) or diversity (Figure 16), suggesting a relatively stable system after one fire (Figure 15). However, cheatgrass cover had a strong negative effect on both the Shannon-Weaver ($\beta = -0.23$; $p \ll 0.05$; Marginal $R^2 = 0.56$) and Pielou's Evenness ($\beta = -.009$; $p \ll 0.05$; Marginal $R^2 = 0.59$) indexes of alpha diversity (Figure 16).

Both IGA analyses were well fit and very similar to each other (Figure 17). The Gelman–Rubin convergence diagnostics and effective sample sizes indicated good model convergence, and posterior predictive checks showed that >99% the observed values fell within the predicted intervals. The gradient estimated by the model was relatively weak. All species except *Lepidium perfoliatum* had their 89% credible intervals cross zero, while *L. perfoliatum* was fully negative. All sites had their credible intervals cross zero as well. This is not necessarily surprising because all of the sites had similar species compositions. Even the unburned, shrub-dominated plots had generally one or two species of shrub (*Artemisia tridentata* and *Ericameria nauseosa*), and the species that was most dominant in the burned sites, *Bromus tectorum*, was removed from this analysis because it was present at every site. Nevertheless, there was still a pattern. The positive side of the gradient was associated with greater native species occurrence, higher diversity and evenness, more shrub cover

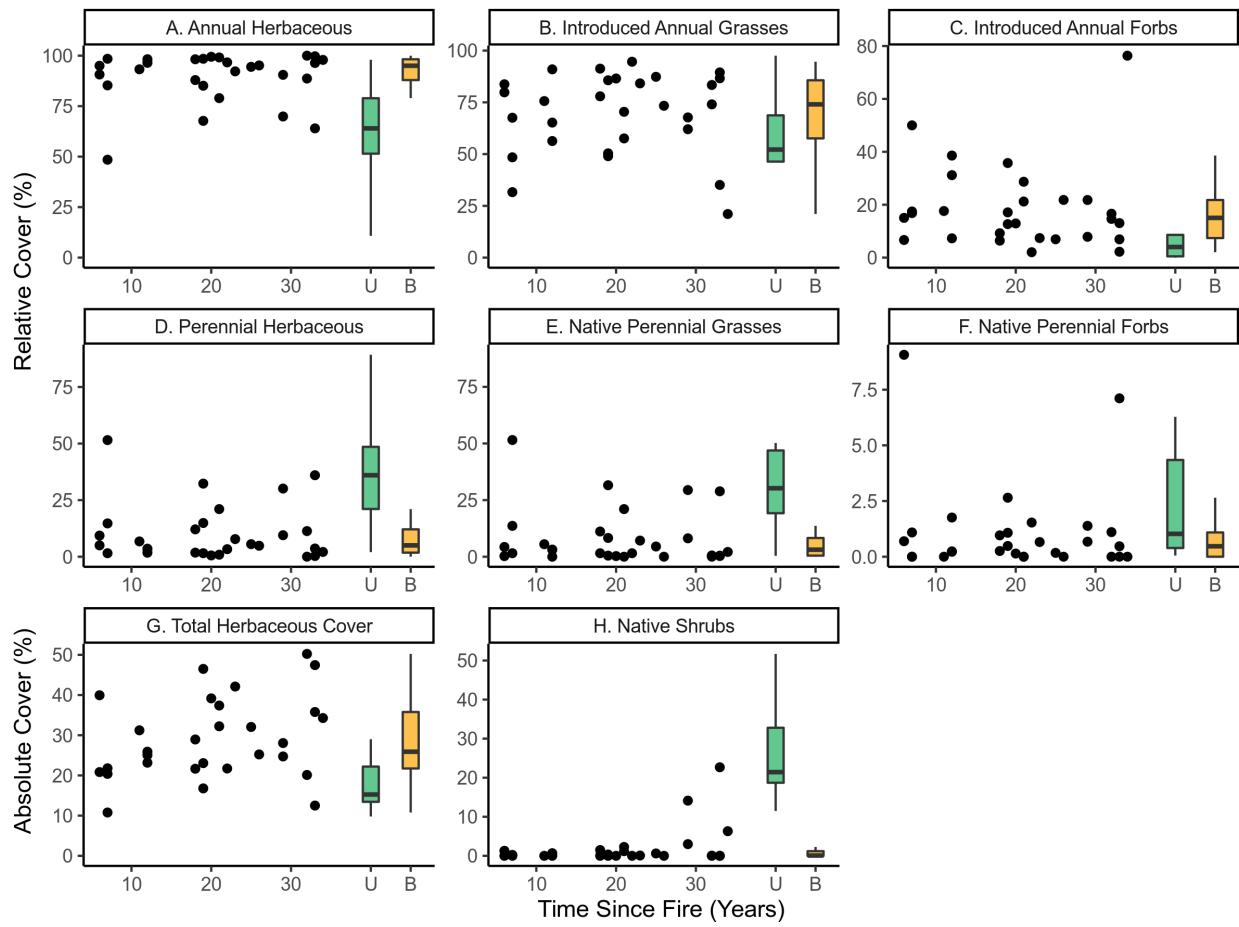


Figure 15: Bivariate relationships between last year burned and relative plant cover partitioned by functional group. Each point represents one 250 m^2 sampling location. Boxplots represent the distributions for all unburned locations (U) and burned locations (B). Bar represents the median, the upper and lower box ends are the 25th and 75th quantiles, and the whiskers extend to $1.5 * \text{the interquartile range}$.

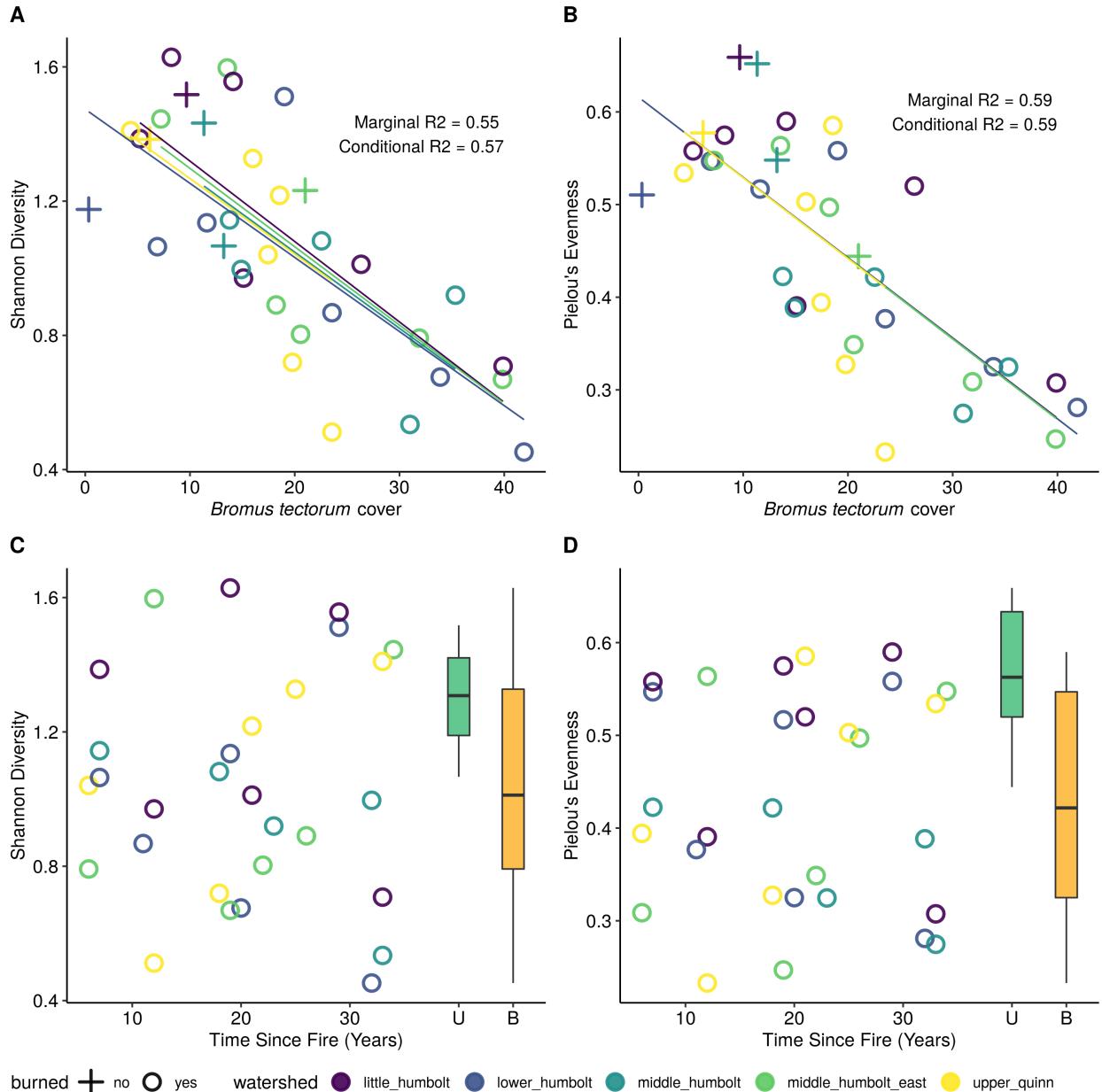


Figure 16: The relationship between *Bromus tectorum* cover and Shannon diversity is in a and Pielou's evenness in b. Colors represent watersheds, shapes indicate burned (circles) or unburned (crosses). Lines are the predictions from linear mixed models. The relationship between time since fire and Shannon diversity is in c and Pielou's evenness in d, along with boxplots showing the differences between burned (B) and unburned (U) plots.

and lower grazing intensity (Figure 17). The negative side of the gradient was associated with higher cheatgrass cover, greater exotic species occurrence, and higher grazing intensity (Figure 17).

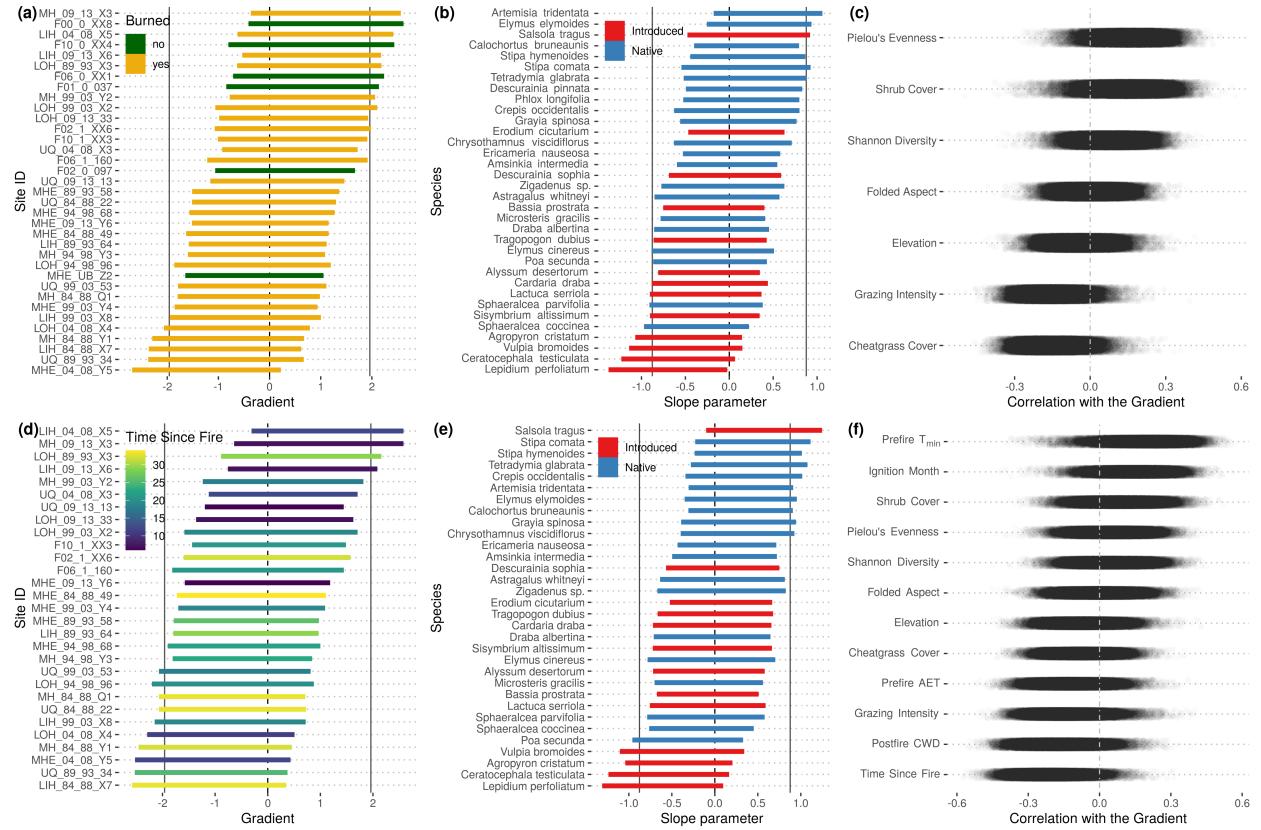


Figure 17: Indirect Gradient Analysis results. The top row (a-c) shows the results for the model with all plots. (a) shows where each site lies along the latent gradient, with bars representing the 95% confidence interval. The color of the bar represents whether or not the plot has burned since 1984. (b) shows where each species lies along the gradient. Bars represent the 95% confidence interval and are colored according to whether they are native. (c) shows the correlations of environmental metrics with the posterior distribution of the gradient. The bottom row (d-f) is the same but for the model with burned plots only. In (d), color corresponds to time since fire.

For the IGA model that included all plots, grazing intensity and *B. tectorum* cover had completely negative credible intervals, while Pielou's evenness was completely positive (Table S1, Figure 17c). For the IGA model for only the burned plots, time since fire was completely negative (Figure 17f, table S1). Most fire year climatic variables did not have strong associations, with a few exceptions. In the months before a fire occurred, the median minimum temperature (hereafter prefire T_{min}) was positively correlated with the gradient, while minimum actual evapotranspiration (hereafter, prefire AET) were negatively correlated with the gradient (Figure 17f). In the months

following fire, the maximum climatic water deficit (postfire CWD) was negatively correlated with the gradient (Figure 17f). These three fire year climate variables were used in the JSDM created for the burned plots.

The JSDMs we created had good model convergence and relatively low explanatory power (mean $R^2 = 0.2$). As with the IGA models, low explanatory was expected given that all of the plots had very similar species compositions. Furthermore, the average time since fire was 20 ± 9 years, so we expected the effects of the fire year climate and ignition month to be faint. The JSDM for the burned plots only showed that time since fire had negative effects on 8 native species and 2 non-natives, with positive effects on 3 of the most prevalent species (Figure 18a). Many species had positive relationships with elevation and negative relationships with folded aspect - indicating greater success on cooler, wetter sites. Postfire CWD had exclusively positive relationships with 14 native and 3 non-native species. Prefire T_{min} had positive relationships with 9 native and 4 non-native species, and negative effects on 3 natives and 1 non-native. Prefire AET had negative effects on 5 species, 4 native and 1 non-native. Grazing intensity had positive effects on 4 native species and 4 non-native species, and negative effects on one native species (Figures 5-7).

From the JSDM that included all plots, grazing intensity had the strongest environmental filtering effects, while fire had weaker but consistent effects. Grazing intensity positively affected the occurrence of short statured herbaceous plants as well as a resprouting shrub, *Ericameria nauseosa*. *Sisymbrium altissimum*, the most commonly occurring introduced plant was positively effected by fire occurrence, while all native plants were either unaffected or negatively affected by fire occurrence (Figure 20). *B. tectorum* cover had a negative effect on 3 native species: *A. t. wyomingensis*, our keystone species, *Tetradymia glabrata*, a native shrub, and *Phlox longifolia* a common forb (Figure 18).

4. Discussion

4.1. Hypothesis 1: Evidence against native plant community recovery

After removing the effect of fire frequency on community composition for low elevation ($< 1500\text{m}$) areas where *A. tridentata* communities have become dominated by annual grasses, we found that instead of returning towards the pre-fire composition, plant communities were becoming

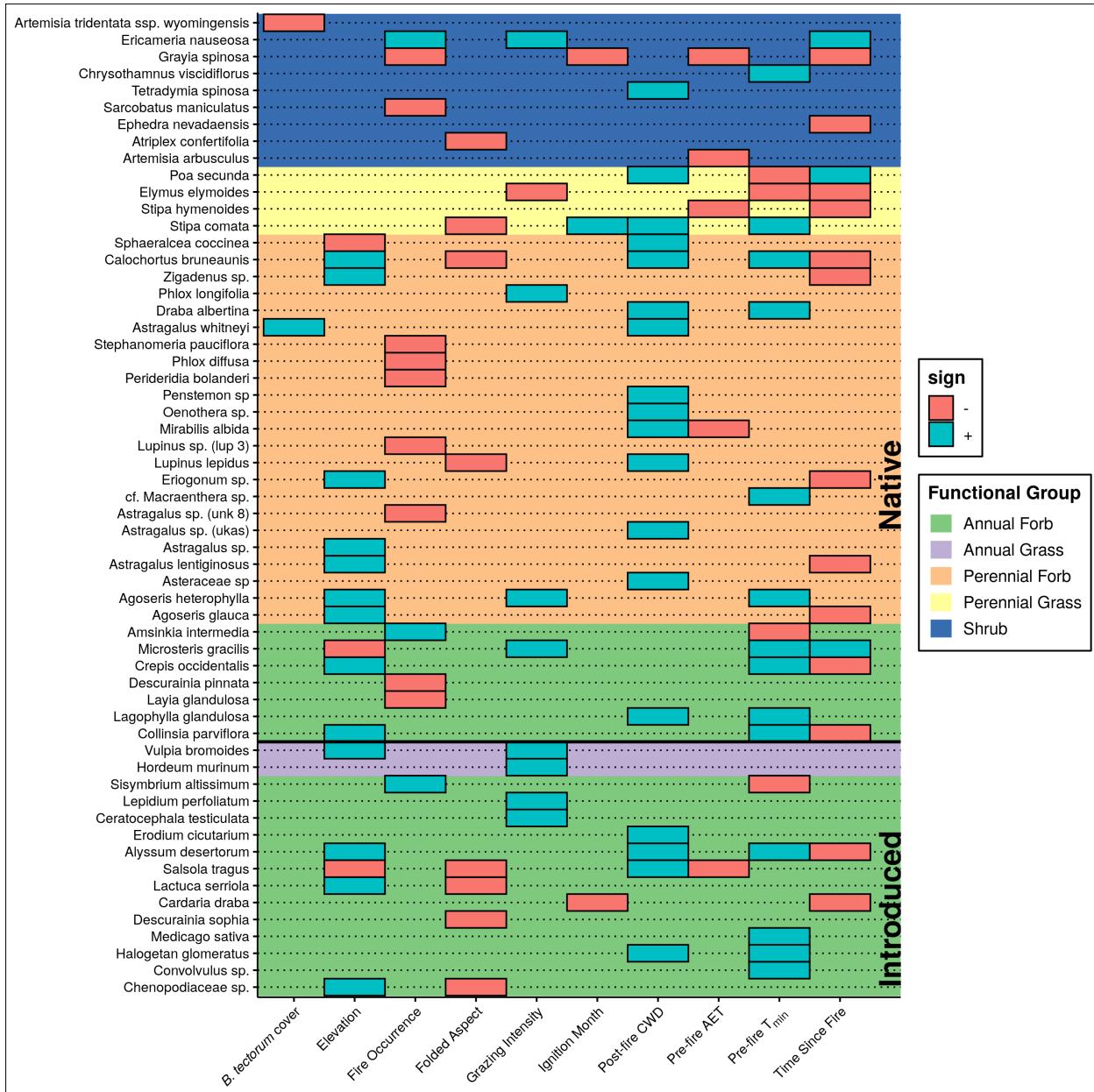


Figure 18: Environmental variables that had 89% support by species. Color indicates the sign, blue for positive, red for negative. Shading of the background corresponds to the plant functional group. Fire occurrence is from the JSMD on all plots, and all other variables are from the JSMD on post-fire plots.

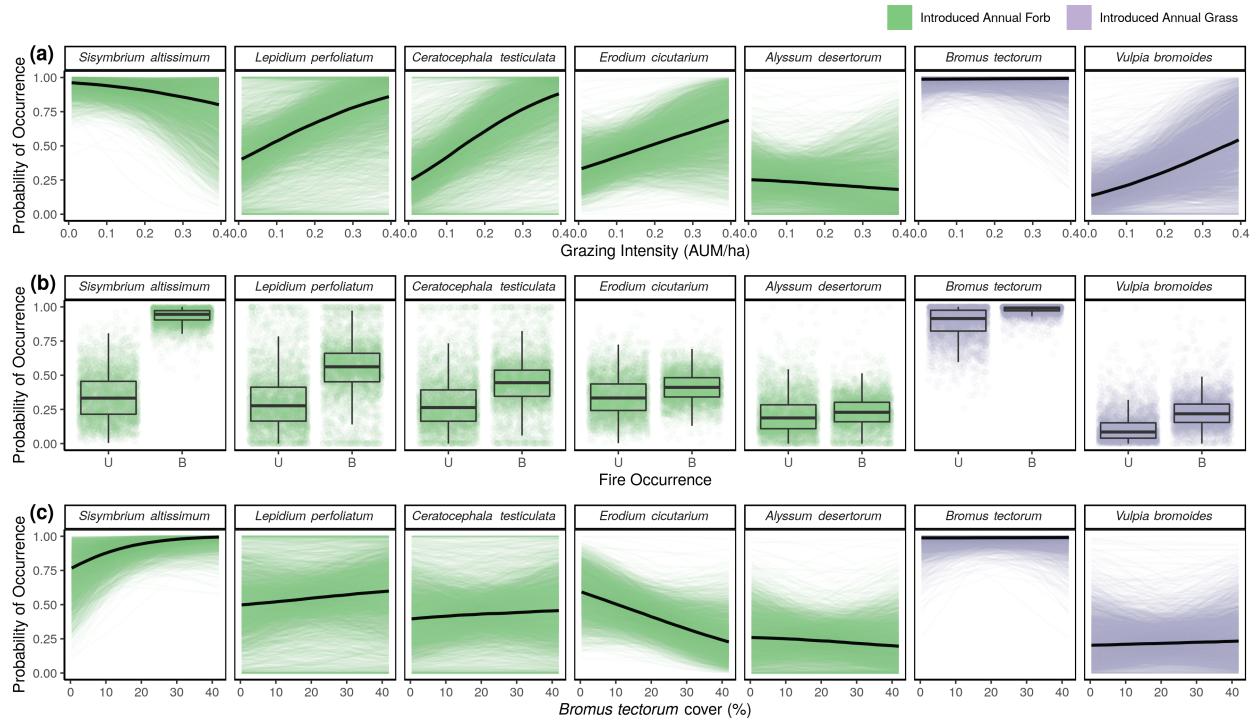


Figure 19: Predicted species occurrence from JSMD on all plots for the seven most prevalent non-native species along gradients of (a) grazing intensity, (b) fire occurrence and (c) *Bromus tectorum* cover. In (a) and (c), each colored line (or point) represents a single posterior sample, and the black line is the mean. In (b), the horizontal bar represents the median and box plots illustrate the quantiles of the distribution. Abbreviations: B = burned; U = unburned.

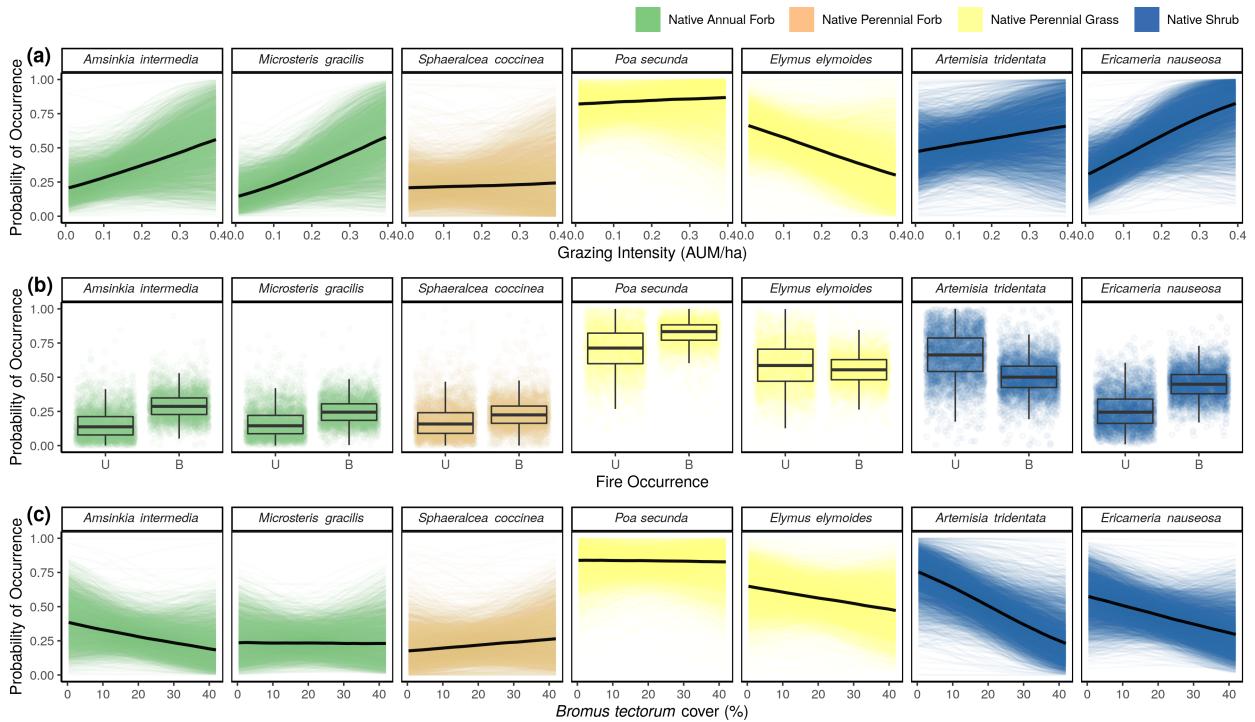


Figure 20: Predicted species occurrence from JSMD on all plots for the seven most prevalent native species along gradients of (a) grazing intensity, (b) fire occurrence and (c) *Bromus tectorum* cover. In (a) and (c), each colored line (or point) represents a single posterior sample, and the black line is the mean. In (b), the horizontal bar represents the median and box plots illustrate the quantiles of the distribution. Abbreviations: B = burned; U = unburned.

increasingly dominated by introduced annual plants as time passed. The lack of any relationship between time since fire and functional group cover or diversity (Figure 15), combined with the negative relationships between time since fire and native species occurrence from the IGAs and JSDMs is indicative of a stable ecological state (Pausas and Bond 2020). Furthermore, we found evidence that both grazing pressure and abundance of *B. tectorum* were key forces for decreasing diversity and maintaining the post-fire species assemblage.

4.2. Hypothesis 2: Long-term grazing pressure and annual grass abundance control community composition

It was surprising that despite clear effects on diversity, and a strong correlation with the IGA gradient, *B. tectorum* abundance did not have a pronounced influence on the occurrence of more individual species. It could be that it acts indirectly through its negative influence on *A. t. wyomingensis* and through neutral or even facilitative effects on other co-dominant annual introduced species. One of the ways in which taller plants often displace ruderal species like *B. tectorum* is by outgrowing and eventually shading out the shorter statured grasses. If *B. tectorum* is inhibiting the establishment of shrubs more generally, it could be negatively affecting native forbs indirectly since shrubs act as sources of shade and provide islands of increased soil moisture and fertility.

Grazing pressure increased the probability of occurrence for four of the five most prevalent introduced annuals that were co-dominant with *B. tectorum* in post-fire environments (Figure 18). While our grazing intensity measure was only a coarse approximation, it still correlated more strongly with the posterior distribution of the IGA than any other single variable and it had the strongest effect sizes for both JSDMs, and it corroborates prior work showing that grazing pressure benefits *B. tectorum* (Williamson et al. 2019). Superficially, the IGAs and JSDMs appear to disagree about grazing. For the IGAs, grazing intensity was associated with more introduced species and more degraded sites, while the JSDMs indicated that grazing intensity mostly had positive effects on both native and introduced species. But the particular species that were positively affected is important to distinguish. Prior work has shown that grazing pressure favors plant species that are annual over perennial, that are shorter statured over taller statured, and that have stoloniferous or

rosette architectures over tussock architectures (Díaz et al. 2007). Here, all of the native species that were positively influenced by grazing in Figure 18 were either shorter-statured (*Phlox longifolia* & *Microsteris gracilis*) or perennials with rosette architectures (*Agoseris* spp.), and one is a resprouting shrub (*Ericameria nauseosa*). The native grass that was negatively influenced, *Elymus elymoides*, has a tussock architecture and is also a key perennial grass for resisting cheatgrass invasion (Booth, Stark, and Caldwell 2003; MacKown et al. 2009). Likewise, the introduced species that were positively affected were all annuals (Figure 19). Here, we likely would not have been able to see *B. tectorum* being influenced by any of the environmental variables in our JSDMs because it occurred at every plot. However, another possible mechanism that could be acting in concert is that high grazing intensity could reduce the abundance of dominant annual grasses, opening up the canopy enough so that forb species can find their niche.

4.3 Fire-year climate effects

The negative correlation of Postfire CWD with the IGA gradient (Figure 17f) suggests that high values of CWD after the fire negatively impact the germination and establishment of the plant species that recolonize after the fire. However the JSDM showed generally positive effects on many native species. Again, which particular species were positively affected may shed light on why. In this case all of the native species except one were perennial. In desert ecosystems, perennial plants have deep, expansive root systems (Gibbens and Lenz 2001; Ottaviani et al. 2020). *B. tectorum* and other annual grasses are known to have shallow root systems [30 cm for *B. tectorum*; Klemmendson and Smith (1964); Cline, Uresk, and Rickard (1977)], and to be highly sensitive to interannual variability in water availability (Prevéy and Seastedt 2015). Higher CWD immediately after the fire may reduce the abundance of introduced annuals (David S. Pilliod, Welty, and Arkle 2017; Boyte, Wylie, and Major 2019), and by extension the density of their shallow root systems, during the critical period in which the seeds of native plants are germinating and developing their root systems. Once the introduced annuals inevitably achieve dominance, the root systems of the native perennials are deep enough to be stratified below most annual root systems, avoiding competition for soil water with *B. tectorum* and other introduced annuals.

Prefire AET being negatively correlated with the IGA gradient suggests that increased water

availability in the months leading up to a fire leads to higher and more spatially continuous fine fuel loads (K. W. Davies and Nafus 2013). This leads to fires that burn more contiguously with fewer unburned patches, and thus fire-intolerant plants are less likely to avoid mortality by fire. This idea was corroborated by the JSDM, which had negative effects for all 5 plant species that had strong evidence of environmental filtering from prefire AET. Prefire T_{min} being positively correlated with the IGA gradient, and with mostly positive effects on native forbs from the JSDM, could indicate that an earlier onset of warmer spring temperatures leads to a longer period of growth before the fire season, giving native plants more time to reach reproductive maturity and produce more seeds, and thus more propagules would be available for recolonization post-fire.

Climate projections for the late 21st century for the western US indicate that there will be higher temperatures across all drylands (Bradford et al. 2020). The projections for mean annual precipitation are geographically mixed (Bradford et al. 2020), with generally fewer precipitation events, but with more precipitation per event (Polade et al. 2014). For the cold desert areas studied here, winter soil water availability is projected to remain the same or increase, while the temperature on the hottest, driest days is predicted to increase (Bradford et al. 2020). This means there will be likely be more wet winters that will stimulate fine fuel growth from annual plants followed by hot, dry summers that will encourage large fires and negatively impact sagebrush recovery after fire. These regional climatic changes will be exacerbated locally because the loss of shrubs and subsequent dominance by annuals has been shown to have major ecohydrological consequences, including higher soil temperatures and evaporation, leading to dryer microclimates and more drought stress for re-establishing native plants (Wilcox et al. 2012; Turnbull et al. 2012).

In addition to external drivers, there are intraspecific dynamics at play in each species. Allee effects (C. M. Taylor and Hastings 2005) may cause low or even negative growth rates at low population densities. In long-lived species like *A. tridentata* the changing of the population's age structure can lead to slow population growth or even population declines as the population transitions between being composed mostly of high-mortality seedlings to high-fecundity, low-mortality adults (Shriver et al. 2019). These transient dynamics are exacerbated by lower water availability, since lower water availability suppresses growth rates of individual plants (Shriver et al. 2019).

4.4 Management Implications

Low-elevation areas that have already lost their shrub cover and are dominated by introduced annuals are not likely to see the return of woody plant cover, and the associated carbon sequestration, even after decades of fire exclusion. The return of the native shrubland community will likely require active restoration. These lower elevation sites are extensive (K. W. Davies et al. 2011), and have been notoriously difficult to restore (Knutson et al. 2014). Determining a successful approach that could restore shrub cover could be widely impactful for both carbon sequestration and reducing fire risk. Our results suggest that some native species can successfully tolerate fire and grazing pressure (Figure 20). Including resprouting, fire- and grazing-tolerant shrubs like *E. nauseosa* in initial restoration efforts would provide structural heterogeneity, aboveground carbon storage and islands of soil fertility more rapidly than only seeding in *A. tridentata* which often takes 30+ years to reach meaningful cover (Harniss and Murray 1973), but more often fails to establish (Shriver et al. 2019). Targeted grazing treatments may be effective in temporarily reducing annual grass cover (K. W. Davies et al. 2010; Williamson et al. 2019). Seeding in resprouting, fire- and grazing-tolerant shrubs with short-statured native forbs and focusing grazing on those sites for a few years after the initial seeding may allow for shrubs and forbs to establish and at the expense of invasive plant cover. In subsequent rounds of seeding or live planting, more diverse species mixtures accompanied by seed obligate shrub species could be used, with already established shrubs acting as nurse plants, providing critically important shade and protection from grazers (Padilla and Pugnaire 2006; Montesinos-Navarro et al. 2017).

It is already well-established that antecedent climatic conditions are predictive of fire activity (Abatzoglou 2013). The fact that antecedent climatic conditions may also be predictive of which species will gain a foothold and persist may be advantageous in that land managers would have lead time to use that information to prepare for restoration efforts in concert with preparations for the fire season. Further research is needed on which prefire climatic variables encourage or discourage which species or which functional traits. Increased understanding in this area could allow for the selection of species for seed mixtures that are tailored to the current year climatic conditions.

Acknowledgements

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Chapter 4. Cover-based allometric estimate of aboveground biomass of a non-native, invasive annual grass (*Bromus tectorum* L.) in the Great Basin, USA

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Abstract

Cheatgrass (*Bromus tectorum* L.) presence in the Great Basin is associated with an increase in fire frequency and size, likely due to increased spatial continuity of fine fuel biomass. Measurements of the extent and cover of cheatgrass steadily are improving, but the strength of the correlation between cover and aboveground biomass (AGB) is unclear. A reliable relationship between cover and AGB of cheatgrass would allow for improved incorporation of regional estimates of cover into models of fire activity, carbon storage, and net primary productivity, all of which rely on biomass. We measured cover and AGB of cheatgrass at 60 locations in the north-central Great Basin and used these measurements to model the relationship. We also explored the effects of sample aggregation on this relationship with samples from 320 additional locations in the central, northern, western, and eastern Great Basin. We found a strong linear relationship ($b = 6.94$; pseudo $R^2 = 0.81$) between percent cover and AGB. These results show that cheatgrass cover can reliably predict AGB. Given

the strong, linear relationship between cover and biomass for this annual grass, it is likely that allometric equations based on cover will also apply to other grass species.

1. Introduction

The aboveground biomass (AGB) of plants is an important ecological property and a key indicator of how terrestrial ecosystem function responds to global change. Invasions of non-native grasses have altered the abundance and spatial distribution of AGB in many areas across the United States (Fusco et al. 2019) and other parts of the world (G. Miller et al. 2010; Milton 2004; Setterfield et al. 2010). This can lead to the modification of fire activity, often leading to loss of human life and property, substantial financial costs, and loss of ecosystem function (Brooks et al. 2004; D'Antonio and Vitousek 1992). One of the most well-documented examples of a fire-prone, non-native grass is cheatgrass (*Bromus tectorum* L.). Cheatgrass has colonized much of the western United States, and is particularly damaging in the Great Basin. In the Great Basin, cheatgrass increases the horizontal fuel continuity such that fire spreads through colonized landscapes more readily than through native, perennial-dominated landscapes (K. W. Davies and Nafus 2013). As a result, in areas dominated by cheatgrass, fires are twice as likely to occur and to become much larger than in the native vegetation (Jennifer K. Balch et al. 2013; Bradley et al. 2018). This has disrupted ecosystem functioning (Turnbull et al. 2012; Wilcox et al. 2012) and led to a loss of biodiversity (Mahood and Balch 2019).

Cover is a measure of abundance that is much faster to measure than AGB and does not require destructive sampling. Cover of cheatgrass has been modeled throughout the Great Basin (Boyte, Wylie, and Major 2019; Boyte and Wylie 2016; Bradley et al. 2018, 2006; Peterson 2005). However, AGB is a more directly informative ecological property than cover, a more accurate proxy of carbon storage and net primary productivity than cover, and necessary for modeling fire occurrence (Hantson et al. 2016; David S. Pilliod, Welty, and Arkle 2017) and emissions (Kennedy et al. 2020). Nevertheless, the relationship between cover and AGB of cheatgrass remains largely unexplored.

Annual estimates of cheatgrass cover at regional extents have been derived from remotely sensed images (e.g., Peterson 2005; Bradley et al. 2006, 2018; Boyte and Wylie 2016; Boyte, Wylie, and Major 2019). The accuracy and spatial and temporal resolution of these estimates is increasing

consistently. For example, Boyte, Wylie, and Major (2019) modeled cheatgrass cover across the Great Basin at 250 m resolution with a mean absolute error of 12.6%. These approaches (Peterson 2005; Bradley et al. 2006, 2018; Boyte and Wylie 2016) suggest that regional estimates of cheatgrass cover can be derived from remotely sensed data in near real time (Boyte, Wylie, and Major 2019). If these models of cover could be reliably converted to AGB with an allometric equation, fire risk assessment could be improved, and the outputs of these models could more easily transfer to models of net primary productivity and carbon storage, and perhaps be integrated into global dynamic vegetation models.

The main question about the relationship between AGB and cover is whether it is linear or exponential. For many species of herbaceous plants, when cover is low, the relationship appears to be linear (Axmanová et al. 2012; Chieppa et al. 2020; Flombaum and Sala 2007; Muukkonen et al. 2006). As cover approaches 100%, the relationship can become asymptotic (Figure 21) while AGB increases linearly (Axmanová et al. 2012; Marushia and Allen 2011). This behavior is more likely when plant height varies considerably, creating a complex canopy with many layers, which is more likely to occur when there are many species, or perennial plants of different ages. Species-specific allometric equations may be more accurate than allometric equations for functional groups or for total cover of all species (Chieppa et al. 2020). Annual plants, in particular, are more likely to grow to similar heights and have a simple canopy. In our case, cheatgrass often occurs in a near monoculture, with a single canopy layer. Therefore, the AGB to cover relationship may remain linear even as cover approaches 100%.

One possible confounding factor in the relationship between cover and AGB is the response of annual plants to interannual climatic variations. Annual plants in the Great Basin, especially cheatgrass, are highly responsive to precipitation, aridity, and temperature (Larson, Lehnhoff, and Rew 2017; Mangla, Sheley, and James 2011). Not only is the abundance of cheatgrass responsive to interannual variation, but the specific leaf area, or leaf area per unit biomass, can vary as a function of moisture availability (Butterfield et al. 2017; Fernández and Reynolds 2000; Poulin et al. 2007; Sandel and Low 2019; Tardella et al. 2017). If the relationship between cover and AGB is highly variable among years, predicting AGB as a function of cover may require accounting for functional trait response to interannual climate variability.

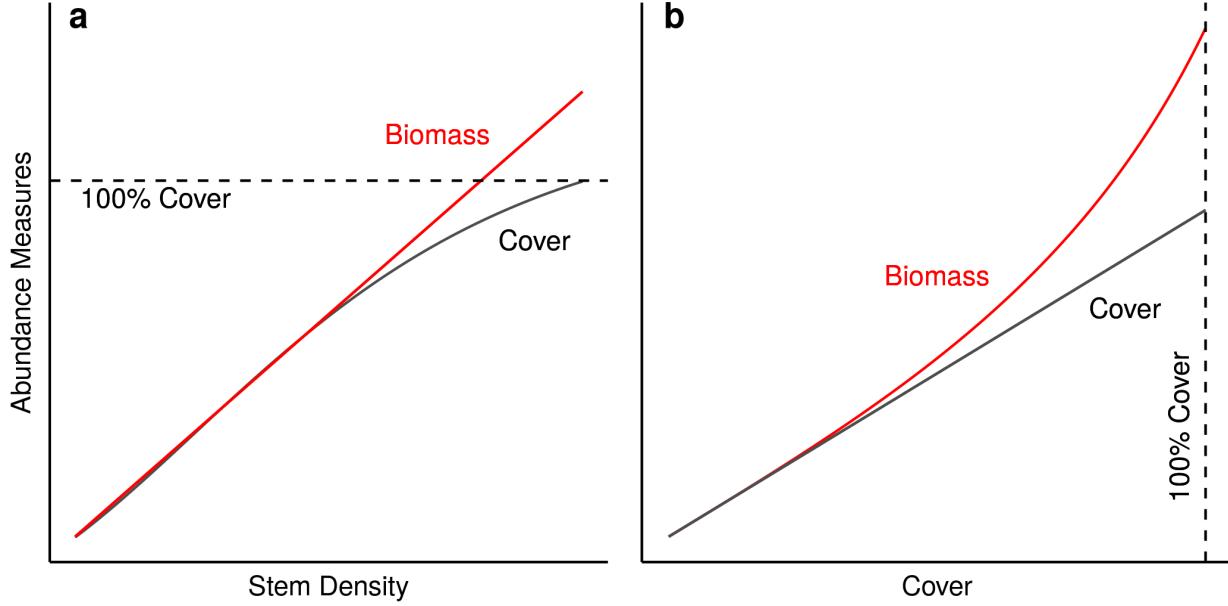


Figure 21: The saturation effect, where aboveground biomass increases linearly with stem density, but cover becomes asymptotic as it approaches 100 percent (panel a), and the expected appearance of the cover to biomass relationship with this effect (panel b). This relationship would lead to greater inherent sampling error at higher values of cover.

Here, we sampled cover and AGB of cheatgrass, and modeled the relationship, at 380 locations across the Great Basin from 2016-2019. We hypothesized that at low cover values, the relationship between cover and biomass is linear, but could become non-linear at high cover values if high cover also relates to greater height. We also examined the effect of sample size and aggregation on estimates of AGB. At 60 locations, we aggregated samples from 1 m^2 quadrats to represent cover at the level of 30-50 m transects. At 320 locations, we collected and processed samples at the level of the individual 1 m^2 quadrat to represent the full range of cover values.

2. Methods

We used two sampling methods to measure cover and AGB of cheatgrass. The first method aimed to capture the variation of cover and AGB approximating the scale of a Landsat pixel by measuring cover using ocular estimates and clipping all standing cheatgrass biomass in multiple 0.1 m^2 quadrats along 30-50 m transects. Cover data were averaged and biomass aggregated for this method (hereafter, transect-level). The second method aimed to encompass the full range of possible

cover values up to 100% by measuring cover using ocular estimates in individual 1 m² quadrats, and clipping a 0.1 m² subset that appeared to be representative of the 1 m² quadrat (hereafter, quadrat-level). We dried all biomass samples at 60° C and weighed them when the mass stabilized.

2.1 Transect-level sampling design

We implemented two different designs for sampling along transects. In June 2016, we sampled cheatgrass at its peak AGB at 20 locations in the north-central Great Basin (Figure 22). We selected locations after reviewing fire and soil maps from the US Bureau of Land Management (BLM) and consulting with land managers from the BLM's Winnemucca Field Office. The slopes (0-5%) and elevations (1297-1607 m) of the locations were similar, and locations were separated by at least 1.5 km. Eleven locations were dominated by sagebrush (*Artemesia tridentata*). Cheatgrass cover in the understory of six of these sites was <5%. Native shrubs were not present in nine sites, which instead were dominated by cheatgrass (>5% cover) and annual forbs. Permitted levels of livestock grazing in summer and autumn were similar among locations.

At each location, we established three pairs of parallel, 50-m transects separated by 20 m. We sampled 0.1 m² quadrats every 5 m along each transect, for a total of 60 transects each composed of 22 quadrats measurements of cover (averaged for each transect) and biomass (aggregated for each transect).

In the first week of July in 2017 and 2018, and in September 2019, we sampled 40 locations in the north-central Great Basin (Figure 22). Sampling in 2017 and 2018 coincided with peak AGB of cheatgrass. Sampling in 2019 followed senescence and seed dispersal. Half of the sites were dominated by sagebrush and half were dominated by cheatgrass and annual forbs. Elevations ranged from 1200-1700 m, and all locations had a history of livestock grazing. At each location, we established one 30-m transect with five 0.1 m² quadrats randomly located along the transect. In 2017-2018, we averaged cover and aggregated biomass across the five quadrats to calculate transect-level cover and biomass. For locations sampled in 2019, we recorded cover and AGB from each quadrat separately. This allowed us to evaluate whether aggregation affected the relationship between AGB and cover.

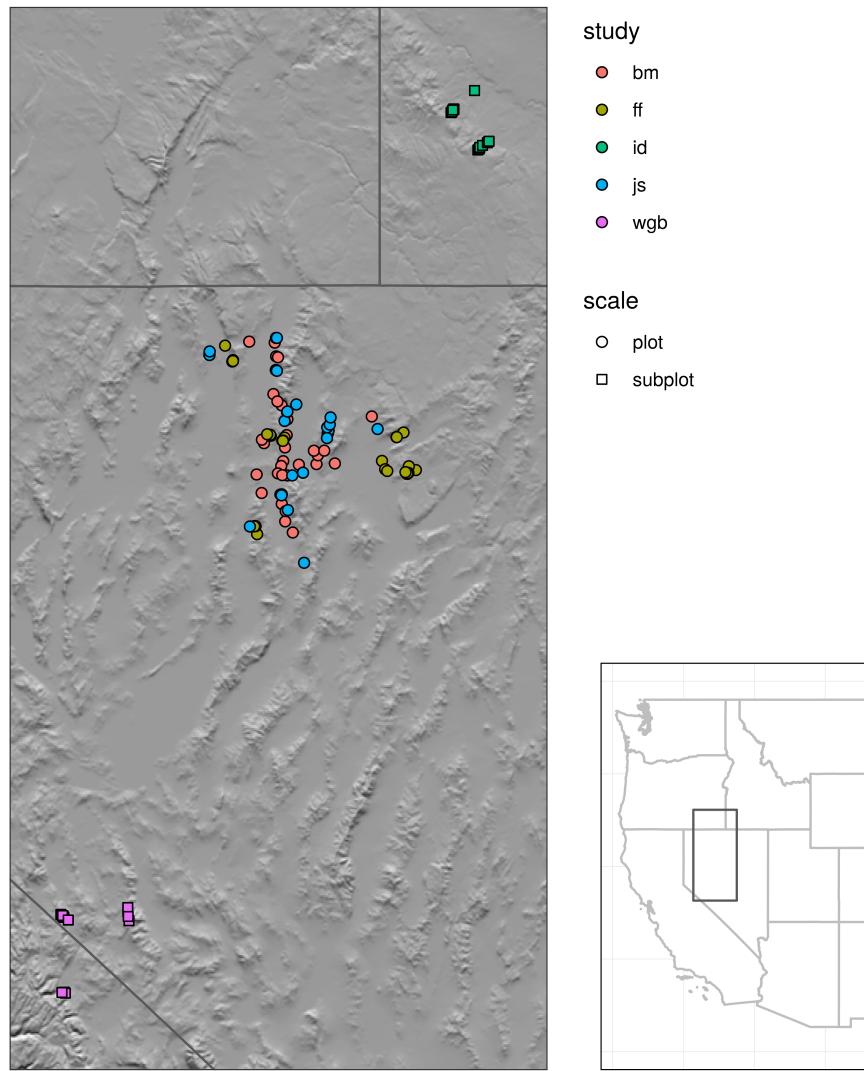


Figure 22: Study area and sampling sites. Circles represent the locations of 1m² quadrat-level samples, which were collected from 2016-2019. Squares represent the locations of transect-level samples collected from 2016-2019. T (note that the same transect sites were resampled from 2017-2019).

2.2 Quadrat-level sampling design

We sampled quadrats at 90 locations in the northern Great Basin (Owyhee County, Idaho; 30 in late June and early July 2016, 20 in late June and early-mid July 2017, and 40 in June 2018), 33 locations in the eastern Great Basin (Tooele County, Utah) in June 2017, 90 locations in the central Great Basin (Lander, Nye, and Eureka Counties, Nevada; 40 in June and early July 2018 and 50 in June and early July 2019), and 124 locations in the western Great Basin (Mono and Alpine Counties, California and Mineral, Lyon, and Douglas Counties, Nevada; 50 in June-August 2016, 34 in June 2017, and 40 in June-July 2018; Figure 22). Many locations were tens of km apart (e.g., some locations in the central Great Basin were 90 km apart).

2.3 Statistical Modeling

We used linear models to estimate the relationship between percent cover and AGB from the transect-level samples collected at peak AGB (June 2016, July 2017, and July 2018). First, we created a set of ordinary least squares (OLS) models, each with data from one year, and another OLS model with the data from all three years. Cover was the predictor and AGB was the dependent variable. Next, we created a linear mixed model using the data from all three years with the year of sampling as a random effect, a random slope, and the intercept fixed at zero. To determine if this mixed model was a better fit than the simple OLS model with all of the years aggregated, we compared the models with Akaike's Information Criterion (AIC) and selected the mixed model if its AIC was lower than that of the OLS model by more than two (Burnham and Anderson 2002).

To evaluate whether aggregating the AGB collected in individual quadrats affected the relationship between percent cover and AGB, we aggregated the data collected in September 2019 by location, and created separate OLS models with the aggregated and unaggregated data. Because the two OLS models were not nested, we compared them by examining R^2 and standard errors of the coefficients.

We also created linear models from the samples collected at the quadrat level, but the coefficients appeared to be unrealistically low, and many models did not pass diagnostic tests, even when restricted to low cover values (Figure 23). Exponential and non-linear models had similar problems. There are at least three possible reasons for this. First, samples were not consistently

collected at peak biomass. Second, estimating cover at 1 m² while collecting AGB in a 0.1 m² subset of that square meter led to high levels of sampling error due to heterogeneity within the 1 m² quadrat. Third, as indicated in an exploratory analysis in which we included the identity of the observer as a random effect in a mixed model, there was strong among-observer variation in cover estimates. Therefore, we were concerned that these data were not reliable, and excluded them from the final estimation of the relationship between biomass and cover.

Data and code to reproduce the analysis is at http://www.github.com/admahood/cg_biomass.

3. Results

We found statistically significant, linear relationships between percent cover and AGB of cheatgrass. For transect-level samples collected from 2016-2019, coefficients ranged from 3.1-8 g m⁻² per 1% cover (Figure 24). However, because the 2019 sample was collected in September, cheatgrass seeds already had shed, and so the model does not represent the relationship at peak AGB. Accordingly, we used our transect-level measurements from 2016-2018 to estimate the allometric equation for calculating AGB from cover at peak biomass. The linear mixed model we used to estimate this relationship had a pseudo R² value of 0.81 (Figure 25). The allometric equation we estimated was:

$$AGB(gm^{-2}) = 6.94(\pm 0.5) * cover(\%)$$

For our comparison of aggregated versus unaggregated samples, the coefficients were the same, but the variance explained was somewhat greater when samples were aggregated by transects ($R^2 = 0.89$, $p < 0.05$) than when samples were not aggregated ($R^2 = 0.84$, $p < 0.05$; Figure 25).

For the samples collected at the quadrat level, we also found significant relationships between cover and AGB of cheatgrass in all cases. However, although in some cases the linear models fit well, in most cases the models did not pass diagnostic tests for homoscedasticity or normally distributed residuals. In addition, the estimated coefficients were much lower, ranging from 0.95 - 3.1 across years and locations, (Figure 23) and variance explained was lower (overall $R^2 = 0.57$). Nevertheless, there is some visual evidence of a saturation effect (higher than expected biomass at high cover values; Figure 21), with more outliers at high cover values (e.g., Figure 23g).

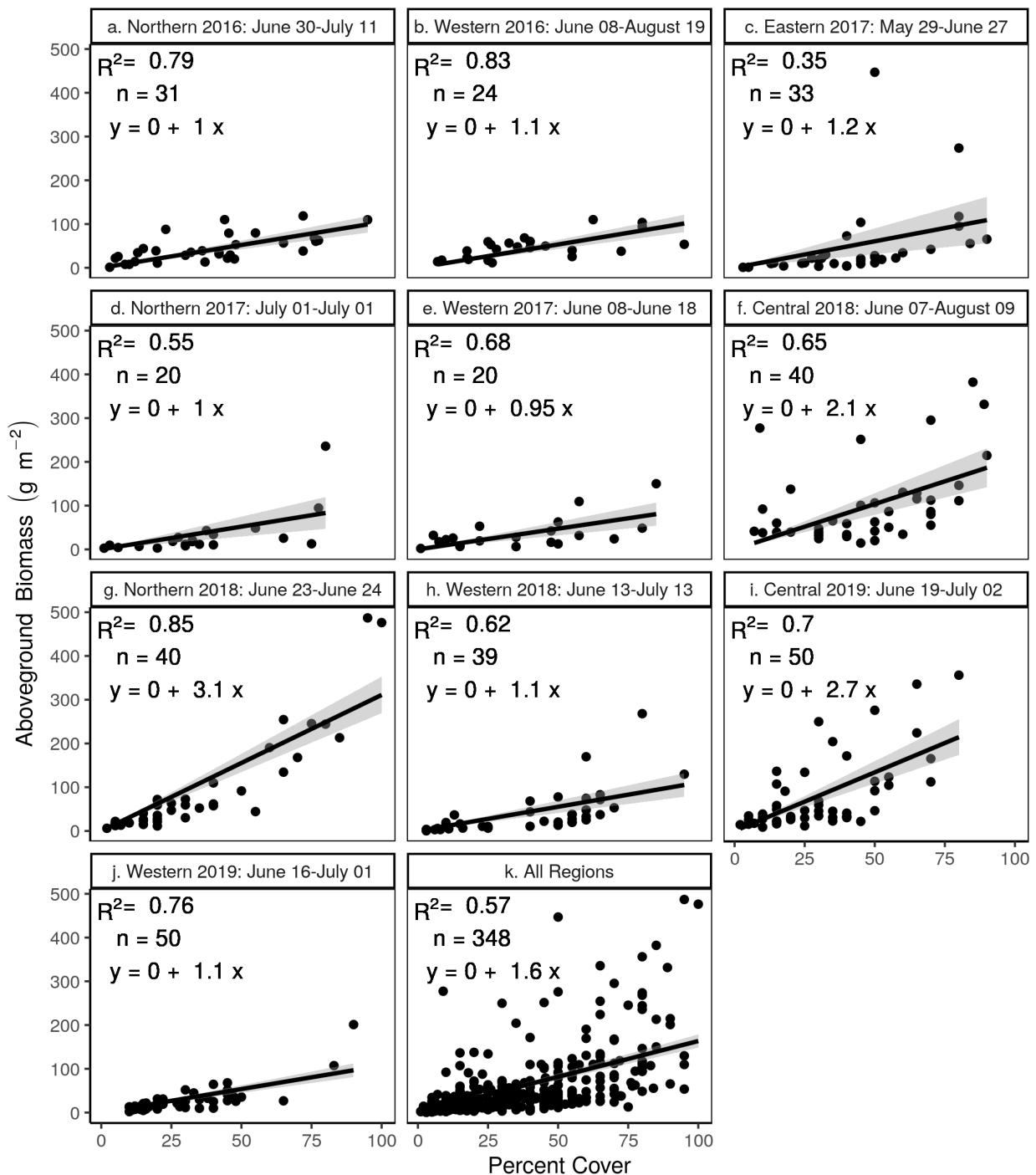


Figure 23: Aboveground biomass collected within 0.1 m^2 of a 1 m^2 quadrat within which we estimated percent cover. All relationships were statistically significant ($p < 0.05$). Samples captured the full gradient of percent cover. The lower coefficients may reflect the difficulty of collecting a representative sample of biomass within 1 m^2 given the high spatial heterogeneity of biomass at that resolution.

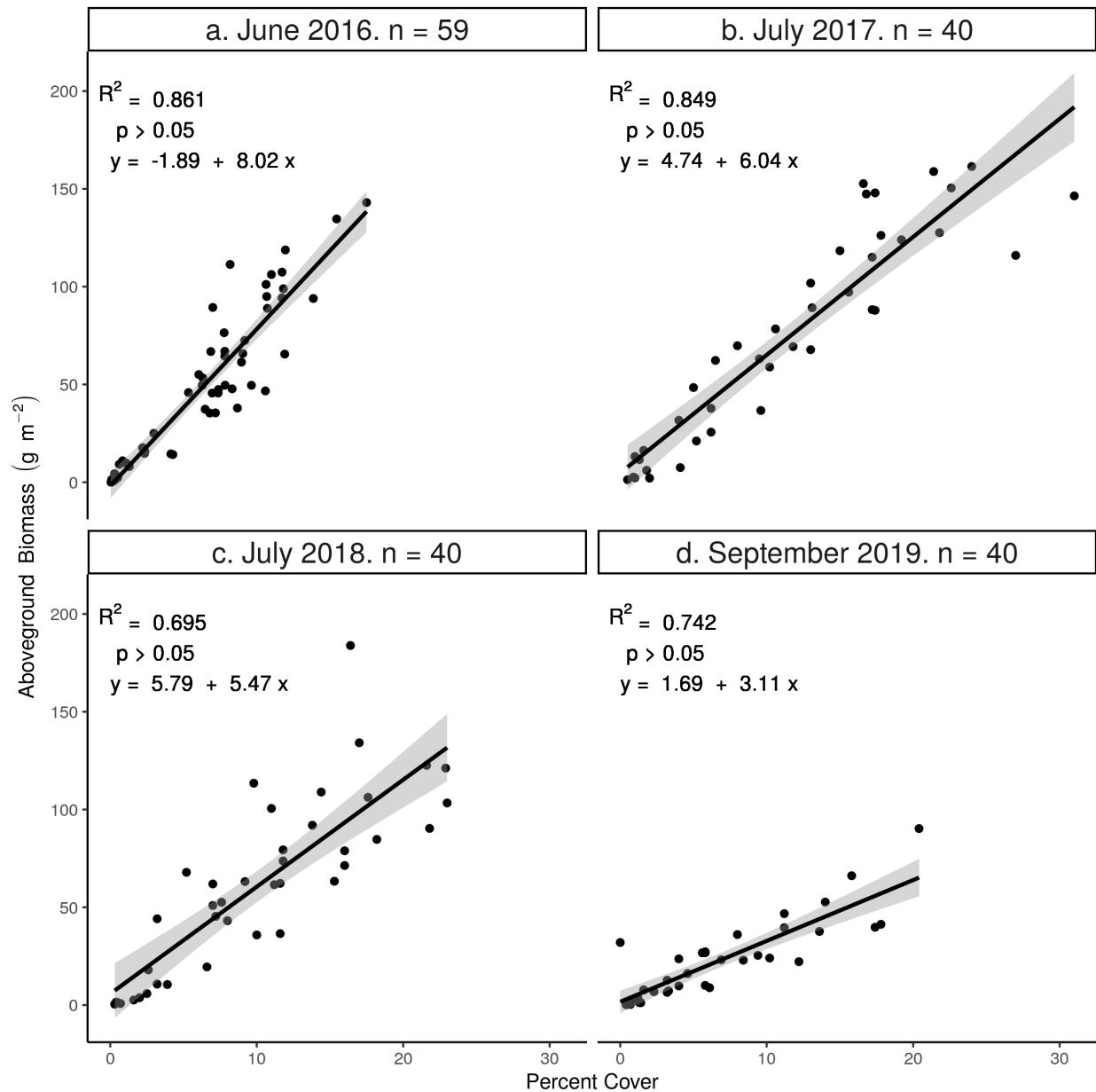


Figure 24: Percent cover and aboveground biomass of cheatgrass were linearly related. Lines are estimates from ordinary least squares regression models. The shaded area is the 95% confidence interval. Data in 2016-2018 were collected at peak AGB. Data in 2019 were collected in September, which was at the end of the growing season and well past peak AGB.

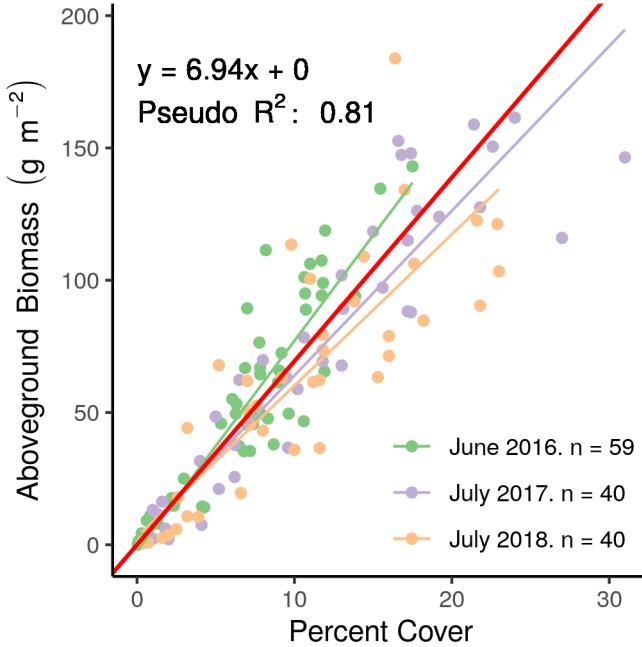


Figure 25: Results of a linear mixed model with random slopes and intercepts for the three years of transect-level data collected at peak biomass. Finer lines are the predicted values grouped by year. The bold red line is the overall relationship.

4. Discussion

The relationship between AGB and cover of cheatgrass appeared to be linear and quite strong at the transect level, where all cover values were less than 40% (Figures 3 and 4). Our allometric equation of a 6.94 g m⁻² increase in AGB for a 1% increase in cover is similar to the equations estimated by Chieppa et al. (2020) for short-lived grasses (6.06) and long-lived grasses (6.54).

We found suggestive evidence that biomass continued to increase as cover values approached 100% (e.g Figure 23g). However, our inferences from those data are tentative for the reasons outlined above (see Methods). Biomass may increase as cover saturates, leading to higher sampling error at higher cover values (as in Boyte, Wylie, and Major 2019). However, because cheatgrass cover rarely exceeds 50% at the resolution of a 30m Landsat pixel, even where it grows in dense monocultures (Boyte, Wylie, and Major 2019), this phenomenon may not be problematic for regional biomass modelling for most areas.

Despite high variability in cover among years (Bradley et al. 2006), the relationship between cover and AGB at the time of peak biomass appears to be relatively stable. However, because our

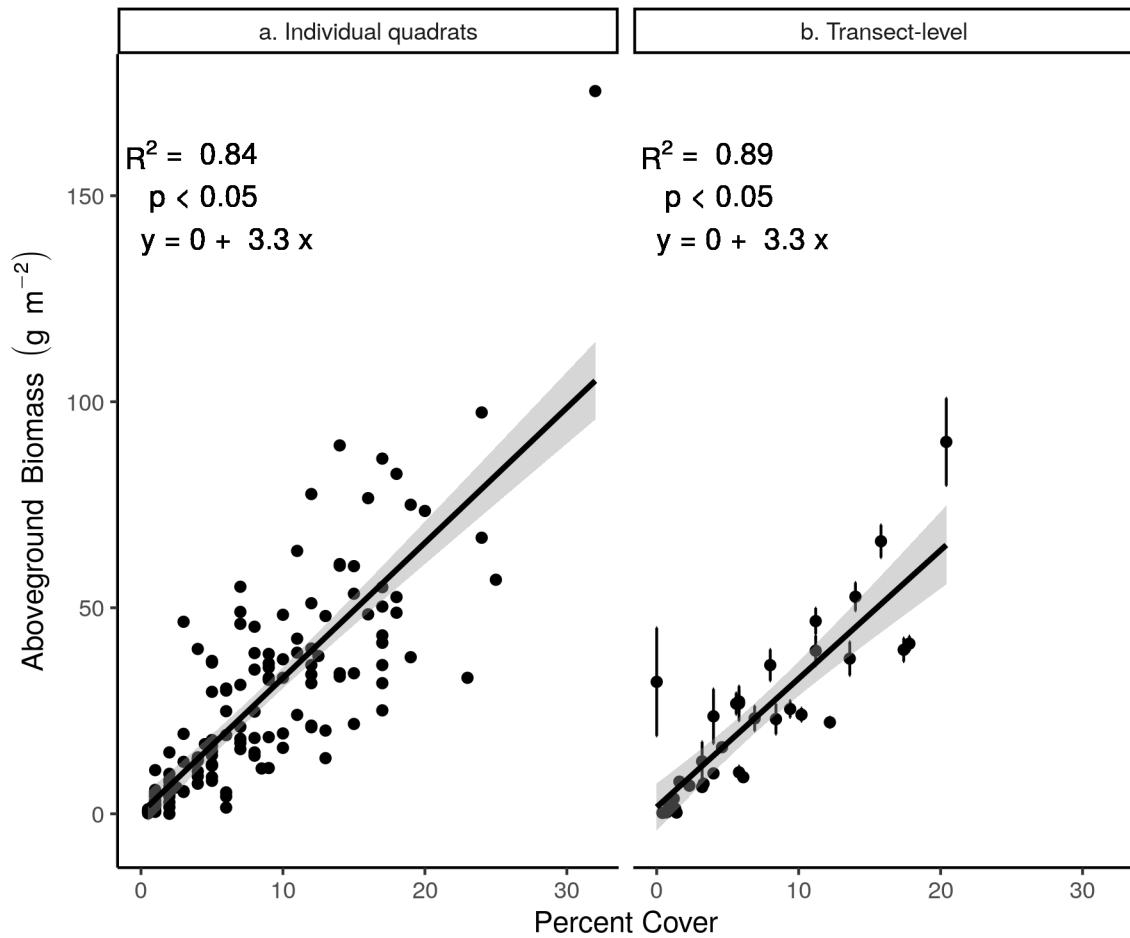


Figure 26: The effect of sample aggregation on the relationship between cover and AGB of cheatgrass for samples collected in September 2019. In panel a, each point represents the cover and AGB measured within a single 0.1 m^2 quadrat. In panel b, each point represents the mean percent cover and AGB of five 0.1 m^2 samples collected along each 30 m transect. The shaded areas represent 95% confidence intervals. Vertical lines in panel b represent the 95% confidence interval of the mean. The model that was based on the aggregated data had the same coefficient, but explained more variation.

random effects model explained more variation than a global OLS model, there may still be subtle interannual differences in the relationship. The model could be made more universally applicable by accounting for the drivers of these differences. One such driver may be intraspecific variation in plant functional traits. These traits vary spatially along topographic and moisture gradients [measured as soil moisture, supplemental watering, climatic water deficit, topographic position, and precipitation, respectively; Butterfield et al. (2017); Fernández and Reynolds (2000); Poulin et al. (2007); Sandel and Low (2019); Tardella et al. (2017)], and temporally throughout the growing season (Svejcar 1990). If one considers percent cover to be a function of leaf area, then the relationship between AGB and percent cover would be a function of specific leaf area (SLA; leaf area divided by leaf dry mass). SLA and leaf area can vary among individuals of the same species, and within and among communities. If SLA is higher, a given cover value would predict a lower AGB value, so the cover to AGB coefficient would be lower.

Cheatgrass SLA has been documented to be higher at lower elevations (Ziska, Reeves, and Blank 2005), and SLA within individual cheatgrass plants reaches a maximum at peak biomass and then declines as the growing season progresses (Svejcar 1990). We explored the first effect by extracting elevation from a 10m digital elevation model at each transect-level sampling location and adding it to our transect-level model from Figure 25. We found that elevation was not statistically significant. With respect to the second effect, we found that the coefficient of the cover to biomass relationship was lower in samples collected later in the growing season (Figure 24d) than at peak biomass (Figure 24a-c), the opposite of what one would expect if SLA was the principal driver of changes in the cover-biomass relationship as the growing season progresses. Rather, this variation is likely to be more strongly influenced by seed shedding.

The SLA values of grass species in general have also been observed to be sensitive to interannual variation in precipitation. As precipitation increases, SLA tends to increase (Butterfield et al. 2017; Fernández and Reynolds 2000; Poulin et al. 2007; Sandel and Low 2019; Tardella et al. 2017). Therefore, one would expect a higher slope of the cover to AGB relationship in dry years. However, we detected only slight (but not negligible) interannual differences in the coefficients for samples collected at peak biomass (Figures 3 and 4). The discrepancy between the documented variation in SLA in other studies and our results might be due to differences among species in strategies for

surviving drought. Cheatgrass mitigates the effects of seasonal drought by germinating in early spring as soon as moisture is available and completing its life cycle before soil moisture decreases, and atmospheric vapor pressure deficit increases, during summer. Perennial grasses, in contrast, must allocate fewer resources to aboveground growth during the period when moisture availability is high, and more to underground carbon storage to survive the summer drought. These differences in resource allocation strategies may explain why the SLA of cheatgrass, unlike the SLA of other grasses, does not appear to be sensitive to precipitation.

Height may be another confounding factor, especially at high values of cover. Estimating AGB as cover approaches 100% is challenging because plant height still can increase after canopy cover reaches a maximum. One could incorporate vegetation height into a model of AGB, but several of the largest existing sets of training data, which include tens of thousands of data points, do not include measurements of height (see Boyte, Wylie, and Major 2019). Models of canopy height derived from remote sensing typically focus on tree or shrub cover (Alonzo et al. 2018; Narine et al. 2019). Annual grass height is much more difficult to model with satellite remote sensing. Therefore, there are trade-offs between increases in model accuracy and the prompt availability of data. It may be possible to model cheatgrass height on the basis of topography and current year climate, and incorporate those values into models of AGB. These concerns may be moot, however, given that Chieppa et al. (2020) found no improvement in model accuracy when they added height to models of AGB predicted by cover for grass species.

Several other annual grass species have become dominant in other areas of the western United States. These include various species of *Bromus* and *Avena* throughout California, red brome (*Bromus rubens* L.) in the Mojave Desert, and Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) in the northern Great Basin. Like cheatgrass, these species generally have a simple, single-layer canopy. We believe that AGB of these species likely also could be estimated from allometric equations based on cover. Differences among species in, for example, SLA, height, and seed mass may prevent application of the identical equation. However, we believe that a linear allometric equation between biomass and cover is likely to be consistently applicable, and that it may be possible to apply allometric equations within functional groups more generally.

5. Acknowledgements

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Conclusion

Synopsis

Our research was guided by two overarching questions. Our first question asked whether the post-fire annual grassland is an alternative stable state. Rather than setting up manipulative experiments designed to detect the classic hysteresis S-shaped curve (Schmitz 2004), we used an observational approach designed to measure the components of hypothesized self-reinforcing feedback loops at sites distributed across a broad region. Evidence of stabilizing feedbacks would suggest the occurrence of hysteresis, and one might even argue it is even better evidence, since here we're looking at the physical mechanisms that would cause hysteresis. In each case, we found evidence that vegetation had stabilizing feedbacks with fire (chapter 1), soil nutrients (chapter 2), cheatgrass cover (chapter 3) and cattle grazing (chapter 3).

Our second question asked what impacts the conversion to annual grassland has on ecosystem function. Because we found evidence of self-reinforcing feedbacks, this question is tightly interwoven with the first, since the impacts of vegetation change may also be the drivers that maintain the stability of the new state. Nevertheless, We found evidence in chapter 2 that the conversion to annual grass dominance from perennial grass and shrub dominance transformed soil C and N cycling, from net nutrient storage to net nutrient loss.

Synthesis

Evidence for an alternative stable state

The first three chapters of this dissertation provide evidence of multiple redundant, and sometimes synergistic, self-reinforcing mechanisms that maintain the annual grassland as an alternative stable state after fire in low elevation Wyoming big sagebrush ecosystems. Fire initiates the alternate state through impacts on aboveground (Chapter 3) and seed-bank (Chapter 1) species composition that favor non-native annuals. After fire has removed the shrub canopy, annual grass dominance transforms the pathways through which carbon, nitrogen and other soil nutrients travel, leading to long-term soil degradation and loss of fertility islands (Chapter 2). Annual grass invasion also decreases biodiversity and the occurrence of sagebrush (Chapter 3). The loss of aboveground

biodiversity may limit the capacity of the system to recover its structural diversity over time. The persistent loss of the shrub canopy and perennial plant cover represents a loss of aboveground structural diversity, while the loss of soil fertility islands represents a loss of belowground structural diversity. The loss of aboveground and belowground structural diversity results in decreased niche diversity and compartmentalization. In this novel environment, native species must compete directly against fast-growing annual grasses for moisture in order to reestablish — a difficult task. Native species that could compete against introduced annuals, like *Elymus elymoides*, are suppressed by long-term grazing pressure (Chapter 3).

Carbon accounting considerations

These results also have important implications for carbon accounting. In chapter two we made the case that the change in functional group composition from perennial grasses to annual grasses after fire reverses an important pathway that carbon travels within the ecosystem. The likely mechanism for this is that perennial grasses store carbon in their deep root systems, and those root systems persist, alive, underground even when the plant is dormant. Annual grasses grow, reproduce and die in a single growing season. As a consequence, much of the carbon in their tissues, besides that which is stored in produce seeds, is deposited as litter and eventually respired through decomposition. Thus estimates of biomass from cover (Chapter 4) may be combined with estimates of the fraction of tissue that is respired to contribute to estimations of long-term carbon loss that results from conversion to annual grasslands. Another key result from chapter two is that there is substantive interannual variability in plant tissue carbon concentrations within and among species (estimated marginal means 38%-45%, Chapter 2, Figure 11). Other efforts to estimate carbon from aboveground herbaceous biomass set the percentage of carbon as a constant (47%, M. O. Jones et al. 2018; Robinson et al. 2019). These findings present an opportunity to improve those estimates.

Interannual variability must be accounted for

An often overlooked driver of ecosystem function that is especially important in arid regions is interannual climate variability (Werner et al. 2020). Not only can interannual climate variability obscure the effects of invasion, fire and other disturbances on ecosystem processes, it is also a crucial consideration for ecosystem restoration applications (Hardegree et al. 2018). We found in chapter

two that there are large changes from year to year in soil and plant nutrients, for every variable that we measured. We found in chapter three that climate during the year of the fire had lasting effects on the occurrence of many different species. Taken together, this implies that the effects of fire on ecosystem recovery depends substantially on antecedent and contemporary climate. Years where climate causes depleted soil nutrient content may hamper the ability of native or introduced species to germinate and establish. Fires that occur after several successive years where perennials are not able to add to their belowground carbon stocks may result in a decreased capacity to compete with invasive annuals. This work highlights the long-recognized need for long-term monitoring of ecological systems. Capturing the range of interannual variability will allow for the comparison of trajectories of change rather than comparing annual snapshots.

Management implications

In chapter two we found that soil fertility islands may be lost after fire removes the shrub canopy. Desert ecosystems are often dependent upon this type of heterogeneous distribution of resources, and so effective restoration may require restoring the heterogeneous shrub and shrub interspace structure. We found that some native resprouting shrubs and short-statured forbs were tolerant of grazing, as predicted by theory (Díaz et al. 2007, Chapter 3). These species could be used as resource island pioneers, and as nurse plants to aid in the establishment of perennial grasses and keystone species like *Artemisia*. Fire year climate also impacted many native forb species. Land managers could use climatic conditions in the winter leading up to the fire season along with summer and fall forecasts to prepare for restoration ahead of the fire season (Hardegree et al. 2018). Future research could focus on further teasing out the effects of fire year climate on species occurrence. Determining which climatic variables are most important for which species, and which functional traits, could provide land managers and restoration practitioners with recipes tailored for the idiosyncrasies of the current year. This could include species mixes, restoration methodological strategies (e.g. seeding vs live plantings), as well as climatic limits that determine when it is better to not waste the effort (Schuurman et al. 2020). Another key management strategy that may be helpful in preserving native biodiversity is to incentive fire suppression crews to use tactics that reduce burn severity and maximize unburned patches (Steenvoorden et al. 2019).

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Appendix. Additional tables

Table S1: Soil series at each site extracted from the web soil survey (Ogeen 2017, <https://casoilresource.lawr.ucdavis.edu/gmap/>). Sites 4, 5, 19, 20 and 21 were not resampled in 2016

Site	Invasion Stage	Elevation (m)	CaCO ₃	Soil Series
1	Intact sagebrush	1462	0	Fine, montmorillonitic, mesic Xerollic Durargids
2	Intact sagebrush	1608	0	Loamy, mixed, superactive, mesic, shallow Cambidic Haplodurids
3	Intact sagebrush	1539	0	Loamy, mixed, superactive, mesic, shallow Cambidic Haplodurids
4	Intact sagebrush	1479	5%	Ashy over loamy, glassy over mixed, superactive, mesic Durinodic Haplocambids
5	Intact sagebrush	1434	1%	Loamy-skeletal, mixed, mesic Typic Camborthids
6	Intact sagebrush	1348	0	Coarse-loamy, mixed, mesic Haploixerollic Durorthids
7	Intact sagebrush	1600	0	Coarse-loamy, mixed, mesic Haploixerollic Durorthids
8	Intact sagebrush	1529	1-5%	Loamy, mixed, mesic, shallow Haploixerollic Durorthids
10	Invaded sagebrush	1416	0	Fine-loamy, mixed, mesic Xerollic Nadurargids
11	Invaded sagebrush	1394	0	Coarse-loamy, mixed, mesic Durixerollic Camborthids
12	Invaded sagebrush	1478	0	Coarse-loamy, mixed, mesic Durixerollic Camborthids
13	Invaded sagebrush	1376	0	Clayey over sandy or sandy-skeletal, montmorillonitic, mesic Durixerollic Natrargids
14	Invaded sagebrush	1316	0	Sandy-skeletal, mixed, mesic Xerollic Camborthids
16	Cheatgrass dominated	1521	0	Fine, montmorillonitic, mesic Xerollic Durargids
18	Cheatgrass dominated	1412	0	Clayey over sandy or sandy-skeletal, montmorillonitic, mesic Durixerollic Natrargids
19	Cheatgrass dominated	1315	0	Sandy-skeletal, mixed, mesic Xerollic Camborthids
20	Cheatgrass dominated	1302	0	Sandy-skeletal, mixed, mesic Xerollic Camborthids
21	Cheatgrass dominated	1300	0	Sandy-skeletal, mixed, mesic Xerollic Camborthids
22	Cheatgrass dominated	1494	0	Fine, montmorillonitic, mesic Xerollic Durargids
23	Cheatgrass dominated	1448	1%	Loamy, mixed, mesic, shallow Entic Durorthids
24	Cheatgrass dominated	1297	0	Sandy-skeletal, mixed, mesic Xerollic Camborthids
25	Cheatgrass Die-off	1441	0	Fine, montmorillonitic, mesic Xerollic Durargids
26	Cheatgrass Die-off	1451	0	Fine-loamy, mixed, mesic Xerollic Nadurargids
27	Cheatgrass Die-off	1469	0	Coarse-loamy over sandy or sandy-skeletal, mixed, mesic Durixerollic Camborthids
28	Cheatgrass Die-off	1384	0	Loamy, mixed, superactive, mesic, shallow Xeric Natridurids

Table S2: Species list

Species	Species
<i>Achnatherum thurberianum</i>	<i>Grayia spinosa</i>
<i>Agropyron cristatum</i>	<i>Hesperostipa comata</i>
<i>Allium sp.</i>	<i>Lactuca seriola</i>
<i>Alyssum desertorum</i>	<i>Lepidium perfoliatum</i>
<i>Amsinckia intermedia</i>	<i>Leymus cinereus</i>
<i>Artemisia tridentata</i>	<i>Lomatium sp.</i>
<i>Astragalus lentiformis</i>	<i>Machaeranthera canescens</i>
<i>Bromus tectorum</i>	<i>Mentzelia albicaulis</i>
<i>Calochortus bruneaunis</i>	<i>Microsteris gracilis</i>
<i>Carex sp.</i>	<i>Oryzopsis hymenoides</i>
<i>Ceratocephala testiculata</i>	<i>Pascopyrum smithii</i>
<i>Chaenactis douglasii</i>	<i>Phlox diffusa</i>
<i>Chrysothamnus viscidiflorus</i>	<i>Phlox hoodii</i>
<i>Collinsia parviflora</i>	<i>Phlox longifolia</i>
<i>Crepis acuminata</i>	<i>Poa secunda</i>
<i>Cryptantha watsonii</i>	<i>Salsola tragus</i>
<i>Cymopterus ibapensis</i>	<i>Sisymbrium altissimum</i>
<i>Descurainia pinnata</i>	<i>Stellaria media</i>
<i>Descurainia sophia</i>	<i>Taeniatherum caput-medusae</i>
<i>Elymus elymoides</i>	<i>Tetradymia glabrata</i>
<i>Ericameria nauseosa</i>	<i>Tragopogon dubius</i>
<i>Eriogonum ovalifolium</i>	<i>Vulpia bromoides</i>
<i>Erodium cicutarium</i>	

Table S3: Significant ($p < 0.5$) Correlations of plant function group cover and plant tissue concentrations with the NMS ordination. Soil variables were also tested but none were significantly correlated with the ordination.

Variable	NMDS1	NMDS2	R ²	p
Plant Functional Groups				
AIG	0.70	-0.71	0.92	0.0001
AIF	0.60	0.80	0.70	0.0001
PNG	-0.89	-0.46	0.92	0.0001
PNF	-0.31	0.95	0.43	0.0001
Annuals	1.00	-0.01	0.95	0.0001
Perennials	-1.00	0.01	0.95	0.0001
Forbs	0.16	0.99	0.87	0.0001
Grasses	-0.16	-0.99	0.87	0.0001
Soil Nutrients				
Soil Total N	-0.29	0.29	0.17	0.0243
Soil Total C	-0.24	0.32	0.16	0.0250
Plant Tissue Nutrients				
Litter N	0.12	-0.35	0.14	0.0401
Litter C	0.26	0.26	0.14	0.0424
Other N	0.37	0.08	0.15	0.0399
Other C	0.56	-0.21	0.35	0.0002
Poa C	0.23	-0.36	0.19	0.0475
Poa C:N	0.14	-0.41	0.18	0.0463
Bromus C	0.38	-0.29	0.22	0.0074

Table S4: Standard deviations of three replicated samples at each site, grouped by invasion stage and then averaged. Letters indicate significantly different groups according to a Bonferroni-adjusted Kruskal-Wallis test.

	I. Intact Sagebrush	II. Invaded Sagebrush	III. Cheatgrass-dominated	IV. Cheatgrass Dieoff
Litter N (%)	0.1	0.1	0.1	0.1
Litter C (%)	3.2	2.3	2.5	2.6
Litter C:N	6.8	4.7	6.4	6.9
Soil SurSo ₄ (kg/ha)	0.8	2.2	1.7	1.5
Soil Ca (kg/ha)	443.5	1595.6	470.5	275.8
Soil Mg (kg/ha)	69.8	88.9	56.9	60.0
Soil C:N	1.0 ab	1.8 a	0.7 b	0.8 ab
Soil Total N (kg/ha)	109.1	78.2	91.4	75.7
Soil Total C (kg/ha)	1425.4 a	1065.0 ab	957.9 ab	667.4 b

Table S5: Mean understory cover values for each invasion stage.

variable	Intact Sagebrush	Invaded Sagebrush	Cheatgrass-Dominated	Cheatgrass Dieoff
2013				
Bare Ground	73.46	44.02	14.21	33.38
Litter	23.56	52.99	81.70	50.14
Biological Soil Crust	0.48	0.17	0.00	0.03
Rock	0.15	1.12	1.80	12.65
Annual Introduced Grass	0.21	2.38	4.15	2.72
Annual Introduced Forb	0.01	0.05	4.27	4.10
Perennial Native Forb	0.65	0.05	0.19	0.77
Perennial Native Grass	5.32	3.03	0.51	2.93
Annual Native Forb	0.03	0.07	0.07	0.08
2016				
Bare Ground	51.64	41.35	15.52	25.87
Litter	39.50	48.25	80.46	70.02
Biological Soil Crust	4.01	3.14	0.03	0.04
Rock	1.67	3.80	0.70	1.65
Annual Introduced Grass	1.93	6.36	10.44	6.82
Annual Introduced Forb	0.53	0.98	6.48	12.73
Perennial Native Forb	0.28	0.03	0.01	0.01
Perennial Native Grass	6.46	4.47	0.52	1.80
Annual Native Forb	0.12	0.10	0.00	0.01

Table S6: Path model results and fit indices.

Model	df	p	X ²	CFI	TLI	RMSEA	SRMR
Soil C and N							
Stages I and II	11	0.99	3.18	1	1.32	0	0.03
Stages III and IV	2	0.90	0.21	1	1.15	0	0.01
Plant Tissue C:N							
Bromus C:N	4	0.70	2.20	1	1.09	0	0.02
Poa C:N	9	0.80	5.42	1	1.10	0	0.02
Other C:N	16	0.93	8.56	1	1.11	0	0.03

Note:

CFI: Comparative Fit Index.

TLI: Tucker-Lewis Index.

RMSEA: Root Mean Square Error of Approximation.

SRMR: Standardized Root Mean Square Residual.

Table S7: Covariance matrix for the Soil C and N path model for invasion stages I and II

x	sN	sC	ICN	PNG	NF	aet	p2	Shrubs	BSC	sd_cwd
sN	0.026	0.026	0.008	0.030	0.051	-0.004	-0.011	0.000	0.029	0.003
sC	0.026	0.042	0.030	0.031	0.080	-0.004	-0.028	-0.004	0.052	0.013
ICN	0.008	0.030	0.076	-0.006	0.046	-0.002	-0.028	-0.003	0.013	-0.003
PNG	0.030	0.031	-0.006	0.182	0.112	0.006	0.005	-0.042	0.084	0.007
NF	0.051	0.080	0.046	0.112	0.587	0.010	-0.078	0.015	0.404	0.012
aet	-0.004	-0.004	-0.002	0.006	0.010	0.056	-0.022	0.018	0.020	-0.013
p2	-0.011	-0.028	-0.028	0.005	-0.078	-0.022	0.075	0.014	-0.129	-0.009
Shrubs	0.000	-0.004	-0.003	-0.042	0.015	0.018	0.014	0.069	-0.045	-0.018
BSC	0.029	0.052	0.013	0.084	0.404	0.020	-0.129	-0.045	0.873	0.009
sd_cwd	0.003	0.013	-0.003	0.007	0.012	-0.013	-0.009	-0.018	0.009	0.024

Table S8: Covariance matrix for the Soil C and N path model for invasion stages III and IV

x	sN	sC	AIG	AIF	sd_cwd	p2	aet	tmn
sN	0.035	0.052	-0.031	-0.005	0.008	-0.003	0.005	0.012
sC	0.052	0.085	-0.078	-0.046	0.009	-0.021	0.009	0.011
AIG	-0.031	-0.078	0.315	0.143	0.018	0.120	-0.025	0.020
AIF	-0.005	-0.046	0.143	0.853	0.027	0.120	0.041	0.048
sd_cwd	0.008	0.009	0.018	0.027	0.017	0.011	-0.010	0.006
p2	-0.003	-0.021	0.120	0.120	0.011	0.074	-0.011	0.032
aet	0.005	0.009	-0.025	0.041	-0.010	-0.011	0.032	0.006
tmn	0.012	0.011	0.020	0.048	0.006	0.032	0.006	0.037

Table S9: Covariance matrix for the Bromus C:N path model

x	BCN	AIG	AIF	PNG	p2	Shrubs	aet	tmn	sd_cwd
BCN	0.116	0.112	0.100	0.030	0.069	0.020	0.002	0.007	-0.001
AIG	0.112	0.447	0.229	-0.185	0.077	-0.181	0.001	-0.034	0.003
AIF	0.100	0.229	0.694	-0.223	0.056	-0.333	0.004	-0.021	-0.009
PNG	0.030	-0.185	-0.223	0.423	0.016	0.260	0.018	0.027	0.011
p2	0.069	0.077	0.056	0.016	0.077	0.016	-0.018	0.021	0.000
Shrubs	0.020	-0.181	-0.333	0.260	0.016	0.465	0.029	0.051	0.018
aet	0.002	0.001	0.004	0.018	-0.018	0.029	0.047	0.001	-0.011
tmn	0.007	-0.034	-0.021	0.027	0.021	0.051	0.001	0.054	0.006
sd_cwd	-0.001	0.003	-0.009	0.011	0.000	0.018	-0.011	0.006	0.023

Table S10: Covariance matrix for the Poa C:N path model

x	OCN	AIG	AIF	Litter	PNG	tmn	aet	p2	sd_cwd	Shrubs	BSC
OCN	0.148	0.019	-0.008	-0.013	0.088	0.018	-0.002	0.060	0.014	0.094	0.003
AIG	0.019	0.452	0.236	0.168	-0.189	-0.017	0.006	0.081	0.002	-0.205	-0.196
AIF	-0.008	0.236	0.677	0.171	-0.223	-0.023	-0.002	0.064	-0.010	-0.330	-0.304
Litter	-0.013	0.168	0.171	0.150	-0.170	-0.013	-0.006	0.027	-0.005	-0.177	-0.186
PNG	0.088	-0.189	-0.223	-0.170	0.421	0.017	0.013	0.007	0.021	0.292	0.257
tmn	0.018	-0.017	-0.023	-0.013	0.017	0.055	0.002	0.023	0.006	0.038	0.011
aet	-0.002	0.006	-0.002	-0.006	0.013	0.002	0.045	-0.017	-0.010	0.026	0.023
p2	0.060	0.081	0.064	0.027	0.007	0.023	-0.017	0.075	0.001	0.008	-0.069
sd_cwd	0.014	0.002	-0.010	-0.005	0.021	0.006	-0.010	0.001	0.022	0.015	0.023
Shrubs	0.094	-0.205	-0.330	-0.177	0.292	0.038	0.026	0.008	0.015	0.473	0.292
BSC	0.003	-0.196	-0.304	-0.186	0.257	0.011	0.023	-0.069	0.023	0.292	0.696

Table S11: Covariance matrix for the other plants C:N path model

x	PCN	AIG	Litter	PNG	tmn	aet	p2	sd_cwd	Shrubs
PCN	0.138	0.108	0.032	0.028	-0.013	-0.003	0.062	0.000	0.022
AIG	0.108	0.463	0.185	-0.166	-0.010	0.028	0.086	-0.005	-0.193
Litter	0.032	0.185	0.143	-0.145	0.000	0.003	0.044	-0.007	-0.148
PNG	0.028	-0.166	-0.145	0.362	-0.032	-0.013	-0.033	0.011	0.166
tmn	-0.013	-0.010	0.000	-0.032	0.047	-0.002	0.012	0.000	0.002
aet	-0.003	0.028	0.003	-0.013	-0.002	0.045	-0.017	-0.012	-0.002
p2	0.062	0.086	0.044	-0.033	0.012	-0.017	0.070	-0.008	-0.011
sd_cwd	0.000	-0.005	-0.007	0.011	0.000	-0.012	-0.008	0.019	0.015
Shrubs	0.022	-0.193	-0.148	0.166	0.002	-0.002	-0.011	0.015	0.444