Title: Non-native grass invasion drives biodiversity loss after a single fire in a semi-arid shrubland

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0. Abstract

In the Great Basin of the western United States, annual grass invasion has initiated a novel grass-fire cycle that has transformed vast areas of semi-arid shrublands into non-native annual grasslands that now burn frequently. After the initial transformation, the system is so fire prone that it is difficult to find areas that have not burned repeatedly. We evaluated how the ecosystem responds in the absence of repeated fire to determine if management interventions preventing it could be used to restore the native shrubland.

We created a regional-scale chronosequence of areas that burned only once from 1984-2017 using Landsat-derived burned area products, and collected species composition data across a gradient of 4-32 years since fire. We used linear mixed models to look for evidence of native plant recovery, and used indirect gradient analysis and joint species distribution models to examine the response of species occurrence to a) fire occurrence and timing and pre- and post-fire climate; and b) topography, grazing, and annual grass dominance.

Native diversity and perennial herbaceous cover were unrelated to time since fire and negatively associated with annual grass cover. The occurrence of a single fire had mostly negative associations with native species and mostly positive associations with non-native species. Grazing intensity did not affect the dominant post-fire annual grass, but non-native annual forbs sorted along a gradient towards two groups based on grazing intensity, annual grass cover, and topography.

Annual grass competition will likely maintain the post-fire invasive-dominated plant community even if management interventions successfully stop the grass-fire cycle.

Keywords: *Bromus tectorum*, Non-native annuals, Biodiversity, Fire, Great Basin, Joint Species Distribution Model, Sagebrush ecosystems

1. Introduction

Understanding ecosystem transformations is one of the most important challenges facing ecologists in the 21st century (Sutherland *et al.*, 2013). A myriad of global change forces including non-native species introductions, climate change, and changes in disturbance regimes are altering the structure and function of ecosystems around the world and making them vulnerable to permanent changes in composition and reductions in biodiversity (Brooks *et al.*, 2004; Berdugo *et al.*, 2020). These interconnected forces affect ecosystems over different time scales (Jentsch and White, 2019). Over long time periods, chronic, low-intensity disturbances or stressors (‘presses’) like the invasion of non-native plants, drought, and livestock grazing can alter ecosystem structure, composition, functioning, and biogeochemical cycling (Hooker *et al.*, 2008; van der Putten *et al.*, 2013; Williamson *et al.*, 2020; Mahood *et al.*, 2022; Bates and Davies, 2023; Maxwell *et al.*, 2024). Over very short time scales, pulse disturbances, like fire, can radically shift species composition and ecosystem function (Shinneman, McIlroy and de Graaff, 2021).

In the Great Basin in the Western United States, interactions between press and pulse disturbances have led to widespread ecosystem transformation (Chambers *et al.*, 2021; Crist *et al.*, 2023) in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems. Here, the invasion of the annual cheatgrass (*Bromus tectorum* L.) has steadily increased the connectivity and flammability of fuel beds, which has increased fire activity (Davies and Nafus, 2013; Mahood, Koontz and Balch, 2023; Harrison *et al.*, 2024). As a seed obligate, *A. t. wyomingensis* relies on recolonization from unburned, seed-producing individuals for regeneration (Davies, 2011; Miller *et al.*, 2013; Chambers, Bradley, *et al.*, 2014). When the shrub canopy does not recover, it is usually at warmer and drier sites, which are typically at lower elevation (Chambers *et al.*, 2007, 2017). In contrast, at cooler and wetter sites at higher elevations, the first individuals to colonize the burned area may establish within 5 years of the fire and reach a mature size class in as few as 15 years (Nelson, Weisberg and Kitchen, 2014; Shinneman and McIlroy, 2016). At warmer and drier sites, initial signs of recovery can be followed by mortality and population decline (Shriver *et al.*, 2019). Annual grasses and forbs often become dominant after fire (Urza *et al.*, 2024), leading to the initiation of a grass-fire cycle where larger, more frequent, and more spatially contiguous fires beget increased dominance by non-native annuals (Balch *et al.*, 2013; Keeley and Pausas, 2019). Because fire probability and ability to spread is dependent on total vegetation cover, rather than annual grass and forb cover specifically (Mahood, Koontz and Balch, 2023), the extent of annual grass and forb invasion only needs to be enough to fill in the space between shrubs and perennial grasses to increase fuel continuity and thus fire risk (Bradley *et al.*, 2018).

Repeated fires occur when the fire rotation is less than the recovery time of the ecosystem. The increase in fire activity caused by annual grass invasion is so widespread that areas affected by repeated fire are becoming more common (Crist *et al.*, 2023)(**Figure 1a**). In intact *A. t. wyomingensis* systems, the fire rotation has been estimated at 100-342 years (Baker, 2006; Bukowski and Baker, 2013), whereas in annual grass- and forb-dominated areas, it has been estimated at 78 years and may be as low as 3-5 years in some areas (Balch *et al.*, 2013). In this system, even a single fire can radically alter plant community composition and decrease species diversity;

repeated fires exacerbate these effects (Mahood and Balch, 2019; Shinneman, McIlroy and de Graaff, 2021). Repeated fires may be the dominant control on post-fire community assembly in many Wyoming big sagebrush ecosystems obscuring the effects of other processes on post-fire regeneration and assembly. These processes could include livestock grazing, climate and weather patterns, and competition of native perennial grasses and forbs with non-native plants.

Burning is a short-term pulse disturbance that increases the probability of annual grass dominance after fire (Urza *et al.*, 2024). However,there is also widespread transformation of sagebrush ecosystems to non-native annual dominance in the absence of fire (Smith *et al.*, 2023; Urza *et al.*, 2024). At coarse scales, biophysical suitability to *B. tectorum* and other non-native annuals varies across gradients of climate, soils, and elevation (Chambers *et al.*, 2007; McMahon *et al.*, 2021). In addition, site conditions and the relative abundance of perennial grasses and forbs strongly influence post-fire outcomes (Urza *et al.*, 2017; Barker *et al.*, 2019; Porensky *et al.*, 2021). For example, on relatively cooler and wetter sites with relatively high cover of perennial grasses and forbs, *B. tectorum* may be abundant initially, but can be largely out-competed by native species over time (Mata-González *et al.*, 2007; Taylor *et al.*, 2014; Moffet, Taylor and Booth, 2015; Ellsworth *et al.*, 2016; Shinneman and McIlroy, 2016). As conditions become warmer and drier, the ability of *A. t. wyomingensis* and other native perennials to recover after fire declines (Chambers, Bradley, *et al.*, 2014; Shriver *et al.*, 2019; Urza *et al.*, 2021), increasing the opportunity for non-native annuals to reproduce and increase during favorable years (Chambers *et al.*, 2007). Therefore, the composition and relative abundance of *B. tectorum* and other non-native annuals is likely to depend on both climatic conditions and the relative abundance of perennial grasses and forbs.

The effects of the long-term press of livestock grazing depend largely on the relative resistance of the site to the invaders and the duration, intensity and timing of grazing. Globally, livestock grazing has been found to favor annual over perennial species (Díaz *et al.*, 2007). In *A. t. wyomingensis* ecosystems, resistance to non-native annuals is generally low due to high climatic suitability (i.e., warm and dry to moist climatic regimes) (Chambers, Bradley, *et al.*, 2014; McMahon *et al.*, 2021; Rigge, Shi and Postma, 2021; Terry *et al.*, 2024) but is influenced by the species composition of the native community. Perennial grasses are strong competitors with *B. tectorum* (e.g. *Elymus elymoides* L.) (Booth, Caldwell and Stark, 2003; Chambers *et al.*, 2007; Leger, 2008; Reisner *et al.*, 2013; Leger and Goergen, 2017); their capacity to regrow after wildfire ensures recovery in a system where the dominant shrubs are killed by fire (Chambers, Miller, *et al.*, 2014).

Studies of grazing effects after wildfire are limited in *A. t. wyomingensis* ecosystems, but there is observational evidence that grazing occurrence is associated with increased presence of *B. tectorum* at landscape scales regardless of wildfire (Williamson *et al.*, 2020). A short-term grazing experiment following wildfire on a warm and dry site with relatively low resistance to invasion indicated that cattle grazing to achieve 50% utilization had largely neutral associations with the abundance of both perennial native species and annual grasses as well as species richness (Bruce *et al.*, 2007). At a site with higher resistance dominated by perennial bunchgrasses, cattle grazing following prescribed fire had neutral effects in the short term (Bates *et al.*, 2009), and after 20 years resulted in higher cover of *B. tectorum* at light grazing intensities, and higher cover of non-native annual forbs at high grazing intensity, although interannual variability was high (Bates and Davies, 2023). Cattle grazing had no effect on the perennial native plants they analyzed.

Because Wyoming big sagebrush ecosystems have low resistance to invasion by many non-native annuals (Chambers, Bradley, *et al.*, 2014; Chambers, Brown, Bradford, Board, *et al.*, 2023), increases in annual grass and forb abundance are almost inevitable a few years after a wildfire (Balch *et al.*, 2013; Urza *et al.*, 2024). The fall and spring after a wildfire provide a critical window of opportunity for regrowth and establishment of native plants (Strand *et al.*, 2014; Hardegree *et al.*, 2018; Tarbox *et al.*, 2024). The climatic conditions for the two years preceding the fire influence the growth and reproduction of non-native annuals (Pilliod, Welty and Arkle 2017) and determine the biomass and moisture content of the fine fuels on the landscape (Nafus and Davies 2013). In turn, these fuels drive the severity, intensity, and extent of fire (Abatzoglou and

Kolden, 2013; Pilliod, Welty and Arkle, 2017). Historically, most fires in Wyoming big sagebrush ecosystems occurred at the end of the growing season when many species are dormant (Chambers *et al.*, 2019). However, fire seasons are changing globally and little is known about how earlier fire seasons are affecting plant communities (Miller *et al.*, 2013, 2019; Jolly *et al.*, 2015; Cattau *et al.*, 2020). Fires that remove perennial shrubs and herbaceous species release a pulse of soil water and nutrient resources that are available to plants for fall regrowth and establishment, given sufficient fall precipitation, and for spring and early summer establishment and growth when soil water availability is highest (Strain, Brady and Hanan, 2024). It is during this time when plants have the opportunity to colonize newly available niche spaces via resprouting, germination from seedbank reserves or dispersal from adjacent unburned areas (Urza *et al.*, 2024). However, low soil moisture or high atmospheric demand can severely limit regeneration (O'Connor *et al.*, 2020; Schönbeck *et al.*, 2022), and postfire nitrogen may be exported from the system via erosion before plants break dormancy (Homyak *et al.*, 2014).

Postfire Wyoming big sagebrush ecosystems are often converted to annual grasslands dominated largely by *B. tectorum* (Mack, 1981; Miller *et al.*, 2013; Chambers, Bradley, *et al.*, 2014)*.* However, these landscapes have diverse and complex fire histories (**Figure 1**), and when examined in detail the communities are almost never characterized exclusively by *B. tectorum* - *B. tectorum* is almost always accompanied by an assortment of annual forbs. Here, we evaluated the effects of single fires (i.e., areas that have burned only once in recent history) on plant community composition and the associated effects of climate and cattle grazing in Wyoming big sagebrush ecosystems. We constructed a 32 year, satellite-derived fire history atlas of areas that burned only once across a 36,000 km^2 area to examine if there was evidence of a return to pre-fire composition after a single fire. We focused on two questions. First, was there evidence of native plant recovery in the absence of repeated fire; and second, what were the drivers of post-fire species composition and persistence after a single fire? For the first question, we hypothesized that shrub cover, native perennial grass cover, and native plant diversity would increase with time since fire (TSF). For the second question we explored the short-term pulse and long-term press disturbances associated with maintaining the post-fire state. For the short-term pulse disturbance, fire, we examined fire occurrence and timing, as well as fire-year climate. For the long-term press disturbances, we focused on annual grass dominance and long-term grazing intensity. Our approach allowed us to evaluate how the press vs pulse disturbances were associated with the overall changes in plant functional groups and plant community composition and thus to identify the factors contributing to annual grass- versus annual forb-dominated alternative states. We discuss the implications of postfire dominance of these alternative states for management.

2. Methods

2.1 Study area

The study was conducted across a 36,000 km^2 area in northern Nevada (**Figure 1**). The region has hot, dry summers and cold, wet winters. Annual precipitation averaged 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, 2024). The region consists of mountain ranges that run north to south, and the Wyoming big sagebrush ecosystems generally lie on the lower slopes of the mountains. At all sites sampled, *A. t. wyomingensis* was the dominant shrub, and *Poa secunda* was the most common understory perennial grass. Sites were limited further to areas where soils were clay loams according to the Web Soil Survey (O’Geen, Walkinshaw and Beaudette, 2017), and this soil texture was confirmed on site. Our sites ranged from 1275 to 1631 m in elevation (mean 1460, sd 93). No sites were located within wild horse and burro herd management areas. To ensure statistical independence, all but one pair of sites were located more than a kilometer apart. Within each watershed, the mean distance between plots was 20-40 km. One anomalously close pair of plots was 374 meters, and one of those was an unburned control.

2.2 Fire History Atlas

We created a fire history atlas, from which we selected plot locations along a gradient of TSF (**Figure 1**). In order to avoid the confounding effects of fire frequency on community composition, we kept fire frequency after 1984 constant. 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 30 m resolution yearly burn severity mosaics from the Monitoring Trends in Burn Severity (MTBS) database (www.mtbs.gov) (Eidenshink *et al.*, 2007). We extracted low to high burn severity classifications (from 2, low severity, to 4, high severity) from this product, effectively removing potential unburned pixels from the insides of 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 30 m resolution USGS Burned Area Essential Climate Variable (BAECV) product of annual fire occurrence (Hawbaker *et al.*, 2017). With this dataset 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 was a fire history layer where we could be reasonably certain that those areas on the map had burned only once since 1984 (**Figure 1b**). 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 out all land not managed by the Bureau of Land management and all land that was more than 2 km from roads (for logistical purposes). We confined the study to the Central Basin and Range ecoregion (Omernik and Griffith, 2014) to keep coarse-scale environmental conditions relatively consistent. We corroborated our assumption that sites were unburned shrublands prior to the single fire in the dataset by using a linear model to compare the marginal means of the shrub cover estimates from the 30 m resolution Rangelands Analyses Platform (Allred *et al.*, 2021) for three groups: years before and after the fire at burned sites, and unburned controls (**Figure 1c**). We also assessed whether pre-fire sites were likely to be more invaded than unburned sites, and thus more likely to burn, by comparing pre-fire cover of annual and perennial herbaceous functional groups with unburned controls (**Figure 1e**). Time since fire was uncorrelated with elevation.

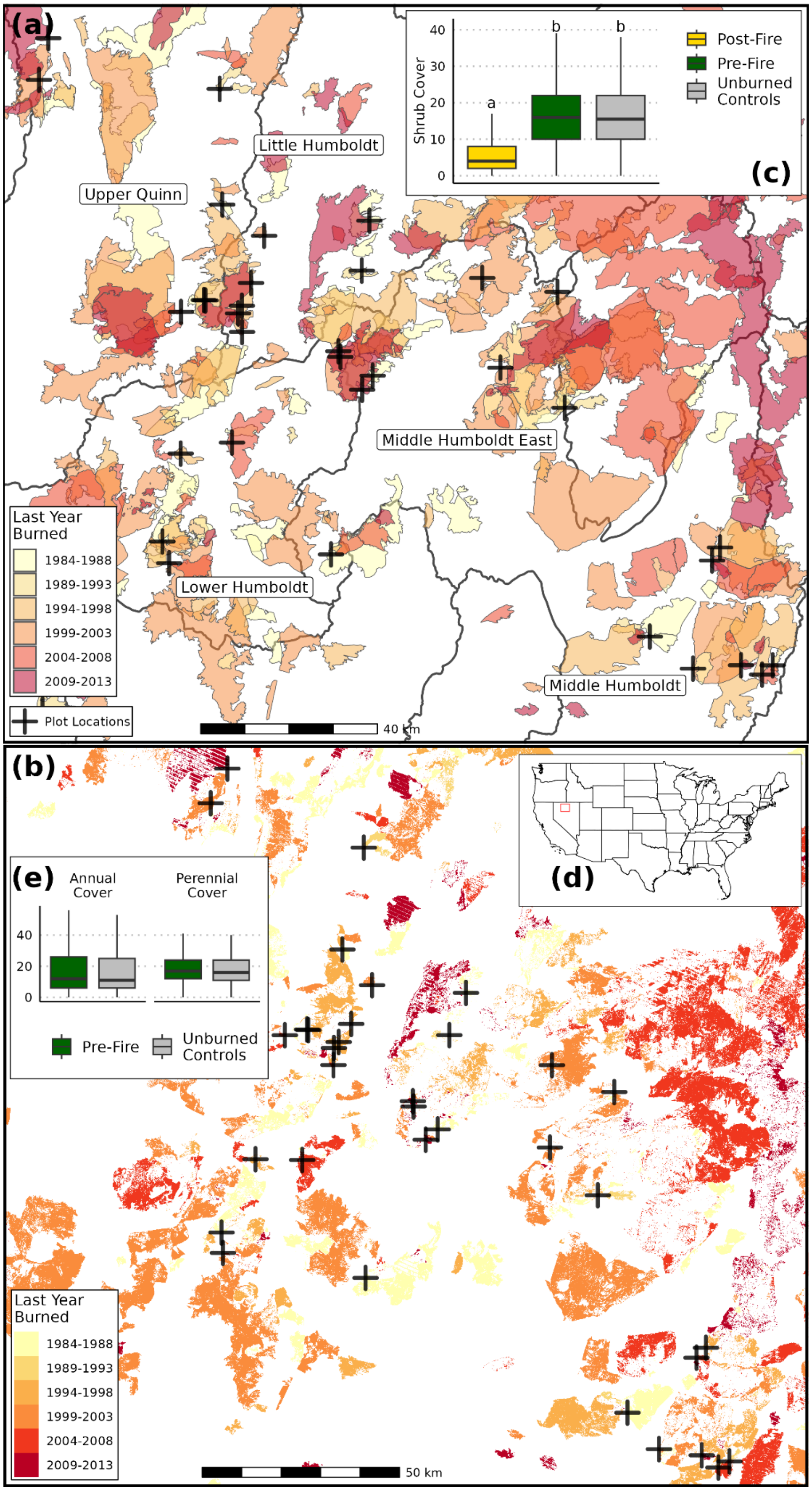
(a)
Little Humboldt
Upper Quinn
Middle Humboldt East
Lower Humboldt
Middle Humboldt
Last Year Burned
1984-1988
1989-1993
1994-1998
1999-2003
2004-2008
2009-2013
Plot Locations
40 km
Shrub Cover
40
30
20
10
0
a
b
b
Post-Fire
Pre-Fire
Unburned Controls
(c)
(b)
(e)
Annual Cover
Perennial Cover
40
20
0
Pre-Fire
Unburned Controls
(d)
Last Year Burned
1984-1988
1989-1993
1994-1998
1999-2003
2004-2008
2009-2013
50 km

Figure 1. *Fire history of the study area from 1984-2015. In panel a, partially transparent MTBS fire perimeters illustrate the prevalence of repeated fire. Panel b shows the burned area in the study after filtering out repeated fires and unburned patches, but before excluding private land. Boxplots in panel c shows shrub cover at unburned controls, and each burned plot before and after fire occurrence. The boxplots indicate that most areas were shrublands before the first fire was recorded. Panel d shows the broader setting. Boxplots in panel e compare pre-fire cover of annual and perennial herbaceous plants to unburned controls.*

2.3 Sampling design

We stratified the sampling space spatially and temporally (**Figure 1**). Spatially, we divided the region into five study blocks using 1:250,000-scale hydrologic units [hereafter, watersheds; (Steeves and Nebert, 1994)]. The watersheds were Upper Quinn, Lower Humboldt, Little Humboldt, and Middle Humboldt. Middle Humboldt was divided into two blocks, because it was larger than the other 5 watersheds and consisted of two broad areas connected by a small isthmus. Most of the fire history that we were sampling was in the two areas on either side of the isthmus. We divided the last year burned into six, five-year bins from 1984-2013. Candidate sampling areas were further restricted to include only pixels classified as Inter-Mountain Basins Big Sagebrush Shrubland vegetation alliance in LANDFIRE's Biophysical Setting product. In each of the five study blocks, we established one 50 m by 50 m plot from each of the six temporal bins plus one 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. 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. All plots experienced similar temperatures and precipitation during the period from 1984-2017 (**Figure S1**).

2.4 Field sampling

Field sampling was conducted in June 2017. At each sampling location, we delineated a 50 m x 50 m plot and placed nine, randomly located 1 m^2 subplots within each plot. In each subplot three observers conducted ocular estimates of the cover of every species through consensus, or via averaging if a consensus could not be reached. We then did a systematic, gridded plant walk throughout the plot to detect any species that were not present in the subplots. Because this method tends to underestimate shrubs, we used the point-centered quarter method (Pilliod and Arkle, 2013) to estimate shrub cover if shrubs were present. The point-centered quarter method 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.

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 (4 km) 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 1 to the month before the fire) and following (month after fire to December 30) the fire, as well as the month in which the fire occurred. Livestock grazing is ubiquitous in the sagebrush biome, and all of our sites have been grazed historically by cattle. In order to account for its influence, we acquired data for billed 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. Our study sites were widely distributed, so almost every site was within its own unique allotment. In addition, billed AUMs did not change much from year to year in this region. Thus, we felt confident that this was an appropriate metric of long-term grazing pressure for our particular application.

2.6 Statistical analysis

2.6.1 Associations of functional group cover with fire occurrence and time since fire

We grouped our plant cover data into functional groups: native perennial grasses (NPG), native perennial forbs (NPF), native annual forbs (NAF), native shrubs (NW), introduced annual grass (IAG), introduced perennial grass (IPG), introduced annual forb (IAF), and introduced shrubs (IW). For our analyses of functional group abundance, we excluded NAF, IPG and IW due to rarity, and aggregated all annuals into annual herbaceous, all perennials into perennial herbaceous, and all herbaceous groups into total herbaceous cover, for a total of 8 groups that were analysed further. We converted all groups that characterized the composition of the understory layer—everything except total herbaceous cover and native shrub cover—to relative cover (cover / total cover * 100). Analyzing relative cover instead of absolute cover allowed for better comparison of components of the plant community across sites (Catford *et al.*, 2012). We used linear mixed models and Wilcoxon rank sum tests (Bauer, 1972) on plot-scale aggregates of cover data (n=35) to examine functional group associations with single fire occurrence and time since fire. We created bivariate linear mixed models (Bates *et al.*, 2015) to examine the relationship between TSF and the cover of each plant functional group, with the watershed as a random intercept. We also created three sets of models to examine Shannon-Wiener alpha diversity (Shannon, 1948) and Pielou's evenness (Pielou, 1966) as response variables. Predictor variables were TSF for the first set *B. tectorum* cover for the second set, and tnon-native annual forb cover for the third set. In addition, we created a model with *B. tectorum* cover as the predictor variable and perennial herbaceous cover as the response variable. All models had watershed as the random effect. For all models we explored non-linear additions to the predictor variables, assessed the fit using marginal and conditional R^2 calculated using the *performance* package (Lüdecke *et al.*, 2021), and used the *DHARMa* package for model diagnostics (Hartig, 2024)(Hartig 2024). All of these analyses focused on examining the effects of *B. tectorum* on the rest of the plant community, so we did a separate analysis to explore the effects of other species on the community, without the effect of *B. tectorum*. To do this, we removed *B. tectorum* from the cover matrix, converted cover to relative cover and ran separate models for each species with the relative cover of that species as the predictor and Shannon-Wiener diversity as the response.

2.6.2 Analyses of species occurrence

We conducted two separate analyses to understand the effects of press and pulse disturbances on species composition at the 1 m^2 subplot scale: joint species distribution models (JSDM) (Tikhonov *et al.*, 2020) and indirect gradient analysis (IGA).

2.6.3 Indirect gradient analysis

Indirect gradient analysis is a method that uses Markov-chain Monte Carlo simulations on presence/absence data to detect a latent variable of the probability of occurrence using Bayesian inference. We followed the workflow of Walker (2015). We set prior means to zero, such that the prior distribution can be thought of as a null model. The prior variance for the gradient was 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). We ran three chains with a burn in of 10,000, after which there were 100,000 iterations, with a thin of 100, for 1,000 total samples per chain, and 3,000 total posterior samples.

Because it uses occurrence data, species that occur at only one site, as well as *B. tectorum*, which occurred at every burned subplot, were removed from the analysis because they add no information. The Indirect Gradient Analysis was performed on 28 species at 261 subplots. The exclusion of *B. tectorum* from the IGA allowed us to test how the cover of *B. tectorum* was associated with the gradient that was estimated, and thus assess the effect of the abundance of *B. tectorum* on the occurrence of other species. We used two methods for model diagnostics: Gelman and Rubin’s potential scale reduction factor (PSRF) convergence diagnostic (Plummer *et al.*, 2006) and effective sample size to assess model convergence. We considered strong convergence of parameters if PSRF was under 1.1, and ideally under 1.01, while ESS values were considered well converged over 400 and ideally closer to the posterior sample size (Vehtari *et al.*, 2021).

To examine how fire year climate, grazing intensity, and TSF 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 computed 95% 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.

2.6.4 Joint species distribution modeling

We used joint species distribution models to model the occurrence, and co-occurrence, of all species within a 1 m^2 quadrat using the R package *Hmsc* (Tikhonov *et al.*, 2020). This method allowed us to better understand how each individual species responded to environmental covariates while accounting for interspecific interactions and incorporating the associations with functional traits of each species. This method can take a wide variety of inputs for fixed and random effects (see (Tikhonov *et al.,* 2020)). For our purposes, we used matrices of species occurrences at each location, environmental covariates at each location, and traits for each species.

Species that occurred in less than five subplots were grouped with other species according to functional group (**Table S1**). Models were created with each 1 m^2 subplot as the unit of analysis, with the identity of the watershed, plot, and subplots as random effects. We created two JSDMs, each with elevation, folded aspect (McCune and Keon, 2002), long-term grazing intensity, perennial cover, annual grass dominance (defined as the relative cover of annual grasses across a given 50 m x 50 m plot) as environmental covariates. The annual grasses encountered were *B. tectorum*, *Hordeum murinum* and *Vulpia bromoides*, but. *B. tectorum* was typically the only species present (92% of subplots), or was 90-99% of the annual grass cover (**Table S1**).

The first JSDM was created to understand the effect of the pulse disturbance, fire, on community composition. The predictor variables for the first model were those given above plus fire occurrence. The second JSDM was created to understand how post-fire community assembly was associated with the various long-term press disturbances, and the legacy of fire-year climate. The predictor variables were those given above plus TSF, shrub cover, ignition month, and the three fire year climate variables that were highly correlated with the IGA gradient on each species' occurrence probability. The second JSDM was created to understand the effect of the pulse disturbance, fire, on community composition. The predictor variables for the first model were those given above plus fire occurrence.

For both models, we included each species' functional group as categorical life history traits in each model: invasive annual grass (IAG), invasive perennial grass (IPG), invasive annual forb (IAF), native annual forb (NAF), native perennial forb (NPF), native perennial grass (NPG) and native woody plants (NW) (**Table S1**).

We used the default priors provided by the *Hmsc* package. We ran four MCMC chains for 1,500,000 iterations. The first 500,000 iterations were removed as burn-in and 1 out of every 1000 remaining iteration was sampled, resulting in 1,000 posterior samples per chain (4,000 total). To assess model convergence and chain mixing we used PSRF and effective sample size. We considered parameters to be well-converged if PSRF was under 1.1, and ideally under 1.01, while ESS values over 400 were considered well converged and ideally closer to the posterior sample size (Vehtari *et al.*, 2021).

To evaluate the explanatory power of the model to predict the occurrence of each species, we used the Tjur R^2, calculated by comparing the posterior predictive distribution to the observed values. To evaluate the strength of the effect of each covariate on each species, we calculated the probability of direction for each parameter (Makowski *et al.*, 2019). Probability of direction is the probability that a parameter is strictly positive or negative, and is strongly correlated to the frequentist p-value. We considered an association to be strong if its probability of direction was greater than 97.5% (analogous to $p < 0.05$). Like the IGA, the JSDM of the burned plots only could not estimate parameters for *B. tectorum* because it occurred at every plot.

In order to examine interspecific interactions, after accounting for environmental filtering and trait associations, we created matrices of residual correlation between species for each model.

Code and data to reproduce the analysis and figures will be available at https://github.com/admahood/time-since-fire upon publication, along with a permanent digital object identifier.

3. Results

3.1 Associations of fire and time since fire with functional group composition and diversity

The occurrence of a single fire was strongly associated with the abundance of almost all plant functional groups compared to unburned controls (**Figure 2**). The cover of annual herbaceous plants, annual forbs, and total herbaceous plants was higher at burned sites, and the cover of shrubs, perennial grasses, and all perennial herbaceous plants was higher at unburned controls (**Figure 2a**). The only functional group that was not significantly different between burned sites and unburned controls was non-native annual grasses.

We found no effect of TSF on functional group cover or diversity, suggesting a relatively stable system dominated by non-native annuals after one fire (**Figure 2b, 3a**). *B. tectorum* cover had a strong negative effect on the Shannon-Weiner (β = -0.23; $p << 0.05$; Marginal R^2= 0.56) and Pielou's Evenness (β = -.009; $p << 0.05$; Marginal R^2= 0.59) indices of alpha diversity (Figure 3b). *B. tectorum* cover also had a nonlinear, negative effect on the cover of perennial herbaceous plants (Marginal R^2 = 0.25) (**Figure 3**). Non-native annual forbs as a functional group (**Figure 3d**), as well as all species individually, either had no relationship with diversity, or significant but weak effects with R^2 values of 0.1 or less. For all mixed models, the watershed had almost no effect on model performance, explaining at most 2% of the variance.

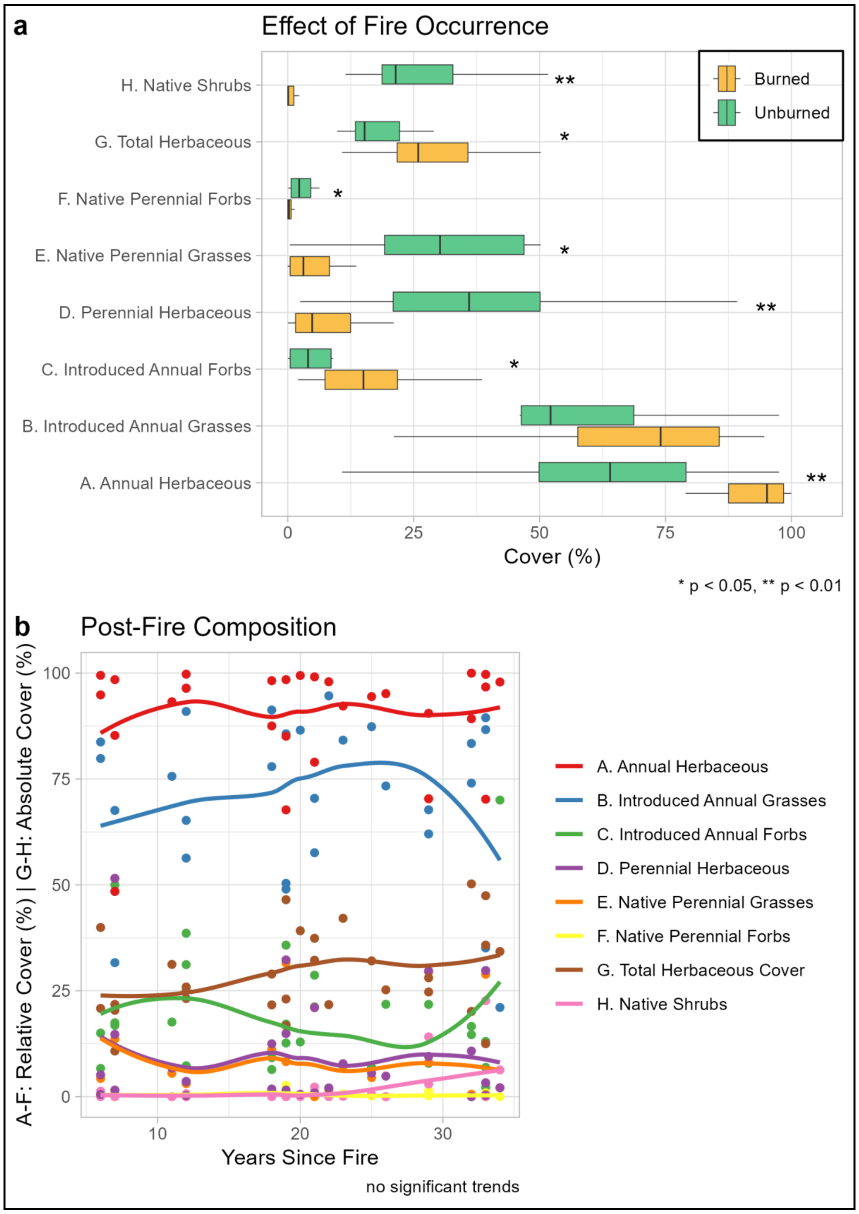

Figure 2: Functional group responses to fire occurrence (a) and time since fire (b). Single fire occurrence was negatively associated with native shrubs, native perennial grasses, and perennial forbs but positively associated with non-native annual forbs and annual herbaceous cover (a). In a, burned plots included all times since fire and significance was tested with a Wilcoxon Rank Sum Test. There were no meaningful relationships of functional group cover with time since fire. Instead of linear model fits, LOESS smoothers are added to aid visualization (b). Note that A-F are relative cover, and G-H are absolute cover. These are plot level means (n=35).

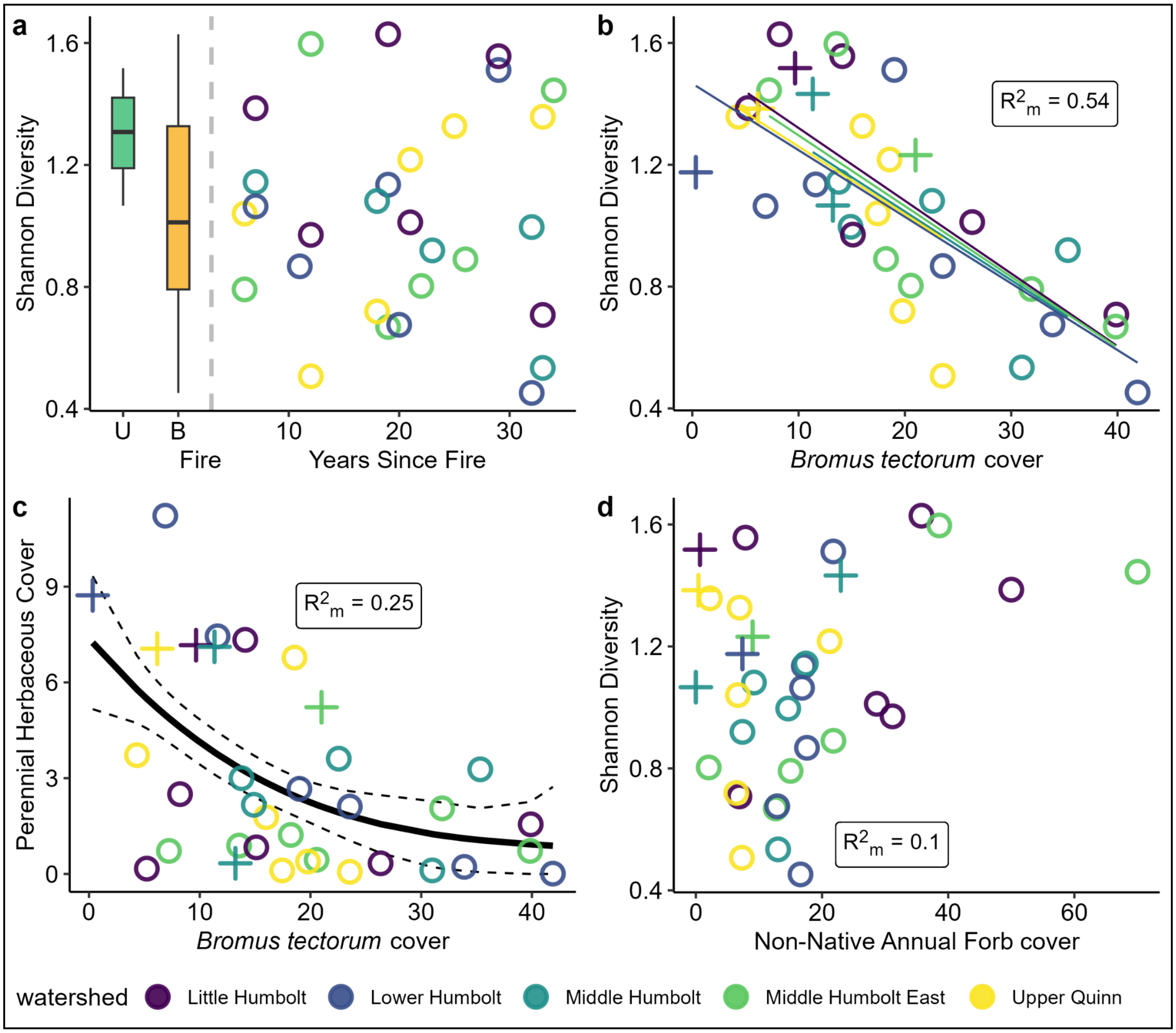

Figure 3. The relationships of the Shannon-Weiner diversity index (Shannon diversity) to years since fire (a), Shannon Diversity to B. tectorum cover (b), perennial herbaceous cover to B. tectorum cover (c), and Shannon diversity to non-native annual forb cover (d). Diversity declined after fire (boxplots in a), and was unrelated to time since fire (the scatter plot portion of a). Bromus tectorum cover was negatively associated with the Shannon diversity index (b) and native perennial grass and forb cover (c). Non-native annual forbs were weakly associated with Shannon diversity (d). The lines in b and c were from a linear mixed models. These are plot-level means (n=35).

3.2 Model Convergence for IGA and JSDMs

The PSRF upper bounds of the Gelman–Rubin convergence diagnostics from the IGA were all below 1.01 and the effective sample sizes ranged from 2,000 to 10,000, indicating good model convergence (**Figure S2**). The JSDM for burned plots alone had close to ideal model convergence (ESS > 400, PSRF < 1.01), but the JSDM for all plots did not. Effective sample sizes were all over 400, but PSRF values were over 1.1 for 23 of the 168 model parameters (**Figure S2**). However, the purpose of the model for all plots was to show the effect of fire occurrence on species, and those parameters that were not well converged were still in agreement. **Figures 4** and **6** show the posterior distributions for each chain, so parameters that are not well-converged can be seen. The JSDM that included all plots explained an average of 30% of the variation per species, ranging from 2% to 72% (**Figure S3**). The JSDM for the burned plots only explained an average of 33% of the variation per species, ranging from 5% to 69% (**Figure S3**).

3.3 Short-term pulse: associations of fire occurrence and timing and fire-year climate with species composition

To evaluate species associations with fire occurrence, timing and fire-year climate, we used joint species distribution models (JSDMs). The overall dataset had 74 total species, 51 of which were in the 1 m^2 subplots. The 28 postfire plots had 58 species, 39 of which were in the 1 m^2 subplots (**Table S1**).

Similar to our functional group analysis (**Figure 2a**), fire had positive associations with most introduced species and mixed associations with native plants (**Figure 4a**). It had strong negative associations with *A. t. wyomingensis* and the other NPF group, and strong positive associations with *P. secunda*, *Sisymbrium altissimum* and *Lepidium perfoliatum*. Later ignition months had mostly neutral associations with native species, and mostly negative associations with introduced species (i.e., earlier ignitions benefitted non-native species), including strong negative associations with *L. perfoliatum, Salsola tragus*, and other IAF, and strong positive associations with other NPG and native legumes. Prefire CWD had positive associations with most native species, except other NPG. It had strong negative associations with other IPF and other IAG, and strong positive associations with *S. altissimum*. Postfire CWD had mostly positive associations with all species, and strong positive relationships with three native and three non-native species. Postfire AET had mixed effects. It had strong negative associations with other NPF and *Alyssum desertorum*, and strong positive associations with other IAG, *S. altissimum*, *L. perfoliatum*, and other IPF. The natives were native legumes, *Sphaeralcea* spp, other NPF, and other NPG; the non-natives were *S. altissimum*, other IAG, and other IPF)

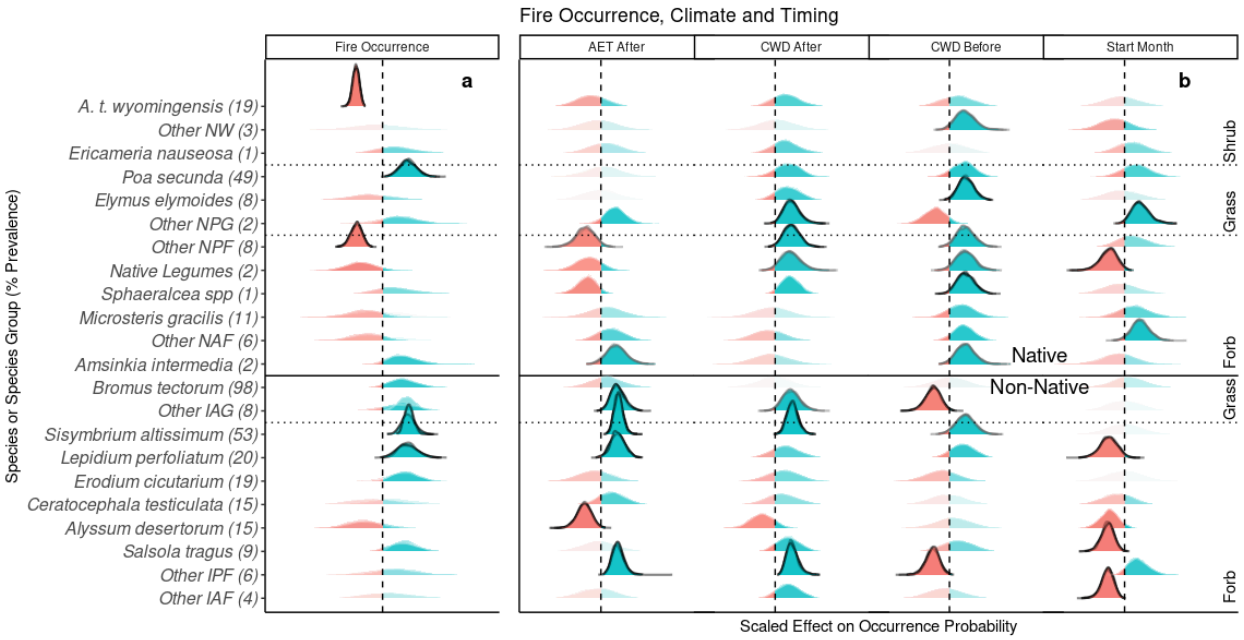

Figure 4. Effect of the short-term pulse, fire, on species occurrence according to joint species distribution models. Each bell curve represents 4 overlapping posterior distributions of a parameter estimate of how species occurrence was associated with environmental covariates. Panel a is from the joint species distribution model of all plots (n=315 subplots at 35 sites), and illustrates how fire occurrence had mostly negative associations with native species and positive associations with non-native species. Panel b is from the model of burned plots only (n=252 subplots at 28 sites), and illustrates how the timing of the fire, and the climatic conditions before and after the fire had many strong associations with species occurrence. Overlap of posterior distributions from each chain illustrates model convergence for that parameter. Vertical dotted lines indicate zero association. Distributions with a median closer to zero are more transparent. Blue is positive, and red is negative. Prevalence (% occurrence) is next to each species name in parenthesis. Native species are above the bold line, non-native below. Dotted lines separate functional groups. Black outlines around distributions represent a 97.5% probability that the effect is strictly positive or negative, grey indicates a 95% probability (analogous to $p < 0.05$ and $p < 0.1$, respectively). Abbreviations: CWD = climatic water deficit; AET = actual evapotranspiration.

3.4 Long-term press: associations of time since fire, annual grass dominance and grazing with species composition

To evaluate associations of the press disturbance, cattle grazing, with species composition, we used both IGA and JSDM. For the IGA, most sites had their credible intervals cross zero, with the exception of several sites with low *B. tectorum* cover (**Figure 5a**). The gradient estimated by the model had positive associations with 7 species (5 non-native and 2 native), and negative associations with one non-native species (*S. altissimum*) (**Figure 5b**). The positive side of the gradient was associated with higher grazing intensity, higher Shannon-Weiner diversity, higher CWD after the fire, and higher shrub cover (**Figure 5c**). The negative side of the gradient was associated with higher CWD before fire, higher *B. tectorum* cover, higher AET after the fire, and warmer aspects (**Figure 5c**).

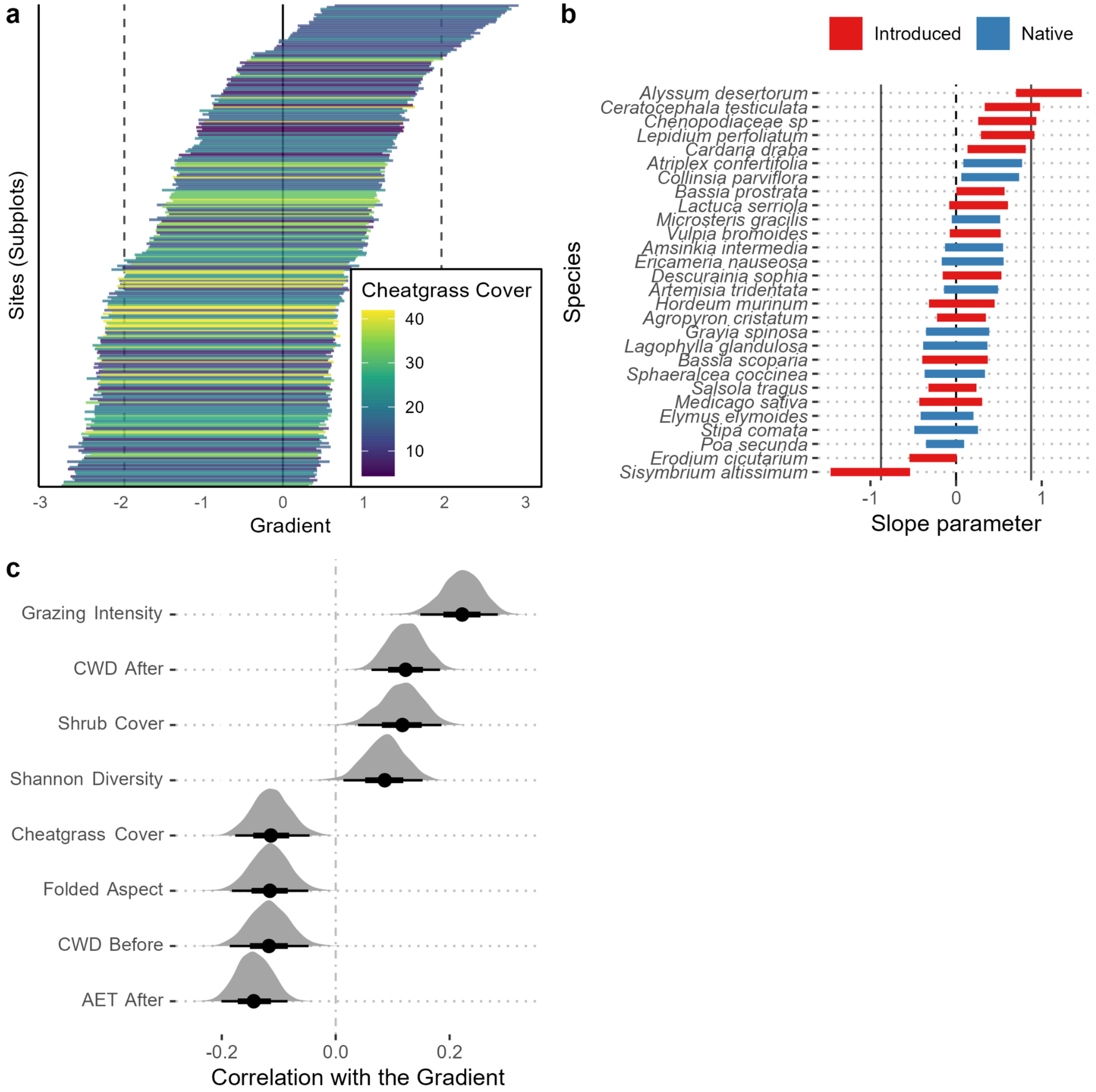

***Figure 5**. Indirect gradient analysis on post-fire plant communities for all species except B. tectorum. Panel a shows that species compositions were similar at most sites, except those with low cover of B. tectorum. Panel b illustrates that the non-native forbs are largely sorted into two groups. Panel c suggests that this sorting is associated with grazing intensity, fire year climate and site variables (n=252 subplots at 28 sites). In panel c, variables with 95% credible intervals crossing zero were omitted. CWD = climatic water deficit; AET = actual evapotranspiration.*

The JSDM of post-fire plots showed that TSF had clear positive associations with the native shrub species that were grouped for the analysis, the native perennial grass, *E. elymoides*, the native perennial forbs, *Sphaeralcea* spp, and *Amsinckia intermedia*, other NPF, and the non-native annual forbs *S. altissimum* and *L. perfoliatum. The TSF* had negative associations with the other NPG, as well as non-native annual forbs *Erodium cicutarium, Ceratocephala testiculata, Salsola tragus,* and *other IPF* (**Figure 6**). Annual grass cover had negative associations with all species except other IAG and *S. altissimum*. Grazing intensity had largely positive associations with the native annual forb, *Microsteris gracilis,* as well as the other IAG, *E. cicutarium, C. testiculata* and other IPF, and negative associations with other NW, *E. elymoides*, other NAF, and *A. intermedia* as well as *S. altissimum*. (**Figure 6**). Many species had positive relationships with elevation and negative relationships with warmer aspects. Shrub cover had positive or neutral associations with most native and non-native species, except for strong negative associations with *S. altissimum* and *A. intermedia*. Perennial herbaceous cover had strong positive associations with *P. secunda* and *S. altissimum*, and strong negative associations with the non-natives *S. tragus* and *A. desertorum*, and the natives *Sphaeralcea* spp, the native legume group and the other native perennial forb group.

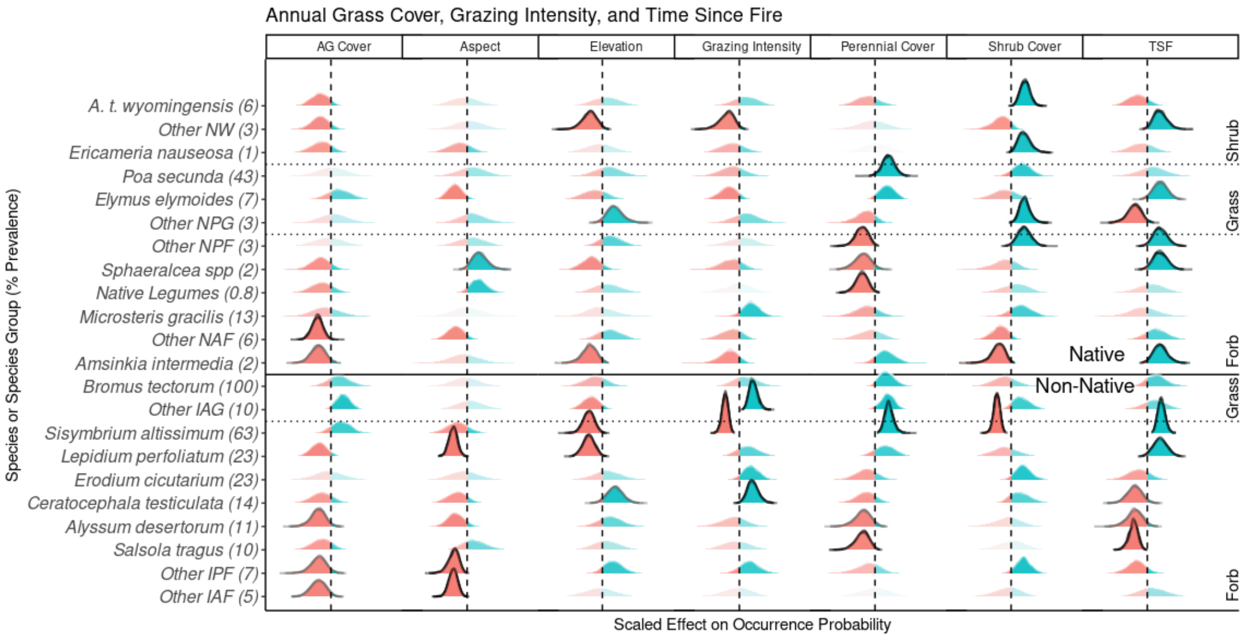

Figure 6. Effect of long-term presses on post-fire species occurrence (n=252 subplots at 28 sites) according to a joint species distribution model. Annual grass cover (AG Cover) had negative associations with all but a few species. Time since fire (TSF) was positively associated with the occurrence of several native species but also S. altissimum *and non-native grasses. Other long-term presses had mixed associations. Plot arrangement is the same as Figure 4.*

3.6 Postfire correlations among species

In the post-fire plots, there were two groups of species that had strong positive associations with each other. The first group had four non-native annual forbs, *C. testiculata*, *L. perfoliatum*, and *A. desertorum*; a non-native perennial grass, *A. cristatum*; and two groups: other IAG and other NAF. These species were negatively associated with another group with positive intra-group associations: the non-native annual forbs *S. altissimum* and *S. tragus*, the native annual forb *A. intermedia*, the native perennial grass *E. elymoides*, and other NPG (**Figure 7**). Weak relationships were expected for *B. tectorum* since the model is occurrence-based and it occurred in almost every 1 m^2 subplot in post-fire sites.

Taken together, our results suggested that long-term presses sorted post-fire communities towards two plant species assemblages that were dominated by non-native species. The first assemblage had high cover of *B. tectorum* and high prevalence of *S. altissimum*, and the second had lower cover of *B. tectorum*, and high prevalence of several non-native annual forbs: *A. desertorum*, *C. testiculata*, and *L. perfoliatum.* This is evident from the indirect gradient analysis (IGA) (**Figure 5**), and the JSDM of burned plots. There were negative associations between many of the forbs in the second group and *B. tectorum* cover (**Figure 6**), and positive residual correlations within the second group of species (**Figure 7**). The first group was associated with low long-term grazing intensity, high annual grass cover, lower elevations, and warmer (i.e. more southwest-facing) aspects (**Figures 5, 6**). The second group was associated with high long-term grazing intensity, lower *B. tectorum* cover, higher elevation, and cooler aspects (**Figures 5, 6**).

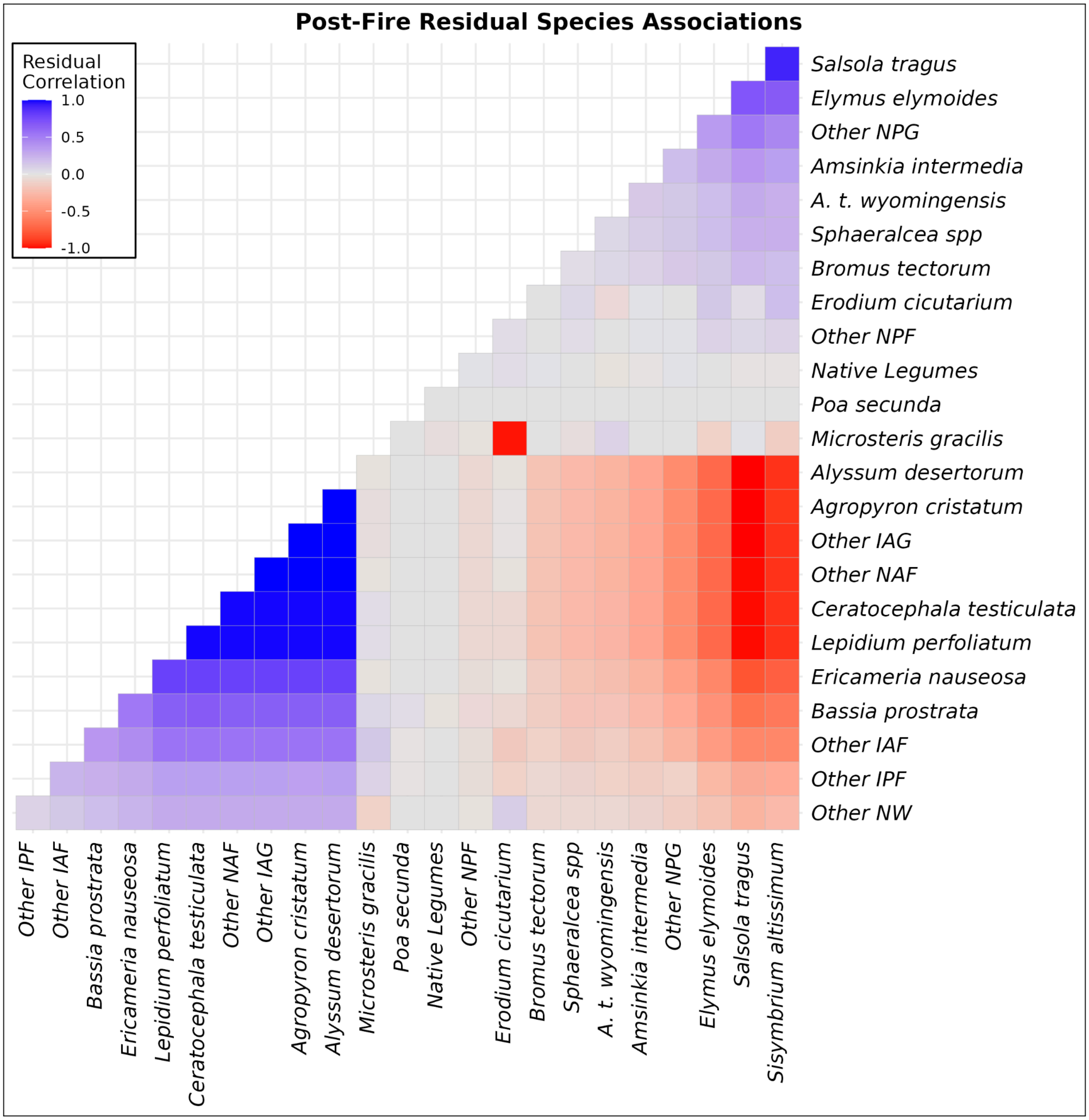
Post-Fire Residual Species Associations
Residual Correlation
1.0
0.5
0.0
-0.5
-1.0
Salsola tragus
Elymus elymoides
Other NPG
Amsinkia intermedia
A. t. wyomingensis
Sphaeralcea spp
Bromus tectorum
Erodium cicutarium
Other NPF
Native Legumes
Poa secunda
Microsteris gracilis
Alyssum desertorum
Agropyron cristatum
Other IAG
Other NAF
Ceratocephala testiculata
Lepidium perfoliatum
Ericameria nauseosa
Bassia prostrata
Other IAF
Other IPF
Other NW
Other IPF
Other IAF
Bassia prostrata
Ericameria nauseosa
Lepidium perfoliatum
Ceratocephala testiculata
Other NAF
Other IAG
Agropyron cristatum
Alyssum desertorum
Microsteris gracilis
Poa secunda
Native Legumes
Other NPF
Erodium cicutarium
Bromus tectorum
Sphaeralcea spp
A. t. wyomingensis
Amsinkia intermedia
Other NPG
Elymus elymoides
Salsola tragus
Sisymbrium altissimum

Figure 7. Residual correlations among species in postfire communities (n=252 subplots at 28 sites) suggest that plant communities are sorting into two groups. These residual correlations account for environmental covariates and are based on a joint species distribution model. Red indicates negative correlations, blue indicates positive correlations.

4. Discussion

Wildfires are converting vast areas of lower elevation *A. t. wyomingensis* ecosystems that burned infrequently in the past into grasslands dominated by invasive annuals that burn frequently. Repeated fires are widely believed to be the primary mechanism maintaining the non-native annual grass and forb communities (Davies, 2011; Balch *et al.*, 2013; Mahood and Balch, 2019; Mahood, Koontz and Balch, 2023). However, we found little evidence of regeneration of native plants in the absence of repeated fire. Our results indicated that the pulse disturbance of a single fire (Jentsch and White, 2019) had little effect on the abundance of invasive annual grasses but increased the abundance of invasive annual forbs. The invasive annuals were negatively associated with most native species and likely acted as a long-term press disturbance that reduced or prevented regeneration of the native species due to strong competition for available resources. The long-term press of cattle grazing tended to be negatively associated with the occurrence of many of the perennial native species but positively associated with the invasive annuals. The increased prevalence of non-native annuals other than *B. tectorum* associated with cattle grazing likely resulted in even greater competition with the native species. Few if any studies have evaluated the entire complement of species after fire in these ecosystems. We found the annual invaders sorted towards two distinct plant species assemblages post-fire that were related to grazing intensity, annual grass cover, and topography. Our results indicate that preemptive management to restore the native community soon after the initial wildfire will be needed to maintain or increase the biodiversity of these ecosystems.

4.1 Fire occurrence, fire timing, and fire year climate

Fire occurrence and circumstances surrounding the time of fire had lasting legacies on community composition. In these systems, it is already well-documented that fire occurrence is associated with altered community composition (Miller *et al.*, 2013; Mahood and Balch, 2019). Here, it was negatively associated with the abundance of native species (**Figure 2a**) and positively associated with the occurrence of non-native species (**Figure 4**). We found that a single fire resulted in a long-term reset of the species composition to one dominated by annual, non-native species (**Figures 2-4**) (Smith *et al.*, 2023; Urza *et al.*, 2024). The abundance of every functional group had significant associations with fire occurrence except for non-native annual grasses (**Figure 2a**). The lack of a significant difference in non-native annual grass abundance at burned and unburned sites in the functional group analysis has been observed in other studies (Case *et al.*, 2024), and underscores the conclusion by Smith et al (2023) that fire needs annual grass more than annual grass needs fire. In contrast to non-native annual grasses, non-native annual forbs and total herbaceous cover increased significantly. In already invaded but unburned shrublands, fire can change species composition by eliminating fire-intolerant native species and increasing non-native annual forbs with little impact on non-native annual grasses.

We found that post-fire plant communities were very similar in their functional group composition regardless of time since fire (TSF) (**Figure 2b, 3a**). The native species that had strong positive associations with TSF were generally of low prevalence, so these associations may be spurious (**Figure 6**). In contrast, the most prevalent annual forbs had strong positive associations with TSF.

Earlier ignition dates were associated with increased probability of occurrence of all but three non-native annual forb species (**Figure 4**). In the Great Basin, most fires occurred historically in late summer to early fall (Miller *et al.*, 2013). Annual grass- and forb-dominated areas dry out earlier in the season than the native perennial ecosystems (Davies and Nafus, 2013), which may lead to early fire ignitions that can spread into areas of intact sagebrush (Balch *et al.*, 2013; Bradley *et al.*, 2018). Native bunchgrasses suffer greater damage from fire earlier in the season during the period of active growth than when they are dormant later in the season (Wright and Klemmedson, 1965). In addition, the non-native annual grasses and forbs in this system tend to have high numbers of seeds in the seedbank (Hassan and West, 1986). *Bromus tectorum* in particular has high seed production postfire due to increased resource availability, has higher seed dispersal due to bare soils in the first few years after fire (Monty, Brown and Johnston, 2013), and has been reported to have smoke induced germination in its invaded range (Fenesi *et al.*, 2016; Naghipour *et al.*, 2016), Suppressed recovery of native bunchgrasses after a spring or early summer burn combined with the fire-adapted traits of non-native annuals help explain our results.

Fire-year climate was associated with the long-term persistence of many native species (**Figure 4**). In dryland ecosystems, perennial plants generally have deep, expansive root systems compared to those of annual species (Gibbens and Lenz, 2001; Ottaviani *et al.*, 2020). Seed production and seedling establishment of annual grasses are highly sensitive to inter-annual variability in water availability (Bradley and Mustard, 2005; Balch *et al.*, 2013; Prevéy and Seastedt, 2014). Higher CWD before the fire may reduce the abundance of non-native annuals (Pilliod, Welty and Arkle, 2017; Boyte, Wylie and Major, 2019). Lower cover of annuals can reduce burn severity as well as the amount of annual seeds in the seed bank after fire (Mahood, Koontz and Balch, 2023), potentially reducing competition between native perennials and non-native annuals during the critical period postfire for regrowth, seed production, and seedling establishment. Regional-scale climatic changes will be exacerbated locally by the loss of shrubs and subsequent dominance by non-native annuals, which can have major ecohydrological consequences. Higher soil temperatures and evaporation on areas dominated by non-native annuals can lead to drier microclimates and increased drought stress for re-establishing native plants (Turnbull *et al.*, 2012; Wilcox *et al.*, 2012).

4.2 Annual grass dominance and cattle grazing as long-term presses

High annual grass abundance was the long-term press that had the strongest negative association with diversity and perennial native cover (**Figure 3)**; it was consistently negatively associated with the persistence of most native species (**Figure 6**). Prior research has shown that annual grasses in this system build substantial seed bank reserves that can persist postfire (Schantz *et al.*, 2016). *Bromus tectorum* competes favorably against seedlings of native annual forbs and perennial bunchgrasses, reducing growth rate and biomass (Humphrey and Schupp, 2004; Parkinson, Zabinski and Shaw, 2013), and ultimately reducing plant establishment (Shriver *et al.*, 2019).

Our long-term grazing intensity metric was a coarse approximation that lacked information about seasonality. Still, the associations between grazing and the plant community from the IGA and JSDM aligned with theory and prior research. Our results indicated that long-term grazing intensity had a neutral relationship with *B. tectorum* and was positively associated with the occurrence of non-native annual grass species other than *B. tectorum*. Prior observational work in post-fire Wyoming big sagebrush ecosystems found positive associations between non-native annual grass presence and grazing at landscape scales (Williamson *et al.*, 2020). Experimental studies on these effects are limited but have not supported the notion that cattle grazing is a major driver of *B. tectorum* abundance. They have showed that in post-fire ecosystems the association of cattle grazing with non-native annual grass abundance varied depending on several factors, including the initial site conditions and interannual climate variability (Bates and Davies, 2023), the timing, intensity and duration of grazing (Davies, Bates and Boyd, 2016; Schroeder *et al.*, 2025), and the severity of the fire (Bates *et al.*, 2009; Davies, Svejcar and Bates, 2009; Bates and Davies, 2023). In post-fire landscapes with low resilience and resistance, like the one studied here, grazing intensity and the timing of livestock reintroduction is particularly important. Selective consumption of plants, seed dispersal of the nonnative annuals (Young, 1987), trampling, and prevention of post-fire recovery of biological soil crust (Belnap, Phillips and Troxler, 2006; Ponzetti, McCune and Pyke, 2007; Dettweiler-Robinson, Bakker and Grace, 2013; Root, Miller and Rosentreter, 2020) can all reduce native recovery and promote non-native annuals.

Rather than directly benefiting *B. tectorum*, long-term grazing intensity appeared to contribute to the sorting of which non-native annual forbs persisted. Globally, grazing pressure favors plant species that are shorter-lived, shorter-statured, and that have stoloniferous or rosette architectures over tussock architectures (Diaz et al 2007). Here, grazing intensity had strong positive associations with *C. testiculata, E. cicutarium*, *M. gracilis* and other IAG (**Figures 5-6**), all of which are shorter-statured. Plants that were negatively associated with grazing were taller (*S. altissimum, E*. *elymoides*, *A.*

intermedia, and *Sphaeralcea* spp.) (**Figure 4**). Both the direct impacts of plant consumption, the trampling of the soil surface and litter removal by cattle favors the establishment and persistence of low-growing forbs like *C. testiculata* and *E. cicutarium* (Reisner *et al.*, 2013). *Sisymbrium altissimum* has low grazing preference but had strong negative associations with grazing intensity, and a positive association with TSF. Evidence from Mahood *et al.* (2023) and here (**Figure 4**) suggests *S. altissimum* is more likely to occur after fire. Prior experimental work has focused on abundance of forbs when aggregated into one or more groups. In the Central Basin and Range pre-fire grazing increased post-fire forb abundance (Gornish *et al,* 2023), but immediate post-fire grazing had no short-term effect (1-2 years; Bruce *et al,* 2007). In the Northern Basin and Range abundance of annual forbs decreased after post-fire fall and winter grazing (Davies *et al.*, 2022), but in another study annual forbs abundance increased only after 20 years of long-term, heavy grazing, but were unaffected at other grazing intensities and shorter time periods after fire (Bates & Davies 2023). Our results illustrate how within a functional group such as annual forbs, the occurrence of species can be driven in different directions by factors such as grazing pressure, climate, and topography, even if abundance of that functional group as a whole is unaffected. These associations can be obscured when analyzing plot-scale averages of forb abundance with all species aggregated.

4.3 Management Implications

One of the most important consequences of a single fire event in intact *A. t. wyomingensis* systems is the persistent change in ecosystem structure and functioning. These low-elevation areas that have lost their shrub canopy are not likely to see the return of woody plants, and the associated ecosystem services, such as carbon sequestration, with passive restoration (Knutson *et al.*, 2014; Germino *et al.*, 2018; Shriver *et al.*, 2019). Because the post-fire annual grassland is likely to be an alternative stable state that is maintained by self-reinforcing feedback mechanisms, the feedbacks that maintain the post-fire assemblage must be identified and preemptive action must be taken to reverse them (Suding, Gross and Houseman, 2004). The evidence here suggests that within the annual grass and forb state, species composition follows gradients of topography, is associated with grazing intensity, and bears the legacy of fire-year climate.

The circumstances surrounding the fire, including the climate and time of ignition, influence long-term post-fire species composition in complex ways (Germino, Kluender and Anthony, 2022). With more detailed research, land managers may be able to use fire-year climate and fire seasonality to inform which species mixtures and propagation methods will be most likely to successfully establish and persist after fire. Multispecies analyses that are specific to the region and local knowledge may allow land managers to predict which species will likely be good candidates for restoration success within a given year, or a given set of circumstances.

In post-fire sites, many native plants were more likely to occur in plots with higher shrub cover (**Figure 6**). Shrubs can facilitate the persistence of understory plants by protecting them from livestock as well as providing an environment with higher soil moisture. Restoration of native shrub cover as a structural component, even if it is not sagebrush, may allow for the establishment and persistence of native plants that might not otherwise be able to persist in the face of annual grass and forb dominance and unfavorable climate (Power *et al.*, 2023; Zaiats *et al.*, 2024). Even though we did find increased probability of occurrence for shrub species with TSF in some models (**Figure 6**), this may not lead to eventual recovery to pre-fire levels of abundance. Allee effects (Taylor and Hastings, 2005) may cause low or even negative growth rates at low population densities. In long-lived species, like *A. t. wyomingensis*, 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. These transient dynamics are exacerbated by lower water availability, since lower water availability suppresses growth rates of individual plants (Shriver *et al.*, 2019).

Restoration of ecosystem structure that is resilient in the face of anticipated increases in fire activity and aridity may allow the system to regain the capacity to sequester soil carbon and the ecohydrological functioning that shrubs and other deep-rooted plants provide (Turnbull *et al.*, 2012). Here, *A. t. wyomingensis* had strong negative associations with fire occurrence, while other native shrubs had neutral relationships (**Figure 4**). Including resprouting, fire- and grazing-tolerant shrubs like *Ericameria nauseosa* or *Chrysothamnus viscidiflorus*, along with short-statured, grazing-tolerant native understory plants in initial restoration treatments would provide structural heterogeneity, aboveground carbon storage, and islands of soil fertility. However, while resprouting shrubs are more resilient against repeated fires than *A. t. wyomingensis*, they may still become locally extirpated with enough repeated fires (Power *et al.*, 2023). A multi-year approach, where resilience indicators (Chambers, Brown, Bradford, Board, *et al.*, 2023) and current climate (Simler-Williamson and Germino, 2022; Mahood *et al.*, 2024) are used to inform the level of investment, species, and methods immediately post-fire, followed by opportunistic repeat treatments in climatically favorable years (Shriver *et al.*, 2018), may be an effective strategy (Svejcar, Davies and Ritchie, 2023). Initial goals should be aimed at restoring structure. 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 to provide critically important shade and protection from grazers (Padilla and Pugnaire, 2006; Montesinos-Navarro *et al.*, 2017).

Prescribed fire is not likely to be a management tool with desirable outcomes in low-elevation *A. t. wyomingensis* systems with relatively low resilience and resistance (Chambers *et al.*, 2024) (**Figure 4**). Fire management should instead be directed towards preventing intact stands of sagebrush with high ecological integrity from burning during wildfires (Doherty, 2022; Chambers, Brown, Bradford, Doherty, *et al.*, 2023). When wildfires cannot be prevented, protecting unburned patches within the fire perimeter should be prioritized to allow for natural recolonization within the fire perimeter (Steenvoorden *et al.*, 2019).

4.4 Study Limitations

This study had limitations that may have affected the results. The spatial scale of the grazing data that we used was coarse relative to our plot data. The median size of the 24 grazing allotments studied was 32,000 ha, whereas we sampled 0.25 ha plots. The Central Basin and Range is topographically complex and relatively dry, and so within each allotment grazing patterns will be spatially heterogeneous and vary according to topography and especially water availability. Similarly, the climate data used was coarser (4 km) than the grain of the field sampling, and summarised across multi-month time scales. Even small areas with gentle topography can have large variations in microclimate (Barnard *et al.*, 2025) that affect plant community composition (Kemppinen *et al.*, 2024; Mahood *et al.*, 2024) and productivity (Macdonald *et al.*, 2025). These variations are not well-represented by coarse-scale data. Finally, while we believe that this is an appropriate use of space-for-time substitution (Walker *et al.*, 2010), it is important not to confound the results reported here as changes through time.

5. Conclusion

Wildfires are converting vast areas of low-elevation *A. t. wyomingensis* ecosystems that historically burned infrequently into grasslands that are burning frequently. These post-fire grasslands are often viewed as static because they are dominated by non-native annual invaders. However, understanding the post-fire dynamics of these ecosystems can provide insights into their restoration. We found that the initial fire acted like a pulse disturbance eliminating shrub cover and reducing perennial grass and forb cover. Persistent, high levels of invasive annual grasses and increases in annual forbs post-fire likely resulted in a long term press that reduced or prevented reestablishment of many native perennials. In addition, cattle grazing appeared to result in a long-term press that favored the persistence of many non-native annuals and structured the composition of the annual forb communities. Additional research into the nature of these interactions may provide information on developing more strategic restoration approaches. Our results clearly indicate that successful restoration of perennial species will require controlling or minimizing increases in non-native annual grasses and forbs post-fire. The timing, amount, or intensity of cattle grazing may need to be adjusted to ensure that it is neither increasing invasive annuals or decreasing the recovery of native perennials.

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Supplemental Figures and Tables

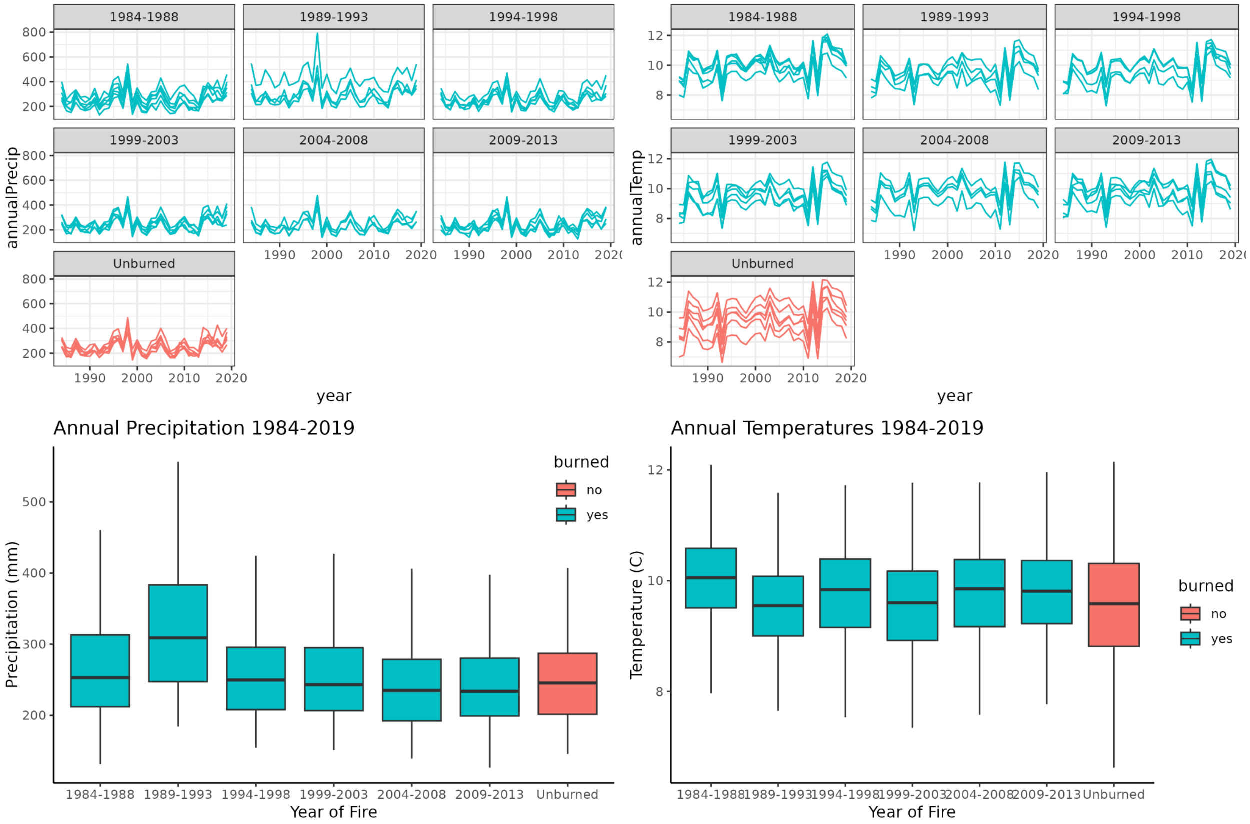

Figure S1. Visualization of annual mean temperatures and precipitation totals for the 35 study plots. Cite rangelands app for weather data

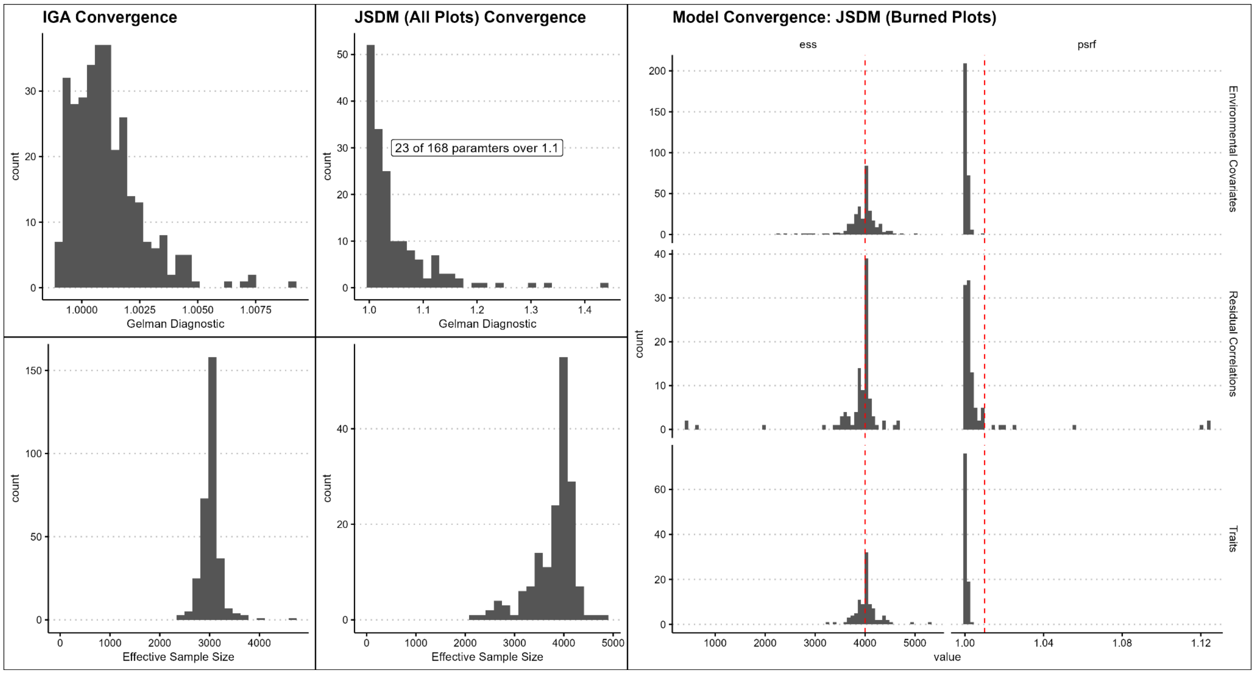

Figure S2. Model convergence diagnostics for the IGA and both JSDMs. Abbreviations: ess = Effective sample size, psrf = potential scale reduction factor.

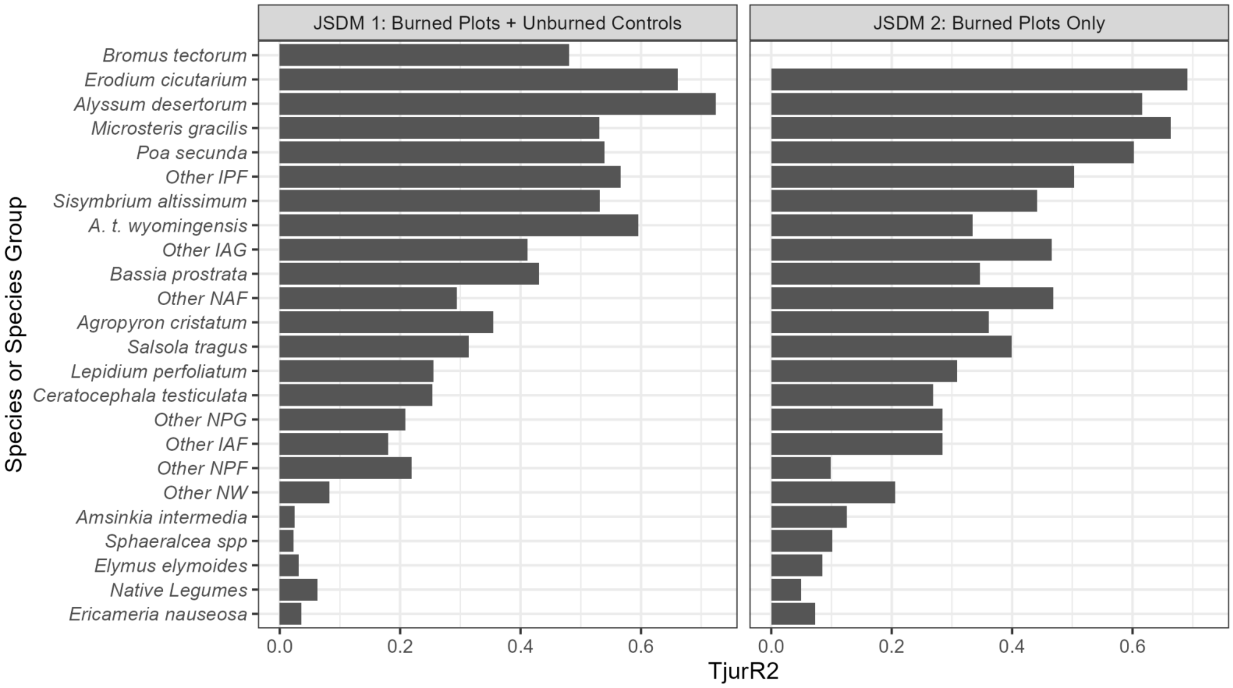

Figure S3. Variance explained (Tjur R^2) for each species in both JSDMs. Bromus tectorum had an R^2 of 0 for the burned-only plots because it occurred in 100% of the suplots and therefore adds not information to an occurrence model. It occurred in 98% of the subplots when unburned controls were included.

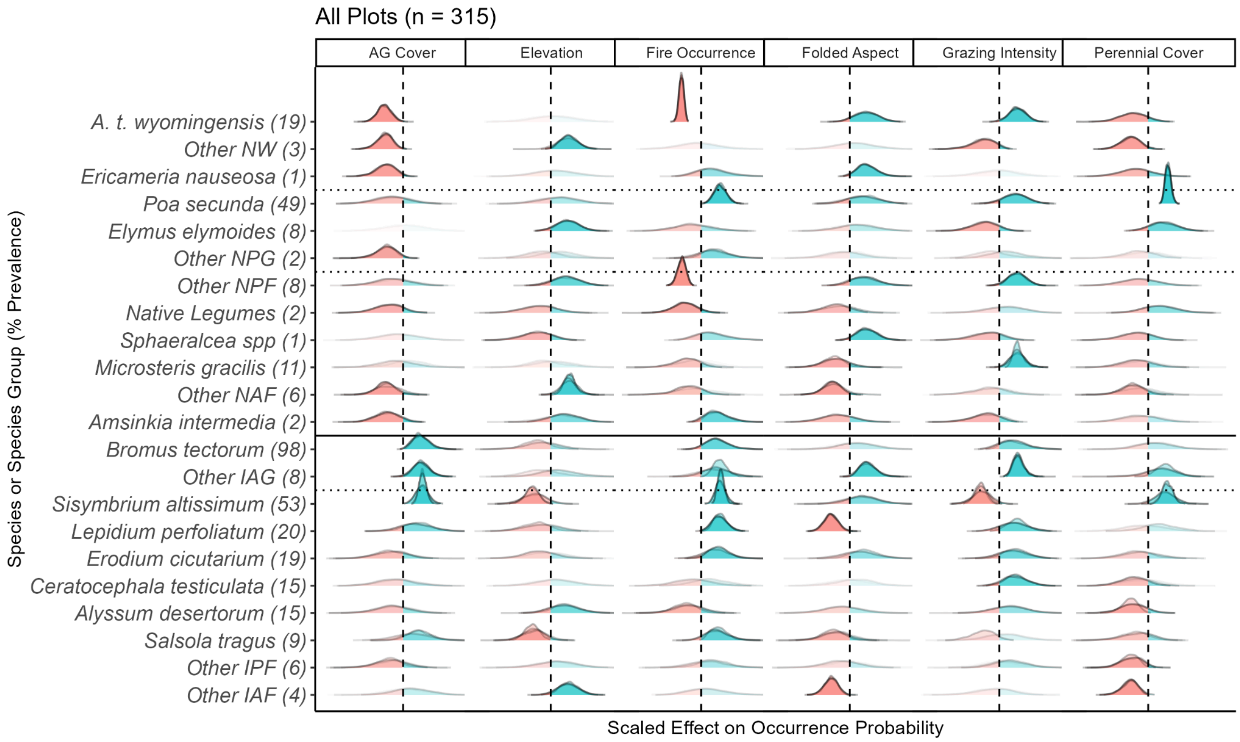

Figure S4. Model parameters from the JSDM of all plots.

Table S1. Species encountered (n=51), and how they were grouped for the JSDMs. Abbreviations: IPG Introduced Perennial Grass; IAF: Introduced Annual Forb; NAF: Native Annual Forb; NW: Native Shrub; NW: Introduced Shrub; IAG: Introduced Annual Grass; NPG: Native Perennial Grass; NC: Native Cactus; IPF: Introduced Perennial Forb.

Species	Functional Group	Group	Number of Plots
Ungrouped Species			
Agropyron cristatum	IPG		11
Alyssum desertorum	IAF		10
Amsinkia intermedia	NAF		10
Artemisia tridentata ssp. *wyomingensis*	NW		20
Bassia prostrata	IW		5
Bromus tectorum	IAG		35
Ceratocephala testiculata	IAF		16
Elymus elymoides	NPG		21
Ericameria nauseosa	NW		15
Erodium cicutarium	IAF		15
Lepidium perfoliatum	IAF		19
Microsteris gracilis	NAF		9
Opuntia sp.	NC		1
Poa secunda	NPG		29
Salsola tragus	IAF		8
Sisymbrium altissimum	IAF		29
Grouped Species		Group	
Sphaeralcea coccinea	NPF	Sphaeralcea_spp	9
Sphaeralcea parvifolia	NPF	Sphaeralcea_spp	4
Vulpia bromoides	IAG	introduced_annual_graminoid	9
Hordeum murinum	IAG	introduced_annual_graminoid	1
Cardaria draba	IPF	introduced_perennial_forb	3
Convolvulus sp	IPF	introduced_perennial_forb	1

Medicago sativa	IPF	introduced_perennial_forb	1
Stipa hymenoides	NPG	native_perennial_graminoid	5
Elymus cinereus	NPG	native_perennial_graminoid	4
Stipa comata	NPG	native_perennial_graminoid	2
Unknown perennial grass	NPG	native_perennial_graminoid	1
Lactuca serriola	IAF	introduced_annual_forb	4
Tragopogon dubius	IAF	introduced_annual_forb	4
Descurainia sophia	IAF	introduced_annual_forb	2
Bassia scoparia	IAF	introduced_annual_forb	1
Halogetan glomeratus	IAF	introduced_annual_forb	1
Draba albertina	NAF	native_annual_forb	2
Chenopodiaceae sp	NAF	native_annual_forb	1
Collinsia parviflora	NAF	native_annual_forb	1
Gayophytum ramosissimum	NAF	native_annual_forb	1
Lagophylla glandulosa	NAF	native_annual_forb	1
Layia glandulosa	NAF	native_annual_forb	1
Astragalus whitneyi	NPF	native_legume_forb	2
Astragalus lentiginosus	NPF	native_legume_forb	1
Astragalus sp 1	NPF	native_legume_forb	1
Astragalus sp 2	NPF	native_legume_forb	1
Astragalus sp 3	NPF	native_legume_forb	1
Lupinus argenteus	NPF	native_legume_forb	1
Lupinus lepidus	NPF	native_legume_forb	1
Lupinus sp	NPF	native_legume_forb	1
Grayia spinosa	NW	native_shrub	5
Chrysothamnus viscidiflorus	NW	native_shrub	4
Tetradymia glabrata	NW	native_shrub	3
Artemisia arbusculus	NW	native_shrub	1
Atriplex confertifolia	NW	native_shrub	1
Ephedra nevadaensis	NW	native_shrub	1

Sarcobatus maniculatus	NW	native_shrub	1
Tetradymia spinosa	NW	native_shrub	1
Atriplex sp	NW	native_shrub	1
Calochortus bruneaunis	NPF	native_perennial_forb	8
Crepis occidentalis	NPF	native_perennial_forb	3
Phlox longifolia	NPF	native_perennial_forb	3
Zigadenus sp	NPF	native_perennial_forb	3
Descurainia pinnata	NPF	native_perennial_forb	2
Agoseris glauca	NPF	native_perennial_forb	1
Agoseris heterophylla	NPF	native_perennial_forb	1
Allium sp	NPF	native_perennial_forb	1
Asteraceae sp	NPF	native_perennial_forb	1
Chaenactis douglasii	NPF	native_perennial_forb	1
Eriogonum sp	NPF	native_perennial_forb	1
Mirabilis albida	NPF	native_perennial_forb	1
Oenothera sp	NPF	native_perennial_forb	1
Penstemon sp	NPF	native_perennial_forb	1
Perideridia bolanderi	NPF	native_perennial_forb	1
Phlox diffusa	NPF	native_perennial_forb	1
Phlox hoodii	NPF	native_perennial_forb	1
Stephanomeria pauciflora	NPF	native_perennial_forb	1
Macraenthera sp	NPF	native_perennial_forb	1