Running head: Burn severity and the grass-fire cycle

Title: Fuel connectivity, burn severity, and seedbank survivorship drive the grass fire cycle in a semi-arid shrubland.

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Open Reseach Statement: Data and code to recreate the analysis are freely available at https://www.github.com/admahood/seed-bank (DOI available after acceptance) and the Dryad data repository (url given after acceptance).

Abstract

Introduced grasses can initiate novel grass-fire cycles that alter ecosystem structure and function, and threaten biodiversity. In sagebrush communities in the western United States, annual grass invasion increases the connectivity of fine fuels, which increases the size and spatial contiguity of fires. This increase in fire size and contiguity results in post-fire plant communities that are dominated by introduced annual grasses (IAG), which are themselves more likely to promote large fires and initiate a novel grass-fire cycle. But the mechanisms by which pre-fire invasion and fire occurrence are linked to higher post-fire flammability are not fully understood.

Here, we investigate the successive mechanisms in a potential positive feedback that maintains the novel annual grass-fire cycle. We used total vegetation cover (TVC) as a proxy for fuel connectivity and found that pre-fire TVC increased burn severity. We then used a Bayesian joint species distribution model to examine how burn severity affected the proportion of IAG in the seed bank, and found that higher burn severity had mostly positive or neutral effects on the occurrence of IAG and other non-native species, and mostly negative or neutral relationships with native species. We found that the abundance of IAG seeds in the seedbank immediately post-fire had a positive effect on the fuel connectivity 3 years after fire, thus completing a positive feedback promoting IAG. These results suggest that measurable characteristics of ecosystem structure (e.g. TVC) and fire (dNBR) may be used to inform management actions to mitigate the negative effects of the grass-fire cycle, perhaps via targeted restoration applications or pre-fire fuel treatments.

Keywords: cheatgrass, sagebrush, grass-fire cycle, joint species distribution model, burn severity, fuel connectivity, *Bromus tectorum*, *Artemisia tridentata*

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 (80, 30 and 0 percent) that occur among overlapping levels of precipitation, and so it is thought that internal, self-reinforcing mechanisms maintain these 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 (The grass-fire cycle, D'Antonio and Vitousek 1992; Staver, Archibald, and Levin 2011).

A classic example of a novel grass-fire cycle in a semi-arid, temperate system is the invasion and persistence 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 (Davies et al. 2011). This has been attributed to a host of causes, including wildfire (Balch et al. 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of annual grasses. At uninvaded sites, the space between shrubs is typically composed of bare ground covered in biological soil crust and dotted with perennial bunch grasses. The lack of fuel connectivity is believed to limit fire spread, with a historical fire regime of infrequent, patchy fires (Baker 2006; Bukowski and Baker 2013; Keeley and Pausas 2019). Annual grass invasion increases fuel connectivity while decreasing fuel moisture (Davies and Nafus 2013), leading to increased fire size and frequency (Whisenant 1990; Knapp 1996; Balch et al. 2013). After fire, the landscape is often dominated by introduced annual grasses and forbs. 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.

The relationship between the species composition of the seed bank and fire severity and/or intensity is relatively understudied. In different systems, individual species have adapted strategies to cope with fires that may be adapted to different severities. 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, beyond simply affecting seed mortality, fire temperature can also alter physical seed dormancy thresholds (Liyanage and Ooi 2017).

In order for an annual like *B. tectorum* it to benefit from fire, which it clearly does (Balch et al. 2013; Mahood and Balch 2019), it would need 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 (Brooks et al. 2004; Jones et al. 2015) and burn severity (defined here as the proportion of biomass burned (Keeley 2009)). Burn severity can be measured after fire *in situ*, or estimated from satellite images by comparing scenes from before and after the fire (J. D. Miller et al. 2009). While in many cases fires that burn at higher temperatures will also burn at higher severities, grass fires may not always have such a relationship. Direct measurements have shown that *B. tectorum* burns at low temperatures (Beckstead et al. 2011; Germino, Chambers, and Brown 2016). Because fire duration is inversely related to soil heating, lower fire temperatures can be inferred from the commonly observed phenomenon that *B. tectorum*-fueled fires burn fast. Soil heating 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* also increases horizontal fuel connectivity (Davies and Nafus 2013), this leads to more contiguously burned areas with fewer unburned plants, and therefore higher burn severity, despite lower fire temperatures.

If increased burn severity is a mechanism by which *B. tectorum* invasion excludes native plants in sagebrush shrublands, then an area with high burn severity should 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 and 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 tolerating drought and opportunistically devoting its resources to producing large seed crops in cool, wet years (Meyer 1994; Perryman et al. 2001; Shriver et al. 2018). When it burns it burns with high intensity, killing individual plants, 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; 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 remain viable for at least two years 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 (Melillo, Richmond, and Yohe 2014; 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 (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). Second, the dominant plant, *B. tectorum*, can out-compete native plants for early spring moisture (Meyer 1994; 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 (Appendix S1, Fig. S1). 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 the day 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 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 *Artemisia* 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 on the unburned side (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 aboveground plant species.

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.

2.3 Post-Fire Vegetation Sampling

We sampled the vegetative occupancy and cover in May 2017, the growing season immediately after the fire and again in September 2019. 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.

2.4 Estimating Burn Severity with Landsat 8 OLI

We downloaded the “fire bundle” of the Hot Pot fire from 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 were likely 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 of each seed bank plot for pixels whose centroids fell inside of the fire perimeter and calculated the mean.

2.5 Statistical Analysis

Our statistical analysis centered around trying to understand each component of the positive feedback loop posited by the 4 hypotheses described above. 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, J. D. Miller et al. 2009) as the response variable. With the field data we collected, we created an ordinary least squares (OLS) linear model with burn severity 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.

We were concerned that because our data were collected at the edge of the fire, the burn severity calculated at each point may have included partially burned pixels. So, as a supplement, we examined the same relationship by creating a model of TVC using Landsat Thematic Mapper (TM) surface reflectance data using TVC from the Bureau of Land Management’s Assessment, Inventory and Monitoring dataset (AIM, 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 surface reflectance 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 surface reflectance values to calculate various vegetation indexes (Appendix S1: Table S1), 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 generalized linear model of TVC with a beta distribution. For this and all linear models, we started with the largest possible model and used backwards selection following the methodology of Zuur et al. (2009). We used the final reduced 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.

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

Equation 2: $NDSVI = \frac{SWIR_1 - Red}{SWIR_1 + Red}$

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 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) 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) as a dependent variable. We used fuel connectivity, elevation, and aspect as independent variables.

All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis are freely available at https://www.github.com/admahood/seed-bank (DOI available after acceptance) and the Dryad data repository (url given after acceptance).

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

1a, Appendix 1: Table S2). For our remotely sensed analysis, our most parsimonious model of TVC explained 35% of the variation and had Green NDVI, NDSVI and their interaction as predictors (Appendix S1: Table S2). Our model of dNBR using the predicted TVC within the fire perimeter as a predictor of dNBR explained 42% of the variation and the relationship between TVC and burn severity was positive and significant ($p \ll 0.01$, Figure 1a, Appendix S1: Table S2).

The vast majority of seeds that germinated in the greenhouse were the two most common grass species, *P secunda* and *B. tectorum* (Appendix S1: Table S3). 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 (Appendix S1: Fig. S2). For H2, the JSDM converged well (Appendix S1: Fig S3). Gelman diagnostics all very close to 1 and the effective sample size centered on 4,000. Elevation had the most significant effects on individual species and explained the most variance on average (36%). Burn severity explained 23% of the variance on average and was supported at the 95% level for 5 species. 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. 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. 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 $R^2 =$

0.75,Figure 1c, Appendix S1: Table S2). For H4 the most parsimonious model (Adj R^2 = 0.89, Appendix S1: Table S2) 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 (β = -0.28, p=0.004, Figure 1d).

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. The 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 (Davies and Nafus 2013). This change in the spatial distribution of fine fuels has been associated with larger and more frequent fires (Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) also increases burn severity (H1, Figure 1a). Higher burn severity was associated with an increased occurrence of introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure 1b). Finally, higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher post-fire fuel connectivity (H3, Figure 1c). In addition, we found evidence that high post-fire fuel connectivity was associated with lower aboveground diversity (H4, Figure 1d). This suggests that during inter-fire intervals, there may be additional mechanisms (e.g. competition) maintaining the post-fire, annual grass-dominated species assemblage.

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 plot locations had mature canopies of native shrubs with the inter-shrub space occupied mostly by native bunchgrasses and forbs, with no fire occurrence since 1984. 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 fire, almost all of the plots were dominated by introduced annuals, and lacked any structural heterogeneity. Thus native plants may have been be able to persist via niche compartmentalization after the initial invasion, but fire burned away most of the seeds (Appendix S1, Fig. S1) and removed 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) allow the process of interspecific competition to be dominant (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) CO_2 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 (Appendix S1, Fig. S3). 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.

Contrasts among forests and shrublands as it pertains to remote sensing

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. 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 (Appendix S1: Fig. S4 a-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 (Appendix S1: Fig. S4 d-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 (Jones et al. 2015) and unconsumed annual and perennial grass bases. 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 discrepancy was not unexpected, as the classified burn severity is known to be of limited use for research (Kolden, Smith, and Abatzoglou 2015).

Spectral reflectance has long been used to characterize wildfire fuels. Unique signatures of remotely-sensed spectral reflectance are typically matched to categorical fuel classifications (CFCs), which describe the physiognomy of vegetation and its potential to support various fire behavior (Ottmar et al. 2007). While different CFCs can provide a general understanding of fuel amount and connectivity, recent efforts using data with finer spatial and spectral resolution may improve fuel classification with more continuous, multi-dimensional measurements (Stavros et al. 2018). The continuous measure of NDVI in western U.S. coniferous forests is a proxy for live fuel biomass, which likely explains its positive association with wildfire severity (Parks et al. 2018; Koontz et al. 2020). NDVI also correlates with vegetation cover in these forested systems, and so greater crown connectivity may also explain the NDVI/severity relationship at local scales. When using a more direct NDVI-derived measure of vegetation connectivity in Sierra Nevada yellow pine/mixed-conifer, Koontz et al. (2020) found that greater variability in forest structure also increased the probability of high-severity fire. Here, we arrived at a combination of NDVI and NDSVI to describe the fuel connectivity of the annual grass invaded Great Basin sagebrush community to better reflect key differences in the physiognomies of forest and arid shrublands. In sagebrush shrublands, the fuel that contributes to large wildfires is a mixture of evergreen shrubs interspersed with herbaceous plants that remain green for only a portion of the growing season, and then become dry and straw-colored. Thus, both the live and dead fuel need to be taken into account in remote measurements of fuel connectivity.

Management implications

These results demonstrate that the strength of the grass-fire cycle in this system is controlled by measurable fire properties and ecosystem structural components. Land managers may be able to increase their chances of restoration success by using existing methods or developing novel ones that manipulate these components to weaken or even break the positive feedback cycle. This work provides further evidence that the post-fire annual grassland is a system where the degraded state represents an alternative species assemblage from that of the restoration target. Because the propagules of the original assemblage are no longer present, methods that rely on natural succession may 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 (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. Our results also suggest that calculating the burn severity using Landsat or Sentinel images may help land managers identify areas with a greater likelihood of successful seeding.

Livestock grazing can reduce fuel connectivity in uninvaded sagebrush (Davies et al. 2010). At the same time, livestock grazing can decrease the resistance to invasion by *B. tectorum* via negative effects on biological soil crust (BSC) (Chambers et al. 2014; 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 may also 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.

Greenhouse or *in situ* germination assays are time-consuming and require botanical expertise, and are very important. There are many studies that only study fire occurrence as it relates to the seed bank. One potential avenue for future research may be linking satellite-derived estimates of burn severity (Parks et al. 2018) and TVC with locations of prior studies in retrospective meta-analyses. Teasing out these mechanisms will increase our understanding of how generalizable these phenomena are, and may provide more insight on how to mediate the negative effects or break the positive feedback loop.

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Figure Captions

Figure 1. On the left side of (a), 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. Panel b shows the 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. In (c), fuel connectivity three years post-fire is modelled by seedbank composition, elevation and pre-fire aboveground species richness. In (d) 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, points are the partial residuals, and dotted lines are the 95% confidence intervals. $p < 0.05$ for black lines, $p > 0.05$ for grey lines.

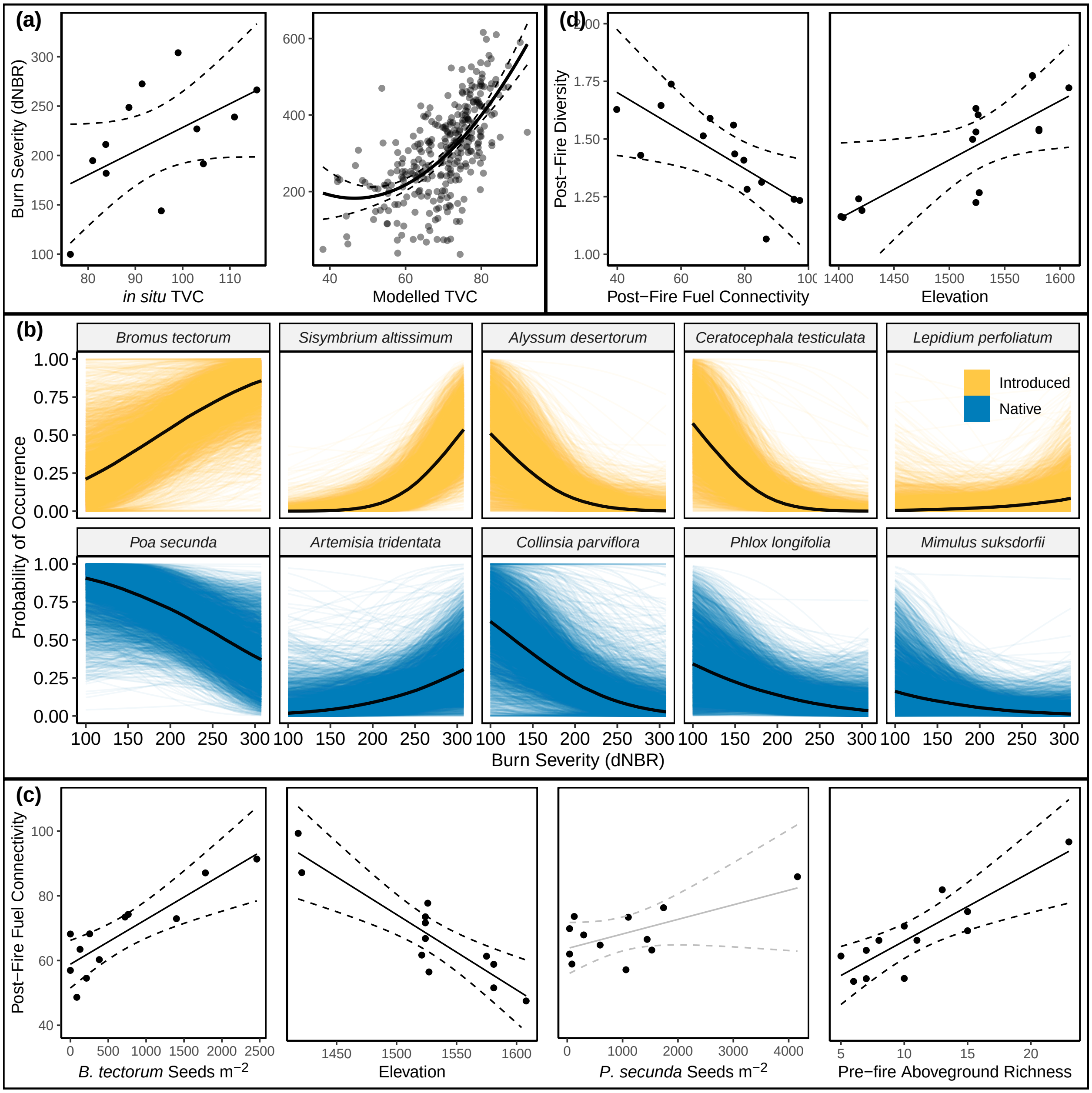
(a)
Burn Severity (dNBR)
300
250
200
150
100
80
90
100
110
in situ TVC
600
400
200
40
60
80
Modelled TVC
(d)
Post−Fire Diversity
2.00
1.75
1.50
1.25
1.00
40
60
80
100
Post−Fire Fuel Connectivity
1400
1450
1500
1550
1600
Elevation
(b)
Bromus tectorum
Sisymbrium altissimum
Alyssum desertorum
Ceratocephala testiculata
Lepidium perfoliatum
Introduced
Native
Poa secunda
Artemisia tridentata
Collinsia parviflora
Phlox longifolia
Mimulus suksdorfii
Probability of Occurrence
1.00
0.75
0.50
0.25
0.00
100
150
200
250
300
Burn Severity (dNBR)
(c)
Post−Fire Fuel Connectivity
100
80
60
40
0
500
1000
1500
2000
2500
B. tectorum Seeds m^{-2}
1450
1500
1550
1600
Elevation
0
1000
2000
3000
4000
P. secunda Seeds m^{-2}
5
10
15
20
Pre−fire Aboveground Richness

Figure 1: .