

Running head: Annual grasses, burn severity, seedbank

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

Title: But wait, there's more: Burn severity is a mechanism for the grass-fire cycle

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¹ Abstract

² Alternative stable states are an important topic in the context of global change in which
³ positive feedbacks maintain two distinct plant communities under the same climatic conditions.
⁴ In sagebrush communities in the western United States, annual grass invasion increases the
⁵ connectivity of fine fuels, which increases the size and spatial contiguity of fires. This results
⁶ in post-fire plant communities that are dominated by introduced annual grasses (IAG). But
⁷ it is unclear exactly how fire directly benefits the IAG. Here, we used total vegetation cover
⁸ (TVC) as a proxy for fuel connectivity and found that pre-fire TVC increased burn severity.
⁹ We then used a joint species distribution model to examine how burn severity affected the
¹⁰ proportion of IAG in the seed bank, and found that higher burn severity had mostly positive
¹¹ or neutral effects on the occurrence of IAG and other non-native species, and mostly negative
¹² or neutral relationships with native species. To complete the positive feedback loop, we found
¹³ that the abundance of IAG seeds in the seedbank immediately post-fire had a positive effect
¹⁴ on the fuel connectivity 3 years after fire. This is the first study that we are aware of in the
¹⁵ western US that shows how burn severity influences seed bank species composition, as well
¹⁶ as examining the full feedback loop between fuel connectivity, burn severity and seed bank
¹⁷ species composition. These results provide measurable ecosystem structure components as
¹⁸ well as fire characteristics that land managers may be able to use to mitigate the effects of
¹⁹ the grass-fire cycle.

²⁰ *Keywords:* cheatgrass, sagebrush, grass-fire cycle, joint species distribution model, burn
²¹ severity, fuel connectivity

²² **1. Introduction**

²³ One of the consequences of global change in the 21st century that is most difficult to reverse
²⁴ is when ecosystems abruptly shift from one stable species assemblage to another (Ratajczak
²⁵ et al. 2018). In tropical ecosystems, three alternative stable states have been identified
²⁶ along a gradient of precipitation: forests, savannas and grasslands (Hirota et al. 2011;
²⁷ Staver, Archibald, and Levin 2011). These three states cluster around values of tree cover
²⁸ (approximately 80, 30 and 0 percent) that occur among overlapping levels of precipitation,
²⁹ and so it is thought that they exhibit states of hysteresis in which internal, self-reinforcing
³⁰ mechanisms maintain alternate states (Andersen et al. 2009). In the forested state there is
³¹ a self-reinforcing positive feedback between evapotranspiration and tree cover (Staal et al.
³² 2020). In the grassland and savanna states, there are feedbacks between grass flammability
³³ and fire occurrence (Staver, Archibald, and Levin 2011; D'Antonio and Vitousek 1992).

³⁴ A classic example of hysteresis in a semi-arid, temperate system is the invasion of *Bromus*
³⁵ *tectorum* L. and other introduced annual grasses in the Great Basin of the western United
³⁶ States. Here, over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*
³⁷ Beetle & Young) ecosystems have been degraded, fragmented or lost completely (Davies
³⁸ et al. 2011). This has been attributed to a host of causes, including wildfire (Balch et al.
³⁹ 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of
⁴⁰ annual grasses. In this open shrubland, the space between shrubs is primarily composed of
⁴¹ bare ground covered in biological soil crust, dotted with perennial bunch grasses. The lack
⁴² of fuel connectivity is believed to have limited fire spread, with a fire regime of infrequent,
⁴³ patchy fires (Keeley and Pausas 2019). Annual grass invasion increases fuel connectivity
⁴⁴ while decreasing fuel moisture (Davies and Nafus 2013), leading to increased fire size and
⁴⁵ frequency (Whisenant 1990; Knapp 1996; Balch et al. 2013). After fire, the landscape is often
⁴⁶ dominated by introduced annual grasses and forbs. This causes a >50% loss of aboveground
⁴⁷ carbon storage (Bradley et al. 2006; Nagy et al. 2020). But in order to understand how

48 the grassland state persists, the mechanisms by which fire benefits the introduced annual
49 grass must be understood. Petraitis and Latham (1999) posited that the maintenance of
50 alternate species assemblages requires first a disturbance that removes the species from the
51 initial assemblage and second the arrival of the species of the alternate assemblage. One
52 understudied mechanism that may explain both is the interaction between burn severity and
53 the species composition of the soil seed bank.

54 The relationship between the species composition of the seed bank and fire severity and/or
55 intensity is understudied, but more attention has been given to the subject recently. In
56 boreal forests, the depth of the burn may be more important than the temperature of
57 the fire, with species-specific effects on recovery depending on whether the species recovers
58 via resprouting or from the seed bank (Morgan and Neuenschwander 1988; Schimmel and
59 Granström 1996). In a wetland study in Japan, high severity fire was found to increase
60 seedbank diversity, and the similarity between the seedbank composition and aboveground
61 composition was higher in places burned at high severity (Kimura and Tsuyuzaki 2011). There
62 have been a handful of studies in temperate, semi-arid regions. Lipoma, Funes, and Díaz
63 (2018) found that in shrubland high-severity fire reduced the overall number of seeds in the
64 seedbank but did not change the floristic or functional composition. Maia et al. (2012) found
65 intraspecific differences in post-fire seedbank densities that were explained by burn severity
66 in a pine plantation in Portugal. Palmer, Denham, and Ooi (2018) found that the residual
67 seedbank after fire varied with severity between two *Acacia* species in Australia. Wright,
68 Latz, and Zuur (2016) found that Australian mulga (*Acacia aneura*) had higher regeneration
69 after higher fire temperatures. In Iran, Heydari et al. (2017) found that low-severity fire
70 increased diversity in the soil seed bank, but high-severity fire led to losses. These studies
71 show that the effects of fire severity on the seed bank are ecosystem- and species-specific.
72 High severity fire can benefit species that use the seedbank (Kimura and Tsuyuzaki 2011), be
73 seedbank-neutral (Lipoma, Funes, and Díaz 2018), or have a negative effect (Heydari et al.
74 2017). Furthermore, beyond simply affecting seed mortality, fire temperature can also alter

75 physical seed dormancy thresholds (Liyanage and Ooi 2017).

76 Because *B. tectorum* is annual, in order for it to benefit from fire, which it clearly does (Balch
77 et al. 2013; Mahood and Balch 2019), it would need enough seeds in the post-fire landscape to
78 achieve a fitness benefit and become well-represented in the post-fire plant assemblage (Bond
79 and Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal, and
80 *B. tectorum* seeds have been shown to have increased dispersal distances after fire (Monty,
81 Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. There
82 is strong evidence that *B. tectorum* builds a well-stocked pool of seeds in the soil and litter,
83 even when it is not well represented in the above-ground plant assemblage (Young and Evans
84 1975; Hassan and West 1986; Boudell, Link, and Johansen 2002). If the increase in fuel
85 connectivity caused by *B. tectorum* increases the severity of fire, it stands to reason that
86 burn severity would influence the community composition of the post-fire seed bank in a way
87 that facilitates the post-fire dominance of *B. tectorum*. To our knowledge, despite several
88 studies on the relationship between fire and the seed bank in this system (Young and Evans
89 1975; Hassan and West 1986; Humphrey and Schupp 2001; Boudell, Link, and Johansen
90 2002; Barga and Leger 2018), no studies to date have examined this potential effect of burn
91 severity on the seed bank.

92 There is strong evidence that *B. tectorum* invasion alters the physical properties of fire,
93 including fire temperature (Brooks et al. 2004; Jones et al. 2015) and burn severity (the
94 proportion of biomass burned (Keeley 2009)). Burn severity can be measured after fire *in situ*,
95 or via satellite by comparing scenes from before and after the fire (J. D. Miller et al. 2009).
96 While in many cases fires that burn at higher temperatures will also burn at higher severities,
97 grass fires may not always have such a relationship. Direct measurements have shown that *B.*
98 *tectorum* burns at low temperatures (Beckstead et al. 2011; Germino, Chambers, and Brown
99 2016). Because fire duration is inversely related to soil heating, lower fire temperatures can
100 be inferred from the commonly observed phenomenon that *B. tectorum*-fueled fires burn fast.

101 Soil heating affects the response of vegetation to fire (Gagnon et al. 2015), including the
102 capacity of the seeds of *B. tectorum* to remain viable after fire (Humphrey and Schupp 2001).
103 Because *B. tectorum* also increases horizontal fuel connectivity (Davies and Nafus 2013), this
104 leads to more contiguously burned areas with fewer unburned plants, and therefore higher
105 burn severity—even with lower fire temperatures.

106 If increased burn severity is a mechanism by which *B. tectorum* excludes native plants in
107 sagebrush shrublands, then an area with high burn severity may have a lower occurrence of
108 viable seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced
109 annual plants. This would lead to the dominance of introduced annual grasses and forbs
110 would result in higher fuel connectivity, closing the positive feedback loop. Prior work has
111 demonstrated that *A. tridentata* communities have historically had long fire rotations (>150
112 years) (Baker 2006; Bukowski and Baker 2013). Plants that are adapted to infrequent fire
113 would be unlikely to produce seeds that are adapted to surviving fire, or dispersal mechanisms
114 to take advantage of the resources available immediately after fire (Davis et al. 2000; Keeley
115 et al. 2011). *A. tridentata* relies on tolerating drought and opportunistically devoting its
116 resources to producing big seed crops in cool, wet years (Meyer 1994; Perryman et al. 2001;
117 Shriver et al. 2018). When it burns it burns with high intensity, killing individual plants,
118 and the remaining unburned neighbors seed the area (*sensu* Schwilk and Kerr 2002). The
119 seeds have a short dispersal distance, the vast majority falling within a few meters of the
120 parent plant (Meyer 1994; Schlaepfer, Lauenroth, and Bradford 2014). They typically lose
121 their viability after one growing season if they remain on the soil surface or under litter, but
122 can retain some viability for at least 24 months if they are buried under a few inches of soil
123 (Wijayratne and Pyke 2009).

124 The Great Basin has not escaped the recent warming and drying trend that the western U.S.
125 has experienced (Melillo, Richmond, and Yohe 2014; Bradford et al. 2020). This is expected
126 to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly

127 by causing the plants to produce lighter seeds (Schlaepfer, Lauenroth, and Bradford 2014).
128 With this in mind, there is another potential self-reinforcing mechanism that could serve to
129 maintain the high fuel connectivity state without fire. That is that the post-fire state with
130 high fuel connectivity is associated with two mechanisms for competitive exclusion of natives.
131 First, it reduces soil moisture which is unfavorable for *Artemisia* seedlings (Turnbull et al.
132 2012; Wilcox et al. 2012). Second, the dominant plant, *B. tectorum*, can out-compete native
133 plants for early spring moisture (Meyer 1994; Chambers et al. 2007).

134 Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot
135 Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July
136 2016. Because it burned a large area in only three days, we could sample a broad area
137 while being reasonably certain that the climatic conditions during the fire were the same
138 at all sites. Because we collected our samples immediately after the fire was extinguished,
139 we felt confident that the seed bank samples did not contain seeds deposited by post-fire
140 dispersal. We put the samples in cold storage and germinated the seeds from those cores in a
141 greenhouse the following spring. In spring 2017 and fall 2019 we collected information on
142 vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel
143 connectivity would be positively related to burn severity; (H2) burn severity would increase
144 the occurrence probability of introduced annual species in the seed bank and reduce the
145 occurrence probability of native species; (H2a) increased fuel connectivity brought on by
146 the invasion of annual grasses already depleted the diversity of the soil seed bank before the
147 fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related
148 to post-fire fuel connectivity. In addition, because in our study system sites with high fuel
149 connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high
150 post-fire fuel connectivity of those near-monocultures would result in lower aboveground
151 species diversity due to competitive pressure.

₁₅₂ **2. Methods**

₁₅₃ *2.1 Study Area*

₁₅₄ The study was conducted in north-central Nevada the day after a large fire (the Hot Pot
₁₅₅ Fire) was extinguished (Figure 1). The Hot Pot Fire burned just over 50,000 hectares in
₁₅₆ less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big
₁₅₇ sagebrush plant communities. The fire occurred after the early season plants, including *B.*
₁₅₈ *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone
₁₅₉ to seed, and before the late season species, including Wyoming big sagebrush, had produced
₁₆₀ flowers. Thus we were able to isolate the effect of the fire without any confounding effects of
₁₆₁ post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged
₁₆₂ from 1397 to 1607 meters in elevation.

₁₆₃ *2.2 Seed Bank Sampling*

₁₆₄ In early July 2016, we collected samples of the soil seed bank at fourteen locations immediately
₁₆₅ after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where
₁₆₆ it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites
₁₆₇ were mature sagebrush communities with no history of fire since at least 1984. Three plots
₁₆₈ had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS)
₁₆₉ fire history (Eidenshink et al. 2007) and had high cover of *B. tectorum*, but still had scattered
₁₇₀ sagebrush cover. We used a metal stake to mark paired burned and unburned sampling
₁₇₁ locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic
₁₇₂ disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the
₁₇₃ perimeter. Within 3 m of each marker, we extracted 12, 6 cm deep, 5 cm diameter, soil cores.
₁₇₄ Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system
₁₇₅ (Shinneman and McIlroy 2016), and so they are not uniformly distributed (Boudell, Link, and
₁₇₆ Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemisia*
₁₇₇ have different germination rates based on the micro-site they find themselves in (i.e. under

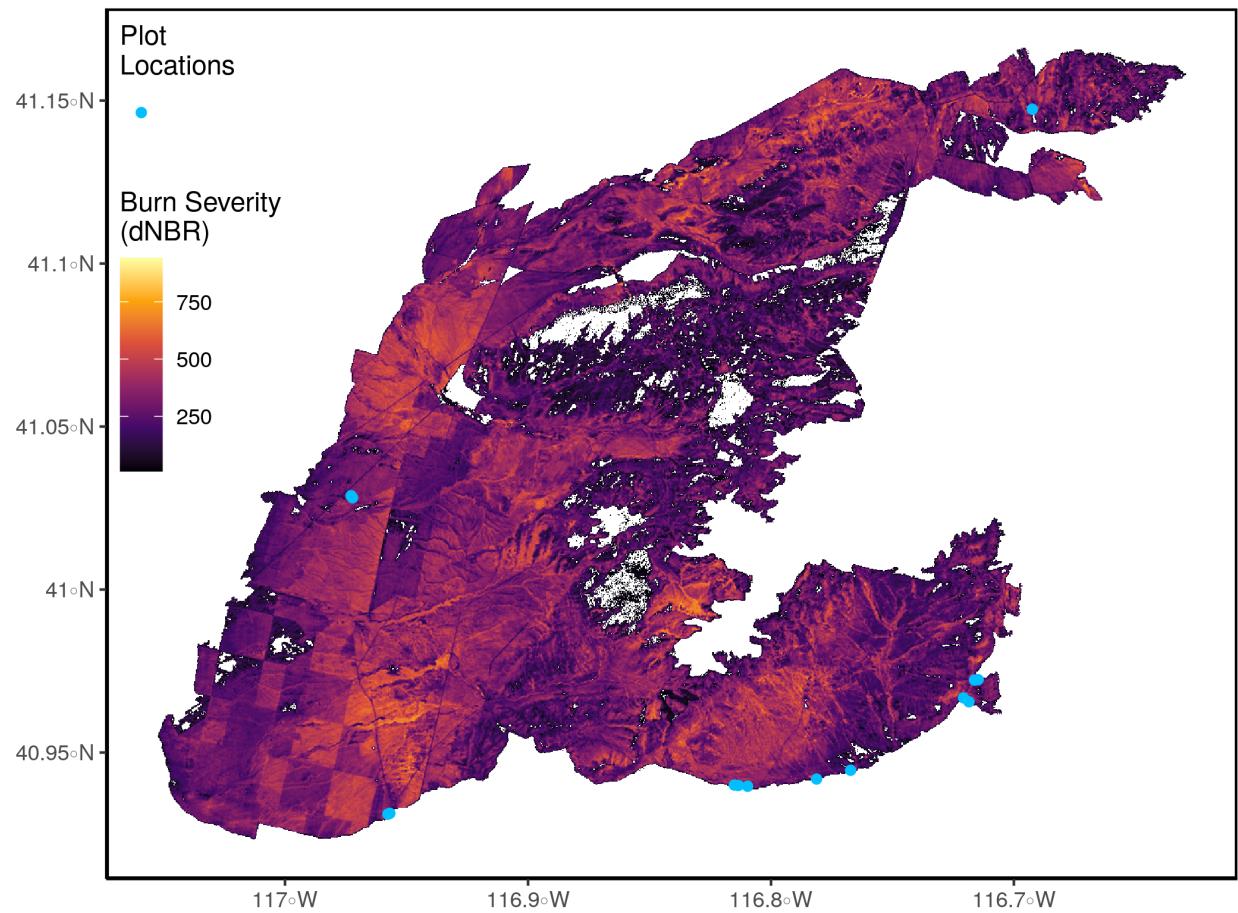


Figure 1: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

¹⁷⁸ a shrub or in the bare ground between shrubs, Eckert et al. 1986). To account for these
¹⁷⁹ potentially confounding effects, we placed half of the core locations under shrubs, and half in
¹⁸⁰ shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even
¹⁸¹ when they were completely incinerated, their imprint remained on the soil surface (Bechtold
¹⁸² and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each
¹⁸³ soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples.
¹⁸⁴ Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and
¹⁸⁵ Mcarthur 2013).

¹⁸⁶ At all sites, to be sure that we were at a site where sagebrush germination could occur we
¹⁸⁷ checked for first year germinants (we found them at all sites), and to ensure that there were
¹⁸⁸ no confounding effects of post-fire seed dispersal, we determined whether or not the sagebrush
¹⁸⁹ were flowering (they were not flowering at all sites), and recorded species occupancy for all
¹⁹⁰ plant species.

¹⁹¹ *2.3 Greenhouse Germination*

¹⁹² We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample
¹⁹³ was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots.
¹⁹⁴ These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were
¹⁹⁵ watered as needed to stay at field capacity. Every week emerging germinants were identified,
¹⁹⁶ counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks
¹⁹⁷ we ended the germination assay.

¹⁹⁸ *2.4 Post-Fire Vegetation Sampling*

¹⁹⁹ In order to understand how the seed bank composition compares to the realized vegetative
²⁰⁰ composition, we sampled the vegetative occupancy and cover in May 2017, the growing
²⁰¹ season immediately after the fire and again in September 2019. In 2017, at each location, we
²⁰² established 50m transects starting at the boundary of the burned and unburned sides of the
²⁰³ perimeter, running perpendicular to the fire perimeter, and marked the transect ends with

204 rebar. We measured the occupancy and abundance of all plant species by measuring cover
205 of every species in 0.1 m² quadrats spaced every 5 m along each transect. We used the line
206 intercept method to measure shrub cover and herbaceous plant cover along the transect. Both
207 live and dead plants were included in these measurements. Total vegetation cover (TVC)
208 was defined as the sum of herbaceous plant cover and shrub cover. In order to assess if sites
209 had the potential for sagebrush regeneration immediately post-fire, we counted all first-year
210 germinants within 50 cm of the transect, which we defined as any sagebrush individual less
211 than 20 cm in height. In September 2019 we resampled the burned transects for occupancy
212 and abundance of all plant species, as well as shrub and fine fuel cover.

213 *2.5 Estimating Burn Severity with Landsat 8 OLI*

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

222 *2.6 Statistical Analysis*

223 Our statistical analysis centered around trying to understand each component of the positive
224 feedback loop posited by the 4 hypotheses described above. In order to understand how
225 pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC)
226 from two separate data sources as a proxy for fuel connectivity, and created separate linear
227 models with TVC as the predictor variable and burn severity (dNBR, J. D. Miller et al.
228 2009) as the response variable. With the field data we collected, we created an ordinary least
229 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 been from only partially burned pixels. So, as a supplement, we examined the relationship using Landsat Thematic Mapper (TM) data and TVC from the Bureau of Land Management's Assessment, Inventory and Monitoring dataset (AIM, U.S. Department of Interior 2018) to represent fuel connectivity. The AIM dataset contained 813 sampling locations within the Central Basin and Range ecoregion (Commission for Environmental Cooperation 2006) that were visited by BLM field crews between 2011 and 2015. They were mostly sampled once but there were some repeats, for 1,117 total measurements. For each of these points, we extracted the values of each Landsat band for the sampling year near peak biomass using a cloud-free scene from May or early June. Then, we used those band values to calculate various vegetation indexes (Table S2), including the Green Normalized Differentiated Vegetation Index (Green NDVI, Equation 1), and Normalized Differentiated Senesced Vegetation Index (NDSVI, Equation 2). We used these indexes to create a beta regression model of TVC, starting with the largest possible model and used backwards selection following the methodology of Zuur et al. (2009). We used 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.

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

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

To examine how burn severity affected the community composition of the seed bank (H2), we created a joint species distribution model (JSDM) in a Bayesian framework (Tikhonov et al. 2020) for the occurrence of all species germinated from the seed bank that were found

256 at more than one location. We created four Markov Chain Monte Carlo (MCMC) chains,
257 each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain
258 and then recorded every 100th for a total of 1,000 posterior samples per chain, and 4,000
259 total. We assessed model convergence using the effective sample size and the potential scale
260 reduction factor (Gelman, Rubin, and others 1992). We used the model to predict the
261 probability of occurrence of germinable seeds of a given species along a gradient of burn
262 severity. We included burn severity, elevation, aspect, pre-fire seedbank diversity and soil
263 depth as independent variables.

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

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

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

280 For all linear and generalized linear models, we used backwards selection to find the most
281 parsimonious model. We fitted the largest possible model first, and removed independent

Table 1: Model performance metrics

Model	R2	R2_adjusted	Sign
H1: TVC ~ NDSVI + Green NDVI	0.35	NA	+
H1: dNBR ~ TVC(modelled)	0.42	0.42	+
H1: dNBR ~ TVC(<i>in situ</i>)	0.27	0.20	+
H3: Post-Fire Fuel Connectivity ~ # Cheatgrass Seeds + covariates	0.84	0.75	+
H4: Post-Fire Diversity ~ Post-Fire Fuel Connectivity	0.92	0.89	-

variables that did not improve the model fit according to Akaike's Information Criterion (AIC), following the guidelines of Zuur et al. (2009).

All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis is freely available on Figshare (link here after acceptance) and GitHub (<https://www.github.com/admahood/seed-bank>).

3. Results

We found support for each hypothesized component of the positive feedback loop. For H1, the most parsimonious model for our *in situ* observations had only TVC as the predictor, which had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$, Figure 2a, Table 1). 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 (Table 1). 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 2a, Table 1).

The vast majority of seeds that germinated in the greenhouse were the two most common grass species, *P. secunda* and *B. tectorum* (Table S1). 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 (Figure S1). For H2, the JSDM converged well (Gelman diagnostics all very close to 1 and the

302 effective sample size centered on 4,000, Figure 3a). Elevation had the most significant effects
303 on individual species (Figure 3b) and explained the most variance on average (36% Figure 3c).
304 Burn severity explained 23% of the variance on average and was supported at the 95% level
305 for 5 species (Figure 3b). For the introduced species, the predictions along a gradient of burn
306 severity were positive for *B. tectorum*, *Sisymbrium altissimum* L. and *Lepidium perfoliatum*
307 L., and negative for *Ceratocephala testiculata* and *Alyssum desertorum* Stapf (Figure 2b).
308 For native species, the effect of burn severity on occurrence was positive for *A. tridentata*,
309 neutral for *P. secunda* and negative for the remaining species (Figure 2b). Testing H2a
310 revealed a positive relationship between pre-fire aboveground species diversity and pre-fire
311 fuel connectivity, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a
312 confounding factor for H2.

313 For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and
314 the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the postfire seedbank
315 was positively associated with the fuel connectivity in 2019 ($\beta = 0.54$, $p = 0.01$, Adj $R^2 =$
316 0.75, Figure 3c, Table 1).

317 For H4 the most parsimonious model (Adj $R^2 = 0.89$, Table 1) had elevation, aspect, fuel
318 connectivity and an interaction between elevation and fuel connectivity as predictors of
319 aboveground Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated
320 with Shannon-Weaver diversity ($\beta = -0.28$, $p=0.004$, Figure 3d).

321 4. Discussion

322 In order to truly consider an annual grass-fire cycle to be maintained by self-reinforcing
323 feedbacks, the mechanisms by which fire occurrence is linked to higher post-fire flammability
324 must be understood. In this study we found evidence that interaction between burn severity
325 and seed bank composition may explain that link. Prior work has shown that annual grass
326 invasion increases fuel connectivity in western US sagebrush ecosystems by filling in shrub

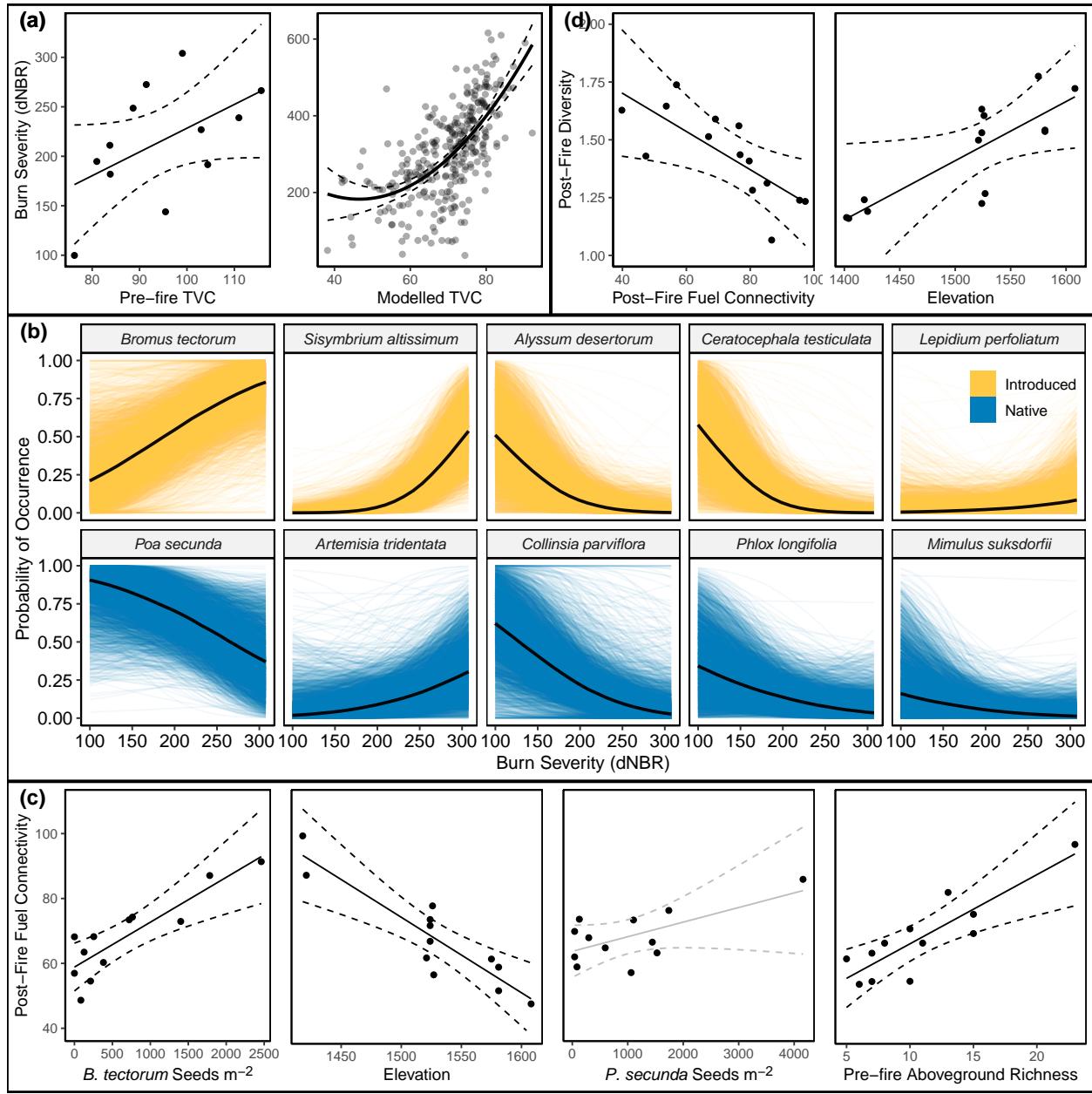


Figure 2: a) Hypothesis 1. On the left, burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Dotted lines are the 95% confidence intervals. b) Hypothesis 2. Modelled occurrence of germinable seeds for all species found at more than one location along a gradient of burn severity, after accounting for soil depth, aspect, elevation and pre-fire diversity. Black line is the mean prediction, each colored line represents one posterior sample. c) Hypothesis 3. Fuel connectivity three years post-fire as modelled by seedbank composition, elevation and pre-fire aboveground species richness. d) Hypothesis 4. Shannon-Weaver diversity index of the aboveground, post-fire community composition, was negatively affected by fuel connectivity after accounting for elevation. For a, c and d, lines are the fitted partial effects (in the case of multiple predictors), points are the partial residuals, dotted lines are the 95% confidence intervals. Black lines indicate that $p < 0.05$, grey lines indicate that $p > 0.05$

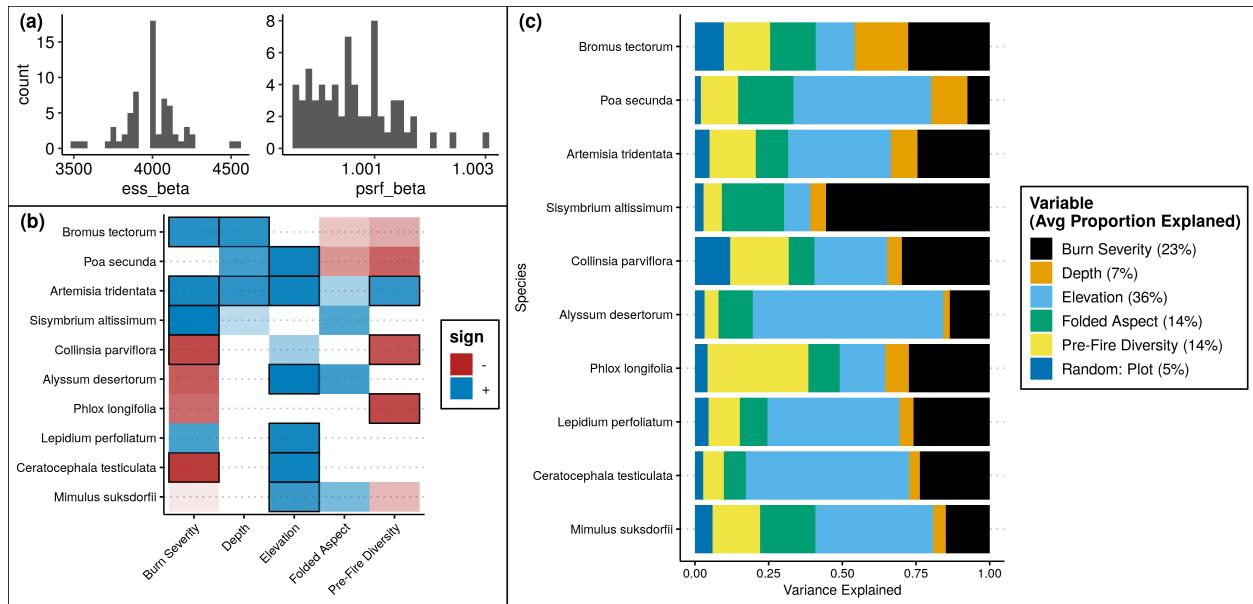


Figure 3: a) Model convergence diagnostics. On the left is the effective sample size after adjusting for autocorrelation (ideally 4,000), and on the right is the Gelman diagnostic, ideally 1. b) Predictor variables that had at least 80% support. Variables with 95% support are outlined in black. The level of transparency corresponds to the level of support. c) Variance partitioning by species. Average across all species per variable is given in the legend. Species are ordered by prevalence.

327 interspaces with a contiguous bed of fine fuels (Davies and Nafus 2013). This change in
328 the spatial distribution of fine fuels has been associated with larger and more frequent fires
329 (Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) increases burn
330 severity (H1, Figure 2a). Higher burn severity was associated with an increased occurrence of
331 introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure
332 2b). Higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher
333 post-fire fuel connectivity (H3, Figure 2c). In addition, we found evidence that high post-fire
334 fuel connectivity was associated with lower aboveground diversity (H4, Figure 2d). This
335 suggests that during inter-fire intervals, there are additional mechanisms maintaining the
336 post-fire species assemblage that is dominated by annual introduced plants.

337 The difference in species composition before and after fire explains an apparent contradiction
338 in results between H2a (positive relationship between pre-fire fuel connectivity and diversity)
339 and H4 (negative relationship between post-fire fuel connectivity and diversity). Most (11
340 out of 14) plot locations had mature canopies of native shrubs and with the inter-shrub space
341 occupied mostly by native bunchgrasses and forbs, with fire history since 1984. The three
342 plots with recent fire history burned in 1984 and were invaded by *B. tectorum*, but they still
343 had significant cover of *A. tridentata*. Even in locations with high annual grass cover between
344 shrubs, shrubs provide ecosystem structural heterogeneity and islands of fertility (Doescher,
345 Miller, and Winward 1984; Bechtold and Inouye 2007), and perennial natives that may have
346 been established before invasion have deep roots established that allow for the avoidance of
347 competition for water with shallow-rooted annuals (Gibbens and Lenz 2001; Ottaviani et al.
348 2020). This may provide enough niche compartmentalization to allow native plants to persist.
349 Three years after the Hot Pot fire, almost all of the plots were dominated by introduced
350 annuals, and lacked any structural heterogeneity. Thus native plants may have been be able
351 to persist via niche compartmentalization after the initial invasion, but fire burns away most
352 of the seeds (Figure S1) and removes all of the structural benefits that shrub cover provides.
353 In this clean slate post-fire environment, the altered species composition of the seedbank and

³⁵⁴ superior post-fire dispersal of *B. tectorum* (Monty, Brown, and Johnston 2013) allows the
³⁵⁵ process of interspecific competition to be dominant (Schlaepfer, Lauenroth, and Bradford
³⁵⁶ 2014).

³⁵⁷ *Global impacts*

³⁵⁸ The grass-fire cycle in the western US is reinforced through providing fitness benefits to
³⁵⁹ the introduced annual grasses and forbs via at least 4 redundant processes: i) changing the
³⁶⁰ composition of the seedbank, ii) competitive exclusion of native plants, iii) CO₂ enrichment
³⁶¹ which may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of
³⁶² annual grass species (Nagel et al. 2004; Smith et al. 2000), strengthening the fuel connectivity
³⁶³ to burn severity to seed composition feedback loop, and iv) ecohydrological feedbacks that
³⁶⁴ create a warmer, drier microclimate (Turnbull et al. 2012; Wilcox et al. 2012). It is likely
³⁶⁵ that some of these feedbacks are idiosyncratic to the system being studied, while others
³⁶⁶ may reflect the fundamental properties of ecosystem function that change when a system is
³⁶⁷ converted from being dominated by woody plants to being dominated by herbaceous plants
³⁶⁸ (Kitzberger et al. 2016). Understanding the mechanisms of hysteresis, and in particular how
³⁶⁹ multiple redundant mechanisms act in concert, will provide important insights for ecosystem
³⁷⁰ change on a global scale. At least 13 grass species initiate self-reinforcing feedbacks with
³⁷¹ fire in the U.S. (Fusco et al. 2019; Tortorelli, Krawchuk, and Kerns 2020), and many more
³⁷² worldwide, including Australia (G. Miller et al. 2010; Setterfield et al. 2010), Brazil (Rossi et
³⁷³ al. 2014) and South Africa (Milton 2004). While the conversion of temperate forests and
³⁷⁴ shrublands to grasslands may have a less per-hectare impact on carbon sequestration than
³⁷⁵ tropical forests, the consequences are still relevant to the global carbon cycle, especially when
³⁷⁶ forests (rather than the shrublands studied here) are replaced by herbaceous ecosystems
³⁷⁷ (Kerns et al. 2020).

³⁷⁸ *Potential limitations*

³⁷⁹ We found fewer species and lower diversity in our seedbank germination assays than we did in

the aboveground sampling (Figure S2). 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 (Figure 6a-c) the dNBR was higher, and the shrubs had completely burned throughout the root system, leaving only a hole in the ground filled with ashes as evidence of their prior presence. In these areas the entirety of the soil surface—underneath shrub canopy and in canopy interspaces—was consumed by fire, and there was little evidence of remaining litter or biological soil crust. In areas with lower fuel connectivity (Figure 6d-f), and lower dNBR, shrubs were usually consumed only to the stumps, and sometimes

406 were left standing and charred, destined for mortality. In these areas the soil surface often
407 still had biological soil crust, partially consumed litter (Jones et al. 2015) and unconsumed
408 annual and perennial grass bases. We note that the manual severity classification provided by
409 MTBS had exclusively low and medium severity, but our observations of essentially complete
410 consumption of plant and litter tissues and very few unburned patches suggested that these
411 should have been mostly medium and high severity. This discrepancy was not unexpected
412 (Kolden, Smith, and Abatzoglou 2015).

413 Other studies that have used spectral indexes to quantify fuel connectivity in forested systems
414 have typically used NDVI (Parks et al. 2018; Koontz et al. 2020). Here, we arrived at green
415 NDVI and NDSVI, this contrast is the manifestation of key differences in the physiognomies
416 of forest and arid shrublands that is essential to understand their relationship to fire. In
417 coniferous forests of the western US, greenness is a good proxy for fuel load and NDVI texture
418 for connectivity. In sagebrush shrublands, the fuel that contributes to large wildfires is a
419 mixture of evergreen shrubs interspersed with herbaceous plants that remain green for only a
420 portion of the growing season, and then become dry and straw-colored.

421 *Management implications*

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

430 This work shows that this is a clear example of a system where the degraded state represents
431 an alternative species assemblage from that of the restoration target, where the propagules

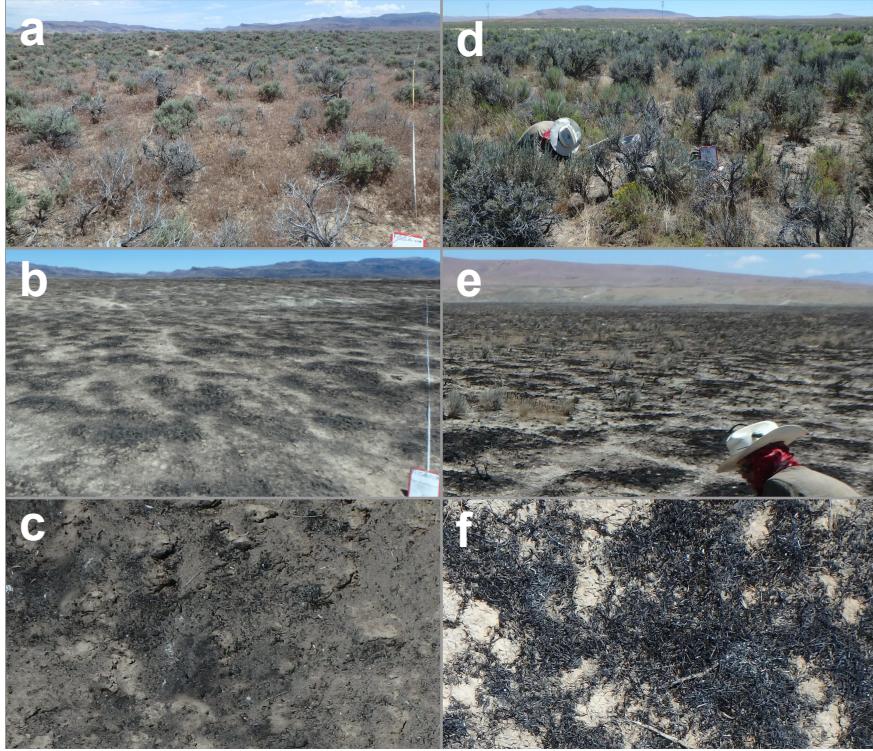


Figure 4: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space being highly invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, and approximately all of the biomass was consumed by the fire. Panel C is a closeup of the soil surface, showing in more detail how the litter was also almost completely consumed by the fire. On the right, the photos in panels d and e were on opposite sides of a fire line in an area that had minimal annual grass invasion over a broad area, and thus lower fuel connectivity. Note the remaining plants and stumps in panel e and the presence of only partially consumed litter in panel f.

432 of the original assemblage are no longer present, and thus methods that rely on natural
433 succession may not be sufficient (Suding, Gross, and Houseman 2004). Our results highlight
434 the importance of prioritizing the preservation of native shrub cover and in particular policies
435 that encourage land managers to maximize the preservation of unburned patches during the
436 suppression of wildfires in this system (Steenvoorden et al. 2019). Commonly encountered
437 native plants and the keystone shrub species *A. tridentata* depend on post-fire seed dispersal
438 from surviving individuals in unburned patches (Schlaepfer, Lauenroth, and Bradford 2014).
439 Once the system achieves a canopy dominated by annual grasses and forbs, the competitive
440 pressure from the annual grass monoculture makes it more difficult if not impossible for
441 perennial native forbs and shrubs to establish from the depleted seedbank. Post-fire seeding
442 efforts may restore native propagules, but if there is dense cover of annuals further effort
443 may be required to reduce fuel connectivity in order to reduce both fire risk and competitive
444 pressure from annuals.

445 Livestock grazing can reduce fuel connectivity in uninvaded sagebrush (Davies et al. 2010).
446 At the same time, grazing can also decrease the resistance to invasion by *B. tectorum* via
447 negative effects on biological soil crust (BSC) (Condon and Pyke 2018), and can reduce the
448 survival of *Artemisia* seedlings that are not protected by shrub canopies (Owens and Norton
449 1992). In wet years, targeted grazing at already invaded sagebrush sites may reduce fuel
450 connectivity and alleviate fire risk. Plant community composition in the years immediately
451 after fire may be highly variable spatially and from year to year. Post-fire grazing may help
452 reduce *B. tectorum* cover, but it would more likely exacerbate the problem by introducing
453 cheatgrass in uninvaded sites (Williamson et al. 2019) or increasing the already superior
454 postfire dispersal of *B. tectorum* seeds (Monty, Brown, and Johnston 2013). We suggest
455 management approaches that are specifically tailored each year to the conditions of a given
456 site, and targeting grazing only in already invaded areas to reduce *B. tectorum* cover where
457 it may aid in native plant restoration.

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