

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.

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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 systems that are dominated by introduced annual grasses. But it is unclear exactly
⁷ how fire directly benefits the introduced annual grasses. 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 introduced annual plants in the seed bank, and found that higher burn severity
¹¹ had mostly positive or neutral effects on the occurrence of non-native species, and mostly
¹² negative or neutral relationships with native species. We then tested if post-fire seed bank
¹³ composition affected post-fire TVC, we found that the abundance of annual grass seeds in
¹⁴ the seedbank immediately post-fire had a positive effect on the fuel connectivity 3 years later.
¹⁵ This is the first study that we are aware of in the western US that shows how burn severity
¹⁶ influences seed bank species composition, as well as examining the full feedback loop with
¹⁷ fuel connectivity.

¹⁸ **1. Introduction**

¹⁹ One of the consequences of global change in the 21st century that is most difficult to reverse
²⁰ is when ecosystems abruptly shift from one stable species assemblage to another (Ratajczak
²¹ et al. 2018). In tropical ecosystems, three alternative stable states have been identified
²² along a gradient of precipitation: forests, savannas and grasslands (Hirota et al. 2011;
²³ Staver, Archibald, and Levin 2011). These three states cluster around values of tree cover
²⁴ (approximately 80, 30 and 0 percent) that occur among overlapping levels of precipitation,
²⁵ and so it is thought that they exhibit states of hysteresis in which internal, self-reinforcing
²⁶ mechanisms maintain alternate states (Andersen et al. 2009). In the forested state there is

²⁷ a self-reinforcing positive feedback between evapotranspiration and tree cover (Staal et al.
²⁸ 2020). In the grassland and savanna states, there are feedbacks between grass flammability
²⁹ and fire occurrence (Staver, Archibald, and Levin 2011; D'Antonio and Vitousek 1992).

³⁰ A classic example of hysteresis in a semi-arid, temperate system is the invasion of *Bromus*
³¹ *tectorum* L. and other introduced annual grasses in the Great Basin of the western United
³² States. Here, over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*
³³ Beetle & Young) ecosystems have been degraded, fragmented or lost completely (Davies
³⁴ et al. 2011). This has been attributed to a host of causes, including wildfire (Balch et al.
³⁵ 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of
³⁶ annual grasses. In this open shrubland, the space between shrubs is primarily composed of
³⁷ bare ground covered in biological soil crust, dotted with perennial bunch grasses. The lack
³⁸ of fuel connectivity is believed to have limited fire spread, with a fire regime of infrequent,
³⁹ patchy fires (Keeley and Pausas 2019). Annual grass invasion increases fuel connectivity
⁴⁰ while decreasing fuel moisture (Davies and Nafus 2013), leading to increased fire size and
⁴¹ frequency (Whisenant 1990; Knapp 1996; Balch et al. 2013). After fire, the landscape is often
⁴² dominated by introduced annual grasses and forbs. This causes a >50% loss of aboveground
⁴³ carbon storage (Bradley et al. 2006; Nagy et al. 2020). But in order to understand how
⁴⁴ the grassland state persists, the mechanisms by which fire benefits the introduced annual
⁴⁵ grass must be understood. Petraitis and Latham (1999) posited that the maintenance of
⁴⁶ alternate species assemblages requires first a disturbance that removes the species from the
⁴⁷ initial assemblage and second the arrival of the species of the alternate assemblage. One
⁴⁸ understudied mechanism that may explain both is the interaction between burn severity and
⁴⁹ the species composition of the soil seed bank.

⁵⁰ Studies that directly examine the relationship between the species composition of the seed
⁵¹ bank and fire severity and/or intensity are uncommon, but more attention has been given to
⁵² the subject recently. In boreal forests, the depth of the burn may be more important more

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

74 Because *B. tectorum* is annual, in order for it to benefit from fire, which it clearly does
75 (Balch et al. 2013; Mahood and Balch 2019), it would have to have enough seeds in the
76 post-fire landscape to achieve a fitness benefit and become well-represented in the post-fire
77 plant assemblage (Bond and Midgley 1995). If the fire is patchy, this can happen through
78 post-fire seed dispersal, and *B. tectorum* seeds have been shown to have increased dispersal
79 distances after fire (Monty, Brown, and Johnston 2013). Without unburned patches, seeds

80 must survive the fire. There is strong evidence that *B. tectorum* builds a well-stocked pool of
81 seeds in the soil and litter, even when it is not well represented in the above-ground plant
82 assemblage (Young and Evans 1975; Hassan and West 1986; Boudell, Link, and Johansen
83 2002). If the increase in fuel connectivity caused by *B. tectorum* increases the severity of
84 fire, it stands to reason that burn severity would influence the community composition of
85 the post-fire seed bank in a way that facilitates the post-fire dominance of *B. tectorum*. To
86 our knowledge, despite several studies on the relationship between fire and the seed bank in
87 this system (Young and Evans 1975; Hassan and West 1986; Humphrey and Schupp 2001;
88 Boudell, Link, and Johansen 2002; Barga and Leger 2018), no studies to date have examined
89 this potential effect of burn severity on the seed bank.

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

102 If increased burn severity is a mechanism by which *B. tectorum* excludes native plants in
103 sagebrush shrublands, then an area with high burn severity may have a lower occurrence of
104 viable seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced
105 annual plants. This would lead to the dominance of introduced annual grasses and forbs

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

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

¹³² 2016. Because it burned a large area in only three days, we could sample a broad area
¹³³ while being reasonably certain that the climatic conditions during the fire were the same
¹³⁴ at all sites. Because we collected our samples immediately after the fire was extinguished,
¹³⁵ we felt confident that the seed bank samples did not contain seeds deposited by post-fire
¹³⁶ dispersal. We put the samples in cold storage and germinated the seeds from those cores in a
¹³⁷ greenhouse the following spring. In spring 2017 and fall 2019 we collected information on
¹³⁸ vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel
¹³⁹ connectivity would be positively related to burn severity; (H2) burn severity would increase
¹⁴⁰ the occurrence probability of introduced annual species in the seed bank and reduce the
¹⁴¹ occurrence probability of native species; (H2a) increased fuel connectivity brought on by
¹⁴² the invasion of annual grasses already depleted the diversity of the soil seed bank before the
¹⁴³ fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related
¹⁴⁴ to post-fire fuel connectivity. In addition, because in our study system sites with high fuel
¹⁴⁵ connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high
¹⁴⁶ post-fire fuel connectivity of those near-monocultures would result in lower aboveground
¹⁴⁷ species diversity due to competitive pressure.

¹⁴⁸ 2. Methods

¹⁴⁹ 2.1 Study Area

¹⁵⁰ The study was conducted in north-central Nevada the day after a large fire (the Hot Pot
¹⁵¹ Fire) was extinguished (Figure 1). The Hot Pot Fire burned just over 50,000 hectares in
¹⁵² less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big
¹⁵³ sagebrush plant communities. The fire occurred after the early season plants, including *B.*
¹⁵⁴ *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone
¹⁵⁵ to seed, and before the late season species, including Wyoming big sagebrush, had produced
¹⁵⁶ flowers. Thus we were able to isolate the effect of the fire without any confounding effects of
¹⁵⁷ post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged

₁₅₈ from 1397 to 1607 meters in elevation.

₁₅₉ *2.2 Seed Bank Sampling*

₁₆₀ In early July 2016, we collected samples of the soil seed bank at fourteen locations immediately
₁₆₁ after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where
₁₆₂ it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites
₁₆₃ were mature sagebrush communities with no history of fire since at least 1984. Three plots
₁₆₄ had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS)
₁₆₅ fire history (Eidenshink et al. 2007) and had high cover of *B. tectorum*, but still had scattered
₁₆₆ sagebrush cover. We used a metal stake to mark paired burned and unburned sampling
₁₆₇ locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic
₁₆₈ disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the
₁₆₉ perimeter. Within 3 m of each marker, we extracted 12, 6 cm deep, 5 cm diameter, soil cores.
₁₇₀ Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system
₁₇₁ (Shinneman and McIlroy 2016), and so they are not uniformly distributed (Boudell, Link, and
₁₇₂ Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemisia*
₁₇₃ have different germination rates based on the micro-site they find themselves in (i.e. under
₁₇₄ a shrub or in the bare ground between shrubs, Eckert et al. 1986). To account for these
₁₇₅ potentially confounding effects, we placed half of the core locations under shrubs, and half in
₁₇₆ shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even
₁₇₇ when they were completely incinerated, their imprint remained on the soil surface (Bechtold
₁₇₈ and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each
₁₇₉ soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples.
₁₈₀ Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and
₁₈₁ Mcarthur 2013).

₁₈₂ At all sites, to be sure that we were at a site where sagebrush germination could occur we
₁₈₃ checked for first year germinants (we found them at all sites), and to ensure that there were

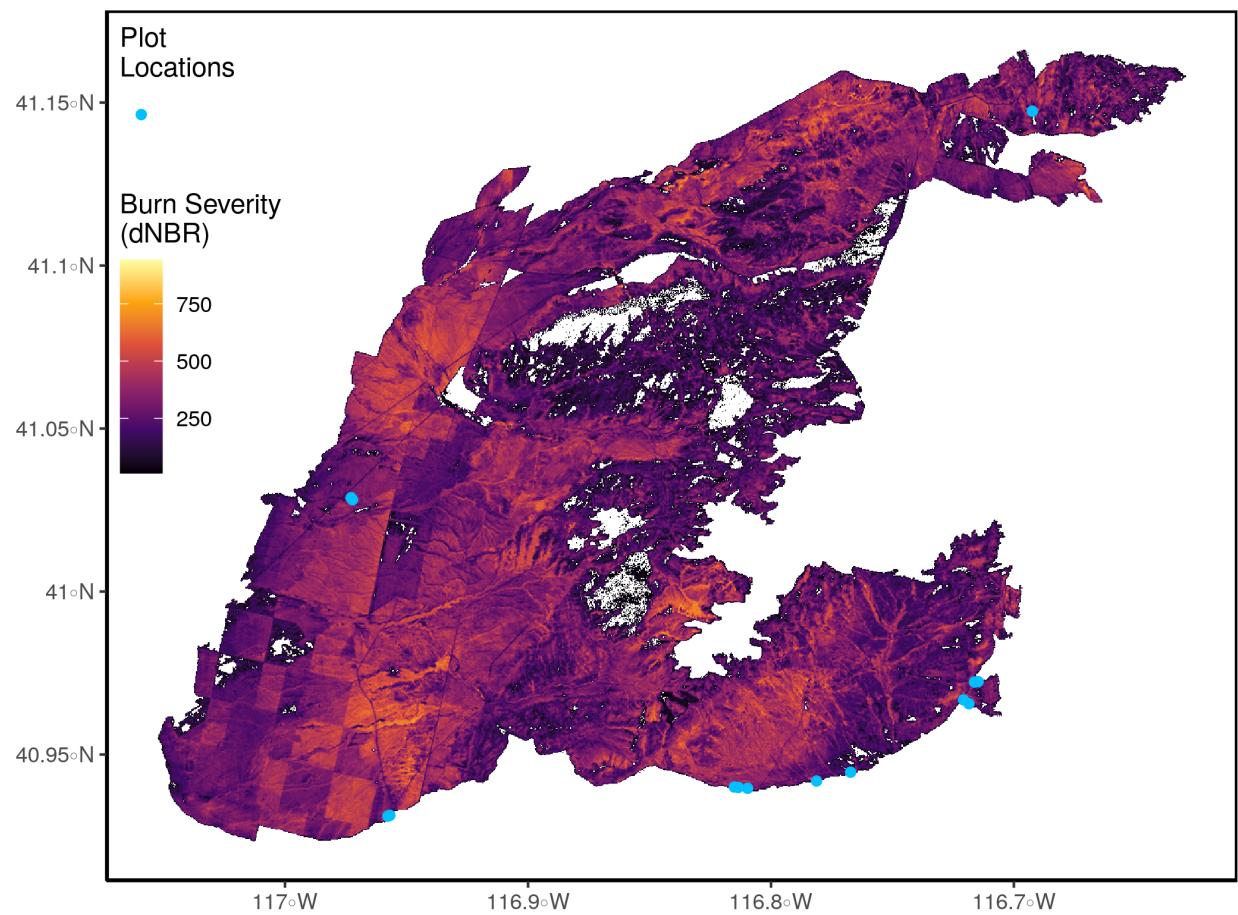


Figure 1: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

¹⁸⁴ no confounding effects of post-fire seed dispersal, we determined whether or not the sagebrush
¹⁸⁵ were flowering (they were not flowering at all sites), and recorded species occupancy for all
¹⁸⁶ plant species.

¹⁸⁷ *2.3 Greenhouse Germination*

¹⁸⁸ We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample
¹⁸⁹ was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots.
¹⁹⁰ These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were
¹⁹¹ watered as needed to stay at field capacity. Every week emerging germinants were identified,
¹⁹² counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks
¹⁹³ we ended the germination assay.

¹⁹⁴ *2.4 Post-Fire Vegetation Sampling*

¹⁹⁵ In order to understand how the seed bank composition compares to the realized vegetative
¹⁹⁶ composition, we sampled the vegetative occupancy and cover in May 2017, the growing
¹⁹⁷ season immediately after the fire and again in September 2019. In 2017, at each location, we
¹⁹⁸ established 50m transects starting at the boundary of the burned and unburned sides of the
¹⁹⁹ perimeter, running perpendicular to the fire perimeter, and marked the transect ends with
²⁰⁰ rebar. We measured the occupancy and abundance of all plant species by measuring cover
²⁰¹ of every species in 0.1 m² quadrats spaced every 5 m along each transect. We used the line
²⁰² intercept method to measure shrub cover and herbaceous plant cover along the transect. Both
²⁰³ live and dead plants were included in these measurements. Total vegetation cover (TVC)
²⁰⁴ was defined as the sum of herbaceous plant cover and shrub cover. In order to assess if sites
²⁰⁵ had the potential for sagebrush regeneration immediately post-fire, we counted all first-year
²⁰⁶ germinants within 50 cm of the transect, which we defined as any sagebrush individual less
²⁰⁷ than 20 cm in height. In September 2019 we resampled the burned transects for occupancy
²⁰⁸ and abundance of all plant species, as well as shrub and fine fuel cover.

²⁰⁹ *2.5 Estimating Burn Severity with Landsat 8 OLI*

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

217 *2.6 Statistical Analysis*

218 Our statistical analysis centered around trying to understand each component of the positive
219 feedback loop posited by the 4 hypotheses described previously. In order to understand
220 how pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover
221 (TVC) from two separate data sources as a proxy for fuel connectivity, and created separate
222 linear models with TVC as the predictor variable and burn severity (dNBR) as the response
223 variable. With the field data we collected, we created an ordinary least squares (OLS) linear
224 model with burn severity (dNBR) as the dependent variable and TVC (defined as shrub cover
225 plus herbaceous plant cover from the unburned side of the paired plots), elevation and aspect
226 as independent variables. As a supplement, we examined the relationship using Landsat
227 Thematic Mapper data and TVC from the Bureau of Land Management’s Assessment,
228 Inventory and Monitoring dataset [AIM; U.S. Department of Interior (2018)] to represent
229 fuel connectivity. The AIM dataset contained 813 sampling locations within the Central
230 Basin and Range ecoregion (Commission for Environmental Cooperation 2006) that were
231 visited by BLM field crews between 2011 and 2015. They were mostly sampled once but there
232 were some repeats, for 1,117 total measurements. For each of these points, we extracted the
233 values of each Landsat band for the sampling year near peak biomass using a cloud-free scene
234 from May or early June. Then, we used those band values to calculate various vegetation
235 indices (Table S2), including the Green Normalized Differenced Vegetation Index (Green

²³⁶ NDVI, band 5 - band 3 / band 5 + band 3), and Normalized Differenced Senesced Vegetation
²³⁷ Index (NDSVI, band 6 - band 4 / band 6 + band 4). We used these indexes to create a
²³⁸ beta regression model of TVC, starting with the largest possible model and used backwards
²³⁹ selection following the methodology of Zuur et al. (2009). We used this model to create
²⁴⁰ a layer of predicted TVC for the study area for the pre-fire scene, and extracted both our
²⁴¹ predictions of TVC and dNBR of the fire from 1000 regularly-spaced points within the fire
²⁴² perimeter. Finally, to quantify the effect of TVC on burn severity, we created an OLS linear
²⁴³ model with our modeled TVC and its second-order polynomial as predictor variables and
²⁴⁴ burn severity as the response variable.

²⁴⁵ To examine how burn severity affected the community composition of the seed bank (H2),
²⁴⁶ we created a joint species distribution model (JSDM) in a Bayesian framework (Tikhonov et
²⁴⁷ al. 2020) for the occurrence of all species germinated from the seed bank that were found
²⁴⁸ at more than one location. We created four Markov Chain Monte Carlo (MCMC) chains,
²⁴⁹ each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain
²⁵⁰ and then recorded every 100th for a total of 1,000 posterior samples per chain, and 4,000
²⁵¹ total. We assessed model convergence using the effective sample size and the potential scale
²⁵² reduction factor (Gelman, Rubin, and others 1992). We used the model to predict the
²⁵³ probability of occurrence of germinable seeds of a given species along a gradient of burn
²⁵⁴ severity. We included burn severity, elevation, aspect, pre-fire seedbank diversity and soil
²⁵⁵ depth as independent variables.

²⁵⁶ To account for the possibility of H2a as a confounding factor, we included the Shannon-Weaver
²⁵⁷ diversity index (Shannon and Weaver 1949; Hill 1973) in the paired, unburned seed bank
²⁵⁸ samples as one of the predictor variables in our JSDM. We also created OLS models with
²⁵⁹ the unburned species richness and Shannon-Weaver diversity index predicted by prefire fuel
²⁶⁰ connectivity, with the expectation that pre-fire fuel connectivity would have had a negative
²⁶¹ effect on the prefire seedbank diversity.

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

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

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

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

279 3. Results

280 We found support for each hypothesized component of the positive feedback loop. For H1,
281 the most parsimonious model for our *in situ* observations had only TVC as the predictor,
282 which had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$,
283 Figure 2a). For our remotely sensed analysis, our most parsimonious model of TVC explained
284 34% of the variation and had Green NDVI, NDSVI and their interaction as predictors (Table
285 1???). Our model of dNBR using the predicted TVC within the fire perimeter as a predictor
286 of dNBR explained 41% of the variation and the relationship between TVC and burn severity

287 was positive and significant ($p < 0.01$, Figure 2a).

288 The vast majority of seeds that germinated in the greenhouse were the two most common grass
289 species, *P. secunda* and *B. tectorum* (Table S1). Eight forb species were found in more than
290 one location, and these 10 prevalent species are those that were used in our JSDM. Burned
291 plots had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14 in the bottom 4 cm.
292 Unburned plots had an average of 299 ± 170 in the top 2 cm and 59 ± 29 in the bottom 4 cm
293 (Figure S1). For H2, the JSDM converged well (Gelman diagnostics all very close to 1 and the
294 effective sample size centered on 4,000, Figure 3a). Elevation had the most significant effects
295 on individual species (Figure 3b) and explained the most variance on average (36% Figure 3c).
296 Burn severity explained 23% of the variance on average and was supported at the 95% level
297 for 5 species (Figure 3b). For the introduced species, the predictions along a gradient of burn
298 severity were positive for *B. tectorum*, *Sisymbrium altissimum* L. and *Lepidium perfoliatum*
299 L., and negative for *Ceratocephala testiculata* and *Alyssum desertorum* Staph (Figure 2b).
300 For native species, the effect of burn severity on occurrence was positive for *A. tridentata*,
301 neutral for *P. secunda* and negative for the remaining species (Figure 2b). Testing H2a
302 revealed a positive relationship between pre-fire aboveground species diversity and pre-fire
303 fuel connectivity, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a
304 confounding factor for H2.

305 For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and
306 the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the postfire seedbank
307 was positively associated with the fuel connectivity in 2019 ($\beta = 0.54$, $p = 0.01$, Adj $R^2 =$
308 0.74, Figure 3c).

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

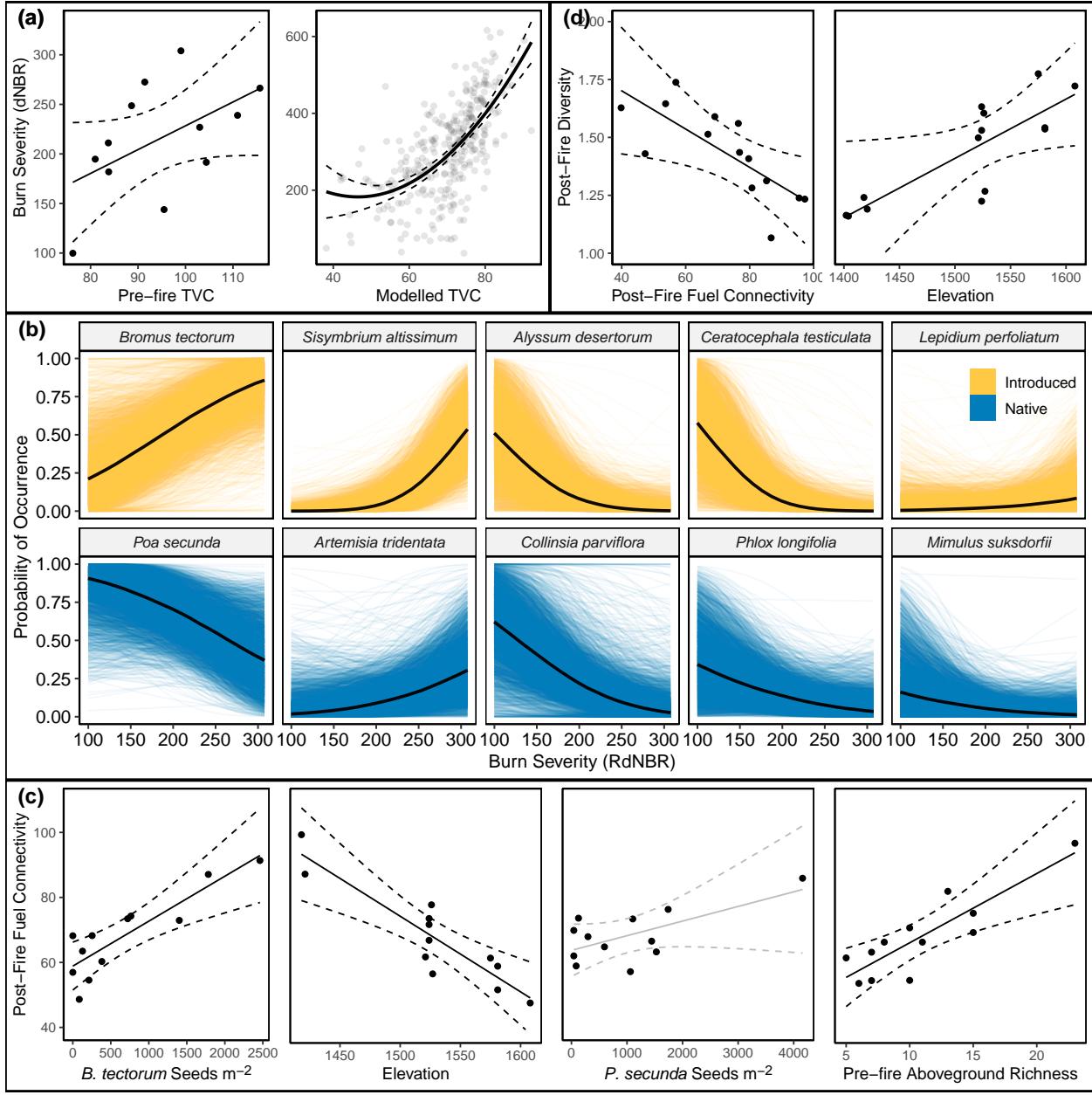


Figure 2: a) Hypothesis 1. On the left, burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Dotted lines are the 95% confidence intervals. b) Hypothesis 2. Modelled occurrence 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.

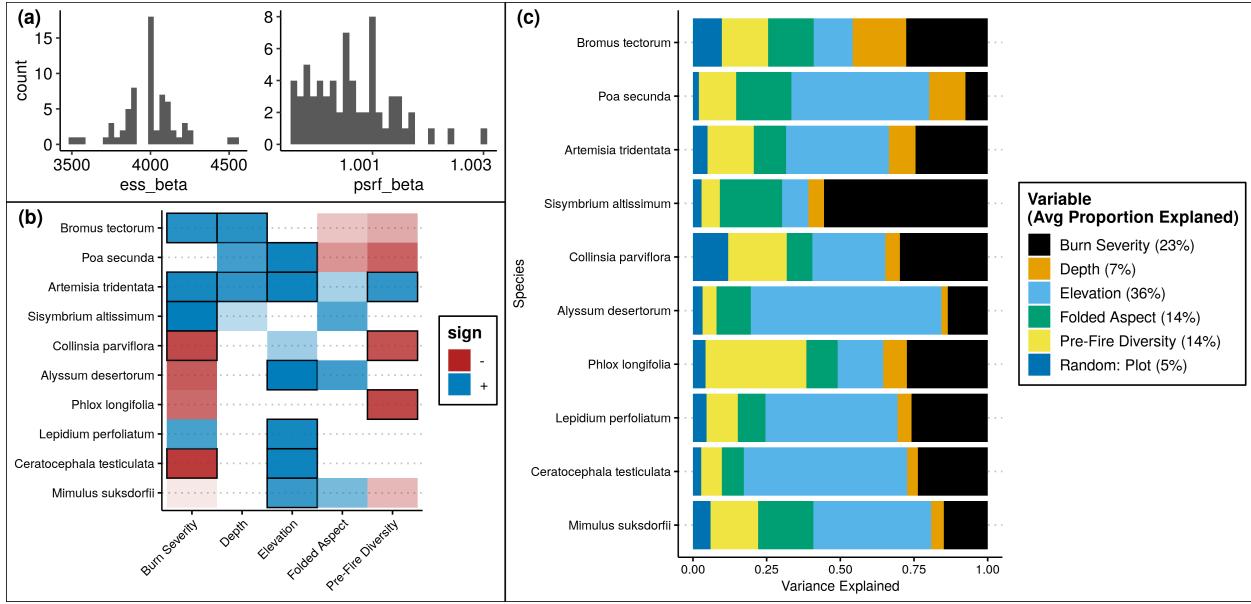


Figure 3: a) Model convergence diagnostics. On the left is the effective sample size after adjusting for autocorrelation (ideally 4,000), and on the right is the Gelman diagnostic, ideally 1. b) Predictor variables that had at least 80% support. Variables with 95% support are outlined in black. The level 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.

313 4. Discussion

314 In order to truly consider an annual grass-fire cycle to be maintained by self-reinforcing
 315 feedbacks, the mechanisms by which fire occurrence is linked to higher post-fire flammability
 316 must be understood. In this study we found evidence that interaction between burn severity
 317 and seed bank composition may explain that link. Prior work has shown that annual grass
 318 invasion increases fuel connectivity in western US sagebrush ecosystems by filling in shrub
 319 interspaces with a contiguous bed of fine fuels (Davies and Nafus 2013). This change in
 320 the spatial distribution of fine fuels has been associated with larger and more frequent fires
 321 (Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) increases burn
 322 severity (H1, Figure 2a). Higher burn severity was associated with an increased occurrence of
 323 introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure
 324 2b). Higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher

325 post-fire fuel connectivity (H3, Figure 2c). In addition, we found evidence that high post-fire
326 fuel connectivity was associated with lower aboveground diversity (H4, Figure 2d). This
327 suggests that during inter-fire intervals, there are additional mechanisms maintaining the
328 post-fire species assemblage that is dominated by annual introduced plants.

329 The difference in species composition before and after fire explains an apparent contradiction
330 in results between H2a (positive relationship between pre-fire fuel connectivity and diversity)
331 and H4 (negative relationship between post-fire fuel connectivity and diversity). Most (11
332 out of 14) plot locations had mature canopies of native shrubs and with the inter-shrub space
333 occupied mostly by native bunchgrasses and forbs, with fire history since 1984. The three
334 plots with recent fire history burned in 1984 and were invaded by *B. tectorum*, but they still
335 had significant cover of *A. tridentata*. Even in locations with high annual grass cover between
336 shrubs, shrubs provide ecosystem structural heterogeneity and islands of fertility (Doescher,
337 Miller, and Winward 1984; Bechtold and Inouye 2007), and perennial natives that may have
338 been established before invasion have deep roots established that allow for the avoidance of
339 competition for water with shallow-rooted annuals (Gibbens and Lenz 2001; Ottaviani et al.
340 2020). This may provide enough niche compartmentalization to allow native plants to persist.
341 Three years after the Hot Pot fire, almost all of the plots were dominated by introduced
342 annuals, and lacked any structural heterogeneity. Thus native plants may have been able
343 to persist via niche compartmentalization after the initial invasion, but fire burns away most
344 of the seeds (Figure S1) and removes all of the structural benefits that shrub cover provides.
345 In this clean slate post-fire environment, the altered species composition of the seedbank and
346 superior post-fire dispersal of *B. tectorum* (Monty, Brown, and Johnston 2013) allows the
347 process of interspecific competition to be dominant (Schlaepfer, Lauenroth, and Bradford
348 2014).

349 *Global impacts*

350 The grass-fire cycle in the western US is reinforced through providing fitness benefits to

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

370 *Potential limitations*

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).

³⁷⁷ Nevertheless, for those species that were prevalent in our germination studies, we still found
³⁷⁸ consistent relationships between their abundance and occurrence by biogeographic origin,
³⁷⁹ and those species that were prevalent in the postfire seedbank germination assays were also
³⁸⁰ those most common in the aboveground community postfire.

³⁸¹ Burn severity metrics like dNBR were conceived of in the context of forested ecosystems (J.
³⁸² D. Miller et al. 2009), and calibrated using the composite burn index (Key and Benson 1999),
³⁸³ tree mortality, and percent change in tree canopy cover. These do not apply in shrubland
³⁸⁴ systems. Here we estimated burn severity using dNBR and understand it to be a proxy for the
³⁸⁵ amount of biomass that was burned in the fire. We recorded qualitative observations of burn
³⁸⁶ severity while we were sampling, mainly to ensure that we sampled a range of severities, and
³⁸⁷ the dNBR we used appears to be a good proxy for our observations. However, we note that
³⁸⁸ the manual severity classification provided by MTBS had exclusively low and medium severity,
³⁸⁹ but our observations of essentially complete consumption of plant and litter tissues and very
³⁹⁰ few unburned patches suggested that these should have been mostly medium and high severity.
³⁹¹ This was not unexpected (Kolden, Smith, and Abatzoglou 2015). The Hot Pot fire took place
³⁹² during a high wind event, burning 50,000 ha in only 3 days, so the scale of weather-driven fire
³⁹³ spread overtook any possibility of fuel disconnectivity on the scale of a few meters stopping
³⁹⁴ the spread of the fire. In areas where the space between shrubs was well-connected by fine
³⁹⁵ fuels (Figure 6a-c) the dNBR was higher, and the shrubs had completely burned throughout
³⁹⁶ the root system, leaving only a hole in the ground filled with ashes as evidence of their prior
³⁹⁷ presence. In these areas the entirety of the soil surface—underneath shrub canopy and in
³⁹⁸ canopy interspaces—was consumed by fire, and there was little evidence of remaining litter
³⁹⁹ or biological soil crust. In areas with lower fuel connectivity (Figure 6d-f), and lower dNBR,
⁴⁰⁰ shrubs were usually consumed only to the stumps, and sometimes were left standing and
⁴⁰¹ charred, destined for mortality. In these areas the soil surface often still had biological soil
⁴⁰² crust, partially consumed litter (Jones et al. 2015) and unconsumed annual and perennial
⁴⁰³ grass bases.

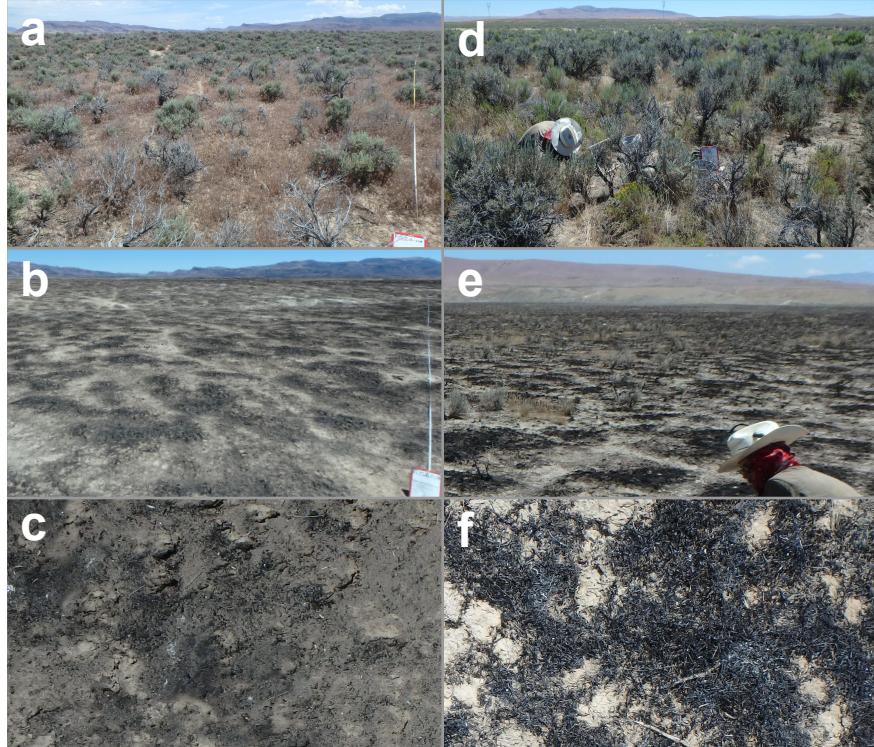


Figure 4: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space being highly invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, and approximately all of the biomass was consumed 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.

404 *Management implications*

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

413 This work shows that this is a clear example of a system where the degraded state represents
414 an alternative species assemblage from that of the restoration target, where the propagules
415 of the original assemblage are no longer present, and thus methods that rely on natural
416 succession may not be sufficient (Suding, Gross, and Houseman 2004). Our results highlight
417 the importance of prioritizing the preservation of native shrub cover and in particular policies
418 that encourage land managers to maximize the preservation of unburned patches during the
419 suppression of wildfires in this system (Steenvoorden et al. 2019). Commonly encountered
420 native plants and the keystone shrub species *A. tridentata* depend on post-fire seed dispersal
421 from surviving individuals in unburned patches (Schlaepfer, Lauenroth, and Bradford 2014).
422 Once the system achieves a canopy dominated by annual grasses and forbs, the competitive
423 pressure from the annual grass monoculture makes it more difficult if not impossible for
424 perennial native forbs and shrubs to establish from the depleted seedbank. Post-fire seeding
425 efforts may restore native propagules, but if there is dense cover of annuals further effort
426 may be required to reduce fuel connectivity in order to reduce both fire risk and competitive
427 pressure from annuals.

428 Livestock grazing can reduce fuel connectivity in uninvaded sagebrush (Davies et al. 2010).
429 At the same time, grazing can also decrease the resistance to invasion by *B. tectorum* via

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

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