

Running head: Burn severity and the grass fire cycle

Title: Mechanisms of the grass-fire cycle: 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
⁶ results in post-fire plant communities that are dominated by introduced annual grasses
⁷ (IAG). But in order to truly consider this annual grass-fire cycle to be maintained by self-
⁸ reinforcing feedbacks, the mechanisms by which fire occurrence is linked to higher post-fire
⁹ flammability must be understood. Here, we used total vegetation cover (TVC) as a proxy
¹⁰ for fuel connectivity and found that pre-fire TVC increased burn severity. We then used
¹¹ a joint species distribution model to examine how burn severity affected the proportion of
¹² IAG in the seed bank, and found that higher burn severity had mostly positive or neutral
¹³ effects on the occurrence of IAG and other non-native species, and mostly negative or neutral
¹⁴ relationships with native species. To complete the positive feedback loop, we found that
¹⁵ the abundance of IAG seeds in the seedbank immediately post-fire had a positive effect on
¹⁶ the fuel connectivity 3 years after fire. This is the first study that we are aware of in the
¹⁷ western US that shows how burn severity influences seed bank species composition, as well
¹⁸ as examining the full feedback loop between fuel connectivity, burn severity and seed bank
¹⁹ species composition. These results provide measurable ecosystem structure components as
²⁰ well as fire characteristics that land managers may be able to use to mitigate the effects of
²¹ the grass-fire cycle.

²² *Keywords:* cheatgrass, sagebrush, grass-fire cycle, joint species distribution model, burn
²³ severity, fuel connectivity, *Bromus tectorum*, *Artemisia tridentata*

²⁴ **1. Introduction**

²⁵ One of the consequences of global change in the 21st century that is most difficult to reverse
²⁶ is when ecosystems abruptly shift from one stable species assemblage to another (Ratajczak
²⁷ et al. 2018). In tropical ecosystems, three alternative stable states have been identified
²⁸ along a gradient of precipitation: forests, savannas and grasslands (Hirota et al. 2011;
²⁹ Staver, Archibald, and Levin 2011). These three states cluster around values of tree cover
³⁰ (approximately 80, 30 and 0 percent) that occur among overlapping levels of precipitation,
³¹ and so it is thought that they exhibit states of hysteresis in which internal, self-reinforcing
³² mechanisms maintain alternate states (Andersen et al. 2009). In the forested state there is
³³ a self-reinforcing positive feedback between evapotranspiration and tree cover (Staal et al.
³⁴ 2020). In the grassland and savanna states, there are feedbacks between grass flammability
³⁵ and fire occurrence (Staver, Archibald, and Levin 2011; D'Antonio and Vitousek 1992).

³⁶ A classic example of hysteresis in a semi-arid, temperate system is the invasion of *Bromus*
³⁷ *tectorum* L. and other introduced annual grasses in the Great Basin of the western United
³⁸ States. Here, over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*
³⁹ Beetle & Young) ecosystems have been degraded, fragmented or lost completely (Davies
⁴⁰ et al. 2011). This has been attributed to a host of causes, including wildfire (Balch et al.
⁴¹ 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of
⁴² annual grasses. Before invasion, the space between shrubs is primarily composed of bare
⁴³ ground covered in biological soil crust and dotted with perennial bunch grasses. The lack of
⁴⁴ fuel connectivity is believed to limit fire spread, with a historical fire regime of infrequent,
⁴⁵ patchy fires (Baker 2006; Bukowski and Baker 2013; Keeley and Pausas 2019). Annual grass
⁴⁶ invasion increases fuel connectivity while decreasing fuel moisture (Davies and Nafus 2013),
⁴⁷ leading to increased fire size and frequency (Whisenant 1990; Knapp 1996; Balch et al. 2013).
⁴⁸ After fire, the landscape is often dominated by introduced annual grasses and forbs. But in
⁴⁹ order to understand how the grassland state persists, the mechanisms by which fire benefits

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

55 The relationship between the species composition of the seed bank and fire severity and/or
56 intensity is understudied, but more attention has been given to the subject recently. In
57 boreal forests, the depth of the burn may be more important than the temperature of
58 the fire, with species-specific effects on recovery depending on whether the species recovers
59 via resprouting or from the seed bank (Morgan and Neuenschwander 1988; Schimmel and
60 Granström 1996). In a wetland study in Japan, high severity fire was found to increase
61 seedbank diversity, and the similarity between the seedbank composition and aboveground
62 composition was higher in places burned at high severity (Kimura and Tsuyuzaki 2011). There
63 have been a handful of studies in temperate, semi-arid regions. Lipoma, Funes, and Díaz
64 (2018) found that in shrubland high-severity fire reduced the overall number of seeds in the
65 seedbank but did not change the floristic or functional composition. Maia et al. (2012) found
66 intraspecific differences in post-fire seedbank densities that were explained by burn severity
67 in a pine plantation in Portugal. Palmer, Denham, and Ooi (2018) found that the residual
68 seedbank after fire varied with severity between two *Acacia* species in Australia. Wright,
69 Latz, and Zuur (2016) found that Australian mulga (*Acacia aneura*) had higher regeneration
70 after higher fire temperatures. In Iran, Heydari et al. (2017) found that low-severity fire
71 increased diversity in the soil seed bank, but high-severity fire led to losses. These studies
72 show that the effects of fire severity on the seed bank are ecosystem- and species-specific.
73 High severity fire can benefit species that use the seedbank (Kimura and Tsuyuzaki 2011), be
74 seedbank-neutral (Lipoma, Funes, and Díaz 2018), or have a negative effect (Heydari et al.
75 2017). Furthermore, beyond simply affecting seed mortality, fire temperature can also alter
76 physical seed dormancy thresholds (Liyanage and Ooi 2017).

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

93 There is strong evidence that *B. tectorum* invasion alters the physical properties of fire,
94 including fire temperature (Brooks et al. 2004; Jones et al. 2015) and burn severity (the
95 proportion of biomass burned (Keeley 2009)). Burn severity can be measured after fire *in situ*,
96 or via satellite by comparing scenes from before and after the fire (J. D. Miller et al. 2009).
97 While in many cases fires that burn at higher temperatures will also burn at higher severities,
98 grass fires may not always have such a relationship. Direct measurements have shown that *B.*
99 *tectorum* burns at low temperatures (Beckstead et al. 2011; Germino, Chambers, and Brown
100 2016). Because fire duration is inversely related to soil heating, lower fire temperatures can
101 be inferred from the commonly observed phenomenon that *B. tectorum*-fueled fires burn fast.
102 Soil heating affects the response of vegetation to fire (Gagnon et al. 2015), including the
103 capacity of the seeds of *B. tectorum* to remain viable after fire (Humphrey and Schupp 2001).

¹⁰⁴ Because *B. tectorum* also increases horizontal fuel connectivity (Davies and Nafus 2013), this
¹⁰⁵ leads to more contiguously burned areas with fewer unburned plants, and therefore higher
¹⁰⁶ burn severity—even with lower fire temperatures.

¹⁰⁷ If increased burn severity is a mechanism by which *B. tectorum* excludes native plants in
¹⁰⁸ sagebrush shrublands, then an area with high burn severity may have a lower occurrence of
¹⁰⁹ viable seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced
¹¹⁰ annual plants. This would lead to the dominance of introduced annual grasses and forbs
¹¹¹ would result in higher fuel connectivity, closing the positive feedback loop. Prior work has
¹¹² demonstrated that *A. tridentata* communities have historically had long fire rotations (>150
¹¹³ years) (Baker 2006; Bukowski and Baker 2013). Plants that are adapted to infrequent fire
¹¹⁴ would be unlikely to produce seeds that are adapted to surviving fire, or dispersal mechanisms
¹¹⁵ to take advantage of the resources available immediately after fire (Davis et al. 2000; Keeley
¹¹⁶ et al. 2011). *A. tridentata* relies on tolerating drought and opportunistically devoting its
¹¹⁷ resources to producing big seed crops in cool, wet years (Meyer 1994; Perryman et al. 2001;
¹¹⁸ Shriver et al. 2018). When it burns it burns with high intensity, killing individual plants,
¹¹⁹ and the remaining unburned neighbors seed the area (*sensu* Schwilk and Kerr 2002). The
¹²⁰ seeds have a short dispersal distance, the vast majority falling within a few meters of the
¹²¹ parent plant (Meyer 1994; Schlaepfer, Lauenroth, and Bradford 2014). They typically lose
¹²² their viability after one growing season if they remain on the soil surface or under litter, but
¹²³ can retain some viability for at least 24 months if they are buried under a few inches of soil
¹²⁴ (Wijayratne and Pyke 2009).

¹²⁵ The Great Basin has not escaped the recent warming and drying trend that the western U.S.
¹²⁶ has experienced (Melillo, Richmond, and Yohe 2014; Bradford et al. 2020). This is expected
¹²⁷ to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly
¹²⁸ by causing the plants to produce lighter seeds (Schlaepfer, Lauenroth, and Bradford 2014).
¹²⁹ With this in mind, there is another potential self-reinforcing mechanism that could serve to

¹³⁰ maintain the high fuel connectivity state without fire. That is that the post-fire state with
¹³¹ high fuel connectivity is associated with two mechanisms for competitive exclusion of natives.
¹³² First, it reduces soil moisture which is unfavorable for *Artemisia* seedlings (Turnbull et al.
¹³³ 2012; Wilcox et al. 2012). Second, the dominant plant, *B. tectorum*, can out-compete native
¹³⁴ plants for early spring moisture (Meyer 1994; Chambers et al. 2007).

¹³⁵ Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot
¹³⁶ Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July
¹³⁷ 2016. Because it burned a large area in only three days, we could sample a broad area
¹³⁸ while being reasonably certain that the climatic conditions during the fire were the same
¹³⁹ at all sites. Because we collected our samples immediately after the fire was extinguished,
¹⁴⁰ we felt confident that the seed bank samples did not contain seeds deposited by post-fire
¹⁴¹ dispersal. We put the samples in cold storage and germinated the seeds from those cores in a
¹⁴² greenhouse the following spring. In spring 2017 and fall 2019 we collected information on
¹⁴³ vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel
¹⁴⁴ connectivity would be positively related to burn severity; (H2) burn severity would increase
¹⁴⁵ the occurrence probability of introduced annual species in the seed bank and reduce the
¹⁴⁶ occurrence probability of native species; (H2a) increased fuel connectivity brought on by
¹⁴⁷ the invasion of annual grasses already depleted the diversity of the soil seed bank before the
¹⁴⁸ fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related
¹⁴⁹ to post-fire fuel connectivity. In addition, because in our study system sites with high fuel
¹⁵⁰ connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high
¹⁵¹ post-fire fuel connectivity of those near-monocultures would result in lower aboveground
¹⁵² species diversity due to competitive pressure.

¹⁵³ 2. Methods

¹⁵⁴ 2.1 Study Area

¹⁵⁵ The study was conducted in north-central Nevada the day after a large fire (the Hot Pot
¹⁵⁶ Fire) was extinguished (Figure 1). The Hot Pot Fire burned just over 50,000 hectares in
¹⁵⁷ less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big
¹⁵⁸ sagebrush plant communities. The fire occurred after the early season plants, including *B.*
¹⁵⁹ *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone
¹⁶⁰ to seed, and before the late season species, including Wyoming big sagebrush, had produced
¹⁶¹ flowers. Thus we were able to isolate the effect of the fire without any confounding effects of
¹⁶² post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged
¹⁶³ from 1397 to 1607 meters in elevation.

¹⁶⁴ *2.2 Seed Bank Sampling*

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

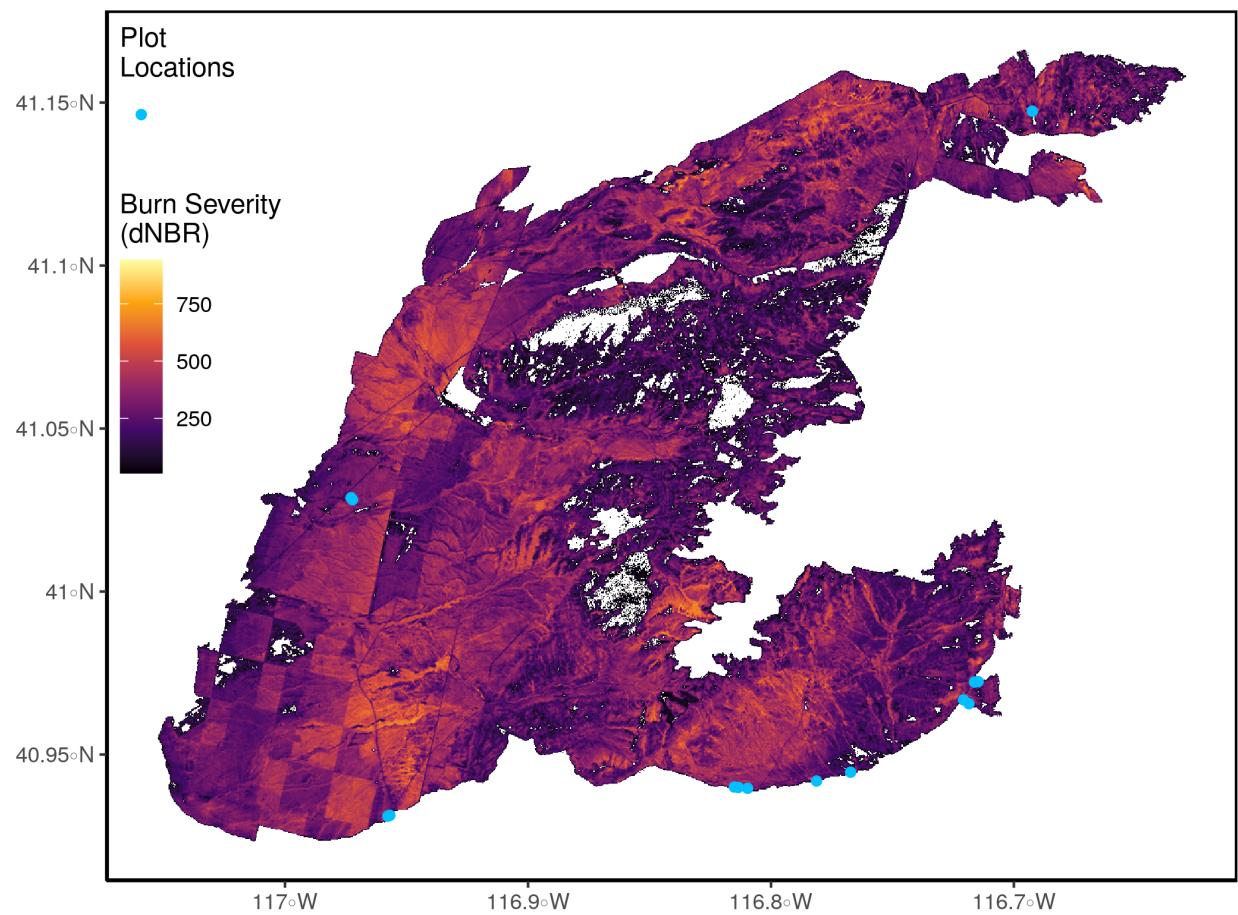


Figure 1: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

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

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

192 *2.3 Greenhouse Germination*

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

199 *2.4 Post-Fire Vegetation Sampling*

200 In order to understand how the seed bank composition compares to the realized vegetative
201 composition, we sampled the vegetative occupancy and cover in May 2017, the growing
202 season immediately after the fire and again in September 2019. In 2017, at each location, we
203 established 50m transects starting at the boundary of the burned and unburned sides of the
204 perimeter, running perpendicular to the fire perimeter, and marked the transect ends with
205 rebar. We measured the occupancy and abundance of all plant species by measuring cover
206 of every species in 0.1 m² quadrats spaced every 5 m along each transect. We used the line

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

214 *2.5 Estimating Burn Severity with Landsat 8 OLI*

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

223 *2.6 Statistical Analysis*

224 Our statistical analysis centered around trying to understand each component of the positive
225 feedback loop posited by the 4 hypotheses described above. In order to understand how
226 pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC)
227 from two separate data sources as a proxy for fuel connectivity, and created separate linear
228 models with TVC as the predictor variable and burn severity (dNBR, [J. D. Miller et al.](#)
229 [2009](#)) as the response variable. With the field data we collected, we created an ordinary least
230 squares (OLS) linear model with burn severity as the dependent variable and TVC (defined as
231 shrub cover plus herbaceous plant cover from the unburned side of the paired plots), elevation
232 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 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: $\text{Green NDVI} = \frac{\text{NIR-Green}}{\text{NIR+Green}}$

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 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 is freely available on Figshare (link here after acceptance) and GitHub (<https://www.github.com/admahood/seed-bank>).

²⁸⁵ **3. Results**

²⁸⁶ We found support for each hypothesized component of the positive feedback loop. For H1,
²⁸⁷ the most parsimonious model for our *in situ* observations had only TVC as the predictor,
²⁸⁸ which had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$,
²⁸⁹ Figure 2a, Table S2). For our remotely sensed analysis, our most parsimonious model of
²⁹⁰ TVC explained 35% of the variation and had Green NDVI, NDSVI and their interaction as
²⁹¹ predictors (Table S2). Our model of dNBR using the predicted TVC within the fire perimeter
²⁹² as a predictor of dNBR explained 42% of the variation and the relationship between TVC
²⁹³ and burn severity was positive and significant ($p \ll 0.01$, Figure 2a, Table S2).

²⁹⁴ The vast majority of seeds that germinated in the greenhouse were the two most common
²⁹⁵ grass species, *P. secunda* and *B. tectorum* (Table S1). Eight forb species were found in more
²⁹⁶ than one location, and these 10 prevalent species are those that were used in our JSDM.
²⁹⁷ Burned plots had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14 in the
²⁹⁸ bottom 4 cm. Unburned plots had an average of 299 ± 170 in the top 2 cm and 59 ± 29
²⁹⁹ in the bottom 4 cm (Figure S1). For H2, the JSDM converged well (Gelman diagnostics
³⁰⁰ all very close to 1 and the effective sample size centered on 4,000, Figure S2a). Elevation
³⁰¹ had the most significant effects on individual species (Figure S2b) and explained the most
³⁰² variance on average (36% Figure S2c). Burn severity explained 23% of the variance on
³⁰³ average and was supported at the 95% level for 5 species (Figure S2b). For the introduced
³⁰⁴ species, the predictions along a gradient of burn severity were positive for *B. tectorum*,
³⁰⁵ *Sisymbrium altissimum* L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala*
³⁰⁶ *testiculata* and *Alyssum desertorum* Stapf (Figure 2b). For native species, the effect of burn
³⁰⁷ severity on occurrence was positive for *A. tridentata*, neutral for *P. secunda* and negative
³⁰⁸ for the remaining species (Figure 2b). Testing H2a revealed a positive relationship between
³⁰⁹ pre-fire aboveground species diversity and pre-fire fuel connectivity, and so we felt it was
³¹⁰ reasonable to rule out pre-fire fuel connectivity as a confounding factor for H2.

³¹¹ For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and
³¹² the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the postfire seedbank
³¹³ was positively associated with the fuel connectivity in 2019 ($\beta = 0.54$, $p = 0.01$, Adj $R^2 =$
³¹⁴ 0.75, Figure 3c, Table S2).

³¹⁵ For H4 the most parsimonious model (Adj $R^2 = 0.89$, Table S2) had elevation, aspect, fuel
³¹⁶ connectivity and an interaction between elevation and fuel connectivity as predictors of
³¹⁷ aboveground Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated
³¹⁸ with Shannon-Weaver diversity ($\beta = -0.28$, $p=0.004$, Figure 3d).

³¹⁹ 4. Discussion

³²⁰ In order to truly consider an annual grass-fire cycle to be maintained by self-reinforcing
³²¹ feedbacks, the mechanisms by which fire occurrence is linked to higher post-fire flammability
³²² must be understood. In this study we found evidence that interaction between burn severity
³²³ and seed bank composition may explain that link. Prior work has shown that annual grass
³²⁴ invasion increases fuel connectivity in western US sagebrush ecosystems by filling in shrub
³²⁵ interspaces with a contiguous bed of fine fuels (Davies and Nafus 2013). This change in
³²⁶ the spatial distribution of fine fuels has been associated with larger and more frequent fires
³²⁷ (Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) increases burn
³²⁸ severity (H1, Figure 2a). Higher burn severity was associated with an increased occurrence of
³²⁹ introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure
³³⁰ 2b). Higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher
³³¹ post-fire fuel connectivity (H3, Figure 2c). In addition, we found evidence that high post-fire
³³² fuel connectivity was associated with lower aboveground diversity (H4, Figure 2d). This
³³³ suggests that during inter-fire intervals, there are additional mechanisms maintaining the
³³⁴ post-fire species assemblage that is dominated by annual introduced plants.

³³⁵ The difference in species composition before and after fire explains an apparent contradiction

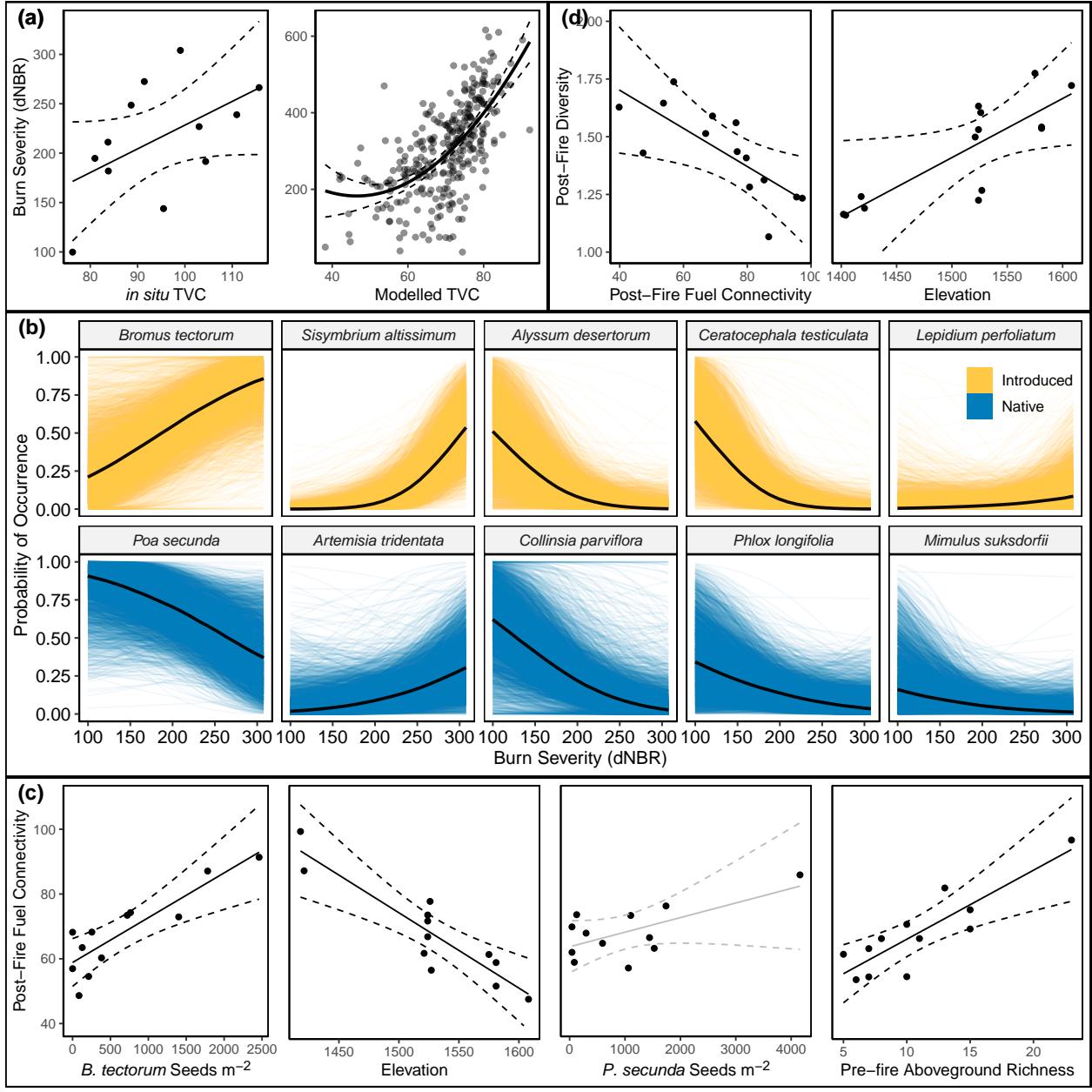


Figure 2: On the left side of (a), burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Panel b shows the modelled occurrence of germinable seeds for all species found at more 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

336 in results between H2a (positive relationship between pre-fire fuel connectivity and diversity)
337 and H4 (negative relationship between post-fire fuel connectivity and diversity). Most (11
338 out of 14) plot locations had mature canopies of native shrubs and with the inter-shrub space
339 occupied mostly by native bunchgrasses and forbs, with fire history since 1984. The three
340 plots with recent fire history burned in 1984 and were invaded by *B. tectorum*, but they still
341 had significant cover of *A. tridentata*. Even in locations with high annual grass cover between
342 shrubs, shrubs provide ecosystem structural heterogeneity and islands of fertility ([Doescher,](#)
343 [Miller, and Winward 1984; Bechtold and Inouye 2007](#)), and perennial natives that may have
344 been established before invasion have deep roots established that allow for the avoidance of
345 competition for water with shallow-rooted annuals ([Gibbens and Lenz 2001; Ottaviani et al.](#)
346 [2020](#)). This may provide enough niche compartmentalization to allow native plants to persist.
347 Three years after the Hot Pot fire, almost all of the plots were dominated by introduced
348 annuals, and lacked any structural heterogeneity. Thus native plants may have been able
349 to persist via niche compartmentalization after the initial invasion, but fire burns away most
350 of the seeds (Figure S1) and removes all of the structural benefits that shrub cover provides.
351 In this clean slate post-fire environment, the altered species composition of the seedbank and
352 superior post-fire dispersal of *B. tectorum* ([Monty, Brown, and Johnston 2013](#)) allows the
353 process of interspecific competition to be dominant ([Schlaepfer, Lauenroth, and Bradford](#)
354 [2014](#)).

355 *Global impacts*

356 The grass-fire cycle in the western US is reinforced through providing fitness benefits to
357 the introduced annual grasses and forbs via at least 4 redundant processes: i) changing the
358 composition of the seedbank, ii) competitive exclusion of native plants, iii) CO₂ enrichment
359 which may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of
360 annual grass species ([Nagel et al. 2004; Smith et al. 2000](#)), strengthening the fuel connectivity
361 to burn severity to seed composition feedback loop, and iv) ecohydrological feedbacks that

362 create a warmer, drier microclimate (Turnbull et al. 2012; Wilcox et al. 2012). It is likely
363 that some of these feedbacks are idiosyncratic to the system being studied, while others
364 may reflect the fundamental properties of ecosystem function that change when a system is
365 converted from being dominated by woody plants to being dominated by herbaceous plants
366 (Kitzberger et al. 2016). Understanding the mechanisms of hysteresis, and in particular how
367 multiple redundant mechanisms act in concert, will provide important insights for ecosystem
368 change on a global scale. At least 13 grass species initiate self-reinforcing feedbacks with
369 fire in the U.S. (Fusco et al. 2019; Tortorelli, Krawchuk, and Kerns 2020), and many more
370 worldwide, including Australia (G. Miller et al. 2010; Setterfield et al. 2010), Brazil (Rossi et
371 al. 2014) and South Africa (Milton 2004). While the conversion of temperate forests and
372 shrublands to grasslands may have a less per-hectare impact on carbon sequestration than
373 tropical forests, the consequences are still relevant to the global carbon cycle, especially when
374 forests (rather than the shrublands studied here) are replaced by herbaceous ecosystems
375 (Kerns et al. 2020).

376 *Potential limitations*

377 We found fewer species and lower diversity in our seedbank germination assays than we did in
378 the aboveground sampling (Figure S3). This result may be influenced by the methodological
379 limitations inherent to greenhouse germination trials (Vandvik et al. 2016). In particular
380 our results may be understating the occurrence of native species in the seedbank. Habitat
381 specialists have been shown to emerge more in *in situ* germination assays than in greenhouse
382 germination assays, while the opposite has been found for ruderal species (Plue et al. 2017).
383 Nevertheless, for those species that were prevalent in our germination studies, we still found
384 consistent relationships between their abundance and occurrence by biogeographic origin,
385 and those species that were prevalent in the postfire seedbank germination assays were also
386 those most common in the aboveground community postfire.

387 *Contrasts among forests and shrublands as it pertains to remote sensing*

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

411 Other studies that have used spectral indexes to quantify fuel connectivity in forested systems
412 have typically used NDVI (Parks et al. 2018; Koontz et al. 2020). Here, we arrived at green
413 NDVI and NDSVI, this contrast is the manifestation of key differences in the physiognomies
414 of forest and arid shrublands that is essential to understand their relationship to fire. In

415 coniferous forests of the western US, greenness is a good proxy for fuel load and NDVI texture
416 for connectivity. In sagebrush shrublands, the fuel that contributes to large wildfires is a
417 mixture of evergreen shrubs interspersed with herbaceous plants that remain green for only a
418 portion of the growing season, and then become dry and straw-colored.

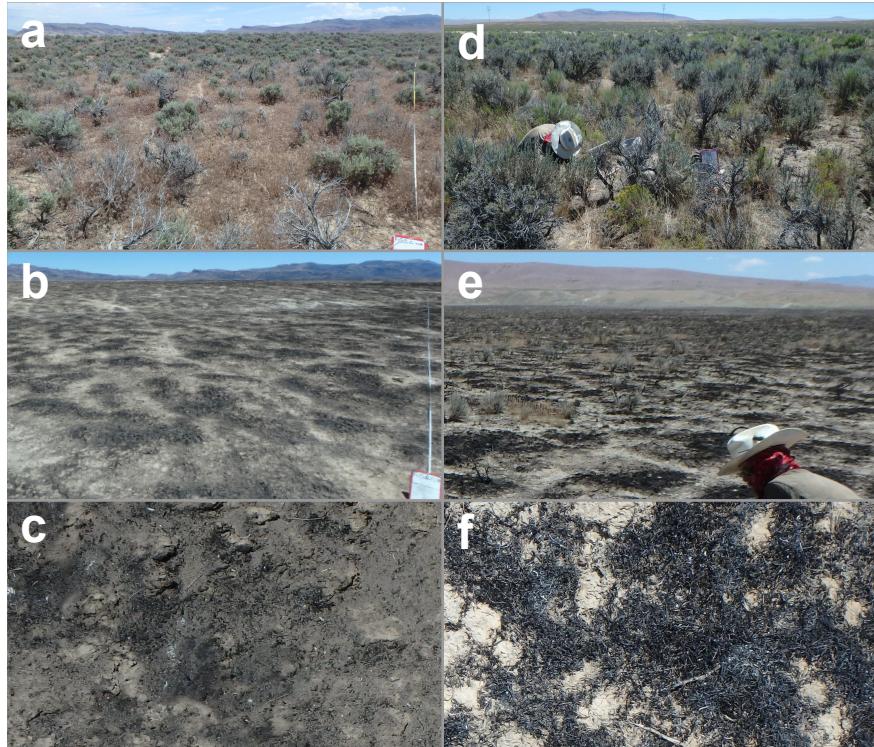


Figure 3: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space being highly invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, and approximately all of the biomass was consumed 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.

419 Management implications

420 Greenhouse or *in situ* germination assays are time-consuming and require botanical expertise,
421 and are very important. One potential avenue for future research may be linking remote
422 sensing data with retrospective meta-analyses of prior studies. There are many studies that
423 only study fire occurrence as it relates to the seed bank. Fire history, including burn severity,

424 is now possible to calculate for anywhere on earth at a 30 meter resolution from 1984 to
425 present with Landsat images ([Parks et al. 2018](#)). Teasing out these mechanisms will increase
426 our understanding of how generalizable these phenomena are, and where and when it may be
427 possible to reverse the process.

428 This work shows that the post-fire annual grassland is a system where the degraded state
429 represents an alternative species assemblage from that of the restoration target, where the
430 propagules of the original assemblage are no longer present, and thus methods that rely on
431 natural succession may not be sufficient ([Suding, Gross, and Houseman 2004](#)). These results
432 provide measurable fire properties and ecosystem structural components that compose the
433 self-reinforcing feedback. This information may be useful for land managers for identifying
434 new methods for breaking these feedbacks, in order to increase the likelihood for successful
435 restoration.

436 Our results highlight the importance of prioritizing the preservation of native shrub cover
437 and in particular policies that encourage land managers to maximize the preservation of
438 unburned patches during the suppression of wildfires in this system ([Steenvoorden et al.](#)
439 [2019](#)). Commonly encountered native plants and the keystone shrub species *A. tridentata*
440 depend on post-fire seed dispersal from surviving individuals in unburned patches ([Schlaepfer,](#)
441 [Lauenroth, and Bradford 2014](#)). Once the system achieves a canopy dominated by annual
442 grasses and forbs, the competitive pressure from the annual grass monoculture makes it more
443 difficult if not impossible for perennial native forbs and shrubs to establish from the depleted
444 seedbank. Post-fire seeding efforts may restore native propagules, but if there is dense cover
445 of annuals further effort may be required to reduce fuel connectivity in order to reduce both
446 fire risk and competitive pressure from annuals. Our results also suggest that calculating the
447 burn severity using remote sensing may help land managers identify areas that may be have
448 a greater likelihood of successful seeding.

449 Livestock grazing can reduce fuel connectivity in uninvaded sagebrush ([Davies et al. 2010](#)).

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

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