

Running head: Burn severity and the grass fire cycle

Title: Burn severity, fuel connectivity and seed bank survivorship drive the annual-grass fire cycle in a semi-arid shrubland.

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¹ Abstract

² Introduced grasses can initiate novel grass-fire cycles that alter ecosystem structure and
³ function, and threaten biodiversity. In sagebrush communities in the western United States,
⁴ annual grass invasion increases the connectivity of fine fuels, which increases the size and
⁵ spatial contiguity of fires. This increase in fire size and contiguity results in post-fire plant
⁶ communities that are dominated by introduced annual grasses (IAG), which are themselves
⁷ more likely to promote large fires and initiate a novel grass-fire cycle. But the mechanisms
⁸ by which pre-fire invasion and fire occurrence are linked to higher post-fire flammability are
⁹ not fully understood.

¹⁰ Here, we used total vegetation cover (TVC) as a proxy for fuel connectivity and found that
¹¹ pre-fire TVC increased burn severity. We then used a Bayesian joint species distribution
¹² model to examine how burn severity affected the proportion of IAG in the seed bank, and
¹³ found that higher burn severity had mostly positive or neutral effects on the occurrence of
¹⁴ IAG and other non-native species, and mostly negative or neutral relationships with native
¹⁵ species. To complete the positive feedback loop, we found that the abundance of IAG seeds
¹⁶ in the seedbank immediately post-fire had a positive effect on the fuel connectivity 3 years
¹⁷ after fire. This is the first study that we are aware of in the western US that shows how burn

18 severity influences seed bank species composition, as well as examining the full feedback loop
19 between fuel connectivity, burn severity and seed bank species composition. These results
20 suggest that measurable characteristics of ecosystem structure (e.g. TVC) and fire (dNBR)
21 may be used to inform management actions to mitigate the negative effects of the grass-fire
22 cycle, perhaps via targeted restoration applications or pre-fire fuel treatments.

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

25 1. Introduction

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

37 A classic example of a novel grass-fire cycle in a semi-arid, temperate system is the invasion
38 and persistence of *Bromus tectorum* L. and other introduced annual grasses in the Great
39 Basin of the western United States. Here, over half of Wyoming big sagebrush (*Artemisia*
40 *tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems have been degraded, fragmented or
41 lost completely (Davies et al. 2011). This has been attributed to a host of causes, including
42 wildfire (Balch et al. 2013), grazing (Williamson et al. 2019), land use/land cover change,

43 and the invasion of annual grasses. At uninvaded sites, the space between shrubs is typically
44 composed of bare ground covered in biological soil crust and dotted with perennial bunch
45 grasses. The lack of fuel connectivity is believed to limit fire spread, with a historical fire
46 regime of infrequent, patchy fires (Baker 2006; Bukowski and Baker 2013; Keeley and Pausas
47 2019). Annual grass invasion increases fuel connectivity while decreasing fuel moisture
48 (Davies and Nafus 2013), leading to increased fire size and frequency (Whisenant 1990;
49 Knapp 1996; Balch et al. 2013). After fire, the landscape is often dominated by introduced
50 annual grasses and forbs. But in order to understand how the grassland state persists, the
51 mechanisms by which fire benefits the introduced annual grass must be understood. Petraitis
52 and Latham (1999) posited that the maintenance of alternate species assemblages requires
53 first a disturbance that removes the species from the initial assemblage and second the arrival
54 of the species of the alternate assemblage. One understudied mechanism that may explain
55 both is the interaction between burn severity and the species composition of the soil seed
56 bank.

57 The relationship between the species composition of the seed bank and fire severity and/or
58 intensity is relatively understudied. In different systems, individual species have adapted
59 strategies to cope with fires that may be adapted to different severities. In boreal forests,
60 the depth of the burn may be more important than the temperature of the fire, with
61 species-specific effects on recovery depending on whether the species recovers via resprouting
62 or from the seed bank (Morgan and Neuenschwander 1988; Schimmel and Granström 1996).
63 In a wetland study in Japan, high severity fire was found to increase seedbank diversity, and
64 the similarity between the seedbank composition and aboveground composition was higher in
65 places burned at high severity (Kimura and Tsuyuzaki 2011). There have been a handful
66 of studies in temperate, semi-arid regions. Lipoma, Funes, and Díaz (2018) found that in
67 shrubland high-severity fire reduced the overall number of seeds in the seedbank but did
68 not change the floristic or functional composition. Maia et al. (2012) found intraspecific
69 differences in post-fire seedbank densities that were explained by burn severity in a pine

70 plantation in Portugal. Palmer, Denham, and Ooi (2018) found that the residual seedbank
71 after fire varied with severity between two *Acacia* species in Australia. Wright, Latz, and
72 Zuur (2016) found that Australian mulga (*Acacia aneura*) had higher regeneration after
73 higher fire temperatures. In Iran, Heydari et al. (2017) found that low-severity fire increased
74 diversity in the soil seed bank, but high-severity fire led to losses. These studies show that the
75 effects of fire severity on the seed bank are ecosystem- and species-specific. High severity fire
76 can benefit species that use the seedbank (Kimura and Tsuyuzaki 2011), be seedbank-neutral
77 (Lipoma, Funes, and Díaz 2018), or have a negative effect (Heydari et al. 2017). Furthermore,
78 beyond simply affecting seed mortality, fire temperature can also alter physical seed dormancy
79 thresholds (Liyanage and Ooi 2017).

80 In order for an annual like *B. tectorum* it to benefit from fire, which it clearly does (Balch et
81 al. 2013; Mahood and Balch 2019), it would need enough seeds in the post-fire landscape to
82 achieve a fitness benefit and become well-represented in the post-fire plant assemblage (Bond
83 and Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal, and
84 *B. tectorum* seeds have been shown to have increased dispersal distances after fire (Monty,
85 Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. There
86 is strong evidence that *B. tectorum* builds a well-stocked pool of seeds in the soil and litter,
87 even when it is not well represented in the above-ground plant assemblage (Young and Evans
88 1975; Hassan and West 1986; Boudell, Link, and Johansen 2002). If the increase in fuel
89 connectivity caused by *B. tectorum* increases the severity of fire, it stands to reason that
90 burn severity would influence the community composition of the post-fire seed bank in a way
91 that facilitates the post-fire dominance of *B. tectorum*. To our knowledge, despite several
92 studies on the relationship between fire and the seed bank in this system (Young and Evans
93 1975; Hassan and West 1986; Humphrey and Schupp 2001; Boudell, Link, and Johansen
94 2002; Barga and Leger 2018), no studies to date have examined this potential effect of burn
95 severity on the seed bank.

96 There is strong evidence that *B. tectorum* invasion alters the physical properties of fire,
97 including fire temperature (Brooks et al. 2004; Jones et al. 2015) and burn severity (defined
98 here as the proportion of biomass burned (Keeley 2009)). Burn severity can be measured
99 after fire *in situ*, or estimated from satellite images by comparing scenes from before and after
100 the fire (J. D. Miller et al. 2009). While in many cases fires that burn at higher temperatures
101 will also burn at higher severities, grass fires may not always have such a relationship. Direct
102 measurements have shown that *B. tectorum* burns at low temperatures (Beckstead et al.
103 2011; Germino, Chambers, and Brown 2016). Because fire duration is inversely related to soil
104 heating, lower fire temperatures can be inferred from the commonly observed phenomenon
105 that *B. tectorum*-fueled fires burn fast. Soil heating affects the response of vegetation to fire
106 (Gagnon et al. 2015), including the capacity of the seeds of *B. tectorum* to remain viable
107 after fire (Humphrey and Schupp 2001). Because *B. tectorum* also increases horizontal fuel
108 connectivity (Davies and Nafus 2013), this leads to more contiguously burned areas with
109 fewer unburned plants, and therefore higher burn severity, despite lower fire temperatures.

110 If increased burn severity is a mechanism by which *B. tectorum* invasion excludes native plants
111 in sagebrush shrublands, then an area with high burn severity should have a lower occurrence
112 of viable seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced
113 annual plants. This would lead to the dominance of introduced annual grasses and forbs and
114 would result in higher fuel connectivity, closing the positive feedback loop. Prior work has
115 demonstrated that *A. tridentata* communities have historically had long fire rotations (>150
116 years) (Baker 2006; Bukowski and Baker 2013). Plants that are adapted to infrequent fire
117 would be unlikely to produce seeds that are adapted to surviving fire, or dispersal mechanisms
118 to take advantage of the resources available immediately after fire (Davis et al. 2000; Keeley
119 et al. 2011). *A. tridentata* relies on tolerating drought and opportunistically devoting its
120 resources to producing large seed crops in cool, wet years (Meyer 1994; Perryman et al. 2001;
121 Shriver et al. 2018). When it burns it burns with high intensity, killing individual plants, and
122 the remaining unburned neighbors seed the area (*sensu* Schwilk and Kerr 2002). The seeds

¹²³ have a short dispersal distance, the vast majority falling within a few meters of the parent
¹²⁴ plant (Meyer 1994; Schlaepfer, Lauenroth, and Bradford 2014). They typically lose their
¹²⁵ viability after one growing season if they remain on the soil surface or under litter, but can
¹²⁶ remain viable for at least two years if they are buried under a few inches of soil (Wijayratne
¹²⁷ and Pyke 2009).

¹²⁸ The Great Basin has not escaped the recent warming and drying trend that the western U.S.
¹²⁹ has experienced (Melillo, Richmond, and Yohe 2014; Bradford et al. 2020). This is expected
¹³⁰ to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly
¹³¹ by causing the plants to produce lighter seeds (Schlaepfer, Lauenroth, and Bradford 2014).
¹³² With this in mind, there is another potential self-reinforcing mechanism that could serve to
¹³³ maintain the high fuel connectivity state without fire. That is that the post-fire state with
¹³⁴ high fuel connectivity is associated with two mechanisms for competitive exclusion of natives.
¹³⁵ First, it reduces soil moisture which is unfavorable for *Artemisia* seedlings (Turnbull et al.
¹³⁶ 2012; Wilcox et al. 2012). Second, the dominant plant, *B. tectorum*, can out-compete native
¹³⁷ plants for early spring moisture (Meyer 1994; Chambers et al. 2007).

¹³⁸ Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot
¹³⁹ Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July
¹⁴⁰ 2016. Because it burned a large area in only three days, we could sample a broad area
¹⁴¹ while being reasonably certain that the climatic conditions during the fire were the same
¹⁴² at all sites. Because we collected our samples immediately after the fire was extinguished,
¹⁴³ we felt confident that the seed bank samples did not contain seeds deposited by post-fire
¹⁴⁴ dispersal. We put the samples in cold storage and germinated the seeds from those cores in a
¹⁴⁵ greenhouse the following spring. In spring 2017 and fall 2019 we collected information on
¹⁴⁶ vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel
¹⁴⁷ connectivity would be positively related to burn severity; (H2) burn severity would increase
¹⁴⁸ the occurrence probability of introduced annual species in the seed bank and reduce the

¹⁴⁹ occurrence probability of native species; (H2a) increased fuel connectivity brought on by
¹⁵⁰ the invasion of annual grasses already depleted the diversity of the soil seed bank before the
¹⁵¹ fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related
¹⁵² to post-fire fuel connectivity. In addition, because in our study system sites with high fuel
¹⁵³ connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high
¹⁵⁴ post-fire fuel connectivity of those near-monocultures would result in lower aboveground
¹⁵⁵ species diversity due to competitive pressure.

¹⁵⁶ 2. Methods

¹⁵⁷ 2.1 Study Area

¹⁵⁸ The study was conducted in north-central Nevada the day after a large fire (the Hot Pot
¹⁵⁹ Fire) was extinguished (Figure 1). The Hot Pot Fire burned just over 50,000 hectares in
¹⁶⁰ less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big
¹⁶¹ sagebrush plant communities. The fire occurred after the early season plants, including *B.*
¹⁶² *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone
¹⁶³ to seed, and before the late season species, including Wyoming big sagebrush, had produced
¹⁶⁴ flowers. Thus we were able to isolate the effect of the fire without any confounding effects of
¹⁶⁵ post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged
¹⁶⁶ from 1397 to 1607 meters in elevation.

¹⁶⁷ 2.2 Seed Bank Sampling

¹⁶⁸ In early July 2016, we collected samples of the soil seed bank at fourteen locations the day
¹⁶⁹ after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where
¹⁷⁰ it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites
¹⁷¹ were mature sagebrush communities with no history of fire since at least 1984. Three plots
¹⁷² had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS)
¹⁷³ fire history ([Eidenshink et al. 2007](#)) and had high cover of *B. tectorum*, but still had scattered

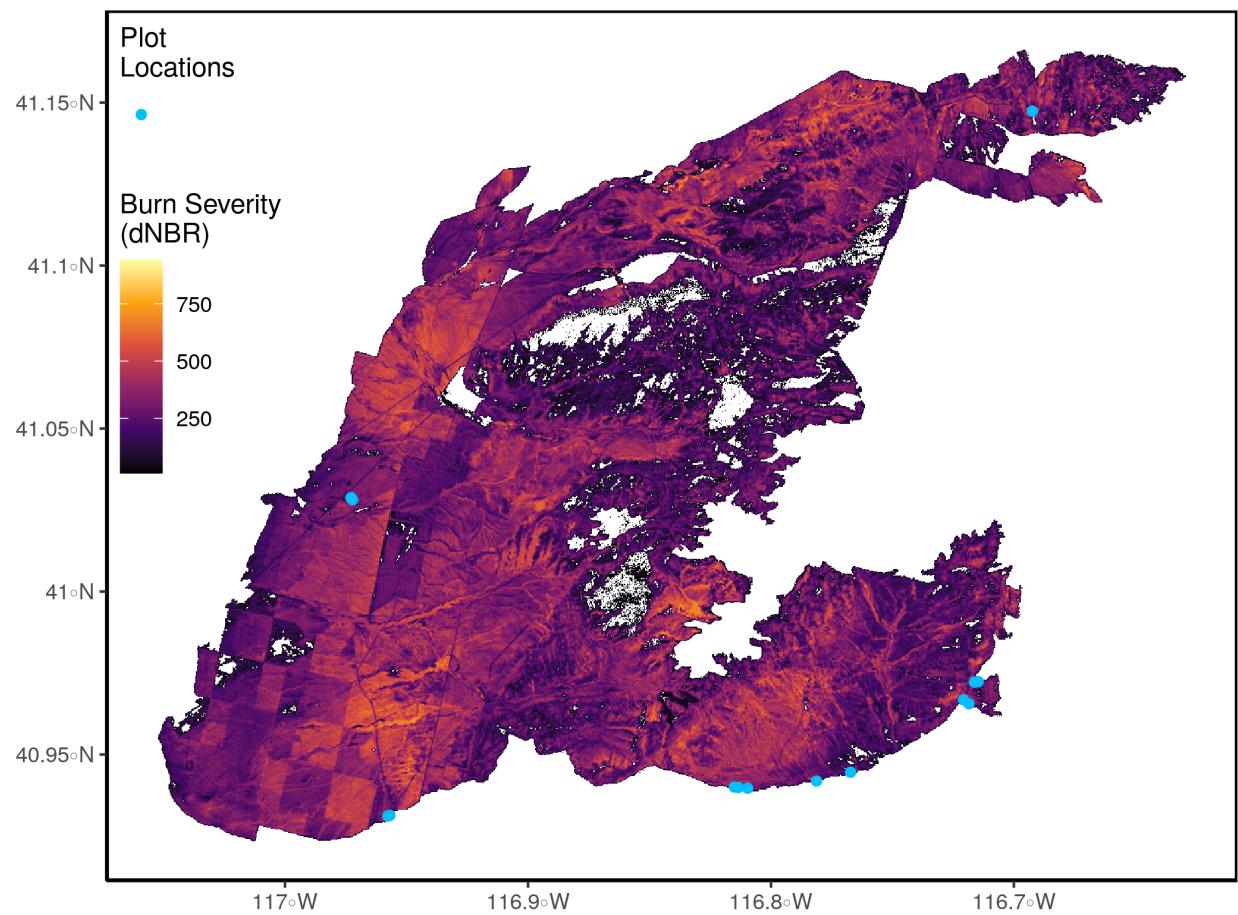


Figure 1: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

¹⁷⁴ sagebrush cover. We used a metal stake to mark paired burned and unburned sampling
¹⁷⁵ locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic
¹⁷⁶ disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the
¹⁷⁷ perimeter. Within 3 m of each marker, we extracted 12, 6 cm deep, 5 cm diameter, soil cores.
¹⁷⁸ Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system
¹⁷⁹ (Shinneman and McIlroy 2016), and so they are not uniformly distributed (Boudell, Link, and
¹⁸⁰ Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemesia*
¹⁸¹ have different germination rates based on the micro-site they find themselves in (i.e. under
¹⁸² a shrub or in the bare ground between shrubs, Eckert et al. 1986). To account for these
¹⁸³ potentially confounding effects, we placed half of the core locations under shrubs, and half in
¹⁸⁴ shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even
¹⁸⁵ when they were completely incinerated, their imprint remained on the soil surface (Bechtold
¹⁸⁶ and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each
¹⁸⁷ soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples.
¹⁸⁸ Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and
¹⁸⁹ McArthur 2013). At all sites, to be sure that we were at a site where sagebrush germination
¹⁹⁰ could occur we checked for first year germinants on the unburned side (we found them at all
¹⁹¹ sites), and to ensure that there were no confounding effects of post-fire seed dispersal, we
¹⁹² determined whether or not the sagebrush were flowering (they were not flowering at all sites),
¹⁹³ and recorded species occupancy for all aboveground plant species.

¹⁹⁴ We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample
¹⁹⁵ was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots.
¹⁹⁶ These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were
¹⁹⁷ watered as needed to stay at field capacity. Every week emerging germinants were identified,
¹⁹⁸ counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks
¹⁹⁹ we ended the germination assay.

200 *2.3 Post-Fire Vegetation Sampling*

201 We sampled the vegetative occupancy and cover in May 2017, the growing season immediately
202 after the fire and again in September 2019. At each location, we established 50m transects
203 starting at the boundary of the burned and unburned sides of the perimeter, running
204 perpendicular to the fire perimeter, and marked the transect ends with rebar. We measured
205 the occupancy and abundance of all plant species by measuring cover of every species in
206 0.1 m² quadrats spaced every 5 m along each transect. We used the line intercept method
207 to measure shrub cover and herbaceous plant cover along the transect. Both live and dead
208 plants were included in these measurements. Total vegetation cover (TVC) was defined as
209 the sum of herbaceous plant cover and shrub cover.

210 *2.4 Estimating Burn Severity with Landsat 8 OLI*

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

219 *2.5 Statistical Analysis*

220 Our statistical analysis centered around trying to understand each component of the positive
221 feedback loop posited by the 4 hypotheses described above. In order to understand how
222 pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC)
223 from two separate data sources as a proxy for fuel connectivity, and created separate linear
224 models with TVC as the predictor variable and burn severity (dNBR, [J. D. Miller et al.](#)
225 [2009](#)) as the response variable. With the field data we collected, we created an ordinary

226 least squares (OLS) linear model with burn severity as the dependent variable and TVC
227 (defined as shrub cover plus herbaceous plant cover from the unburned side of the paired
228 plots), elevation and aspect as independent variables.

229 We were concerned that because our data were collected at the edge of the fire, the burn severity
230 calculated at each point may have included partially burned pixels. So, as a supplement,
231 we examined the same relationship by creating a model of TVC using Landsat Thematic
232 Mapper (TM) surface reflectance data using TVC from the Bureau of Land Management's
233 Assessment, Inventory and Monitoring dataset (AIM, [U.S. Department of Interior 2018](#)). The
234 AIM dataset contained 813 sampling locations within the Central Basin and Range ecoregion
235 ([Commission for Environmental Cooperation 2006](#)) that were visited by BLM field crews
236 between 2011 and 2015. They were mostly sampled once but there were some repeats, for
237 1,117 total measurements. For each of these points, we extracted the surface reflectance
238 values of each Landsat band for the sampling year near peak biomass using a cloud-free scene
239 from May or early June. Then, we used those surface reflectance values to calculate various
240 vegetation indexes (Table S1), including the Green Normalized Differentiated Vegetation Index
241 (Green NDVI, Equation 1), and Normalized Differentiated Senesced Vegetation Index (NDSVI,
242 Equation 2). We used these indexes to create generalized linear model of TVC with a beta
243 distribution. For this and all linear models, we started with the largest possible model and
244 used backwards selection following the methodology of [Zuur et al. \(2009\)](#). We used the final
245 reduced model to create a layer of predicted TVC for the study area for the pre-fire scene,
246 and extracted both our predictions of TVC and dNBR of the fire from 1000 regularly-spaced
247 points within the fire perimeter. Finally, to quantify the effect of TVC on burn severity, we
248 created an OLS linear model with our modeled TVC and its second-order polynomial as
249 predictor variables and burn severity as the response variable.

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

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

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

263 To account for the possibility of H2a as a confounding factor, we included the Shannon-Weaver
264 diversity index ([Shannon and Weaver 1949](#)) in the paired, unburned seed bank samples as
265 one of the predictor variables in our JSDM. We also created OLS models with the unburned
266 species richness and Shannon-Weaver diversity index predicted by prefire fuel connectivity,
267 with the expectation that pre-fire fuel connectivity would have had a negative effect on the
268 prefire seedbank diversity. To examine how community composition and burn severity then
269 affected subsequent fuel connectivity (H3), we created OLS models with fuel connectivity
270 three years post-fire as the dependent variable, and burn severity, seed counts for *B. tectorum*,
271 *P. secunda* and other species, elevation, aspect, depth, and alpha diversity as independent
272 variables. To examine how the resulting fuel connectivity was related to biodiversity (H4), we
273 used the diversity data and connectivity data that we collected in 2019 to create a Poisson
274 GLM with number of species encountered aboveground at each plot location as the dependent
275 variable, as well as an OLS linear model with the Shannon-Weaver index ([Shannon and](#)
276 [Weaver 1949](#)) as a dependent variable. We used fuel connectivity, elevation, and aspect as
277 independent variables.

278 All analyses were done in R ([R Core Team 2020](#)). Data and code to recreate the analysis
279 is freely available at <https://www.github.com/admahood/seed-bank> (DOI available after
280 acceptance).

281 3. Results

282 We found support for each hypothesized component of the positive feedback loop. For H1,
283 the most parsimonious model for our *in situ* observations had only TVC as the predictor,
284 which had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$,
285 Figure 2a, Table S3). For our remotely sensed analysis, our most parsimonious model of
286 TVC explained 35% of the variation and had Green NDVI, NDSVI and their interaction as
287 predictors (Table S3). Our model of dNBR using the predicted TVC within the fire perimeter
288 as a predictor of dNBR explained 42% of the variation and the relationship between TVC
289 and burn severity was positive and significant ($p \ll 0.01$, Figure 2a, Table S3).

290 The vast majority of seeds that germinated in the greenhouse were the two most common
291 grass species, *P. secunda* and *B. tectorum* (Table S2). Eight forb species were found in more
292 than one location, and these 10 prevalent species are those that were used in our JSDM.
293 Burned plots had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14 in the
294 bottom 4 cm. Unburned plots had an average of 299 ± 170 in the top 2 cm and 59 ± 29
295 in the bottom 4 cm (Figure S1). For H2, the JSDM converged well (Gelman diagnostics
296 all very close to 1 and the effective sample size centered on 4,000, Figure S2a). Elevation
297 had the most significant effects on individual species (Figure S2b) and explained the most
298 variance on average (36% Figure S2c). Burn severity explained 23% of the variance on
299 average and was supported at the 95% level for 5 species (Figure S2b). For the introduced
300 species, the predictions along a gradient of burn severity were positive for *B. tectorum*,
301 *Sisymbrium altissimum* L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala*
302 *testiculata* and *Alyssum desertorum* Stapf (Figure 2b). For native species, the effect of burn
303 severity on occurrence was positive for *A. tridentata*, neutral for *P. secunda* and negative

304 for the remaining species (Figure 2b). Testing H2a revealed a positive relationship between
305 pre-fire aboveground species diversity and pre-fire fuel connectivity, and so we felt it was
306 reasonable to rule out pre-fire fuel connectivity as a confounding factor for H2.

307 For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and
308 the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the postfire seedbank
309 was positively associated with the fuel connectivity in 2019 ($\beta = 0.54$, $p = 0.01$, Adj R^2
310 = 0.75, Figure 3c, Table S3). For H4 the most parsimonious model (Adj $R^2 = 0.89$, Table
311 S3) had elevation, aspect, fuel connectivity and an interaction between elevation and fuel
312 connectivity as predictors of aboveground Shannon-Weaver alpha diversity. Fuel connectivity
313 was negatively associated with Shannon-Weaver diversity ($\beta = -0.28$, $p=0.004$, Figure 3d).

314 4. Discussion

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

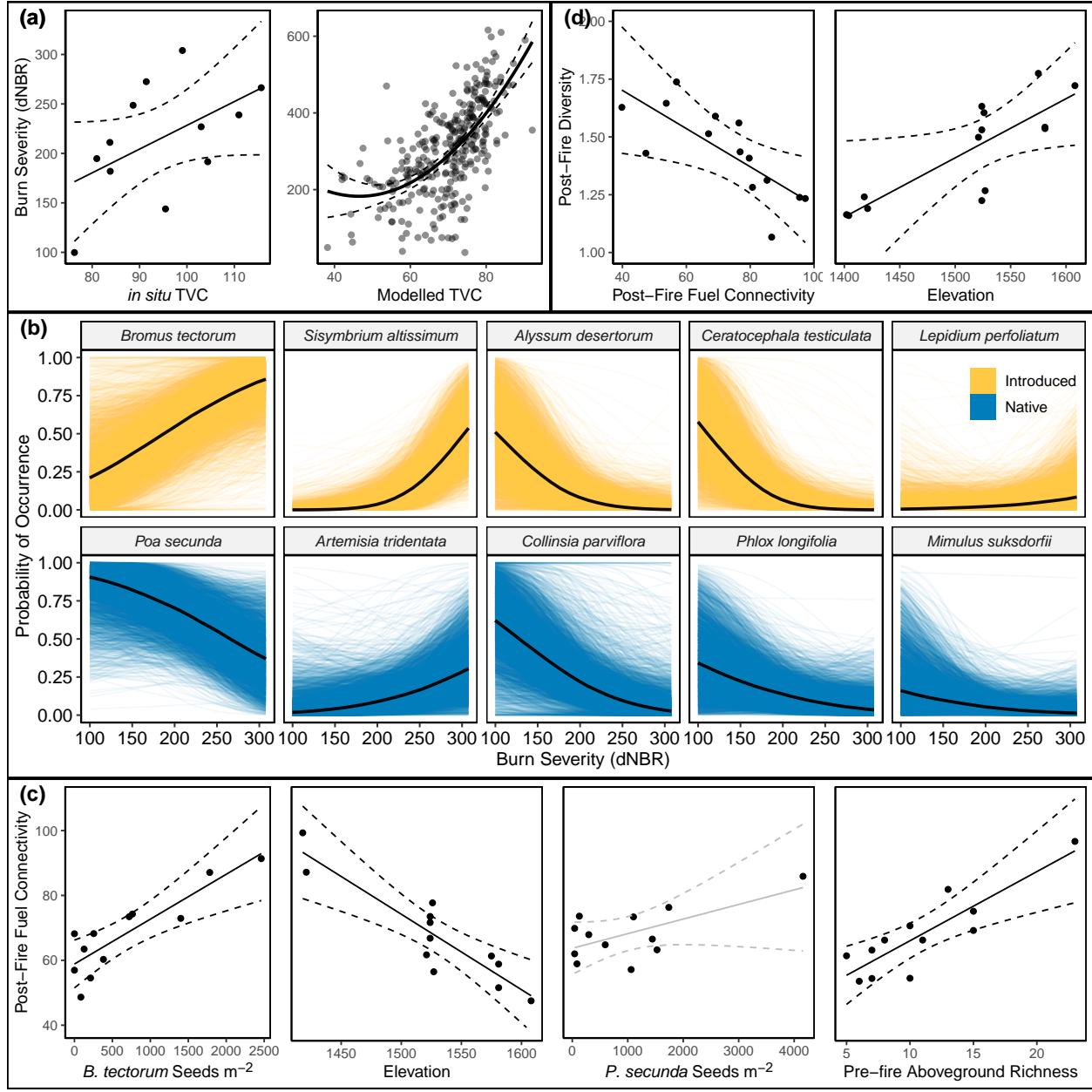


Figure 2: On the left side of (a), burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Panel b shows the modelled occurrence of germinable seeds for all species found at more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

330 The difference in species composition before and after fire explains an apparent contradiction
331 in results between H2a (positive relationship between pre-fire fuel connectivity and diversity)
332 and H4 (negative relationship between post-fire fuel connectivity and diversity). Most plot
333 locations had mature canopies of native shrubs and with the inter-shrub space occupied mostly
334 by native bunchgrasses and forbs, with no fire occurrence since 1984. Even in locations with
335 high annual grass cover between shrubs, shrubs provide ecosystem structural heterogeneity
336 and islands of fertility (Doescher, Miller, and Winward 1984; Bechtold and Inouye 2007), and
337 perennial natives that may have been established before invasion have deep roots established
338 that allow for the avoidance of competition for water with shallow-rooted annuals (Gibbens
339 and Lenz 2001; Ottaviani et al. 2020). This may provide enough niche compartmentalization
340 to allow native plants to persist. Three years after the Hot Pot fire, almost all of the plots
341 were dominated by introduced annuals, and lacked any structural heterogeneity. Thus native
342 plants may have been able to persist via niche compartmentalization after the initial
343 invasion, but fire burns away most of the seeds (Figure S1) and removes all of the structural
344 benefits that shrub cover provides. In this clean slate post-fire environment, the altered
345 species composition of the seedbank and superior post-fire dispersal of *B. tectorum* (Monty,
346 Brown, and Johnston 2013) allows the process of interspecific competition to be dominant
347 (Schlaepfer, Lauenroth, and Bradford 2014).

348 *Global impacts*

349 The grass-fire cycle in the western US is reinforced through providing fitness benefits to
350 the introduced annual grasses and forbs via at least 4 redundant processes: i) changing the
351 composition of the seedbank, ii) competitive exclusion of native plants, iii) CO₂ enrichment
352 which may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of
353 annual grass species (Nagel et al. 2004; Smith et al. 2000), strengthening the fuel connectivity
354 to burn severity to seed composition feedback loop, and iv) ecohydrological feedbacks that
355 create a warmer, drier microclimate (Turnbull et al. 2012; Wilcox et al. 2012). It is likely

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

369 *Potential limitations*

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

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

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

405 Spectral reflectance has long been used to characterize wildfire fuels. Unique signatures of
406 remotely-sensed spectral reflectance are typically matched to categorical fuel classifications
407 (CFCs), which describe the physiognomy of vegetation and its potential to support various fire
408 behavior (Ottmar et al. 2007). While different CFCs can provide a general understanding of

⁴⁰⁹ fuel amount and connectivity, recent efforts using data with finer spatial and spectral resolution
⁴¹⁰ may improve fuel classification with more continuous, multi-dimensional measurements
⁴¹¹ (Stavros et al. 2018). The continuous measure of NDVI in western U.S. coniferous forests is a
⁴¹² proxy for live fuel biomass, which likely explains its positive association with wildfire severity
⁴¹³ (Parks et al. 2018; Koontz et al. 2020). NDVI also correlates with vegetation cover in these
⁴¹⁴ forested systems, and so greater crown connectivity may also explain the NDVI/severity
⁴¹⁵ relationship at local scales. When using a more direct NDVI-derived measure of vegetation
⁴¹⁶ connectivity in Sierra Nevada yellow pine/mixed-conifer, Koontz et al. (2020) found that
⁴¹⁷ greater variability in forest structure also increased the probability of high-severity fire. Here,
⁴¹⁸ we arrived at a combination of NDVI and NDSVI to describe the fuel connectivity of the
⁴¹⁹ annual grass invaded Great Basin sagebrush community to better reflect key differences in
⁴²⁰ the physiognomies of forest and arid shrublands. In sagebrush shrublands, the fuel that
⁴²¹ contributes to large wildfires is a mixture of evergreen shrubs interspersed with herbaceous
⁴²² plants that remain green for only a portion of the growing season, and then become dry and
⁴²³ straw-colored. Thus, both the live and dead fuel need to be taken into account in remote
⁴²⁴ measurements of fuel connectivity.

⁴²⁵ *Management implications*

⁴²⁶ These results demonstrate that the strength of the grass-fire cycle in this system is controlled
⁴²⁷ by measurable fire properties and ecosystem structural components. Land managers may be
⁴²⁸ able to increase their chances of restoration success by using existing methods or developing
⁴²⁹ novel ones that manipulate these components to weaken or even break the positive feedback
⁴³⁰ cycle. This work provides further evidence that the post-fire annual grassland is a system
⁴³¹ where the degraded state represents an alternative species assemblage from that of the
⁴³² restoration target. Because the propagules of the original assemblage are no longer present,
⁴³³ methods that rely on natural succession may not be sufficient (Suding, Gross, and Houseman
⁴³⁴ 2004). Our results highlight the importance of prioritizing the preservation of native shrub

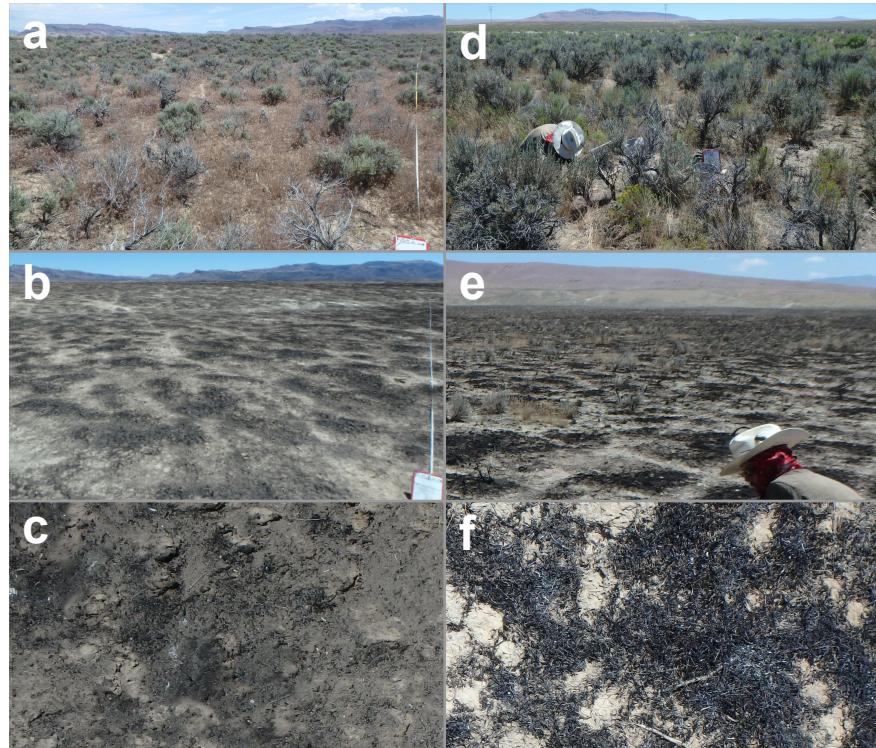


Figure 3: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, days after all of the biomass was consumed by the fire. Panel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

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

447 Livestock grazing can reduce fuel connectivity in uninvaded sagebrush ([Davies et al. 2010](#)).
448 At the same time, livestock grazing can decrease the resistance to invasion by *B. tectorum* via
449 negative effects on biological soil crust (BSC) ([Chambers et al. 2014; Condon and Pyke 2018](#)),
450 and can reduce the survival of *Artemisia* seedlings that are not protected by shrub canopies
451 ([Owens and Norton 1992](#)). In wet years, targeted grazing at already invaded sagebrush sites
452 may reduce fuel connectivity and alleviate fire risk. Plant community composition in the
453 years immediately after fire may be highly variable spatially and from year to year. Post-fire
454 grazing may help reduce *B. tectorum* cover, but it may also exacerbate the problem by
455 introducing cheatgrass in uninvaded sites ([Williamson et al. 2019](#)) or increasing the already
456 superior postfire dispersal of *B. tectorum* seeds ([Monty, Brown, and Johnston 2013](#)). We
457 suggest management approaches that are specifically tailored each year to the conditions of a
458 given site, and targeting grazing only in already invaded areas to reduce *B. tectorum* cover
459 where it may aid in native plant restoration.

460 Greenhouse or *in situ* germination assays are time-consuming and require botanical expertise,

461 and are very important. There are many studies that only study fire occurrence as it relates
462 to the seed bank. One potential avenue for future research may be linking satellite-derived
463 estimates of burn severity ([Parks et al. 2018](#)) and TVC with locations of prior studies in
464 retrospective meta-analyses. Teasing out these mechanisms will increase our understanding
465 of how generalizable these phenomena are, and may provide more insight on how to mediate
466 the negative effects or break the positive feedback loop.

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