

Running head: Burn severity and the grass-fire cycle

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

Adam L. Mahood^{1,2,*}, Michael J. Koontz², Jennifer K. Balch^{1,2}

¹ Department of Geography, University of Colorado Boulder, Boulder, CO, USA

² Earth Lab, University of Colorado, Boulder, CO, USA

* Corresponding author: admahood@gmail.com

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

¹ **Abstract**

² Exotic plant invasions can alter ecosystem structure and disturbance regimes. This can lead
³ to permanent state changes and biodiversity losses. In sagebrush shrublands in the western
⁴ United States, annual grass invasion increases vegetation connectivity, which increases the size
⁵ and 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). The novel grassland
⁷ state is persistent, and more likely to promote large fires than the shrubland it replaced. But
⁸ the mechanisms by which pre-fire invasion and fire occurrence are linked to higher post-fire
⁹ flammability are not fully understood.

¹⁰ Here, we investigate the successive mechanisms of a positive feedback that maintains a novel,
¹¹ persistent, and more flammable ecosystem. We used total vegetation cover (TVC) as a proxy
¹² for vegetation connectivity and found that pre-fire TVC increased burn severity. We then
¹³ used a Bayesian joint species distribution model to examine how burn severity affected the
¹⁴ proportion of IAG in the seed bank, and found that higher burn severity had mostly positive
¹⁵ or neutral effects on the occurrence of IAG and other non-native species, and mostly negative
¹⁶ or neutral relationships with native species. Finally, we found that the abundance of IAG
¹⁷ seeds in the seedbank immediately post-fire had a positive effect on the fuel connectivity 3
¹⁸ years after fire, thus completing a positive feedback promoting IAG. These results suggest that
¹⁹ the strength of the positive feedback is controlled by measurable characteristics of ecosystem
²⁰ structure (e.g. TVC) and disturbance (dNBR), and so it is possible that they can be used to
²¹ inform management actions to mitigate the undesirable effects of the grass-fire cycle, perhaps
²² 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 Global change drivers like exotic species invasion and changes in land use, land cover and
27 climate can alter ecosystem structure. Altered structure can alter many facets of ecosystem
28 function and composition. The combined effects of altered structure on function can cascade,
29 interact and ultimately lead to permanent ecosystem state change and losses of biodiversity
30 and ecosystem services (Ratajczak et al. 2018). These impacts are most difficult to mitigate
31 when internal, self-reinforcing mechanisms are manifested from those structural changes
32 that then maintain the new altered state (Andersen et al. 2009). Alternative stable states
33 have been documented at broad scales in tropical ecosystems, where forests, savannas and
34 grasslands are considered self-maintaining states because they cluster around three values of
35 tree cover (80, 30 and 0 percent) while occurring along overlapping ranges of precipitation
36 (Hirota et al. 2011; Staver, Archibald, and Levin 2011). In the forested state there is thought
37 to be a self-reinforcing positive feedback between evapotranspiration and tree cover (Staal et
38 al. 2020). In the grassland and savanna states, there are feedbacks between grass flammability
39 and fire occurrence (The grass-fire cycle, D'Antonio and Vitousek 1992; Staver, Archibald,
40 and Levin 2011).

41 A classic example of altered vegetation structure leading to a novel ecosystem state that
42 is persistent is the invasion of *Bromus tectorum* L. and other introduced annual grasses in
43 the Great Basin of the western United States. Here, over half of Wyoming big sagebrush
44 (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems have been degraded,
45 fragmented or lost completely (Davies et al. 2011). This has been attributed to a host of
46 causes, including wildfire (Balch et al. 2013), grazing (Williamson et al. 2019), land use/land
47 cover change, and the invasion of annual grasses. At uninvaded sites, the space between
48 shrubs is typically composed of bare ground covered in biological soil crust and dotted with
49 perennial plants. The lack of fuel connectivity is believed to limit fire spread, with a historical
50 fire regime of infrequent, patchy fires (Baker 2006; Bukowski and Baker 2013). Annual

51 grass invasion increases fuel connectivity while decreasing fuel moisture ([Davies and Nafus](#)
52 [2013](#)), leading to increased fire size and frequency ([Knapp 1996](#); [Balch et al. 2013](#)). After
53 fire, the landscape is often dominated by introduced annual grasses and forbs. But in order
54 to understand how the grassland state persists, the mechanisms by which fire benefits the
55 introduced annual grass must be understood. [Petraitis and Latham \(1999\)](#) posited that the
56 maintenance of alternate species assemblages requires first a disturbance that removes the
57 species from the initial assemblage and second the arrival of the species of the alternate
58 assemblage. One understudied mechanism that may explain both is the interaction between
59 burn severity and the species composition of the soil seed bank.

60 The relationship between the species composition of the seed bank and fire severity and/or
61 intensity is relatively understudied. In different systems, individual species have adapted
62 strategies to cope with fires that may be adapted to different severities. In boreal forests,
63 the depth of the burn may be more important than the temperature of the fire, with
64 species-specific effects on recovery depending on whether the species recovers via resprouting
65 or from the seed bank ([Morgan and Neuenschwander 1988](#); [Schimmel and Granström 1996](#)).
66 In a wetland study in Japan, high severity fire was found to increase seedbank diversity, and
67 the similarity between the seedbank composition and aboveground composition was higher in
68 places burned at high severity ([Kimura and Tsuyuzaki 2011](#)). There have been a handful
69 of studies in temperate, semi-arid regions. [Lipoma, Funes, and Díaz \(2018\)](#) found that in
70 shrubland high-severity fire reduced the overall number of seeds in the seedbank but did
71 not change the floristic or functional composition. [Maia et al. \(2012\)](#) found intraspecific
72 differences in post-fire seedbank densities that were explained by burn severity in a pine
73 plantation in Portugal. [Palmer, Denham, and Ooi \(2018\)](#) found that the residual seedbank
74 after fire varied with severity between two *Acacia* species in Australia. [Wright, Latz, and](#)
75 [Zuur \(2016\)](#) found that Australian mulga (*Acacia aneura*) had higher regeneration after
76 higher fire temperatures. In Iran, [Heydari et al. \(2017\)](#) found that low-severity fire increased
77 diversity in the soil seed bank, but high-severity fire led to losses. These studies show that the

78 effects of fire severity on the seed bank are ecosystem- and species-specific. High severity fire
79 can benefit species that use the seedbank (Kimura and Tsuyuzaki 2011), be seedbank-neutral
80 (Lipoma, Funes, and Díaz 2018), or have a negative effect (Heydari et al. 2017). Furthermore,
81 beyond simply affecting seed mortality, fire temperature can also alter physical seed dormancy
82 thresholds (Liyanage and Ooi 2017).

83 In order for an annual like *B. tectorum* it to benefit from fire, which it clearly does (Balch et
84 al. 2013; Mahood and Balch 2019), it would need enough seeds in the post-fire landscape to
85 achieve a fitness benefit and become well-represented in the post-fire plant assemblage (Bond
86 and Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal, and
87 *B. tectorum* seeds have been shown to have increased dispersal distances after fire (Monty,
88 Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. There
89 is strong evidence that *B. tectorum* builds a well-stocked pool of seeds in the soil and litter,
90 even when it is not well represented in the above-ground plant assemblage (Young and Evans
91 1975; Hassan and West 1986; Boudell, Link, and Johansen 2002). If the increase in fuel
92 connectivity caused by *B. tectorum* increases the severity of fire, it stands to reason that
93 burn severity would influence the community composition of the post-fire seed bank in a way
94 that facilitates the post-fire dominance of *B. tectorum*. To our knowledge, despite several
95 studies on the relationship between fire and the seed bank in this system (Young and Evans
96 1975; Hassan and West 1986; Humphrey and Schupp 2001; Boudell, Link, and Johansen
97 2002; Barga and Leger 2018), no studies to date have examined this potential effect of burn
98 severity on the seed bank.

99 There is strong evidence that *B. tectorum* invasion alters the physical properties of fire,
100 including fire temperature (Brooks et al. 2004; Jones et al. 2015) and burn severity (defined
101 here as the proportion of biomass burned (Keeley 2009)). Burn severity can be measured
102 after fire *in situ*, or estimated from satellite images by comparing scenes from before and after
103 the fire (J. D. Miller et al. 2009). While in many cases fires that burn at higher temperatures

104 will also burn at higher severities, grass fires may not always have such a relationship. Direct
105 measurements have shown that *B. tectorum* burns at low temperatures (Beckstead et al.
106 2011; Germino, Chambers, and Brown 2016). Because fire duration is inversely related to soil
107 heating, lower fire temperatures can be inferred from the commonly observed phenomenon
108 that *B. tectorum*-fueled fires burn fast. Soil heating affects the response of vegetation to fire
109 (Gagnon et al. 2015), including the capacity of the seeds of *B. tectorum* to remain viable
110 after fire (Humphrey and Schupp 2001). Because *B. tectorum* also increases horizontal fuel
111 connectivity (Davies and Nafus 2013), this leads to more contiguously burned areas with
112 fewer unburned plants, and therefore higher burn severity, despite lower fire temperatures.

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

131 The Great Basin has not escaped the recent warming and drying trend that the western U.S.
132 has experienced (Melillo, Richmond, and Yohe 2014; Bradford et al. 2020). This is expected
133 to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly
134 by causing the plants to produce lighter seeds (Schlaepfer, Lauenroth, and Bradford 2014).
135 With this in mind, there is another potential self-reinforcing mechanism that could serve to
136 maintain the high fuel connectivity state without fire. That is that the post-fire state with
137 high fuel connectivity is associated with two mechanisms for competitive exclusion of natives.
138 First, it reduces soil moisture which is unfavorable for *Artemisia* seedlings (Turnbull et al.
139 2012; Wilcox et al. 2012). Second, the dominant plant, *B. tectorum*, can out-compete native
140 plants for early spring moisture (Meyer 1994; Chambers et al. 2007).

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

¹⁵⁸ species diversity due to competitive pressure.

¹⁵⁹ 2. Methods

¹⁶⁰ 2.1 Study Area

¹⁶¹ The study was conducted in north-central Nevada the day after a large fire (the Hot Pot Fire)
¹⁶² was extinguished (Appendix S1, Fig. S1). The Hot Pot Fire burned just over 50,000 hectares
¹⁶³ in less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big
¹⁶⁴ sagebrush plant communities. The fire occurred after the early season plants, including *B.*
¹⁶⁵ *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone
¹⁶⁶ to seed, and before the late season species, including Wyoming big sagebrush, had produced
¹⁶⁷ flowers. Thus we were able to isolate the effect of the fire without any confounding effects of
¹⁶⁸ post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged
¹⁶⁹ from 1397 to 1607 meters in elevation.

¹⁷⁰ 2.2 Seed Bank Sampling

¹⁷¹ In early July 2016, we collected samples of the soil seed bank at fourteen locations the day
¹⁷² after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where
¹⁷³ it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites
¹⁷⁴ were mature sagebrush communities with no history of fire since at least 1984. Three plots
¹⁷⁵ had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS)
¹⁷⁶ fire history ([Eidenshink et al. 2007](#)) and had high cover of *B. tectorum*, but still had scattered
¹⁷⁷ sagebrush cover. We used a metal stake to mark paired burned and unburned sampling
¹⁷⁸ locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic
¹⁷⁹ disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the
¹⁸⁰ perimeter. Within 3 m of each marker, we extracted 12, 6 cm deep, 5 cm diameter, soil cores.
¹⁸¹ Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system
¹⁸² ([Shinneman and McIlroy 2016](#)), and so they are not uniformly distributed ([Boudell, Link, and](#)

¹⁸³ Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemesia*
¹⁸⁴ have different germination rates based on the micro-site they find themselves in (i.e. under
¹⁸⁵ a shrub or in the bare ground between shrubs, Eckert et al. 1986). To account for these
¹⁸⁶ potentially confounding effects, we placed half of the core locations under shrubs, and half in
¹⁸⁷ shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even
¹⁸⁸ when they were completely incinerated, their imprint remained on the soil surface (Bechtold
¹⁸⁹ and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each
¹⁹⁰ soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples.
¹⁹¹ Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and
¹⁹² Mcarthur 2013). At all sites, to be sure that we were at a site where sagebrush germination
¹⁹³ could occur we checked for first year germinants on the unburned side (we found them at all
¹⁹⁴ sites), and to ensure that there were no confounding effects of post-fire seed dispersal, we
¹⁹⁵ determined whether or not the sagebrush were flowering (they were not flowering at all sites),
¹⁹⁶ and recorded species occupancy for all aboveground plant species.

¹⁹⁷ We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample
¹⁹⁸ was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots.
¹⁹⁹ These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were
²⁰⁰ watered as needed to stay at field capacity. Every week emerging germinants were identified,
²⁰¹ counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks
²⁰² we ended the germination assay.

²⁰³ 2.3 Post-Fire Vegetation Sampling

²⁰⁴ We sampled the vegetative occupancy and cover in May 2017, the growing season immediately
²⁰⁵ after the fire and again in September 2019. At each location, we established 50m transects
²⁰⁶ starting at the boundary of the burned and unburned sides of the perimeter, running
²⁰⁷ perpendicular to the fire perimeter, and marked the transect ends with rebar. We measured
²⁰⁸ the occupancy and abundance of all plant species by measuring cover of every species in

209 0.1 m² quadrats spaced every 5 m along each transect. We used the line intercept method
210 to measure shrub cover and herbaceous plant cover along the transect. Both live and dead
211 plants were included in these measurements. Total vegetation cover (TVC) was defined as
212 the sum of herbaceous plant cover and shrub cover.

213 *2.4 Estimating Burn Severity with Landsat 8 OLI*

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

222 *2.5 Statistical Analysis*

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

232 We were concerned that because our data were collected at the edge of the fire, the burn severity
233 calculated at each point may have included partially burned pixels. So, as a supplement, we
234 examined the same relationship by creating a model of TVC using Landsat Thematic Mapper

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

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

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

255 To examine how burn severity affected the community composition of the seed bank (H2),
256 we created a joint species distribution model (JSDM) in a Bayesian framework ([Tikhonov et](#)
257 [al. 2020](#)) for the occurrence of all species germinated from the seed bank that were found
258 at more than one location. We created four Markov Chain Monte Carlo (MCMC) chains,
259 each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain
260 and then recorded every 100th for a total of 1,000 posterior samples per chain, and 4,000

total. We assessed model convergence using the effective sample size and the potential scale reduction factor (Gelman, Rubin, and others 1992). We used the model to predict the probability of occurrence of germinable seeds of a given species along a gradient of burn severity. We included burn severity, elevation, aspect, pre-fire seedbank diversity and soil depth as independent variables.

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

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

²⁸⁴ **3. Results**

²⁸⁵ We found support for each hypothesized component of the positive feedback loop. For H1, the
²⁸⁶ most parsimonious model for our *in situ* observations had only TVC as the predictor, which
²⁸⁷ had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$, Figure
²⁸⁸ 1a, Appendix 1: Table S2). For our remotely sensed analysis, our most parsimonious model
²⁸⁹ of TVC explained 35% of the variation and had Green NDVI, NDSVI and their interaction
²⁹⁰ as predictors (Appendix S1: Table S2). Our model of dNBR using the predicted TVC within
²⁹¹ the fire perimeter as a predictor of dNBR explained 42% of the variation and the relationship
²⁹² between TVC and burn severity was positive and significant ($p \ll 0.01$, Figure 1a, Appendix
²⁹³ S1: 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* (Appendix S1: Table S3). Eight forb species were
²⁹⁶ found in more than one location, and these 10 prevalent species are those that were used in
²⁹⁷ our JSDM. Burned plots had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14
²⁹⁸ in the bottom 4 cm. Unburned plots had an average of 299 ± 170 in the top 2 cm and $59 \pm$
²⁹⁹ 29 in the bottom 4 cm (Appendix S1: Fig. S2). For H2, the JSDM converged well (Appendix
³⁰⁰ S1: Fig S3). Gelman diagnostics all very close to 1 and the effective sample size centered
³⁰¹ on 4,000. Elevation had the most significant effects on individual species and explained the
³⁰² most variance on average (36%). Burn severity explained 23% of the variance on average
³⁰³ and was supported at the 95% level for 5 species. For the introduced species, the predictions
³⁰⁴ along a gradient of burn severity were positive for *B. tectorum*, *Sisymbrium altissimum*
³⁰⁵ L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala testiculata* and *Alyssum*
³⁰⁶ *desertorum* Stapf. For native species, the effect of burn severity on occurrence was positive
³⁰⁷ for *A. tridentata*, neutral for *P. secunda* and negative for the remaining species. Testing H2a
³⁰⁸ revealed a positive relationship between pre-fire aboveground species diversity and pre-fire
³⁰⁹ fuel connectivity, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a

310 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 1c, Appendix S1: Table S2). For H4 the most parsimonious model (Adj $R^2 =$
315 0.89, Appendix S1: Table S2) had elevation, aspect, fuel connectivity and an interaction
316 between elevation and fuel connectivity as predictors of aboveground Shannon-Weaver alpha
317 diversity. Fuel connectivity was negatively associated with Shannon-Weaver diversity ($\beta =$
318 -0.28, $p=0.004$, Figure 1d).

319 4. Discussion

320 Here we document the mechanisms by which changes in ecosystem structure brought on
321 by invasion led to cascading effects on ecosystem function and composition via changes
322 in the disturbance regime. It has already been shown that *B. tecroum* invasion increases
323 fire frequency ([Balch et al. 2013](#)), and from this we can infer the existence of a grass-fire
324 cycle. However, in order to truly consider an annual grass-fire cycle to be maintained
325 by self-reinforcing feedbacks, the mechanisms by which fire occurrence is linked to higher
326 post-fire flammability must be understood. The interaction between burn severity and
327 seed bank composition may explain that link. Prior work has shown that annual grass
328 invasion increases fuel connectivity in western US sagebrush ecosystems by filling in shrub
329 interspaces with a contiguous bed of fine fuels ([Davies and Nafus 2013](#)). This change in
330 the spatial distribution of fine fuels has been associated with larger and more frequent fires
331 ([Balch et al. 2013](#)). Here, we found higher fuel connectivity (via TVC) also increases burn
332 severity (H1, Figure 1a). Higher burn severity was associated with an increased occurrence
333 of introduced annuals in the seedbank and a decreased occurrence of native plants (H2,
334 Figure 1b). Finally, higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted
335 in higher post-fire fuel connectivity (H3, Figure 1c). In addition, we found evidence that

³³⁶ high post-fire fuel connectivity was associated with lower aboveground diversity (H4, Figure
³³⁷ 1d). This suggests that during inter-fire intervals, there may be additional mechanisms
³³⁸ (e.g. competition) maintaining the post-fire, annual grass-dominated species assemblage.

³³⁹ The difference in species composition before and after fire explains an apparent contradiction
³⁴⁰ in results between H2a (positive relationship between pre-fire fuel connectivity and diversity)
³⁴¹ and H4 (negative relationship between post-fire fuel connectivity and diversity). Most plot
³⁴² locations had mature canopies of native shrubs with the inter-shrub space occupied mostly
³⁴³ by native bunchgrasses and forbs, with no fire occurrence since 1984. Even in locations with
³⁴⁴ high annual grass cover between shrubs, shrubs provide ecosystem structural heterogeneity
³⁴⁵ and islands of fertility (Doescher, Miller, and Winward 1984; Bechtold and Inouye 2007), and
³⁴⁶ perennial natives that may have been established before invasion have deep roots established
³⁴⁷ that allow for the avoidance of competition for water with shallow-rooted annuals (Gibbens
³⁴⁸ and Lenz 2001; Ottaviani et al. 2020). This may provide enough niche compartmentalization
³⁴⁹ to allow native plants to persist. Three years after fire, almost all of the plots were dominated
³⁵⁰ by introduced annuals, and lacked any structural heterogeneity. Thus native plants may have
³⁵¹ been able to persist via niche compartmentalization after the initial invasion, but fire
³⁵² burned away most of the seeds (Appendix S1, Fig. S1) and removed all of the structural
³⁵³ benefits that shrub cover provides. In this clean slate post-fire environment, the altered
³⁵⁴ species composition of the seedbank and superior post-fire dispersal of *B. tectorum* (Monty,
³⁵⁵ Brown, and Johnston 2013) allow the process of interspecific competition to be dominant
³⁵⁶ (Schlaepfer, Lauenroth, and Bradford 2014).

³⁵⁷ *Global impacts*

³⁵⁸ Understanding the mechanisms of hysteresis, and in particular how multiple redundant
³⁵⁹ mechanisms act in concert, will provide important insights for ecosystem change on a global
³⁶⁰ scale. At least 13 grass species initiate self-reinforcing feedbacks with fire in the U.S. (Fusco
³⁶¹ et al. 2019; Tortorelli, Krawchuk, and Kerns 2020), and many more worldwide, including

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

³⁷⁷ *Potential limitations*

³⁷⁸ We found fewer species and lower diversity in our seedbank germination assays than we did
³⁷⁹ in the aboveground sampling (Appendix S1, Fig. S3). This result may be influenced by the
³⁸⁰ methodological limitations inherent to greenhouse germination trials (Vandvik et al. 2016).
³⁸¹ In particular our results may be understating the occurrence of native species in the seedbank.
³⁸² Habitat specialists have been shown to emerge more in *in situ* germination assays than in
³⁸³ greenhouse germination assays, while the opposite has been found for ruderal species (Plue et
³⁸⁴ al. 2017). Nevertheless, for those species that were prevalent in our germination studies, we
³⁸⁵ still found consistent relationships between their abundance and occurrence by biogeographic
³⁸⁶ origin, and those species that were prevalent in the postfire seedbank germination assays
³⁸⁷ were also those most common in the aboveground community postfire.

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

389 Burn severity metrics like dNBR were conceived of in the context of forested ecosystems ([J.](#)
390 [D. Miller et al. 2009](#)), and calibrated using the composite burn index ([Key and Benson 1999](#)),
391 tree mortality, and percent change in tree canopy cover. These do not apply in shrubland
392 systems. Here we estimated burn severity using dNBR and understand it to be a proxy for
393 the amount of biomass that was burned in the fire. We recorded qualitative observations of
394 burn severity while we were sampling, mainly to ensure that we sampled a range of severities,
395 and the dNBR we used appears to correspond with our observations. In areas where the
396 space between shrubs was well-connected by fine fuels (Appendix S1: Fig. S4 a-c) the dNBR
397 was higher, and the shrubs had completely burned throughout the root system, leaving only
398 a hole in the ground filled with ashes as evidence of their prior presence. In these areas
399 the entirety of the soil surface—underneath shrub canopy and in canopy interspaces—was
400 consumed by fire, and there was little evidence of remaining litter or biological soil crust. In
401 areas with lower fuel connectivity (Appendix S1: Fig. S4 d-f), and lower dNBR, shrubs were
402 usually consumed only to the stumps, and sometimes were left standing and charred, destined
403 for mortality. In these areas the soil surface often still had biological soil crust, partially
404 consumed litter ([Jones et al. 2015](#)) and unconsumed annual and perennial grass bases. The
405 manual severity classification provided by MTBS had exclusively low and medium severity,
406 but our observations of essentially complete consumption of plant and litter tissues and very
407 few unburned patches suggested that these should have been mostly medium and high severity.
408 This discrepancy was not unexpected, as the ordinal burn severity classifications produced by
409 MTBS are known to be of limited use for research ([Kolden, Smith, and Abatzoglou 2015](#)).
410 Spectral reflectance has long been used to characterize ecosystem structure, including wildfire
411 fuels. Unique signatures of remotely-sensed spectral reflectance are typically matched to
412 categorical fuel classifications (CFCs), which describe the physiognomy of vegetation and
413 its potential to support various fire behavior ([Ottmar et al. 2007](#)). While different CFCs

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

430 *Management implications*

431 These results demonstrate that the strength of the grass-fire cycle in this system is controlled
432 by measurable fire properties and ecosystem structural components. Land managers may be
433 able to increase their chances of restoration success by using existing methods or developing
434 novel ones that manipulate these components to weaken or even break the positive feedback
435 cycle. This work provides further evidence that the post-fire annual grassland is a system
436 where the degraded state represents an alternative species assemblage from that of the
437 restoration target. Because the propagules of the original assemblage are no longer present,
438 methods that rely on natural succession may not be sufficient ([Suding, Gross, and Houseman](#)
439 [2004](#)). Our results highlight the importance of prioritizing the preservation of native shrub

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

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

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

466 and are very important. There are many studies that study fire occurrence as it relates to
467 the seed bank but do not incorporate severity. One potential avenue for future research may
468 be linking satellite-derived estimates of burn severity ([Parks et al. 2018](#)) and ecosystem
469 structure with locations of prior seedbank studies in retrospective meta-analyses.

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783 **Figure Captions**

784 **Figure 1.** On the left side of (a), burn severity (dNBR) as predicted by total vegetation cover
785 (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is
786 predicted by modelled TVC. Panel b shows the modelled occurrence of germinable seeds for
787 all species found at more than one location along a gradient of burn severity, after accounting
788 for soil depth, aspect, elevation and pre-fire diversity. Black line is the mean prediction, each
789 colored line represents one posterior sample. In (c), fuel connectivity three years post-fire is
790 modelled by seedbank composition, elevation and pre-fire aboveground species richness. In
791 (d) shannon-Weaver diversity index of the aboveground, post-fire community composition,
792 was negatively affected by fuel connectivity after accounting for elevation. For a, c and d,
793 lines are the fitted partial effects, points are the partial residuals, and dotted lines are the
794 95% confidence intervals. $p < 0.05$ for black lines, $p > 0.05$ for grey lines.

795 **Figure 2.** Visual illustration of the relationship between fuel connectivity and burn severity.
796 On the left, panel a shows the intershrub space invaded by annual grasses. The photo in
797 panel b was taken in the exact same place two weeks later, days after all of the biomass was
798 consumed by the fire. Panel C is a closeup of the soil surface, showing in more detail how the
799 litter was also almost completely consumed by the fire. On the right, the photos in panels d
800 and e were on opposite sides of a fire line in an area that had minimal annual grass invasion
801 over a broad area, and thus lower fuel connectivity. Note the remaining plants and stumps in
802 panel e and the presence of only partially consumed litter in panel f.

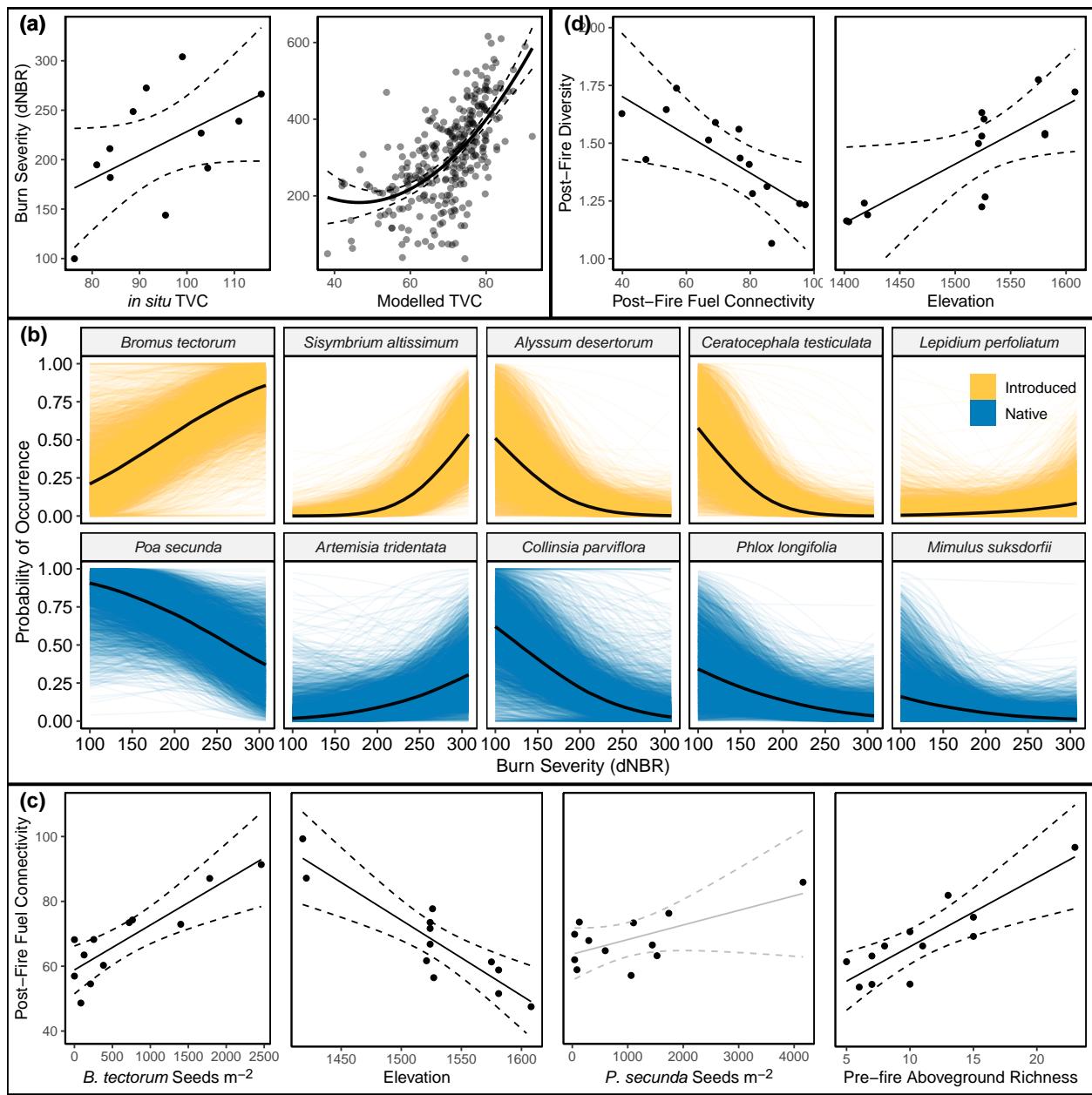


Figure 1: .

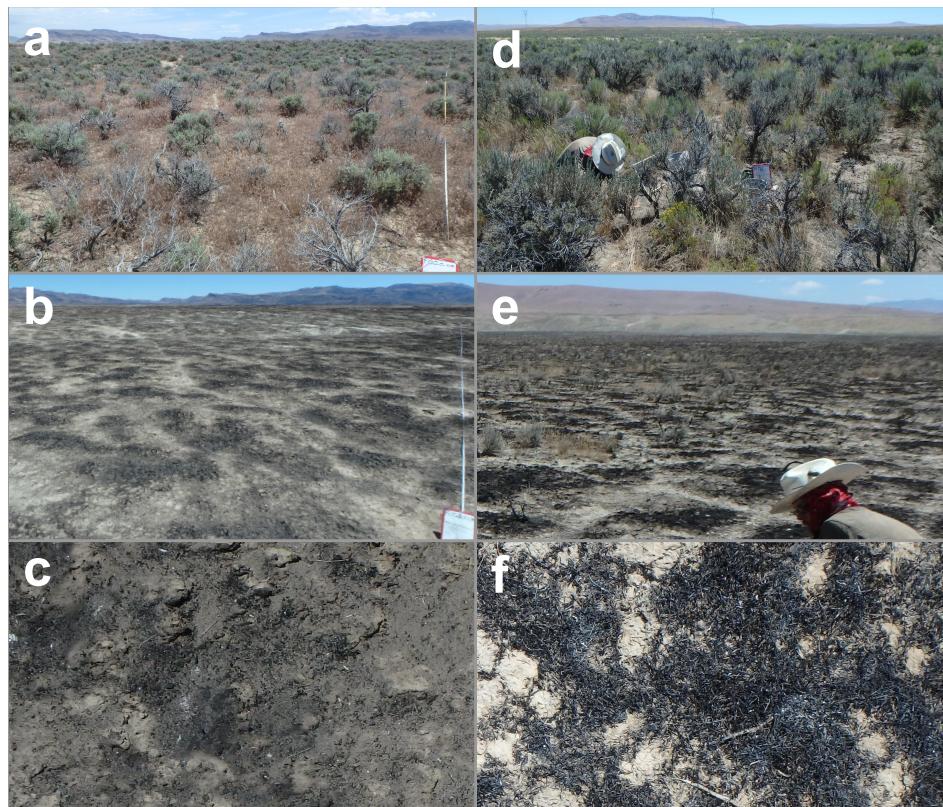


Figure 2: .