

Running head: Burn severity and ecosystem transformation

Title: Fuel connectivity, burn severity, and seedbank survivorship drive ecosystem transformation in a semi-arid shrubland.

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¹ **Abstract**

² A key challenge in ecology is understanding how multiple drivers interact to precipitate
³ persistent vegetation state changes. These state changes may be both precipitated and
⁴ maintained by disturbances, but predicting whether the state change is fleeting or persistent
⁵ requires an understanding of the mechanisms by which disturbance affects the alternative
⁶ communities. In the sagebrush shrublands of the western United States, widespread annual
⁷ grass invasion has increased fuel connectivity, which increases the size and spatial contiguity
⁸ of fires, leading to post-fire monocultures of introduced annual grasses (IAG). The novel
⁹ grassland state can be persistent, and more likely to promote large fires than the shrubland
¹⁰ it replaced. But the mechanisms by which pre-fire invasion and fire occurrence are linked
¹¹ to higher post-fire flammability are not fully understood. A natural experiment to explore
¹² these interactions presented itself when we arrived in northern Nevada immediately after a
¹³ 50,000 ha wildfire was extinguished.

¹⁴ We hypothesized that the novel grassland state is maintained via a reinforcing feedback
¹⁵ where higher fuel connectivity increases burn severity, which subsequently increases post-fire
¹⁶ IAG dispersal, seed survivorship, and fuel connectivity. We used a Bayesian joint species
¹⁷ distribution model and structural equation model framework to assess the strength of the
¹⁸ support for each element in this feedback pathway. We found that pre-fire fuel connectivity
¹⁹ increased burn severity and that higher burn severity had mostly positive effects on the oc-
²⁰ currence of IAG and another non-native species, and mostly negative or neutral relationships
²¹ with all other species. Finally, we found that the abundance of IAG seeds in the seedbank
²² immediately post-fire had a positive effect on the fuel connectivity 3 years after fire, comple-
²³ ting a positive feedback promoting IAG. These results demonstrate that the strength of the
²⁴ positive feedback is controlled by measurable characteristics of ecosystem structure, compo-
²⁵ sition and disturbance. Further, each node in the loop is affected independently by multiple
²⁶ global change drivers. It is possible that these characteristics can be modeled to predict

27 threshold behavior and inform management actions to mitigate or slow the establishment of
28 the grass-fire cycle, perhaps via targeted restoration applications or pre-fire fuel treatments.

29 *Keywords:* *Artemisia tridentata*, *Bromus tectorum*, burn severity, cheatgrass, fuel connectiv-
30 ity, grass-fire cycle, joint species distribution model, sagebrush

31 1. Introduction

32 Ecosystems around the world are being affected simultaneously by multiple facets of global
33 change. For example, changes in land use can facilitate exotic plant invasions ([Allan et al.](#)
34 [2015](#)), which can alter ecosystem structure ([Davies and Nafus 2013](#)). Altered structure can
35 change the likelihood of a disturbance, the properties of a disturbance and the capacity of the
36 system to recover after a disturbance ([Brooks et al. 2004](#)). Global climate change can also
37 directly affect the magnitude of disturbances ([S. A. Parks and Abatzoglou 2020](#)), and act
38 as a demographic filter that influences how ecosystems recover after disturbances ([Rother,](#)
39 [Veblen, and Furman 2015](#); [Davis et al. 2019](#)) via impacts on adult plant survival and seed
40 dispersal ([Davis, Higuera, and Sala 2018](#); [Eskelinen et al. 2020](#)). The combined effects
41 of global change forces on structure, function and disturbance can cascade and interact.
42 For example, while burn severity (or the proportion of biomass burned ([Keeley 2009](#))) is
43 influenced by vegetation structure ([Koontz et al. 2020](#); [Sean A. Parks et al. 2018](#)), it also
44 increases with temperature and aridity ([S. A. Parks and Abatzoglou 2020](#)). These forces
45 can ultimately lead to permanent compositional change, biodiversity losses and the loss of
46 ecosystem services ([Ratajczak et al. 2018](#); [Mahood and Balch 2019](#); [Mahood et al. 2022](#))
47 due to internal, self-reinforcing mechanisms that arise from those structural and functional
48 changes which then maintain an alternative stable state ([Marten Scheffer and Carpenter](#)
49 [2003](#); [Ratajczak et al. 2018](#)).

50 There is a long history of univariate time series observations that show sudden state changes
51 ([Marten Scheffer and Carpenter 2003](#)), and these have informed the development of theories

52 that help us understand how systems of any type can change state suddenly, and exist in per-
53 sistent alternative stable states (Marten Scheffer et al. 2015; Ratajczak et al. 2018). These
54 theories typically represent the system's state with a single variable, of which the mean is
55 observed to abruptly change in time or space (Marten Scheffer et al. 2015). Descriptive
56 evidence of alternative stable states has been documented at broad scales in tropical ecosys-
57 tems, where forests, savannas and grasslands are considered alternative stable states because
58 they are floristically distinct (Aleman et al. 2020) and cluster around static values of woody
59 cover (80, 30 and 0 percent) while occurring along overlapping ranges of precipitation (Hirota
60 et al. 2011; Staver, Archibald, and Levin 2011). The forested state has a self-reinforcing,
61 positive feedback between evapotranspiration and tree cover (Staal et al. 2020), while the
62 grassland and savanna states are maintained by feedbacks between grass flammability and
63 fire occurrence (D'Antonio and Vitousek 1992; Staver, Archibald, and Levin 2011). Al-
64 ternative stable states are believed to be widespread (M. Scheffer et al. 2001), but their
65 existence is rarely proven at broader scales, with most demonstrative studies having been
66 conducted in greenhouse and laboratory microcosm experiments (Schröder, Persson, and De
67 Roos 2005). One of the reasons for this is that ecological systems are much more complex
68 than a simple bivariate system with a single driver and a single response. There may be
69 multiple drivers, and the state is the product of interactions between organisms and their
70 immediate environment, as well as countless inter- and intra-specific interactions.

71 A central challenge in ecology in the 21st century is to move from describing how plant
72 communities are affected by global change to the capacity to predict how species pools will
73 assemble and persist in response to global change (Davis, Higuera, and Sala 2018; Keddy and
74 Laughlin 2021). Prediction of community response to multi-faceted global change drivers
75 is enhanced with a better understanding of the mechanisms that underlie community sta-
76 bility in the face of disturbances. A classic example of an ecosystem that appears to have
77 disturbance-mediated alternative stable states (but see Morris and Leger (2016)), but whose
78 stability mechanisms aren't well understood is the invasion of *Bromus tectorum* L. and other

introduced annual grasses in the Great Basin of the western United States. Here, it is well documented how the interaction of annual grass invasion, fire (Balch et al. 2013) and grazing (Williamson et al. 2019) are associated with the degradation or loss of over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems (Davies et al. 2011). These systems had a precolonial fire regime of infrequent, patchy fires (Bukowski and Baker 2013). In uninvaded areas, the space between shrubs is typically composed of bare ground covered in biological soil crust and caespitose perennial plants. Because fire does not spread readily below a threshold of approximately 60% cover of flammable vegetation (Archibald, Staver, and Levin 2012), the low fuel connectivity in these areas limits fire spread. Annual grass invasion increases fuel connectivity while decreasing fuel moisture (Brooks et al. 2004; Davies and Nafus 2013), leading to increased fire size and frequency (Balch et al. 2013). Sagebrush stands with high native perennial cover might need only a small amount of additional annual grass cover to alter ecosystem structure enough to alter the fire regime (Appendix S1, Fig. S1). After fire, the landscape is typically dominated by introduced annual grasses. But in order to understand how fire drives the persistence of the grassland state, we need to understand the demographic mechanisms by which fire impacts propagule dispersal and benefits the alternative state (Davis, Higuera, and Sala 2018). As with forested systems, propagule dispersal is a key filter through which species must pass in order to establish and persist in a post-fire landscape (Gill et al. 2022).

Petraitis and Latham (1999) posited that the maintenance of alternate species assemblages requires first a disturbance that removes the species from the initial assemblage and second the arrival of the species of the alternate assemblage. One understudied mechanism that may explain both for the *Artemisia/Bromus* system is the interaction between the species composition of the soil seed bank and burn severity. Because the invading species are annual, and many of the key native plant species are seed obligates, the seed is the key life history stage that fire must act upon to benefit the invading plants. Seeds and seedlings are particularly vulnerable to climate, competition and disturbance (Enright et al. 2015). Warmer and drier

106 conditions simultaneously reduce recruitment, growth, and survival of seeds and seedlings
107 (Enright et al. 2015; Schlaepfer, Lauenroth, and Bradford 2014), while also increasing burn
108 severity (S. A. Parks and Abatzoglou 2020). In fire prone ecosystems, seed obligate species
109 typically have life history strategies to cope with fires that burn at different severities (Maia
110 et al. 2012; Wright, Latz, and Zuur 2016; Palmer, Denham, and Ooi 2018). Soil heating from
111 fire affects the response of vegetation to fire (Gagnon et al. 2015), including the capacity of
112 seeds to remain viable after fire (Humphrey and Schupp 2001). High severity fire can affect
113 species that use the seedbank positively (Kimura and Tsuyuzaki 2011), negatively (Heydari
114 et al. 2017), or have no effect (Lipoma, Funes, and Díaz 2018), depending on species-specific
115 adaptations. Both the depth of the burn and fire temperature can affect subsequent recovery
116 by seed germination (Morgan and Neuenschwander 1988; Schimmel and Granström 1996),
117 as well as seed mortality and physical seed dormancy mechanisms (Liyanage and Ooi 2017).

118 In addition to size and frequency, exotic plant invasions can alter fire temperature (Brooks
119 et al. 2004; R. O. Jones et al. 2015) and burn severity. While in many cases fires that
120 burn at higher temperatures will also consume more biomass (i.e. burn at higher severity),
121 grass fires may not always have such a relationship. Direct measurements have shown that
122 *B. tectorum* burns at low temperatures (Beckstead et al. 2011; Germino, Chambers, and
123 Brown 2016), but because it also increases horizontal fuel connectivity (Davies and Nafus
124 2013), it leads to more contiguously burned areas and therefore higher burn severity, despite
125 lower fire temperatures. To benefit from fire, *B. tectorum* would need to gain a fitness benefit
126 relative to other species

127 One way to achieve this is to disperse more viable seeds into the post-fire landscape than
128 the other species and become well-represented in the post-fire plant assemblage (Bond and
129 Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal (Monty,
130 Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. If the
131 increase in fuel connectivity caused by *B. tectorum* increases the severity of fire, one way
132 burn severity might then influence the community composition of the post-fire seed bank to

133 facilitate the post-fire dominance of *B. tectorum* would be to burn a contiguous area at a
134 temperature high enough to kill fire-intolerant native seeds, but low enough that *B. tectorum*
135 seeds survive and germinate more readily from fire-induced germination cues (Naghripour et
136 al. 2016; Fenesi et al. 2016). In other words, an area with high burn severity should have a
137 lower relative occurrence of viable seeds of native species, and a higher relative occurrence
138 of the seeds of fire-tolerant introduced annual plants. This would allow for the for the
139 often-observed dominance of introduced annual grasses after a few years and would result
140 in higher fuel connectivity, closing the positive feedback loop. Plants that are not adapted
141 to frequent fire would be less likely to produce seeds that are adapted to surviving fire,
142 or dispersal mechanisms to take advantage of the resources available immediately after fire
143 (Keeley et al. 2011). To our knowledge, despite several studies on the relationship between
144 fire occurrence and the seed bank in this system (Hassan and West 1986; Humphrey and
145 Schupp 2001; Boudell, Link, and Johansen 2002), no studies to date have examined the effect
146 of burn severity on the seed bank. Burn severity is more ecologically meaningful than fire
147 occurrence, and is more useful for understanding threshold effects and stable states than a
148 binary variable.

149 Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot
150 Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July
151 2016. Each location had paired burned and unburned samples. Because it burned a large
152 area in only three days, we could sample a broad area while being reasonably certain that
153 the weather conditions during the fire were similar at all sites. Because we collected our
154 samples immediately after the fire was extinguished, we felt confident that the seed bank
155 samples did not contain seeds deposited by post-fire dispersal. We put the samples in cold
156 storage and germinated the seeds from those cores in a greenhouse the following spring. In
157 spring 2017 and fall 2019 we collected information on vegetation structure and diversity at
158 each location. We tested four hypotheses in this study that are depicted in Figure 1a and
159 described here: (H1) Pre-fire fuel connectivity would be positively related to burn severity;

160 (H2) burn severity would increase the occurrence probability of introduced annual species
161 in the seed bank and reduce the occurrence probability of native species. An alternative to
162 H2 is H2a, in which increased fuel connectivity brought on by the invasion of annual grasses
163 may have already depleted the diversity of the soil seed bank before the fire occurred; (H3)
164 the abundance of post-fire *B. tectorum* seeds in the seedbank would be positively related
165 to post-fire fuel connectivity. In addition, because in our study system post-fire sites are
166 floristically distinct from the pre-fire state ([Mahood and Balch 2019](#)), typically with near
167 monocultures of *B. tectorum*, we hypothesized that (H4) high post-fire fuel connectivity of
168 those near-monocultures would result in lower aboveground species diversity due to compet-
169 itive exclusion of native plants.

170 2. Methods

171 2.1 Study Area

172 The study was conducted in north-central Nevada the day after a large fire (the Hot Pot Fire)
173 was extinguished (Appendix S1, Fig. S2). The Hot Pot Fire burned just over 50,000 hectares
174 in less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big
175 sagebrush plant communities. The fire occurred after the early season plants, including *B.*
176 *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone
177 to seed, and before the late season species, including Wyoming big sagebrush, had produced
178 flowers. Thus we were able to isolate the effect of the fire without any confounding effects of
179 post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged
180 from 1,397 to 1,607 meters in elevation.

181 2.2 Seed Bank Sampling

182 In early July 2016, we collected samples of the soil seed bank at fourteen locations the day
183 after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where
184 it was clearly delineated by a bulldozer line or in one case a narrow dirt road. We were

185 confident paired sites were of the same pre-fire composition because we had been working in
186 these areas all summer collecting data for another study. Eleven sites were mature sagebrush
187 communities with no history of fire since at least 1984. Three sites had previously burned in
188 1984 according to the Monitoring Trends in Burn Severity (MTBS) fire history ([Eidenshink](#)
189 [et al. 2007](#)) and had high cover of *B. tectorum*, but still had scattered sagebrush cover. We
190 used a metal stake to mark paired burned and unburned sampling locations on each side of
191 the perimeter, 10 m from the nearest evidence of anthropogenic disturbance (i.e. bulldozer
192 effects, footprints) associated with active fire suppression along the perimeter. Within 3 m of
193 each marker, we extracted twelve, 6 cm deep, 5 cm diameter, soil cores. Seeds of sagebrush
194 generally do not fall far (<30 m) from their parent plants in this system ([Shinneman and](#)
195 [McIlroy 2016](#)), and so they are not uniformly distributed ([Boudell, Link, and Johansen 2002](#)).
196 In addition, seeds from *B. tectorum* and *Artemisia* have different germination rates based
197 on the micro-site they find themselves in (i.e. under a shrub or in the bare ground between
198 shrubs, [Eckert et al. 1986](#)). To account for these potentially confounding effects, we placed
199 half of the core locations under shrubs, half in shrub interspaces, and aggregated the cores
200 for each site. In the burned areas, it was obvious where shrubs had been located. Even
201 when they were completely incinerated, their imprint remained on the soil surface ([Bechtold](#)
202 [and Inouye 2007](#)). To examine the effect of seed depth, we divided each soil core into 0-2
203 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples. Samples were then
204 placed in cold storage (~2 deg C) for 3 months ([Meyer, Monsen, and Mcarthur 2013](#)). At all
205 sites, to be sure that we were at a site where sagebrush germination could occur we checked
206 for first year germinants on the unburned side (we found them at all sites), and to ensure
207 that there were no confounding effects of post-fire seed dispersal, we determined whether or
208 not the sagebrush were flowering (they were not flowering at all sites), and recorded species
209 occupancy for all aboveground plant species.

210 We followed the methodology of Ter Heert et al. ([1996](#)) to germinate the seeds. Each
211 sample was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4

212 pots. These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand.
213 Pots were watered as needed to stay at field capacity. Every week emerging germinants were
214 identified, counted and removed. Most of the germination occurred within 6 weeks, and after
215 8 weeks we ended the germination assay.

216 *2.3 Post-Fire Vegetation Sampling*

217 We sampled the aboveground fuel structure and plant diversity in May 2017, the growing
218 season immediately after the fire and again in September 2019. At each location, we es-
219 tablished 50m transects starting at the boundary of the burned and unburned sides of the
220 perimeter, running perpendicular to the fire perimeter, and marked the transect ends with
221 rebar. In order to characterize aboveground plant diversity, we measured the occupancy and
222 abundance of all plant species by measuring cover of every species in 0.1 m² quadrats spaced
223 every 5 m along each transect. We measured shrub cover (coarse fuels) and herbaceous
224 plant cover (fine fuels) using the line intercept method along the transect, a commonly-used
225 approach for characterizing fuel structure ([Elzinga, Salzer, and Willoughby 1998](#)). We cal-
226 culated total vegetation cover (TVC) as the sum of the fine and coarse fuel measurements.
227 Both live and dead plants were included in these measurements.

228 *2.4 Remotely-Sensed Burn Severity*

229 We downloaded the “fire bundle” of the Hot Pot fire from [www.mtbs.gov](#). This included
230 cloud-free Landsat 8 scenes collected before the Hot Pot fire, and already calculated layers
231 of the Differenced Normalized Burn Ratio (dNBR, Equations 1 & 2, [J. D. Miller et al. 2009](#)).
232 Because our sites were generally within 10 meters of the burn perimeter, The pixels directly
233 intersecting the site locations were likely to be mixed pixels (i.e. containing burned and
234 unburned ground). To minimize this effect, we extracted all the dNBR values within a 120
235 meter buffer of each seed bank site for pixels whose centroids fell inside of the fire perimeter
236 and calculated the mean.

237 **Equation 1:** $NBR = (NIR - SWIR_1)/(NIR + SWIR_1)$

238 **Equation 2:** $dNBR = (NRB_{prefire} - NBR_{postfire}) * 1000$

239 *2.5 Statistical Analysis*

240 Our statistical analysis centered around trying to understand each component of the positive
241 feedback loop posited by the 4 hypotheses described above. In order to understand how pre-
242 fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC)
243 from two separate data sources as a proxy for fuel connectivity, and created separate linear
244 models with TVC as the predictor variable and burn severity (dNBR, [J. D. Miller et al.](#)
245 [2009](#)) as the response variable. With the field data we collected, we created an ordinary
246 least squares (OLS) linear model with burn severity as the dependent variable and TVC
247 (defined as shrub cover plus herbaceous plant cover from the unburned side of the paired
248 sites), elevation and aspect as independent variables.

249 We were concerned that because our data were collected at the edge of the fire, the burn
250 severity calculated at each point may have included partially burned pixels. So, as a sup-
251 plement, we examined the same relationship by creating a model of TVC using Landsat
252 Thematic Mapper (TM) surface reflectance data using field measurements of TVC from the
253 Bureau of Land Management's Assessment, Inventory and Monitoring dataset (AIM, [U.S.](#)
254 [Department of Interior 2018](#)). The AIM dataset contained 813 sampling locations within
255 the Central Basin and Range ecoregion ([Commission for Environmental Cooperation 2006](#))
256 that were visited by BLM field crews between 2011 and 2015. They were mostly sampled
257 once but there were some repeats, for 1,117 total measurements. For each of these points,
258 we extracted the surface reflectance values of each Landsat band for the sampling year near
259 peak biomass using a cloud-free scene from May or early June. Then, we used those surface
260 reflectance values to calculate various vegetation indexes (Appendix S1: Table S1), including
261 the Green Normalized Differenced Vegetation Index (Green NDVI, Equation 3), and Nor-
262 malized Differenced Senesced Vegetation Index (NDSVI, Equation 4). We used these two
263 indexes and their interactions as predictors in a generalized linear model of TVC with a

264 beta distribution. We used the model to create a layer of estimated pre-fire TVC for the
265 study area, and extracted both our predictions of TVC and dNBR of the fire from 1000
266 regularly-spaced points within the fire perimeter. Finally, to quantify the effect of TVC on
267 burn severity, we created an OLS linear model with our modeled TVC and its second-order
268 polynomial as predictor variables and burn severity as the response variable.

269 **Equation 3:** $\text{Green NDVI} = \frac{\text{NIR}-\text{Green}}{\text{NIR}+\text{Green}}$

270 **Equation 4:** $\text{NDSVI} = \frac{\text{SWIR}_1-\text{Red}}{\text{SWIR}_1+\text{Red}}$

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

282 To account for the possibility that increased fuel connectivity brought on by the invasion
283 of annual grasses may have already depleted the diversity of the soil seed bank before the
284 fire occurred (H2a) as a confounding factor, we included the Shannon-Weaver diversity in-
285 dex ([Shannon and Weaver 1949](#)) in the paired, unburned seed bank samples as one of the
286 predictor variables in our JSDM. We also created OLS models with the unburned species
287 richness and Shannon-Weaver diversity index predicted by prefire fuel connectivity, with the
288 expectation that pre-fire fuel connectivity would have had a negative effect on the prefire
289 seedbank diversity. To examine how community composition and burn severity then affected

290 subsequent fuel connectivity (H3), we created OLS models with fuel connectivity three years
291 post-fire as the dependent variable, and burn severity, seed counts for *B. tectorum*, *P. secunda*
292 and other species, elevation, aspect, depth, and alpha diversity as independent variables. To
293 examine how the resulting fuel connectivity was related to biodiversity (H4), we used the
294 aboveground diversity data and connectivity data that we collected in 2019 to create a Pois-
295 son GLM with number of species encountered at each site as the dependent variable, as well
296 as an OLS linear model with the Shannon-Weaver index for the plant species as a dependent
297 variable. We used fuel connectivity, elevation, and aspect as independent variables.

298 In order to examine hypotheses 1-3 in a single framework we constructed a path model
299 (Rosseel 2012, fig. 1a). We had paths leading from pre-fire connectivity, through burn
300 severity to the log of the post-fire count of *B. tectorum* seeds in the seedbank, and finally to
301 post-fire connectivity. Pre-fire cover of *B. tectorum*, elevation, pre-fire seed bank diversity
302 and pre-fire aboveground diversity were also accounted for.

303 All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis
304 are freely available at <https://doi.org/10.5281/zenodo.5293996>.

305 3. Results

306 We found support for each hypothesized component of the positive feedback loop indepen-
307 dently and when combined in the path model ($\chi^2 = 3.17$, $p = 0.39$, Figure 1a). For H1,
308 TVC had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$,
309 Figure 1b, Appendix S1: Table S2). For our remotely sensed analysis, Green NDVI, NDSVI
310 and their interaction explained 35% of the variation in pre-fire TVC (Appendix S1: Table
311 S2). This predicted TVC had a positive relationship with burn severity ($p \ll 0.01$, $R^2 = .42$,
312 Figure 1b, Appendix S1: Table S2).

313 The majority of seeds that germinated in the greenhouse were the two most common grass
314 species, *P. secunda* and *B. tectorum* (Appendix S1: Table S3, Fig. S3). Eight dicot species

were found in more than one location, and these 10 prevalent species are those that were used in our JSDM. Burned sites had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14 in the bottom 4 cm. Unburned sites had an average of 299 ± 170 in the top 2 cm and 59 ± 29 in the bottom 4 cm (Appendix S1: Fig. S4). For H2, the JSDM converged well (Appendix S1: Fig S5). Gelman diagnostics were all very close to 1 and the effective sample size centered on 4,000, which indicated good model convergence. Elevation had the strongest effects on individual species occurrence and explained the most variance on average (36%). Burn severity explained 23% of the variance on average and was supported at the 95% level for 5 species (Appendix S1: Fig S3b). For the introduced species, the predictions along a gradient of burn severity were positive for *B. tectorum*, *Sisymbrium altissimum* L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala testiculata* and *Alyssum desertorum* Stapf (Figure 1e). For native species, the effect of burn severity on occurrence was positive for *A. tridentata*, likely due to high severity fire removing litter and competitors immediately after fire ([Schlaepfer, Lauenroth, and Bradford 2014](#)), but the mean predictions were still low, never rising above 50%. It was neutral for *P. secunda* and negative for the remaining species. Testing H2a revealed a positive relationship between pre-fire aboveground species diversity and pre-fire fuel connectivity in the single model, and neutral relationships in the path model, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a confounding factor for H2.

For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the post-fire seedbank was positively associated with the fuel connectivity in 2019 ($\beta = 0.54$, $p = 0.01$, Adj R² = 0.75, Figure 1c, Appendix S1: Table S2). For H4 the most parsimonious model (Adj R² = 0.89, Appendix S1: Table S2) had elevation, aspect, fuel connectivity and an interaction between elevation and fuel connectivity as predictors of aboveground Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated with Shannon-Weaver diversity ($\beta = -0.28$, $p=0.004$, Figure 1d).

³⁴² **4. Discussion**

³⁴³ Here we document how changes in ecosystem structure brought on by invasion can lead
³⁴⁴ to cascading effects on ecosystem function and composition via changes in the disturbance
³⁴⁵ regime. It has already been shown that *B. tectorum* invasion increases fire frequency ([Balch
346 et al. 2013](#)), and is indicative of a grass-fire cycle. However, an understanding of the positive
³⁴⁷ feedback mechanisms that link *B. tectorum* invasion success to fire occurrence is required
³⁴⁸ to infer the long-term persistence of such a cycle. The interaction between burn severity
³⁴⁹ and seed bank composition documented here may explain that link. Prior work has shown
³⁵⁰ that annual grass invasion increases fuel connectivity by filling in shrub interspaces with a
³⁵¹ contiguous bed of fine fuels ([Davies and Nafus 2013](#)). This change in the spatial distribution
³⁵² of fine fuels has been associated with larger and more frequent fires ([Balch et al. 2013](#)).
³⁵³ Here, we found higher fuel connectivity (via TVC) increased burn severity (H1, Figure 1b).
³⁵⁴ Higher burn severity was associated with an increased occurrence of introduced annuals in
³⁵⁵ the post-fire seedbank and a decreased occurrence of native plants (H2, Figure 1e). Finally,
³⁵⁶ greater abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher post-fire
³⁵⁷ fuel connectivity (H3, Figure 1c). In addition, we found evidence that high post-fire fuel
³⁵⁸ connectivity was associated with lower aboveground diversity (H4, Figure 1d). This suggests
³⁵⁹ that during inter-fire intervals, there may be additional mechanisms (e.g. competition, altered
³⁶⁰ ecohydrology) maintaining the post-fire, annual grass-dominated species assemblage.

³⁶¹ The difference in species composition before and after fire explains an apparent contradiction
³⁶² in results between H2a (positive to neutral relationship between pre-fire fuel connectivity and
³⁶³ diversity) and H4 (negative relationship between post-fire fuel connectivity and diversity).
³⁶⁴ Most site locations had mature canopies of native shrubs with the inter-shrub space occu-
³⁶⁵ pied mostly by native bunchgrasses and forbs, with no fire occurrence since 1984. Even in
³⁶⁶ locations with high annual grass cover between shrubs, shrubs provide ecosystem structural
³⁶⁷ heterogeneity and islands of fertility ([Doescher, Miller, and Winward 1984](#); [Bechtold and](#)

368 Inouye 2007), and perennial natives that may have been established before invasion have
369 deep roots established that allow for the avoidance of competition for water with shallow-
370 rooted annuals (Gibbens and Lenz 2001; Ottaviani et al. 2020). This may provide enough
371 niche compartmentalization to allow native plants to persist in spite of the invasion prior to
372 fire occurrence. Three years after fire, almost all of the sites were dominated by introduced
373 annuals, and lacked any structural heterogeneity (Appendix S1, Fig. S6c). Thus native
374 plants may have been able to persist via niche compartmentalization after the initial inva-
375 sion, but fire burned away most of the seeds (Appendix S1, Fig. S3, S7) and removed all
376 of the structural benefits, and microclimatic refugia that shrub cover provides. In this clean
377 slate post-fire environment, the altered species composition of the seedbank and superior
378 post-fire dispersal of *B. tectorum* (Monty, Brown, and Johnston 2013) allow the process of
379 interspecific competition to be dominant (Schlaepfer, Lauenroth, and Bradford 2014).

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,
382 and calibrated using the composite burn index (Key and Benson 1999), tree mortality, and
383 percent change in tree canopy cover (J. D. Miller et al. 2009). It is unclear how well
384 these metrics carry over to shrubland systems. We recorded qualitative observations of burn
385 severity while we were sampling, mainly to ensure that we sampled a range of severities, and
386 the dNBR we used appears to correspond with our observations. In areas where the space
387 between shrubs was well-connected by fine fuels (Figure 2 a-c) the burn severity was higher,
388 and the shrubs had completely burned throughout the root system, leaving only a hole in the
389 ground filled with ashes as evidence of their prior presence. In these areas the entirety of the
390 soil surface—underneath shrub canopy and in canopy interspaces—was consumed by fire,
391 and there was little evidence of remaining litter or biological soil crust. Areas with lower fuel
392 connectivity had lower burn severity (Figure 2 d-f). Here, shrubs were usually consumed
393 only to the stumps, and sometimes left standing and charred, destined for mortality. In
394 these areas the soil surface often still had biological soil crust, partially consumed litter

395 (R. O. Jones et al. 2015) and unconsumed annual and perennial grass bases. The manual
396 severity classification provided by MTBS had exclusively low and medium severity, but our
397 observations of essentially complete consumption of plant and litter tissues and very few
398 unburned patches suggested that these should have been mostly medium and high severity.
399 This discrepancy was not unexpected, as the ordinal burn severity classifications produced
400 by MTBS are known to be flawed for research use (Kolden, Smith, and Abatzoglou 2015).

401 Spectral reflectance has long been used to characterize ecosystem structure, including wildfire
402 fuels. Unique signatures of remotely-sensed spectral reflectance are typically matched to
403 categorical fuel classifications (CFCs), which describe the physiognomy of vegetation and
404 its potential to support various fire behavior (Ottmar et al. 2007). While different CFCs
405 can provide a general understanding of fuel amount and connectivity, recent efforts using
406 data with finer spatial and spectral resolution may improve fuel classification with more
407 continuous, multi-dimensional measurements (Stavros et al. 2018). The continuous measure
408 of NDVI in western U.S. coniferous forests is a proxy for live fuel biomass, which likely
409 explains its positive association with wildfire severity (Sean A. Parks et al. 2018; Koontz et al.
410 2020). NDVI also correlates with vegetation cover in these forested systems, and so greater
411 crown connectivity may also explain the NDVI/severity relationship at local scales. When
412 using a more direct NDVI-derived measure of vegetation connectivity in Sierra Nevada yellow
413 pine/mixed-conifer, Koontz et al. (2020) found that greater variability in forest structure,
414 decreased the probability of high-severity fire, likely due to decreased fuel connectivity (i.e.,
415 live tree canopies in the yellow pine/mixed-conifer forest). Here, we arrived at a combination
416 of NDVI and NDSVI to describe the fuel connectivity of the annual grass invaded Great Basin
417 sagebrush community to better reflect key differences in the physiognomies of forest and arid
418 shrublands. In sagebrush shrublands, the fuel that contributes to large wildfires is a mixture
419 of evergreen shrubs interspersed with herbaceous plants that remain green for only a portion
420 of the growing season, and then become dry and straw-colored. Thus, both the live and
421 dead fuel need to be taken into account in remote measurements of fuel connectivity for this

422 system.

423 ***Management implications***

424 These results demonstrate that the strength of the grass-fire cycle in this system is controlled
425 by measurable fire properties and ecosystem structural components. We found that annual
426 grass cover was not the single variable that explained burn severity and fuel connectivity
427 (Appendix S1, Fig S6). Rather, it was the contribution of annual grass cover to the total
428 connectivity of the system (Appendix S1, Fig. S1). The most important areas to prioritize
429 for management interventions could paradoxically be areas with relatively low levels of an-
430 nual grass cover that join previously disconnected vegetation. Land managers may be able
431 to increase their chances of restoration success by using existing methods or developing novel
432 ones that manipulate these components to weaken or even break the positive feedback cycle.
433 This work provides further evidence that the post-fire annual grassland is a system where
434 the degraded state represents an alternative species assemblage from that of the restoration
435 target. Because the propagules of the original assemblage are no longer present, methods
436 that rely on natural succession may not be sufficient ([Suding, Gross, and Houseman 2004](#)).
437 Estimating burn severity using satellite imagery may be used in conjunction with site suit-
438 ability and climate forecasts to help land managers identify areas with a greater likelihood
439 of successful seeding. Our results highlight the importance of prioritizing the preservation of
440 existing native shrub cover and in particular policies that encourage land managers to max-
441 imize the preservation of unburned patches within the fire perimeter during the suppression
442 of wildfires in this system ([Steenvoorden et al. 2019](#)), as these are the primary sources of
443 native propagules.

444 Livestock grazing can reduce fuel connectivity in uninvaded sagebrush ([Davies et al. 2010](#)).
445 At the same time, livestock grazing can decrease the resistance to invasion by *B. tectorum* via
446 negative effects on biological soil crust (BSC) ([Condon and Pyke 2018](#)), and can reduce the
447 survival of *Artemisia* seedlings that are not protected by shrub canopies ([Owens and Norton](#)

448 1992). Targeted spring grazing in annual grass monocultures may reduce fuel connectivity
449 and alleviate fire risk. Post-fire grazing may help reduce *B. tectorum* cover, but it may
450 also exacerbate the problem by introducing *B. tectorum* in uninvaded sites (Williamson et
451 al. 2019) or increasing the already superior post-fire dispersal of *B. tectorum* seeds (Monty,
452 Brown, and Johnston 2013). Management interventions should be specifically tailored each
453 year to the conditions of a given site, and focused on native plant restoration.

454 Herbaceous cover in these dryland systems has high interannual variability (Mahood et al.
455 2022). Because the components of ecosystem structure and disturbance severity in positive
456 feedback cycle described here are continuous mechanistic variables, it may be possible to
457 develop theoretical models (*sensu* (Archibald, Staver, and Levin 2012)) to estimate the
458 threshold of vegetation cover that will lead to high burn severity. These can then be applied
459 in conjunction with near real time fuel loading forecasts (M. O. Jones et al. 2021) to identify
460 areas that are vulnerable to high severity fire, which can be used by land managers to take
461 preemptive measures in high value areas.

462 ***Global environmental change implications***

463 Understanding how different facets of global environmental change create multiple mecha-
464 nisms that act in concert to drive ecosystem transformation will provide important insights
465 about ecosystem change from regional to global scales. The system studied here has at
466 least four external processes that may influence the positive feedback we documented. First,
467 land use change via livestock grazing facilitates invasion (Ponzetti, Mccune, and Pyke 2007;
468 Williamson et al. 2019). Second, the introduction of exotic grasses increases fuel connec-
469 tivity (Davies and Nafus 2013), affects burn severity. Third, increasing temperatures due
470 to climate change increase burn severity in forests (S. A. Parks and Abatzoglou 2020). We
471 expect this to be true for shrublands, and is an important area for future research. Increas-
472 ing temperatures simultaneously decrease seed viability and seedling survival (Schlaepfer,
473 Lauenroth, and Bradford 2014; Enright et al. 2015). Fourth, CO₂ enrichment may prefer-

⁴⁷⁴ entially enhance biomass (i.e. higher fuel connectivity) and seed production of annual grass
⁴⁷⁵ species ([Smith et al. 2000](#); [Nagel et al. 2004](#)). All four of these external drivers are globally
⁴⁷⁶ ubiquitous consequences of global change.

⁴⁷⁷ An ecosystem “state” is the product of countless endogenous interactions. The grass-fire
⁴⁷⁸ cycle studied here is strengthened through providing fitness benefits to the introduced annual
⁴⁷⁹ grasses via at least three reinforcing processes. First, we document how it changes the
⁴⁸⁰ composition of the seedbank. Second, introduced annual grasses competitively exclude native
⁴⁸¹ plants. Third, the dominance of introduced annual grasses initiates ecohydrological feedbacks
⁴⁸² to create a warmer, drier microclimate ([Turnbull et al. 2012](#)). It is possible that some
⁴⁸³ of these feedbacks are idiosyncratic to the system being studied, while others may reflect
⁴⁸⁴ fundamental properties of ecosystem function that change when a system is converted from
⁴⁸⁵ being dominated by deep-rooted woody plants to being dominated by annual herbaceous
⁴⁸⁶ plants ([Kitzberger et al. 2016](#)). At least 13 grass species initiate self-reinforcing feedbacks
⁴⁸⁷ with fire in the U.S. alone ([Fusco et al. 2019](#); [Tortorelli, Krawchuk, and Kerns 2020](#)). There
⁴⁸⁸ are many more fire-inducing grass invasions worldwide, with documented cases in Australia
⁴⁸⁹ ([G. Miller et al. 2010](#)), Brazil ([Rossi et al. 2014](#)) and South Africa ([Milton 2004](#)). The
⁴⁹⁰ conversion of forests and shrublands to grasslands may have consequences relevant to the
⁴⁹¹ global carbon cycle, especially when ecosystems dominated by deep-rooted plants that store
⁴⁹² carbon belowground are replaced by shallow-rooted ecosystems that lose carbon to grazing
⁴⁹³ and fire ([Kerns et al. 2020](#); [Mahood et al. 2022](#)).

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819 **Figure Captions**

820 **Figure 1.** Panel a is a Path model showing the theorized hypotheses. Red arrows are nega-
821 tive relationships, blue arrows are positive relationships, and grey arrows are not significant
822 ($p > 0.1$) but still accounted for in the model. Abbreviations: pre = pre-fire; post = post-
823 fire; cv = cover; elv = elevation; ag = aboveground; sb = seed bank; sev = severity; div =
824 diversity. On the left side of (b), burn severity (dNBR) as predicted by total vegetation cover
825 (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is
826 predicted by modelled TVC. Panel e shows the modelled occurrence of germinable seeds for
827 all species found at more than one location along a gradient of burn severity, after accounting
828 for soil depth, aspect, elevation and pre-fire diversity. Black line is the mean prediction, each
829 colored line represents one posterior sample. In (c), fuel connectivity three years post-fire is
830 modelled by seedbank composition, elevation and pre-fire aboveground species richness. In
831 (d) shannon-Weaver diversity index of the aboveground, post-fire community composition,
832 was negatively affected by fuel connectivity after accounting for elevation. For a, c and d,
833 lines are the fitted partial effects, points are the partial residuals, and dotted lines are the
834 95% confidence intervals. $p < 0.05$ for black lines, $p > 0.05$ for grey lines.

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

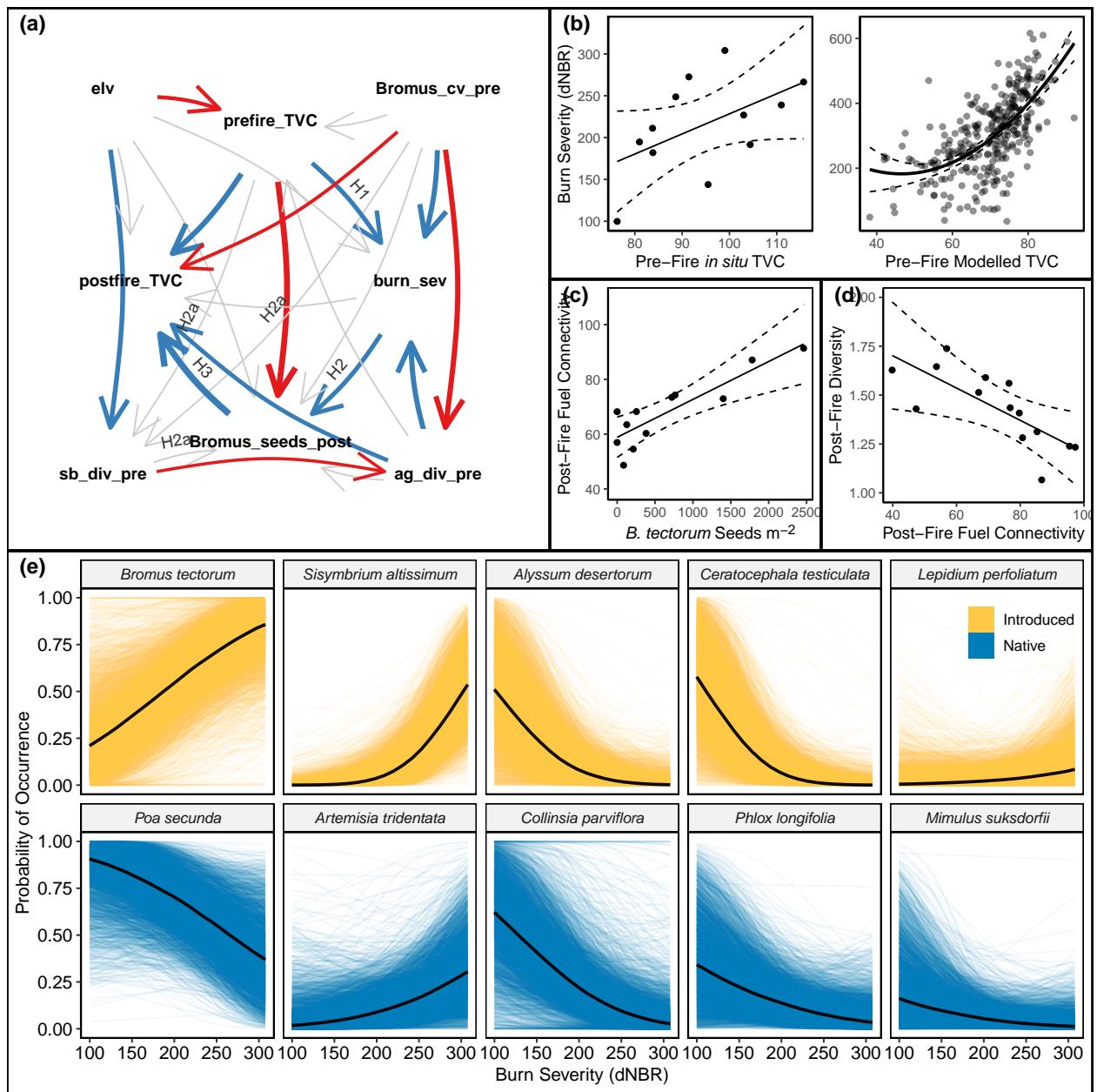


Figure 1: .

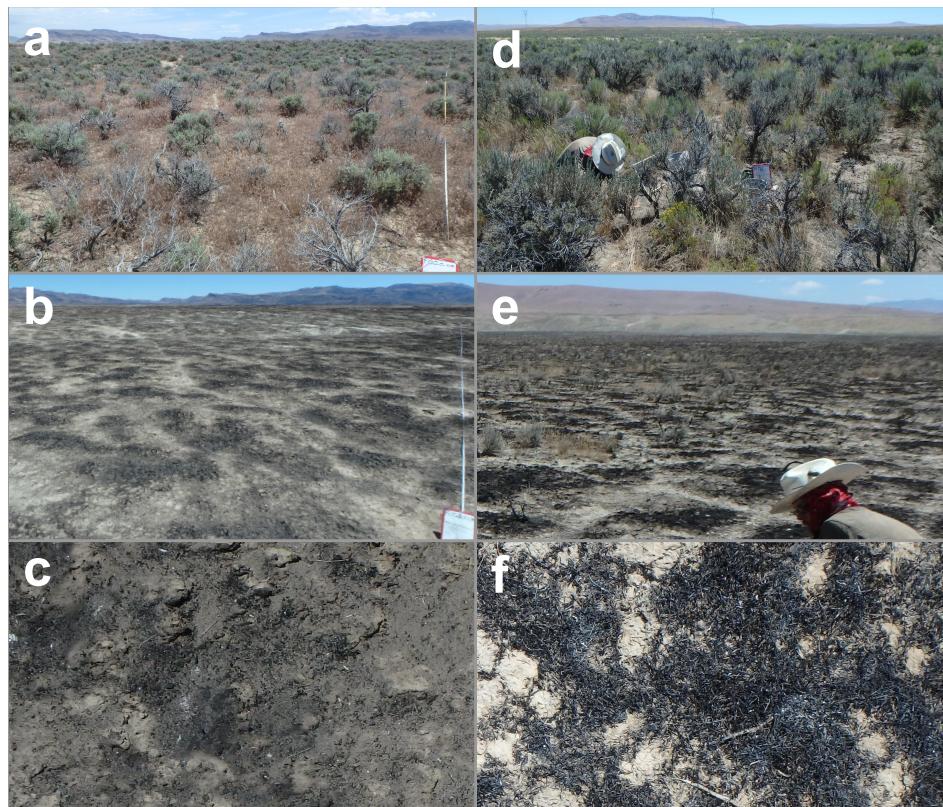


Figure 2: .