

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*, alternative stable states, *Bromus tectorum*, burn severity,
30 cheatgrass, fuel connectivity, grass-fire cycle, joint species distribution model, resilience,
31 sagebrush

32 1. Introduction

33 Ecosystems around the world are being affected simultaneously by multiple facets of global
34 change. For example, changes in land use can facilitate exotic plant invasions ([Allan et al. 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](#)).

51 There is a long history of univariate time series observations that show sudden state changes

52 (Marten Scheffer and Carpenter 2003), and these have informed the development of theories
53 that help us understand how systems of any type can change state suddenly, and exist in per-
54 sistent alternative stable states (Marten Scheffer et al. 2015; Ratajczak et al. 2018). These
55 theories typically represent the system's state with a single variable, of which the mean is
56 observed to abruptly change in time or space (Marten Scheffer et al. 2015). Descriptive
57 evidence of alternative stable states has been documented at broad scales in tropical ecosys-
58 tems, where forests, savannas and grasslands are considered alternative stable states because
59 they are floristically distinct (Aleman et al. 2020) and cluster around static values of woody
60 cover (80, 30 and 0 percent) while occurring along overlapping ranges of precipitation (Hirota
61 et al. 2011; Staver, Archibald, and Levin 2011). The forested state has a self-reinforcing,
62 positive feedback between evapotranspiration and tree cover (Staal et al. 2020), while the
63 grassland and savanna states are maintained by feedbacks between grass flammability and
64 fire occurrence (D'Antonio and Vitousek 1992; Staver, Archibald, and Levin 2011). Al-
65 ternative stable states are believed to be widespread (M. Scheffer et al. 2001), but their
66 existence is rarely proven at broader scales, with most demonstrative studies having been
67 conducted in greenhouse and laboratory microcosm experiments (Schröder, Persson, and De
68 Roos 2005). One of the reasons for this is that ecological systems are much more complex
69 than a simple bivariate system with a single driver and a single response. There may be
70 multiple drivers, and the state is the product of interactions between organisms and their
71 immediate environment, as well as countless inter- and intra-specific interactions.

72 A central challenge in ecology in the 21st century is to move from describing how plant
73 communities are affected by global change to the capacity to predict how species pools will
74 assemble and persist in response to global change (Davis, Higuera, and Sala 2018; Keddy and
75 Laughlin 2021). Prediction of community response to multi-faceted global change drivers
76 is enhanced with a better understanding of the mechanisms that underlie community sta-
77 bility in the face of disturbances. A classic example of an ecosystem that appears to have
78 disturbance-mediated alternative stable states (but see Morris and Leger (2016)), but whose

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

99 Petraitis and Latham (1999) posited that the maintenance of alternate species assemblages
100 requires first a disturbance that removes the species from the initial assemblage and second
101 the arrival of the species of the alternate assemblage. One understudied mechanism that may
102 explain both for the *Artemisia/Bromus* system is the interaction between the species compo-
103 sition of the soil seed bank and burn severity. Because the invading species are annual, and
104 many of the key native plant species are seed obligates, the seed is the key life history stage
105 that fire must act upon to benefit the invading plants. Seeds and seedlings are particularly

¹⁰⁶ vulnerable to climate, competition and disturbance (Enright et al. 2015). Warmer and drier
¹⁰⁷ conditions simultaneously reduce recruitment, growth, and survival of seeds and seedlings
¹⁰⁸ (Enright et al. 2015; Schlaepfer, Lauenroth, and Bradford 2014), while also increasing burn
¹⁰⁹ severity (S. A. Parks and Abatzoglou 2020). In fire prone ecosystems, seed obligate species
¹¹⁰ typically have life history strategies to cope with fires that burn at different severities (Maia
¹¹¹ et al. 2012; Wright, Latz, and Zuur 2016; Palmer, Denham, and Ooi 2018). Soil heating from
¹¹² fire affects the response of vegetation to fire (Gagnon et al. 2015), including the capacity of
¹¹³ seeds to remain viable after fire (Humphrey and Schupp 2001). High severity fire can affect
¹¹⁴ species that use the seedbank positively (Kimura and Tsuyuzaki 2011), negatively (Heydari
¹¹⁵ et al. 2017), or have no effect (Lipoma, Funes, and Díaz 2018), depending on species-specific
¹¹⁶ adaptations. Both the depth of the burn and fire temperature can affect subsequent recovery
¹¹⁷ by seed germination (Morgan and Neuenschwander 1988; Schimmel and Granström 1996),
¹¹⁸ as well as seed mortality and physical seed dormancy mechanisms (Liyanage and Ooi 2017).

¹¹⁹ In addition to size and frequency, exotic plant invasions can alter fire temperature (Brooks
¹²⁰ et al. 2004; R. O. Jones et al. 2015) and burn severity. While in many cases fires that
¹²¹ burn at higher temperatures will also consume more biomass (i.e. burn at higher severity),
¹²² grass fires may not always have such a relationship. Direct measurements have shown that
¹²³ *B. tectorum* burns at low temperatures (Beckstead et al. 2011; Germino, Chambers, and
¹²⁴ Brown 2016), but because it also increases horizontal fuel connectivity (Davies and Nafus
¹²⁵ 2013), it leads to more contiguously burned areas and therefore higher burn severity, despite
¹²⁶ lower fire temperatures. To benefit from fire, *B. tectorum* would need to gain a fitness benefit
¹²⁷ relative to other species

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

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

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

described here: (H1) Pre-fire fuel connectivity would be positively related to burn severity; (H2) burn severity would increase the occurrence probability of introduced annual species in the seed bank and reduce the occurrence probability of native species. An alternative to H2 is H2a, in which increased fuel connectivity brought on by the invasion of annual grasses may have already depleted the diversity of the soil seed bank before the fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds in the seedbank would be positively related to post-fire fuel connectivity. In addition, because in our study system post-fire sites are floristically distinct from the pre-fire state (Mahood and Balch 2019), typically with near monocultures of *B. tectorum*, we hypothesized that (H4) high post-fire fuel connectivity of those near-monocultures would result in lower aboveground species diversity due to competitive exclusion of native plants.

2. Methods

2.1 Study Area

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

2.2 Seed Bank Sampling

In early July 2016, we collected samples of the soil seed bank at fourteen locations the day after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where

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

We followed the methodology of Ter Heert et al. ([1996](#)) to germinate the seeds. Each

212 sample was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4
213 pots. These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand.
214 Pots were watered as needed to stay at field capacity. Every week emerging germinants were
215 identified, counted and removed. Most of the germination occurred within 6 weeks, and after
216 8 weeks we ended the germination assay.

217 *2.3 Post-Fire Vegetation Sampling*

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

229 *2.4 Remotely-Sensed Burn Severity*

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

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

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

240 *2.5 Statistical Analysis*

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

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

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

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

271 **Equation 4:** $NDSVI = \frac{SWIR_1-Red}{SWIR_1+Red}$

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

283 To account for the possibility that increased fuel connectivity brought on by the invasion
284 of annual grasses may have already depleted the diversity of the soil seed bank before the
285 fire occurred (H2a) as a confounding factor, we included the Shannon-Weaver diversity in-
286 dex ([Shannon and Weaver 1949](#)) in the paired, unburned seed bank samples as one of the
287 predictor variables in our JSDM. We also created OLS models with the unburned species
288 richness and Shannon-Weaver diversity index predicted by prefire fuel connectivity, with the
289 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 aboveground diversity data and connectivity data that we collected in 2019 to create a Poisson GLM with number of species encountered at each site as the dependent variable, as well as an OLS linear model with the Shannon-Weaver index for the plant species as a dependent variable. We used fuel connectivity, elevation, and aspect as independent variables.

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

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

3. Results

We found support for each hypothesized component of the positive feedback loop independently and when combined in the path model ($\chi^2 = 3.17$, $p = 0.39$, Figure 1a, Appendix S1, Tables S4 & S5). For H1, TVC had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$, Figure 1b, Appendix S1: Table S2). For our remotely sensed analysis, Green NDVI, NDSVI and their interaction explained 35% of the variation in pre-fire TVC (Appendix S1: Table S2). This predicted TVC had a positive relationship with burn severity ($p \ll 0.01$, $R^2 = .42$, Figure 1b, Appendix S1: Table S2).

The majority of seeds that germinated in the greenhouse were the two most common grass

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 \pm 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 $R^2 = 0.75$, Figure 1c, Appendix S1: Table S2). For H4 the most parsimonious model (Adj $R^2 = 0.89$, 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 ($\beta =$

³⁴² -0.28, p=0.004, Figure 1d).

³⁴³ 4. Discussion

³⁴⁴ Here we document how changes in ecosystem structure brought on by invasion can lead
³⁴⁵ to cascading effects on ecosystem function and composition via changes in the disturbance
³⁴⁶ regime. It has already been shown that *B. tectorum* invasion increases fire frequency ([Balch
347 et al. 2013](#)), and is indicative of a grass-fire cycle. However, an understanding of the positive
³⁴⁸ feedback mechanisms that link *B. tectorum* invasion success to fire occurrence is required
³⁴⁹ to infer the long-term persistence of such a cycle. The interaction between burn severity
³⁵⁰ and seed bank composition documented here may explain that link. Prior work has shown
³⁵¹ that annual grass invasion increases fuel connectivity by filling in shrub interspaces with a
³⁵² contiguous bed of fine fuels ([Davies and Nafus 2013](#)). This change in the spatial distribution
³⁵³ of fine fuels has been associated with larger and more frequent fires ([Balch et al. 2013](#)).
³⁵⁴ Here, we found higher fuel connectivity (via TVC) increased burn severity (H1, Figure 1b).
³⁵⁵ Higher burn severity was associated with an increased occurrence of introduced annuals in
³⁵⁶ the post-fire seedbank and a decreased occurrence of native plants (H2, Figure 1e). Finally,
³⁵⁷ greater abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher post-fire
³⁵⁸ fuel connectivity (H3, Figure 1c). In addition, we found evidence that high post-fire fuel
³⁵⁹ connectivity was associated with lower aboveground diversity (H4, Figure 1d). This suggests
³⁶⁰ that during inter-fire intervals, there may be additional mechanisms (e.g. competition, altered
³⁶¹ ecohydrology) maintaining the post-fire, annual grass-dominated species assemblage.
³⁶² The difference in species composition before and after fire explains an apparent contradiction
³⁶³ in results between H2a (positive to neutral relationship between pre-fire fuel connectivity and
³⁶⁴ diversity) and H4 (negative relationship between post-fire fuel connectivity and diversity).
³⁶⁵ Most site locations had mature canopies of native shrubs with the inter-shrub space occu-
³⁶⁶ pied mostly by native bunchgrasses and forbs, with no fire occurrence since 1984. Even in

locations with high annual grass cover between shrubs, shrubs provide ecosystem structural heterogeneity and islands of fertility (Doescher, Miller, and Winward 1984; Bechtold and Inouye 2007), and perennial natives that may have been established before invasion have deep roots established that allow for the avoidance of competition for water with shallow-rooted annuals (Gibbens and Lenz 2001; Ottaviani et al. 2020). This may provide enough niche compartmentalization to allow native plants to persist in spite of the invasion prior to fire occurrence. Three years after fire, almost all of the sites were dominated by introduced annuals, and lacked any structural heterogeneity (Appendix S1, Fig. S6c). Thus native plants may have been able to persist via niche compartmentalization after the initial invasion, but fire burned away most of the seeds (Appendix S1, Fig. S3, S7) and removed all of the structural benefits, and microclimatic refugia that shrub cover provides. In this clean slate post-fire environment, the altered species composition of the seedbank and superior post-fire dispersal of *B. tectorum* (Monty, Brown, and Johnston 2013) allow the process of interspecific competition to be dominant (Schlaepfer, Lauenroth, and Bradford 2014).

Contrasts among forests and shrublands as it pertains to remote sensing

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

only to the stumps, and sometimes left standing and charred, destined for mortality. In these areas the soil surface often still had biological soil crust, partially consumed litter (R. O. Jones et al. 2015) and unconsumed annual and perennial grass bases. The manual severity classification provided by MTBS had exclusively low and medium severity, but our observations of essentially complete consumption of plant and litter tissues and very few unburned patches suggested that these should have been mostly medium and high severity. This discrepancy was not unexpected, as the ordinal burn severity classifications produced by MTBS are known to be flawed for research use (Kolden, Smith, and Abatzoglou 2015).

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

421 of the growing season, and then become dry and straw-colored. Thus, both the live and
422 dead fuel need to be taken into account in remote measurements of fuel connectivity for this
423 system.

424 ***Management implications***

425 These results demonstrate that the strength of the grass-fire cycle in this system is controlled
426 by measurable fire properties and ecosystem structural components. We found that annual
427 grass cover was not the single variable that explained burn severity and fuel connectivity
428 (Appendix S1, Fig S6). Rather, it was the contribution of annual grass cover to the total
429 connectivity of the system (Appendix S1, Fig. S1). The most important areas to prioritize
430 for management interventions could paradoxically be areas with relatively low levels of an-
431 nual grass cover that join previously disconnected vegetation. Land managers may be able
432 to increase their chances of restoration success by using existing methods or developing novel
433 ones that manipulate these components to weaken or even break the positive feedback cycle.

434 This work provides further evidence that the post-fire annual grassland is a system where
435 the degraded state represents an alternative species assemblage from that of the restoration
436 target. Because the propagules of the original assemblage are no longer present, methods
437 that rely on natural succession may not be sufficient ([Suding, Gross, and Houseman 2004](#)).

438 Estimating burn severity using satellite imagery may be used in conjunction with site suit-
439 ability and climate forecasts to help land managers identify areas with a greater likelihood
440 of successful seeding. Our results highlight the importance of prioritizing the preservation of
441 existing native shrub cover and in particular policies that encourage land managers to max-
442 imize the preservation of unburned patches within the fire perimeter during the suppression
443 of wildfires in this system ([Steenvoorden et al. 2019](#)), as these are the primary sources of
444 native propagules.

445 Livestock grazing can reduce fuel connectivity in uninvaded sagebrush ([Davies et al. 2010](#)).
446 At the same time, livestock grazing can decrease the resistance to invasion by *B. tectorum* via

⁴⁴⁷ negative effects on biological soil crust (BSC) ([Condon and Pyke 2018](#)), and can reduce the
⁴⁴⁸ survival of *Artemisia* seedlings that are not protected by shrub canopies ([Owens and Norton](#)
⁴⁴⁹ [1992](#)). Targeted spring grazing in annual grass monocultures may reduce fuel connectivity
⁴⁵⁰ and alleviate fire risk. Post-fire grazing may help reduce *B. tectorum* cover, but it may
⁴⁵¹ also exacerbate the problem by introducing *B. tectorum* in uninvaded sites ([Williamson et](#)
⁴⁵² [al. 2019](#)) or increasing the already superior post-fire dispersal of *B. tectorum* seeds ([Monty,](#)
⁴⁵³ [Brown, and Johnston 2013](#)). Management interventions should be specifically tailored each
⁴⁵⁴ year to the conditions of a given site, and focused on native plant restoration.

⁴⁵⁵ Herbaceous cover in these dryland systems has high interannual variability ([Mahood et al.](#)
⁴⁵⁶ [2022](#)). Because the components of ecosystem structure and disturbance severity in positive
⁴⁵⁷ feedback cycle described here are continuous mechanistic variables, it may be possible to
⁴⁵⁸ develop theoretical models (*sensu* ([Archibald, Staver, and Levin 2012](#))) to estimate the
⁴⁵⁹ threshold of vegetation cover that will lead to high burn severity. These can then be applied
⁴⁶⁰ in conjunction with near real time fuel loading forecasts ([M. O. Jones et al. 2021](#)) to identify
⁴⁶¹ areas that are vulnerable to high severity fire, which can be used by land managers to take
⁴⁶² preemptive measures in high value areas.

⁴⁶³ ***Global environmental change implications***

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

473 ing temperatures simultaneously decrease seed viability and seedling survival (Schlaepfer,
474 Lauenroth, and Bradford 2014; Enright et al. 2015). Fourth, CO₂ enrichment may prefer-
475 entially enhance biomass (i.e. higher fuel connectivity) and seed production of annual grass
476 species (Smith et al. 2000; Nagel et al. 2004). All four of these external drivers are globally
477 ubiquitous consequences of global change.

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

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820 **Figure Captions**

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

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

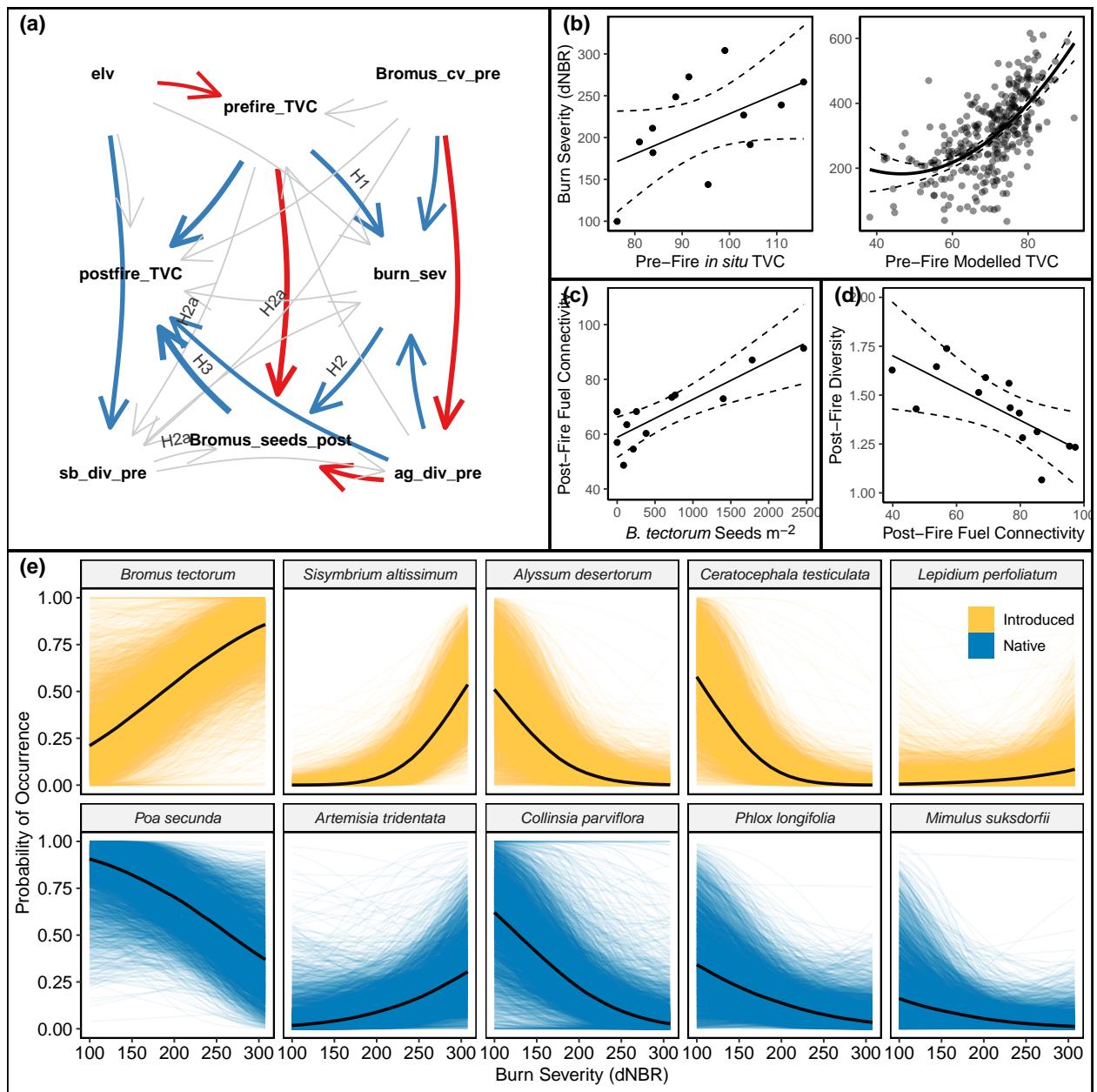


Figure 1: .

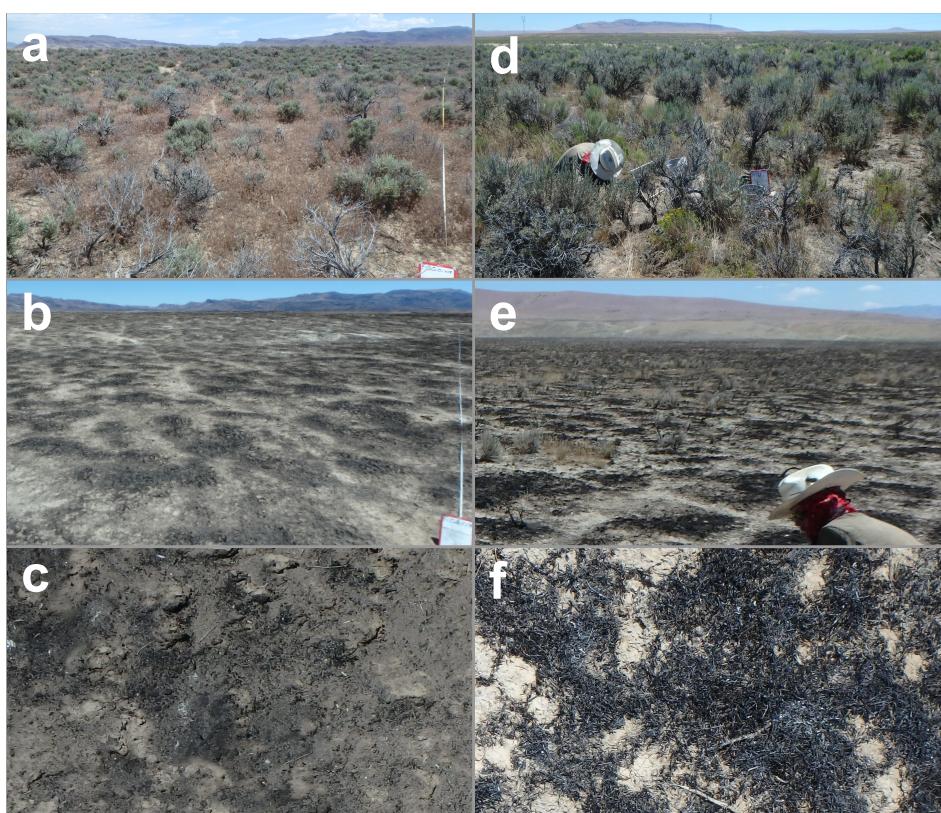


Figure 2: .

Appendix S1 for: “Fuel connectivity, burn severity, and seedbank survivorship drive ecosystem transformation in a semi-arid shrubland.”

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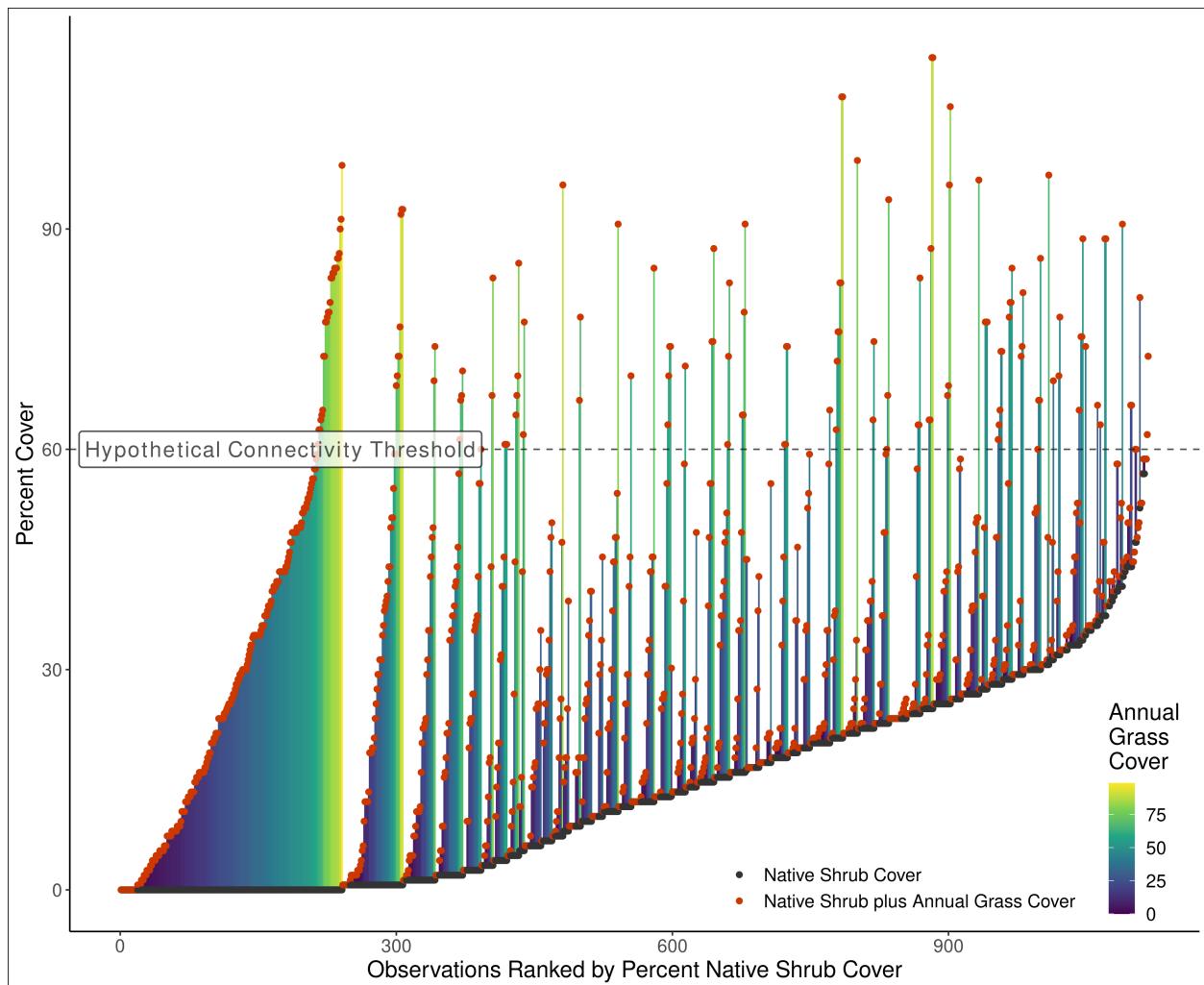


Figure S1: Sites with little to no shrub cover require high IAG cover to meet the threshold necessary to carry a fire, while sites with higher shrub cover may reach that threshold with much lower IAG cover. Therefore, annual grass cover alone may not be sufficient for quantifying fire risk. Data Source: the Bureau of Land Management's Assessment, Inventory and Monitoring dataset.

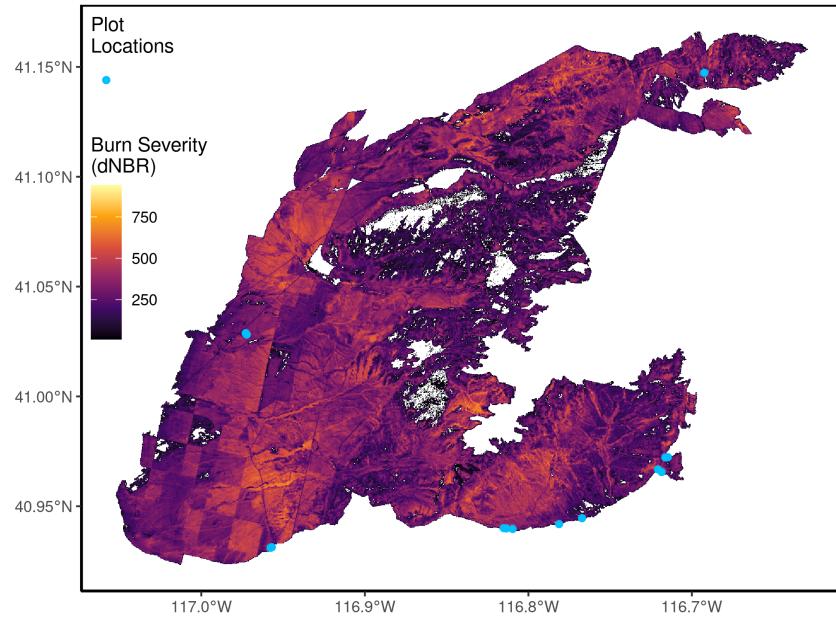


Figure S2: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

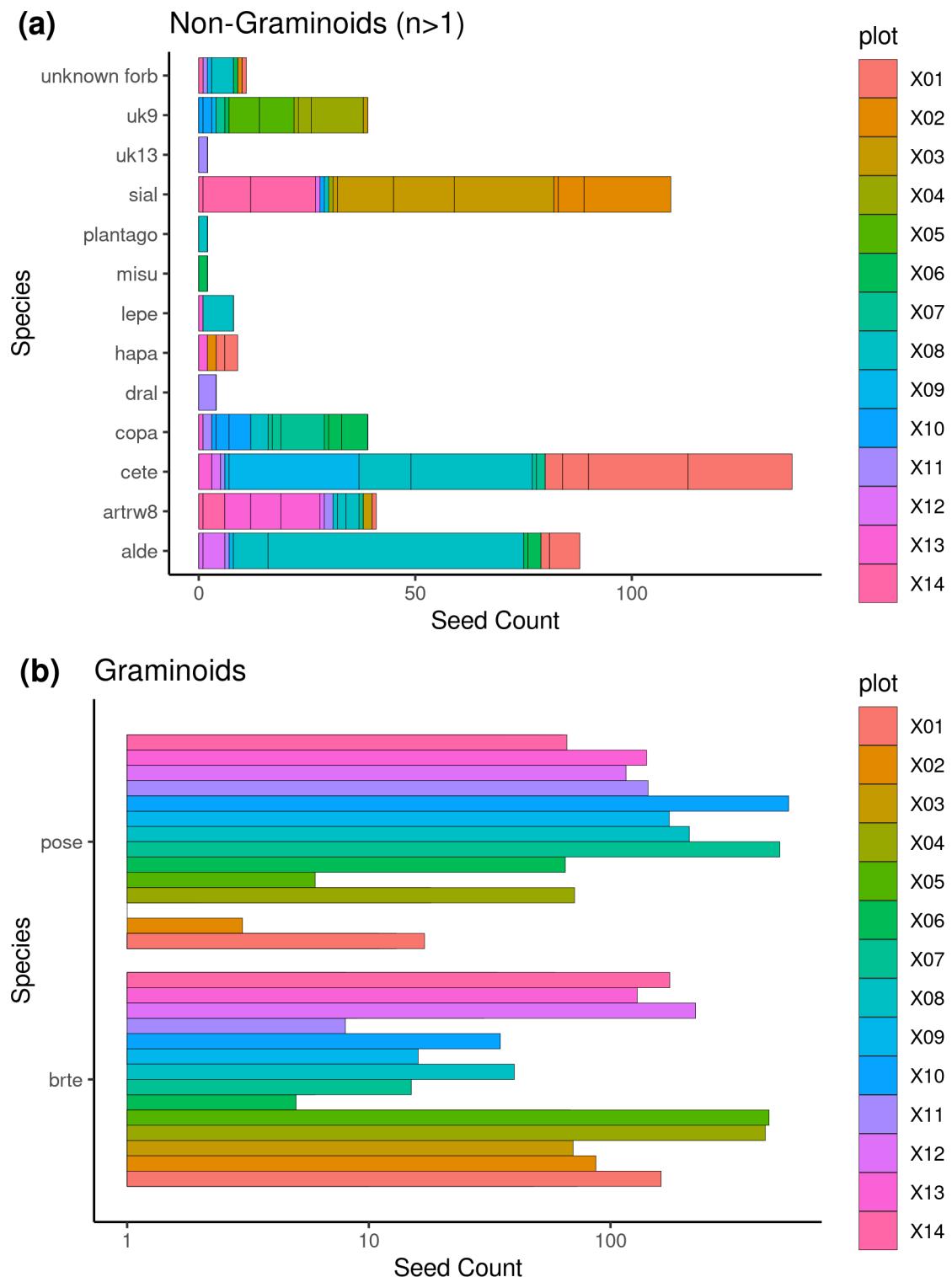


Figure S3: Seed counts by species that occurred more than once. Panel a shows non-graminoids, b shows graminoids.

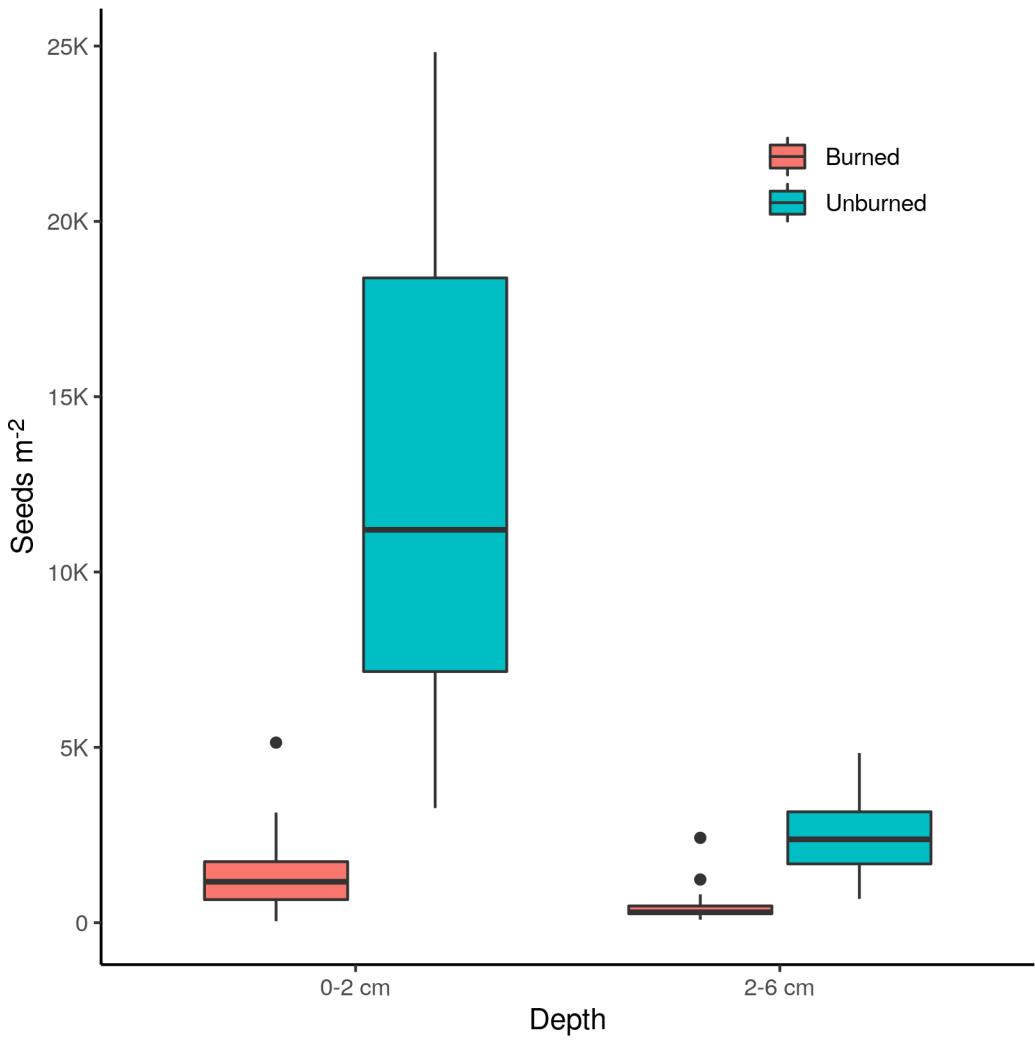


Figure S4: Total seed counts per plot.

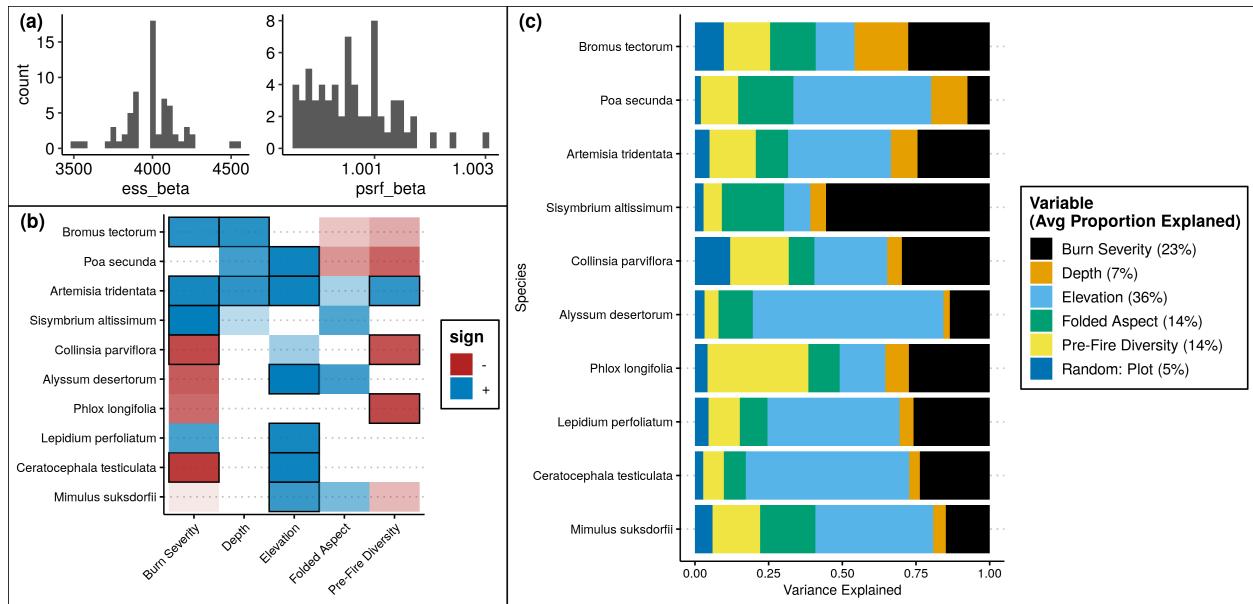


Figure S5: a) Model convergence diagnostics. On the left is the effective sample size after adjusting for autocorrelation (ideally 4,000), and on the right is the Gelman diagnostic, ideally 1. b) Predictor variables that had at least 80% support. Variables with 95% support are outlined in black. The level of transparency corresponds to the level of support. c) Variance partitioning by species. Average across all species per variable is given in the legend. Species are ordered by prevalence.

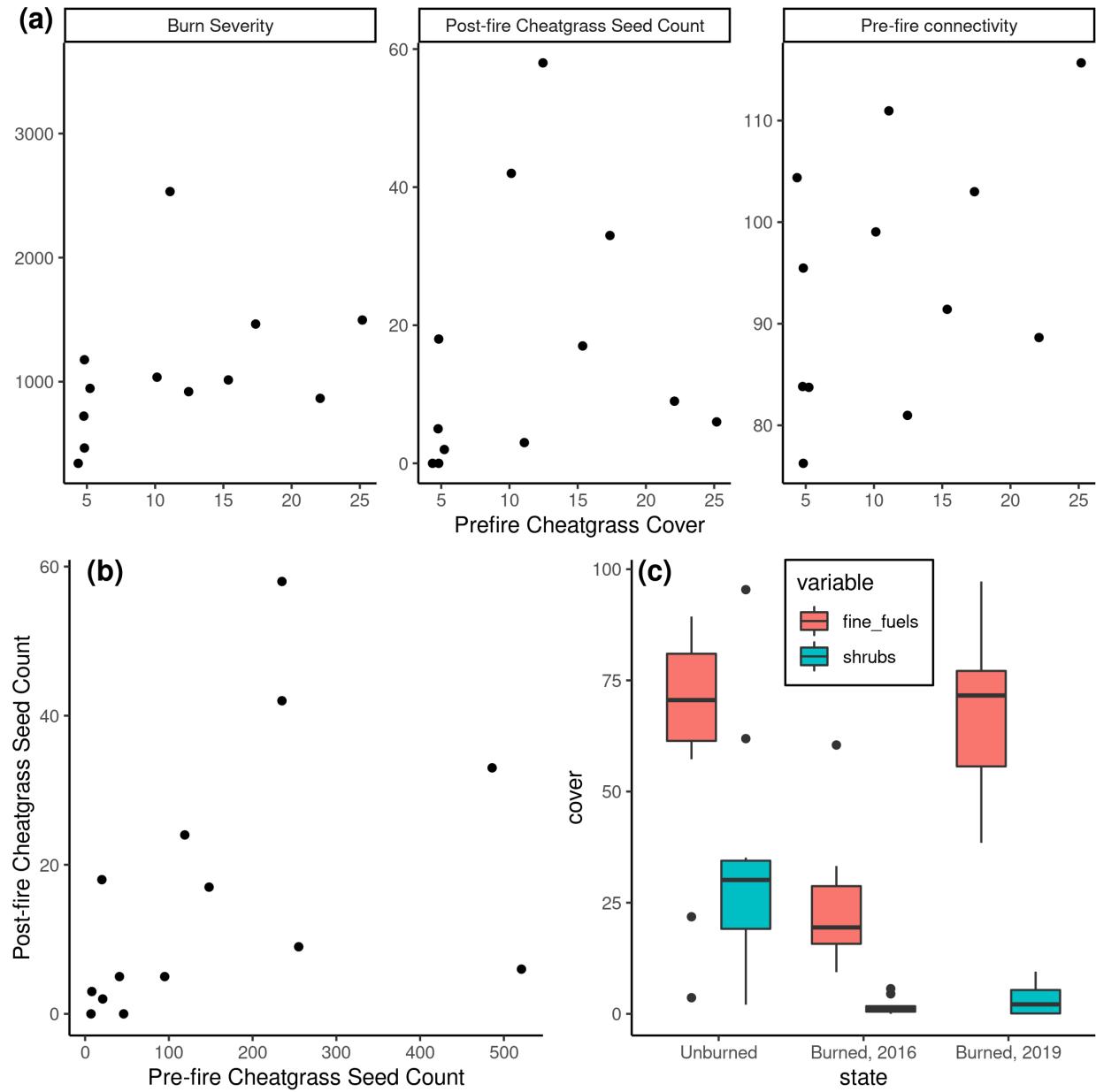


Figure S6: Panel a illustrates how we did not find convincing evidence that pre-fire cheatgrass cover alone was predictive of any of the key components of our hypothesized feedback loop. Panel b shows how even pre-fire cheatgrass seed counts were not predictive of post-fire seed counts. Panel c shows the general change in structural composition, from woody to herbaceous, before and after the fire.

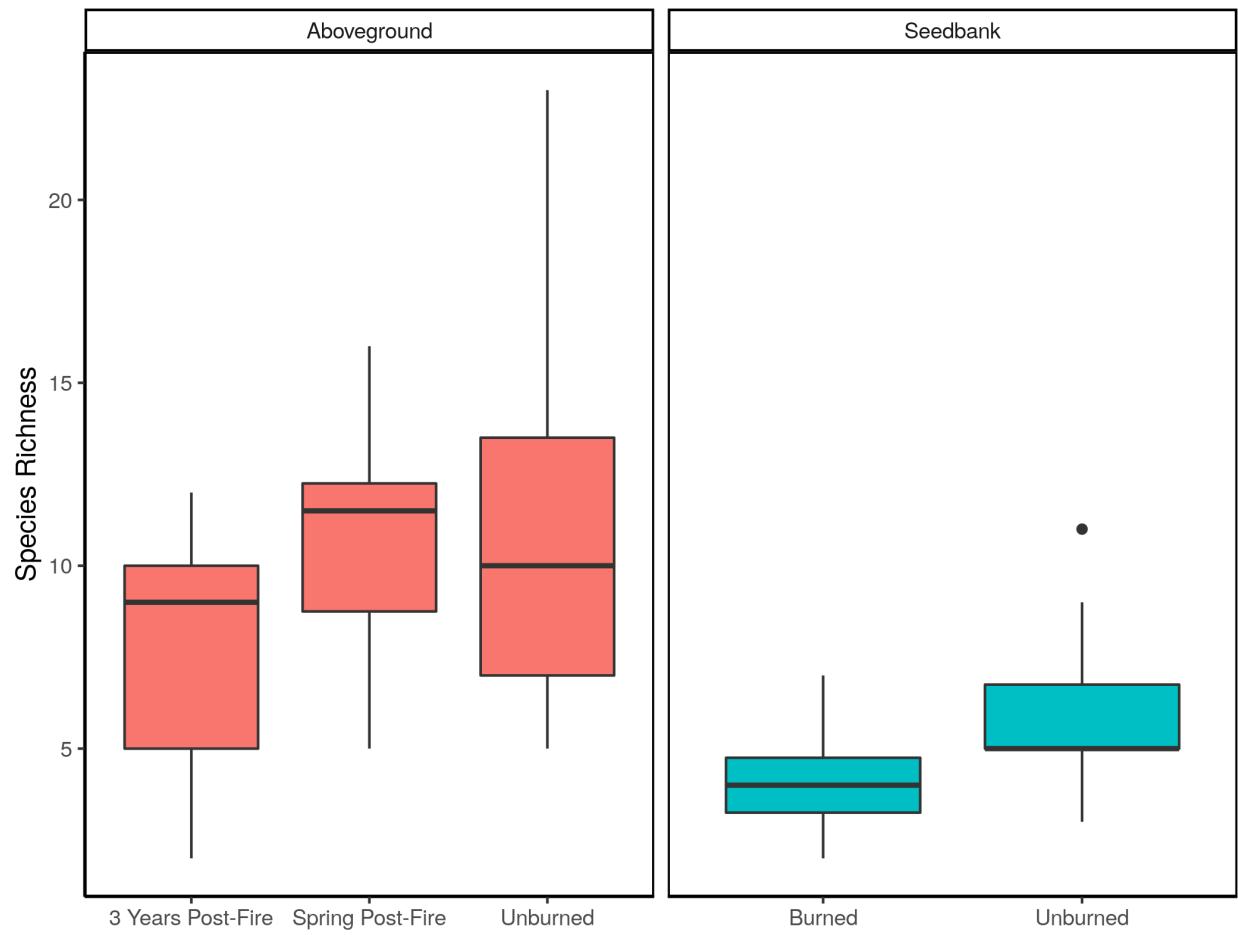


Figure S7: Species richness at different sampling times and locations.

Table S1. Vegetation indexes that were explored in the remote sensing analysis for hypothesis 1.

Index Name	Equation
Green NDVI	$\frac{NIR-Green}{NIR+Green}$
SAVI	$\frac{NIR-Red}{NIR+Red} + 1.5$
NDVI	$\frac{NIR-Red}{NIR+Red}$
EVI	$\frac{NIR-Red}{NIR+(6*Red)-(7.5*Blue)+1} * 2.5$
NDSVI	$\frac{SWIR_1-Red}{SWIR_1+Red}$
NDTI	$\frac{SWIR_1-SWIR_2}{SWIR_1+SWIR_2}$

Table S2: Model performance metrics.

Model	R2	R2_adjusted	Sign
H1: TVC ~ NDSVI + Green NDVI	0.35		+
H1: dNBR ~ TVC(modelled)	0.42	0.42	+
H1: dNBR ~ TVC(<i>in situ</i>)	0.27	0.20	+
H3: Post-Fire Fuel Connectivity ~ # Cheatgrass Seeds + covariates	0.84	0.75	+
H4: Post-Fire Diversity ~ Post-Fire Fuel Connectivity	0.92	0.89	-

Table S3: Seeds germinated in the greenhouse from the cores we collected.

Plot	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10	p11	p12	p13	p14
Burn Severity (dNBR)	195	307	300	226	266	143	211	191	99	181	238	248	272	304
<i>B. tectorum</i>														
U_T2	162	87	70	437	453	5	15	40	16	35	8	225	129	176
U_B4	73	32	25	49	68	2	6	6	4	6	0	30	19	59
B_T2	48	19	4	29	1	0	1	0	15	5	3	9	11	34
B_B4	10	5	1	4	5	0	1	0	3	0	0	0	6	8
<i>P. secunda</i>														
U_T2	17	3	1	71	6	65	502	212	175	546	143	116	141	66
U_B4	13	0	0	18	2	10	55	24	19	49	29	19	29	51
B_T2	11	0	0	2	1	3	21	0	37	32	5	28	8	63
B_B4	3	0	0	0	0	0	4	1	4	4	2	6	18	35
<i>A. tridentata</i>														
U_T2	1	0	0	0	0	0	1	2	0	0	0	1	7	0
U_B4	0	0	0	0	0	0	0	3	0	0	2	0	6	1
B_T2	1	0	2	0	0	0	1	1	0	0	0	0	9	5
B_B4	0	0	0	0	0	0	0	1	0	0	0	0	1	2
<i>A. desertorum</i>														
U_T2	0	0	0	0	0	0	0	59	1	0	0	5	0	0
U_B4	0	0	0	0	0	0	0	8	0	0	1	1	0	0
B_T2	7	0	0	0	0	1	0	0	0	0	0	1	0	0
B_B4	2	0	0	0	0	3	0	0	0	0	0	0	0	0
<i>C. testiculatum</i>														
U_T2	24	0	0	0	0	0	2	28	30	0	1	2	3	0
U_B4	23	0	0	0	0	0	1	12	0	0	0	0	0	0
B_T2	6	0	0	0	0	0	0	0	0	0	0	0	0	0
B_B4	4	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>C. parviflora</i>														
U_T2	0	0	0	0	0	6	10	0	0	3	0	0	1	0
U_B4	0	0	0	0	0	3	0	4	0	1	2	0	0	0
B_T2	0	0	0	0	0	0	2	0	0	3	0	0	0	0
B_B4	0	0	0	0	0	1	1	4	0	5	0	0	0	0
<i>S. altissimum</i>														
U_T2	0	20	23	0	0	0	0	1	0	1	0	0	0	1
U_B4	0	6	13	0	0	0	0	0	0	0	0	1	0	0
B_T2	0	1	14	1	0	0	0	0	0	0	0	0	0	15
B_B4	0	0	1	0	0	0	0	0	0	0	0	1	0	11
<i>M. gracilis</i>														
U_T2	0	0	0	1	0	1	0	0	0	0	0	0	0	0
U_B4	0	0	1	12	8	0	2	0	0	1	0	0	0	0
B_T2	0	0	0	0	0	0	0	0	0	2	0	0	0	0
B_B4	0	0	0	3	7	0	0	1	1	0	0	0	0	0
Other species														
All treatments	9	3	0	0	0	4	0	17	2	0	11	1	11	6

Note:

U = Unburned

B = Burned

T2 = Top 2 cm

B4 = Bottom 4 cm

Table S4: Covariance matrix for the path model.

x	Bromus_seeds_post	prefire_TVC	ag_div_pre	sb_div_pre	burn_sev	postfire_TVC	elv	Bromus_cv_pre
Bromus_seeds_post	0.000	0.006	0.035	0.002	0.019	0.016	-0.075	0.048
prefire_TVC	0.006	0.000	-0.040	-0.003	-0.025	-0.007	-0.005	-0.001
ag_div_pre	0.035	-0.040	0.000	0.000	0.005	-0.012	0.088	0.000
sb_div_pre	0.002	-0.003	0.000	0.000	0.000	0.028	-0.001	0.000
burn_sev	0.019	-0.025	0.005	0.000	0.000	-0.002	0.048	-0.002
postfire_TVC	0.016	-0.007	-0.012	0.028	-0.002	0.000	-0.036	0.046
elv	-0.075	-0.005	0.088	-0.001	0.048	-0.036	0.000	0.000
Bromus_cv_pre	0.048	-0.001	0.000	0.000	-0.002	0.046	0.000	0.000

Table S5: Path model fit measures.

measure	value
degrees of freedom	4.00
p-value	0.92
Chi-Square	0.93
Comparative Fit Index	1.00
Tucker-Lewis Index	1.47
Root Mean Square Error of Approximation	0.00
Standardized Root Mean Square Residual	0.03