

Running head: Burn severity and the grass fire cycle

Title: Mechanisms of the grass-fire cycle: high fuel connectivity from annual grass invasion increases burn severity, which alters seedbank composition leading higher fuel connectivity.

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## <sup>1</sup> Abstract

<sup>2</sup> The spread of introduced grasses and their effects on ecosystem structure and function,  
<sup>3</sup> especially when a novel grass-fire cycle is initiated, is a substantial threat to global biodiversity.  
<sup>4</sup> In sagebrush communities in the western United States, annual grass invasion increases the  
<sup>5</sup> connectivity of fine fuels, which increases the size and spatial contiguity of fires. This results  
<sup>6</sup> in post-fire plant communities that are dominated by introduced annual grasses (IAG). But  
<sup>7</sup> the mechanisms by which pre-fire invasion and fire occurrence are linked to higher post-fire  
<sup>8</sup> flammability are not fully understood.

<sup>9</sup> Here, we used total vegetation cover (TVC) as a proxy for fuel connectivity and found that  
<sup>10</sup> pre-fire TVC increased burn severity. We then used a Bayesian joint species distribution  
<sup>11</sup> model to examine how burn severity affected the proportion of IAG in the seed bank, and  
<sup>12</sup> found that higher burn severity had mostly positive or neutral effects on the occurrence of  
<sup>13</sup> IAG and other non-native species, and mostly negative or neutral relationships with native  
<sup>14</sup> species. To complete the positive feedback loop, we found that the abundance of IAG seeds  
<sup>15</sup> in the seedbank immediately post-fire had a positive effect on the fuel connectivity 3 years  
<sup>16</sup> after fire. This is the first study that we are aware of in the western US that shows how burn  
<sup>17</sup> severity influences seed bank species composition, as well as examining the full feedback loop  
<sup>18</sup> between fuel connectivity, burn severity and seed bank species composition. These results  
<sup>19</sup> provide measurable ecosystem structure components as well as fire characteristics that land  
<sup>20</sup> managers may be able to use to mitigate the effects of the grass-fire cycle.

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<sup>21</sup> *Keywords:* cheatgrass, sagebrush, grass-fire cycle, joint species distribution model, burn  
<sup>22</sup> severity, fuel connectivity, *Bromus tectorum*, *Artemisia tridentata*

<sup>23</sup> **1. Introduction**

<sup>24</sup> One of the consequences of global change in the 21<sup>st</sup> century that is most difficult to reverse  
<sup>25</sup> is when ecosystems abruptly shift from one stable species assemblage to another (Ratajczak  
<sup>26</sup> et al. 2018). In tropical ecosystems, three alternative stable states have been identified  
<sup>27</sup> along a gradient of precipitation: forests, savannas and grasslands (Hirota et al. 2011;  
<sup>28</sup> Staver, Archibald, and Levin 2011). These three states cluster around values of tree cover  
<sup>29</sup> (approximately 80, 30 and 0 percent) that occur among overlapping levels of precipitation,  
<sup>30</sup> and so it is thought that internal, self-reinforcing mechanisms maintain these alternate states  
<sup>31</sup> (Andersen et al. 2009). In the forested state there is a self-reinforcing positive feedback  
<sup>32</sup> between evapotranspiration and tree cover (Staal et al. 2020). In the grassland and savanna  
<sup>33</sup> states, there are feedbacks between grass flammability and fire occurrence (The grass-fire  
<sup>34</sup> cycle, D'Antonio and Vitousek 1992; Staver, Archibald, and Levin 2011).

<sup>35</sup> A classic example of a novel grass-fire cycle in a semi-arid, temperate system is the invasion  
<sup>36</sup> of *Bromus tectorum* L. and other introduced annual grasses in the Great Basin of the  
<sup>37</sup> western United States. Here, over half of Wyoming big sagebrush (*Artemisia tridentata* ssp.  
<sup>38</sup> *wyomingensis* Beetle & Young) ecosystems have been degraded, fragmented or lost completely  
<sup>39</sup> (Davies et al. 2011). This has been attributed to a host of causes, including wildfire (Balch et  
<sup>40</sup> al. 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of  
<sup>41</sup> annual grasses. At uninvaded sites, the space between shrubs is typically composed of bare  
<sup>42</sup> ground covered in biological soil crust and dotted with perennial bunch grasses. The lack of  
<sup>43</sup> fuel connectivity is believed to limit fire spread, with a historical fire regime of infrequent,  
<sup>44</sup> patchy fires (Baker 2006; Bukowski and Baker 2013; Keeley and Pausas 2019). Annual grass  
<sup>45</sup> invasion increases fuel connectivity while decreasing fuel moisture (Davies and Nafus 2013),  
<sup>46</sup> leading to increased fire size and frequency (Whisenant 1990; Knapp 1996; Balch et al. 2013).  
<sup>47</sup> After fire, the landscape is often dominated by introduced annual grasses and forbs. But in  
<sup>48</sup> order to understand how the grassland state persists, the mechanisms by which fire benefits

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

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

<sup>76</sup> affecting seed mortality, fire temperature can also alter physical seed dormancy thresholds  
<sup>77</sup> (Liyanage and Ooi 2017).

<sup>78</sup> Because *B. tectorum* is annual, in order for it to benefit from fire, which it clearly does (Balch  
<sup>79</sup> et al. 2013; Mahood and Balch 2019), it would need enough seeds in the post-fire landscape to  
<sup>80</sup> achieve a fitness benefit and become well-represented in the post-fire plant assemblage (Bond  
<sup>81</sup> and Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal, and  
<sup>82</sup> *B. tectorum* seeds have been shown to have increased dispersal distances after fire (Monty,  
<sup>83</sup> Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. There  
<sup>84</sup> is strong evidence that *B. tectorum* builds a well-stocked pool of seeds in the soil and litter,  
<sup>85</sup> even when it is not well represented in the above-ground plant assemblage (Young and Evans  
<sup>86</sup> 1975; Hassan and West 1986; Boudell, Link, and Johansen 2002). If the increase in fuel  
<sup>87</sup> connectivity caused by *B. tectorum* increases the severity of fire, it stands to reason that  
<sup>88</sup> burn severity would influence the community composition of the post-fire seed bank in a way  
<sup>89</sup> that facilitates the post-fire dominance of *B. tectorum*. To our knowledge, despite several  
<sup>90</sup> studies on the relationship between fire and the seed bank in this system (Young and Evans  
<sup>91</sup> 1975; Hassan and West 1986; Humphrey and Schupp 2001; Boudell, Link, and Johansen  
<sup>92</sup> 2002; Barga and Leger 2018), no studies to date have examined this potential effect of burn  
<sup>93</sup> severity on the seed bank.

<sup>94</sup> There is strong evidence that *B. tectorum* invasion alters the physical properties of fire,  
<sup>95</sup> including fire temperature (Brooks et al. 2004; Jones et al. 2015) and burn severity (defined  
<sup>96</sup> here as the proportion of biomass burned (Keeley 2009)). Burn severity can be measured  
<sup>97</sup> after fire *in situ*, or estimated from satellite images by comparing scenes from before and after  
<sup>98</sup> the fire (J. D. Miller et al. 2009). While in many cases fires that burn at higher temperatures  
<sup>99</sup> will also burn at higher severities, grass fires may not always have such a relationship. Direct  
<sup>100</sup> measurements have shown that *B. tectorum* burns at low temperatures (Beckstead et al.  
<sup>101</sup> 2011; Germino, Chambers, and Brown 2016). Because fire duration is inversely related to soil

heating, lower fire temperatures can be inferred from the commonly observed phenomenon that *B. tectorum*-fueled fires burn fast. Soil heating affects the response of vegetation to fire (Gagnon et al. 2015), including the capacity of the seeds of *B. tectorum* to remain viable after fire (Humphrey and Schupp 2001). Because *B. tectorum* also increases horizontal fuel connectivity (Davies and Nafus 2013), this leads to more contiguously burned areas with fewer unburned plants, and therefore higher burn severity, despite lower fire temperatures.

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

The Great Basin has not escaped the recent warming and drying trend that the western U.S. has experienced (Melillo, Richmond, and Yohe 2014; Bradford et al. 2020). This is expected

<sup>128</sup> to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly  
<sup>129</sup> by causing the plants to produce lighter seeds (Schlaepfer, Lauenroth, and Bradford 2014).

<sup>130</sup> With this in mind, there is another potential self-reinforcing mechanism that could serve to  
<sup>131</sup> maintain the high fuel connectivity state without fire. That is that the post-fire state with  
<sup>132</sup> high fuel connectivity is associated with two mechanisms for competitive exclusion of natives.

<sup>133</sup> First, it reduces soil moisture which is unfavorable for *Artemesia* seedlings (Turnbull et al.  
<sup>134</sup> 2012; Wilcox et al. 2012). Second, the dominant plant, *B. tectorum*, can out-compete native  
<sup>135</sup> plants for early spring moisture (Meyer 1994; Chambers et al. 2007).

<sup>136</sup> Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot  
<sup>137</sup> Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July  
<sup>138</sup> 2016. Because it burned a large area in only three days, we could sample a broad area  
<sup>139</sup> while being reasonably certain that the climatic conditions during the fire were the same  
<sup>140</sup> at all sites. Because we collected our samples immediately after the fire was extinguished,  
<sup>141</sup> we felt confident that the seed bank samples did not contain seeds deposited by post-fire  
<sup>142</sup> dispersal. We put the samples in cold storage and germinated the seeds from those cores in a  
<sup>143</sup> greenhouse the following spring. In spring 2017 and fall 2019 we collected information on  
<sup>144</sup> vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel  
<sup>145</sup> connectivity would be positively related to burn severity; (H2) burn severity would increase  
<sup>146</sup> the occurrence probability of introduced annual species in the seed bank and reduce the  
<sup>147</sup> occurrence probability of native species; (H2a) increased fuel connectivity brought on by  
<sup>148</sup> the invasion of annual grasses already depleted the diversity of the soil seed bank before the  
<sup>149</sup> fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related  
<sup>150</sup> to post-fire fuel connectivity. In addition, because in our study system sites with high fuel  
<sup>151</sup> connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high  
<sup>152</sup> post-fire fuel connectivity of those near-monocultures would result in lower aboveground  
<sup>153</sup> species diversity due to competitive pressure.

<sup>154</sup> **2. Methods**

<sup>155</sup> *2.1 Study Area*

<sup>156</sup> The study was conducted in north-central Nevada the day after a large fire (the Hot Pot  
<sup>157</sup> Fire) was extinguished (Figure 1). The Hot Pot Fire burned just over 50,000 hectares in  
<sup>158</sup> less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big  
<sup>159</sup> sagebrush plant communities. The fire occurred after the early season plants, including *B.*  
<sup>160</sup> *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone  
<sup>161</sup> to seed, and before the late season species, including Wyoming big sagebrush, had produced  
<sup>162</sup> flowers. Thus we were able to isolate the effect of the fire without any confounding effects of  
<sup>163</sup> post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged  
<sup>164</sup> from 1397 to 1607 meters in elevation.

<sup>165</sup> *2.2 Seed Bank Sampling*

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

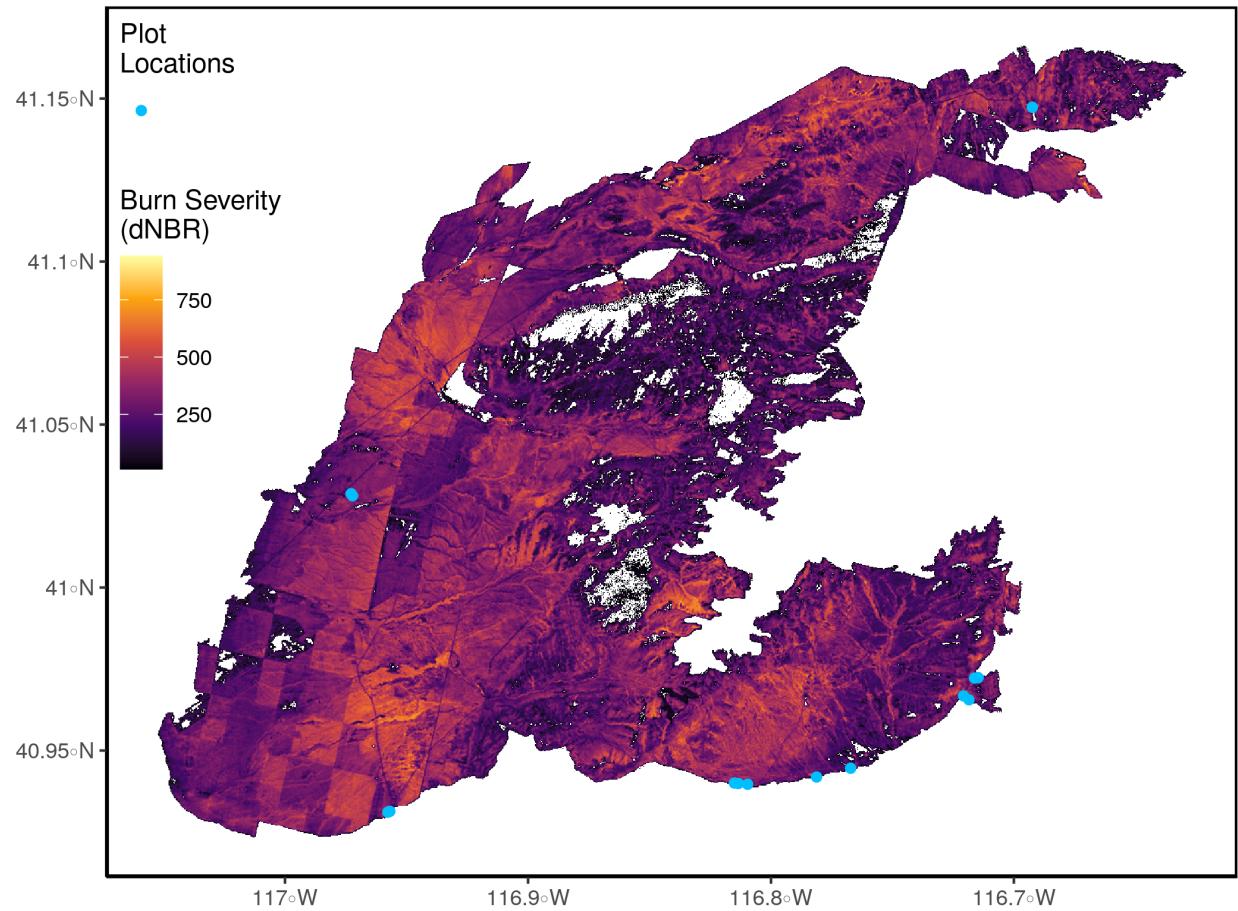


Figure 1: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

<sup>180</sup> a shrub or in the bare ground between shrubs, [Eckert et al. 1986](#)). To account for these  
<sup>181</sup> potentially confounding effects, we placed half of the core locations under shrubs, and half in  
<sup>182</sup> shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even  
<sup>183</sup> when they were completely incinerated, their imprint remained on the soil surface ([Bechtold](#)  
<sup>184</sup> and [Inouye 2007](#); [Germino et al. 2018](#)). To examine the effect of seed depth, we divided each  
<sup>185</sup> soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples.  
<sup>186</sup> Samples were then placed in cold storage (~2 deg C) for 3 months ([Meyer, Monsen, and](#)  
<sup>187</sup> [McArthur 2013](#)).

<sup>188</sup> At all sites, to be sure that we were at a site where sagebrush germination could occur we  
<sup>189</sup> checked for first year germinants on the unburned side (we found them at all sites), and  
<sup>190</sup> to ensure that there were no confounding effects of post-fire seed dispersal, we determined  
<sup>191</sup> whether or not the sagebrush were flowering (they were not flowering at all sites), and recorded  
<sup>192</sup> species occupancy for all aboveground plant species.

### <sup>193</sup> *2.3 Greenhouse Germination*

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

### <sup>200</sup> *2.4 Post-Fire Vegetation Sampling*

<sup>201</sup> We sampled the vegetative occupancy and cover in May 2017, the growing season immediately  
<sup>202</sup> after the fire and again in September 2019. At each location, we established 50m transects  
<sup>203</sup> starting at the boundary of the burned and unburned sides of the perimeter, running  
<sup>204</sup> perpendicular to the fire perimeter, and marked the transect ends with rebar. We measured  
<sup>205</sup> the occupancy and abundance of all plant species by measuring cover of every species in

206 0.1 m<sup>2</sup> quadrats spaced every 5 m along each transect. We used the line intercept method  
207 to measure shrub cover and herbaceous plant cover along the transect. Both live and dead  
208 plants were included in these measurements. Total vegetation cover (TVC) was defined as  
209 the sum of herbaceous plant cover and shrub cover.

210 *2.5 Estimating Burn Severity with Landsat 8 OLI*

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

219 *2.6 Statistical Analysis*

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

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

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

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

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

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

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

To account for the possibility of H2a as a confounding factor, we included the Shannon-Weaver diversity index (Shannon and Weaver 1949) in the paired, unburned seed bank samples as one of the predictor variables in our JSDM. We also created OLS models with the unburned species richness and Shannon-Weaver diversity index predicted by prefire fuel connectivity, with the expectation that pre-fire fuel connectivity would have had a negative effect on the prefire seedbank diversity.

To examine how community composition and burn severity then affected subsequent fuel connectivity (H3), we created OLS models with fuel connectivity three years post-fire as the dependent variable, and burn severity, seed counts for *B. tectorum*, *P. secunda* and other species, elevation, aspect, depth, and alpha diversity as independent variables.

To examine how the resulting fuel connectivity was related to biodiversity (H4), we used the diversity data and connectivity data that we collected in 2019 to create a Poisson GLM with number of species encountered aboveground at each plot location as the dependent variable, as well as an OLS linear model with the Shannon-Weaver index (Shannon and Weaver 1949) as a dependent variable. We used fuel connectivity, elevation, and aspect as independent variables.

All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis is freely available on Figshare (link here after acceptance) and GitHub (<https://www.github.com/admahood/seed-bank>).

<sup>282</sup> **3. Results**

<sup>283</sup> We found support for each hypothesized component of the positive feedback loop. For H1,  
<sup>284</sup> the most parsimonious model for our *in situ* observations had only TVC as the predictor,  
<sup>285</sup> which had a weak positive relationship with burn severity ( $\beta = 2.4$ ,  $p = 0.083$ ,  $R^2 = 0.27$ ,  
<sup>286</sup> Figure 2a, Table S3). For our remotely sensed analysis, our most parsimonious model of  
<sup>287</sup> TVC explained 35% of the variation and had Green NDVI, NDSVI and their interaction as  
<sup>288</sup> predictors (Table S3). Our model of dNBR using the predicted TVC within the fire perimeter  
<sup>289</sup> as a predictor of dNBR explained 42% of the variation and the relationship between TVC  
<sup>290</sup> and burn severity was positive and significant ( $p \ll 0.01$ , Figure 2a, Table S3).

<sup>291</sup> The vast majority of seeds that germinated in the greenhouse were the two most common  
<sup>292</sup> grass species, *P. secunda* and *B. tectorum* (Table S2). Eight forb species were found in more  
<sup>293</sup> than one location, and these 10 prevalent species are those that were used in our JSDM.  
<sup>294</sup> Burned plots had an average of  $34 \pm 32$  total seeds in the top 2 cm, and  $12 \pm 14$  in the  
<sup>295</sup> bottom 4 cm. Unburned plots had an average of  $299 \pm 170$  in the top 2 cm and  $59 \pm 29$   
<sup>296</sup> in the bottom 4 cm (Figure S1). For H2, the JSDM converged well (Gelman diagnostics  
<sup>297</sup> all very close to 1 and the effective sample size centered on 4,000, Figure S2a). Elevation  
<sup>298</sup> had the most significant effects on individual species (Figure S2b) and explained the most  
<sup>299</sup> variance on average (36% Figure S2c). Burn severity explained 23% of the variance on  
<sup>300</sup> average and was supported at the 95% level for 5 species (Figure S2b). For the introduced  
<sup>301</sup> species, the predictions along a gradient of burn severity were positive for *B. tectorum*,  
<sup>302</sup> *Sisymbrium altissimum* L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala*  
<sup>303</sup> *testiculata* and *Alyssum desertorum* Stapf (Figure 2b). For native species, the effect of burn  
<sup>304</sup> severity on occurrence was positive for *A. tridentata*, neutral for *P. secunda* and negative  
<sup>305</sup> for the remaining species (Figure 2b). Testing H2a revealed a positive relationship between  
<sup>306</sup> pre-fire aboveground species diversity and pre-fire fuel connectivity, and so we felt it was  
<sup>307</sup> reasonable to rule out pre-fire fuel connectivity as a confounding factor for H2.

<sup>308</sup> For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and  
<sup>309</sup> the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the postfire seedbank  
<sup>310</sup> was positively associated with the fuel connectivity in 2019 ( $\beta = 0.54$ ,  $p = 0.01$ , Adj  $R^2 =$   
<sup>311</sup> 0.75, Figure 3c, Table S3).

<sup>312</sup> For H4 the most parsimonious model (Adj  $R^2 = 0.89$ , Table S3) had elevation, aspect, fuel  
<sup>313</sup> connectivity and an interaction between elevation and fuel connectivity as predictors of  
<sup>314</sup> aboveground Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated  
<sup>315</sup> with Shannon-Weaver diversity ( $\beta = -0.28$ ,  $p=0.004$ , Figure 3d).

## <sup>316</sup> 4. Discussion

<sup>317</sup> In order to truly consider an annual grass-fire cycle to be maintained by self-reinforcing  
<sup>318</sup> feedbacks, the mechanisms by which fire occurrence is linked to higher post-fire flammability  
<sup>319</sup> must be understood. In this study we found evidence that interaction between burn severity  
<sup>320</sup> and seed bank composition may explain that link. Prior work has shown that annual grass  
<sup>321</sup> invasion increases fuel connectivity in western US sagebrush ecosystems by filling in shrub  
<sup>322</sup> interspaces with a contiguous bed of fine fuels (Davies and Nafus 2013). This change in  
<sup>323</sup> the spatial distribution of fine fuels has been associated with larger and more frequent fires  
<sup>324</sup> (Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) increases burn  
<sup>325</sup> severity (H1, Figure 2a). Higher burn severity was associated with an increased occurrence of  
<sup>326</sup> introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure  
<sup>327</sup> 2b). Higher abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher  
<sup>328</sup> post-fire fuel connectivity (H3, Figure 2c). In addition, we found evidence that high post-fire  
<sup>329</sup> fuel connectivity was associated with lower aboveground diversity (H4, Figure 2d). This  
<sup>330</sup> suggests that during inter-fire intervals, there are additional mechanisms maintaining the  
<sup>331</sup> post-fire species assemblage that is dominated by annual introduced plants.

<sup>332</sup> The difference in species composition before and after fire explains an apparent contradiction

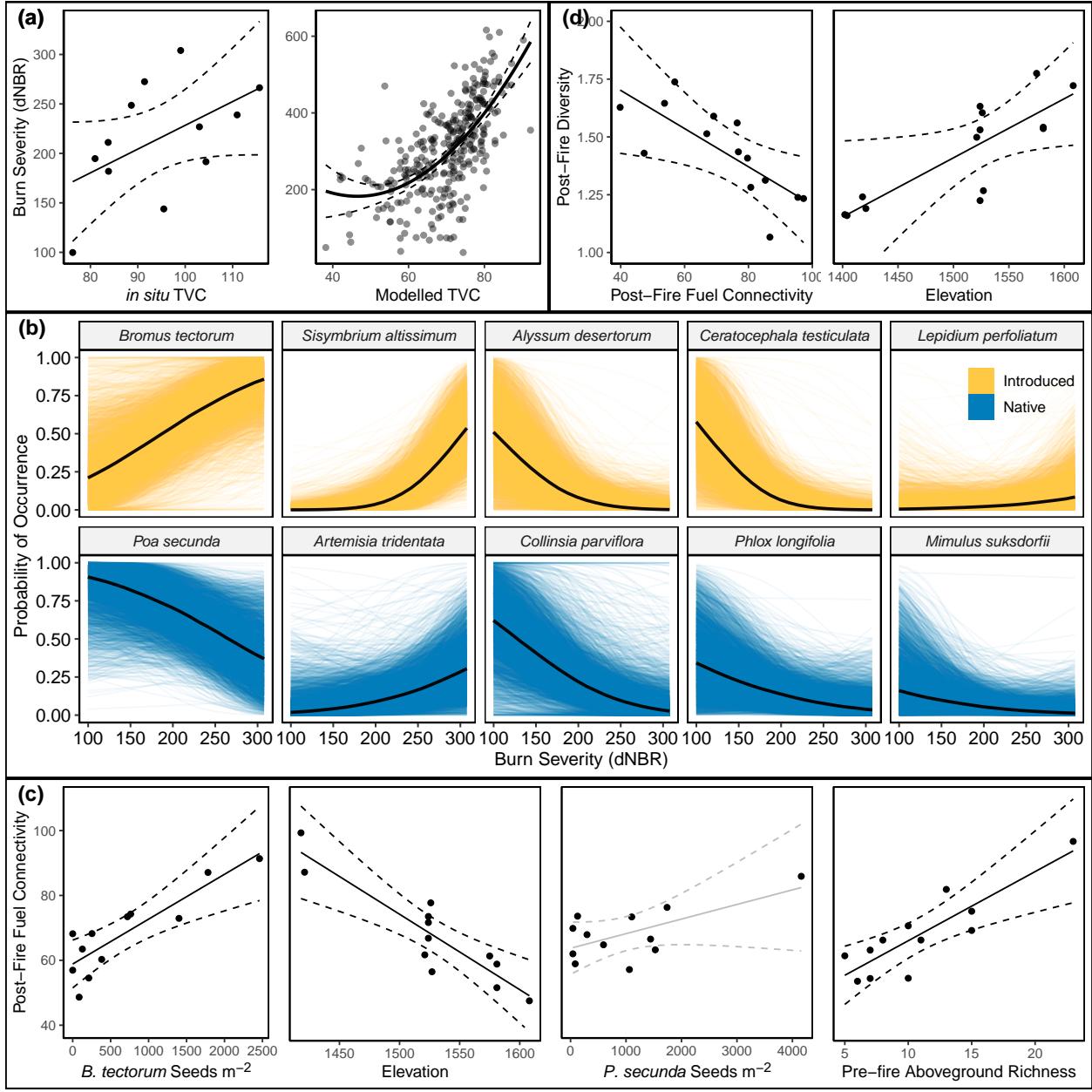


Figure 2: On the left side of (a), burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Panel b shows the modelled occurrence of germinable seeds for all species found at more than one location along a gradient of burn severity, after accounting for soil depth, aspect, elevation and pre-fire diversity. Black line is the mean prediction, each colored line represents one posterior sample. In (c), fuel connectivity three years post-fire is modelled by seedbank composition, elevation and pre-fire aboveground species richness. In (d) shannon-Weaver diversity index of the aboveground, post-fire community composition, was negatively affected by fuel connectivity after accounting for elevation. For a, c and d, lines are the fitted partial effects, points are the partial residuals, and dotted lines are the 95% confidence intervals.  $p < 0.05$  for black lines,  $p > 0.05$  for grey lines

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

352 *Global impacts*

353 The grass-fire cycle in the western US is reinforced through providing fitness benefits to  
354 the introduced annual grasses and forbs via at least 4 redundant processes: i) changing the  
355 composition of the seedbank, ii) competitive exclusion of native plants, iii) CO<sub>2</sub> enrichment  
356 which may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of  
357 annual grass species ([Nagel et al. 2004; Smith et al. 2000](#)), strengthening the fuel connectivity  
358 to burn severity to seed composition feedback loop, and iv) ecohydrological feedbacks that

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

### 373 *Potential limitations*

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

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

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

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

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

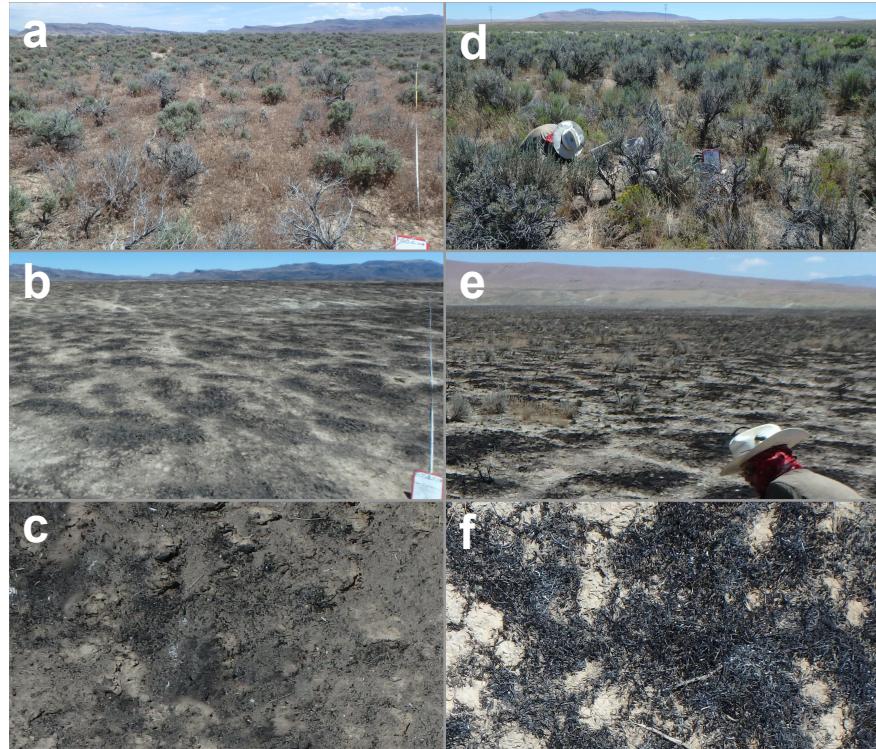


Figure 3: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space being highly invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, and approximately all of the biomass was consumed by the fire. Panel C is a closeup of the soil surface, showing in more detail how the litter was also almost completely consumed by the fire. On the right, the photos in panels d and e were on opposite sides of a fire line in an area that had minimal annual grass invasion over a broad area, and thus lower fuel connectivity. Note the remaining plants and stumps in panel e and the presence of only partially consumed litter in panel f.

#### 416 *Management implications*

417 These results provide measurable fire properties and ecosystem structural components that  
418 compose the self-reinforcing feedback. This information may be useful for land managers  
419 for identifying new methods for breaking these feedbacks, in order to increase the likelihood  
420 for successful restoration. Greenhouse or *in situ* germination assays are time-consuming and

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

427 This work provides further evidence that the post-fire annual grassland is a system where  
428 the degraded state represents an alternative species assemblage from that of the restoration  
429 target. Because the propagules of the original assemblage are no longer present, methods  
430 that rely on natural succession may not be sufficient ([Suding, Gross, and Houseman 2004](#)).  
431 Our results highlight the importance of prioritizing the preservation of native shrub cover  
432 and in particular policies that encourage land managers to maximize the preservation of  
433 unburned patches during the suppression of wildfires in this system ([Steenvoorden et al.](#)  
434 [2019](#)). Commonly encountered native plants and the keystone shrub species *A. tridentata*  
435 depend on post-fire seed dispersal from surviving individuals in unburned patches ([Schlaepfer,](#)  
436 [Lauenroth, and Bradford 2014](#)). Once the system achieves a canopy dominated by annual  
437 grasses and forbs, the competitive pressure from the annual grass monoculture makes it more  
438 difficult if not impossible for perennial native forbs and shrubs to establish from the depleted  
439 seedbank. Post-fire seeding efforts may restore native propagules, but if there is dense cover  
440 of annuals further effort may be required to reduce fuel connectivity in order to reduce both  
441 fire risk and competitive pressure from annuals. Our results also suggest that calculating the  
442 burn severity using remote sensing may help land managers identify areas that may have  
443 a greater likelihood of successful seeding.

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) ([Chambers et al. 2014; Condon and Pyke 2018](#)),

447 and can reduce the survival of *Artemisia* seedlings that are not protected by shrub canopies  
448 (Owens and Norton 1992). In wet years, targeted grazing at already invaded sagebrush sites  
449 may reduce fuel connectivity and alleviate fire risk. Plant community composition in the  
450 years immediately after fire may be highly variable spatially and from year to year. Post-fire  
451 grazing may help reduce *B. tectorum* cover, but it may also exacerbate the problem by  
452 introducing cheatgrass in uninvaded sites (Williamson et al. 2019) or increasing the already  
453 superior postfire dispersal of *B. tectorum* seeds (Monty, Brown, and Johnston 2013). We  
454 suggest management approaches that are specifically tailored each year to the conditions of a  
455 given site, and targeting grazing only in already invaded areas to reduce *B. tectorum* cover  
456 where it may aid in native plant restoration.

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