

Running head: Annual grasses, burn severity, seedbank

Title: High fuel connectivity from annual grass invasion increases burn severity, which alters seedbank composition to favor annual grass invasion.

Adam L. Mahood<sup>1,2,\*</sup>, Michael J. Koontz<sup>2</sup>, Jennifer K. Balch<sup>1,2</sup>

<sup>1</sup> Department of Geography, University of Colorado Boulder, Boulder, CO, USA

<sup>2</sup> Earth Lab, University of Colorado, Boulder, CO, USA

\* Corresponding author: admahood@gmail.com

<sup>1</sup> **Abstract**

<sup>2</sup> Alternative stable states are an important topic in the context of global change in which  
<sup>3</sup> positive feedbacks maintain two distinct plant communities under the same climatic conditions.  
<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> it is unclear exactly how fire directly benefits the IAG. Here, we used total vegetation cover  
<sup>8</sup> (TVC) as a proxy for fuel connectivity and found that pre-fire TVC increased burn severity.  
<sup>9</sup> We then used a joint species distribution model to examine how burn severity affected the  
<sup>10</sup> proportion of IAG in the seed bank, and found that higher burn severity had mostly positive  
<sup>11</sup> or neutral effects on the occurrence of IAG and other non-native species, and mostly negative  
<sup>12</sup> or neutral relationships with native species. To complete the positive feedback loop, we found  
<sup>13</sup> that the abundance of IAG seeds in the seedbank immediately post-fire had a positive effect  
<sup>14</sup> on the fuel connectivity 3 years after fire. This is the first study that we are aware of in the  
<sup>15</sup> western US that shows how burn severity influences seed bank species composition, as well  
<sup>16</sup> as examining the full feedback loop between fuel connectivity, burn severity and seed bank  
<sup>17</sup> species composition.

<sup>18</sup> **1. Introduction**

<sup>19</sup> One of the consequences of global change in the 21<sup>st</sup> century that is most difficult to reverse  
<sup>20</sup> is when ecosystems abruptly shift from one stable species assemblage to another (Ratajczak  
<sup>21</sup> et al. 2018). In tropical ecosystems, three alternative stable states have been identified  
<sup>22</sup> along a gradient of precipitation: forests, savannas and grasslands (Hirota et al. 2011;  
<sup>23</sup> Staver, Archibald, and Levin 2011). These three states cluster around values of tree cover  
<sup>24</sup> (approximately 80, 30 and 0 percent) that occur among overlapping levels of precipitation,  
<sup>25</sup> and so it is thought that they exhibit states of hysteresis in which internal, self-reinforcing  
<sup>26</sup> mechanisms maintain alternate states (Andersen et al. 2009). In the forested state there is

<sup>27</sup> a self-reinforcing positive feedback between evapotranspiration and tree cover (Staal et al.  
<sup>28</sup> 2020). In the grassland and savanna states, there are feedbacks between grass flammability  
<sup>29</sup> and fire occurrence (Staver, Archibald, and Levin 2011; D'Antonio and Vitousek 1992).

<sup>30</sup> A classic example of hysteresis in a semi-arid, temperate system is the invasion of *Bromus*  
<sup>31</sup> *tectorum* L. and other introduced annual grasses in the Great Basin of the western United  
<sup>32</sup> States. Here, over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*  
<sup>33</sup> Beetle & Young) ecosystems have been degraded, fragmented or lost completely (Davies  
<sup>34</sup> et al. 2011). This has been attributed to a host of causes, including wildfire (Balch et al.  
<sup>35</sup> 2013), grazing (Williamson et al. 2019), land use/land cover change, and the invasion of  
<sup>36</sup> annual grasses. In this open shrubland, the space between shrubs is primarily composed of  
<sup>37</sup> bare ground covered in biological soil crust, dotted with perennial bunch grasses. The lack  
<sup>38</sup> of fuel connectivity is believed to have limited fire spread, with a fire regime of infrequent,  
<sup>39</sup> patchy fires (Keeley and Pausas 2019). Annual grass invasion increases fuel connectivity  
<sup>40</sup> while decreasing fuel moisture (Davies and Nafus 2013), leading to increased fire size and  
<sup>41</sup> frequency (Whisenant 1990; Knapp 1996; Balch et al. 2013). After fire, the landscape is often  
<sup>42</sup> dominated by introduced annual grasses and forbs. This causes a >50% loss of aboveground  
<sup>43</sup> carbon storage (Bradley et al. 2006; Nagy et al. 2020). But in order to understand how  
<sup>44</sup> the grassland state persists, the mechanisms by which fire benefits the introduced annual  
<sup>45</sup> grass must be understood. Petraitis and Latham (1999) posited that the maintenance of  
<sup>46</sup> alternate species assemblages requires first a disturbance that removes the species from the  
<sup>47</sup> initial assemblage and second the arrival of the species of the alternate assemblage. One  
<sup>48</sup> understudied mechanism that may explain both is the interaction between burn severity and  
<sup>49</sup> the species composition of the soil seed bank.

<sup>50</sup> Studies that directly examine the relationship between the species composition of the seed  
<sup>51</sup> bank and fire severity and/or intensity are uncommon, but more attention has been given to  
<sup>52</sup> the subject recently. In boreal forests, the depth of the burn may be more important more

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

74 Because *B. tectorum* is annual, in order for it to benefit from fire, which it clearly does  
75 (Balch et al. 2013; Mahood and Balch 2019), it would have to have enough seeds in the  
76 post-fire landscape to achieve a fitness benefit and become well-represented in the post-fire  
77 plant assemblage (Bond and Midgley 1995). If the fire is patchy, this can happen through  
78 post-fire seed dispersal, and *B. tectorum* seeds have been shown to have increased dispersal  
79 distances after fire (Monty, Brown, and Johnston 2013). Without unburned patches, seeds

80 must survive the fire. There is strong evidence that *B. tectorum* builds a well-stocked pool of  
81 seeds in the soil and litter, even when it is not well represented in the above-ground plant  
82 assemblage (Young and Evans 1975; Hassan and West 1986; Boudell, Link, and Johansen  
83 2002). If the increase in fuel connectivity caused by *B. tectorum* increases the severity of  
84 fire, it stands to reason that burn severity would influence the community composition of  
85 the post-fire seed bank in a way that facilitates the post-fire dominance of *B. tectorum*. To  
86 our knowledge, despite several studies on the relationship between fire and the seed bank in  
87 this system (Young and Evans 1975; Hassan and West 1986; Humphrey and Schupp 2001;  
88 Boudell, Link, and Johansen 2002; Barga and Leger 2018), no studies to date have examined  
89 this potential effect of burn severity on the seed bank.

90 There is strong evidence that *B. tectorum* invasion alters the physical properties of fire,  
91 including fire temperature (Jones et al. 2015; Brooks et al. 2004) and burn severity (the  
92 proportion of biomass burned (Keeley 2009; J. D. Miller et al. 2009)). Direct measurements  
93 have shown low temperature (Beckstead et al. 2011; Germino, Chambers, and Brown 2016),  
94 and lower fire temperatures can be inferred from the commonly observed phenomenon that *B.*  
95 *tectorum*-fueled fires burn fast. Fire duration is inversely related to soil heating and therefore  
96 affects the response of vegetation to fire (Gagnon et al. 2015), including the capacity of  
97 the seeds of *B. tectorum* to remain viable after fire (Humphrey and Schupp 2001). Because  
98 *B. tectorum* increases horizontal fuel connectivity (Davies and Nafus 2013), this leads to  
99 more contiguously burned areas with fewer unburned plants, and therefore higher burn  
100 severity—even with lower fire temperatures. The fire featured in this study is a perfect  
101 example. It burned about 50,000 hectares in less than a week.

102 If increased burn severity is a mechanism by which *B. tectorum* excludes native plants in  
103 sagebrush shrublands, then an area with high burn severity may have a lower occurrence of  
104 viable seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced  
105 annual plants. This would lead to the dominance of introduced annual grasses and forbs

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 successfully tolerating drought and opportunistically devoting its resources to producing big seed crops in wet years (Meyer 1994; Perryman et al. 2001). When it burns it burns with high intensity, individual plants do not survive or resprout vegetatively, 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 retain some viability for at least 24 months 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 (Bradford et al. 2020). This is expected to affect *A. tridentata* directly by decreasing germination and seedling survival, and indirectly by causing the plants to produce lighter seeds (Schlaepfer, Lauenroth, and Bradford 2014). With this in mind, there is another potential self-reinforcing mechanism that could serve to maintain the high fuel connectivity state without fire. That is that the post-fire state with high fuel connectivity is associated with two mechanisms for competitive exclusion of natives. First, it reduces soil moisture which is unfavorable for *Artemisia* seedlings (Turnbull et al. 2012; Wilcox et al. 2012), and second the dominant plant, *B. tectorum*, can out-compete native plants for early spring moisture (Meyer 1994; Chambers et al. 2007).

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

<sup>132</sup> 2016. Because it burned a large area in only three days, we could sample a broad area  
<sup>133</sup> while being reasonably certain that the climatic conditions during the fire were the same  
<sup>134</sup> at all sites. Because we collected our samples immediately after the fire was extinguished,  
<sup>135</sup> we felt confident that the seed bank samples did not contain seeds deposited by post-fire  
<sup>136</sup> dispersal. We put the samples in cold storage and germinated the seeds from those cores in a  
<sup>137</sup> greenhouse the following spring. In spring 2017 and fall 2019 we collected information on  
<sup>138</sup> vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel  
<sup>139</sup> connectivity would be positively related to burn severity; (H2) burn severity would increase  
<sup>140</sup> the occurrence probability of introduced annual species in the seed bank and reduce the  
<sup>141</sup> occurrence probability of native species; (H2a) increased fuel connectivity brought on by  
<sup>142</sup> the invasion of annual grasses already depleted the diversity of the soil seed bank before the  
<sup>143</sup> fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds would be positively related  
<sup>144</sup> to post-fire fuel connectivity. In addition, because in our study system sites with high fuel  
<sup>145</sup> connectivity are often near monocultures of *B. tectorum*, we hypothesized that (H4) high  
<sup>146</sup> post-fire fuel connectivity of those near-monocultures would result in lower aboveground  
<sup>147</sup> species diversity due to competitive pressure.

## <sup>148</sup> 2. Methods

### <sup>149</sup> 2.1 Study Area

<sup>150</sup> The study was conducted in north-central Nevada the day after a large fire (the Hot Pot  
<sup>151</sup> Fire) was extinguished (Figure 1). The Hot Pot Fire burned just over 50,000 hectares in  
<sup>152</sup> less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big  
<sup>153</sup> sagebrush plant communities. The fire occurred after the early season plants, including *B.*  
<sup>154</sup> *tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone  
<sup>155</sup> to seed, and before the late season species, including Wyoming big sagebrush, had produced  
<sup>156</sup> flowers. Thus we were able to isolate the effect of the fire without any confounding effects of  
<sup>157</sup> post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged

<sub>158</sub> from 1397 to 1607 meters in elevation.

<sub>159</sub> *2.2 Seed Bank Sampling*

<sub>160</sub> In early July 2016, we collected samples of the soil seed bank at fourteen locations immediately  
<sub>161</sub> after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where  
<sub>162</sub> it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites  
<sub>163</sub> were mature sagebrush communities with no history of fire since at least 1984. Three plots  
<sub>164</sub> had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS)  
<sub>165</sub> fire history (Eidenshink et al. 2007) and had high cover of *B. tectorum*, but still had scattered  
<sub>166</sub> sagebrush cover. We used a metal stake to mark paired burned and unburned sampling  
<sub>167</sub> locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic  
<sub>168</sub> disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the  
<sub>169</sub> perimeter. Within 3 m of each marker, we extracted 12, 6 cm deep, 5 cm diameter, soil cores.  
<sub>170</sub> Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system  
<sub>171</sub> (Shinneman and McIlroy 2016), and so they are not uniformly distributed (Boudell, Link, and  
<sub>172</sub> Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemisia*  
<sub>173</sub> have different germination rates based on the micro-site they find themselves in (i.e. under  
<sub>174</sub> a shrub or in the bare ground between shrubs, Eckert et al. 1986). To account for these  
<sub>175</sub> potentially confounding effects, we placed half of the core locations under shrubs, and half in  
<sub>176</sub> shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even  
<sub>177</sub> when they were completely incinerated, their imprint remained on the soil surface (Bechtold  
<sub>178</sub> and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each  
<sub>179</sub> soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples.  
<sub>180</sub> Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and  
<sub>181</sub> Mcarthur 2013).  
  
<sub>182</sub> At all sites, to be sure that we were at a site where sagebrush germination could occur we  
<sub>183</sub> checked for first year germinants (we found them at all sites), and to ensure that there were

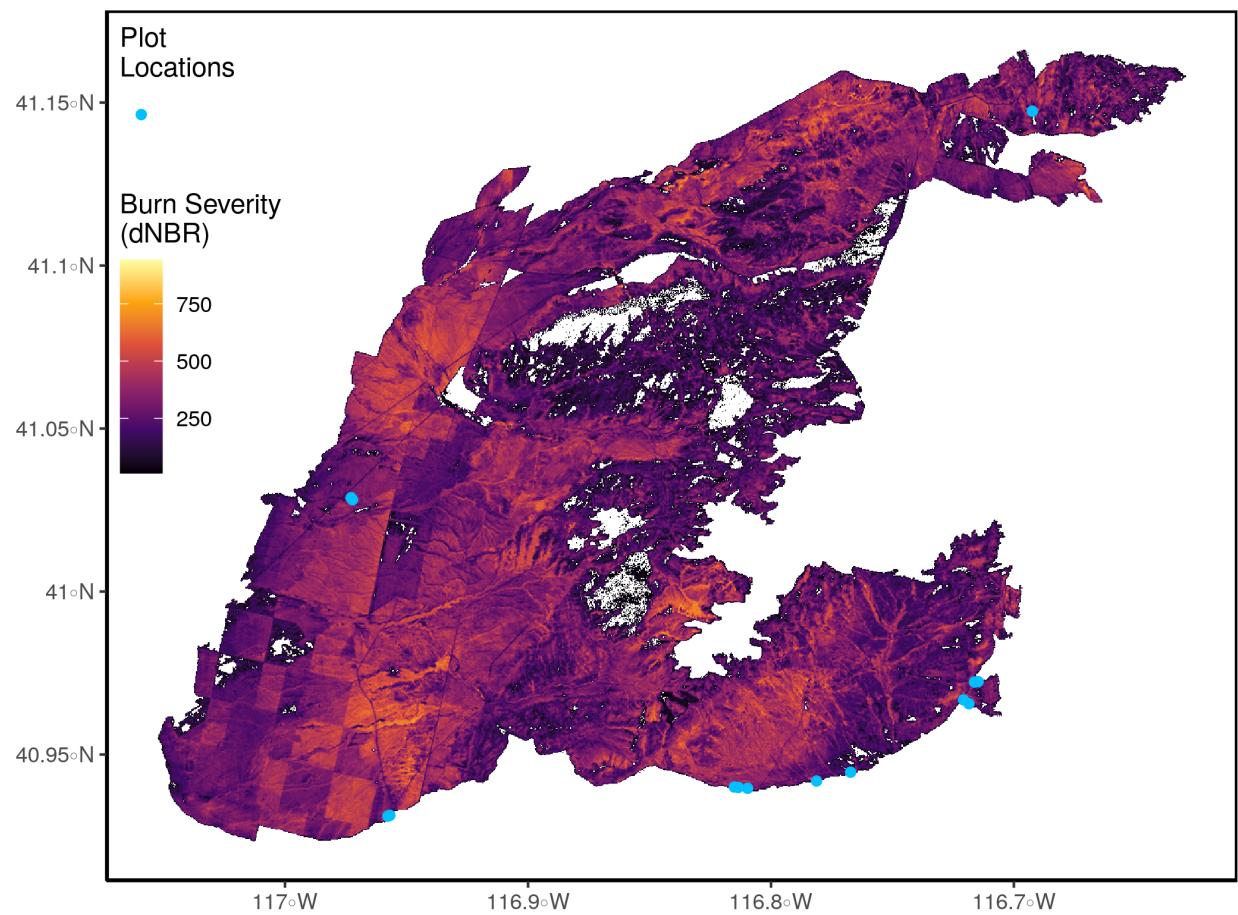


Figure 1: The 2016 Hot Pot Fire. Blue points represent sampling locations and the shaded color is the burn severity. The checkerboard pattern on the lower left corresponds to patterns of land ownership.

<sup>184</sup> no confounding effects of post-fire seed dispersal, we determined whether or not the sagebrush  
<sup>185</sup> were flowering (they were not flowering at all sites), and recorded species occupancy for all  
<sup>186</sup> plant species.

<sup>187</sup> *2.3 Greenhouse Germination*

<sup>188</sup> We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample  
<sup>189</sup> was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots.  
<sup>190</sup> These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were  
<sup>191</sup> watered as needed to stay at field capacity. Every week emerging germinants were identified,  
<sup>192</sup> counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks  
<sup>193</sup> we ended the germination assay.

<sup>194</sup> *2.4 Post-Fire Vegetation Sampling*

<sup>195</sup> In order to understand how the seed bank composition compares to the realized vegetative  
<sup>196</sup> composition, we sampled the vegetative occupancy and cover in May 2017, the growing  
<sup>197</sup> season immediately after the fire and again in September 2019. In 2017, at each location, we  
<sup>198</sup> established 50m transects starting at the boundary of the burned and unburned sides of the  
<sup>199</sup> perimeter, running perpendicular to the fire perimeter, and marked the transect ends with  
<sup>200</sup> rebar. We measured the occupancy and abundance of all plant species by measuring cover  
<sup>201</sup> of every species in 0.1 m<sup>2</sup> quadrats spaced every 5 m along each transect. We used the line  
<sup>202</sup> intercept method to measure shrub cover and herbaceous plant cover along the transect. Both  
<sup>203</sup> live and dead plants were included in these measurements. Total vegetation cover (TVC)  
<sup>204</sup> was defined as the sum of herbaceous plant cover and shrub cover. In order to assess if sites  
<sup>205</sup> had the potential for sagebrush regeneration immediately post-fire, we counted all first-year  
<sup>206</sup> germinants within 50 cm of the transect, which we defined as any sagebrush individual less  
<sup>207</sup> than 20 cm in height. In September 2019 we resampled the burned transects for occupancy  
<sup>208</sup> and abundance of all plant species, as well as shrub and fine fuel cover.

<sup>209</sup> *2.5 Estimating Burn Severity with Landsat 8 OLI*

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

217 *2.6 Statistical Analysis*

218 Our statistical analysis centered around trying to understand each component of the positive  
219 feedback loop posited by the 4 hypotheses described above. In order to understand how  
220 pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC)  
221 from two separate data sources as a proxy for fuel connectivity, and created separate linear  
222 models with TVC as the predictor variable and burn severity (dNBR, J. D. Miller et al.  
223 2009) as the response variable. With the field data we collected, we created an ordinary least  
224 squares (OLS) linear model with burn severity as the dependent variable and TVC (defined as  
225 shrub cover plus herbaceous plant cover from the unburned side of the paired plots), elevation  
226 and aspect as independent variables. We were concerned that because our data were collected  
227 at the edge of the fire, the burn severity calculated at each point may have been from only  
228 partially burned pixels. So, as a supplement, we examined the relationship using Landsat  
229 Thematic Mapper (TM) data and TVC from the Bureau of Land Management’s Assessment,  
230 Inventory and Monitoring dataset (AIM, U.S. Department of Interior 2018) to represent fuel  
231 connectivity. The AIM dataset contained 813 sampling locations within the Central Basin  
232 and Range ecoregion (Commission for Environmental Cooperation 2006) that were visited by  
233 BLM field crews between 2011 and 2015. They were mostly sampled once but there were  
234 some repeats, for 1,117 total measurements. For each of these points, we extracted the values  
235 of each Landsat band for the sampling year near peak biomass using a cloud-free scene from

<sup>236</sup> May or early June. Then, we used those band values to calculate various vegetation indexes  
<sup>237</sup> (Table S2), including the Green Normalized Differentiated Vegetation Index (Green NDVI,  
<sup>238</sup> Equation 1), and Normalized Differentiated Senesced Vegetation Index (NDSVI, Equation 2).  
<sup>239</sup> We used these indexes to create a beta regression model of TVC, starting with the largest  
<sup>240</sup> possible model and used backwards selection following the methodology of Zuur et al. (2009).  
<sup>241</sup> We used this model to create a layer of predicted TVC for the study area for the pre-fire scene,  
<sup>242</sup> and extracted both our predictions of TVC and dNBR of the fire from 1000 regularly-spaced  
<sup>243</sup> points within the fire perimeter. Finally, to quantify the effect of TVC on burn severity, we  
<sup>244</sup> created an OLS linear model with our modeled TVC and its second-order polynomial as  
<sup>245</sup> predictor variables and burn severity as the response variable.

<sup>246</sup> **Equation 1:** *Green NDVI* =  $\frac{NIR-Green}{NIR+Green}$

<sup>247</sup> **Equation 2:** *NDSVI* =  $\frac{SWIR_1-Red}{SWIR_1+Red}$

<sup>248</sup> To examine how burn severity affected the community composition of the seed bank (H2),  
<sup>249</sup> we created a joint species distribution model (JSDM) in a Bayesian framework (Tikhonov et  
<sup>250</sup> al. 2020) for the occurrence of all species germinated from the seed bank that were found  
<sup>251</sup> at more than one location. We created four Markov Chain Monte Carlo (MCMC) chains,  
<sup>252</sup> each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain  
<sup>253</sup> and then recorded every 100th for a total of 1,000 posterior samples per chain, and 4,000  
<sup>254</sup> total. We assessed model convergence using the effective sample size and the potential scale  
<sup>255</sup> reduction factor (Gelman, Rubin, and others 1992). We used the model to predict the  
<sup>256</sup> probability of occurrence of germinable seeds of a given species along a gradient of burn  
<sup>257</sup> severity. We included burn severity, elevation, aspect, pre-fire seedbank diversity and soil  
<sup>258</sup> depth as independent variables.

<sup>259</sup> To account for the possibility of H2a as a confounding factor, we included the Shannon-Weaver  
<sup>260</sup> diversity index (Shannon and Weaver 1949; Hill 1973) in the paired, unburned seed bank  
<sup>261</sup> samples as one of the predictor variables in our JSDM. We also created OLS models with

262 the unburned species richness and Shannon-Weaver diversity index predicted by prefire fuel  
263 connectivity, with the expectation that pre-fire fuel connectivity would have had a negative  
264 effect on the prefire seedbank diversity.

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

269 To examine how the resulting fuel connectivity was related to biodiversity (H4), we used  
270 the diversity data and connectivity data that we collected in 2019 to create a Poisson GLM  
271 with number of species encountered aboveground at each plot location as the dependent  
272 variable, as well as an OLS linear model with the Shannon-Weaver index (Shannon and  
273 Weaver 1949; Hill 1973) as a dependent variable. We used fuel connectivity, elevation, and  
274 aspect as independent variables.

275 For all linear and generalized linear models, we used backwards selection to find the most  
276 parsimonious model. We fitting the largest possible model first, and removed variables that  
277 did not improve the model fit according to Akaike's Information Criterion (AIC), following  
278 the methodology of Zuur et al. (2009).

279 All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis is  
280 freely available on Figshare (link here after acceptance) and GitHub ([https://www.github.com/admahood/seed\\_bank](https://www.github.com/admahood/seed_bank)).

### 282 3. Results

283 We found support for each hypothesized component of the positive feedback loop. For H1,  
284 the most parsimonious model for our *in situ* observations had only TVC as the predictor,  
285 which had a weak positive relationship with burn severity ( $\beta = 2.4$ ,  $p = 0.083$ ,  $R^2 = 0.27$ ,  
286 Figure 2a). For our remotely sensed analysis, our most parsimonious model of TVC explained

<sup>287</sup> 34% of the variation and had Green NDVI, NDSVI and their interaction as predictors (Table  
<sup>288</sup> 1???). Our model of dNBR using the predicted TVC within the fire perimeter as a predictor  
<sup>289</sup> of dNBR explained 41% of the variation and the relationship between TVC and burn severity  
<sup>290</sup> was positive and significant ( $p \ll 0.01$ , Figure 2a).

<sup>291</sup> The vast majority of seeds that germinated in the greenhouse were the two most common grass  
<sup>292</sup> species, *P. secunda* and *B. tectorum* (Table S1). Eight forb species were found in more than  
<sup>293</sup> one location, and these 10 prevalent species are those that were used in our JSDM. Burned  
<sup>294</sup> plots had an average of  $34 \pm 32$  total seeds in the top 2 cm, and  $12 \pm 14$  in the bottom 4 cm.  
<sup>295</sup> Unburned plots had an average of  $299 \pm 170$  in the top 2 cm and  $59 \pm 29$  in the bottom 4 cm  
<sup>296</sup> (Figure S1). For H2, the JSDM converged well (Gelman diagnostics all very close to 1 and the  
<sup>297</sup> effective sample size centered on 4,000, Figure 3a). Elevation had the most significant effects  
<sup>298</sup> on individual species (Figure 3b) and explained the most variance on average (36% Figure 3c).  
<sup>299</sup> Burn severity explained 23% of the variance on average and was supported at the 95% level  
<sup>300</sup> for 5 species (Figure 3b). For the introduced species, the predictions along a gradient of burn  
<sup>301</sup> severity were positive for *B. tectorum*, *Sisymbrium altissimum* L. and *Lepidium perfoliatum*  
<sup>302</sup> L., and negative for *Ceratocephala testiculata* and *Alyssum desertorum* Stapf (Figure 2b).  
<sup>303</sup> For native species, the effect of burn severity on occurrence was positive for *A. tridentata*,  
<sup>304</sup> neutral for *P. secunda* and negative for the remaining species (Figure 2b). Testing H2a  
<sup>305</sup> revealed a positive relationship between pre-fire aboveground species diversity and pre-fire  
<sup>306</sup> fuel connectivity, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a  
<sup>307</sup> 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> 0.74, Figure 3c).

<sup>312</sup> For H4 the most parsimonious model (Adj  $R^2 = 0.89$ ) had elevation, aspect, fuel connectivity

<sup>313</sup> and an interaction between elevation and fuel connectivity as predictors of aboveground  
<sup>314</sup> Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated with Shannon-  
<sup>315</sup> 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  
<sup>333</sup> in results between H2a (positive relationship between pre-fire fuel connectivity and diversity)  
<sup>334</sup> and H4 (negative relationship between post-fire fuel connectivity and diversity). Most (11  
<sup>335</sup> out of 14) plot locations had mature canopies of native shrubs and with the inter-shrub space  
<sup>336</sup> occupied mostly by native bunchgrasses and forbs, with fire history since 1984. The three  
<sup>337</sup> plots with recent fire history burned in 1984 and were invaded by *B. tectorum*, but they still  
<sup>338</sup> had significant cover of *A. tridentata*. Even in locations with high annual grass cover between

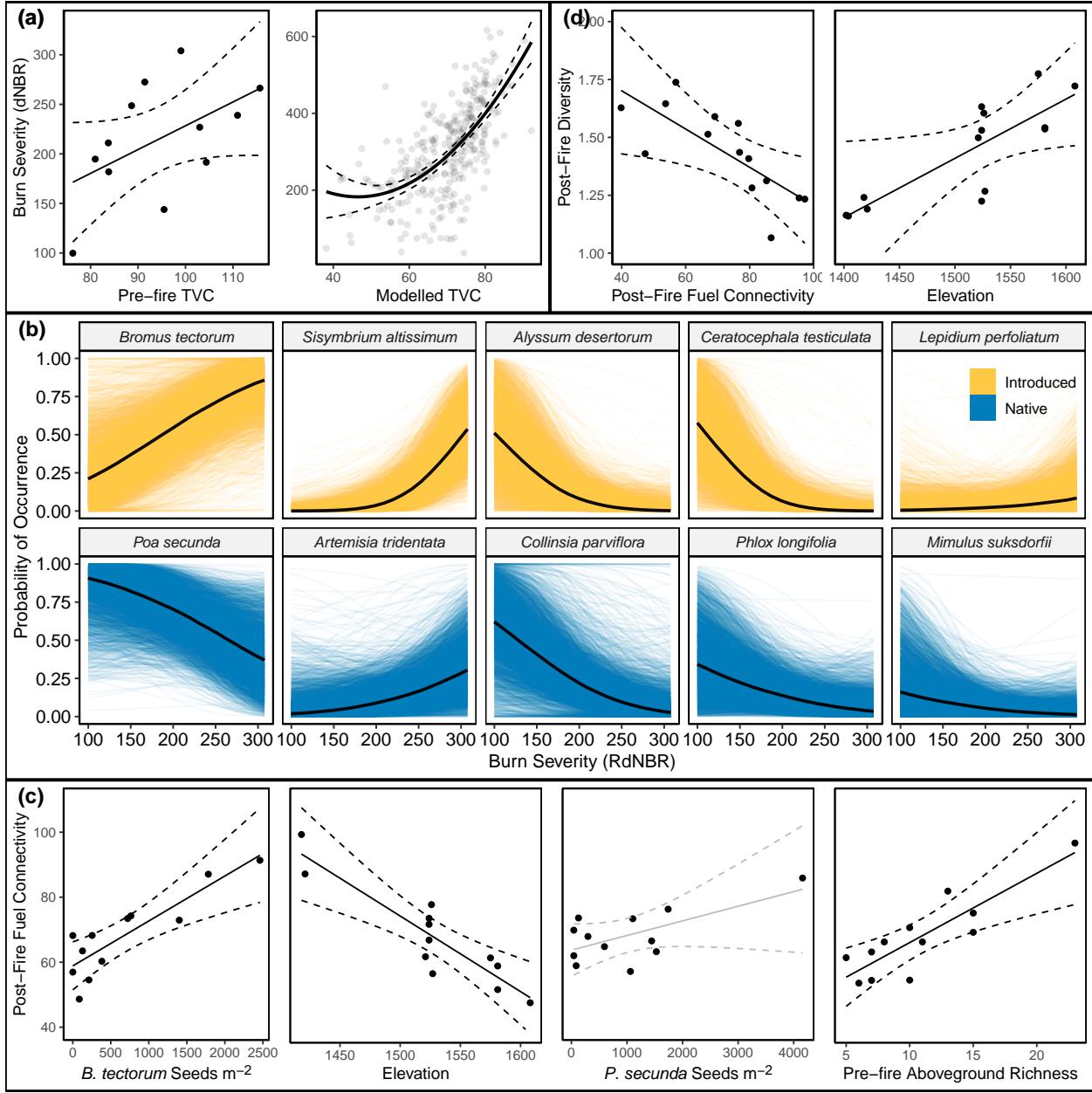


Figure 2: a) Hypothesis 1. On the left, burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Dotted lines are the 95% confidence intervals. b) Hypothesis 2. Modelled occurrence 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. c) Hypothesis 3. Fuel connectivity three years post-fire as modelled by seedbank composition, elevation and pre-fire aboveground species richness. d) Hypothesis 4. 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 (in the case of multiple predictors), points are the partial residuals, dotted lines are the 95% confidence intervals.

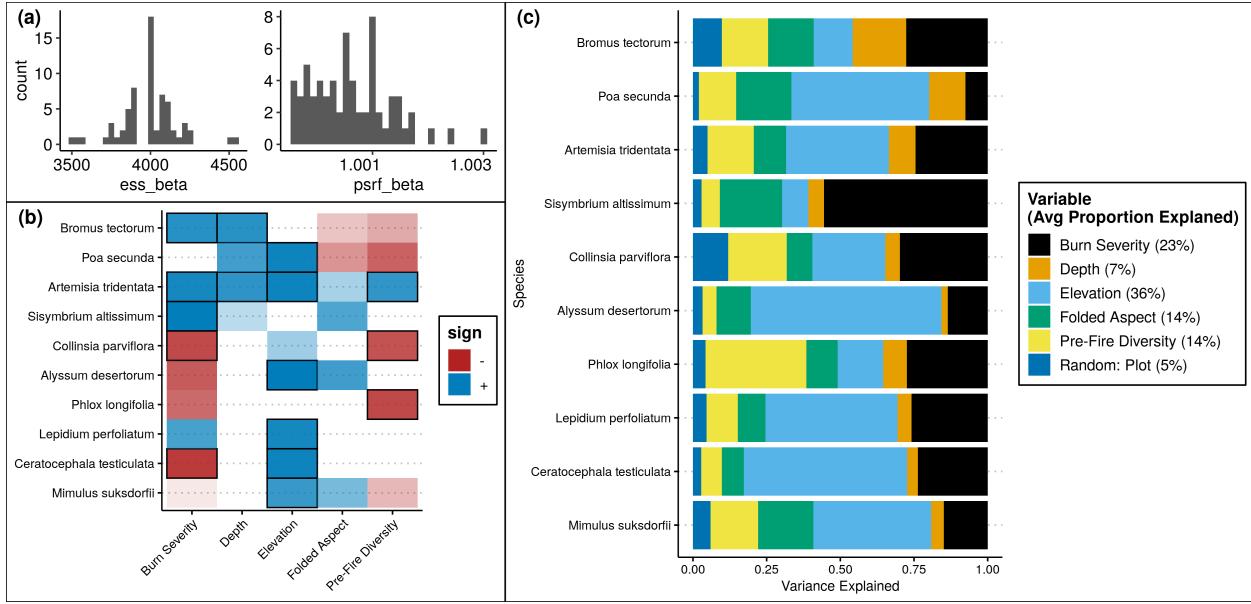


Figure 3: a) Model convergence diagnostics. On the left is the effective sample size after adjusting for autocorrelation (ideally 4,000), and on the right is the Gelman diagnostic, ideally 1. b) Predictor variables that had at least 80% support. Variables with 95% support are outlined in black. The level 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.

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).

<sup>352</sup> *Global impacts*

<sup>353</sup> The grass-fire cycle in the western US is reinforced through providing fitness benefits to  
<sup>354</sup> the introduced annual grasses and forbs via at least 4 redundant processes: i) changing the  
<sup>355</sup> composition of the seedbank, ii) competitive exclusion of native plants, iii) CO<sub>2</sub> enrichment  
<sup>356</sup> which may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of  
<sup>357</sup> annual grass species (Nagel et al. 2004; Smith et al. 2000), strengthening the fuel connectivity  
<sup>358</sup> to burn severity to seed composition feedback loop, and iv) ecohydrological feedbacks that  
<sup>359</sup> create a warmer, drier microclimate (Turnbull et al. 2012; Wilcox et al. 2012). It is likely  
<sup>360</sup> that some of these feedbacks are idiosyncratic to the system being studied, while others  
<sup>361</sup> may reflect the fundamental properties of ecosystem function that change when a system is  
<sup>362</sup> converted from being dominated by woody plants to being dominated by herbaceous plants  
<sup>363</sup> (Kitzberger et al. 2016). Understanding the mechanisms of hysteresis, and in particular how  
<sup>364</sup> multiple redundant mechanisms act in concert, will provide important insights for ecosystem  
<sup>365</sup> change on a global scale. At least 13 grass species initiate self-reinforcing feedbacks with  
<sup>366</sup> fire in the U.S. (Fusco et al. 2019; Tortorelli, Krawchuk, and Kerns 2020), and many more  
<sup>367</sup> worldwide, including Australia (G. Miller et al. 2010; Setterfield et al. 2010), Brazil (Rossi et  
<sup>368</sup> al. 2014) and South Africa (Milton 2004). While the conversion of temperate forests and  
<sup>369</sup> shrublands to grasslands may have a less per-hectare impact on carbon sequestration than  
<sup>370</sup> tropical forests, the consequences are still relevant to the global carbon cycle, especially when  
<sup>371</sup> forests (rather than the shrublands studied here) are replaced by herbaceous ecosystems  
<sup>372</sup> (Kerns et al. 2020).

<sup>373</sup> *Potential limitations*

<sup>374</sup> We found fewer species and lower diversity in our seedbank germination assays than we did in  
<sup>375</sup> the aboveground sampling (Figure S2). This result may be influenced by the methodological  
<sup>376</sup> limitations inherent to greenhouse germination trials (Vandvik et al. 2016). In particular  
<sup>377</sup> 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.

416 *Management implications*

417 Greenhouse or *in situ* germination assays are time-consuming and require botanical expertise,  
418 and are very important. One potential avenue for future research may be linking remote  
419 sensing data with retrospective meta-analyses of prior studies. There are many studies that  
420 only study fire occurrence as it relates to the seed bank. Fire history, including burn severity,  
421 is now possible to calculate for anywhere on earth at a 30 meter resolution from 1984 to  
422 present with Landsat images (Parks et al. 2018). Teasing out these mechanisms will increase  
423 our understanding of how generalizable these phenomena are, and this will allow us to know  
424 how best to manage these ecosystems and where and when it is possible to reverse the process.

425 This work shows that this is a clear example of a system where the degraded state represents  
426 an alternative species assemblage from that of the restoration target, where the propagules  
427 of the original assemblage are no longer present, and thus methods that rely on natural  
428 succession may not be sufficient (Suding, Gross, and Houseman 2004). Our results highlight  
429 the importance of prioritizing the preservation of native shrub cover and in particular policies

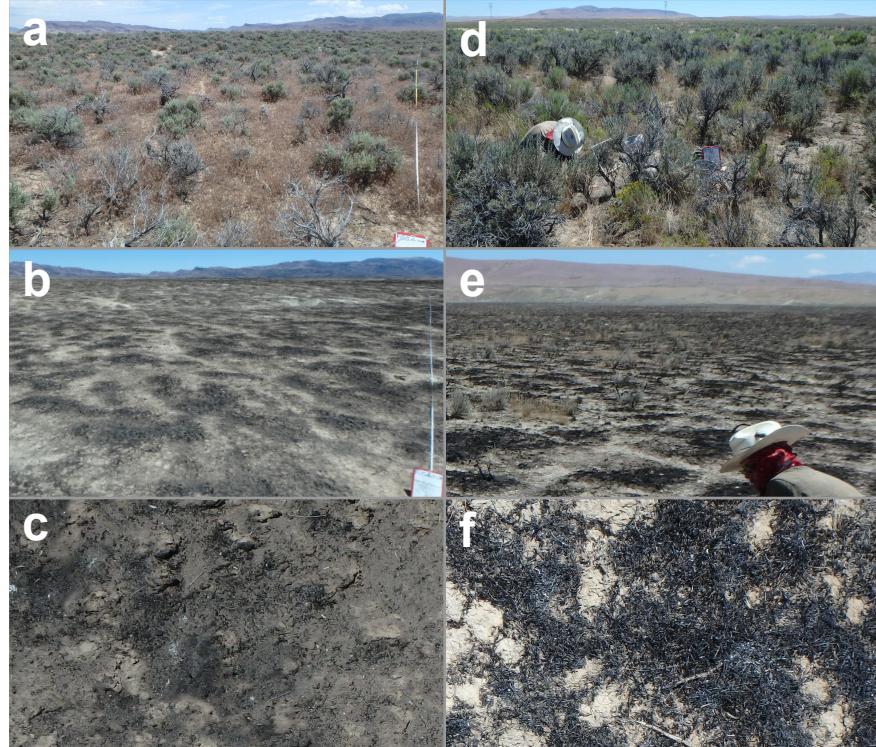


Figure 4: Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space being highly invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, and approximately all of the biomass was consumed 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.

430 that encourage land managers to maximize the preservation of unburned patches during the  
431 suppression of wildfires in this system (Steenvoorden et al. 2019). Commonly encountered  
432 native plants and the keystone shrub species *A. tridentata* depend on post-fire seed dispersal  
433 from surviving individuals in unburned patches (Schlaepfer, Lauenroth, and Bradford 2014).  
434 Once the system achieves a canopy dominated by annual grasses and forbs, the competitive  
435 pressure from the annual grass monoculture makes it more difficult if not impossible for  
436 perennial native forbs and shrubs to establish from the depleted seedbank. Post-fire seeding  
437 efforts may restore native propagules, but if there is dense cover of annuals further effort  
438 may be required to reduce fuel connectivity in order to reduce both fire risk and competitive  
439 pressure from annuals.

440 Livestock grazing can reduce fuel connectivity in uninvasd sagebrush (Davies et al. 2010).  
441 At the same time, grazing can also decrease the resistance to invasion by *B. tectorum* via  
442 negative effects on biological soil crust (BSC) (Condon and Pyke 2018), and can reduce the  
443 survival of *Artemisia* seedlings that are not protected by shrub canopies (Owens and Norton  
444 1992). In wet years, targeted grazing at already invaded sagebrush sites may reduce fuel  
445 connectivity and alleviate fire risk. Plant community composition in the years immediately  
446 after fire may be highly variable spatially and from year to year. Post-fire grazing may help  
447 reduce *B. tectorum* cover, but it would more likely exacerbate the problem by introducing  
448 cheatgrass in uninvasd sites (Williamson et al. 2019) or increasing the already superior  
449 postfire dispersal of *B. tectorum* seeds (Monty, Brown, and Johnston 2013). We suggest  
450 management approaches that are specifically tailored each year to the conditions of a given  
451 site, and targeting grazing only in already invaded areas to reduce *B. tectorum* cover where  
452 it may aid in native plant restoration.

## 453 Acknowledgements

454 We thank Abdelhakim Farid, Julia Lopez, Dylan Murphy and C. Nick Whittemore for their  
455 help in the field and in the greenhouse. We also greatly appreciate the use of the University

456 of Colorado Boulder's Ecology Evolution and Biology Greenhouse. We thank Lindsay P.  
457 Chiquoine for help with methodology and Thomas T. Veblen for constructive feedback that  
458 greatly improved the manuscript. This project was funded in part by the University of  
459 Colorado Boulder Geography department's Adam Kolff Memorial Graduate Research Grant  
460 and CU Boulder's Undergraduate Research Opportunities Program.

## 461 References

- 462 Andersen, Tom, Jacob Carstensen, Emilio Hernández-García, and Carlos M. Duarte. 2009.  
463 “Ecological thresholds and regime shifts: approaches to identification.” *Trends in Ecology  
464 and Evolution* 24 (1): 49–57. <https://doi.org/10.1016/j.tree.2008.07.014>.
- 465 Baker, William L. 2006. “Fire and restoration of sagebrush ecosystems.” *Wildlife Society  
466 Bulletin* 34 (1): 177–85. [https://doi.org/10.2193/0091-7648\(2006\)34%5B177:farose%5D2  
.0.co;2](https://doi.org/10.2193/0091-7648(2006)34%5B177:farose%5D2<br/>467 .0.co;2).
- 468 Balch, Jennifer K., Bethany A. Bradley, Carla M. D'Antonio, and José Gómez-Dans. 2013.  
469 “Introduced annual grass increases regional fire activity across the arid western USA  
470 (1980–2009).” *Global Change Biology* 19 (1): 173–83. <https://doi.org/10.1111/gcb.12046>.
- 471 Barga, Sarah, and Elizabeth A. Leger. 2018. “Shrub cover and fire history predict seed bank  
472 composition in Great Basin shrublands.” *Journal of Arid Environments* 154 (November  
473 2017): 40–50. <https://doi.org/10.1016/j.jaridenv.2018.03.004>.
- 474 Bechtold, H. A., and R. S. Inouye. 2007. “Distribution of carbon and nitrogen in sage-  
475 brush steppe after six years of nitrogen addition and shrub removal.” *Journal of Arid  
476 Environments* 71 (1): 122–32. <https://doi.org/10.1016/j.jaridenv.2007.02.004>.
- 477 Beckstead, Julie, Laura E. Street, Susan E. Meyer, and Phil S. Allen. 2011. “Fire effects on  
478 the cheatgrass seed bank pathogen Pyrenophora semeniperda.” *Rangeland Ecology and  
479 Management* 64 (2): 148–57. <https://doi.org/10.2111/REM-D-10-00052.1>.
- 480 Bond, William J., and Jeremy J. Midgley. 1995. “Kill Thy Neighbour: An Individualistic  
481 Argument for the Evolution of Flammability.” *Oikos* 73 (1): 79. <https://doi.org/10.2307/3545728>.
- 483 Boudell, JA, SO Link, and JR Johansen. 2002. “Effect of soil microtopography on seed  
484 bank distribution in the shrub-steppe.” *Western North American Naturalist* 62 (1): 14–24.  
485 <https://doi.org/10.2307/41717153>.
- 486 Bradford, John B., Daniel R. Schlaepfer, William K. Lauenroth, and Kyle A. Palmquist.  
487 2020. “Robust ecological drought projections for drylands in the 21st century.” *Global  
488 Change Biology* 26 (7): 3906–19. <https://doi.org/10.1111/gcb.15075>.

- 489 Bradley, Bethany A., R. A. Houghton, John F. Mustard, and Steven P. Hamburg. 2006.  
490 “Invasive grass reduces aboveground carbon stocks in shrublands of the Western US.” *Global*  
491 *Change Biology* 12 (10): 1815–22. <https://doi.org/10.1111/j.1365-2486.2006.01232.x>.
- 492 Brooks, Matthew L., Carla M. D’Antonio, David M. Richardson, James B. Grace, Jon E.  
493 Keeley, Joseph M. DiTomaso, Richard J. Hobbs, Mike Pellatt, and David Pyke. 2004.  
494 “Effects of Invasive Alien Plants on Fire Regimes.” *BioScience* 54 (7): 677–88.
- 495 Bukowski, Beth, and William L. Baker. 2013. “Historical fire regimes, reconstructed from  
496 land-survey data, led to complexity and fluctuation in sagebrush landscapes.” *Ecological*  
497 *Applications* 23 (3): 546–64.
- 498 Chambers, Jeanne C., Bruce A. Roundy, Robert R. Blank, Susan E. Meyer, and A. Whittaker.  
499 2007. “What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? ”  
500 *Ecological Monographs* 77 (1): 117–45. <https://doi.org/10.1890/05-1991>.
- 501 Commission for Environmental Cooperation. 2006. “Ecological regions of North America –  
502 Levels I, II, and III: Montreal, Quebec, Canada, Commission for Environmental Cooper-  
503 ation, scale 1:10,000,000.” <https://www.epa.gov/eco-research/ecoregions-north-america>.
- 504 Condon, Lea A., and David A. Pyke. 2018. “Fire and Grazing Influence Site Resistance to  
505 Bromus tectorum Through Their Effects on Shrub, Bunchgrass and Biocrust Communities  
506 in the Great Basin (USA).” *Ecosystems* 21 (7): 1416–31. <https://doi.org/10.1007/s10021-018-0230-8>.
- 508 D’Antonio, Carla M., and Peter M. Vitousek. 1992. “Biological invasions by exotic grasses,  
509 the grass/fire cycle, and global change.” *Annual Review of Ecological Systems* 23: 63–87.
- 510 Davies, Kirk W., Jonathan D. Bates, Tony J. Svejcar, and Chad S. Boyd. 2010. “Effects  
511 of long-term livestock grazing on fuel characteristics in rangelands: An example from  
512 the sagebrush steppe.” *Rangeland Ecology and Management* 63 (6): 662–69. <https://doi.org/10.2111/REM-D-10-00006.1>.
- 514 Davies, Kirk W., Chad S. Boyd, Jeffrey L. Beck, Jon D. Bates, Tony J. Svejcar, and  
515 Michael A. Gregg. 2011. “Saving the sagebrush sea: An ecosystem conservation plan  
516 for big sagebrush plant communities.” *Biological Conservation* 144 (11): 2573–84. <https://doi.org/10.1016/j.biocon.2011.07.016>.
- 518 Davies, Kirk W., and Aleta M. Nafus. 2013. “Exotic annual grass invasion alters fuel amounts,  
519 continuity and moisture content.” *International Journal of Wildland Fire* 22 (3): 353–58.  
520 <https://doi.org/10.1071/WF11161>.
- 521 Davis, Mark A., J P Grime, Ken Thompson, and J Philip. 2000. “Fluctuating resources in  
522 plant communities: a general of invasibility theory.” *Journal of Ecology* 88 (3): 528–34.  
523 <https://doi.org/10.1046/j.1365-2745.2000.00473.x>.
- 524 Doescher, Paul S., Richard F. Miller, and Alma H. Winward. 1984. “Soil Chemical Patterns  
525 under Eastern Oregon Plant Communities Dominated by Big Sagebrush.” <https://doi.org/10.2136/sssaj1984.03615995004800030038x>.

- 527 Eckert, Richard E., Frederick F. Peterson, Michael S. Meurisse, and L. Stephens. 1986.  
528     “Effects of Soil-Surface Morphology on Emergence and Survival of Seedlings in Big  
529     Sagebrush Communities.” *Journal of Range Management* 39 (5): 414–20. <http://www.jstor.org/stable/3899441>.
- 531 Eidenshink, Jeff, Brian Schwind, Ken Brewer, Zhi-liang Zhu, Brad Quayle, and Stephen  
532     Howard. 2007. “A Project for Monitoring Trends in Burn Severity.” *Fire Ecology* 3 (1):  
533     3–21. <https://doi.org/10.4996/fireecology.0301003>.
- 534 Fusco, Emily J., John T. Finn, Jennifer K. Balch, R. Chelsea Nagy, and Bethany A. Bradley.  
535     2019. “Invasive Grasses Increase Fire Occurrence and Frequency Across US Ecoregions.”  
536     *Proceedings of the National Academy of Sciences* 116 (47): 23594–99. <https://doi.org/10.1073/pnas.1908253116>.
- 538 Gagnon, Paul R., Heather A. Passmore, Matthew Slocum, Jonathan A. Myers, Kyle E.  
539     Harms, William J. Platt, and C. E. Timothy Paine. 2015. “Fuels and fires influence  
540     vegetation via above- and belowground pathways in a high-diversity plant community.”  
541     *Journal of Ecology* 103 (4): 1009–19. <https://doi.org/10.1111/1365-2745.12421>.
- 542 Gelman, Andrew, Donald B Rubin, and others. 1992. “Inference from Iterative Simulation  
543     Using Multiple Sequences.” *Statistical Science* 7 (4): 457–72.
- 544 Germino, Matthew J., David M. Barnard, Bill E. Davidson, Robert S. Arkle, David S.  
545     Pilliod, Matthew R. Fisk, and Cara Applestein. 2018. “Thresholds and hotspots for  
546     shrub restoration following a heterogeneous megafire.” *Landscape Ecology* 33 (7): 1177–94.  
547     <https://doi.org/10.1007/s10980-018-0662-8>.
- 548 Germino, Matthew J., Jeanne C. Chambers, and Cynthia S. Brown. 2016. *Exotic Bromegrasses in Arid and Semiarid Ecosystems of the Western US Causes, Consequences, and Management Implications*. <http://www.springer.com/series/412>.
- 551 Gibbens, Robert P., and James M. Lenz. 2001. “Root systems of some Chihuahuan Desert  
552     plants.” *Journal of Arid Environments* 49: 221–63.
- 553 Hassan, M. A., and N. E. West. 1986. “Dynamics of Soil Seed Pools in Burned and Unburned  
554     Sagebrush Semi-Deserts.” *Ecology* 67 (1): 269–72.
- 555 Heerdt, G. N. J. Ter, G. L. Verweij, R. M. Bekker, and J. P. Bakker. 1996. “An Improved  
556     Method for Seed-Bank Analysis: Seedling Emergence After Removing the Soil by Sieving.”  
557     *Functional Ecology* 10 (1): 144. <https://doi.org/10.2307/2390273>.
- 558 Heydari, Mehdi, Reza Omidipour, Mehdi Abedi, and Carol Baskin. 2017. “Effects of  
559     fire disturbance on alpha and beta diversity and on beta diversity components of soil  
560     seed banks and aboveground vegetation.” *Plant Ecology and Evolution* 150 (3): 247–56.  
561     <https://doi.org/10.5091/plecevo.2017.1344>.
- 562 Hill, M. O. 1973. “Diversity and Evenness: A Unifying Notation and Its Consequences.”  
563     *Ecology* 54 (2): 427–32.
- 564 Hirota, Marina, Milena Holmgren, Egbert H. Van Nes, and Marten Scheffer. 2011. “Global  
565     resilience of tropical forest and savanna to critical transitions.” *Science* 334 (6053): 232–35.

- 566 https://doi.org/10.1126/science.1210657.
- 567 Humphrey, L David, and Eugene W Schupp. 2001. "Seed banks of *Bromus tectorum*-  
568 dominated communities in the Great Basin." *Western North American Naturalist* 61 (1):  
569 85–92. https://doi.org/10.2307/41717080.
- 570 Jones, Rachel O., Jeanne C. Chambers, David I. Board, Dale W. Johnson, and Robert R.  
571 Blank. 2015. "The role of resource limitation in restoration of sagebrush ecosystems  
572 dominated by cheatgrass (*Bromus tectorum*)."*Ecosphere* 6 (7): 1–21.
- 573 Keeley, Jon E. 2009. "Fire intensity, fire severity and burn severity: A brief review and  
574 suggested usage." *International Journal of Wildland Fire* 18 (1): 116–26. https://doi.org/  
575 10.1071/WF07049.
- 576 Keeley, Jon E., and Juli G. Pausas. 2019. "Distinguishing disturbance from perturbations  
577 in fire-prone ecosystems." *International Journal of Wildland Fire* 28 (4): 282–87. https:  
578 //doi.org/10.1071/WF18203.
- 579 Keeley, Jon E., Juli G. Pausas, Philip W. Rundel, William J. Bond, and Ross A. Bradstock.  
580 2011. "Fire as an evolutionary pressure shaping plant traits." *Trends in Plant Science* 16  
581 (8): 406–11. https://doi.org/10.1016/j.tplants.2011.04.002.
- 582 Kerns, Becky K., Claire Tortorelli, Michelle A. Day, Ty Nietupski, Ana M. G. Barros, John  
583 B. Kim, and Meg A. Krawchuk. 2020. "Invasive grasses: A new perfect storm for  
584 forested ecosystems?" *Forest Ecology and Management* 463 (November 2019): 117985.  
585 https://doi.org/10.1016/j.foreco.2020.117985.
- 586 Key, Carl H, and Nathan C Benson. 1999. "The Composite Burn Index (CBI): Field Rating  
587 of Burn Severity." *USGS, NRMSC Research,[online] Available: Http://Nrmsc. Usgs.  
588 Gov/Research/Cbi. Htm [3/14/2006]*.
- 589 Kimura, Hideo, and Shiro Tsuyuzaki. 2011. "Fire severity affects vegetation and seed bank  
590 in a wetland." *Applied Vegetation Science* 14 (3): 350–57. https://doi.org/10.1111/j.1654-  
591 109X.2011.01126.x.
- 592 Kitzberger, Thomas, G. L. W. Perry, J. Paritsis, J. H. Gowda, A. J. Tepley, A. Holz, and T.  
593 T. Veblen. 2016. "Fire–vegetation feedbacks and alternative states: common mechanisms  
594 of temperate forest vulnerability to fire in southern South America and New Zealand."  
595 *New Zealand Journal of Botany* 54 (2): 247–72. https://doi.org/10.1080/0028825X.2016.  
596 1151903.
- 597 Knapp, Paul A. 1996. "Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin  
598 Desert." *Global Environmental Change* 6 (1): 37–52. https://doi.org/10.1016/0959-  
599 3780(95)00112-3.
- 600 Kolden, Crystal A, Alistair M S Smith, and John T. Abatzoglou. 2015. "Limitations and  
601 utilisation of Monitoring Trends in Burn Severity products for assessing wildfire severity  
602 in the USA." *International Journal of Wildland Fire* 24: 1023–28.
- 603 Koontz, Michael J, Malcolm P North, Chhaya M Werner, Stephen E Fick, and Andrew M  
604 Latimer. 2020. "Local Forest Structure Variability Increases Resilience to Wildfire in Dry

- 605 Western US Coniferous Forests." *Ecology Letters* 23 (3): 483–94.
- 606 Lipoma, M. Lucrecia, Guillermo Funes, and Sandra Díaz. 2018. "Fire effects on the soil  
607 seed bank and post-fire resilience of a semi-arid shrubland in central Argentina." *Austral  
608 Ecology* 43 (1): 46–55. <https://doi.org/10.1111/aec.12533>.
- 609 Liyanage, Ganesha S., and Mark K. J. Ooi. 2017. "Do dormancy-breaking temperature  
610 thresholds change as seeds age in the soil seed bank?" *Seed Science Research* 27 (1): 1–11.  
611 <https://doi.org/10.1017/S0960258516000271>.
- 612 Mahood, Adam L., and Jennifer K. Balch. 2019. "Repeated fires reduce plant diversity  
613 in low-elevation Wyoming big sagebrush ecosystems (1984 – 2014)." *Ecosphere* 10 (2):  
614 e02591. <https://doi.org/10.1002/ecs2.2591>.
- 615 Maia, P., J. G. Pausas, V. Arcenegui, C. Guerrero, A. Pérez-Bejarano, J. Mataix-Solera, M.  
616 E. T. Varela, I. Fernandes, E. T. Pedrosa, and J. J. Keizer. 2012. "Wildfire effects on the  
617 soil seed bank of a maritime pine stand - The importance of fire severity." *Geoderma* 191:  
618 80–88. <https://doi.org/10.1016/j.geoderma.2012.02.001>.
- 619 Meyer, Susan E. 1994. "Germination and establishment ecology of big sagebrush: implications  
620 for community restoration." In *Symposium on Management, Ecology, and Restoration of  
621 Intermountain Annual Rangelands, Boise, ID, May 18-21, 1992*, 244–51.
- 622 Meyer, Susan E, Stephen B Monsen, and E Durant McArthur. 2013. "Germination Response  
623 of Artemisia tridentata (Asteraceae) to Light and Chill: Patterns of Between-Population  
624 Variation." *Botanical Gazette* 151 (2): 176–83.
- 625 Miller, Georgia, Margaret Friedel, Paul Adam, and Vanessa Chewings. 2010. "Ecological  
626 impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central Australia does field  
627 evidence support a fire-invasion feedback?" *The Rangeland Journal* 32 (4): 353–65.  
628 <https://doi.org/10.1071/RJ09076>.
- 629 Miller, Jay D., Eric E. Knapp, Carl H. Key, Carl N. Skinner, Clint J. Isbell, R. Max Creasy,  
630 and Joseph W. Sherlock. 2009. "Calibration and validation of the relative difference  
631 Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada  
632 and Klamath Mountains, California, USA." *Remote Sensing of Environment* 113 (3):  
633 645–56. <https://doi.org/10.1016/j.rse.2008.11.009>.
- 634 Milton, Sue J. 2004. "Grasses as invasive alien plants in South Africa." *South African Journal  
635 of Science* 100 (1-2): 69–75.
- 636 Monty, Arnaud, Cynthia S. Brown, and Danielle B. Johnston. 2013. "Fire promotes downy  
637 brome (*Bromus tectorum* L.) seed dispersal." *Biological Invasions* 15 (5): 1113–23.  
638 <https://doi.org/10.1007/s10530-012-0355-1>.
- 639 Morgan, P., and L. F. Neuenschwander. 1988. "Seed-Bank Contributions to Regeneration of  
640 Shrub Species After Clear-Cutting and Burning." *Canadian Journal of Botany* 66 (1):  
641 169–72. <https://doi.org/10.1139/b88-026>.
- 642 Nagel, Jennifer M., Travis E. Huxman, Kevin L. Griffin, and Stanley D. Smith. 2004. "CO<sub>2</sub>  
643 enrichment reduces the energetic cost of biomass construction in an invasive desert grass."

- 644      *Ecology* 85 (1): 100–106. <https://doi.org/10.1890/02-3005>.
- 645      Nagy, R. Chelsea, Emily J. Fusco, Jennifer K. Balch, John T. Finn, Adam Mahood, Jenica  
646      M. Allen, and Bethany A. Bradley. 2020. “A synthesis of the effects of cheatgrass  
647      invasion on U.S. Great Basin carbon storage.” *Journal of Applied Ecology*, no. May: 1–11.  
648      <https://doi.org/10.1111/1365-2664.13770>.
- 649      Ottaviani, Gianluigi, Rafael Molina-Vegas, Tristan Charles-Dominique, Stefano Chelli,  
650      Giandiego Campetella, Roberto Canullo, and Jitka Klimešová. 2020. “The Neglected  
651      Belowground Dimension of Plant Dominance.” *Trends in Ecology and Evolution* 35 (9):  
652      763–66. <https://doi.org/10.1016/j.tree.2020.06.006>.
- 653      Owens, M. K., and B. E. Norton. 1992. “Interactions of Grazing and Plant Protection on  
654      Basin Big Sagebrush (*Artemisia tridentata* ssp. *tridentata*) Seedling Survival.” *Journal*  
655      *of Range Management* 45 (3): 257–62. <http://www.jstor.org/stable/4002974>.
- 656      Palmer, Harrison D., Andrew J. Denham, and Mark K. J. Ooi. 2018. “Fire severity drives  
657      variation in post-fire recruitment and residual seed bank size of Acacia species.” *Plant*  
658      *Ecology* 219 (5): 527–37. <https://doi.org/10.1007/s11258-018-0815-5>.
- 659      Parks, Sean A., Lisa M. Holsinger, Morgan A. Voss, Rachel A. Loehman, and Nathaniel  
660      P. Robinson. 2018. “Mean composite fire severity metrics computed with google earth  
661      engine offer improved accuracy and expanded mapping potential.” *Remote Sensing* 10  
662      (6): 1–15. <https://doi.org/10.3390/rs10060879>.
- 663      Perryman, Barry L, Aaron M Maier, Ann L Hild, and Richard A Olson. 2001. “Demographic  
664      characteristics of 3 *Artemisia tridentata* Nutt. subspecies.” *Journal of Range Management*  
665      54 (2): 166–70.
- 666      Petraitis, Peter S., and Roger Earl Latham. 1999. “The importance of scale in testing the  
667      origins of alternative community states.” *Ecology* 80 (2): 429–42. [https://doi.org/10.1890/0012-9658\(1999\)080%5B0429:TIOSIT%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080%5B0429:TIOSIT%5D2.0.CO;2).
- 669      Plue, J., F. Colas, A. G. Auffret, and S. A. O. Cousins. 2017. “Methodological bias in the  
670      seed bank flora holds significant implications for understanding seed bank community  
671      functions.” *Plant Biology* 19 (2): 201–10. <https://doi.org/10.1111/plb.12516>.
- 672      R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna,  
673      Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- 674      Ratajczak, Zak, Stephen R. Carpenter, Anthony R. Ives, Christopher J. Kucharik, Tanjona  
675      Ramiadantsoa, M. Allison Stegner, John W. Williams, Jien Zhang, and Monica G. Turner.  
676      2018. “Abrupt Change in Ecological Systems: Inference and Diagnosis.” *Trends in Ecology*  
677      *and Evolution* 33 (7): 513–26. <https://doi.org/10.1016/j.tree.2018.04.013>.
- 678      Rossi, Rafael Drumond, Carlos Romero Martins, Pedro Lage Viana, Evandro Luís Rodrigues,  
679      and José Eugênio Côrtes Figueira. 2014. “Impact of invasion by molasses grass (*Melinis*  
680      *minutiflora* P. Beauv.) on native species and on fires in areas of campo-cerrado in Brazil.”  
681      *Acta Botanica Brasilica* 28 (4): 631–37. <https://doi.org/10.1590/0102-33062014abb3390>.

- 682 Schimmel, Johnny, and Anders Granström. 1996. "Fire Severity and Vegetation Response in  
683 the Boreal Swedish Forest." *Ecology* 77 (5): 1436–50.
- 684 Schlaepfer, Daniel R., William K. Lauenroth, and John B. Bradford. 2014. "Natural  
685 Regeneration Processes in Big Sagebrush (*Artemisia tridentata*)."*Rangeland Ecology &*  
686 *Management* 67 (4): 344–57. <https://doi.org/10.2111/REM-D-13-00079.1>.
- 687 Schwilk, Dylan W., and Benjamin Kerr. 2002. "Genetic niche-hiking: An alternative  
688 explanation for the evolution of flammability." *Oikos* 99 (3): 431–42. <https://doi.org/10.1034/j.1600-0706.2002.11730.x>.
- 689
- 690 Setterfield, Samantha A., Natalie A. Rossiter-Rachor, Lindsay B. Hutley, Michael M. Douglas,  
691 and Richard J. Williams. 2010. "Turning up the heat: The impacts of Andropogon gayanus  
692 (gamba grass) invasion on fire behaviour in northern Australian savannas." *Diversity and*  
693 *Distributions* 16 (5): 854–61. <https://doi.org/10.1111/j.1472-4642.2010.00688.x>.
- 694 Shannon, CE, and W Weaver. 1949. "The Mathematical Theory of Communication. University  
695 of Illinois Press, Urbana-Champaign, Illinois, USA, 117 p."
- 696 Shinneman, Douglas J., and Susan K. McIlroy. 2016. "Identifying key climate and environmental  
697 factors affecting rates of post-fire big sagebrush (*Artemisia tridentata*) recovery in  
698 the northern Columbia Basin, USA." *International Journal of Wildland Fire* 25: 933–45.  
699 <https://doi.org/10.1071/WF16013>.
- 700 Smith, Stanley D., Travis E. Huxman, Stephen F. Zitzer, Therese N. Charlet, David C.  
701 Housman, James S. Coleman, Lynn K. Fenstermaker, Jeffrey R. Seemann, and Robert S.  
702 Nowak. 2000. "Elevated CO<sub>2</sub> increases productivity and invasive species success in an  
703 arid ecosystem." *Nature* 408 (6808): 79–82. <https://doi.org/10.1038/35040544>.
- 704 Staal, Arie, Ingo Fetzer, Lan Wang-Erlandsson, Joyce H. C. Bosmans, Stefan C. Dekker,  
705 Egbert H. van Nes, Johan Rockström, and Obbe A. Tuinenburg. 2020. "Hysteresis  
706 of tropical forests in the 21st century." *Nature Communications* 11 (1): 1–8. <https://doi.org/10.1038/s41467-020-18728-7>.
- 707
- 708 Staver, A. Carla, Sally Archibald, and Simon A. Levin. 2011. "The global extent and  
709 determinants of savanna and forest as alternative biome states." *Science* 334 (6053):  
710 230–32. <https://doi.org/10.1126/science.1210465>.
- 711 Steenvoorden, Jasper, Arjan J. H. Meddens, Anthony J. Martinez, Lee J. Foster, and W.  
712 Daniel Kissling. 2019. "The potential importance of unburned islands as refugia for the  
713 persistence of wildlife species in fire-prone ecosystems." *Ecology and Evolution* 9 (15):  
714 8800–8812. <https://doi.org/10.1002/ece3.5432>.
- 715 Suding, Katharine N., Katherine L. Gross, and Gregory R. Houseman. 2004. "Alternative  
716 states and positive feedbacks in restoration ecology." *Trends in Ecology & Evolution* 19  
717 (1): 46–53. <https://doi.org/10.1016/j.tree.2003.10.005>.
- 718 Tikhonov, Gleb, Otso Ovaskainen, Jari Oksanen, Melinda de Jonge, Øystein Opdal, and  
719 Tad Dallas. 2020. *Hmsc: Hierarchical Model of Species Communities*. <https://CRAN.R-project.org/package=Hmsc>.
- 720

- 721 Tortorelli, Claire M., Meg A. Krawchuk, and Becky K. Kerns. 2020. "Expanding the  
722 invasion footprint: Ventenata dubia and relationships to wildfire, environment, and plant  
723 communities in the Blue Mountains of the Inland Northwest, USA." *Applied Vegetation  
724 Science*, no. May: 1–13. <https://doi.org/10.1111/avsc.12511>.
- 725 Turnbull, Laura, Bradford P. Wilcox, J. Benlap, S. Ravi, P. D'Odorico, D. Childers, W.  
726 Gwenzi, et al. 2012. "Understanding the role of ecohydrological feedbacks in ecosystem  
727 state change in drylands." *Ecohydrology* 5: 174–83. <https://doi.org/10.1002/eco>.
- 728 U.S. Department of Interior, Bureau of Land Management (BLM). 2018. "BLM AIM  
729 TerrADat TerrestrialAIM point." BLM National Operations Center: BLM. [https://gis.bl  
m.gov/AIMdownload/layerpackages/BLM\\_AIM\\_Terrestrial.lpk](https://gis.bl<br/>730 m.gov/AIMdownload/layerpackages/BLM_AIM_Terrestrial.lpk).
- 731 Vandvik, Vigdis, Kari Klanderud, Eric Meineri, Inger E. Måren, and Joachim Töpper. 2016.  
732 "Seed banks are biodiversity reservoirs: Species-area relationships above versus below  
733 ground." *Oikos* 125 (2): 218–28. <https://doi.org/10.1111/oik.02022>.
- 734 Whisenant, Steven G. 1990. "Changing fire frequencies on Idaho's Snake River plains:  
735 ecological and management implications." In *Proceedings of the Symposium on Cheatgrass  
736 Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management.*, edited  
737 by E D McArthur, E M Romney, S D Smith, and P T Tueller, 4–10. Intermountain  
738 Research Station, Las Vegas, NV: Forest Service General Technical Report INT-276.  
739 [https://doi.org/10.1016/0006-3207\(92\)90659-B](https://doi.org/10.1016/0006-3207(92)90659-B).
- 740 Wijayratne, U. C, and D. A Pyke. 2009. "Investigating seed longevity of big sagebrush  
741 (*Artemisia tridentata*): U.S. Geological Survey Open-File Report 2009-1146."
- 742 Wilcox, Bradford P., Laura Turnbull, Michael H. Young, C. Jason Williams, Sujith Ravi,  
743 Mark S. Seyfried, David R. Bowling, et al. 2012. "Invasion of shrublands by exotic grasses:  
744 ecohydrological consequences in cold versus warm deserts Bradford." *Ecohydrology* 5:  
745 160–73. <https://doi.org/10.1002/eco.247>.
- 746 Williamson, Matthew A., Erica Fleishman, Ralph C. Mac Nally, Jeanne C. Chambers,  
747 Bethany A. Bradley, David S. Dobkin, David I. Board, et al. 2019. "Fire, livestock  
748 grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass  
749 (*Bromus tectorum*) in the central Great Basin, USA." *Biological Invasions* 22 (2): 663–80.  
750 <https://doi.org/10.1007/s10530-019-02120-8>.
- 751 Wright, Boyd R., Peter K. Latz, and A. F. Zuur. 2016. "Fire severity mediates seedling  
752 recruitment patterns in slender mulga (*Acacia aptaneura*), a fire-sensitive Australian  
753 desert shrub with heat-stimulated germination." *Plant Ecology* 217 (6): 789–800. <https://doi.org/10.1007/s11258-015-0550-0>.
- 755 Young, James A ., and Raymond A . Evans. 1975. "Germinability of Seed Reserves in a Big  
756 Sagebrush Community." *Weed Science* 23 (5): 358–64. [http://www.jstor.org/stable/404  
2337](http://www.jstor.org/stable/404<br/>757 2337).
- 758 Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects  
759 Models and Extensions in Ecology with R*. Springer. [https://doi.org/10.1007/978-0-387-  
87458-6](https://doi.org/10.1007/978-0-387-<br/>760 87458-6).