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2 **Title:** Climate before and after planting drive divergent outcomes ten years after restoration of a  
3 wheat field to grassland

4 **Authors:** Adam L. Mahood\*, David M. Barnard, Jacob A. Macdonald, Timothy R. Green, Robert  
5 H. Erskine

6

7 \*corresponding author: [admahood@gmail.com](mailto:admahood@gmail.com)

8

9 **Affiliations:** Water Resources, USDA-ARS

10

11 **ORCIDs:** ALM: 0000-0003-3791-9654

12 DMB: 0000-0003-1877-3151

13 TRG: 0000-0002-1441-8008

14

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18

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20 Restoration, Interannual Climate Variability, Plant Functional Groups, Pascopyrum smithii,  
21 Western Wheatgrass

22

## 23 Abstract

24 Converting croplands to grasslands can restore ecosystem functions and services, but there is  
25 uncertainty about why some restoration treatments succeed and others do not. Existing  
26 restoration strategies tailor species compositions of seed mixes according to long-term climate  
27 means and hardiness zones. However, individual years typically deviate from average climate  
28 norms such that restoration activities may be better informed by recent conditions than with  
29 climate averages. We monitored a field in eastern Colorado that was converted from winter  
30 wheat-fallow to native perennial grassland via seeding. The same seed mix was used to seed  
31 half of the strips in 2013 (drier) and the other half in 2014 (wetter). In the strips seeded in 2013,  
32 only one native grass and one shrub species from the seed mix established widely, whereas in  
33 2014 all native grasses established. Higher soil moisture preceding seed application was  
34 positively associated with perennial grasses, while rhizomatous grasses, shrubs and introduced  
35 annuals were associated with other variables. After seeding, high summer soil moisture was  
36 positively associated with a rhizomatous C3 grass, while the planted C4 bunchgrasses were  
37 negatively associated with high summer soil moisture and positively associated with high fall soil  
38 temperatures. We found evidence of facilitatory interactions between grasses and forbs, and  
39 antagonistic interactions between native perennial grasses and introduced annuals. These  
40 findings highlight the potential for land managers to improve upon current approaches by  
41 considering antecedent and forecasted conditions during restoration planning.

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## 46 Introduction

47 Understanding how species diversity develops in novel ecosystems such as post agricultural  
48 landscapes is one of most important questions in plant science today ([Armstrong et al., 2023](#);  
49 [Bell et al., 2023](#)). Globally, about 15 Mkm<sup>2</sup> (10% of global land area) are currently managed as  
50 croplands, resulting in an estimated 133 Pg in cumulative carbon (C) emissions throughout  
51 human history ([Sanderman, Hengl and Fiske, 2017](#)). Reestablishing native perennial plant  
52 cover in post agricultural landscapes is an important way to restore these systems to C sinks  
53 and enhance soil stabilization, biodiversity and other ecosystem functions and services.

54 However, in order to realize these benefits, native perennial plants need to be successfully  
55 established, and this has proven difficult for many restoration practitioners in arid and semi-arid  
56 grasslands. The task is even more difficult in areas managed for long periods as intensive  
57 agriculture, because often the native seed bank is depleted, soil fertility has declined, non-native  
58 plants are abundant, and ecohydrological function is altered ([Turnbull et al., 2012](#); [Shackelford  
et al., 2021](#)). Furthermore, restoration practitioners are often guided by mean annual climate  
59 conditions when selecting species for seed mixes. But a typical year will tend to have a  
60 combination of high, low or average seasonal values of temperature, precipitation and other  
61 climate variables, and precipitation in particular can be very difficult to predict. Therefore, “mean  
62 conditions” rarely capture climate extremes that drive community responses, especially in  
63 drylands.

65

66 In the United States, the Department of Agriculture Farm Service Agency has a program called  
67 the Conservation Reserve Program (CRP) that has been paying farmers to convert cultivated  
68 land to perennial vegetation since 1985. As of 2020 there were 8.9 million hectares enrolled,  
69 with the Western Great Plains being a region with the greatest enrollment ([USDA, 2023](#)).

Landowners typically follow state- or regional-level guidelines that adhere to national prescriptions for seed application (Taliga, 2011). Often, the plant community established by CRP remains on the land with all of its associated benefits even after contracts expire (Vandever et al., 2023). Successful establishment of perennial vegetation under the CRP program has been shown to increase soil microbial function (Li et al., 2018) and biomass (Bach, Baer and Six, 2012), preserve freshwater ecosystem services (Huang et al., 2019), improve pollinator health (Ricigliano et al., 2019), and increase soil carbon mineralization (Bach, Baer and Six, 2012). More generally, conversion from cultivated annual crops to perennial grassland can increase soil organic carbon (Ye et al., 2023), and moderate soil temperatures (Huang et al., 2023). It is typically assumed that the community will reach some stable state of perennial cover after twenty or more years (Munson and Lauenroth, 2012). However, projections based on successional theory don't always come to pass (Drury and Nisbet, 1973), and divergent outcomes in restoring shortgrass prairie have been documented even 50 years after restoration (Coffin, Lauenroth and Burke, 1996).

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In addition to challenging site conditions, increasing temperatures and aridity have led to widespread declines in soil moisture (Lal et al., 2023). Regional guidance for species selection, seeding rates and timing of treatment currently follows seeding zones based on ecological site type and annual climate means (Taliga, 2011). However, as the climate continues to become warmer, drier and more variable (Yuan et al., 2023), static prescriptions may be less reliable, and it may become increasingly important to account for current and antecedent climatic conditions (Barr, Jonas and Paschke, 2017; Barak et al., 2023). Seed germination and seedling establishment are especially sensitive to short-term fluctuations in climatic conditions (Larson et al., 2015; Shriver et al., 2018), even if mean annual temperature or precipitation is suitable for a given species' climatic niche. The inter- and intra-annual timing of moisture availability and heat stress within the year of a restoration treatment is of tantamount importance for determining

96 germination, seed establishment, and community assembly (Young *et al.*, 2015; O'Connor *et al.*,  
97 2020; Werner *et al.*, 2020) compositional differences due to climate variability can have decadal  
98 legacies (Eckhoff *et al.*, 2023).

99

100 After seeding a former agricultural field to native species, the community composition changes  
101 for decades as perennial plants establish and spread, leaving less room for volunteer annuals  
102 as time passes (Munson and Lauenroth, 2012). The particular species that do establish after  
103 disturbance or a restoration treatment is dependent upon the abiotic circumstances and inter-  
104 specific ecological processes including the strength and timing of competition (Young *et al.*,  
105 2015). For example, introduced annuals can be well-adapted to unpredictable conditions  
106 (Symonides, 1988), and when abundant, can slow down the colonization of perennials due to  
107 competition for resources (Bakker *et al.*, 2003), altered nutrient fluxes (Mahood *et al.*, 2022;  
108 Yang *et al.*, 2023) and changes to hydraulic connectivity (Turnbull *et al.*, 2012). In arid  
109 grasslands, some native perennial species compete well against introduced annuals. For  
110 example, the perennial grass *Elymus elymoides* and native forbs compete favorably against one  
111 of the most notorious introduced annuals, cheatgrass (*Bromus tectorum*), by outcompeting *B.*  
112 *tectorum* for soil water in the fall (Booth, Caldwell and Stark, 2003; Leger, Goergen and Forbis  
113 De Queiroz, 2014; Porensky *et al.*, 2014). Including species in seed mixes that are able to  
114 compete against introduced annuals may speed the development of stable perennial cover  
115 (Csákvári *et al.*, 2023).

116

117 Here, we explored how antecedent environmental conditions affected long-term persistence of  
118 seeded species in a wheat field converted to grassland through CRP in North Central Colorado,  
119 USA (Fig. 1). An identical mix of eight species (Table S1) was applied in alternating strips of a  
120 wheat-fallow agricultural field for two successive years, on April 29, 2013 and May 1, 2014. Both  
121 years had similar mean annual precipitation but occurring at different times, and with different

122 antecedent climate conditions, resulting in much lower soil moisture during the 2013 seed  
123 application. Our objectives were to characterize the plant community diversity and composition  
124 in the two sets of strips, and to model how interannual climate variability affected long-term  
125 outcomes. We hypothesized that the wetter year would have greater diversity, and that pre- and  
126 post-treatment climate variables would be significant predictors of decadal outcomes for  
127 species' occurrence.

## 128 Materials and Methods

### 129 Site Description

130 The field site is located in northern Colorado on the western Great Plains of the USA (latitude =  
131 40.61 °N, longitude = 104.84 °W). Native shortgrass steppe in this region was tilled for dryland  
132 farming going back to the 1870's. The field site has a relative upland topographic position and  
133 relief of 29 m within the current 109 ha field ([Erskine et al., 2006](#)). To reduce wind and water  
134 erosion under winter wheat/fallow crop rotation during fallow periods (14 out of every 24  
135 months), the original half section (320 ac = 129.5 ha) of land was divided into strips of  
136 approximately 135 m width and ~800 m lengths oriented north-south. The field was planted into  
137 native grasses under CRP for the first time in circa 1988, and an eastern portion of the half  
138 section (not studied here) remained in grassland upon subsequent development of an oil well.  
139 The portion west of the oil well (109 ha) was tilled again in the 1990's into 12 alternating strips of  
140 wheat/fallow, each with a new declination of ~12° east of true north and ~120 m width (**Fig 1**).  
141 The original strips are apparent in 1985 Landsat images, and relics remain in later imagery  
142 indicating the potential for legacy seed bank effects that may have impacted current plant  
143 communities. Mapped soil units are Wagonwheel coarse silty loam (a coarse-silty, mixed,  
144 superactive, mesic Aridic Calciustept), Colby fine silty loam (a fine-silty, mixed, superactive,

145 calcareous, mesic Aridic Ustorthent), and Kim fine sandy loam (a fine-loamy, mixed, active,  
146 calcareous, mesic Ustic Torriorthents). Detailed soil horizons and textural information are given  
147 in Green and Erskine (2011, Table 1 therein).

148

149 The mean annual precipitation (2002-2022) is 308 mm, while the mean annual potential  
150 evapotranspiration is ~1200 mm, with a corresponding aridity index of 3.9. Annual precipitation  
151 was 384 mm in 2013 and 396 mm in 2014. Average temperature for the years preceding  
152 planting were 9.6 degrees C for 2013 and 9.0 degrees C for 2014. All together, the 12 month  
153 Standardized Precipitation Evaporation Index (SPEI) (Vicente-Serrano, Beguería and López-  
154 Moreno, 2010) was anomalously low prior to the 2013 seeding application, and closer to normal  
155 preceding the second seed application (**Fig. 1A**).

156

157 The existing CRP treatment was implemented via drill seeding in two stages, with the same  
158 seed mix of 8 species (**Table S1** has seed application rates). One set of alternating crop strips  
159 (**Fig. 1B**) was planted on April 29, 2013, and the second set was planted on May 1, 2014, with  
160 no post-seeding management interventions. Prior to the CRP plantings, the first set was planted  
161 to winter wheat on Oct. 3, 2011, which was harvested on July 5, 2012, then maintained in fallow  
162 prior to CRP seed application using shallow tillage. The second set was planted into the same  
163 variety of wheat on Oct. 5, 2012 and never harvested due to low grain yield. After planting,  
164 some “volunteer” wheat was observed along with the CRP mix of species. In both sets of strips,  
165 alfalfa was dominant in the first year. We note that, after the establishment of perennial  
166 vegetation under CRP, there has been no surface runoff whereas numerous runoff events were  
167 observed pre-CRP.

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172 **Field sampling**

173 In June 2022, we sampled 88 5 m x 5 m plots that were collocated with areas previously  
174 sampled for soil macronutrients ([Sherrod, Erskine and Green, 2015](#)), aligned with a 5m digital  
175 elevation model (DEM) ([Erskine et al., 2006](#)). Each of the 12 strips had about 7 plots, with 49  
176 plots in the strips seeded in 2014, and 39 plots sampled for the strips sampled in 2013 )Figure  
177 S1). Within each plot, we established 4, 0.1 m<sup>2</sup> subplots (31.6 cm x 31.6 cm) at random  
178 locations. In each subplot, we used ocular estimates to measure the fractional cover of every  
179 species, as well as the cover of bare ground, litter, and rocks. We measured the maximum  
180 height of each species in each subplot, and did a gridded plant walkabout to detect all species  
181 in the 25 m<sup>2</sup> plot.

182 **Ancillary data**

183 Erskine et al. ([2006](#)) described the topographic attributes based on a survey-grade 5-m digital  
184 elevation model (DEM), which revealed potential flowpaths and accumulation areas along with  
185 variable slopes up to 13%. The DEM was used to create grids of topographic wetness index  
186 (TWI), topographic position index (TPI), slope, and folded aspect. Four or more frequency  
187 domain sensors (Sentek™) ([Schwank et al., 2006](#)) were installed at 18 locations at depths  
188 ranging from 30 to 170 cm to measure hourly soil moisture from 2002-2018. Each of 18  
189 locations has sensors at a depth of 30 cm. Soil temperature was measured using stand-alone  
190 thermocouple sensors (Onset WaterTempPro™) at a 30 cm depth near each Sentek probe  
191 ([Green and Erskine, 2011](#)). Sixteen of these sensors were installed in two lines in adjacent  
192 strips in the eastern side of the field that captured the range of topographic variability of the  
193 field, and 2 more were placed at the far western edge of the field. The 30cm sensors represent

194 soil moisture from 25-35 cm. Sensors needed to be buried at this depth to allow the farmer to  
195 apply shallow tillage while the field was in wheat/fallow rotation.

196

197

198 We used the topographic layers as predictors in a spatial process model ([Nychka et al., 2021](#)) to  
199 estimate seasonal averages of 30 cm soil temperature and moisture at a 5 m resolution (**Fig.**  
200 **S1**) for three time periods preceding seeding, and three post-seeding. Pre-seeding time periods  
201 were March and April to capture the conditions immediately preceding seeding, December,  
202 January and February to capture winter freezing conditions, and September,- November, since  
203 many species actually germinate in fall and overwinter before growing in the spring. Post-  
204 seeding time periods were May and June to capture the early summer when most plants are  
205 actively growing and peak greenness occurs, July-September to capture the hottest part of the  
206 summer when most drought stress occurs, and October-December to capture the onset of cold  
207 after seeding. Soil total nitrogen content was measured from soil cores at each sampling  
208 location in 2012 ([Sherrod, Erskine and Green, 2015](#)).

## 209 Statistical analysis

210 We used nonmetric multidimensional scaling (NMDS) ([Minchin, 1987](#)) to examine how species  
211 composition and abundance differed between the two CRP applications at the plot scale. We  
212 created one ordination using cover data to understand abundances, and another after  
213 converting the abundance matrix to an occurrence matrix to examine species composition. We  
214 used stress plots to assess the fit of the NMDS ordinations. To examine how individual species  
215 drove the ordinations, we used a permutational correlation with an alpha of  $p < 0.001$  to account  
216 for multiple tests. We calculated the Shannon-Weaver diversity index ([Shannon and Weaver,](#)  
217 [1949](#)) and the species richness for each plot for native species.

218

219 To investigate the persistence of individual species in response to pre- and post-treatment  
220 conditions, we created a joint species distribution model (JSDM) in a Bayesian hierarchical  
221 framework ([Tikhonov et al., 2020](#)) for the occurrence of all species at the 0.1 m<sup>2</sup> quadrat scale  
222 (4 per plot). We modeled occurrence rather than abundance because abundance can be much  
223 more variable from year to year than occurrence, and we were primarily interested in capturing  
224 long-term persistence. This model allowed us to estimate the probability of species occurrence  
225 while also accounting for inter-specific interactions and species traits. Because the model is  
226 estimating the occurrence of species, it has difficulty with species that only occur at one or two  
227 plots. Therefore, we grouped locally rare species with other functionally similar species (**Table**  
228 **S1**). The covariates were the seasonal averages of soil temperature and soil moisture surfaces,  
229 along with the total nitrogen content in the top 15 cm of soil measured in 2012, 2022 bare  
230 ground cover, year of seed application, and topographic wetness index. Random effects were  
231 the strip number and the plot identity. Traits included in the model were presence in the seed  
232 mix, maximum height, introduced, perennial, woody, graminoid, rhizomatous, and  
233 photosynthetic pathway (C3 or C4; **Table S4**).

234

235 We created four Markov Chain Monte Carlo (MCMC) chains, each consisting of 7,500,000  
236 iterations. We discarded the first 2,500,000 iterations for each chain and then recorded every  
237 5,000th sample for a total of 1,000 posterior samples per chain, and 4,000 total. We assessed  
238 model convergence using the effective sample size (ESS) and the potential scale reduction  
239 factor ( $\hat{R}$ ) (Gelman and Rubin, 1992). We used Tjur R<sup>2</sup> to assess explanatory power of the  
240 model.

241

242 We observed throughout much of the field either high abundance of *P. smithii* or *B. tectorum*,  
243 but usually not both, and so we hypothesized that *P. smithii* was competing directly with *B.*

244 *tectorum*. The approach described above quantifies interspecific interactions using occurrence  
245 data, and we wanted to examine this interaction further using abundance data. Therefore, we  
246 created a Bayesian hierarchical model (Bürkner, 2017) with *B. tectorum* occurrence in a 0.1 m<sup>2</sup>  
247 subplot as a Bernoulli-distributed response, with the cover of *P. smithii* and other prevalent  
248 species and bare ground as predictors, with plot as a random effect. We also created an  
249 opposite model with the occurrence of the other prevalent species as a multivariate response  
250 variable, *B. tectorum* and bare ground cover as predictors, with plot as a random effect.

251

252 All of the analyses were conducted in R (R Core Team, 2021). **Table S2** lists all packages used.

253

## 254 Results

### 255 Species composition outcomes

256 The long-term outcomes in species composition after restoration were markedly different  
257 depending on seeding year. Across the field three introduced species, *B. tectorum*, *Bassia*  
258 *scoparia*, and *Salsola tragus*, along with the native *P. smithii*, were ubiquitous regardless of strip  
259 number and year of seed application. Strips seeded in 2013 were characterized by low density  
260 of *Atriplex canescens*, abundant cover of *P. smithii* and low cover of other perennial grass  
261 species (**Fig. S2**). Strips seeded in 2014 had only a few scattered individuals of *A. canescens*,  
262 and had abundant native perennials from the CRP mix. The strips seeded in 2014 had higher  
263 native diversity (**Fig. 2**). Our NMDS analyses in **Figure 2** reflected this, with the occurrence-  
264 based ordination (non-metric fit R<sup>2</sup> = 0.954) showing little overlap between the two years of seed  
265 application, but with more overlap from the abundance-based ordination (non-metric fit R<sup>2</sup> =  
266 0.932), reflecting the high relative abundance of the four species. We found scattered

267 individuals of 15 native forb, grass and shrub species not in the species mix (**Table S1**). Of  
268 those species, six (all forbs) were found in 0.1 m<sup>2</sup> subplots and included in the model, grouped  
269 together as native forbs.

## 270 Interspecific analysis

271 The joint species distribution model converged well. The environmental filter and trait  
272 parameters had high ESS (close to the posterior sample sizes) and  $\hat{R}$  values near 1.0, while  
273 residual species associations were slightly less well converged but still acceptable (**Fig. S3**).  
274 Tjur R<sup>2</sup> values ranged from near zero to 0.75 (**Fig. S4**), The dominant species mentioned above  
275 had R<sup>2</sup> values from 0.15 - 0.65. The “Introduced Annual Bromus” group (**Table S1**) from the  
276 model groups together *B. tectorum*, which was very common and abundant, with *B. secalinus*,  
277 of which we encountered one individual plant. Hereafter we will refer to this group as simply *B.*  
278 *tectorum*. The “Introduced Cichorioideae” group contains three species, *Tragopogon dubius*  
279 Scop., *Taraxacum officinale* L., and *Scorzonera laciniata* L. which are all rosette-forming, wind-  
280 dispersed, non-native species in the Cichorioideae subfamily of Asteraceae.

281

282 Pre-treatment conditions had predictable effects on species occurrence that showed patterns  
283 among functional types (**Fig. 3**). Caespitose perennial native grasses all had strong positive  
284 associations with spring soil moisture. The most prevalent annual introduced grasses, (*S.*  
285 *cereale* & *B. tectorum*) were insensitive to spring soil moisture but positively associated with  
286 spring soil temperature, while the most prevalent introduced forbs, *B. scoparia* and *S. tragus*  
287 were more strongly associated with fall and winter conditions before seeding. *A. canescens*, the  
288 shrub that was widely established in the strips seeded in 2013, was more sensitive to higher soil  
289 temperatures in the fall preceding seeding, and more exposed topographic positions (i.e. low

290 TWI, **Fig. 3**). The three highly prevalent non-native species (*B. tectorum*, *B. scoparia*, and *S.*  
291 *tragus*) all had weak associations with spring soil moisture.  
292 Post-treatment conditions also had predictable effects on species occurrence that showed  
293 patterns among functional types groups (**Fig. 4**). Effects of the conditions immediately after  
294 treatment were mostly weak. High soil moisture conditions in the hottest part of the summer  
295 were positively associated with the occurrence of the rhizomatous C3 grass *P. smithii*, and  
296 negatively associated with the C4 bunchgrasses. Warmer fall soil temperatures after seeding  
297 were positively associated with the seeded C4 bunchgrasses, and *P. smithii* had no response.  
298 For the highly prevalent introduced plants, *B. tectorum* had strong negative associations with  
299 high summer soil temperatures, while *S. tragus* and *B. scoparia* had strong positive associations  
300 with spring soil moisture and fall soil temperatures, and strong negative associations with  
301 summer soil temperatures.

302

303 There were several associations between life history traits and climate around the time of  
304 planting (**Fig. S5**). Fall soil temperature after planting was positively associated with C4 species  
305 and negatively associated with height. High spring soil moisture before planting was associated  
306 positively with Perennials. High spring soil temperature before planting was associated with  
307 graminoids. High summer soil moisture after treatment was negatively associated with C4  
308 species and positively associated with height. Summer soil temperatures after planting were  
309 positively associated with height. High topographic wetness index was associated negatively  
310 with height.

311

312 After accounting for the effect of environment and life history traits, there were two main groups  
313 of species that were positively correlated within the group, and negatively correlated between  
314 the two groups (**Fig. 5**). The first group (G1) was composed of the introduced annuals *B.*  
315 *tectorum*, *B. secalinus* (grouped) and *B. scoparia*. The second group (G2) consisted of all of the

316 perennial native grasses in the CRP mix except *N. viridis*, along with *S. tragus*, introduced  
317 annual mustards, and native forbs.

318

319 Our models of the interaction of *B. tectorum* with *P. smithii* converged well (all Rhat values  
320 approximately 1, ESS > 1000) and suggested that *B. tectorum* and *P. smithii* appear to compete  
321 directly, aligning with our field observations. For most of the species that had strong residual  
322 correlations with *B. tectorum* in the occurrence model, their abundances had weak effects on  
323 the occurrence of *B. tectorum*. Only the abundances of *P. smithii*, invasive annual Brassicaceae  
324 species, and *B. curtipendula* had strong negative associations with *B. tectorum* occurrence (**Fig.**  
325 **S5**). In the other direction, *B. tectorum* abundance only had negative effects on *P. smithii*  
326 occurrence (**Fig. S5**).

## 327 Discussion

328 We found that climate and soil moisture conditions before and after planting strongly affected  
329 long-term restoration outcomes in terms of species composition. Reaching community stability  
330 and restoring ecosystem function may take as long as 20 years ([Munson and Lauenroth, 2012](#)),  
331 which implies that we are looking at a snapshot along the recovery trajectory, and that full  
332 perennial cover may not be guaranteed or even expected ([Drury and Nisbet, 1973](#); [Coffin,](#)  
333 [Lauenroth and Burke, 1996](#)). Thus far, our observations follow established understanding, as  
334 germination and seedling survival are highly dependent upon abiotic conditions during the short  
335 period of time that plants are in those stages of their life cycles ([Larson et al., 2015](#); [O'Connor](#)  
336 [et al., 2020](#)). They also align with other results in more mesic great plains post-agricultural  
337 landscapes showing that year effects resulting from interannual climate variability can persist for  
338 as much as a decade ([Adler and Levine, 2007](#); [Manning and Baer, 2018](#); [Eckhoff et al., 2023](#)).

339

340 There is some uncertainty about why soil moisture was different for the two seed applications.  
341 We believe weather was the main driver, but it is possible that this was complicated by  
342 differential management pre-planting. The first planting was preceded by wheat harvest in July  
343 2012 and subsequent shallow tillage to maintain the fallow state, and the wheat stubble and  
344 residue may have provided some mulching effect, limiting evaporative losses. For the second  
345 planting, the wheat crop was unproductive and not harvested, with less stem density than the  
346 prior year's wheat residue and stubble, but with greater standing biomass. It is possible that  
347 shading/mulching was greater in these strips, but we argue these effects would have been  
348 minimal. We included strip identity and planting year as random and fixed effects, respectively,  
349 in the JSDM and those terms had minimal effects. Planting year had neutral effects on every  
350 species and explained 4.9% of the variation for the average species, while strip identity  
351 explained 3.5% on average. These potential confounding effects would not invalidate the model  
352 since we used direct measurements of soil moisture rather than downscaled climate data.

353

354 There were positive residual associations between grasses and forbs in both introduced annual  
355 groups (G1) and native species groups (G2) (**Fig. 5**). Grass-forb mutualisms may be an  
356 adaptation to interannual climate variability in grasslands ([Hallett et al., 2019](#)). Native grasses  
357 positively associated with each other in G2 suggests facilitation between species, and so  
358 planting these species together may increase their probability of persistence. Future research  
359 over a broader geographical range that includes more species could examine inter-specific  
360 associations in greater detail, and provide insight on which species to seed together in order to  
361 incorporate facilitative interactions with different climatic responses to improve restoration  
362 outcomes. Positive association of non-seeded native forbs with native grasses within G2 (**Fig.**  
363 **5**) highlights the potential for low-diversity CRP treatments, such as that included in this study,  
364 to facilitate volunteer establishment of native plants from nearby areas or from the seed bank  
365 over long periods of time. Positive residual correlations also existed between *B. tectorum* and *B.*

366 *scoparia* (G1), and this group had negative associations with the mostly native G2. This  
367 suggests that introduced annual forbs may play a role in facilitating the persistence and  
368 dominance of introduced annual grasses. Residual correlations in occurrence should be viewed  
369 skeptically because they are not necessarily definitive evidence of mechanistic interactions  
370 between species ([Blanchet, Cazelles and Gravel, 2020](#)). Still, if there were mechanistic  
371 interactions between species, we would likely see residual correlations in their occurrence. With  
372 this in mind, we used abundance data to explore the interaction between *B. tectorum* and *P.*  
373 *smithii* in more detail.

374

375 *Bromus tectorum* is one of the most problematic introduced annual grasses in the western US  
376 (Mack, 1981). The work here adds to the evidence that it can have detrimental effects on plant  
377 communities in the short-grass prairie as well ([Prevéy and Seastedt, 2014](#)). *P. smithii* may be  
378 tractable as a competitively dominant native that may have a competitive advantage over *B.*  
379 *tectorum* and other introduced annuals in seed mixes (**Fig. 5**). The effect of *B. tectorum*  
380 abundance on *P. smithii* occurrence is strong, as is the opposite case. Since *P. smithii* is  
381 perennial, once it is established it may be less affected by the competitive pressure from *B.*  
382 *tectorum*, whereas *B. tectorum* occurrence in the presence of established *P. smithii* is subject to  
383 direct competition for moisture annually while it germinates and becomes established.

384

385 The *M. sativa* cover crop was anecdotally observed to be highly abundant throughout the field in  
386 the years immediately following planting. Its association with G2 (**Fig. 5**) suggests it was either  
387 an effective facilitator of seeded perennial grasses, its long-term persistence was aided by  
388 perennial grass establishment, or both. *M. sativa* is an introduced agricultural crop, but it  
389 typically does not persist in high abundance without supplemental irrigation, making it an  
390 effective temporary cover crop. Native forbs have been shown to be effective at repelling annual  
391 invasives ([Leger, Goergen and Forbis De Queiroz, 2014](#)) in Great Basin restoration treatments,

392 and perhaps native forbs could be used as cover crops in Western Great Plains CRP  
393 applications.

394

395 The near complete failure of establishment for *A. canescens* in 2014 underscores the notion  
396 that in order to have the best chance of restoring all structural and functional strata, seed mixes  
397 should have multiple species per functional group. We did not see strong residual associations  
398 between *A. canescens* and other species, which would have suggested that competition  
399 inhibited its establishment. This leaves climate around the time of planting, or competition with  
400 the temporarily dominant *M. sativa* cover crop as two potential explanations for its divergent  
401 outcomes. In this study and others, the responses of particular species to abiotic conditions  
402 corresponded broadly to functional groups (**Fig. 3**) ([Manning and Baer, 2018](#); [Eckhoff et al., 2023](#)). This suggests that in addition to following previously outlined recommendations to have  
403 high diversity in seed mixtures ([Barr, Jonas and Paschke, 2017](#)), land managers may be able to  
404 tailor species mixes according to observed antecedent conditions along with near-term forecasts  
405 while planning restoration actions, perhaps using a recruitment niche framework ([Larson et al 2023](#)).  
406  
407

408

409 Mean annual precipitation corresponds broadly to species richness and composition in more  
410 mesic restored great plains post agricultural landscapes ([Watson et al., 2021](#)). But in many  
411 places, especially in drylands, "mean conditions" might not be particularly common. At the study  
412 site, both the sum of annual precipitation (313 +- 87 mm), and the time of year that the  
413 precipitation falls are highly variable (**Table 1**). Anticipating and accounting for combinations of  
414 seasonal temperature and precipitation conditions might be a more useful approach for land  
415 managers than assuming mean annual conditions. With more research on the effects of  
416 antecedent and post-planting conditions on long-term outcomes on a broader mix of species,  
417 land managers may be able to develop regionally specific, native seed mixes tailored for

418 combinations of typical, non-mean temperature and moisture conditions (i.e. warm/dry, cold/dry,  
419 warm/wet, cold/wet). It is likely that antecedent conditions are predictive for some species, while  
420 others are more dependent on conditions following planting, or a mixture of the two. Therefore,  
421 seed mixes may have a combination of species where antecedent conditions will facilitate their  
422 establishment, along with a mixture of species that may or may not be successful depending on  
423 what conditions emerge after seeding.

424

425 Seed mixes tailored towards wet/cold conditions might take advantage of the opportunity to  
426 have success with high-diversity mixtures, with multiple species in each functional group as a  
427 bet-hedging strategy to promote the enhanced function and structure of the ecosystem. Mixes  
428 planned for warm/dry conditions could be weighted towards high abundances of competitively  
429 dominant natives to ward off introduced plants ([Leger, Goergen and Forbis De Queiroz, 2014](#);  
430 [Csákvari et al., 2023](#)), with the hope of establishing diverse mixtures in subsequent years, or  
431 even later in the same year, with subsequent treatments. Another approach may be to  
432 strategically consider seed source location when developing the seed mix. Seed sourced from  
433 hotter locations in years with hot antecedent conditions may have a greater probability of  
434 establishment.

## 435 Conclusion

436 In many places, especially drylands, above- or below-average climate conditions prevail more  
437 commonly than mean conditions, and seasonal combinations of extremes are expected. The  
438 effects of interannual and seasonal variability in climate have predictable effects on seed  
439 germination and establishment, but there are few, if any, species-level analyses of long-term  
440 outcomes after restoration seed applications ([Vaughn and Young, 2010](#)). Our results suggest  
441 that the conditions immediately before and after planting govern community assembly and leave

442 a lasting legacy. Restoration practitioners may be able to take advantage of the fact that the  
443 resultant plant communities are assembled in accordance with the response of plant functional  
444 groups and life history strategies to those conditions. Long-term restoration outcomes may be  
445 improved by composing regionally specific seed mixes tailored for common circumstances of  
446 temperature and moisture availability, and using an intra- and interannual, repeated or split  
447 seeding approach to opportunistically take advantage of favorable conditions. Regionally  
448 specific, go/no-go thresholds based on antecedent conditions may also help avoid wasting  
449 resources when success seems unlikely, if funding mechanisms allow for delay of seed  
450 application. Future research on more species at more sites may allow us to quantify  
451 regeneration niches and tease out groups of positively associated native species that, when  
452 planted together, may be more likely to persist.

## 453 Authors' contributions

454 Conceptualization: ALM, DB, TRG; Data curation: ALM, RHE; Formal Analysis: ALM; Funding  
455 acquisition: DB; Investigation: ALM, JM, RHE, TRG, DB; Methodology: ALM, JM, RHE; Project  
456 administration: ALM; Resources: ALM; Software: ALM; Supervision: DB; Validation: ALM;  
457 Visualization: ALM, JM; Writing – original draft: ALM, TRG, DB; Writing – review & editing: ALM,  
458 TRG, DB, JM, RHE

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## 463 References

- 464 Adler, P.B. and Levine, J.M. (2007) 'Contrasting relationships between precipitation and species  
465 richness in space and time', *Oikos*, 116(2), pp. 221–232. Available at:  
466 <https://doi.org/10.1111/j.0030-1299.2007.15327.x>.
- 467 Armstrong, E.M. *et al.* (2023) 'One hundred important questions facing plant science: an  
468 international perspective', *New Phytologist*, 238(2), pp. 470–481. Available at:  
469 <https://doi.org/10.1111/nph.18771>.
- 470 Bach, E.M., Baer, S.G. and Six, J. (2012) 'Plant and Soil Responses to High and Low Diversity  
471 Grassland Restoration Practices', *Environmental Management*, 49(2), pp. 412–424. Available  
472 at: <https://doi.org/10.1007/s00267-011-9787-0>.
- 473 Bakker, J.D. *et al.* (2003) 'Contingency of grassland restoration on year, site, and competition  
474 from introduced grasses', *Ecological Applications*, 13(1), pp. 137–153. Available at:  
475 [https://doi.org/10.1890/1051-0761\(2003\)013\[0137:COGROY\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0137:COGROY]2.0.CO;2).
- 476 Barak, R.S. *et al.* (2023) 'Phylogenetically and functionally diverse species mixes beget diverse  
477 experimental prairies, whether from seeds or plugs', *Restoration Ecology*, 31(1). Available at:  
478 <https://doi.org/10.1111/rec.13737>.
- 479 Barr, S., Jonas, J.L. and Paschke, M.W. (2017) 'Optimizing seed mixture diversity and seeding  
480 rates for grassland restoration: Optimizing grassland seeding', *Restoration Ecology*, 25(3),  
481 pp. 396–404. Available at: <https://doi.org/10.1111/rec.12445>.
- 482 Bell, S.M. *et al.* (2023) 'Quantifying the recarbonization of post-agricultural landscapes', *Nature  
483 Communications*, 14(1), p. 2139. Available at: <https://doi.org/10.1038/s41467-023-37907-w>.
- 484 Blanchet, F.G., Cazelles, K. and Gravel, D. (2020) 'Co-occurrence is not evidence of ecological  
485 interactions', *Ecology Letters*. Edited by E. Jeffers, 23(7), pp. 1050–1063. Available at:  
486 <https://doi.org/10.1111/ele.13525>.
- 487 Booth, M.S., Caldwell, M.M. and Stark, J.M. (2003) 'Overlapping resource use in three Great

- 488 Basin species: implications for community invasibility and vegetation dynamics', *Journal of*  
489 *Ecology*, p. 13.
- 490 Bürkner, P.-C. (2017) 'brms : An R Package for Bayesian Multilevel Models Using Stan',  
491 *Journal of Statistical Software*, 80(1). Available at: <https://doi.org/10.18637/jss.v080.i01>.
- 492 Coffin, D.P., Lauenroth, W.K. and Burke, I.C. (1996) 'Recovery of Vegetation in a Semiarid  
493 Grassland 53 Years after Disturbance', *Ecological Applications*, 6(2), pp. 538–555. Available  
494 at: <https://doi.org/10.2307/2269390>.
- 495 Csákvari, E. *et al.* (2023) 'Native species can reduce the establishment of invasive alien species  
496 if sown in high density and using competitive species', *Restoration Ecology* [Preprint].  
497 Available at: <https://doi.org/10.1111/rec.13901>.
- 498 Drury, W.H. and Nisbet, I.C.T. (1973) 'Succession', *Journal of the Arnold Arboretum*, 54(3), pp.  
499 331–368.
- 500 Eckhoff, K.D. *et al.* (2023) 'Persistent decadal differences in plant communities assembled  
501 under contrasting climate conditions', *Ecological Applications*, 33(3), p. e2823. Available at:  
502 <https://doi.org/10.1002/eap.2823>.
- 503 Erskine, R.H. *et al.* (2006) 'Comparison of grid-based algorithms for computing upslope  
504 contributing area: COMPARISON OF GRID-BASED ALGORITHMS', *Water Resources*  
505 *Research*, 42(9). Available at: <https://doi.org/10.1029/2005WR004648>.
- 506 Gelman, A. and Rubin, D.B. (1992) 'Inference from iterative simulation using multiple  
507 sequences', *Statistical science*, pp. 457–472.
- 508 Green, T.R. and Erskine, R.H. (2011) 'Measurement and inference of profile soil-water  
509 dynamics at different hillslope positions in a semiarid agricultural watershed: PROFILE SOIL-  
510 WATER DYNAMICS', *Water Resources Research*, 47(12). Available at:  
511 <https://doi.org/10.1029/2010WR010074>.
- 512 Hallett, L.M. *et al.* (2019) 'Rainfall variability maintains grass-forb species coexistence', *Ecology*  
513 *Letters*. Edited by R. Snyder, 22(10), pp. 1658–1667. Available at:

- 514 <https://doi.org/10.1111/ele.13341>.
- 515 Huang, L. *et al.* (2019) 'Land conservation can mitigate freshwater ecosystem services  
516 degradation due to climate change in a semiarid catchment: The case of the Portneuf River  
517 catchment, Idaho, USA', *Science of The Total Environment*, 651, pp. 1796–1809. Available  
518 at: <https://doi.org/10.1016/j.scitotenv.2018.09.260>.
- 519 Huang, Y. *et al.* (2023) *Plant diversity stabilizes soil temperature*. preprint. Ecology. Available at:  
520 <https://doi.org/10.1101/2023.03.13.532451>.
- 521 Lal, P. *et al.* (2023) 'Spatiotemporal evolution of global long-term patterns of soil moisture',  
522 *Science of The Total Environment*, 867, p. 161470. Available at:  
523 <https://doi.org/10.1016/j.scitotenv.2023.161470>.
- 524 Larson, J.E. *et al.* (2015) 'Seed and seedling traits affecting critical life stage transitions and  
525 recruitment outcomes in dryland grasses', *Journal of Applied Ecology*. Edited by M. Cadotte,  
526 52(1), pp. 199–209. Available at: <https://doi.org/10.1111/1365-2664.12350>.
- 527 Leger, E.A., Goergen, E.M. and Forbis De Queiroz, T. (2014) 'Can native annual forbs reduce  
528 Bromus tectorum biomass and indirectly facilitate establishment of a native perennial grass?',  
529 *Journal of Arid Environments*, 102, pp. 9–16. Available at:  
530 <https://doi.org/10.1016/j.jaridenv.2013.10.015>.
- 531 Li, C. *et al.* (2018) 'Soil microbial community restoration in Conservation Reserve Program  
532 semi-arid grasslands', *Soil Biology and Biochemistry*, 118, pp. 166–177. Available at:  
533 <https://doi.org/10.1016/j.soilbio.2017.12.001>.
- 534 Mack, R.N. (1981) 'Invasion of Bromus tectorum L. into Western North America: An ecological  
535 chronicle', *Agro-Ecosystems*, 7(2), pp. 145–165. Available at: [https://doi.org/10.1016/0304-3746\(81\)90027-5](https://doi.org/10.1016/0304-3746(81)90027-5).
- 537 Mahood, A.L. *et al.* (2022) 'Interannual climate variability mediates changes in carbon and  
538 nitrogen pools caused by annual grass invasion in a semiarid shrubland', *Global Change  
539 Biology*, 28(1), pp. 267–284. Available at: <https://doi.org/10.1111/gcb.15921>.

- 540 Manning, G.C. and Baer, S.G. (2018) 'Interannual variability in climate effects on community  
541 assembly and ecosystem functioning in restored prairie', *Ecosphere*, 9(6). Available at:  
542 <https://doi.org/10.1002/ecs2.2327>.
- 543 Minchin, P.R. (1987) 'An evaluation of the relative robustness of techniques for ecological  
544 ordination', *Vegetatio*, 69, pp. 89–107.
- 545 Munson, S.M. and Lauenroth, W.K. (2012) 'Plant Community Recovery Following Restoration in  
546 Semiarid Grasslands', *Restoration Ecology*, 20(5), pp. 656–663. Available at:  
547 <https://doi.org/10.1111/j.1526-100X.2011.00808.x>.
- 548 Nychka, D. *et al.* (2021) 'fields: Tools for spatial data'. Boulder, CO, USA: University Corporation  
549 for Atmospheric Research. Available at: <https://github.com/dnnychka/fieldsRPackage>.
- 550 O'Connor, R.C. *et al.* (2020) 'Small-scale water deficits after wildfires create long-lasting  
551 ecological impacts', *Environmental Research Letters*, 15(4), p. 044001. Available at:  
552 <https://doi.org/10.1088/1748-9326/ab79e4>.
- 553 Porensky, L.M. *et al.* (2014) 'Arid old-field restoration: Native perennial grasses suppress weeds  
554 and erosion, but also suppress native shrubs', *Agriculture, Ecosystems & Environment*, 184,  
555 pp. 135–144. Available at: <https://doi.org/10.1016/j.agee.2013.11.026>.
- 556 Prevéy, J.S. and Seastedt, T.R. (2014) 'Seasonality of precipitation interacts with exotic species  
557 to alter composition and phenology of a semi-arid grassland', *Journal of Ecology*. Edited by  
558 S. Wilson, 102(6), pp. 1549–1561. Available at: <https://doi.org/10.1111/1365-2745.12320>.
- 559 R Core Team (2021) *R: A Language and Environment for Statistical Computing*. Vienna,  
560 Austria: R Foundation for Statistical Computing. Available at: <https://www.R-project.org/>.
- 561 Ricigliano, V.A. *et al.* (2019) 'Honey bee colony performance and health are enhanced by apiary  
562 proximity to US Conservation Reserve Program (CRP) lands', *Scientific Reports*, 9(1), p.  
563 4894. Available at: <https://doi.org/10.1038/s41598-019-41281-3>.
- 564 Sanderman, J., Hengl, T. and Fiske, G.J. (2017) 'Soil carbon debt of 12,000 years of human  
565 land use', *Proceedings of the National Academy of Sciences*, 114(36), pp. 9575–9580.

- 566 Available at: <https://doi.org/10.1073/pnas.1706103114>.
- 567 Schwank, M. *et al.* (2006) 'Laboratory characterization of a commercial capacitance sensor for  
568 estimating permittivity and inferring soil water content', *Vadose Zone Journal*, 5(3), pp. 1048–  
569 1064.
- 570 Shackelford, N. *et al.* (2021) 'Drivers of seedling establishment success in dryland restoration  
571 efforts', *Nature Ecology & Evolution*, 5(9), pp. 1283–1290. Available at:  
572 <https://doi.org/10.1038/s41559-021-01510-3>.
- 573 Shannon, C.E. and Weaver, W. (1949) 'A mathematical model of communication', *Urbana, IL:*  
574 *University of Illinois Press*, 11, pp. 11–20.
- 575 Sherrod, L.A., Erskine, R.H. and Green, T.R. (2015) 'Spatial Patterns and Cross-Correlations of  
576 Temporal Changes in Soil Carbonates and Surface Elevation in a Winter Wheat-Fallow  
577 Cropping System', *Soil Science Society of America Journal*, 79(2), pp. 417–427. Available at:  
578 <https://doi.org/10.2136/sssaj2014.05.0222>.
- 579 Shriver, R.K. *et al.* (2018) 'Adapting management to a changing world: Warm temperatures, dry  
580 soil, and interannual variability limit restoration success of a dominant woody shrub in  
581 temperate drylands', *Global Change Biology*, 24(10), pp. 4972–4982. Available at:  
582 <https://doi.org/10.1111/gcb.14374>.
- 583 Symonides, E. (1988) 'On the ecology and evolution of annual plants in disturbed  
584 environments', *Vegetatio*, 77, pp. 21–31.
- 585 Taliga, C. (2011) *Plant Suitability and Seeding Rates for Conservation Plantings in Colorado.*  
586 *Plant materials technical note no. 59 (revised)*.
- 587 Tikhonov, G. *et al.* (2020) 'Joint species distribution modelling with the r -package H msc',  
588 *Methods in Ecology and Evolution*. Edited by N. Golding, 11(3), pp. 442–447. Available at:  
589 <https://doi.org/10.1111/2041-210X.13345>.
- 590 Turnbull, L. *et al.* (2012) 'Understanding the role of ecohydrological feedbacks in ecosystem  
591 state change in drylands', *Ecohydrology*, 5(2), pp. 174–183. Available at:

- 592 <https://doi.org/10.1002/eco.265>.
- 593 USDA, F.S.A. (2023) *Conservation Reserve Program*, *Conservation Reserve Program*.
- 594 Available at: <https://www.fsa.usda.gov/programs-and-services/conservation-programs/>
- 595 conservation-reserve-program/index.
- 596 Vandever, M.W. *et al.* (2023) 'Persistence and quality of vegetation cover in expired
- 597 Conservation Reserve Program fields', *Ecosphere*, 14(1). Available at:
- 598 <https://doi.org/10.1002/ecs2.4359>.
- 599 Vaughn, K.J. and Young, T.P. (2010) 'Contingent Conclusions: Year of Initiation Influences
- 600 Ecological Field Experiments, but Temporal Replication is Rare', *Restoration Ecology*,
- 601 18(s1), pp. 59–64. Available at: <https://doi.org/10.1111/j.1526-100X.2010.00714.x>.
- 602 Vicente-Serrano, S.M., Beguería, S. and López-Moreno, J.I. (2010) 'A Multiscalar Drought Index
- 603 Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index',
- 604 *Journal of Climate*, 23(7), pp. 1696–1718. Available at:
- 605 <https://doi.org/10.1175/2009JCLI2909.1>.
- 606 Watson, D.F. *et al.* (2021) 'Plant community responses to grassland restoration efforts across a
- 607 large-scale precipitation gradient', *Ecological Applications*, 31(6). Available at:
- 608 <https://doi.org/10.1002/eap.2381>.
- 609 Werner, C.M. *et al.* (2020) 'Year effects: Interannual variation as a driver of community
- 610 assembly dynamics', *Ecology*, 101(9). Available at: <https://doi.org/10.1002/ecy.3104>.
- 611 Yang, H. *et al.* (2023) 'The detection and attribution of extreme reductions in vegetation growth
- 612 across the global land surface', *Global Change Biology*, p. gcb.16595. Available at:
- 613 <https://doi.org/10.1111/gcb.16595>.
- 614 Ye, C. *et al.* (2023) 'Soil organic carbon and its stability after vegetation restoration in Zoige
- 615 grassland, eastern Qinghai-Tibet Plateau', *Restoration Ecology* [Preprint]. Available at:
- 616 <https://doi.org/10.1111/rec.13896>.

617 Young, T.P. *et al.* (2015) 'Initial success of native grasses is contingent on multiple interactions  
618 among exotic grass competition, temporal priority, rainfall and site effects', *AoB PLANTS*, 7.  
619 Available at: <https://doi.org/10.1093/aobpla/plu081>.

620 Yuan, X. *et al.* (2023) 'A global transition to flash droughts under climate change', *Science*,  
621 380(6641), pp. 187–191. Available at: <https://doi.org/10.1126/science.abn6301>.

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628 **Tables**

629 **Table 1:** Precipitation (mm) measured at the study site. Highest monthly values are bold.

630 Highest and lowest years are italicized and bold.

Year	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	Mean
<b>Jan</b>	7	1	10	5	1	7	0	0	3	2	1	9	21	3	11	19	9	6	0	3	<b>6</b>
<b>Feb</b>	20	7	8	3	6	2	0	0	10	11	13	7	7	16	12	7	17	3	7	8	<b>8</b>
<b>Mar</b>	6	45	2	33	22	37	13	7	18	8	0	15	26	5	44	29	24	46	29	23	<b>22</b>
<b>Apr</b>	7	<b>64</b>	28	47	9	20	17	69	<b>94</b>	26	13	70	4	56	<b>59</b>	57	16	32	21	48	<b>38</b>
<b>May</b>	<b>42</b>	55	33	37	26	29	41	43	79	<b>119</b>	45	47	82	<b>153</b>	46	<b>111</b>	<b>95</b>	<b>66</b>	<b>47</b>	<b>68</b>	<b>63</b>
<b>Jun</b>	33	43	<b>55</b>	<b>104</b>	6	11	50	83	51	35	15	17	52	51	38	4	33	44	43	21	<b>39</b>
<b>Jul</b>	9	4	28	6	<b>28</b>	<b>62</b>	9	51	75	94	<b>91</b>	43	<b>101</b>	57	12	32	41	21	3	17	<b>39</b>
<b>Aug</b>	16	44	35	14	10	37	<b>105</b>	31	37	5	0	40	24	20	23	54	8	17	11	9	<b>27</b>
<b>Sep</b>	23	11	53	3	16	24	37	12	2	17	40	<b>111</b>	31	2	8	35	5	25	13	11	<b>24</b>
<b>Oct</b>	11	1	24	74	20	0	12	<b>132</b>	18	56	21	21	12	54	10	26	16	15	15	7	<b>27</b>
<b>Nov</b>	10	6	8	6	9	3	2	10	24	10	4	5	16	23	4	9	10	20	8	10	<b>10</b>
<b>Dec</b>	0	8	0	1	<b>28</b>	7	6	18	8	12	3	9	10	22	8	4	1	21	11	8	<b>9</b>
<b>Sum</b>	183	289	285	334	<b>181</b>	238	293	456	418	396	247	394	386	<b>462</b>	276	388	275	316	210	232	<b>313</b>

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632

## 633 Figure Captions

634 **Figure 1:** A shows 12 month SPEI at the site from 2010-2022, and B shows monthly  
635 precipitation for 2013-2014. C shows the alternating strips in summer 2014, before pants had  
636 established in the 2014 strips. D is a high-resolution image showing individual shrub canopies  
637 throughout the 2013 strips and absent in the 2014 strips. E was taken on the ground in 2023 at  
638 the strip boundary. F shows the location.

639 **Figure 2.** Species composition and diversity. A is an NMDS using abundance data, and B is an  
640 NMDS using occurrence data. Four letter species codes (Table S1) correspond with the species  
641 that were significantly correlated ( $p < 0.001$ ) with the ordination. C is the Shannon-Weaver  
642 diversity index, and D is species richness and for each plot. Horizontal black bars in C and C  
643 are the medians. Abbreviations: ATCA = Atriplex canescens, BASC = Bassia scoparia, BOCU =  
644 Bouteloua curtipendula, BRTE = Bromus tectorum, CHBE = Chenopodium belanderia, COAR  
645 Convolvulus arvensis, HEVI Heterotheca villosa, MESA = Medicago sativa, NAVI = Nassella  
646 viridula, PASM = Pascopyrum smithii, SATR = Salsola tragus, SCSC = Schizachyrium  
647 scoparium, SIAL = Sisymbrium altissimum, PAVI = Panicum virgatum

648 **Figure 3.** Posterior distributions of parameter estimates for conditions before seeding by  
649 species. Species are sorted top to bottom according to prevalence. Native species are above  
650 the bold line, introduced below with a grey background, graminoids are above the dotted lines,  
651 and non-graminoids are below. Posterior distributions from each chain overlap to highlight  
652 model convergence. Vertical Dotted lines are zero. Distributions with a median closer to zero  
653 are more transparent. Species above the thick horizontal line are native. Blue is positive, red is  
654 negative. **Abbreviations:** ST = soil temperature, SM = soil moisture, AT = air temperature, TWI  
655 = Topographic Wetness Index. Full species names are given in **Table S1** and **Figure 5**.

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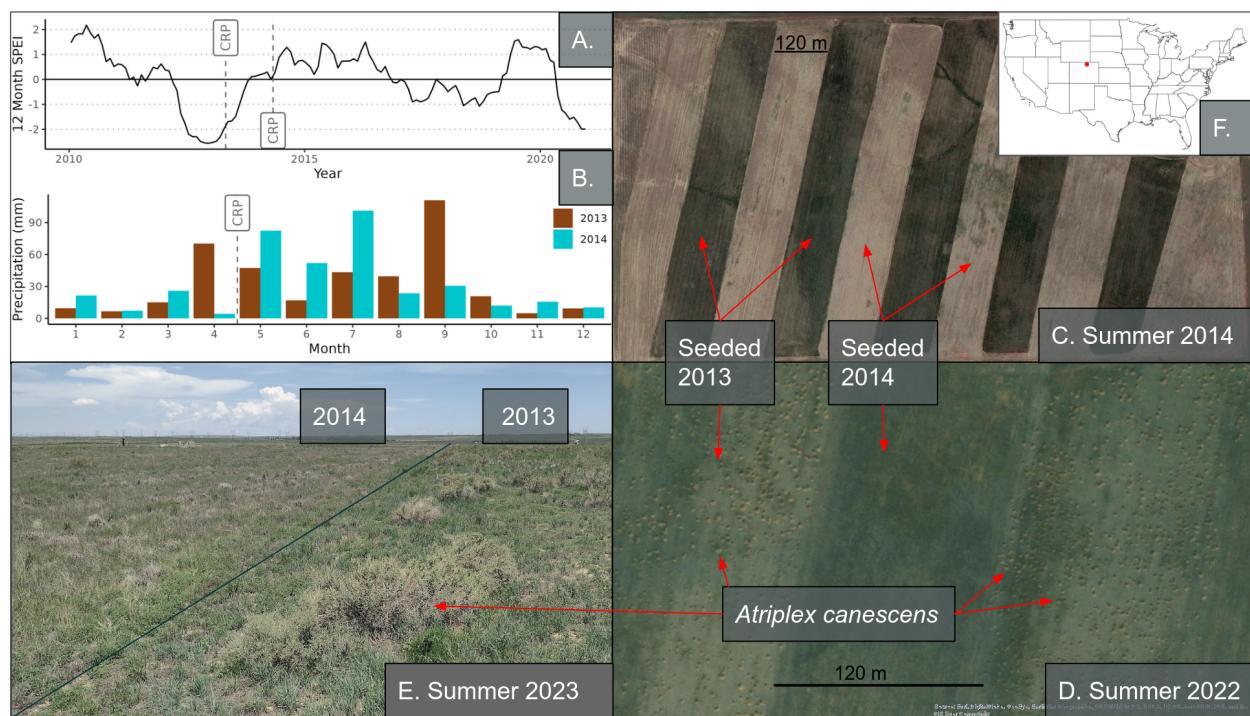
657 **Figure 4.** Posterior distributions of parameter estimates for conditions after seeding by species.  
 658 Plot arrangement is the same as in **Figure 3**.

659

660 **Figure 5:** Residual correlations of species occurrences. The three species at the bottom are  
 661 introduced annual *Bromus* spp, *Secale cereale* and *Bassia scoparia*, a group (G1) with positive  
 662 intragroup associations that appears to be negatively interacting with a group of mostly native  
 663 species (G2, top right) that have positive intragroup associations. Table S1 has abbreviations.

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## 665 Figures



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667 Figure 1

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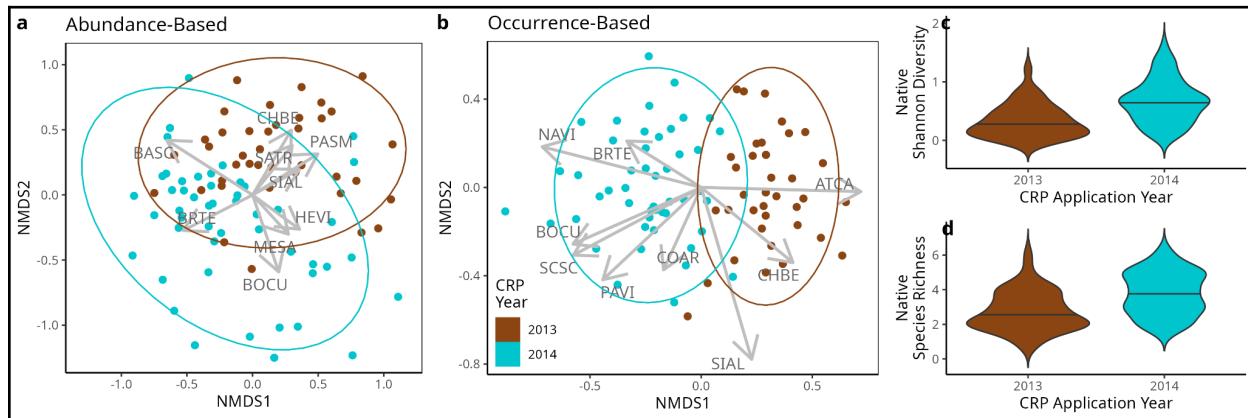
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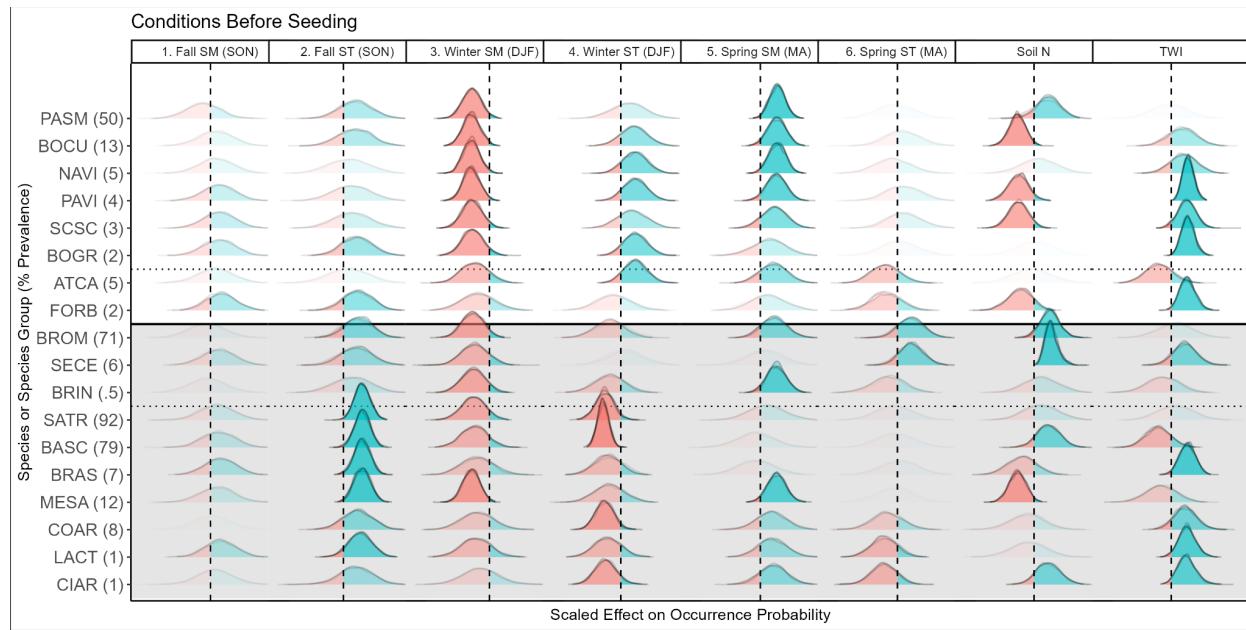
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675 Figure 2

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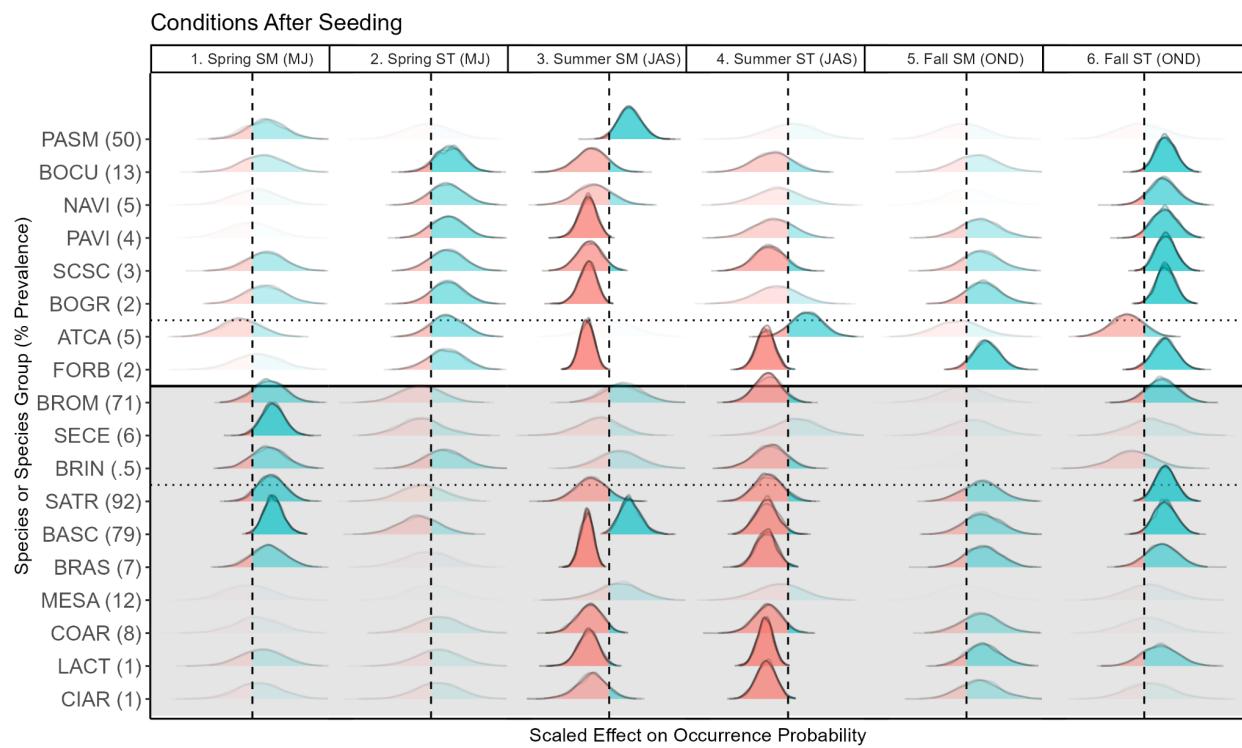


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679 Figure 3

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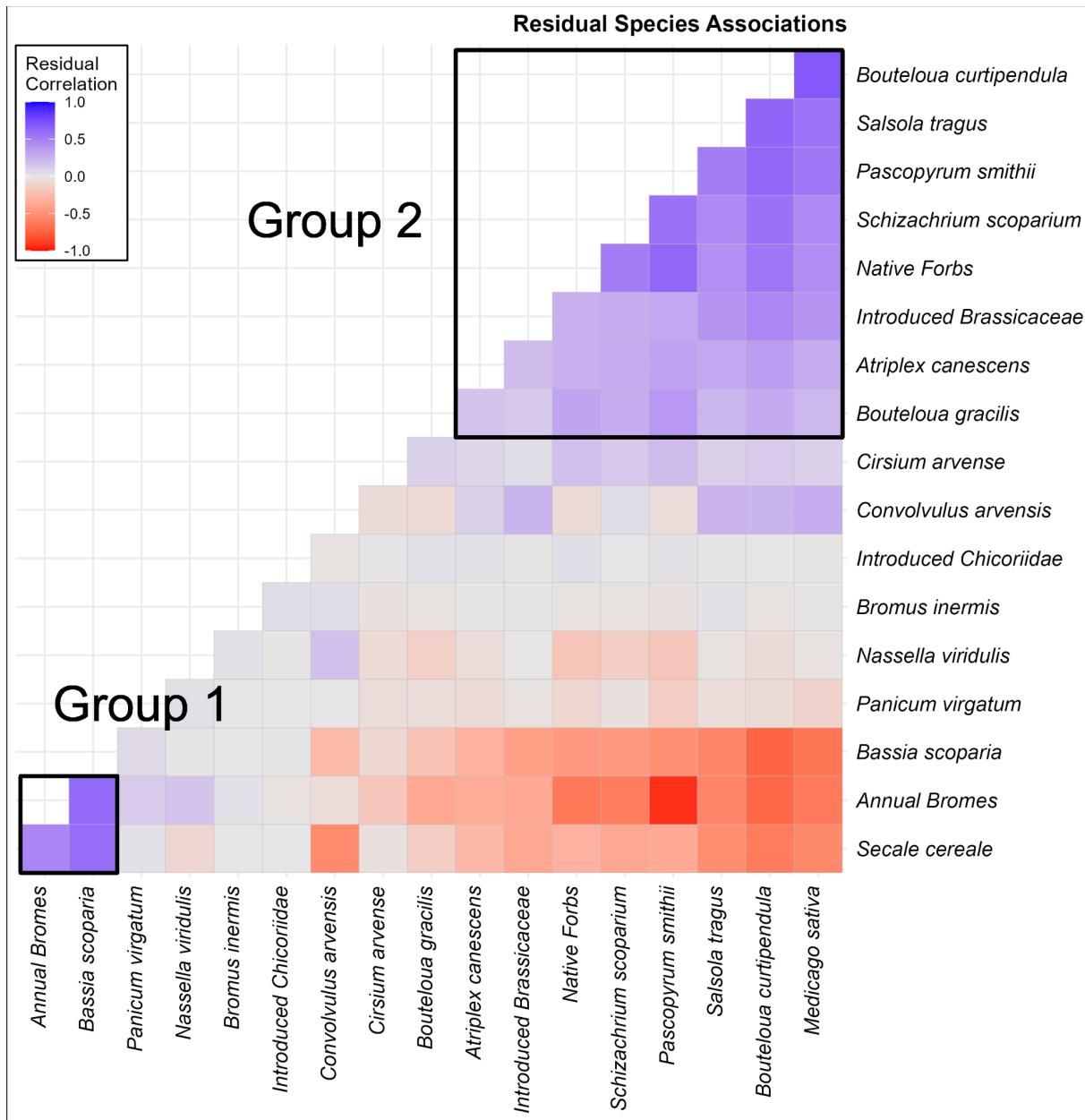
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683 Figure 4

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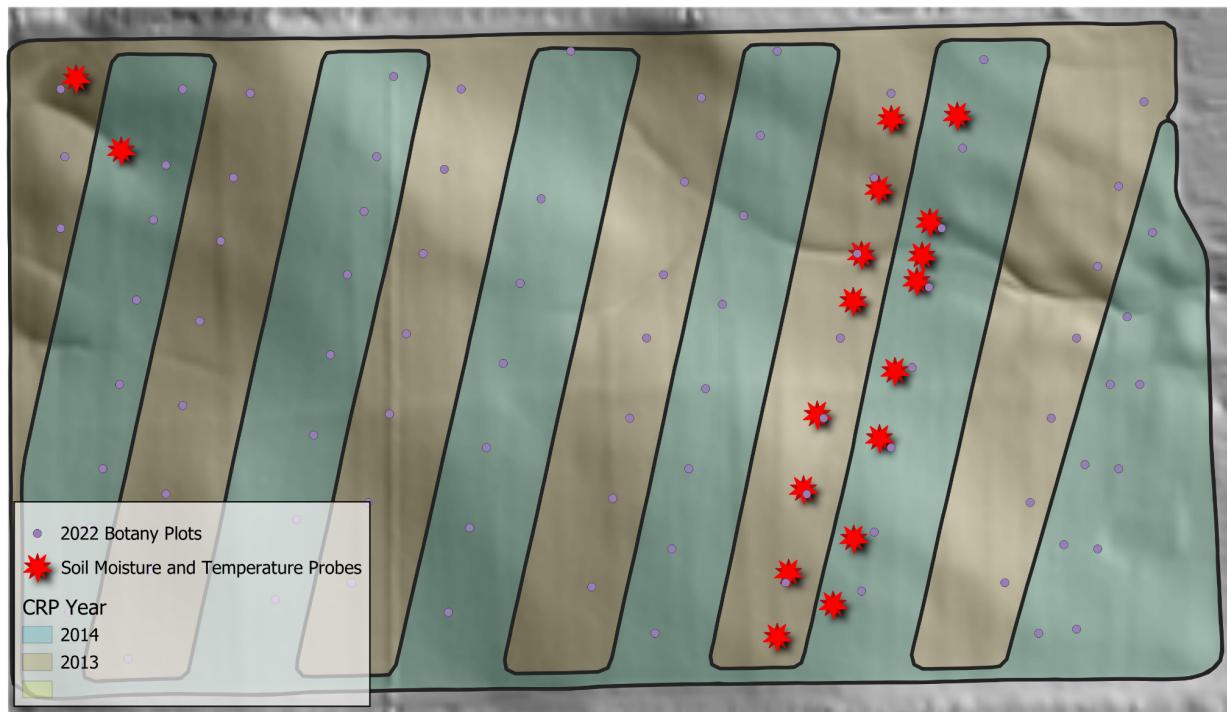
686 Figure 5

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688 

## Supplementary Figures and Tables

689

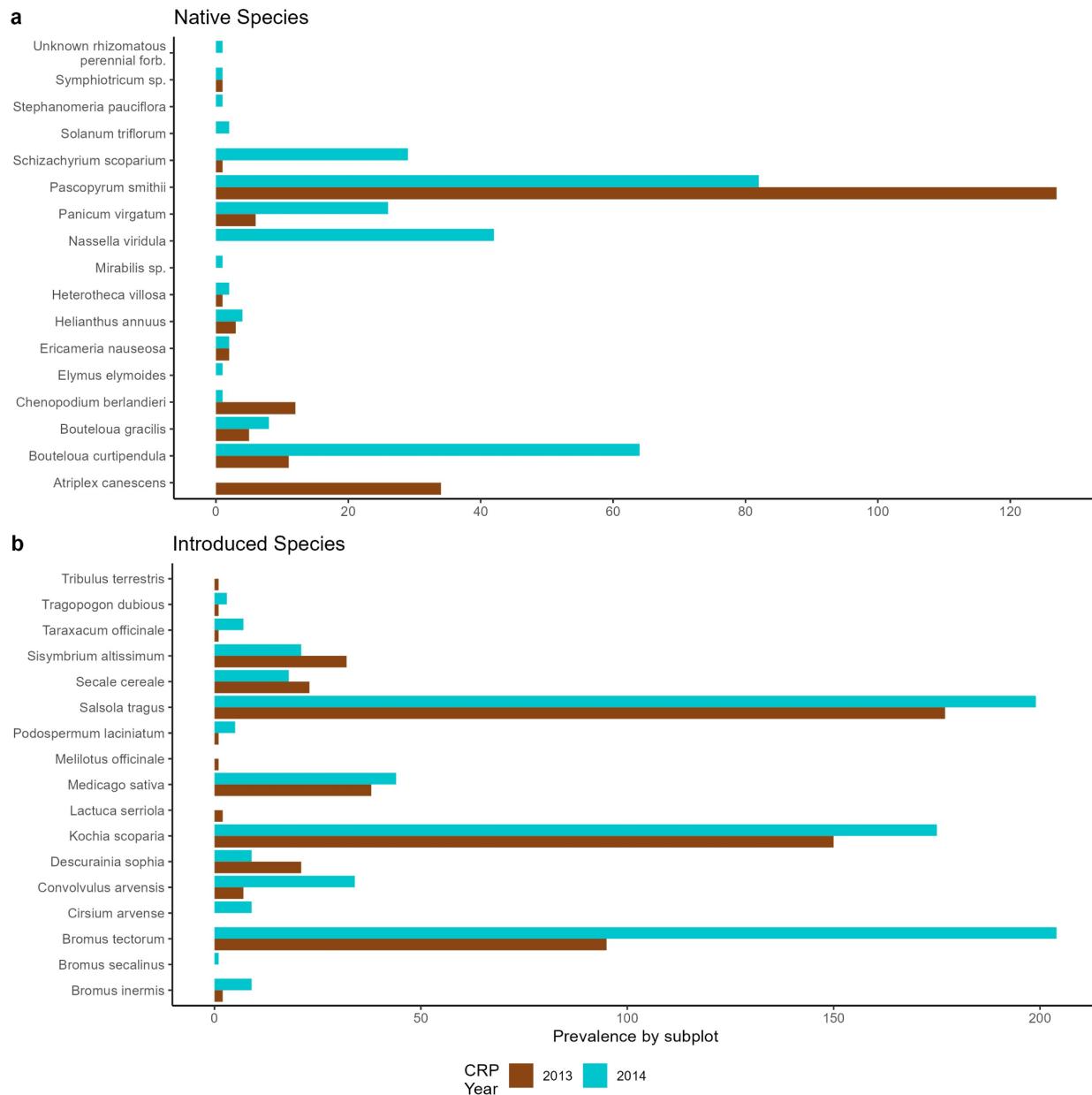


690

691 **Figure S1.** The study site. The background is a 5m digital elevation model, stars indicate the  
692 locations of soil temperature and moisture probes, dots indicate the location of 2022 botany  
693 plots, and the shaded areas indicate the year that the CRP seeding application was conducted.  
694 Probe locations were chosen to represent the range of topographic complexity while also  
695 allowing for the comparison of the effect of management. .

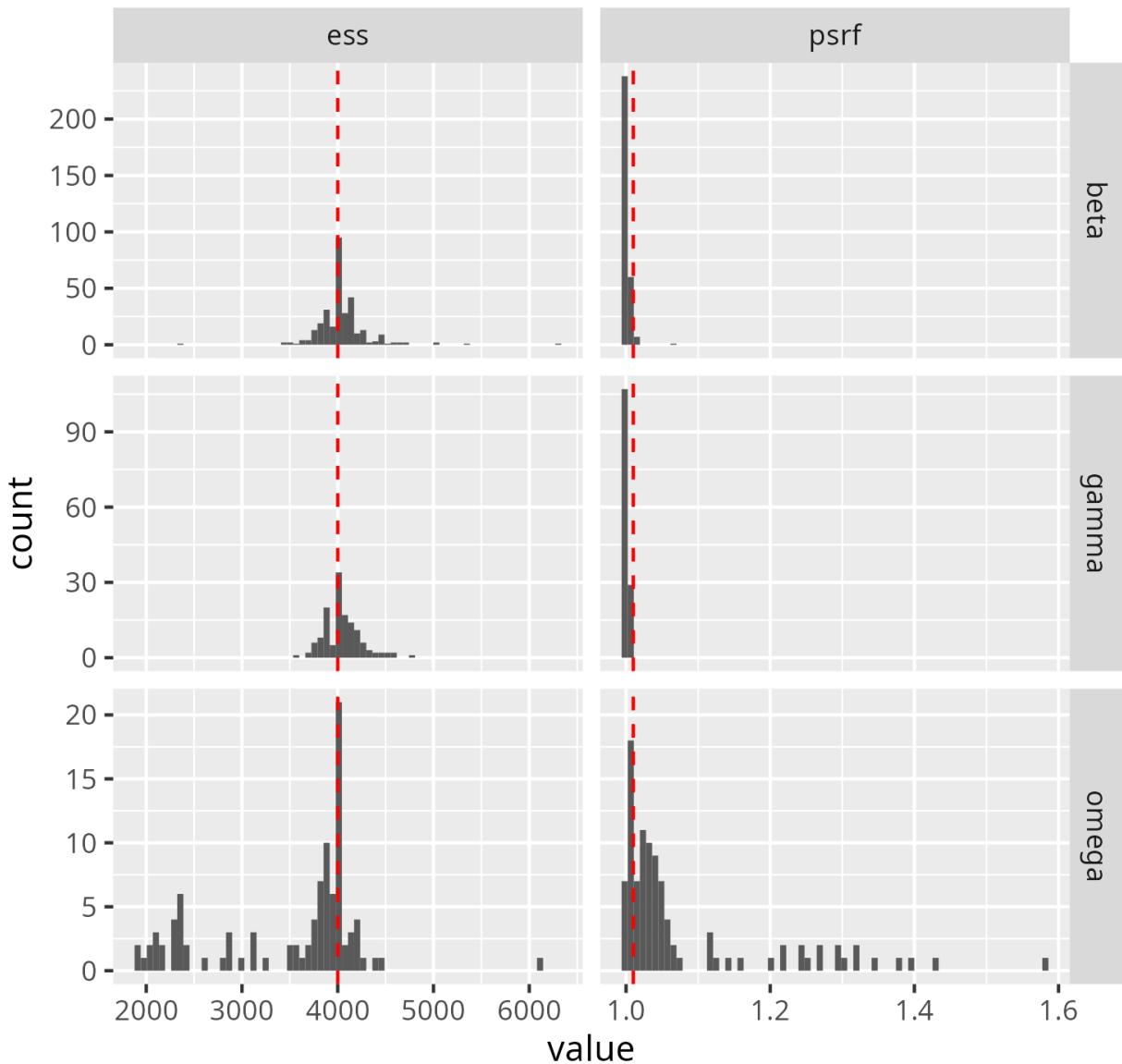
696

697



699 **Figure S2.** Species prevalence. Prevalence (number of plots in which a species was  
700 encountered) for each plant species encountered across the study site for native species (a)  
701 and introduced species (b).

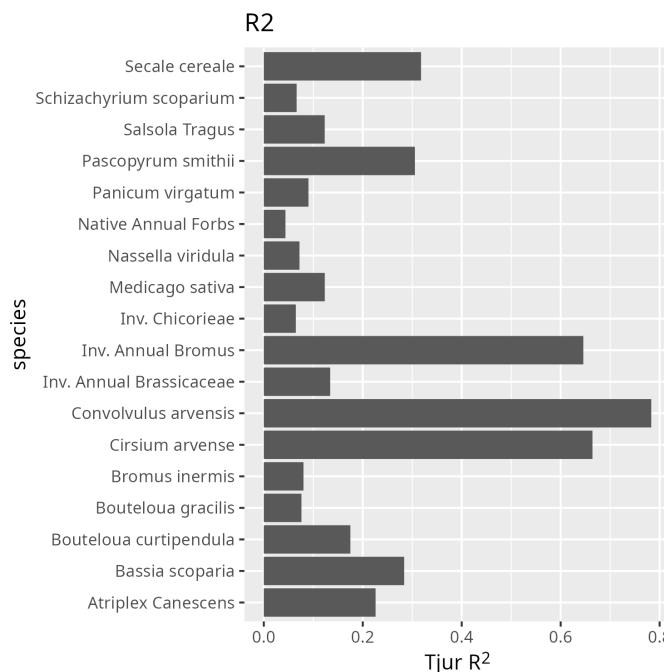
## Model Convergence



702

703 **Figure S3:** Model convergence diagnostics. The potential scale reduction factor (PSRF)  
 704 measures the convergence among chains, and being closer 1.0 is ideal. The vertical red dashed  
 705 line lies at 1.001, a sensible target for most values to be less than. Effective sample size (ESS)  
 706 measures autocorrelation between successive iterations within each chain, and higher values  
 707 are better. Ideally ESS matches the number of posterior samples (indicated by the vertical red  
 708 dashed line), but that is not fully necessary. Betas are the parameters for environmental filters,  
 709 gammas are the parameters for the traits, and omegas are the parameters for the species  
 710 associations.

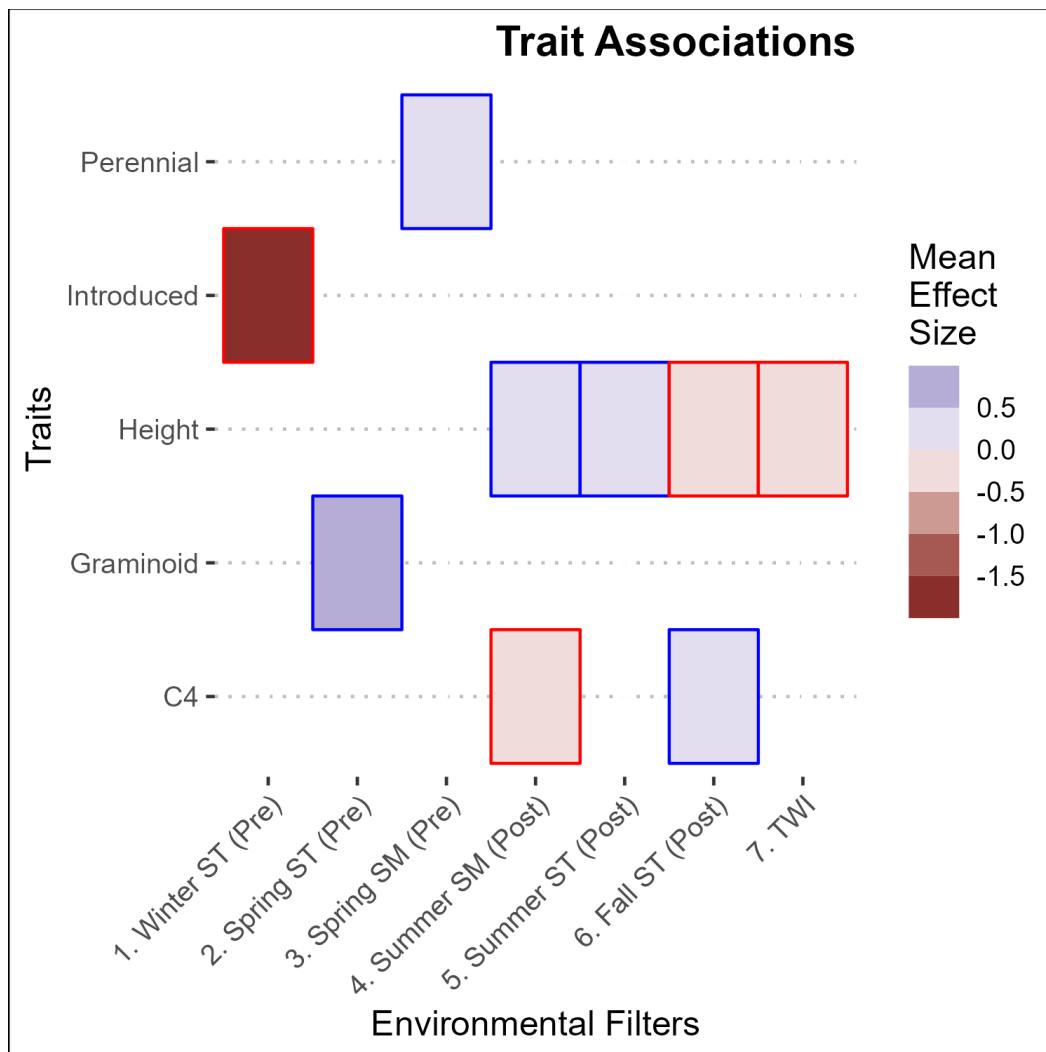
711



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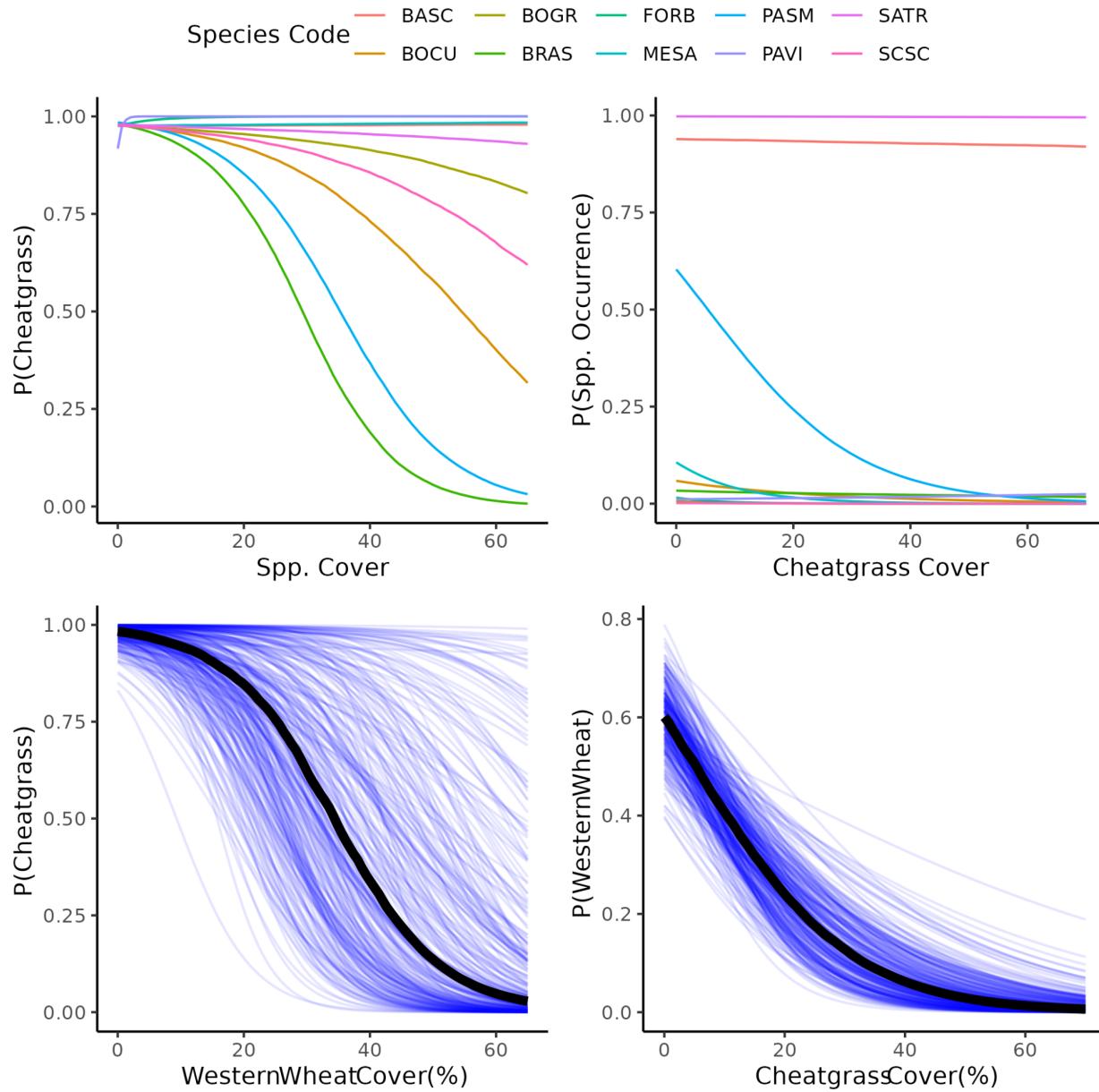
713 **Figure S4:** R2 values for each species or species group.

714



715

716 **Figure S5.** Associations between traits and environmental filters. Only associations whose  
 717 posterior estimates were 89% positive or negative are shown. Boxes with blue outlines  
 718 represent positive associations, red negative.



719

720 **Figure S6.** Western Wheatgrass and Cheatgrass interactions, compared to other species. This  
 721 is using abundance data on the y axes to estimate the occurrence of a given species. *P. smithii*  
 722 and cheatgrass had strong effects on each others' occurrence, compared to other species. This  
 723 was consistent with field observations.

724

725

726 **Table S1:** All species encountered. Many species were encountered outside of the 0.1 m<sup>2</sup>  
 727 quadrats used for the JSMD, and so were not assigned to groups. Those species were still used  
 728 in the diversity calculations.

Family	Genus	Specific epithet	Group			CRP Mix origin	Applied (kg/ha)	Seed
			Code	Group Name	no			
Asteraceae	<i>Gutierrezia</i>	<i>sarothrae</i>	GUSA	<i>Gutierrezia sarothrae</i>	no	native		
Asteraceae	<i>Ericameria</i>	<i>nuaseosa</i>	ERNA	<i>Ericameria nauseosa</i>	no	native		
Asteraceae	<i>Heterotheca</i>	<i>villosa</i>	HEVI	<i>Heterotheca villosa</i>	no	native		
Asteraceae	<i>Helianthus</i>	<i>annuus</i>	HEAN	<i>Helianthus annuus</i>	no	native		
Asteraceae	<i>Stephanomeria</i>	<i>pauciflora</i>	FORB	Native Forbs	no	native		
Asteraceae	cf Aster	d_081_herb_05	FORB	Native Forbs	no	native		
Asteraceae	<i>Antennaria</i>	sp.	ANSP	<i>Antennaria</i> sp	no	native		
Asteraceae	<i>Artemisia</i>	<i>arbuscula</i>	ARAR	<i>Artemisia arbuscula</i>	no	native		
Chenopodiaceae	<i>Atriplex</i>	<i>canescens</i>	ATCA	<i>Atriplex canescens</i>	yes	native	0.2676	
Chenopodiaceae	<i>Chenopodium</i>	<i>berlandieri</i>	FORB	Native Forbs	no	native		
Malvaceae	<i>Sphaeralcea</i>	<i>coccinea</i>	SPCO	<i>Sphaeralcea coccinea</i>	no	native		
Papaveraceae	<i>Argemone</i>	cf <i>hispida</i>	ARHI	<i>Argemone cf hispida</i>	no	native		
Poaceae	<i>Bouteloua</i>	<i>curtipendula</i>	BOCU	<i>Bouteloua curtipendula</i>	yes	native	0.6244	
Poaceae	<i>Panicum</i>	<i>virgatum</i>	PAVI	<i>Panicum virgatum</i>	yes	native	0.1784	
				<i>Schizachyrium</i>				
Poaceae	<i>Schizachyrium</i>	<i>scoparium</i>	SCSC	<i>scoparium</i>	yes	native	0.3568	
Poaceae	<i>Nassella</i>	<i>viridula</i>	NAVI	<i>Nassella viridula</i>	yes	native	0.7136	
Poaceae	<i>Pascopyrum</i>	<i>smithii</i>	PASM	<i>Pascopyrum smithii</i>	yes	native	1.784	
Poaceae	<i>Bouteloua</i>	<i>gracilis</i>	BOGR	<i>Bouteloua gracilis</i>	yes	native	0.1784	

Poaceae	<i>Elymus</i>	<i>elymoides</i>	ELEL	<i>Elymus elymoides</i>	no	native
Solanaceae	<i>Solanum</i>	<i>triflorum</i>	FORB	Native Forbs	no	native
Nyctaginaceae	<i>Mirabilis</i>	sp	FORB	Native Forbs	no	native
		Rhizomatous_p				
unknown	erennial_forb	d_141_herb_09	FORB	Native Forbs	no	native
<hr/>						
				Introduced		
Asteraceae	<i>Scorzonera</i>	<i>laciniata</i>	LACT	Cichorioideae	no	introduced
				Introduced		
Asteraceae	<i>Taraxacum</i>	<i>officinale</i>	LACT	Cichorioideae	no	introduced
				Introduced		
Asteraceae	<i>Tragopogon</i>	<i>dubious</i>	LACT	Cichorioideae	no	introduced
Asteraceae	<i>Cirsium</i>	<i>arvense</i>	CIAR	<i>Cirsium arvense</i>	no	introduced
Asteraceae	<i>Onopordium</i>	<i>acanthium</i>	ONAC	<i>Onopordium acanthium</i>	no	introduced
Asteraceae	<i>Lactuca</i>	<i>serriola</i>	LASE	<i>Lactuca serriola</i>	no	introduced
				Introduced		
Brassicaceae	<i>Sisymbrium</i>	<i>altissimum</i>	BRAS	Brassicaceae	no	introduced
				Introduced		
Brassicaceae	<i>Descurainia</i>	<i>sophia</i>	BRAS	Brassicaceae	no	introduced
Chenopodiaceae	<i>Salsola</i>	<i>tragus</i>	SATR	<i>Salsola tragus</i>	no	introduced
Chenopodiaceae	<i>Bassia</i>	<i>scoparia</i>	BASC	<i>Bassia scoparia</i>	no	introduced
Convolvulaceae	<i>Convolvulus</i>	<i>arvensis</i>	COAR	<i>Convolvulus arvensis</i>	no	introduced
Fabaceae	<i>Medicago</i>	<i>sativa</i>	MESA	<i>Medicago sativa</i>	yes	introduced
Fabaceae	<i>Melilotus</i>	<i>officinale</i>	MEOF	<i>Melilotus officinale</i>	no	introduced
				Introduced Annual		
Poaceae	<i>Bromus</i>	<i>tectorum</i>	BROM	<i>Bromus</i>	no	introduced
Poaceae	<i>Secale</i>	<i>cereale</i>	SECE	<i>Secale cereale</i>	no	introduced
Poaceae	<i>Bromus</i>	<i>inermis</i>	BRIN	<i>Bromus inermis</i>	no	introduced

					Introduced Annual	
Poaceae	<i>Bromus</i>	<i>secalinus</i>	BROM	<i>Bromus</i>	no	introduced
Poaceae	<i>Agropyron</i>	<i>cristatum</i>	AGCR	<i>Agropyron cristatum</i>	no	introduced
Zygophyllaceae	<i>Tribulus</i>	<i>terrestris</i>	TRTE	<i>Tribulus terrestris</i>	no	introduced

729

730

731 Table S2: R packages used in the analysis.

Package	Purpose	Citation
sf	Spatial vector data management	Pebesma 2018
terra	Raster data management	Hijmans 2023a
raster	Raster data management	Hijmans 2023b
vegan	Diversity and NMDS	Oksanen et al 2022
SPEI	Calculating SPEI	Beguería and Vicente-Serrano 2023
microclima	Calculating air temperature	Mosedale et al 2023
NicheMapR	Calculating air temperature	Kearney 2022
topmodel	Calculating TWI	Buytaert 2022
tidyverse	Data wrangling	Wickham et al 2019

lubridate	Date wrangling	Grolemond and Wickham 2011
vroom	Data wrangling	Hester et al 2023
Hmsc	Joint species distribution modeling	Tikhonov et al 2023
snow	parallelization	Tierney et al 2021
fields	spatial process models	Nychka et al 2021
ggpubr	visualization	Kassambara 2023
ggcorrplot	visualization	Kassambara 2022
ggthemes	visualization	Arnold 2021
ggttext	visualization	Wilke 2021
ggrepel	visualization	Slowikowski 2023
gcmc	visualization	Fernandez i Marin 2016
geomtextpath	visualization	Cameron and van den Brand 2022

732

733 **Table S3.** Species included in the CRP mix.

Common Name	Scientific Name	Amount Applied (kg/ha)	Origin
Western wheatgrass	<i>Pascopyrum smithii</i>	1.784	native
Green needlegrass	<i>Nassella viridula</i>	0.7136	native
Sideoats gramma	<i>Bouteloua curtipendula</i>	0.6244	native
Alfalfa	<i>Medicago sativa</i>	0.3568	introduced
Little bluestem	<i>Schizachyrium</i>	0.3568	native

*scoparium*

Fourwing Saltbush	<i>Atriplex canescens</i>	0.2676	native
Blue gramma	<i>Bouteloua gracilis</i>	0.1784	native
Switchgrass	<i>Panicum virgatum</i>	0.1784	native

734

735 Table S4 life history traits of species used in the JSMD analysis.

species group	Mean height	introduced	perennial	woody	graminoid	rhizomatous	Photosynthetic pathway
Invasive Annual <i>Bromus</i>	19	yes	no	no	yes	no	c3
<i>Bassia scoparia</i>	11	yes	no	no	no	no	c3
<i>Salsola tragus</i>	10	yes	no	no	no	no	c4
<i>Pascopyrum smithii</i>	22	no	yes	no	yes	yes	c3
<i>Bouteloua curtipendula</i>	24	no	yes	no	yes	no	c4
<i>Medicago sativa</i>	27.5	yes	yes	no	no	no	c3
Invasive annual Brassicaceae	21	yes	no	no	no	no	c3
<i>Nasella viridulus</i>	41.5	no	yes	no	yes	no	c4
Invasive Chicorioideae	10.5	yes	yes*	no	no	no	c3
Native Forbs	6	no	yes	no	no	no	c4
<i>Cirsium arvense</i>	12	yes	yes	no	no	yes	c3
<i>Convolvulus arvensis</i>	8.5	yes	yes	no	no	yes	c3
<i>Panicum virgatum</i>	27.5	no	yes	no	yes	no	c4
<i>Schizachyrium scoparium</i>	19	no	yes	no	yes	no	c4

<i>Atriplex canescens</i>	115	no	yes	yes	no	no	c4
<i>Bouteloua gracilis</i>	19	no	yes	no	yes	no	c4
<i>Bromus inermis</i>	33	yes	yes	no	yes	yes	c3
<i>Secale cereale</i>	38.5	yes	no	no	yes	no	c3

736 \* two species (5 occurrences) are perennial/biennial, one species (1 occurrence) is annual/biennial

737

738 Supplementary References

739

740 Jeffrey B. Arnold (2021). ggthemes: Extra Themes, Scales and Geoms for 'ggplot2'. R package  
741 version 4.2.4.

742 <https://CRAN.R-project.org/package=ggthemes>

743

744 Santiago Beguería and Sergio M. Vicente-Serrano (2023). SPEI: Calculation of the  
745 Standardized Precipitation-Evapotranspiration Index. R package version 1.8.1.

746 <https://CRAN.R-project.org/package=SPEI>

747

748 Wouter Buytaert (2022). topmodel: Implementation of the Hydrological Model TOPMODEL in R.  
749 R package version 0.7.5.

750 <https://CRAN.R-project.org/package=topmodel>

751

752 Allan Cameron and Teun van den Brand (2022). geomtextpath: Curved Text in 'ggplot2'. R  
753 package version 0.1.1.

754 <https://CRAN.R-project.org/package=geomtextpath>

755

756 Xavier Fernández i Marín (2016). ggmcmc: Analysis of MCMC Samples and Bayesian  
757 Inference. Journal of Statistical Software, 70(9), 1-20  
758 [www.doi.org/10.18637/jss.v070.i09](http://www.doi.org/10.18637/jss.v070.i09)

759

760 Garrett Grolemund, Hadley Wickham (2011). Dates and Times Made Easy with lubridate.  
761 Journal of Statistical Software, 40(3), 1-25.  
762 <https://www.jstatsoft.org/v40/i03/>

763

764 Jim Hester, Hadley Wickham and Jennifer Bryan (2023). vroom: Read and Write Rectangular  
765 Text Data Quickly. R package version 1.6.3.  
766 <https://CRAN.R-project.org/package=vroom>

767

768 Robert J. Hijmans (2023a). terra: Spatial Data Analysis. R package version 1.7-29.  
769 <https://CRAN.R-project.org/package=terra>

770

771 Robert J. Hijmans (2023b). raster: Geographic Data Analysis and Modeling. R package version  
772 3.6-20.  
773 <https://CRAN.R-project.org/package=raster>

774

775 Alboukadel Kassambara (2022). ggcorrplot: Visualization of a Correlation Matrix using 'ggplot2'.  
776 R package  
777 version 0.1.4. <https://CRAN.R-project.org/package=ggcorrplot>

778

779 Alboukadel Kassambara (2023). ggpubr: 'ggplot2' Based Publication Ready Plots. R package  
780 version 0.6.0.  
781 <https://CRAN.R-project.org/package=ggpubr>

782

783 Michael Kearney (2022). NicheMapR: R implementation of Niche Mapper software for  
784 biophysical modelling. R package version 3.2.0.

785 <https://github.com/mrke/NicheMapR>

786

787 Jonathan Mosedale, Jonathan Bennie and James Duffy (2023). microclima: microclimate  
788 modelling with R. R package version 0.1.0.

789 <https://github.com/lyamaclean/microclima>

790

791 Douglas Nychka, Reinhard Furrer, John Paige, Stephan Sain (2021). “fields: Tools for spatial  
792 data.” R package version 14.1.

793 <https://github.com/dnnychka/fieldsRPackage>

794

795 Jari Oksanen, Gavin L. Simpson, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter  
796 R. Minchin, R.B. O'Hara, Peter Solymos, M. Henry H. Stevens, Eduard Szoeecs, Helene

797 Wagner, Matt Barbour, Michael Bedward, Ben Bolker, Daniel Borcard, Gustavo Carvalho,

798 Michael Chirico, Miquel De Caceres, Sebastien Durand, Heloisa Beatriz Antoniazi Evangelista,

799 Rich FitzJohn, Michael Friendly, Brendan Furneaux, Geoffrey Hannigan, Mark O. Hill, Leo Lahti,

800 Dan McGlinn, Marie-Helene Ouellette, Eduardo Ribeiro Cunha, Tyler Smith, Adrian Stier, Cajo

801 J.F. Ter Braak and James Weedon (2022). vegan: Community Ecology Package. R package

802 version 2.6-4.

803 <https://CRAN.R-project.org/package=vegan>

804

805 Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The  
806 R Journal 10 (1), 439-446,

807 <https://doi.org/10.32614/RJ-2018-009>

808

809 Kamil Slowikowski (2023). ggrepel: Automatically Position Non-Overlapping Text Labels with  
810 'ggplot2'. R package version 0.9.3.

811 <https://CRAN.R-project.org/package=ggrepel>

812

813 Gleb Tikhonov, Otso Ovaskainen, Jari Oksanen, Melinda de Jonge, Oystein Opedal and Tad  
814 Dallas (2023). Hmsc: Hierarchical Model of Species Communities. R package version 3.0-14.

815 <https://www.helsinki.fi/en/researchgroups/statistical-ecology/software/hmsc>

816

817 Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A,  
818 Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D,  
819 Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke, Woo K, Yutani H (2019). "Welcome to the  
820 tidyverse." *Journal of Open Source Software*, 4(43), 1686.

821 <https://doi.org/10.21105/joss.01686>

822

823 Claus O. Wilke and Brenton M. Wiernik (2022). ggtext: Improved Text Rendering Support for  
824 'ggplot2'. R package version 0.1.2.

825 <https://CRAN.R-project.org/package=ggtext>

826

827