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

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16   **Open Research Statement:** All data and code are in a public repository,  
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18   acceptance.

19

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22   Western Wheatgrass

23

## 24 Abstract

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

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## 47 Introduction

48 Understanding how species diversity develops in novel ecosystems such as post agricultural  
49 landscapes is one of most important questions in plant science today ([Armstrong et al., 2023](#);  
50 [Bell et al., 2023](#)). Globally, about 15 Mkm<sup>2</sup> (10% of global land area) are currently managed as

51 croplands, resulting in an estimated 133 Pg in cumulative carbon (C) emissions throughout  
52 human history ([Sanderman, Hengl and Fiske, 2017](#)). Reestablishing native perennial plant  
53 cover in post agricultural landscapes is an important way to restore these systems to C sinks  
54 and enhance soil stabilization, biodiversity and other ecosystem functions and services.

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

66

67 In the United States, the Department of Agriculture Farm Service Agency has a program called  
68 the Conservation Reserve Program (CRP) that has been paying farmers to convert cultivated  
69 land to perennial vegetation since 1985. As of 2020 there were 8.9 million hectares enrolled,  
70 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).

85

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

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

100

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

117

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

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

## 129 Materials and Methods

### 130 Site Description

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

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

149

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

157

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

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173 **Field sampling**

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

183 **Ancillary data**

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

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

197

198

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

## 210 Statistical analysis

211 We used nonmetric multidimensional scaling (NMDS) ([Minchin, 1987](#)) to examine how species  
212 composition and abundance differed between the two CRP applications at the plot scale. We  
213 created one ordination using cover data to understand abundances, and another after  
214 converting the abundance matrix to an occurrence matrix to examine species composition. We  
215 used stress plots to assess the fit of the NMDS ordinations. To examine how individual species  
216 drove the ordinations, we used a permutational correlation with an alpha of  $p < 0.001$  to account  
217 for multiple tests. We calculated the Shannon-Weaver diversity index ([Shannon and Weaver,](#)  
218 [1949](#)) and the species richness for each plot for native species.

219

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

235

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

242

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

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

252

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

254

## 255 Results

### 256 Species composition outcomes

257 The long-term outcomes in species composition after restoration were markedly different  
258 depending on seeding year. Across the field three introduced species, *B. tectorum*, *Bassia*  
259 *scoparia*, and *Salsola tragus*, along with the native *P. smithii*, were ubiquitous regardless of strip  
260 number and year of seed application. Strips seeded in 2013 were characterized by low density  
261 of *Atriplex canescens*, abundant cover of *P. smithii* and low cover of other perennial grass  
262 species (**Fig. S2**). Strips seeded in 2014 had only a few scattered individuals of *A. canescens*,  
263 and had abundant native perennials from the CRP mix. The strips seeded in 2014 had higher  
264 native diversity (**Fig. 2**). Our NMDS analyses in **Figure 2** reflected this, with the occurrence-  
265 based ordination (non-metric fit R<sup>2</sup> = 0.954) showing little overlap between the two years of seed  
266 application, but with more overlap from the abundance-based ordination (non-metric fit R<sup>2</sup> =  
267 0.932), reflecting the high relative abundance of the four species. We found scattered

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

## 271 Interspecific analysis

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

282

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

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

303

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

312

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

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

319

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

## 328 Discussion

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

340

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

354

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

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

375

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

385

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

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

395

396 The near complete failure of establishment for *A. canescens* in 2014 underscores the notion  
397 that in order to have the best chance of restoring all structural and functional strata, seed mixes  
398 should have multiple species per functional group. We did not see strong residual associations  
399 between *A. canescens* and other species, which would have suggested that competition  
400 inhibited its establishment. This leaves climate around the time of planting, or competition with  
401 the temporarily dominant *M. sativa* cover crop as two potential explanations for its divergent  
402 outcomes. In this study and others, the responses of particular species to abiotic conditions  
403 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  
404 high diversity in seed mixtures ([Barr, Jonas and Paschke, 2017](#)), land managers may be able to  
405 tailor species mixes according to observed antecedent conditions along with near-term forecasts  
406 while planning restoration actions, perhaps using a recruitment niche framework ([Larson et al 2023](#)).  
407  
408

409

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

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

425

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

## 436 Conclusion

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

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

## 454 Authors' contributions

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

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629 **Tables**

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

631 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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## 634 Figure Captions

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

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

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

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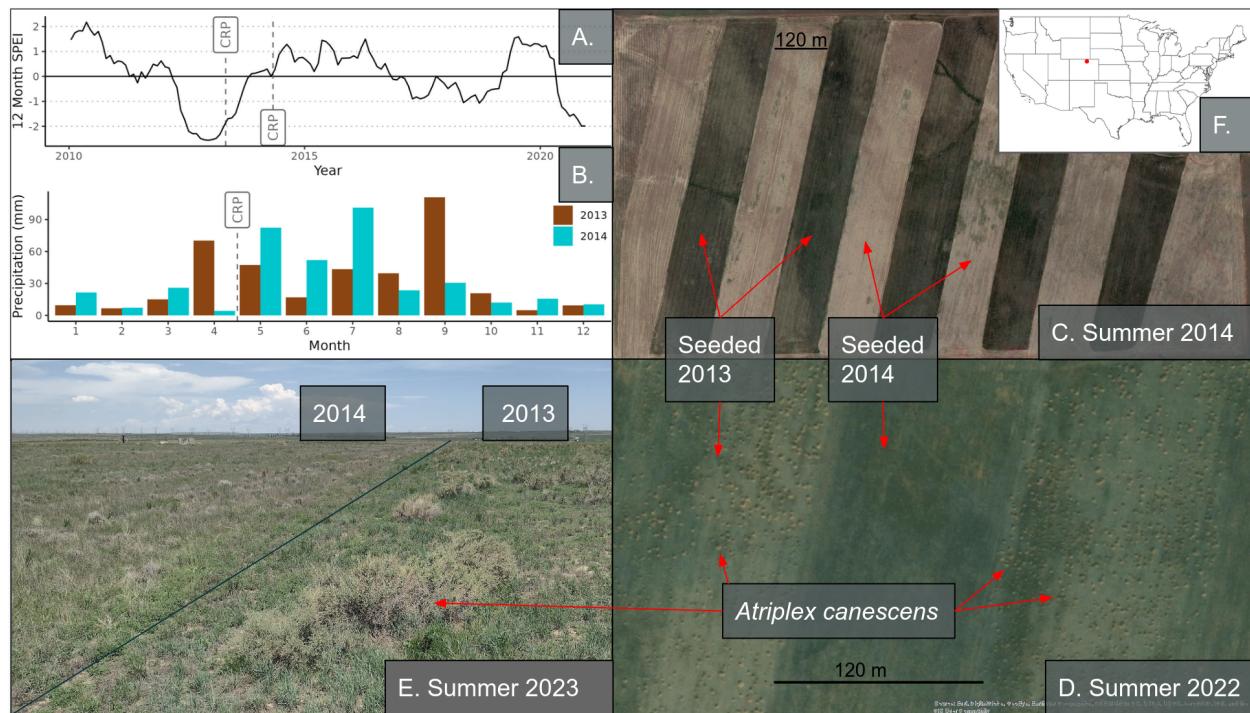
658 **Figure 4.** Posterior distributions of parameter estimates for conditions after seeding by species.  
 659 Plot arrangement is the same as in **Figure 3**.

660

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

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## 666 Figures



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668 Figure 1

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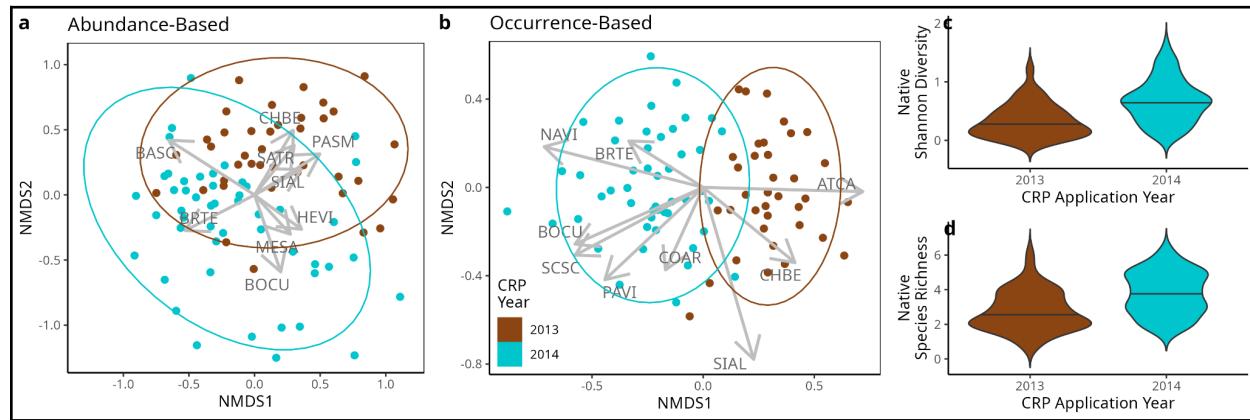
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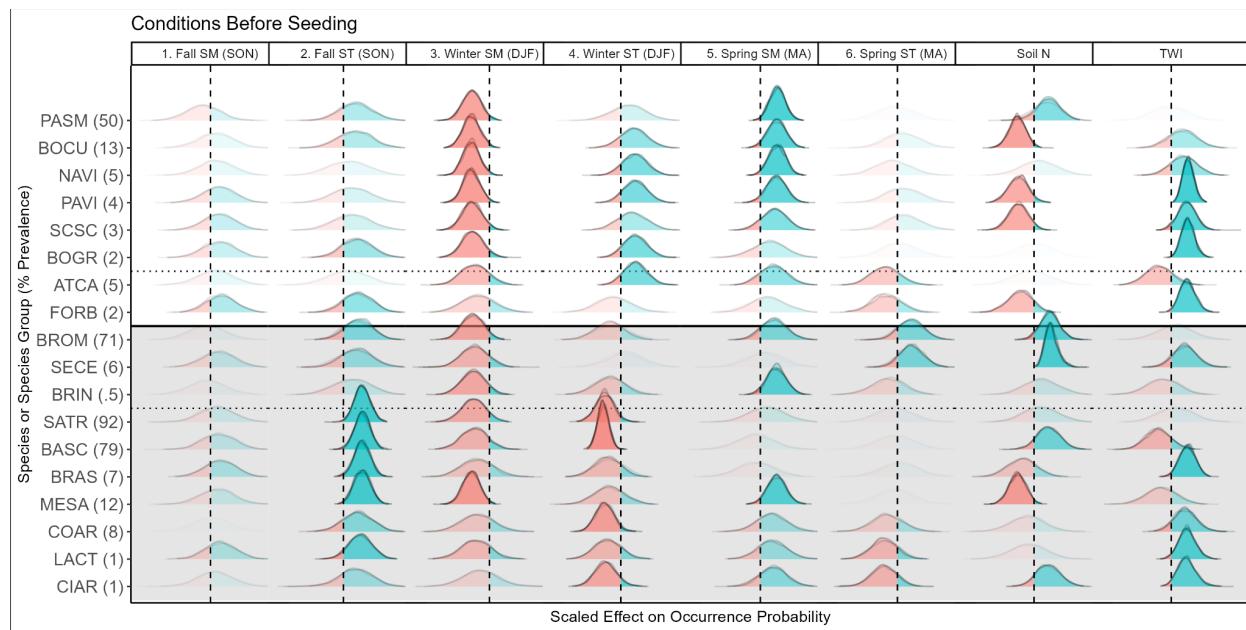
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676 Figure 2

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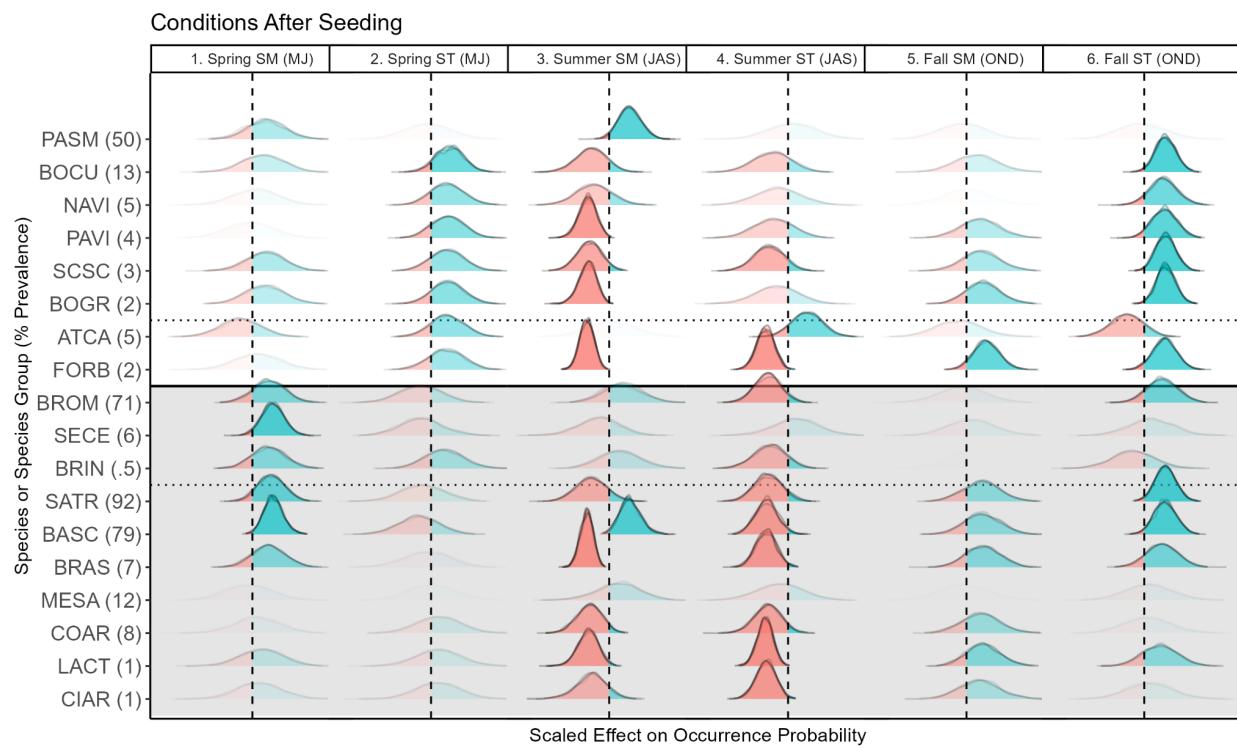


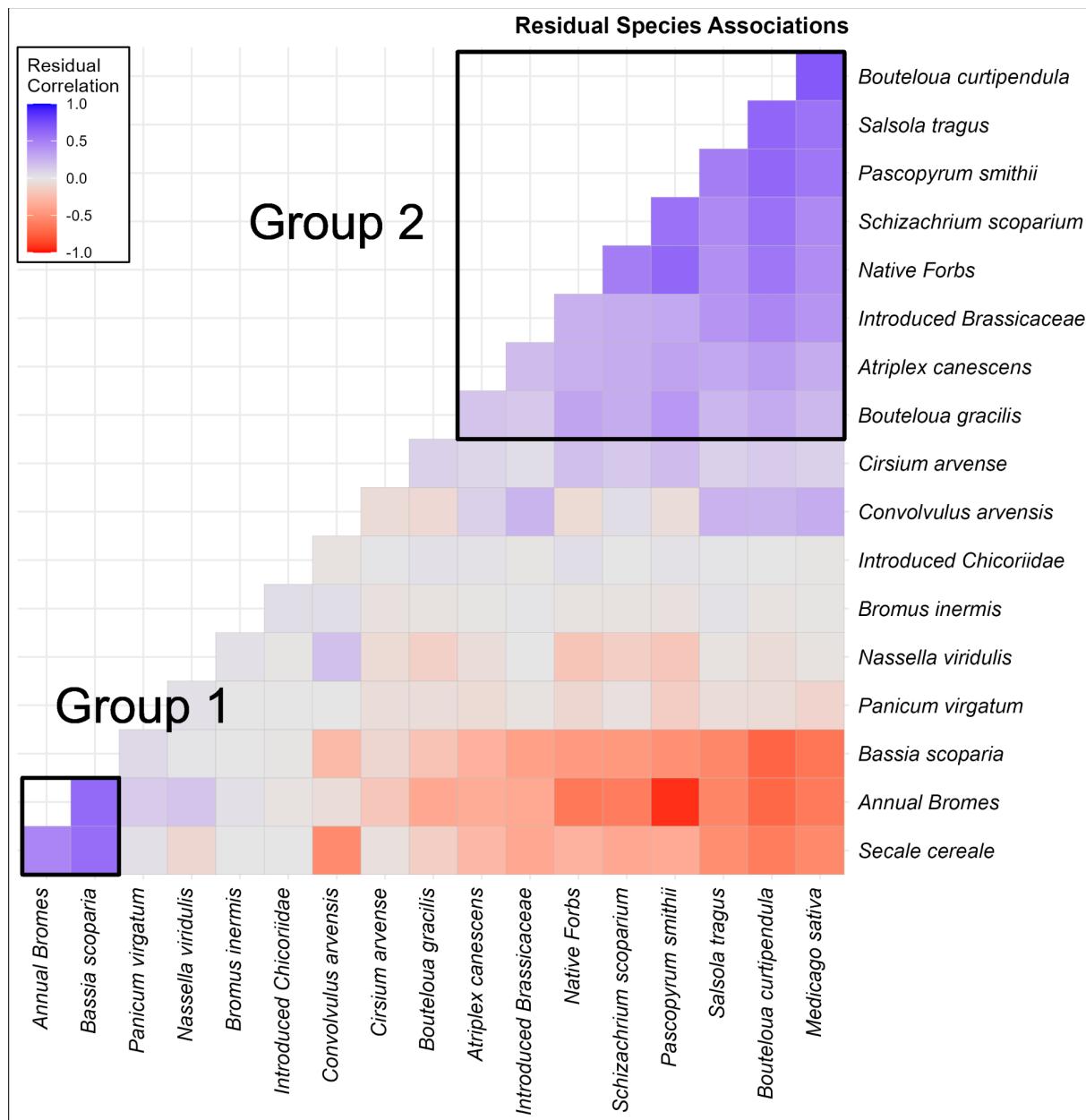
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680 Figure 3

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687 Figure 5

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