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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

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

7

8 *corresponding author: admahood@gmail.com

9

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

11

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

13 DMB: 0000-0003-1877-3151

14 TRG: 0000-0002-1441-8008

15

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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 Mkm² (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 m² 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 m² 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 m² 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 R² 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 m²
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 $R^2 = 0.954$) showing little overlap between the two years of seed
266 application, but with more overlap from the abundance-based ordination (non-metric fit $R^2 =$
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 m² 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 R² values ranged from near zero to 0.75 (**Fig. S4**), The dominant species mentioned above
276 had R² 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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464 References

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

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

- 515 <https://doi.org/10.1111/ele.13341>.
- 516 Huang, L. *et al.* (2019) 'Land conservation can mitigate freshwater ecosystem services
517 degradation due to climate change in a semiarid catchment: The case of the Portneuf River
518 catchment, Idaho, USA', *Science of The Total Environment*, 651, pp. 1796–1809. Available
519 at: <https://doi.org/10.1016/j.scitotenv.2018.09.260>.
- 520 Huang, Y. *et al.* (2023) *Plant diversity stabilizes soil temperature*. preprint. Ecology. Available at:
521 <https://doi.org/10.1101/2023.03.13.532451>.
- 522 Lal, P. *et al.* (2023) 'Spatiotemporal evolution of global long-term patterns of soil moisture',
523 *Science of The Total Environment*, 867, p. 161470. Available at:
524 <https://doi.org/10.1016/j.scitotenv.2023.161470>.
- 525 Larson, J.E. *et al.* (2015) 'Seed and seedling traits affecting critical life stage transitions and
526 recruitment outcomes in dryland grasses', *Journal of Applied Ecology*. Edited by M. Cadotte,
527 52(1), pp. 199–209. Available at: <https://doi.org/10.1111/1365-2664.12350>.
- 528 Leger, E.A., Goergen, E.M. and Forbis De Queiroz, T. (2014) 'Can native annual forbs reduce
529 Bromus tectorum biomass and indirectly facilitate establishment of a native perennial grass?',
530 *Journal of Arid Environments*, 102, pp. 9–16. Available at:
531 <https://doi.org/10.1016/j.jaridenv.2013.10.015>.
- 532 Li, C. *et al.* (2018) 'Soil microbial community restoration in Conservation Reserve Program
533 semi-arid grasslands', *Soil Biology and Biochemistry*, 118, pp. 166–177. Available at:
534 <https://doi.org/10.1016/j.soilbio.2017.12.001>.
- 535 Mack, R.N. (1981) 'Invasion of Bromus tectorum L. into Western North America: An ecological
536 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).
- 538 Mahood, A.L. *et al.* (2022) 'Interannual climate variability mediates changes in carbon and
539 nitrogen pools caused by annual grass invasion in a semiarid shrubland', *Global Change
540 Biology*, 28(1), pp. 267–284. Available at: <https://doi.org/10.1111/gcb.15921>.

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

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

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

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

621 Yuan, X. *et al.* (2023) 'A global transition to flash droughts under climate change', *Science*,
622 380(6641), pp. 187–191. Available at: <https://doi.org/10.1126/science.abn6301>.

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

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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**.

657

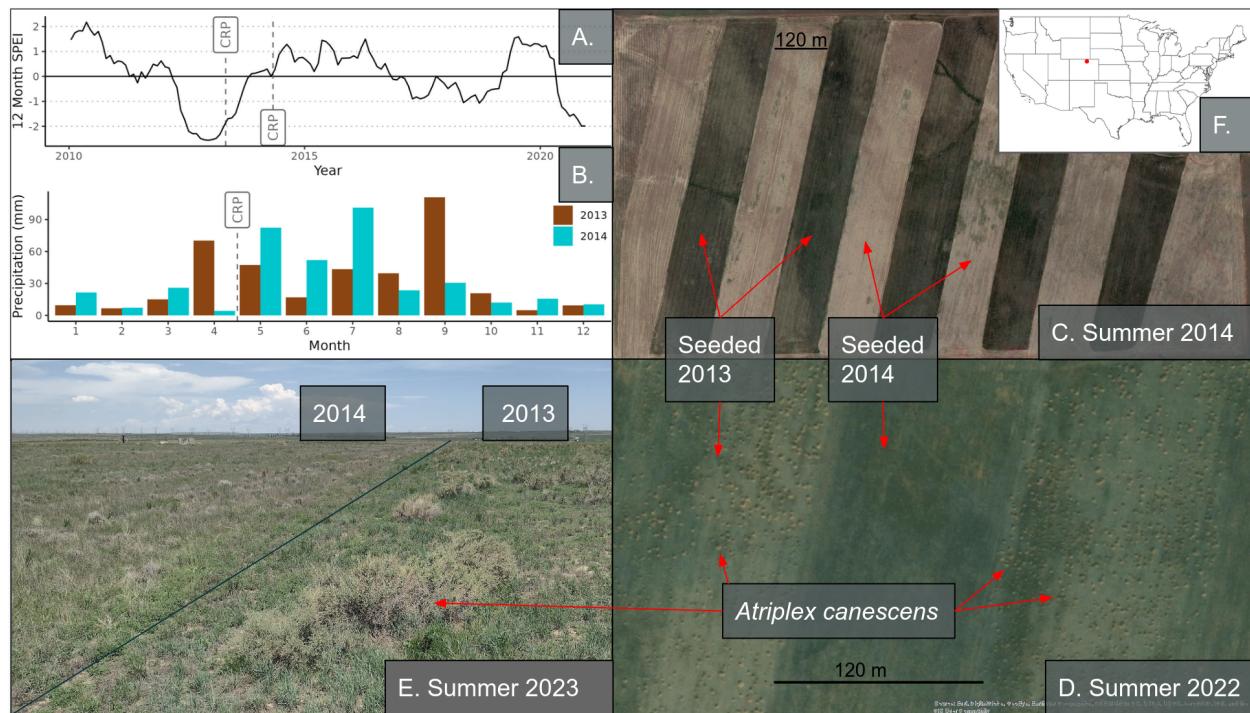
658 **Figure 4.** Posterior distributions of parameter estimates for conditions after seeding by species.
 659 Plot arrangement is the same as in **Figure 3**.

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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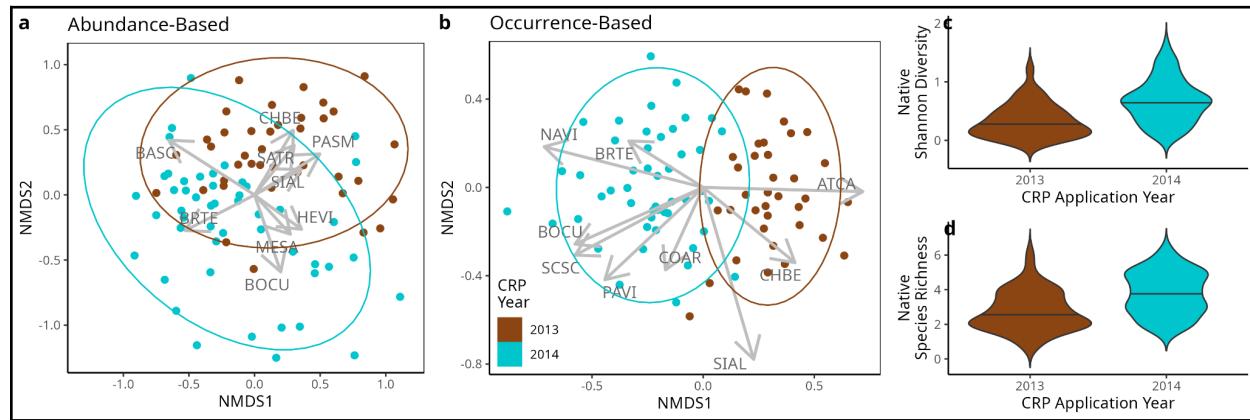
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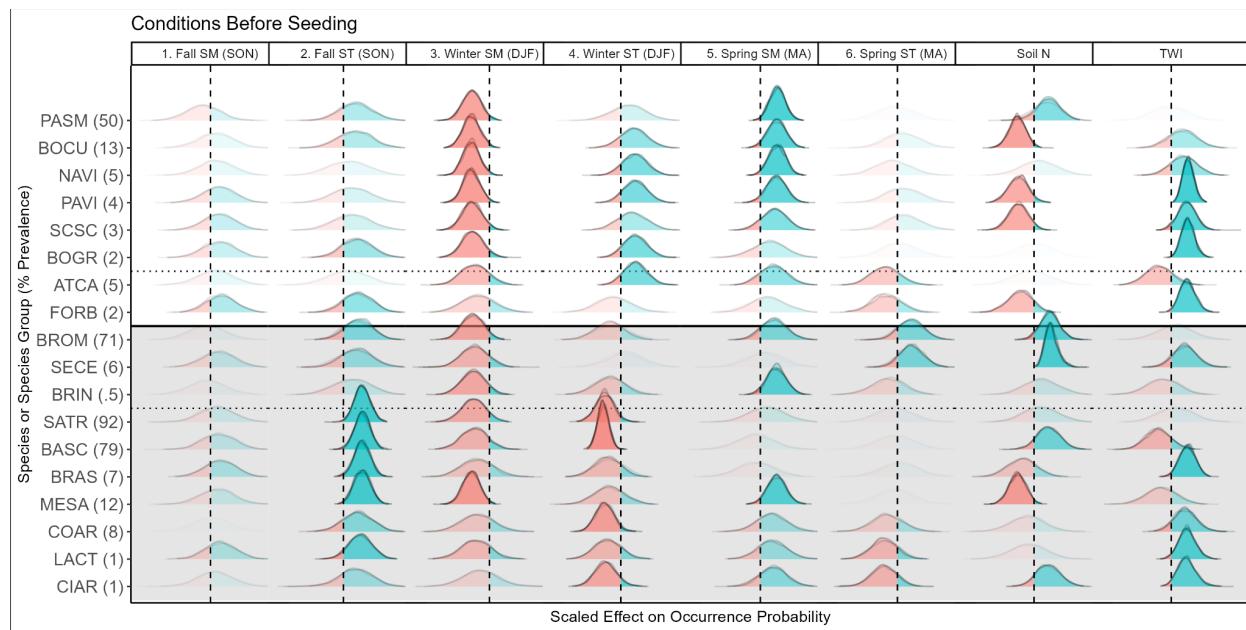
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676 Figure 2

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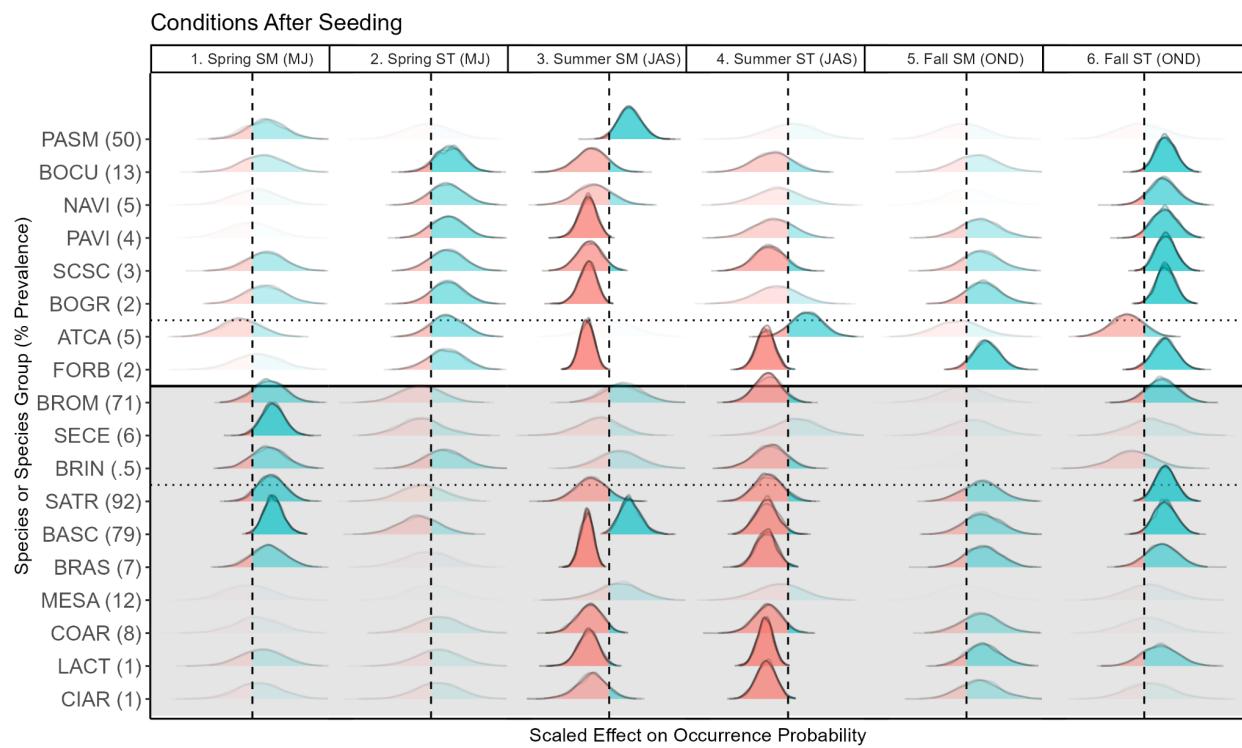


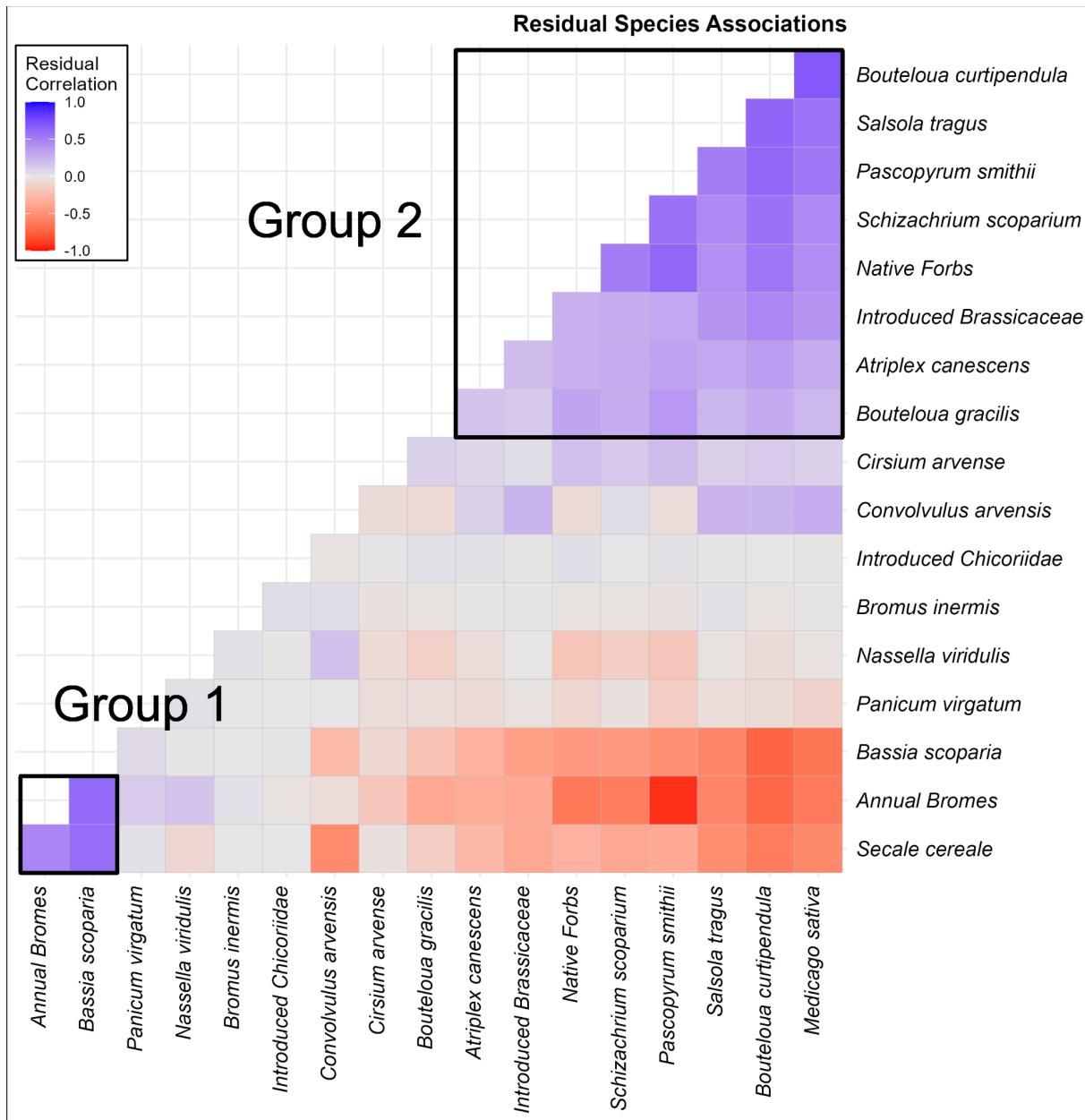
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680 Figure 3

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687 Figure 5

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