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3 **Title:** Antecedent climate drives divergent, long-term restoration outcomes in the Western Great
4 Plains, USA.

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18

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21 Western Wheatgrass

22

23 Abstract

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

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43 Introduction

44 Understanding how species diversity develops in novel ecosystems such as post agricultural
45 landscapes is one of most important questions in plant science today ([Armstrong et al., 2023](#);
46 [Bell et al., 2023](#)). Globally, about 15 Mkm² (10% of global land area) are currently managed as
47 croplands, and this has led to an estimated 133 Pg in cumulative C emissions throughout
48 human history ([Sanderman, Hengl and Fiske, 2017](#)). Reestablishing native perennial plant
49 cover in post agricultural landscapes is an important way to restore these systems to C sinks
50 and enhance ecosystem functions and services. However, restoration practitioners have a
51 difficult task in re-establishing native plants in areas managed for long periods as intensive
52 agriculture, because often the native seed bank is depleted, soil fertility has declined, non-native
53 plants are abundant, and ecohydrological function is altered ([Turnbull et al., 2012](#)). Furthermore,
54 restoration practitioners are often guided by mean annual climate conditions when they decide
55 which species to plant. But a typical year will tend to have a combination of high, low or average
56 seasonal values of temperature, precipitation and other climate variables, and precipitation in
57 particular can be very difficult to predict. Therefore, “mean conditions” rarely capture climate
58 extremes that drive community responses , especially in drylands.

59

60 In the United States, the USDA’s Conservation Reserve Program (CRP) has been paying
61 farmers to convert cultivated land to perennial vegetation since 1985. As of 2020 there were 8.9
62 million hectares enrolled, with the western Great Plains being one of the regions with the
63 greatest enrollment ([USDA, 2023](#)). Landowners typically follow state- or regional-level
64 guidelines that adhere to national prescriptions for seed application ([Taliga, 2011](#)). Often, the
65 plant community established by CRP remains on the land with all of its associated benefits even
66 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).

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, dryer and more variable (Yuan *et al.*, 2023), static prescriptions may be less reliable, and it may become increasingly important to account for current 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 germination, establishment, and community assembly (Young *et al.*, 2015; O'Connor *et al.*, 2020; Werner *et al.*, 2020). Compositional differences due to interannual climate variability can have decadal legacies (Eckhoff *et al.*, 2023).

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

Here, we explored how antecedent climate conditions affected long-term persistence of seeded species in a wheat field converted to CRP in North Central Colorado, USA (**Fig. 1**). A mix of eight species (**Table S1**) was applied in alternating strips of a wheat-fallow agricultural field for two successive years, on April 29, 2013 and May 1, 2014. We measured species composition at 88 plot locations in 2022. Both years had similar mean annual precipitation but it occurred at different times, and with different antecedent climate conditions, resulting in much drier soil moisture during the 2013 seed application. We used non-metric multidimensional scaling (NMDS) (Minchin, 1987) to examine how species composition differed ten years later between treatments, and used a Joint Species Distribution Model (JSDM) in a Bayesian framework (Tikhonov *et al.*, 2020) to test the hypothesis that pretreatment climate variables would be

119 significant predictors of decadal outcomes for species' occurrence. We also tested site
120 topography, and edaphic characteristics as predictors of species occurrence to develop a better
121 understanding of landscape factors driving treatment outcomes and provide useful guidance for
122 restoration practitioners.

123 Materials and Methods

124 Site Description

125 The field site is located in northern Colorado on the western Great Plains of the USA (latitude =
126 40.61 °N, longitude = 104.84 °W). Native shortgrass steppe in this region was tilled for dryland
127 farming going back to the 1870's. The field site has a relative upland topographic position and
128 relief of 29 m within the current 109 ha field ([Erskine et al., 2006](#)). To reduce wind and water
129 erosion under winter wheat/fallow crop rotation during fallow periods (14 out of every 24
130 months), the original half section (320 ac = 129.5 ha) of land was divided into strips of
131 approximately 135 m width and ~800 m lengths oriented north-south. The field was planted into
132 native grasses under CRP for the first time in circa 1988, and an eastern portion of the half
133 section remained in grass upon subsequent development of an oil well. The portion west of the
134 oil well (109 ha) was tilled again in the 1990's into 12 alternating strips of wheat/fallow, each
135 with a new declination of ~12° east of true north and ~120 m width (**Fig 1**). The original strips
136 are apparent in 1985 Landsat images, and relics remain in later imagery indicating the potential
137 for legacy seed bank effects that may have impacted current plant communities.

138

139 The existing CRP was implemented in two stages, with the same seed mix (Table S1). One set
140 of alternating crop strips (**Fig. 1B**) was planted on April 29, 2013, and the second set was
141 planted on May 1, 2014. Prior to the CRP plantings, the first set was planted to winter wheat on

Oct. 3, 2011, which was harvested on July 5, 2012, then maintained in fallow using shallow tillage. The second set was planted into the same variety of wheat on Oct. 5, 2012 and never harvested due to low grain yield. After planting, some “volunteer” wheat was observed along with the CRP mix of species. In both sets of strips, alfalfa was dominant in the first year.

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

Erskine *et al.* ([2006](#)) described the topographic attributes based on a survey-grade 5-m digital elevation model (DEM), which revealed potential flowpaths and accumulation areas along with variable slopes up to 13%. Mapped soil units are Wagonwheel coarse silty loam (a coarse-silty, mixed, superactive, mesic Aridic Calciustept), Colby fine silty loam (a fine-silty, mixed, superactive, calcareous, mesic Aridic Ustorthent), and Kim fine sandy loam (a fine-loamy, mixed, active, calcareous, mesic Ustic Torriorthents). Detailed soil horizons and textural information are given in Green and Erskine ([2011](#), Table 1). We note that, after the establishment of perennial vegetation under CRP, there has been no surface runoff whereas numerous runoff events were observed pre-CRP.

167

168 Field sampling

169 In June 2022, we sampled 88 5 m x 5 m plots that were collocated with areas previously
170 sampled for soil C ([Sherrod, Erskine and Green, 2015](#)), aligned with a 5m digital elevation
171 model (DEM) ([Erskine *et al.*, 2006](#)). Within each plot, we established 4, 0.1 m² subplots at
172 random locations. In each subplot, we used ocular estimates to measure the fractional cover of
173 every species, as well as the cover of bare soil, litter, and rocks. We measured the maximum
174 height of each species in each subplot, and did a gridded plant walkabout to detect all species
175 in the 25 m² plot.

176 Ancillary data

177 The DEM was used to create grids of topographic wetness index (TWI), topographic position
178 index (TPI), slope, and folded aspect. Four or more frequency domain sensors (Sentek™)
179 ([Schwank *et al.*, 2006](#)) were installed at 18 locations at depths ranging from 30 to 170 cm to
180 measure hourly soil moisture from 2002-2018. Each of 18 locations has sensors at a depth of
181 30 cm. Soil temperature was measured using stand-alone thermocouple sensors (Onset
182 WaterTempPro™) at a 30 cm depth near each Sentek probe ([Green and Erskine, 2011](#)).

183

184 We used the topographic layers as predictors in a spatial process model ([Nychka *et al.*, 2021](#)) to
185 estimate seasonal averages of 30 cm soil temperature and moisture at a 5 m resolution (**Fig.**
186 **S1**) for three time periods preceding seeding: March and April to capture the conditions
187 immediately preceding seeding, January and February to capture winter freezing conditions,
188 and September-October, since many species actually germinate in fall and overwinter before

growing in the spring. Soil type, texture and total nitrogen content was measured from soil cores at each sampling location in 2012 (Sherrod, Erskine and Green, 2015). We used a process-based microclimate model (Maclean, Mosedale and Bennie, 2019) to downscale sub-daily data to our DEM to create hourly air temperature surfaces, then aggregated to the mean for the three time periods.

Statistical analysis

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

To investigate the response of individual species to pre-treatment conditions, we created a joint species distribution model (JSDM) in a Bayesian hierarchical framework (Tikhonov *et al.*, 2020) for the occurrence of all species at the 0.1m² quadrat scale. This model allowed us to estimate the probability of species occurrence while also accounting for inter-specific interactions and species traits. Because the model is estimating the occurrence of species, it has difficulty with species that only occur at one or two plots. Therefore, we grouped locally rare species with other functionally similar species (**Table S1**). The covariates were the seasonal averages of soil temperature, soil moisture, and air temperature surfaces, along with the total nitrogen content in the top 15 cm of soil measured in 2012, 2022 bare ground cover, year of seed application, and

topographic wetness index. Random effects were the strip number and the plot identity. Traits included in the model were maximum height, introduced, perennial, woody, graminoid, rhizomatous, and photosynthetic pathway (C3 or C4; **Table S1**).

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

We observed in the field that *P. smithii* appeared to be in direct competition with *B. tectorum*. The approach described above quantifies interspecific interactions using occurrence data, and we wanted to examine this interaction further using abundance data. Therefore, we created a Bayesian hierarchical model (Bürkner, 2017) with *B. tectorum* occurrence in a 0.1 m² subplot as a Bernoulli-distributed response, with the cover of *P. smithii* and other prevalent species and bare ground as predictors, with plot as a random effect. We also created an opposite model with the occurrence of the other prevalent species as a multivariate response variable, *B. tectorum* and bare ground cover as predictors, with plot as a random effect.

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

Results

Species composition outcomes

The long-term outcomes in species composition after CRP seed mix application were markedly different depending on seeding year. Across the field, three introduced species; *B. tectorum*, *Bassia scoparia*, and *Salsola tragus* and the native *P. smithii* were ubiquitous regardless of strip number and year of seed application. Strips seeded in 2013 were characterized by uniformly low density of fourwing saltbush (*Atriplex canescens*), abundant cover of *P. smithii* and low cover of other perennial grass species (**Fig. S2**). Strips seeded in 2014 had only a few scattered individuals of *A. canescens*, and had abundant native perennials from the CRP mix. The strips seeded in 2014 had higher native diversity (**Fig. 2**). Our NMDS analyses in **Figure 2** reflected this, with the occurrence-based ordination (non-metric fit $R^2 = 0.954$) showing little overlap between the two years of seed application, but with more overlap from the abundance-based ordination (non-metric fit $R^2 = 0.932$), reflecting the high relative abundance of the four species. We found scattered individuals of 15 native forb, grass and shrub species not in the species mix (**Table S1**). Of those species, six (all forbs) were found in 0.1 m² subplots and included in the model, grouped together as native forbs.

Interspecific analysis

The model converged well. The environmental filter and trait parameters had high ESS (close to the posterior sample sizes) and \hat{R} values near 1.0, while residual species associations were slightly less well converged but still acceptable (**Fig. S3**). Tjur R^2 values ranged from near zero to 0.75 (**Fig. S4**). The dominant species mentioned above had R^2 values from 0.15 - 0.65.

257 Pre-treatment conditions had predictable effects on species occurrence that showed patterns
258 among functional groups (**Fig. 3**). Caespitose perennial native grasses all had strong positive
259 associations with spring soil moisture. The most prevalent annual introduced grasses, (*S.*
260 *cereale* & *B. tectorum*) were insensitive to spring soil moisture but positively associated with
261 spring soil temperature, while the most prevalent introduced forbs, *B. scoparia* and *S. tragus*
262 were more strongly associated with fall conditions before seeding. *A. canescens*, the shrub that
263 was widely established in the strips seeded in 2013, was more sensitive to higher soil
264 temperatures in the fall preceding seeding, and more exposed topographic positions (i.e. low
265 TWI). The three highly prevalent non-native species (*B. tectorum*, *B. scoparia*, and *S. tragus*) all
266 had weak associations with spring soil moisture. Rather *B. scoparia*, and *S. tragus*, the two
267 most prevalent forbs, were positively associated with fall soil moisture and temperature, and
268 negatively associated with winter soil temperature, while *B. tectorum* was positively associated
269 with spring soil temperature.

270

271 There were only a handful of strong relationships between traits and environmental filters.
272 Perennial occurrence was negatively associated with soil nitrogen, and rhizomatous occurrence
273 had negative associations with spring soil temperature. Taller plants had negative associations
274 with bare ground, as well as grasses, and C4 plants were more likely at sites with high bare
275 ground cover.

276

277 After accounting for the effect of environment and life history traits, there were two main groups
278 of species that were positively correlated within the group, and negatively correlated between
279 the two groups (**Fig. 4**). The first group (G1) was composed of the introduced annuals *B.*
280 *tectorum*, *B. secalinus* (grouped) and *B. scoparia*. The second group (G2) consisted of all of the
281 perennial native grasses in the CRP mix except *N. viridis*, along with *S. tragus*, introduced
282 annual mustards, and native forbs.

283

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

292 Discussion

293 We found that antecedent climate and soil moisture conditions strongly affected long-term
294 restoration outcomes in terms of species composition. While reaching community stability and
295 restoring ecosystem function may take as long as 20 years (Munson and Lauenroth, 2012);
296 implying that we are looking at a snapshot along the recovery trajectory, such a trajectory
297 towards full perennial cover is not necessarily guaranteed or even expected ([Drury and Nisbet,](#)
298 [1973](#); [Coffin, Lauenroth and Burke, 1996](#)). Our observations thus far follow established
299 understanding, as germination and seedling survival are highly dependent upon abiotic
300 conditions during the short period of time that plants are in those stages of their life cycles
301 (Larson *et al.*, 2015; O'Connor *et al.*, 2020). They also align with other results in more mesic
302 great plains post-agricultural landscapes showing that year effects resulting from interannual
303 climate variability can persist for as much as a decade ([Adler and Levine, 2007](#); [Manning and](#)
304 [Baer, 2018](#); [Eckhoff *et al.*, 2023](#)).

305

There were positive residual associations between grasses and forbs in both introduced annual groups (G1) and native species groups (G2) (**Fig. 4**). Grass-forb mutualisms may be an adaptation to interannual climate variability in grasslands (Hallett *et al.*, 2019). Native grasses positively associated with each other in G1 suggests facilitation between species, and so planting these species together may increase their probability of persistence. Future research over a broader geographical range and more species could examine inter-specific associations in more detail, and perhaps provide insight on which species to seed together in order to incorporate facilitative interactions between species with different climatic responses to enhance bet-hedging strategies. Positive association of non-seeded, native forbs with native grasses within G1 (**Fig. 4**) highlights the potential for even low-diversity CRP treatments such as the one studied here to facilitate volunteer establishment of native plants from nearby areas or from the seed bank over long periods of time. Positive residual correlations also existed between *B. tectorum* and *B. scoparia* (G2), and this group had negative associations with the mostly native G1. This suggests that introduced annual forbs may play a role in facilitating the persistence and dominance of introduced annual grasses. Residual correlations in occurrence should be viewed skeptically because they are not necessarily definitive evidence of mechanistic interactions between species (Blanchet, Cazelles and Gravel, 2020). Still, if there were mechanistic interactions between species, we would likely see residual correlations in their occurrence. With this in mind, we used abundance data to explore the interaction between *B. tectorum* and *P. smithii* in more detail.

Bromus tectorum is one of the most problematic introduced annual grasses in the western US (Mack, 1981). The work here adds to the evidence that it can have detrimental effects on plant communities in the short-grass prairie as well (Prevéy and Seastedt, 2014). *P. smithii* may be tractable as a competitively dominant native that may have a competitive advantage over *B. tectorum* and other introduced annuals in seed mixes (**Fig. 4**). The effect of *B. tectorum*

abundance on *P. smithii* occurrence is strong, as is the opposite case. Since *P. smithii* is perennial, once it is established it may be less affected by the competitive pressure from *B. tectorum*, whereas *B. tectorum* occurrence in the presence of established *P. smithii* is subject to direct competition for moisture annually while it germinates and becomes established.

The *M. sativa* cover crop was anecdotally observed to be highly abundant throughout the field in the years immediately following planting. Its association with G1 (**Fig. 4**) suggests it was either an effective facilitator of seeded perennial grasses, its long-term persistence was aided by perennial grass establishment, or both. Native forbs have been shown to be effective at repelling annual invasives ([Leger, Goergen and Forbis De Queiroz, 2014](#)) in Great Basin restoration treatments, and perhaps native forbs could be used as cover crops in western Great Plains CRP applications.

The near complete failure of establishment for *A. canescens* in 2014 underscores the notion that in order to have the best chance of restoring all structural and functional strata, seed mixes should have multiple species per functional group. We did not see strong residual associations between *A. canescens* and other species, which would have suggested that competition inhibited its establishment. This leaves climate around the time of planting, or competition with the temporarily dominant *M. sativa* cover crop as two potential explanations for its divergent outcomes. In this study and others, the responses of particular species to abiotic conditions were not random - they correspond 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 high diversity in seed mixtures ([Barr, Jonas and Paschke, 2017](#)), land managers may be able to tailor species mixes according to antecedent conditions while planning restoration actions.

Mean annual precipitation corresponds broadly to species richness and composition in more mesic restored great plains post agricultural landscapes ([Watson et al., 2021](#)). But in many places, especially in drylands, “mean conditions” might not be particularly common. At the study site, both the sum of annual precipitation (313 +- 87 mm), and the time of year that the precipitation falls are highly variable (**Table 1**). Using antecedent conditions to plan for combinations of seasonal temperature and precipitation conditions might be a more useful approach for land managers than assuming mean annual conditions. With more research on the effects of antecedent and at-planting conditions on long-term outcomes on a broader mix of species, land managers may be able to develop regionally specific, native seed mixes tailored for combinations of typical, non-mean temperature and moisture conditions (i.e. warm/dry, cold/dry, warm/wet, cold/wet). It is likely that antecedent conditions are predictive for some species, while others are more dependent on conditions following planting, or a mixture of the two. Therefore, seed mixes may have a combination of species where antecedent conditions are pointing to their likely success, along with a mixture of species that may or may not be successful depending on what happens after planting.

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

383 Conclusion

384 In many places, especially drylands, above- or below-average climate conditions prevail more
385 commonly than mean conditions, and seasonal combinations of extremes are the norm. The
386 effects of interannual and seasonal variability in climate have predictable effects on seed
387 germination and establishment, but there are few, if any, species-level analyses of long-term
388 outcomes after restoration seed applications. Our results suggest that long-term outcomes are
389 dependent upon the conditions antecedent to planting, and the resultant plant communities fall
390 along functional groups and life history strategies. We found that soil moisture in the two months
391 preceding planting was positively associated with the occurrence of native bunchgrasses, while
392 introduced annual occurrence was less sensitive to the conditions preceding planting. *P. smithii*,
393 a native rhizomatous grass, was able to compete directly against *B. tectorum*. Long-term
394 restoration outcomes may be improved by composing regionally specific seed mixes tailored for
395 common circumstances of temperature and moisture availability, and using an intra- and
396 interannual, repeated seeding approach to opportunistically take advantage of favorable
397 conditions. Regionally specific, go/no-go thresholds based on antecedent conditions may also
398 help avoiding the waste of resources when success seems unlikely, if funding mechanisms
399 allow for delay of seed application. Future research on more species at more sites may allow us
400 to tease out groups of positively associated native species that, when planted together, may be
401 more likely to persist.

402 Authors' contributions

403 Conceptualization: ALM, DB, TG; Data curation: ALM, RHE; Formal Analysis: ALM; Funding
404 acquisition: DB; Investigation: ALM, JM, RHE, TG, DB; Methodology: ALM, JM, RHE; Project
405 administration: ALM; Resources: ALM; Software: ALM; Supervision: DB; Validation: ALM;

406 Visualization: ALM, JM; Writing – original draft: ALM, TG, DB; Writing – review & editing: ALM,
407 TG, DB, JM, RHE

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412 References

- 413 Adler, P.B. and Levine, J.M. (2007) 'Contrasting relationships between precipitation and species
414 richness in space and time', *Oikos*, 116(2), pp. 221–232. Available at:
415 <https://doi.org/10.1111/j.0030-1299.2007.15327.x>.
- 416 Armstrong, E.M. *et al.* (2023) 'One hundred important questions facing plant science: an
417 international perspective', *New Phytologist*, 238(2), pp. 470–481. Available at:
418 <https://doi.org/10.1111/nph.18771>.
- 419 Bach, E.M., Baer, S.G. and Six, J. (2012) 'Plant and Soil Responses to High and Low Diversity
420 Grassland Restoration Practices', *Environmental Management*, 49(2), pp. 412–424. Available
421 at: <https://doi.org/10.1007/s00267-011-9787-0>.
- 422 Bakker, J.D. *et al.* (2003) 'Contingency of grassland restoration on year, site, and competition
423 from introduced grasses', *Ecological Applications*, 13(1), pp. 137–153. Available at:
424 [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).
- 425 Barak, R.S. *et al.* (2023) 'Phylogenetically and functionally diverse species mixes beget diverse
426 experimental prairies, whether from seeds or plugs', *Restoration Ecology*, 31(1). Available at:
427 <https://doi.org/10.1111/rec.13737>.

- 428 Barr, S., Jonas, J.L. and Paschke, M.W. (2017) 'Optimizing seed mixture diversity and seeding
429 rates for grassland restoration: Optimizing grassland seeding', *Restoration Ecology*, 25(3),
430 pp. 396–404. Available at: <https://doi.org/10.1111/rec.12445>.
- 431 Bell, S.M. *et al.* (2023) 'Quantifying the recarbonization of post-agricultural landscapes', *Nature*
432 *Communications*, 14(1), p. 2139. Available at: <https://doi.org/10.1038/s41467-023-37907-w>.
- 433 Blanchet, F.G., Cazelles, K. and Gravel, D. (2020) 'Co-occurrence is not evidence of ecological
434 interactions', *Ecology Letters*. Edited by E. Jeffers, 23(7), pp. 1050–1063. Available at:
435 <https://doi.org/10.1111/ele.13525>.
- 436 Booth, M.S., Caldwell, M.M. and Stark, J.M. (2003) 'Overlapping resource use in three Great
437 Basin species: implications for community invasibility and vegetation dynamics', *Journal of*
438 *Ecology*, p. 13.
- 439 Bürkner, P.-C. (2017) '**brms**: An R Package for Bayesian Multilevel Models Using *Stan*',
440 *Journal of Statistical Software*, 80(1). Available at: <https://doi.org/10.18637/jss.v080.i01>.
- 441 Coffin, D.P., Lauenroth, W.K. and Burke, I.C. (1996) 'Recovery of Vegetation in a Semiarid
442 Grassland 53 Years after Disturbance', *Ecological Applications*, 6(2), pp. 538–555. Available
443 at: <https://doi.org/10.2307/2269390>.
- 444 Csákvári, E. *et al.* (2023) 'Native species can reduce the establishment of invasive alien species
445 if sown in high density and using competitive species', *Restoration Ecology* [Preprint].
446 Available at: <https://doi.org/10.1111/rec.13901>.
- 447 Drury, W.H. and Nisbet, I.C.T. (1973) 'Succession', *Journal of the Arnold Arboretum*, 54(3), pp.
448 331–368.
- 449 Eckhoff, K.D. *et al.* (2023) 'Persistent decadal differences in plant communities assembled
450 under contrasting climate conditions', *Ecological Applications*, 33(3), p. e2823. Available at:
451 <https://doi.org/10.1002/eap.2823>.
- 452 Erskine, R.H. *et al.* (2006) 'Comparison of grid-based algorithms for computing upslope
453 contributing area: COMPARISON OF GRID-BASED ALGORITHMS', *Water Resources*

- 454 *Research*, 42(9). Available at: <https://doi.org/10.1029/2005WR004648>.
- 455 Gelman, A. and Rubin, D.B. (1992) 'Inference from iterative simulation using multiple
456 sequences', *Statistical science*, pp. 457–472.
- 457 Green, T.R. and Erskine, R.H. (2011) 'Measurement and inference of profile soil-water
458 dynamics at different hillslope positions in a semiarid agricultural watershed: PROFILE SOIL-
459 WATER DYNAMICS', *Water Resources Research*, 47(12). Available at:
460 <https://doi.org/10.1029/2010WR010074>.
- 461 Hallett, L.M. *et al.* (2019) 'Rainfall variability maintains grass-forb species coexistence', *Ecology*
462 *Letters*. Edited by R. Snyder, 22(10), pp. 1658–1667. Available at:
463 <https://doi.org/10.1111/ele.13341>.
- 464 Huang, L. *et al.* (2019) 'Land conservation can mitigate freshwater ecosystem services
465 degradation due to climate change in a semiarid catchment: The case of the Portneuf River
466 catchment, Idaho, USA', *Science of The Total Environment*, 651, pp. 1796–1809. Available
467 at: <https://doi.org/10.1016/j.scitotenv.2018.09.260>.
- 468 Huang, Y. *et al.* (2023) *Plant diversity stabilizes soil temperature*. preprint. Ecology. Available at:
469 <https://doi.org/10.1101/2023.03.13.532451>.
- 470 Lal, P. *et al.* (2023) 'Spatiotemporal evolution of global long-term patterns of soil moisture',
471 *Science of The Total Environment*, 867, p. 161470. Available at:
472 <https://doi.org/10.1016/j.scitotenv.2023.161470>.
- 473 Larson, J.E. *et al.* (2015) 'Seed and seedling traits affecting critical life stage transitions and
474 recruitment outcomes in dryland grasses', *Journal of Applied Ecology*. Edited by M. Cadotte,
475 52(1), pp. 199–209. Available at: <https://doi.org/10.1111/1365-2664.12350>.
- 476 Leger, E.A., Goergen, E.M. and Forbis De Queiroz, T. (2014) 'Can native annual forbs reduce
477 *Bromus tectorum* biomass and indirectly facilitate establishment of a native perennial grass?',
478 *Journal of Arid Environments*, 102, pp. 9–16. Available at:
479 <https://doi.org/10.1016/j.jaridenv.2013.10.015>.

- Li, C. *et al.* (2018) 'Soil microbial community restoration in Conservation Reserve Program semi-arid grasslands', *Soil Biology and Biochemistry*, 118, pp. 166–177. Available at: <https://doi.org/10.1016/j.soilbio.2017.12.001>.
- Mack, R.N. (1981) 'Invasion of *Bromus tectorum* L. into Western North America: An ecological 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).
- Maclean, I.M.D., Mosedale, J.R. and Bennie, J.J. (2019) 'Microclima: An R package for modelling meso- and microclimate', *Methods in Ecology and Evolution*. Edited by S. McMahon, 10(2), pp. 280–290. Available at: <https://doi.org/10.1111/2041-210X.13093>.
- Mahood, A.L. *et al.* (2022) 'Interannual climate variability mediates changes in carbon and nitrogen pools caused by annual grass invasion in a semiarid shrubland', *Global Change Biology*, 28(1), pp. 267–284. Available at: <https://doi.org/10.1111/gcb.15921>.
- Manning, G.C. and Baer, S.G. (2018) 'Interannual variability in climate effects on community assembly and ecosystem functioning in restored prairie', *Ecosphere*, 9(6). Available at: <https://doi.org/10.1002/ecs2.2327>.
- Minchin, P.R. (1987) 'An evaluation of the relative robustness of techniques for ecological ordination', *Vegetatio*, 69, pp. 89–107.
- Munson, S.M. and Lauenroth, W.K. (2012) 'Plant Community Recovery Following Restoration in Semiarid Grasslands', *Restoration Ecology*, 20(5), pp. 656–663. Available at: <https://doi.org/10.1111/j.1526-100X.2011.00808.x>.
- Nychka, D. *et al.* (2021) 'fields: Tools for spatial data'. Boulder, CO, USA: University Corporation for Atmospheric Research. Available at: <https://github.com/dnychka/fieldsRPackage>.
- O'Connor, R.C. *et al.* (2020) 'Small-scale water deficits after wildfires create long-lasting ecological impacts', *Environmental Research Letters*, 15(4), p. 044001. Available at: <https://doi.org/10.1088/1748-9326/ab79e4>.
- Porensky, L.M. *et al.* (2014) 'Arid old-field restoration: Native perennial grasses suppress weeds

- 506 and erosion, but also suppress native shrubs', *Agriculture, Ecosystems & Environment*, 184,
507 pp. 135–144. Available at: <https://doi.org/10.1016/j.agee.2013.11.026>.
- 508 Prev  y, J.S. and Seastedt, T.R. (2014) 'Seasonality of precipitation interacts with exotic species
509 to alter composition and phenology of a semi-arid grassland', *Journal of Ecology*. Edited by
510 S. Wilson, 102(6), pp. 1549–1561. Available at: <https://doi.org/10.1111/1365-2745.12320>.
- 511 R Core Team (2021) *R: A Language and Environment for Statistical Computing*. Vienna,
512 Austria: R Foundation for Statistical Computing. Available at: <https://www.R-project.org/>.
- 513 Ricigliano, V.A. *et al.* (2019) 'Honey bee colony performance and health are enhanced by apiary
514 proximity to US Conservation Reserve Program (CRP) lands', *Scientific Reports*, 9(1), p.
515 4894. Available at: <https://doi.org/10.1038/s41598-019-41281-3>.
- 516 Sanderman, J., Hengl, T. and Fiske, G.J. (2017) 'Soil carbon debt of 12,000 years of human
517 land use', *Proceedings of the National Academy of Sciences*, 114(36), pp. 9575–9580.
518 Available at: <https://doi.org/10.1073/pnas.1706103114>.
- 519 Schwank, M. *et al.* (2006) 'Laboratory characterization of a commercial capacitance sensor for
520 estimating permittivity and inferring soil water content', *Vadose Zone Journal*, 5(3), pp. 1048–
521 1064.
- 522 Shannon, C.E. and Weaver, W. (1949) 'A mathematical model of communication', *Urbana, IL:*
523 *University of Illinois Press*, 11, pp. 11–20.
- 524 Sherrod, L.A., Erskine, R.H. and Green, T.R. (2015) 'Spatial Patterns and Cross-Correlations of
525 Temporal Changes in Soil Carbonates and Surface Elevation in a Winter Wheat-Fallow
526 Cropping System', *Soil Science Society of America Journal*, 79(2), pp. 417–427. Available at:
527 <https://doi.org/10.2136/sssaj2014.05.0222>.
- 528 Shriver, R.K. *et al.* (2018) 'Adapting management to a changing world: Warm temperatures, dry
529 soil, and interannual variability limit restoration success of a dominant woody shrub in
530 temperate drylands', *Global Change Biology*, 24(10), pp. 4972–4982. Available at:
531 <https://doi.org/10.1111/gcb.14374>.

- 532 Symonides, E. (1988) 'On the ecology and evolution of annual plants in disturbed
533 environments', *Vegetatio*, 77, pp. 21–31.
- 534 Taliga, C. (2011) *Plant Suitability and Seeding Rates for Conservation Plantings in Colorado*.
535 *Plant materials technical note no. 59 (revised)*.
- 536 Tikhonov, G. *et al.* (2020) 'Joint species distribution modelling with the R -package H_{MSC}',
537 *Methods in Ecology and Evolution*. Edited by N. Golding, 11(3), pp. 442–447. Available at:
538 <https://doi.org/10.1111/2041-210X.13345>.
- 539 Turnbull, L. *et al.* (2012) 'Understanding the role of ecohydrological feedbacks in ecosystem
540 state change in drylands', *Ecohydrology*, 5(2), pp. 174–183. Available at:
541 <https://doi.org/10.1002/eco.265>.
- 542 USDA, F.S.A. (2023) *Conservation Reserve Program, Conservation Reserve Program*.
543 Available at: [https://www.fsa.usda.gov/programs-and-services/conservation-programs/](https://www.fsa.usda.gov/programs-and-services/conservation-programs/conservation-reserve-program/index)
544 [conservation-reserve-program/index](https://www.fsa.usda.gov/programs-and-services/conservation-programs/conservation-reserve-program/index).
- 545 Vandever, M.W. *et al.* (2023) 'Persistence and quality of vegetation cover in expired
546 Conservation Reserve Program fields', *Ecosphere*, 14(1). Available at:
547 <https://doi.org/10.1002/ecs2.4359>.
- 548 Vicente-Serrano, S.M., Beguería, S. and López-Moreno, J.I. (2010) 'A Multiscalar Drought Index
549 Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index',
550 *Journal of Climate*, 23(7), pp. 1696–1718. Available at:
551 <https://doi.org/10.1175/2009JCLI2909.1>.
- 552 Watson, D.F. *et al.* (2021) 'Plant community responses to grassland restoration efforts across a
553 large-scale precipitation gradient', *Ecological Applications*, 31(6). Available at:
554 <https://doi.org/10.1002/eap.2381>.
- 555 Werner, C.M. *et al.* (2020) 'Year effects: Interannual variation as a driver of community
556 assembly dynamics', *Ecology*, 101(9). Available at: <https://doi.org/10.1002/ecy.3104>.
- 557 Yang, H. *et al.* (2023) 'The detection and attribution of extreme reductions in vegetation growth

across the global land surface', *Global Change Biology*, p. gcb.16595. Available at:

<https://doi.org/10.1111/gcb.16595>.

Ye, C. *et al.* (2023) 'Soil organic carbon and its stability after vegetation restoration in Zoige

grassland, eastern QINGHAI-TIBET Plateau', *Restoration Ecology* [Preprint]. Available at:

<https://doi.org/10.1111/rec.13896>.

Young, T.P. *et al.* (2015) 'Initial success of native grasses is contingent on multiple interactions

among exotic grass competition, temporal priority, rainfall and site effects', *AoB PLANTS*, 7.

Available at: <https://doi.org/10.1093/aobpla/plu081>.

Yuan, X. *et al.* (2023) 'A global transition to flash droughts under climate change', *Science*,

380(6641), pp. 187–191. Available at: <https://doi.org/10.1126/science.abn6301>.

574 Tables

575 **Table 1:** Precipitation (mm) measured at drake farm. High values are bold. Highest and lowest
576 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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Figure Captions

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

Figure 2. Species composition and diversity. A is an NMDS using abundance data, and B is an NMDS using occurrence data. Four letter species codes (Table S1) correspond with the species that were significantly correlated ($p < 0.001$) with the ordination. C is the Shannon-Weaver diversity index, and D is species richness and for each plot. Horizontal black bars in C and C are the medians.

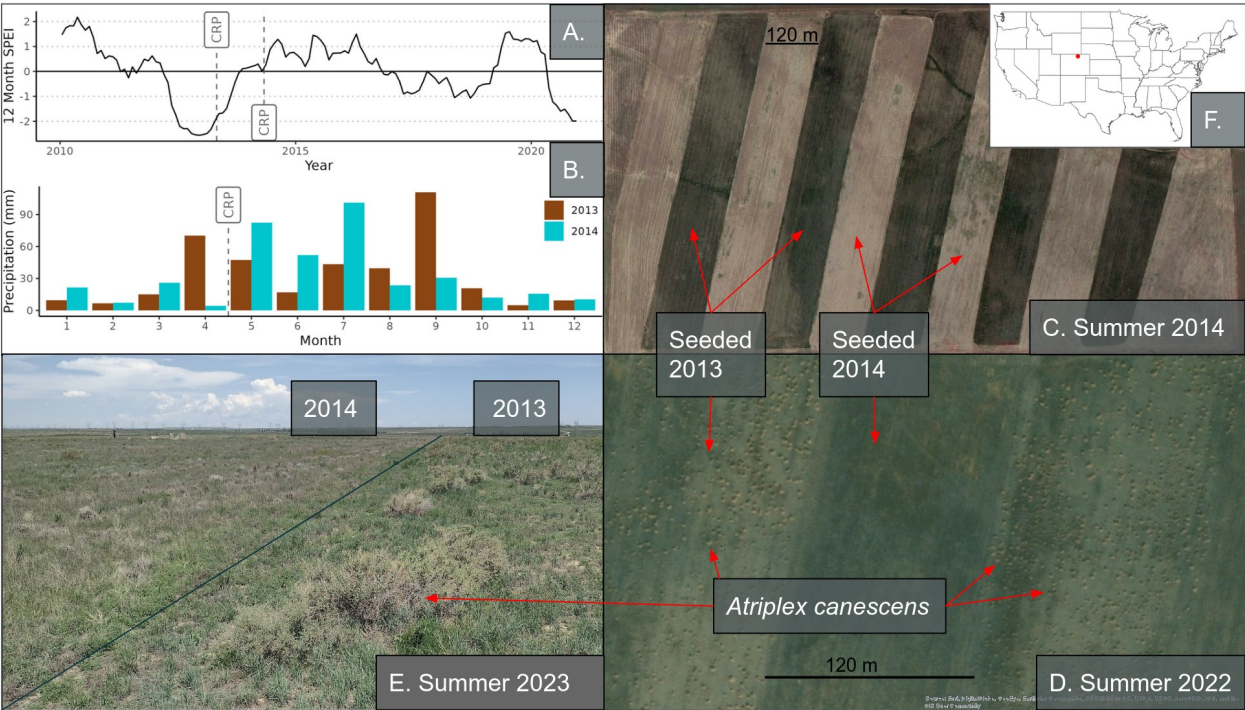
Figure 3. Posterior distributions of parameter estimates for environmental filters by species. Species are sorted top to bottom according to prevalence, origin (native versus introduced), and functional group. Posterior distributions from each chain overlap to highlight model convergence. Vertical Dotted lines are zero. Distributions with a median closer to zero are more transparent. Species above the thick horizontal line are native. Blue is positive, red is negative.

Abbreviations: ST = soil temperature, SM = soil moisture, AT = air temperature, TWI = Topographic Wetness Index. Species and species group abbreviations are in **Table S1**.

Figure 4: Residual correlations of species occurrences. The three species at the bottom are introduced annual *Bromus* spp, *Secale cereale* and *Bassia scoparia*, a group (G1) with positive intragroup associations that appears to be negatively interacting with a group of mostly native species (G2, top right) that have positive intragroup associations. Table S1 has abbreviations.

601

602 **Figures**



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604 **Figure 1**

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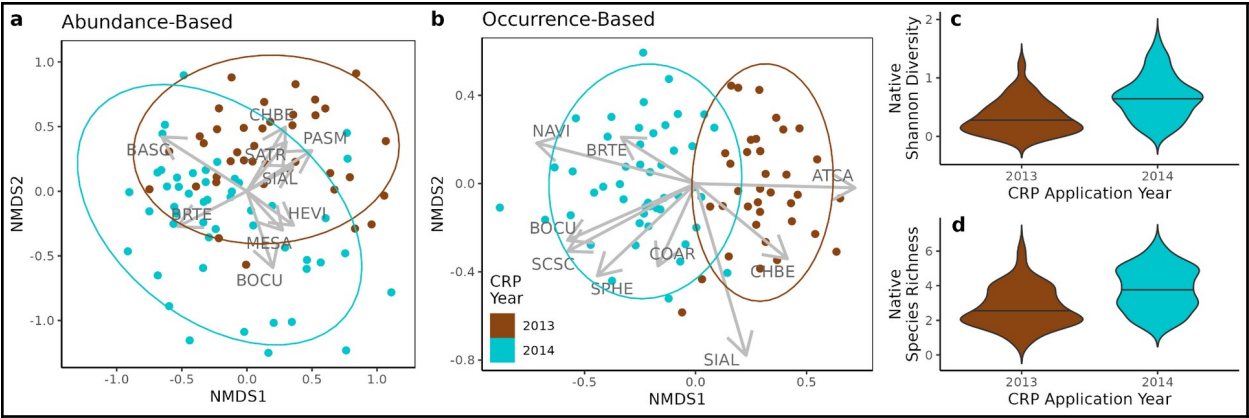


Figure 2

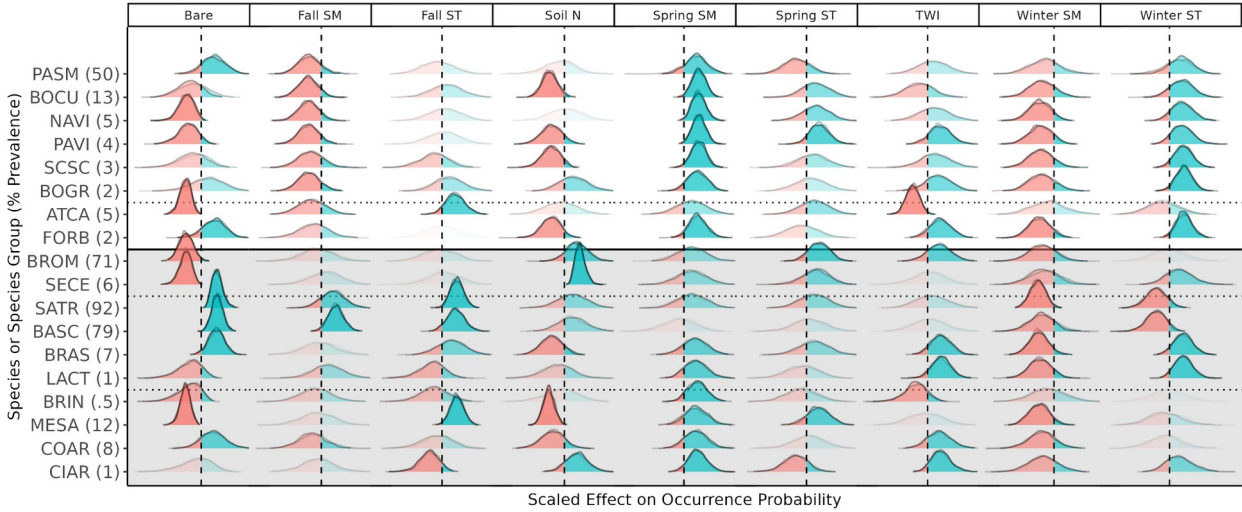
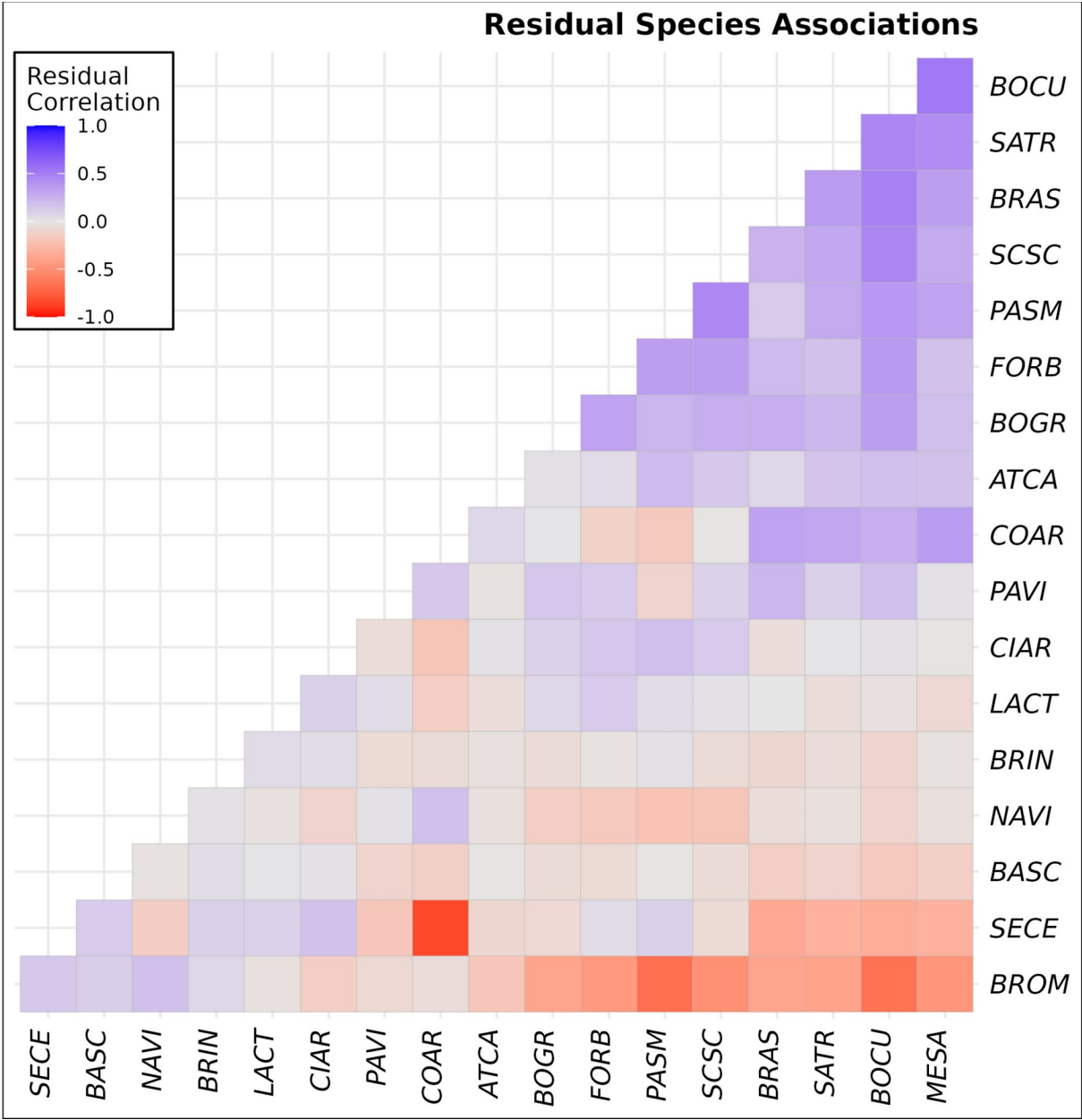


Figure 3



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621 Figure 4