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

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## Abstract

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

# Introduction

Understanding how species diversity develops in novel ecosystems such as post agricultural landscapes is one of most important questions in plant science today ([Armstrong et al., 2023](#); [Bell et al., 2023](#)). Globally, about 15 Mkm<sup>2</sup> (10% of global land area) are currently managed as croplands, and this has led to an estimated 133 Pg in cumulative C emissions throughout human history ([Sanderman, Hengl and Fiske, 2017](#)). Reestablishing native perennial plant cover in post agricultural landscapes is an important way to restore these systems to C sinks and enhance ecosystem functions and services. However, restoration practitioners have a difficult task in re-establishing native plants in areas managed for long periods as intensive agriculture, because often the native seed bank is depleted, soil fertility has declined, non-native plants are abundant, and ecohydrological function is altered ([Turnbull et al., 2012](#)). Furthermore, restoration practitioners are often guided by mean annual climate conditions when they decide which species to plant. But a typical year will tend to have a combination of high, low or average seasonal values of temperature, precipitation and other climate variables, and precipitation in particular can be very difficult to predict. Therefore, “mean conditions” rarely capture climate extremes that drive community responses , especially in drylands.

In the United States, the USDA’s Conservation Reserve Program (CRP) has been paying farmers to convert cultivated land to perennial vegetation since 1985. As of 2020 there were 8.9 million hectares enrolled, with the western Great Plains being one of the regions 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).

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; Shriner *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 (Csákvari 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

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

## Materials and Methods

### Site Description

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

The existing CRP was implemented in two stages, with the same seed mix (Table S1). One set of alternating crop strips (**Fig. 1B**) was planted on April 29, 2013, and the second set was 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.

## Field sampling

In June 2022, we sampled 88 5 m x 5 m plots that were collocated with areas previously sampled for soil C ([Sherrod, Erskine and Green, 2015](#)), aligned with a 5m digital elevation model (DEM) ([Erskine et al., 2006](#)). Within each plot, we established 4, 0.1 m<sup>2</sup> subplots at random locations. In each subplot, we used ocular estimates to measure the fractional cover of every species, as well as the cover of bare soil, litter, and rocks. We measured the maximum height of each species in each subplot, and did a gridded plant walkabout to detect all species in the 25 m<sup>2</sup> plot.

## Ancillary data

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

We used the topographic layers as predictors in a spatial process model ([Nychka et al., 2021](#)) to estimate seasonal averages of 30 cm soil temperature and moisture at a 5 m resolution (**Fig. S1**) for three time periods preceding seeding: March and April to capture the conditions immediately preceding seeding, January and February to capture winter freezing conditions, 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  $0.1\text{m}^2$  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<sup>2</sup> 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 m<sup>2</sup> 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 m<sup>2</sup> 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.

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

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

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

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

## Discussion

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

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.

## Conclusion

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

## Authors' contributions

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

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

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# Tables

**Table 1:** Precipitation (mm) measured at drake farm. High values are bold. Highest and lowest years are italicized and bold.

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

## 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.

# Figures

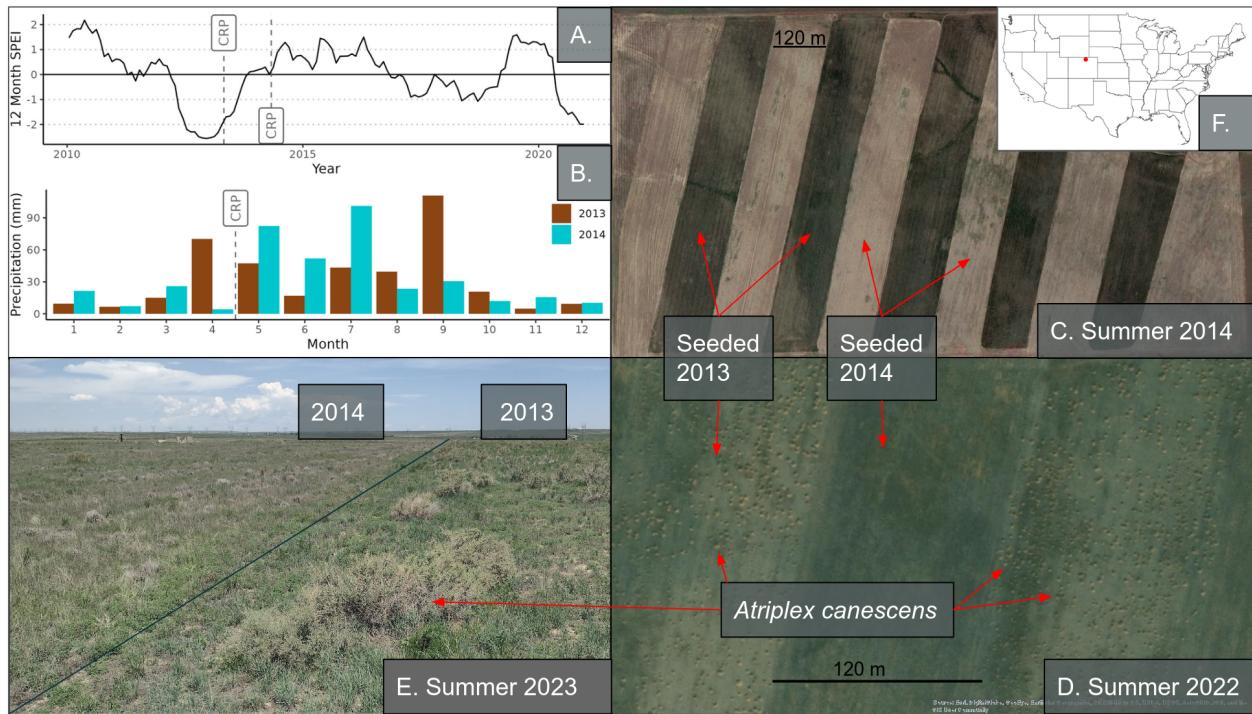


Figure 1

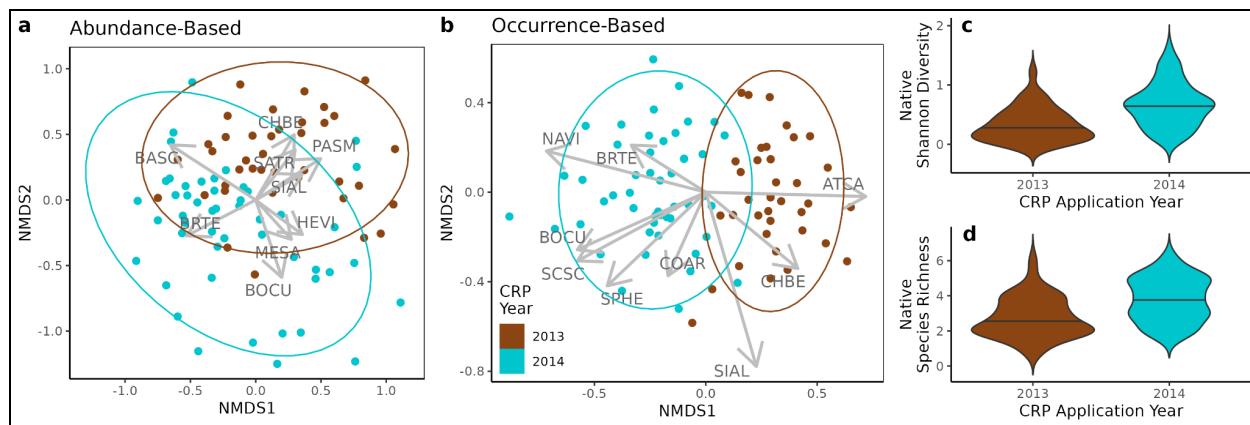


Figure 2

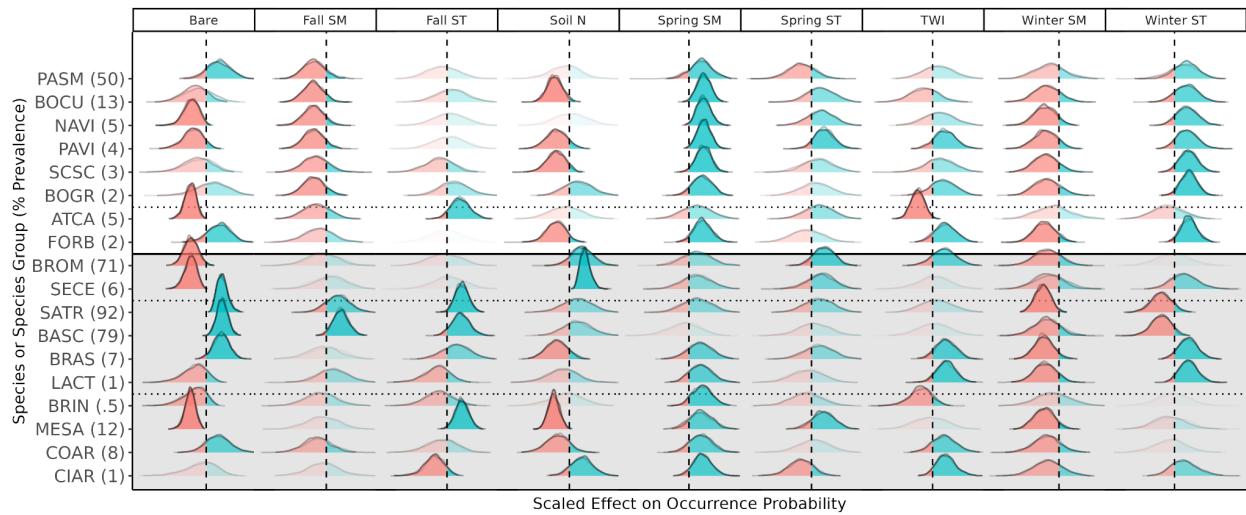


Figure 3

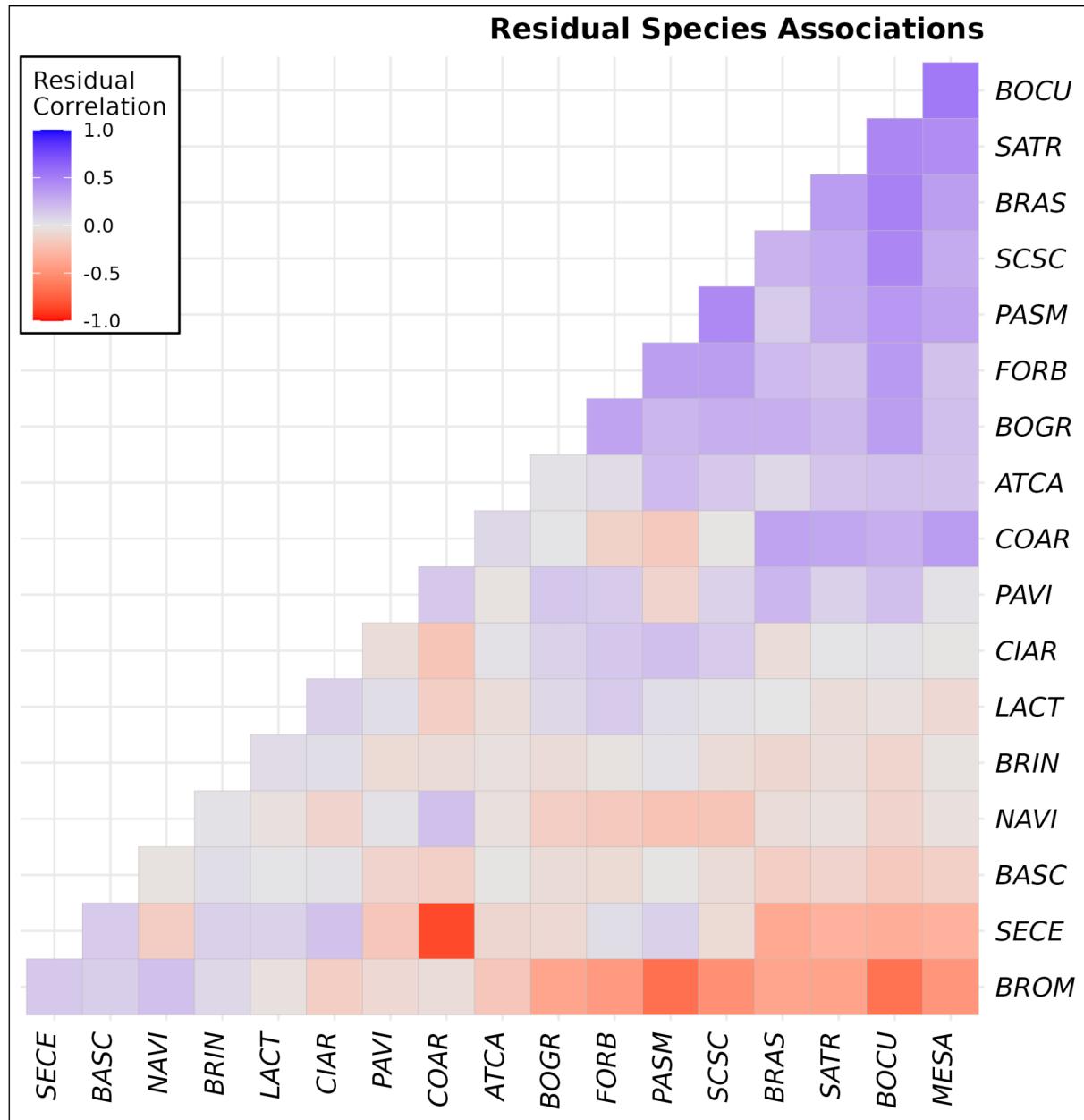
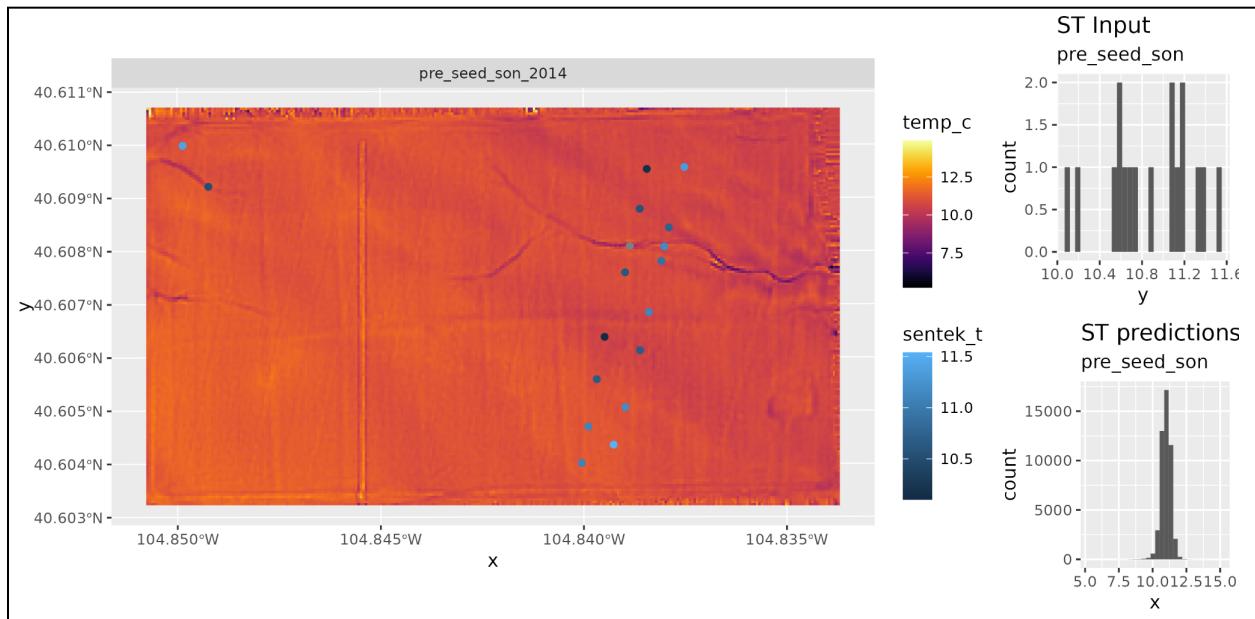
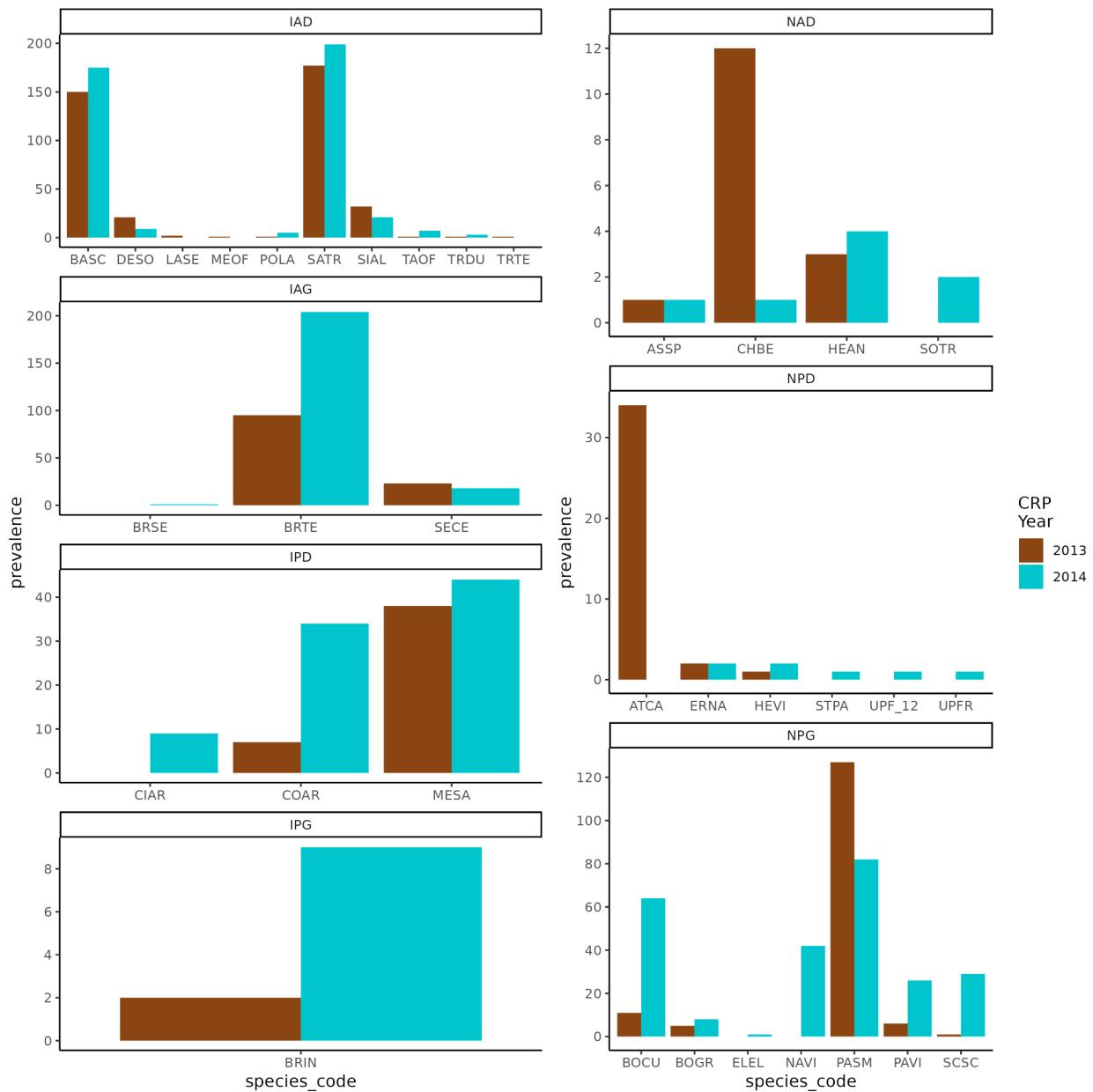


Figure 4

## Supplementary Figures and Tables

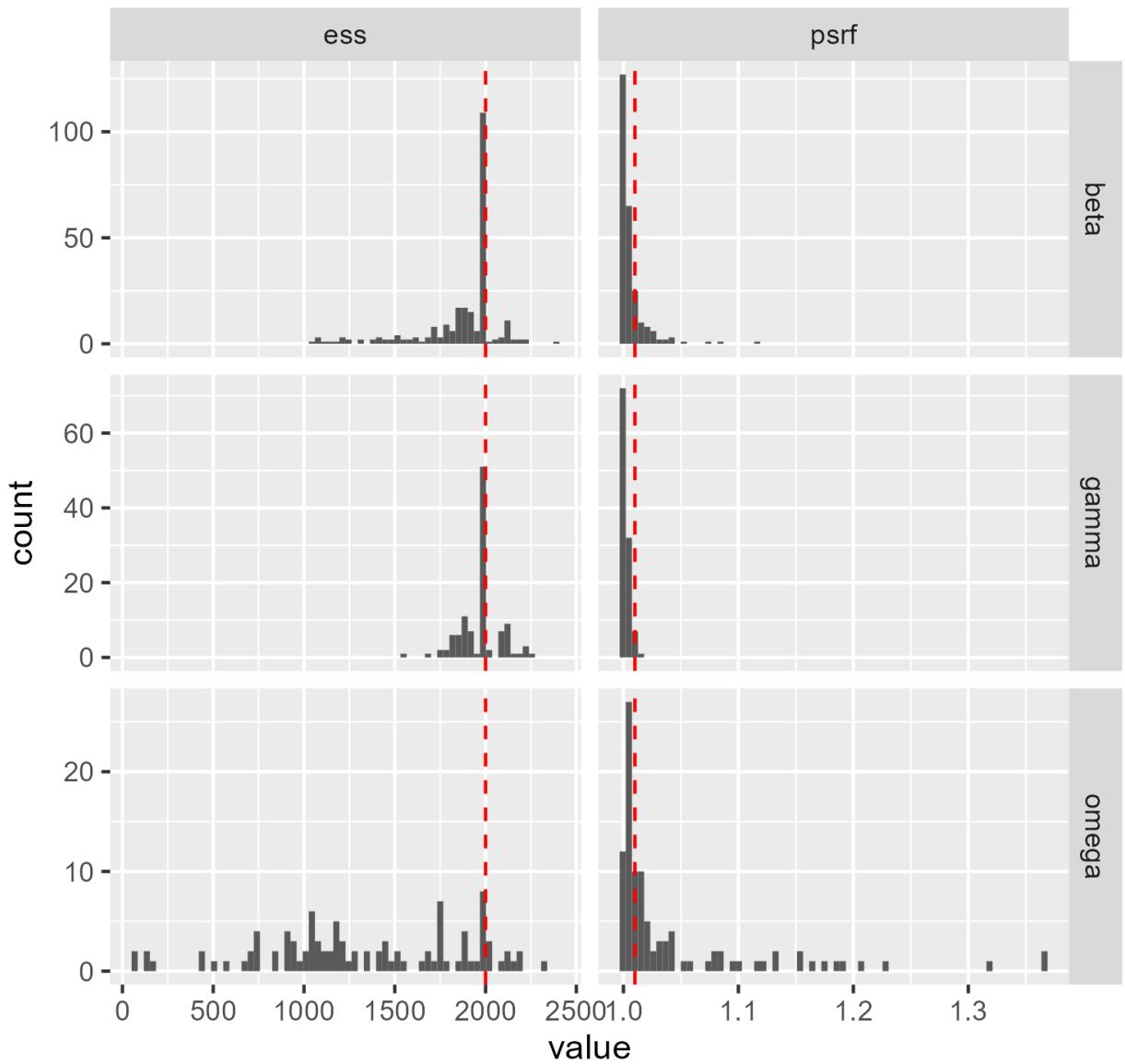


**Figure S1.** One of the surfaces created by spatial process modelling. Blue dots indicate the Sentek sensor locations. Figures for all surfaces used in the analysis, along with the code and data to recreate them, are available in the GitHub repository.

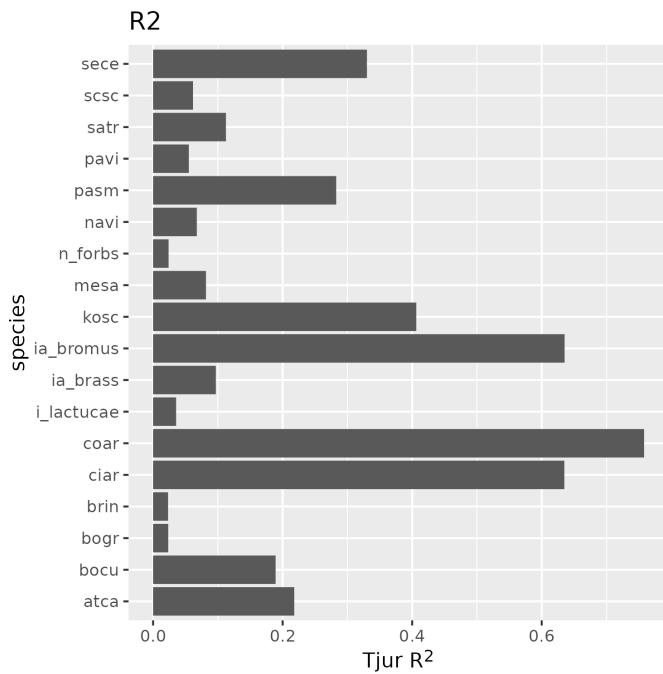


**Figure S2.** Species prevalence. Prevalence (number of plots in which a species was encountered) for each plant species encountered across the study site. Abbreviations: N = native, A = annual, P = perennial, D = dicot, G = graminoid, I = introduced.

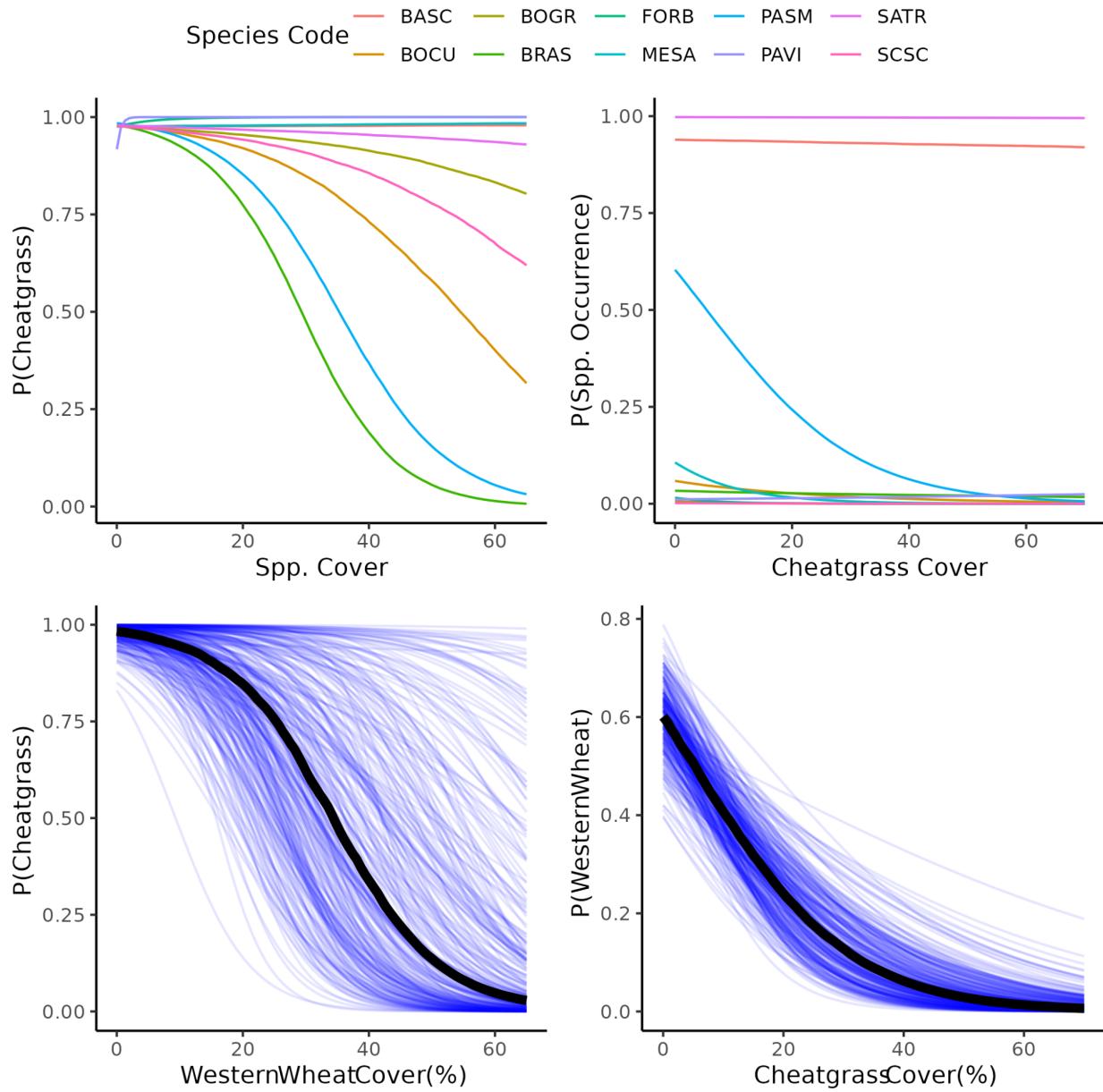
## Model Convergence



**Figure S3:** Model convergence diagnostics. The potential scale reduction factor (PSRF) measures the convergence among chains, and being closer 1.0 is ideal. Effective sample size (ESS) measures autocorrelation between successive iterations within each chain, and higher values are better. Ideally ESS matches the number of posterior samples, but that is not fully necessary. Beta is the parameters for environmental filters, gammas are the parameters for the traits, and omega is the parameters for the species associations.



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



**Figure S5.** Western Wheatgrass and Cheatgrass interactions, compared to other species. This is using abundance data on the y axes to estimate the occurrence of a given species. *P. smithii* and cheatgrass had strong effects on each others' occurrence, compared to other species. THis was consistent with field observations.

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

Family	Genus	Specific epithet	Group Code	Group Name	CRP Mix	origin	Seed Applied (kg/ha)
Asteraceae	<i>Gutierrezia</i>	<i>sarothrae</i>	GUSA	<i>Gutierrezia sarothrae</i>	no	n	
Asteraceae	<i>Ericameria</i>	<i>nauseosa</i>	ERNA	<i>Ericameria nauseosa</i>	no	n	
Asteraceae	<i>Heterotheca</i>	<i>villosa</i>	HEVI	<i>Heterotheca villosa</i>	no	n	
Asteraceae	<i>Helianthus</i>	<i>annuus</i>	HEAN	<i>Helianthus annuus</i>	no	n	
Asteraceae	<i>Stephanomeria</i>	<i>pauciflora</i>	FORB	Native Forbs	no	n	
Asteraceae	cf <i>Aster</i>	d_081_herb_05	FORB	Native Forbs	no	n	
Asteraceae	<i>Antennaria</i>	sp.	ANSP	<i>Antennaria</i> sp	no	n	
Asteraceae	<i>Artemisia</i>	<i>arbuscula</i>	ARAR	<i>Artemisia arbuscula</i>	no	n	
Chenopodiaceae	<i>Atriplex</i>	<i>canescens</i>	ATCA	<i>Atriplex canescens</i>	yes	n	0.2676
Chenopodiaceae	<i>Chenopodium</i>	<i>berlandieri</i>	FORB	Native Forbs	no	n	
Malvaceae	<i>Sphaeralcea</i>	<i>coccinea</i>	SPCO	<i>Sphaeralcea coccinea</i>	no	n	
Papaveraceae	<i>Argemone</i>	cf <i>hispida</i>	ARHI	<i>Argemone cf hispida</i>	no	n	

Poaceae	<i>Bouteloua</i>	<i>curtipendula</i>	BOCU	<i>Bouteloua curtipendula</i>	yes	n	0.6244
Poaceae	<i>Panicum</i>	<i>virgatum</i>	PAVI	<i>Panicum virgatum</i>	yes	n	0.1784
Poaceae	<i>Schizachyrium</i>	<i>scoparium</i>	SCSC	<i>Schizachyrium scoparium</i>	yes	n	0.3568
Poaceae	<i>Nassella</i>	<i>viridula</i>	NAVI	<i>Nassella viridula</i>	yes	n	0.7136
Poaceae	<i>Pascopyrum</i>	<i>smithii</i>	PASM	<i>Pascopyrum smithii</i>	yes	n	1.784
Poaceae	<i>Bouteloua</i>	<i>gracilis</i>	BOGR	<i>Bouteloua gracilis</i>	yes	n	0.1784
Poaceae	<i>Elymus</i>	<i>elymoides</i>	ELEL	<i>Elymus elymoides</i>	no	n	
Solanaceae	<i>Solanum</i>	<i>triflorum</i>	FORB	Native Forbs	no	n	
unknown	Perennial_forb	d_012_herb_01	FORB	Native Forbs	no	n	
unknown	Rhizomatous_p erennial_forb	d_141_herb_09	FORB	Native Forbs	no	n	
Asteraceae	<i>Podospermum</i>	<i>laciniatum</i>	LACT	Introduced Cichorioideae	no	i	
Asteraceae	<i>Taraxacum</i>	<i>officinale</i>	LACT	Introduced Cichorioideae	no	i	
Asteraceae	<i>Tragopogon</i>	<i>dubious</i>	LACT	Introduced Cichorioideae	no	i	
Asteraceae	<i>Cirsium</i>	<i>arvense</i>	CIAR	<i>Cirsium arvense</i>	no	i	
Asteraceae	<i>Onopordium</i>	<i>acanthium</i>	ONAC	<i>Onopordium acanthium</i>	no	i	
Asteraceae	<i>Lactuca</i>	<i>serriola</i>	LASE	<i>Lactuca serriola</i>	no	i	
Brassicaceae	<i>Sisymbrium</i>	<i>altissimum</i>	BRAS	Introduced Brassicaceae	no	i	
Brassicaceae	<i>Descurainia</i>	<i>sophia</i>	BRAS	Introduced Brassicaceae	no	i	
Chenopodiaceae	<i>Salsola</i>	<i>tragus</i>	SATR	<i>Salsola tragus</i>	no	i	
Chenopodiaceae	<i>Bassia</i>	<i>scoparia</i>	BASC	<i>Bassia scoparia</i>	no	i	
Convolvulaceae	<i>Convolvulus</i>	<i>arvensis</i>	COAR	<i>Convolvulus arvensis</i>	no	i	

Fabaceae	<i>Medicago</i>	<i>sativa</i>	MESA	<i>Medicago sativa</i>	yes	i	0.3568
Fabaceae	<i>Melilotus</i>	<i>officinale</i>	MEOF	<i>Melilotus officinale</i>	no	i	
Poaceae	<i>Bromus</i>	<i>tectorum</i>	BROM	Introduced Annual <i>Bromus</i>	no	i	
Poaceae	<i>Secale</i>	<i>cereale</i>	SECE	<i>Secale cereale</i>	no	i	
Poaceae	<i>Bromus</i>	<i>inermis</i>	BRIN	<i>Bromus inermis</i>	no	i	
Poaceae	<i>Bromus</i>	<i>secalinus</i>	BROM	Introduced Annual <i>Bromus</i>	no	i	
Poaceae	<i>Agropyron</i>	<i>cristatum</i>	AGCR	<i>Agropyron cristatum</i>	no	i	
Zygophyllaceae	<i>Tribulus</i>	<i>terrestris</i>	TRTE	<i>Tribulus terrestris</i>	no	i	

Table S2: R packages used in the analysis.

Package	Purpose	Citation
sf	Spatial vector data management	Pebesma 2018
terra	Raster data management	Hijmans 2023a
raster	Raster data management	Hijmans 2023b
vegan	Diversity and NMDS	Oksanen et al 2022
SPEI	Calculating SPEI	Beguería and Vicente-Serrano

2023

microclima	Calculating air temperature	Mosedale et al 2023
NicheMapR	Calculating air temperature	Kearney 2022
topmodel	Calculating TWI	Buytaert 2022
tidyverse	Data wrangling	Wickham et al 2019
lubridate	Date wrangling	Grolemond and Wickham 2011
vroom	Data wrangling	Hester et al 2023
Hmsc	Joint species distribution modeling	Tikhonov et al 2023
snow	parallelization	Tierney et al 2021
fields	spatial process models	Nychka et al 2021
ggpubr	visualization	Kassambara 2023
ggcorrplot	visualization	Kassambara 2022
ggthemes	visualization	Arnold 2021
ggtext	visualization	Wilke 2021

ggrepel	visualization	Slowikowski 2023
gcmc	visualization	Fernandez i Marin 2016
geomtextpath	visualization	Cameron and van den Brand 2022

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

Common Name	Scientific Name	Amount Applied (kg/ha)	Origin
Western wheatgrass	<i>Pascopyrum smithii</i>	1.784	native
Green needlegrass	<i>Nassella viridula</i>	0.7136	native
Sideoats gramma	<i>Bouteloua</i> <i>curtipendula</i>	0.6244	native
Alfalfa	<i>Medicago sativa</i>	0.3568	introduced
Little bluestem	<i>Schizachyrium</i> <i>scoparium</i>	0.3568	native
Fourwing Saltbush	<i>Atriplex canescens</i>	0.2676	native
Blue gramma	<i>Bouteloua gracilis</i>	0.1784	native
Switchgrass	<i>Panicum virgatum</i>	0.1784	native

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## Supplementary References

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