

# Antecedent climate explains divergent, long-term restoration outcomes in the Western Great Plains, USA.

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#### Article

**Keywords:** Ecosystem restoration, cheatgrass (Bromus tectorum), Conservation Reserve Program, western wheatgrass (Pascopyrum smithii), interannual climate variability

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# Title: Antecedent climate drives divergent, long-term

# 2 restoration outcomes in the Western Great Plains,

#### 3 USA.

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#### 12 Abstract

- 13 Converting croplands to grasslands can restore ecosystem functions and services. But there is
- 14 uncertainty about why some restoration treatments succeed and others do not. Existing
- 15 restoration strategies tailor species compositions of seed mixes according to mean conditions in
- 16 hardiness zones. But individual years typically deviate from average climate norms such that
- 17 restoration activities may be better informed by recent conditions than with climate averages in
- 18 order to best direct management strategies. We monitored a field in eastern Colorado that was
- 19 converted from wheat-fallow to native perennial grassland via seeding. The same seed mix was
- 20 used to seed half the strips in 2013 (drier) and the other half in 2014 (wetter). The strips seeded
- 21 in 2013 had only one native grass and shrub species from the seed mix establish, whereas in
- 22 2014 all native grasses established Higher soil moisture preceding seed application was
- 23 positively associated with perennial grasses, while rhizomatous grasses, shrubs and introduced
- 24 annuals were associated with other variables. We found evidence of facilitatory interactions
- 25 between grasses and forbs, and antagonistic interactions between native perennial grasses and
- 26 introduced annuals. These findings can assist land managers to improve upon current
- 27 approaches by considering antecedent conditions during restoration planning.

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- 29 Keywords: Ecosystem restoration, cheatgrass (*Bromus tectorum*), Conservation Reserve
- 30 Program, western wheatgrass (*Pascopyrum smithii*), interannual climate variability

#### Introduction

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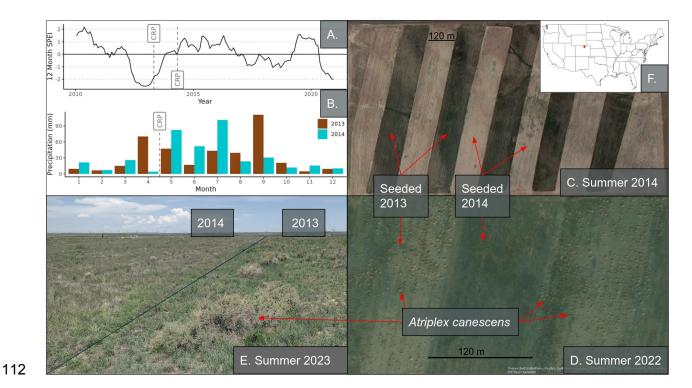
33 landscapes is one of most important questions in plant science today (Armstrong et al., 2023; 34 Bell et al., 2023). Globally, about 15 Mkm<sup>2</sup> (10% of global land area) are currently managed as 35 croplands, and this has led to an estimated 133 Pg in cumulative C emissions throughout 36 human history (Sanderman, Hengl and Fiske, 2017). Reestablishing native perennial plant 37 cover in post agricultural landscapes is an important way to restore these systems to C sinks 38 and enhance ecosystem functions and services. However, restoration practitioners have a 39 difficult task in re-establishing native plants in areas managed for long periods as intensive 40 agriculture, because often the native seed bank is depleted, soil fertility has declined, non-native 41 plants are abundant, and ecohydrological function is altered (Turnbull et al., 2012). Furthermore, 42 restoration practitioners are often guided by mean annual climate conditions when they decide 43 which species to plant. But a typical year will tend to have a combination of high, low or average 44 seasonal values of temperature, precipitation and other climate variables, and precipitation in 45 particular can be very difficult to predict. Therefore, "mean conditions" rarely capture climate 46 extremes that drive community responses, especially in drylands (Zhang et al., 2022). 47 48 In the United States, the USDA's Conservation Reserve Program (CRP) has been paying 49 farmers to convert cultivated land to perennial vegetation since 1985. As of 2020 there were 8.9 50 million hectares enrolled, with the western Great Plains being one of the regions with the 51 greatest enrollment (USDA, 2023). Landowners typically follow state- or regional-level 52 guidelines that adhere to national prescriptions for seed application (Taliga, 2011). Often, the 53 plant community established by CRP remains on the land with all of its associated benefits even 54 after contracts expire (Vandever et al., 2023). Successful establishment of perennial vegetation 55 under the CRP program has been shown to increase soil microbial function (Li et al., 2018) and 56 biomass (Bach, Baer and Six, 2012), preserve freshwater ecosystem services (Huang et al., 57 2019), improve pollinator health (Ricigliano et al., 2019), and increase soil carbon mineralization 58 (Bach, Baer and Six, 2012). More generally, conversion from cultivated annual crops to 59 perennial grassland can increase soil organic carbon (Ye et al., 2023), and moderate soil 60 temperatures (Huang et al., 2023). It is typically assumed that the community will reach some 61 stable state of perennial cover after twenty or more years (Harniss and Murray, 1973; Munson 62 and Lauenroth, 2012). However, assumptions based on successional theory don't always come 63 to pass (Drury and Nisbet, 1973), and starkly divergent outcomes in restoring shortgrass prairie

Understanding how species diversity develops in novel ecosystems such as post agricultural

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     have been documented even 50 years after restoration (Coffin, Lauenroth and Burke, 1996).
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     In addition to challenging site conditions, increasing temperatures and aridity have led to
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     widespread declines in soil moisture (Lal et al., 2023). Regional guidance for species selection,
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     seeding rates and timing of treatment currently follows seeding zones based on ecological site
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     type and annual climate means (Taliga, 2011). However, as the climate continues to become
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     warmer, dryer and more variable (Yuan et al., 2023), static prescriptions may be less reliable,
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     and it may become increasingly important to account for current climatic conditions (Barr, Jonas
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     and Paschke, 2017; Barak et al., 2023). Seed germination and seedling establishment are
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     especially sensitive to short-term fluctuations in climatic conditions (Larson et al., 2015; Shriver
74
     et al., 2018). Even if mean annual temperature or precipitation is suitable for a given species
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     climatic niche. The inter- and intra-annual timing of moisture availability and heat stress within
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     the year of a restoration treatment is of tantamount importance for determining germination,
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     establishment, and community assembly (Young et al., 2015; O'Connor et al., 2020; Werner et
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     al., 2020). Compositional differences due to interannual climate variability can have decadal
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     legacies (Eckhoff et al., 2023).
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     After a seeding treatment, the community composition changes for decades as perennial plants
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     establish and spread, leaving less room for volunteer annuals as time passes (Munson and
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     Lauenroth, 2012). The particular species that do establish after a disturbance or a restoration
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     treatment is dependent upon the abiotic circumstances, and inter-specific ecological processes
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     including the strength and timing of competition (Young et al., 2015). Introduced annuals can be
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     well-adapted to unpredictable conditions (Symonides, 1988), and when abundant can slow
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     down the colonization of perennials, due to competition for resources (Bakker et al., 2003),
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     altered nutrient fluxes (Mahood et al., 2022; Yang et al., 2023) and changes to hydraulic
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     connectivity (Turnbull et al., 2012). Some native perennial species compete against introduced
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     annuals. For example, the perennial grass species Elymus elymoides and native forbs compete
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     favorably against one of the most notorious introduced annuals, cheatgrass (Bromus tectorum),
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     by outcompeting B. tectorum for soil water in the fall (Booth, Caldwell and Stark, 2003; Leger,
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     Goergen and Forbis De Queiroz, 2014; Porensky et al., 2014), Including species in seed mixes
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     that are able to compete against the local introduced annuals may speed the development of
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     stable perennial cover (Csákvári et al., 2023).
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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.



**Figure 1:** Panel A shows the 12 month SPEI at the site from 2010-2022, and B shows the monthly precipitation for 2013 and 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 is a picture taken on the ground in 2023 at the strip boundary. F shows the location in CO.

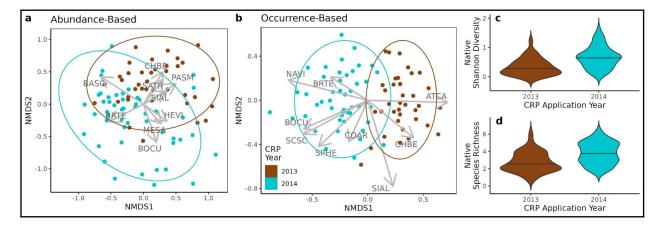
# 118 Results

#### 3.1 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.





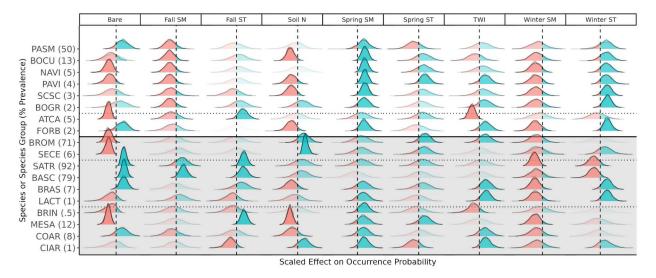
**Figure 2.** Species composition and diversity. Panel (a) is a nonmetric multidimensional scaling ordination (NMDS) using abundance data, and panel (b) is an NMDS using occurrence data. The color and 95% confidence interval ellipses correspond to the year of seed application. Four letter species codes correspond with the species that were significantly correlated (p<0.001) with the ordination. Violin plots of the Shannon-Weaver diversity index (c) and species richness (d) and for each 25 m² plot, by CRP application year. The horizontal black bars in (c) and (d) are the medians. Species abbreviations included in Table S1.

#### 3.2 Interspecific analysis

**JSDM Convergence and fit.** 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<sup>2</sup> values ranged from near zero to 0.75 (**Fig. S4**), The dominant species mentioned above had R<sup>2</sup> values from 0.15 - 0.65.

Environmental filters. 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.



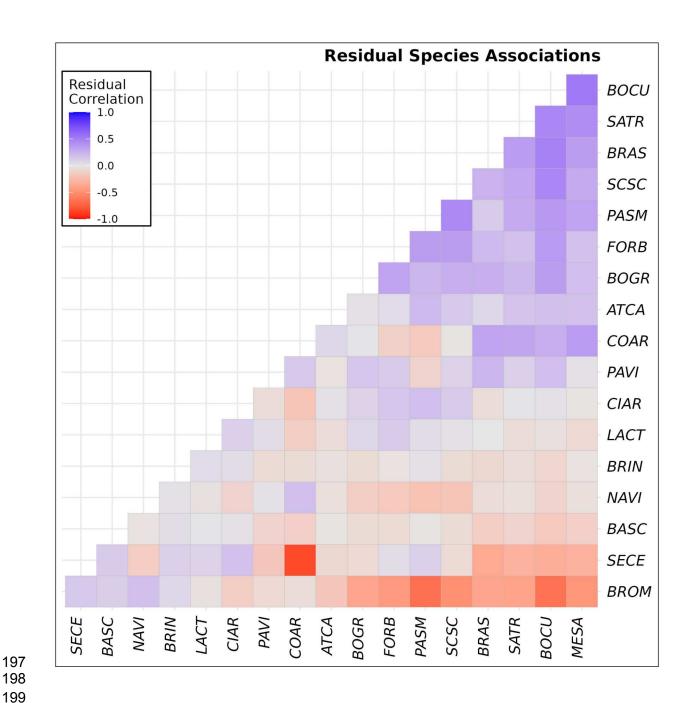
**Figure 3**. Posterior distributions of parameter estimates for environmental filters by species. Species are sorted top to bottom according to prevalence, origin (native versus introduced), and functional group. Posterior distributions from each chain are plotted concurrently to highlight model convergence. Vertical Dotted lines are zero. Distributions with a median closer to zero are more transparent. Species above the thick horizontal line are native (All except native forbs were in the CRP seed mix), the rest are introduced, with only alfalfa in the seed mix. Blue indicates the part of the distribution that is positive, red negative. **Abbreviations:** ST = soil temperature, SM = soil moisture, AT = air temperature, TWI = Topographic Wetness Index. Species and species group abbreviations are in **Table S1**.

*Traits.* 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.

 **Species associations**. 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**).



**Figure 4**: Residual correlations of species occurrences after accounting for the effects of traits and environmental filters. Red values are negative correlations and blue are positive. 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.

### 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; Fuhlendorf *et al.*, 2002), 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; Larson and Funk, 2016; 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

#### Interspecific interactions

groups (G1) and native species groups (G2) (Fig. 4). Grass-forb mutualisms may be an adaptation to interannual climate variability in grasslands (Felton, Zavislan-Pullaro and Smith, 2019; 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.

necessarily definitive evidence of mechanistic interactions between species (Blanchet, Cazelles

Residual correlations in occurrence should be viewed skeptically because they are not

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; Davies *et al.*, 2011). 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 (Keddy and Laughlin, 2021). 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.

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#### Tailoring seed mixes using antecedent climate data

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.

**Table 1:** Precipitation (mm) measured at drake farm. Months with the highest precipitation for a given year are in bold. Annual maximum and minimums are italicized and bold in the bottom row.

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

Seed mixes tailored towards wet/cold conditions might take advantage of the opportunity to have success with high-diversity mixtures (Shriver 2018). When these opportunities arise, high diversity seed mixes, especially when there are multiple species in each functional group, may be a good bet-hedging strategy to promote the enhanced function and structure of the ecosystem. In the context of climate change, mixes planned for the warm/dry end of the spectrum could be more heavily weighted towards high abundances of competitively dominant native graminoids and forbs to ward off competitively dominant 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 a repeated seeding approach (Shriver 2018). Another approach may be to strategically consider seed source location when developing the seed mix. For example, using seed sourced from hotter and drier locations in years with hot and dry antecedent conditions may result in a greater probability of perennial establishment. Current CRP guidelines recommend purchasing seed produced within 100 miles of where it will be planted, so acquiring seeds from a different climatic region may require policy modifications before being implemented.

# 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.

#### Materials and Methods

#### 2.1 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 relics 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

361 Standardized Precipitation Evaporation Index (SPEI) (Vicente-Serrano, Bequería and López-362 Moreno, 2010) was exceptionally anomalously low prior to the 2013 seeding application, and 363 closer to normal preceding the second seed application (Fig. 1A). 364 365 Erskine et al. (2006) described the topographic attributes based on a survey-grade 5-m digital 366 elevation model (DEM), which revealed potential flowpaths and accumulation areas along with 367 variable slopes up to 13%. Mapped soil units are Wagonwheel coarse silty loam (a 368 coarse-silty, mixed, superactive, mesic Aridic Calciustept), Colby fine silty loam (a fine-silty, 369 mixed, superactive, calcareous, mesic Aridic Ustorthent), and Kim fine sandy loam (a fine-370 loamy, mixed, active, calcareous, mesic Ustic Torriorthents). Detailed soil horizons and textural 371 information are given in Green and Erskine (2011, Table 1). We note that, after the 372 establishment of perennial vegetation under CRP, there has been no surface runoff whereas 373

#### 2.2. Plant diversity field sampling

numerous runoff events were observed pre-CRP.

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.

#### 2.3 Ancillary data

383 The 5m DEM with which the plots were aligned was used to create grids of topographic wetness 384 index (TWI), topographic position index (TPI), slope, and folded aspect (McCune and Keon, 385 2002; Hijmans, 2023). Within the field, four or more frequency domain sensors (Sentek<sup>TM</sup>) 386 (Schwank et al., 2006) were installed at 18 locations at depths ranging from 30 to 170 cm to 387 measure hourly soil moisture from 2002-2018. Each of 16 locations on the main transects has 388 sensors at a depth of 30 cm. Soil temperature was measured using stand-alone thermocouple sensors (Onset WaterTempPro<sup>™</sup>) at a 30 cm depth near each Sentek probe (Green and 389 390 Erskine, 2011).

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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. We also had data on soil type, texture and total nitrogen content that was measured from soil cores at each sampling location in 2012 (Sherrod, Erskine and Green, 2015). In order to account for air temperature, we used a process-based microclimate model (Maclean, Mosedale and Bennie, 2019) to downscale sub-daily data to our 5m DEM to create hourly temperature surfaces, then aggregated to the mean for the three time periods.

#### 2.4 Statistical analysis

We used nonmetric multidimensional scaling (Minchin, 1987) to examine how the species composition and abundances 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 understand how the two strips differed in species composition. We used stress plots to assess the fit of the NMDS ordinations. To examine how individual species drove the ordination, we used a permutational correlation with a cutoff of p < 0.001 to account for multiple tests. Since native biodiversity is a common goal for restoration treatments, 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,

424 rhizomatous, and photosynthetic pathway (C3 or C4; **Table S1**). 425 426 We created four Markov Chain Monte Carlo (MCMC) chains, each consisting of 1,500,000 427 iterations. We discarded the first 500,000 iterations for each chain and then recorded every 428 1,000th sample for a total of 1,000 posterior samples per chain, and 4,000 total. We assessed 429 model convergence using the effective sample size (ESS) and the potential scale reduction factor (R) (Gelman and Rubin, 1992; Gelman et al., 2020). We used Tjur R2 to assess 430 431 explanatory power of the model for each species. 432 433 We observed in the field that western wheatgrass (*P. smithii*), a native, rhizomatous grass, 434 appeared to be in direct competition with *B. tectorum*. The approach described above quantifies 435 interspecific interactions in the residual correlations that are calculated, but we wanted to 436 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 437 438 Bernoulli-distributed response, with the cover of *P. smithii* and other species that strongly 439 interacted with B. tectorum, and bare ground cover as predictors, and the plot as a random 440 effect. We also created an opposite model with the occurrence of the strongly interacting 441 species as a multivariate response variable, B. tectorum cover and bare ground cover as 442 predictors, and the plot as a random effect. 443 444 All of the analyses were conducted in R (R Core Team, 2021). Table S2 lists the packages 445 used in the analysis. The code and data needed to reproduce the complete analysis will be 446 publicly available after publication at <a href="https://github.com/admahood/drake-crp">https://github.com/admahood/drake-crp</a>. 447 448

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## **Authors' contributions**

- 637 Conceptualization: ALM, DB, TG
- 638 Data curation: ALM

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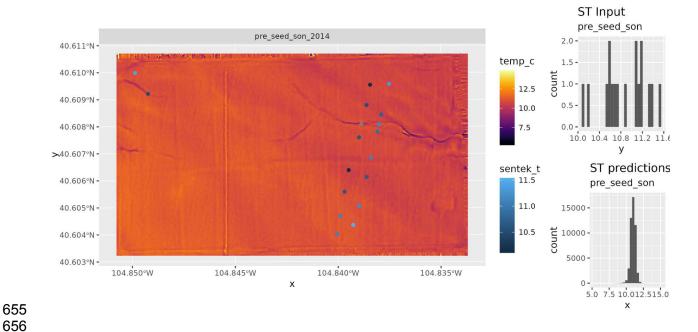
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- 639 Formal Analysis: ALM
- 640 Funding acquisition: DB
- 641 Investigation: ALM, JM, RE, TG, DB
- 642 Methodology: ALM, JM
- 643 Project administration: ALM
- 644 Resources: ALM
- 645 Software: ALM
- 646 Supervision: DB
- 647 Validation: ALM
- 648 Visualization: ALM
- 649 Writing original draft: ALM, TG, DB
- 650 Writing review & editing: ALM, TG, DB, JM

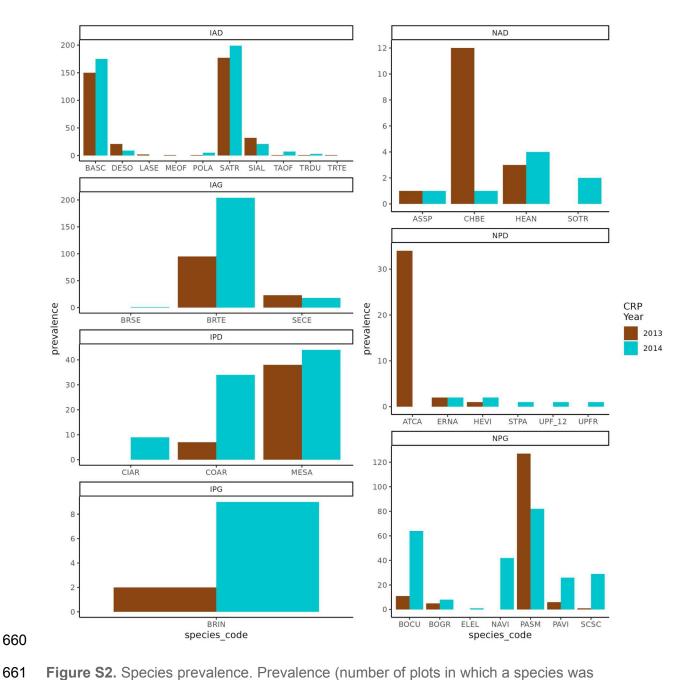
# Acknowledgements

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# 654 Extended Data

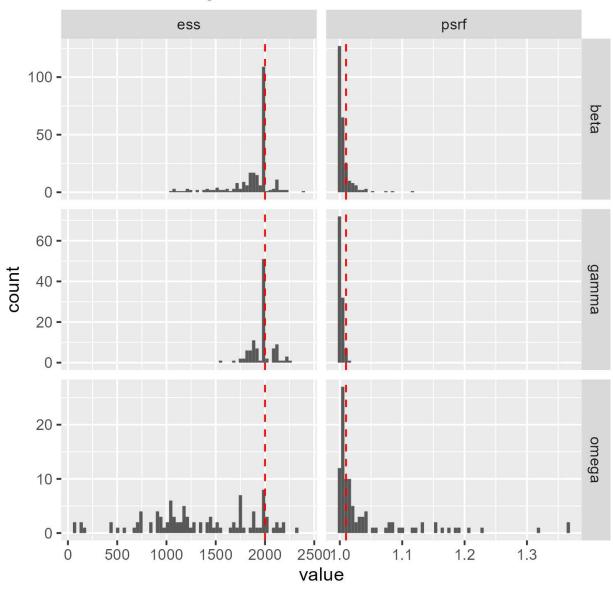


**Figure S1**. One of the surfaces created by spatial process modelling. Blue dots indicate the Sentek sensor locations.

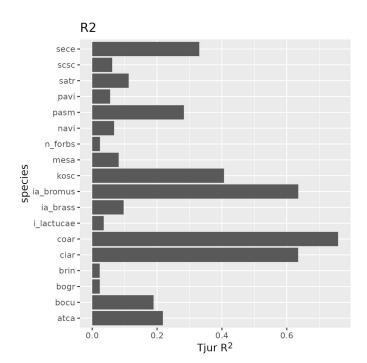


**Figure S2.** Species prevalence. Prevalence (number of plots in which a species was encountered) for each plant species encountered across the study site. Abbreviations: N = native, A = annual, P = perennial, D = dicot, G = graminoid, I = introduced.

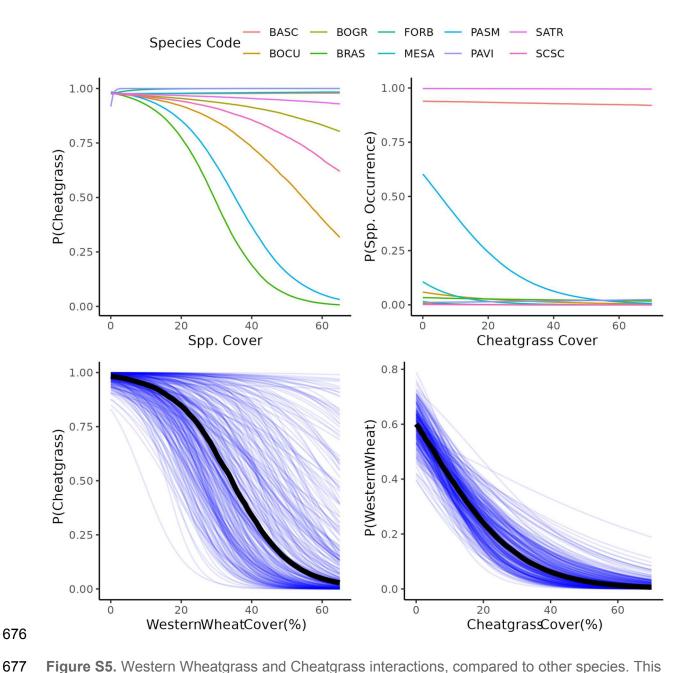
# Model Convergence



**Figure S3:** Model convergence diagnostics. The potential scale reduction factor (PSRF) measures the convergence among chains, and being closer to 1.0 is ideal. Effective sample size (ESS) measures autocorrelation 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 m2 quadrats used for the JSDM, and so were not assigned to groups. Those species were still used in the diversity calculations.

Family	Conun	Specific enithet	Group	Croup Nama	CRP Mix	origin	Seed Applied
Family	Genus	Specific epithet	Code	Group Name		_	(kg/ha)
Asteraceae	Gutierrezia	sarothrae	GUSA	Gutierrezia sarothrae	no	n	
Asteraceae	Ericameria	nauseosa 	ERNA	Ericameria nauseosa	no	n	
Asteraceae	Heterotheca	villosa	HEVI	Heterotheca villosa	no	n	
Asteraceae	Helianthus	annuus	HEAN	Helianthus annuus	no	n	
Asteraceae	Stephanomeria	pauciflora	FORB	Native Forbs	no	n	
Asteraceae	cf Aster	d_081_herb_05	FORB	Native Forbs	no	n	
Asteraceae	Antennaria	sp.	ANSP	Antennaria sp	no	n	
Asteraceae	Artemisia	arbuscula	ARAR	Artemisia arbuscula	no	n	
Chenopodiaceae	Atriplex	canescens	ATCA	Atriplex canescens	yes	n	0.2676
Chenopodiaceae	Chenopodium	berlandieri	FORB	Native Forbs	no	n	
Malvaceae	Sphaerelcea	coccinea	SPCO	Sphaerelcea coccinea	no	n	
Papaveraceae	Argemone	cf hispida	ARHI	Argemone cf hispida	no	n	
Poaceae	Bouteloua	curtipendula	воси	Bouteloua curtipendula	yes	n	0.6244
Poaceae	Panicum	virgatum	PAVI	Panicum virgatum	yes	n	0.1784
Poaceae	Schizachyrium	scoparium	scsc	Schizachyrium scoparium	yes	n	0.3568
Poaceae	Nassella	viridula	NAVI	Nassella viridula	yes	n	0.7136
Poaceae	Pascopyrum	smithii	PASM	Pascopyrum smithii	yes	n	1.784
Poaceae	Bouteloua	gracilis	BOGR	Bouteloua gracilis	yes	n	0.1784
Poaceae	Elymus	elymoides	ELEL	Elymus elymoides	no	n	
Solanaceae	Solanum	triflorum	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	Podospermum	laciniatum	LACT	Introduced Cichorioideae	no	i	
Asteraceae	Taraxacum	officinale	LACT	Introduced Cichorioideae	no	i	
Asteraceae	Tragopogon	dubious	LACT	Introduced Cichorioideae	no	i	
Asteraceae	Cirsium	arvense	CIAR	Cirsium arvense	no	i	
Asteraceae	Onopordium	acanthium	ONAC	Onopordium acanthium	no	i	
Asteraceae	Lactuca	serriola	LASE	Lactuca serriola	no	i	
				Introduced			
Brassicaceae	Sisymbrium	altissimum	BRAS	Brassicaceae	no	i	
Brassicaceae	Descurainia	sophia	BRAS	Introduced Brassicaceae	no	i	
Chenopodiaceae	Salsola	tragus	SATR	Salsola tragus	no	i	
Chenopodiaceae	Bassia	scoparia	BASC	Bassia scoparia	no	i	
Convolvulaceae	Convolvulus	arvensis	COAR	Convolvulus arvensis	no	i	
Fabaceae	Medicago	sativa	MESA	Medicago sativa	yes	i	0.3568

Fabaceae	Melilotus	officinale	MEOF	Melilotus officinale	no	i	
Poaceae	Bromus	tectorum	BROM	Introduced Annual Bromus	no	i	
Poaceae	Secale	cereale	SECE	Secale cereale	no	i	
Poaceae	Bromus	inermis	BRIN	Bromus inermis	no	i	
Poaceae	Bromus	secalinus	BROM	Introduced Annual Bromus	no	i	
Poaceae	Agropyron	cristatum	AGCR	Agropyron cristatum	no	i	
Zygophyllaceae	Tribulus	terrestris	TRTE	Tribulus terrestris	no	i	

Table S2: R packages used in the analysis.

	Г	
Package	purpose	Citation
tidyverse	Data wrangling	
Hmsc	Joint species distribution modeling	In methods
snow	parallelization	
ggpubr	visualization	
ggcorrplot	visualization	
ggthemes	visualization	
ggtext	visualization	
ggrepel	visualization	
sf	Analysis	
fields	Spatial process models	In methods
terra	Analysis	In methods
raster	Analysis	In methods
topmodel	Calculating TWI	
lubridate	Data wrangling	
ggmcmc	visualization	
geomtextpath	visualization	
vroom	Data wrangling	
vegan	Analysis	
SPEI	Analysis	
microclima	Analysis	
NicheMapR	Analysis	

Table S3. Species included in the CRP mix.

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