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RESEARCH ARTICLE

Repeated annual seeding and higher seeding rates show potential to improve recruitment outcomes in a post-fire dryland ecosystem

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Abstract

Introduction: Seeding is a widely used tool to restore drylands after wildfire, yet success is often limited by interannual climate variability. Combining repeated seeding over multiple years with higher seeding rates may increase the likelihood of successful establishment in the face of interannual climate variability while also addressing competitive dominance of invasive, non-native species.

Objective: This study investigates how repeated seeding over multiple years and higher seeding rates interact to influence post-fire restoration outcomes, focusing on sagebrush steppe in the Great Basin (U.S.A).

Methods: Using a fully factorial experimental design, we broadcast seeded a native seed mix (perennial forbs, grasses, and shrubs) at a low or high seeding rate. Seeding occurred either 1 year after a fire, 2 years after, or in both years. Treatments were applied across an elevational gradient to account for local-scale environmental variability.

Results: In the first year, precipitation was below the long-term median and temperatures were above the long-term median. The second year experienced above-median precipitation and below-median temperatures. Perennial forb recruitment was highest in plots seeded during the second year with the high seeding rate. No recruitment was observed for the perennial grasses and shrubs.

Conclusions: Our results show potential for the combined use of repeated annual seeding and higher seeding rates to increase the establishment of perennial forbs by simultaneously increasing the likelihood that seeding occurs during a favorable year and overcoming potential establishment barriers from lower seeding rates when climate conditions are favorable.

Implications for Practice: Drylands experience highly variable and potentially unpredictable interannual climate patterns which can cause post-fire seedings to occur during years with unfavorable climatic conditions. Repeated annual seeding combined with higher seeding rates show promise to improve post-wildfire restoration outcomes in drylands by increasing the likelihood that seeding occurs during a year with favorable weather conditions and overcoming potential establishment barriers from lower seeding rates when weather conditions are favorable. While combining these two techniques is an expensive proposition at large scales, they can be used with other restoration techniques to increase the likelihood of favorable restoration outcomes in targeted restoration projects.

Key words: functional groups, Great Basin, interannual weather, post-fire seeding, sagebrush steppe

Introduction

A significant percentage of the world's drylands are degraded due to a variety of drivers that include climate change, land conversion, invasive species introductions, and altered wildfire regimes (Hoover et al. 2020). The consequences of dryland degradation include the erosion of ecosystem services and biodiversity, which have subsequently prompted an increase in restoration efforts (Davies et al. 2012). Restoration is particularly important following disturbances because disturbance often facilitates ecosystem state changes (D'Antonio & Vitousek 1992), such as the conversion of native-dominated shrublands to non-native dominated grasslands following overgrazing or wildfire (Mahood & Balch 2019). However, a significant proportion of global dryland restoration efforts have been unsuccessful in reversing degradation following disturbance. For example, in an analysis of 174 post-disturbance dryland restoration seeding projects across the world, 17% failed to observe establishment of seeded species (Shackelford et al. 2021). In response to these challenges, new methods are constantly developing to increase the success of post-disturbance dryland restoration outcomes (e.g., Madsen et al. 2012; Davies et al. 2018).

The Great Basin region of the western United States is a semi-arid cold desert that has experienced a significant amount of degradation (Morris & Rowe 2014). Over the last 75 years, millions of hectares have been seeded for wildfire rehabilitation, yet

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successful restoration outcomes have not been widespread (Pilliod et al. 2017). In this region, the invasion of non-native annual grass species has led to drastic changes in wildfire regimes (Bradley et al. 2018) which have contributed to the conversion of significant portions of the Great Basin from sagebrush (*Artemisia* sp.) steppe to annual non-native dominated grasslands (Smith et al. 2022). Success in altering post-wildfire community trajectories away from annual grasslands have been attributed to the establishment of perennial grasses from seeding efforts, which can compete against non-native annual grasses (Schantz et al. 2019). Improving seed-based restoration techniques have the potential to boost establishment outcomes and reduce ecological transitions away from non-native grass dominance in the Great Basin.

Dryland seed-based restoration projects can fail for many reasons, but one widespread driver is low seeding rates. Indeed, the outcomes of many post-disturbance seeding treatments across drylands have been shown to be highly dependent on seeding rates (Shackelford et al. 2021). Higher seeding rates can lead to improved recruitment outcomes by increasing the overall number of germination events that can occur to overcome abiotic germination barriers (Commander et al. 2020) or by overcoming competitive interactions with non-native annual grasses (Schantz et al. 2018). Drawbacks to higher seeding rates include financial and logistical barriers. Seeds are an expensive component of restoration projects and the necessary number of seeds for a high seeding rate may not be available from seed banks or seed producers (Godefroid et al. 2011).

Another driver of successful dryland seed-based restoration projects is interannual variation in precipitation and temperature. Drylands have relatively high interannual climatic variability while also having low overall amounts of precipitation which often leads to few years where weather conditions are favorable for recruitment (Wang et al. 2022). Indeed, varied precipitation amounts and soil temperatures across years can produce vastly different germination and recruitment outcomes from seeding efforts (James et al. 2019; Kövendi-Jakó et al. 2021). Additionally, annual dryland weather conditions are often unpredictable, which can lead to seeding that coincides with unfavorable weather conditions (Hardegree et al. 2018). In response to these variable and unpredictable recruitment constraints, one suggestion to improve seeding success is repeated seeding over multiple years (Shriver et al. 2018; Urza et al. 2021). Because when good years will occur are rarely known in advance, this technique can be thought of as a form of bet hedging in a restoration planning framework that spreads out risk over multiple years and increases the likelihood that seeding occurs during a year with favorable weather conditions. Seeding in multiple years may also leverage life-history strategies, particularly delayed germination, to build up soil seed banks during years with unfavorable conditions, potentially leading to elevated rates of recruitment in subsequent years with more favorable conditions (Larson et al. 2023). However, this strategy is likely only to occur with species that have elevated levels of seed dormancy and/or persistence in the soil.

Environmental gradients are known to mediate the outcomes of seed-based restoration projects by strongly influencing recruitment dynamics. For example, variation in soil texture can affect restoration outcomes by altering how long soils retain moisture and how water moves through soil (Boyd & Davies 2012). The grain size of particles at the soil can affect seed capture and moisture dynamics that can alter seeding outcomes (Chambers et al. 1991). Elevation and aspect are topographic variables with significant effects on recruitment (Parker et al. 2024). Therefore, disentangling the effects of environmental gradients from seeding is necessary to more accurately understand the effects of novel seeding techniques on recruitment outcomes.

While repeated annual seeding and higher seeding rates have each shown promise to increase the likelihood of favorable restoration outcomes (Wilson 2015), there have been few experimental studies looking at how the interaction of these treatments influences post-disturbance recruitment dynamics. It is possible that a strategy of combining repeated annual seeding and higher seeding rates can overcome the challenges each strategy faces. To address the lack of empirical studies on the interaction between these strategies, we established a field experiment across an elevation gradient and measured recruitment outcomes following two seeding rates and repeated annual seeding after a wildfire in a semiarid dryland system (Great Basin, U.S.A.). We addressed four research questions. (1) Does repeated annual seeding improve recruitment compared to seeding in only one year? (2) Do seeding rates interact with repeated annual seeding to influence recruitment outcomes? (3) How do environmental gradients influence recruitment outcomes within the context of these treatments? (4) How do these seeding treatments influence non-native annual grass cover?

Methods

Study Area

Experimental seeding treatments took place within the 12 km^2 footprint of the 2020 Poeville Fire (late June–early July). The fire occurred on the northeast slopes of Peavine Mountain, located on the Humboldt-Toiyabe National Forest about 6 km northwest of Reno, NV, U.S.A. (Fig. 1).

The climate in the area is described as a cold desert, characterized by most of the precipitation falling as snow during the winter months, and seasons that include cold winters and hot summers (Fig. 2). Unburned vegetation communities in the area consist of sagebrush steppe dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*).

Experimental Design

We used a fully crossed randomized block design, replicating seeding rate and repeated annual seeding treatments across six sites that were established across an elevation gradient (1,673 m to 2,005 m in elevation; site 1: lowest elevation, site 6: highest elevation). Sites were selected based on these criteria: within the Poeville fire perimeter, no known history of seeding, aspects ranged from south to east, Burned Area Reflectance Classification (BARC) soil burn severity moderate to high (Hudak et al. 2004), located on USDA Forest Service land, not directly adjacent to human infrastructure (e.g., railroad, recreation/camping area, etc.), were not tree dominated before the fire, and were between 20 m and 300 m of a motorized road or trail. In

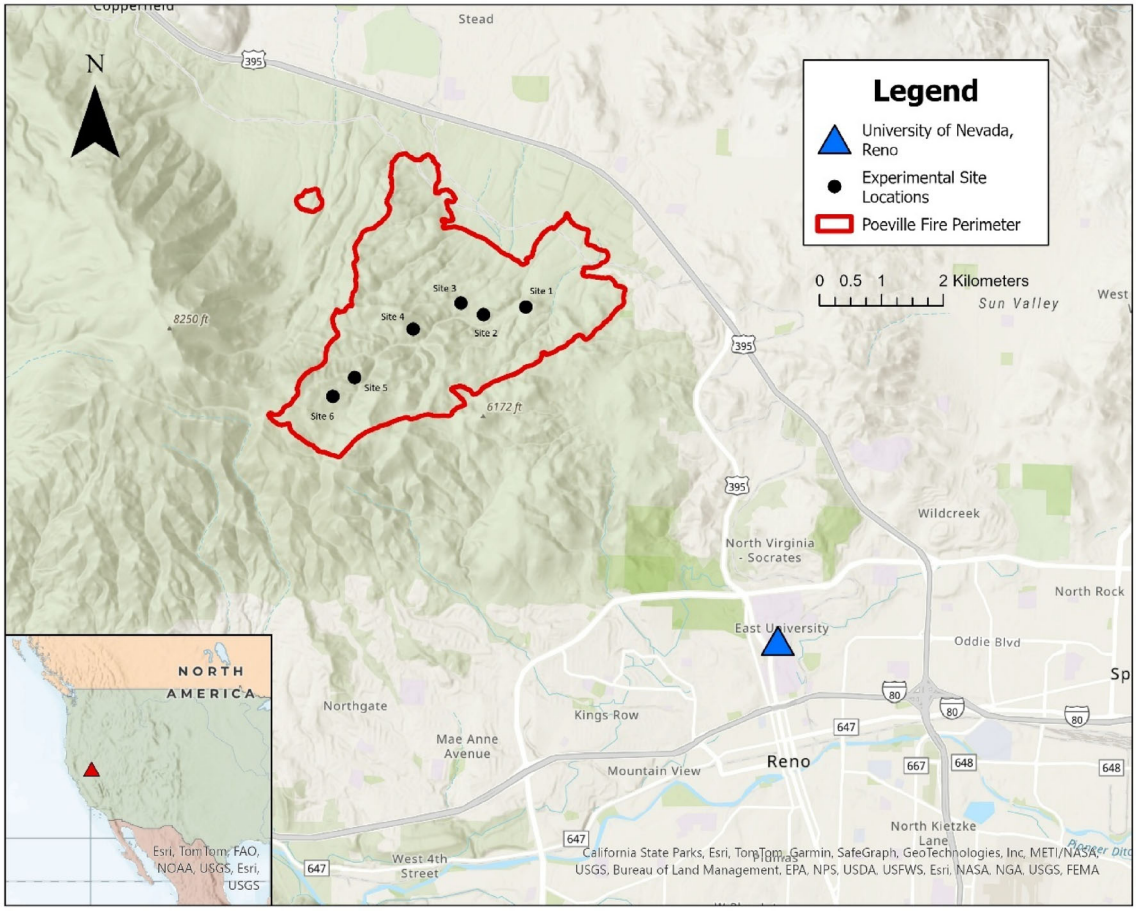

Figure 1. Map of 2020 Poeville Fire perimeter (center of fire perimeter: 39.5859, −119.8842) and the locations of the six experimental sites. Inset map shows the location of the experiment in the western United States.

2021, we established 28 permanently marked experimental seeding plots within each site. Each plot measured four 4-m (16 m^2) and separated from each other by a 2-m buffer. Experimental seeding plots were randomly assigned two seeding rate treatments ("low" or "high" seeding rate) and repeated annual seeding treatments: year 1 only (2021), year 2 only (2022), both years (2021 and 2022), producing six seeding treatment combinations (Fig. S1). Four experimental seeding plots were also assigned as controls (no seeding). Therefore, each seeding treatment combination had four replicates within each site, yielding 24 total experimental plots for each seeding rate and seeding time treatment combination as well as four control plots within each of the six sites ($n = 168$ plots). In the center of each experimental seeding plot, a one 1-m (1-m^2) permanently marked sampling subplot was established to assess recruitment outcomes and vegetation responses to seeding treatments.

Seeding Treatments

The seeds used in this experiment were sourced from seed zones that were matched to the climate of the study area. The seed mix consisted of a mixture of native perennials including grasses, forbs, a nitrogen-fixing forb, and shrubs. Native perennial grass species included Bottlebrush squirreltail (*Elymus elymoides*), Sandberg bluegrass (*Poa secunda*), Great basin wildrye (*Leymus cinereus*), and Western wheatgrass (*Pascopyrum smithii*). Native perennial forbs included Sulfur flower buckwheat (*Eriogonum umbellatum*) and Western yarrow (*Achillea millefolium*), and the nitrogen fixing perennial forb Silvery lupine (*Lupinus argenteus*). Native shrub species included Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) and Antelope bitterbrush (*Purshia tridentata*). To test the effect of varying seeding rates, a "low" and a "high" seeding rate were used for each species (Table 1). The low seeding rates were like those used in Great Basin sagebrush steppe post-fire restoration projects by the Nevada Department of Wildlife (NDOW; M. Freese 2021, NDOW, personal communication). The high seeding rates were 10 times the low seeding rate by pure live seed pounds per acre (PLS). Seeding occurred in late November of 2021 and 2022 and seeds were broadcast seeded and surface tamped (control plots were not surface tamped).

Vegetation Data Collection

We assessed the outcomes of experimental seeding in June of 2022, 2023, and 2024. Within each 1-m^2 permanent sampling

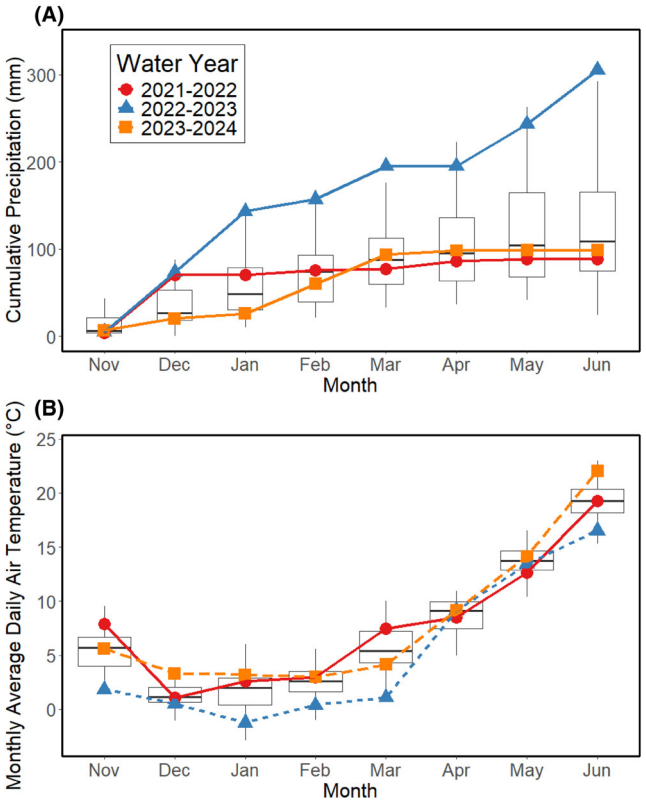

Figure 2. Annual climate data between November–June for the water years during the study from the Cold Springs RAWS Weather station (39.6764, −119.9778; 5,042 ft. elevation; Western Regional Climate Center 2024), around 13 km NW of the study area. Colored symbols and lines represent each distinct water year. (A) Monthly cumulative precipitation. Long-term monthly cumulative precipitation data between 1992 and 2024 are also shown as boxplots. For each boxplot, the black line is the median, box margins show the interquartile range, and whiskers define the 1.5 interquartile range. Outliers are omitted. (B) Monthly average daily air temperatures. Long-term monthly average daily air temperature data between 1992 and 2024 are also shown as boxplots. For each boxplot, the black line is the median, box margins show the interquartile range, and whiskers define the 1.5 interquartile range. Outliers are omitted. Data used in this figure were not used in the environmental data analyses of recruit counts.

subplot, we collected basal area drawings of all perennial plant species in June of each sampling year to measure number of seedlings and number of established plants (Lauenroth & Adler 2008). We also measured visual percent cover of all non-native annual grass species in June of 2024, which included Cheatgrass (*Bromus tectorum*) and Medusahead (*Taeniatherum caput-medusae*) (Supplement S1).

Environmental Data Collection

To investigate how recruitment outcomes are influenced by environmental gradients within our study area, we collected data on several environmental variables that have been shown to influence recruitment outcomes in Great Basin sagebrush steppe: soil texture (percent sand, percent silt, and percent clay), soil surface grain size percentage (bare soil, small gravel, and gravel), solar radiation during summer equinox and during spring/fall equinox, 30-year normal maximum temperature, minimum temperature, and precipitation, and elevation. To measure soil texture, we took a sample of the top 10 cm of soil in each plot, using a 7 cm diameter hand auger. Soil texture for each plot was measured using the rapid soil texturing method developed by Kettler et al. (2001). We measured soil surface grain size percentages by using grid-point intercept of a 16-point 1-m^2 PVC quadrat. Soil surface grain size categories were defined as: bare soil (<0.5 mm), small gravel (0.5–2 mm) and gravel (2–76 mm).

We derived a 1-m^2 resolution raster of solar radiation (watt hours per square meter; WH/m^2) during summer and spring/fall equinox using the Area Solar Radiation tool (ArcGIS Pro, Version 3.3), based on a 1-m^2 resolution digital elevation model (DEM) obtained from the U.S. Geological Society. We then created a 1-m^2 resolution raster for 30-year precipitation and temperature normals by downscaling PRISM 30-year normals (PRISM Climate Group, Oregon State University 2022) using Empirical Bayesian Kriging (ArcGIS Pro, Version 3.3) and the same 1-m^2 resolution DEM. We then located the center of each experimental seeding plot within an error of 0.29 m (Arrow 100 EOS Positioning Systems) and extracted the values of each derived variable to each plot.

Statistical Analysis

To identify how environmental gradients were driving recruitment outcomes with our experimental design, we conducted a principal component analysis (PCA) of our environmental variables using the princomp function in R (R Core Team 2021). Conducting a PCA allowed us to identify environmental gradients while accounting for multicollinearity by collapsing multiple environmental variables into a reduced number of ecologically relevant latent variables that can then be used in a regression with seedling counts (Perkin et al. 2015). Before conducting the PCA, all variables were standardized to a mean of zero and a standard deviation of 1 (*Z*-score standardization) to allow for an appropriate comparison of variables with different units (Gotelli & Ellison 2012). PCA axes were selected for regression with recruitment outcomes by identifying axes that represented logical environmental gradients.

To answer our first three research questions, we fit Bayesian generalized multiple linear regression models in R (R Core Team 2021) using the package RStan (v2.32.5; Stan Development Team 2025) to quantify the effect of seeding rate, repeated annual seeding treatments, and PCA axes on recruitment outcomes. We first pooled the counts of seedlings in each sampling subplot (i.e., density; seedling counts/m^2) into four functional group categories: all seeded species, perennial grasses (*E. elymoides* and *P. secunda*), perennial forbs (*A. millefolium* and *E. umbellatum*), and perennial nitrogen-fixing forbs (*L. argenteus*). Seedling counts of perennial grasses only included seedlings from *E. elymoides* and *P. secunda* because there were no observed seedlings from *L. cinereus* and *P. smithii*. Analysis of shrub seedling counts (*A. tridentata* ssp. *wyomingensis* and *P. tridentata*) was not conducted because

Table 1. Seeding rate for each species. PLS, pure live seed pounds per acre.

Species	*Functional Group*	*Low Seed Rate (PLS)*	*High Seed Rate (PLS)*
Elymus elymoides	Perennial Grass	1.20	12.0
Poa secunda	Perennial Grass	1.00	10.0
Leymus cinereus	Perennial Grass	1.00	10.0
Pascopyrum smithii	Perennial Grass	1.81	18.1
Eriogonum umbellatum	Perennial Forb	0.267	2.67
Achillea millefolium	Perennial Forb	0.317	3.17
Lupinus argenteus	Perennial Nitrogen-Fixing Forb	1.94	19.4
Artemisia tridentata ssp. *wyomingensis*	Shrub	0.20	2.00
Purshia tridentata	Shrub	2.07	20.7

shrubs had very low recruitment across all plots (<6 seedlings; Fig. S2). We modeled the effect of predictor variables on seedling counts using the negative binomial distribution (Eq. 1) with a log link (Eq. 2), while allowing overdispersion to vary based on seeding treatment/year observed and/or site identity (Mutiso et al. 2022).

The full model was:

$$\mathbf{y}_i \sim \text{NegativeBinomial}\left(\mu_i, \phi_{k[i]}\right) \quad (1)$$

$$\log(\mu_i) = \boldsymbol{X}_i\beta \quad (2)$$

where $\boldsymbol{y}$ is the observed counts of seedlings in each sampling subplot (i) in the year directly following seeding, μ is the expected number of seedlings in each plot, and ϕ is an overdispersion parameter that allows the variance to exceed the mean and varies by treatment/year observed and/or site identity (k). $\mathbf{X}$ is a design matrix of each treatment or predictor variable, β is a vector of regression coefficients. Candidate predictor variables included seeding treatment/year observed, principal component axes 1 (PC1) and 2 (PC2) derived from the PCA, an interaction between the top two PCA axes, site identity, and number of established plants observed in the plot during each observation year. Seeding treatment/year observed is the predictor variable used to answer our first two research questions and only included combinations of seeding treatment and year observed as factors in which seeding had occurred in the year prior (e.g., in the first observation year [2022], seeded in first year [2021] and seeded in both years [2021 and 2022] plots were included, but not seeded in second year [2022] plots). PC1, PC2, and an interaction between the two PCA axes are used to answer our third research question. Models were first fit with seeding treatment/year observed, principal component axes 1 and 2, and the interaction between the two PCA axes. Models were then fit by replacing the PCA axes with site identity to test whether there were environmental variables not captured in the PCA that were driving recruitment dynamics. In those cases, overdispersion also varied by site identity. The reference factor for seeding treatment/year observed was control plots observed in 2022 and for site identify it was the lowest elevation site (site 1). The number of established plants observed in the plot during each observation year was included as a predictor variable to capture variation in recruitment due to seed production and recruitment from plants that may have resprouted or recruited after the fire but before seeding occurred. To see if the seeding treatments were an important variable for recruitment, we also fit models with candidate predictor variables individually and with combinations of the various predictor variables, all excluding seeding treatment/year observed.

For the Bayesian generalized multiple linear regression models, coefficients on predictor variables were given normal priors with a mean of 0 and standard deviation of 10. Overdispersion parameters were given a gamma prior with shape of 1 and a rate of 1. Models were fit with three chains, each with a warm-up of 2,000 posterior draws, while 2,000 posterior draws from each chain were kept for inference. Chains were assessed for convergence using the Gelman Rubin statistic ($\hat{R}$) and all $\hat{R}$ values were less than 1.1 (Gelman et al. 2013). We assessed model fit using posterior predictive checks of the deviance, mean, standard deviation, and number of zeros. We assumed models could undergo model comparison and produce reliable inferences when posterior predictive checks produced Bayesian posterior p-values greater than 0.1 or less than 0.9 (Conn et al. 2018). Of the models that passed posterior predictive checks, the most parsimonious models to make inferences of the effect of our predictor variables on seedling counts of each plant functional group were identified using deviance information criteria (DIC; Hooten & Hobbs 2015). To quantify the significance of the difference between factors within our categorical variables, we calculated values analogous to traditional p-values (Bayesian traditional p-value) by quantifying the posterior probability that any one factor coefficient was higher than another. Values above 0.975 (i.e., a 0.975 probability that the treatment is higher) and below 0.025 (i.e., a 0.025 probability that the treatment is lower) indicate a significant difference.

We also tested to see if there was an effect of soil seed banking on recruitment dynamics beyond years when seeding occurred only the year before (2024), by fitting Bayesian multiple linear regression models on the total number of recruits in 2024 ($\mathbf{y}$ is the observed number recruits in 2024), 1.5 years after the final seeding treatment. We used the same Bayesian model fitting and checking process used to model recruitment as in our previous analysis except we only fit models using seeding treatment identity and site identity as predictor variables.

To answer our fourth research question, we fit a Bayesian generalized multiple linear regression model with non-native annual grass percent cover as the response variable and seeding

treatment and site identity as predictor variables. The model fitting process for this analysis can be found in Supplement S1.

Results

Environmental Variation Across Time and Space

Both precipitation and temperature varied across the 3 years of the study (Fig. 2). Between the first seeding and the first vegetation sampling (2021–2022), precipitation amounts were below the long-term median while temperatures were generally at or above the long-term median (dry-warm year). Between seeding in the second year and the second vegetation sampling (2022–2023), precipitation amounts were well above the long-term median while temperatures were consistently below the long-term median (wet-cold year). Before the final vegetation sampling, precipitation amounts were below the long-term median while temperatures were generally above the long-term median (dry-warm year).

The principal component analysis (PCA) captured 64.5% of total variation of environmental variables among plots in the first two principal component axes (45.4% and 19.1%, respectively; Fig. 3). We retained the first two axes as latent variables for subsequent regression with seedling counts as they represent two distinct and ecologically relevant environmental gradients. Principal component axis 1 (PC1) represented a climatic and topographic gradient. Higher PC1 values were associated with higher elevations (correlation coefficient, $r = 0.416$), lower 30-year normal maximum ($r = -0.414$) and minimum ($r = -0.405$) temperature, higher 30-year normal precipitation ($r = 0.405$), and higher summer equinox solar radiation ($r = 0.318$). Principal component axis 2 (PC2) represented a soil texture and soil surface grain size gradient. Higher PC2 values were associated with higher sand ($r = 0.469$), lower silt ($r = -0.445$), and lower clay ($r = -0.338$) soil texture percentages, and lower gravel ($r = -0.466$), higher small gravel ($r = 0.364$), and higher bare soil ($r = 0.257$) surface grain size percentages.

Seeded Species Recruitment

We found that among the 48 models that we fit (12 models for each functional group) to model recruit counts in 2022 and 2023, 32 passed posterior predictive checks and could be used for model comparison. In general, we found that models that included site identity rather than PCA axes explained variability better by having lower deviance information criteria (DIC) scores. The most parsimonious models for all seeded species, seeded perennial forbs (*Achillea millefolium* and *Eriogonum umbellatum*), and the seeded perennial nitrogen-fixing forb (*Lupinus argenteus*) included seeding treatment/year observed and site identity (Table 2). For seeded perennial grasses (*Elymus elymoides* and *Poa secunda*), the most parsimonious model included site identity and number of previously established *E. elymoides* and *P. secunda* plants within the plot (Fig. S3).

For the best model that combined all seeded species, results indicate that the use of a high seeding rate in 2022–2023 (cold-wet year) led to significantly higher numbers of seedlings compared to the control (Fig. 4A). However, the effect of seeding in both years matched the effect of single year seeding treatments in both seeding rates in 2022–2023; in other words, there was no significant difference in the number of seedlings when seeding occurred both years and when seeding only occurred prior to the wet and cool year. Additionally, the number of seedlings when using a low seeding rate was not significantly different compared to the control in both years.

For seeded perennial forbs, the best supported model showed that the use of a low and high seeding rate in 2022–2023 (cold-wet year) led to significantly higher numbers of seedlings compared to the control (Fig. 4B). Additionally, both the low and high seeding rate treatments applied in 2021–2022 (dry-warm year) did not have any significant difference in seedling counts compared to the control.

For *L. argenteus*, the best supported model revealed using both a low and high seeding rate in 2021–2022 (dry-warm year) did not significantly increase the number of seedlings compared to the control (Fig. 4C). In 2022–2023 (cool-wet year), using a high seeding rate significantly increased the number of seedlings compared to the control, while the low seeding rate did not produce significantly more seedlings compared to the control.

For perennial grass seedling counts, the model that included seeding treatment/year observed and site identity showed that after both the first and second year that seeding occurred, there was no significant difference in seedling counts between any of the seeding treatments and not seeding at all (Fig. 4D).

While models that included environmental variable PCA axes to describe plot conditions were not the best supported based on DIC scores, they provided some insight into the environmental conditions driving recruitment variation across sites. For all seeded species, seeded perennial forbs, and *L. argenteus*, the best supported models with environmental variable PCA axes included the interaction between PC1 and PC2 (Table 2), and among all models there was a significantly negative effect of the interaction and no significant effect of each individual principal component axis (Fig. 5A, 5C, & 5E). The negative effect of the interaction indicates that there were more seedlings in sites when PC1 was high and when PC2 was low; more seedlings in sites when both PC1 values were high (higher elevation, higher annual precipitation, lower annual temperatures) and when PC2 values were low (higher proportions of sand texture percentage and soil surface small gravel proportions and with lower proportions of silt and clay texture percentages and soil surface gravel proportions) or when both PC1 values were low and when PC2 values were high (Fig. 5B, 5D, & 5F). For seeded perennial grasses, the best supported model included PC1 and PC2 without the interaction between the PCA axes (Table 2) and showed a positive effect with PC1 and a negative effect with PC2 (Fig. 6).

We found there were significantly more recruits remaining in 2024 for all seeded species combined in the high seeding rate treatment applied in 2022 (Fig. S4a). This effect was primarily driven by the seeded perennial forbs, with all plots to which a high seeding rate was applied in 2022–2023 (cold-wet year) having significantly more recruits compared to not seeding (Fig. S4b). Among *L. argenteus* and the seeded perennial grasses, there was no effect of the seeding treatments on the number of recruits (Fig. S4c & S4d).

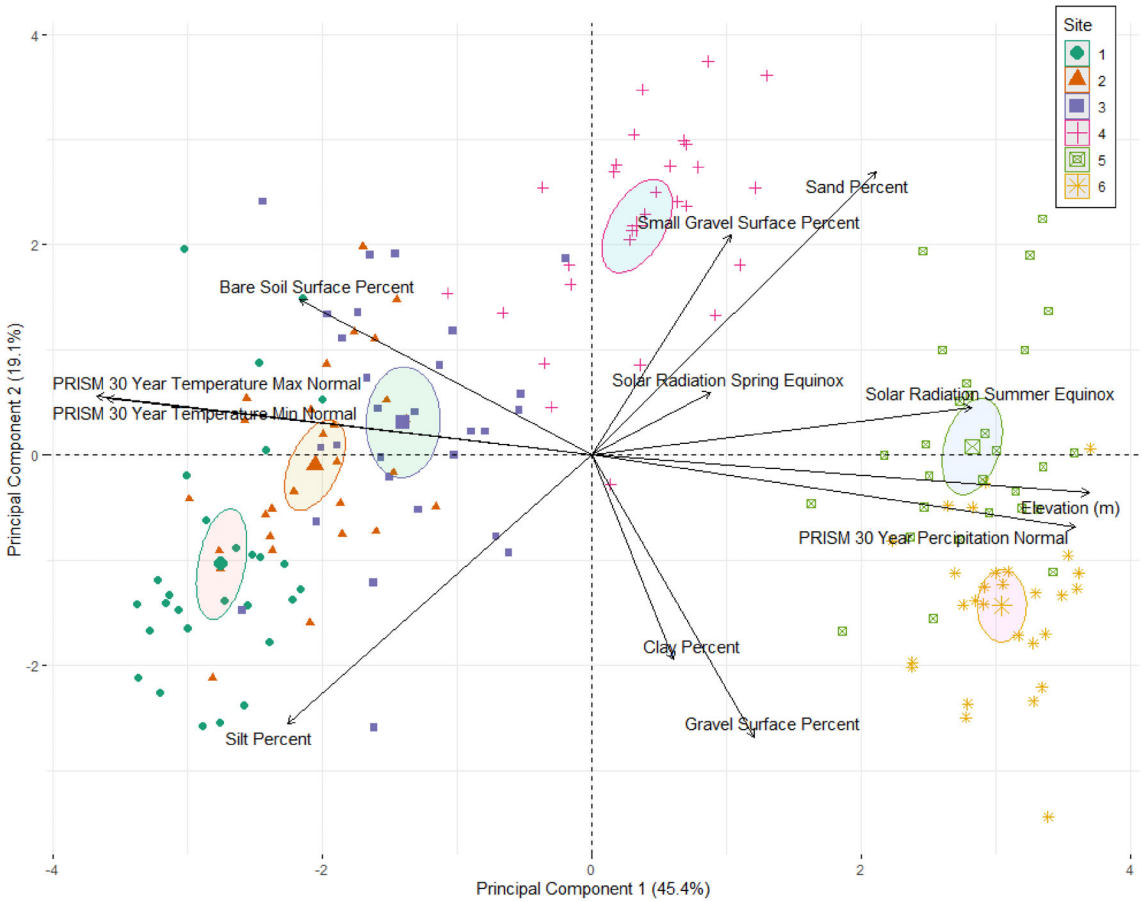

Figure 3. Biplot from environmental variable principal component analysis illustrating principal components (PC) 1 and 2 among 168 plots. Variables include soil texture (percent sand, percent silt, and percent clay), soil surface grain size percentage (bare soil, small gravel, and gravel), solar radiation (watt hours per square meter; WH/m^2) at summer and spring equinox, and PRISM 30-year normal precipitation, maximum temperature, and minimum temperature. The arrows represent each environmental variable, with direction indicating the correlative relationship between all other environmental variables and length indicating the contribution to the two principal component axes. Each point represents a plot and colors/shape represents each site. The position of each point represents the association with both principal component axes. Ellipses represent the 95% confidence area of the mean values of the two PC axes for each site.

We found there to be no difference in non-native grass cover between seeding treatments in 2024 (Supplement S1; Fig. S1).

Discussion

Repeated Annual Seeding and Higher Seeding Rates on Recruitment Outcomes (Q1, Q2)

We found that repeated annual seeding can improve recruitment outcomes compared to seeding in only one year by increasing the likelihood that seeding occurs during a year with favorable weather conditions (Q1). This outcome provides support to the idea that repeated annual seeding can be an effective bet-hedging restoration strategy in variable and unpredictable climates (Shriver et al. 2018; Urza et al. 2021). The utility of bet-hedging from repeated annual seeding stems from the lack of predictability in annual weather conditions. When the predictive accuracy of annual weather conditions is high, the efficacy of bet-hedging by spreading risk across multiple years lessens. There has been significant progress toward developing and integrating weather predictions to aid restoration efforts, but forecast accuracy often depends on a variety of factors including location and forecast lead time (Hagger et al. 2018). Therefore, bet-hedging against interannual climate variability by seeding across multiple years holds value in cases when there is low predictive accuracy of annual weather conditions. One caveat to the benefit of repeated annual seeding is that outcomes depend on the frequency and temporal pattern of years with favorable weather conditions. In areas with less frequent favorable weather conditions, repeated annual seeding can lead to failed restoration outcomes if seeding efforts occur during successive years with unfavorable weather conditions. Therefore, the utility of repeated annual seeding should be weighed against interannual climate patterns of a given restoration site.

In addition to seeding over multiple years, life history strategies such as delayed seed germination can act as a natural bet hedging strategy that lessens the risk of reproductive failure in the face of unpredictable annual climate conditions (Venable 2007). However, this mechanism was likely not a primary driver of improved recruitment outcomes during the first

Table 2. Predictor variables, deviance information criteria (DIC), difference in DIC from the most parsimonious model (ΔDIC), and effective number of parameters (pD), from negative binomial multiple linear regression models modeling seedling counts in 2022 and 2023 of all seeded species and the three seeded functional groups. For all models, $n = 240$. Models included are ones which passed posterior predictive checks (Bayesian p-values >0.1 and <0.9). Models which did not pass posterior predictive checks are listed in Table S1. PC1, principal component axis 1; PC2, principal component axis 2.

Functional Group	*Predictor Variables*	*DIC*	*ΔDIC*	*pD*
A. All seeded species	Seeding treatment/year observed + site identity	680.38	0	18.0
	Seeding treatment/year observed + site identity + number of established plants	682.51	2.13	19.4
	Seeding treatment/year observed + PC1 + PC2 + PC1 × PC2	701.95	21.57	18.8
	Seeding treatment/year observed + PC1 + PC2	723.44	43.06	17.7
	Seeding treatment/year observed	733.66	53.28	14.9
	Site identity	801.45	121.07	10.9
	Site identity + number of established plants	803.84	123.46	12.1
B. Seeded perennial forbs	Seeding treatment/year observed + site identity	314.41	0	11.3
	Seeding treatment/year observed + site identity + number of established plants	315.31	0.9	12.0
	Seeding treatment/year observed + PC1 + PC2 + PC1 × PC2	331.55	17.14	11.1
	Seeding treatment/year observed + PC1 + PC2	338.33	23.92	9.9
	Seeding treatment/year observed + PC1 + PC2 + number of established plants	340.18	25.77	10.6
	Seeding treatment/year observed	343.08	28.67	7.8
	Seeding treatment/year observed + number of established plants	344.93	30.52	8.4
	Site identity	439.07	124.66	9.6
	Site identity + number of established plants	440.35	125.94	10.3
	PC1 + PC2	459.87	145.46	2.9
	Number of established plants	462.38	147.97	10.2
C. Seeded perennial grasses	Site identity + number of established plants	201.97	0	7.3
	Site identity	203.40	1.43	5.8
	Seeding treatment/year observed + site identity	207.87	5.90	12.1
	Seeding treatment/year observed + PC1 + PC2	219.27	17.30	13.4
	Seeding treatment/year observed	225.75	23.78	9.6
D. Seeded perennial nitrogen-fixing forb (*Lupinus argenteus*)	Seeding treatment/year observed + site identity	473.95	0	13.7
	Seeding treatment/year observed + PC1 + PC2 + PC1 × PC2	498.31	24.36	15.3
	Seeding treatment/year observed + PC1 + PC2	510.30	36.35	13.8
	Seeding treatment/year observed	517.95	44.00	11.9
	Site identity	575.26	101.31	11.2
	Site identity + number of established plants	575.30	101.35	11.2
	PC1 + PC2 + number of established plants	592.72	118.77	4.0
	Number of established plants	593.92	119.97	1.93
	PC1 + PC2	594.41	120.66	3.0

two observation years of our study as seeding in two sequential years with distinct weather patterns did not produce better recruitment outcomes than seeding only in the year with seemingly favorable weather conditions for the native perennial forbs. If repeated annual seeding interacted with delayed seed germination, we might have expected to see higher numbers of recruits in the second observation year (2023) in the plots seeded both years compared to plots only seeded the second year. Nonetheless, we did find partial evidence that our seeding treatments may have interacted with delayed germination to influence longer-term recruitment outcomes. We saw that, 1.5 years (dry-warm year, 2024) after the last time seed was applied, there were slightly higher numbers of native perennial forb seedlings in the high seeding rate plots compared to the control, suggesting that the high seeding rate may improve longer-term recruitment outcomes by increasing the overall number of seeds in the seed bank (Commander et al. 2020). Interestingly, the two perennial forbs in our seed mix (*Achillea millifolium* and *Eriogonum umbellatum*) exhibit alternative seed dormancy strategies (Larson et al. 2025), suggesting that other mechanisms related to seed persistence may have been stronger drivers of the results that we found in 2024 (Long et al. 2015). Further studies on seed persistence across our species may reveal whether the observed patterns among the functional groups in our study could have been driven by unique seed persistence characteristics.

We found that while repeated annual seeding can increase the likelihood of seeding during a favorable year, there was a significant interaction between seeding rate and the weather conditions in the year when seeding occurred (Q2). For all seeded species combined, the high seeding rate led to significant increases in the number of seedlings compared to the control only when seeding occurred during the year preceding favorable weather conditions (wet-cold year, 2023) and not in the year preceding unfavorable climate conditions (dry-hot year, 2022). In contrast, the low seeding rate did not produce significantly more seedlings compared to the control during either year. These results suggest a strong interactive effect between seeding rate and interannual climate conditions. This interaction may have been driven by competition for seed safe sites or preemption of soil resources by non-native annual grasses which were alleviated through the high seeding rate (Schantz et al. 2018). One implication of our findings is that seeding rates commonly used in post-fire restoration projects in the Great Basin (our low

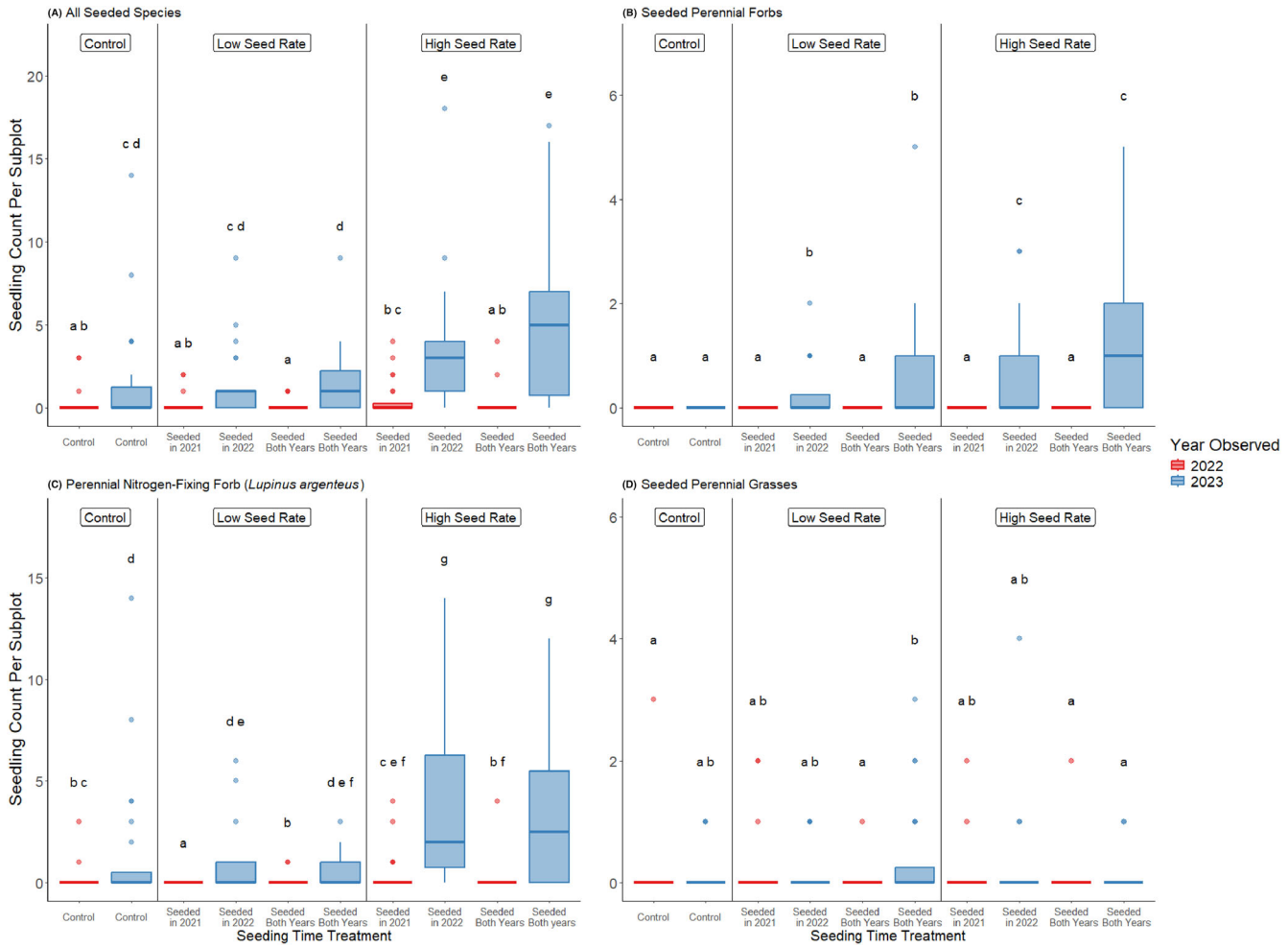

Figure 4. Seedling counts of each functional group category in each seeding rate (control, low rate, high rate) and seeding time (seeded in 2021, seeded in 2022, or seeded both years) treatment measured the year after seeding is applied. For each boxplot, the black line is the median, box margins show the interquartile range, whiskers define the 1.5 interquartile range, and outliers are omitted. Letters above boxplots indicate whether the number of seedlings between seeding treatments/year observed factors are the same (Bayesian traditional p-value >0.25 and <0.975; i.e., same letters above factors indicate statistically similar numbers of seedlings) and were produced from the negative binomial multiple linear regression models that include seeding treatment/year observed and site identity as predictor variables, with overdispersion varying by seeding treatment/year observed and site identity. For all seeded species, perennial forbs (*Achillea millefolium* and *Eriogonum umbellatum*), and the perennial nitrogen-fixing forb (*Lupinus argenteus*) plots, the y-axis has been truncated at 20, 6, and 15 respectively and outliers are not shown for clarity.

seeding rate) may not be more effective to establish native plants than not seeding at all, even in years with favorable climate conditions. However, it may not be necessary to use the high seeding rate we applied to improve restoration success, as even small increases in seeding rates have been shown to have significant benefits for restoration outcomes (Shackelford et al. 2021). Further studies can clarify how repeated annual seeding can interact with a range of seeding rates to identify at what point increases in seeding rates lead to significant improvements in plant recruitment.

In contrast to the perennial forbs and contrary to our expectations, we did not find that the seeding treatments increased perennial grass or shrub seedling counts compared to not seeding at all. We did not find any seedlings of two of the four seeded perennial grasses (*Leymus cinerus* or *Pascopyrum smithii*), and we only found five seedlings of the seeded native perennial shrubs across all plots in 2023 (*Artemisia tridentata* ssp. *wyomingensis* and *Purshia tridentata*). These results suggest that unexpected mechanisms suppressed the effect of the seeding treatments. One mechanism may be a mismatch between locally adapted seed and seedling traits and the climate of our study area. Locally adapted seed and seedling traits have been shown to strongly influence successful recruitment in restoration (Agneray et al. 2022; Larson et al. 2023), and while we attempted to match the seed transfer zone of the seeds used in our experiment to the climate of our study area, there may have been a significant mismatch that overwhelmed any positive effects of our seeding treatments, even during the seemingly favorable climate conditions of 2022–2023. Another reason may be that the high seeding rate was not enough to match seed

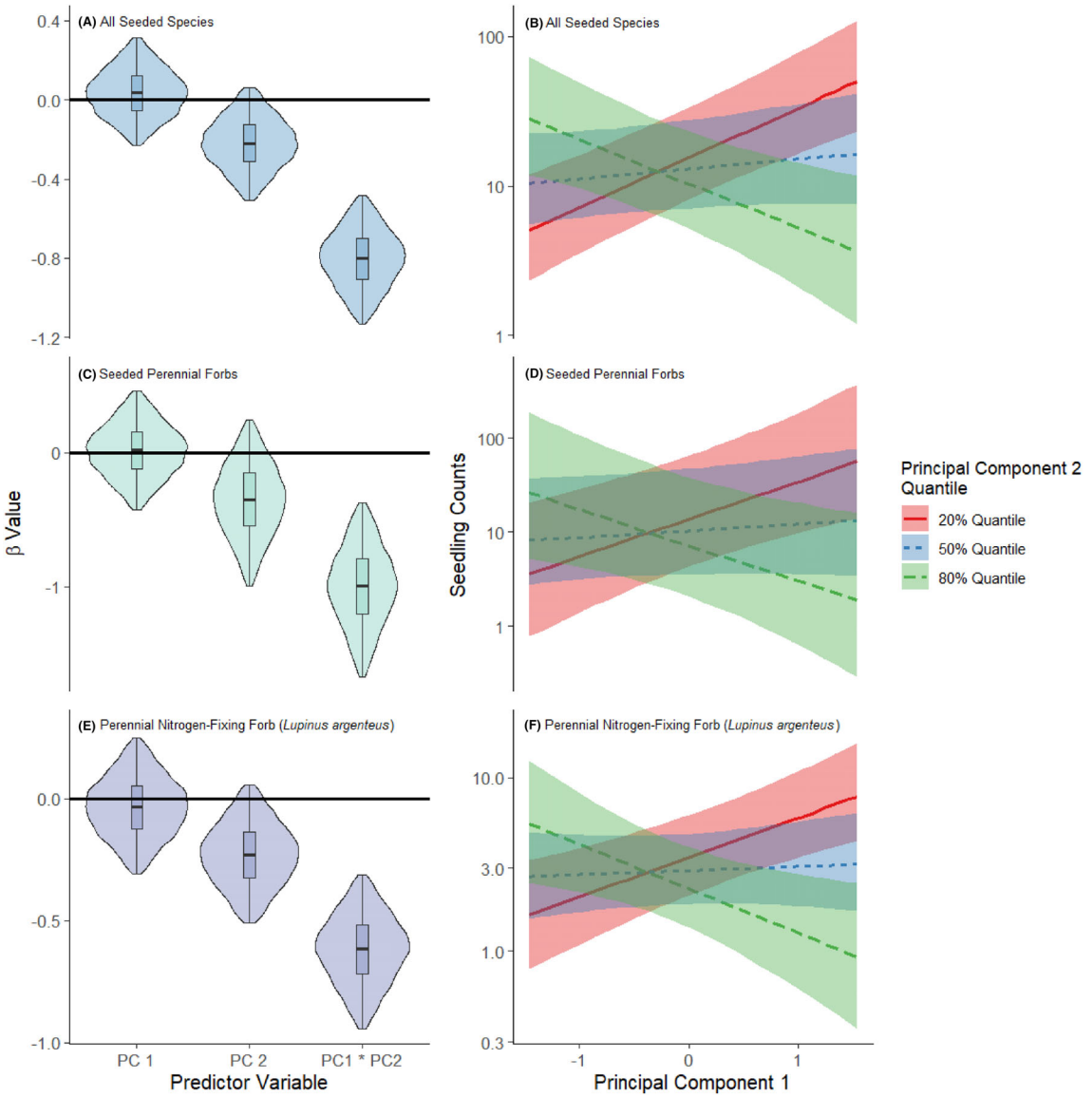

Figure 5. Violin plots of the less than 97.5% and greater than 2.5% posterior distribution effect size of the principal components and interaction between PC1 and PC2 (A, C, E) and marginal effect plots of the 20%, 50%, and 80% PC2 quantile values by PC1 and seeding only in 2022 and observed in 2023 on number of seedlings (B, D, F) from the models that include seeding treatment/year observed and principal components and their interaction as predictor variables with overdispersion varying by seeding treatment/year observed for (A and B) all seeded species, (C and D) seeded perennial forbs (*Achillea millefolium* and *Eriogonum umbellatum*), and (E and F) *Lupinus argenteus*. Marginal effect plots represent the predicted number of seedling counts across the range of PC1 values by the 20% (red-solid), 50% (blue-dashed), and 80% (green-dot dashed) PC2 values.

rain rates necessary for successful recruitment. While few studies have quantified the seed rains that initiate successful recruitment for the species of perennial grasses and shrubs in this experiment, Young et al. (1989) found that the average annual seed production for successful recruitment across several populations of two subspecies of big sagebrush (*A. tridentata* ssp. *vaseyana*, and ssp. *tridentata*) was 1.7 and 0.8 kg seed/0.1 ha, respectively, on par or much higher than the high seeding rate used for *A. tridentata* ssp. *wyomingensis* used in our study (0.897 kg seed/0.1 ha). This provides some evidence that using an even higher seeding rate may be necessary to increase the likelihood of successful recruitment, at least for *A. tridentata* ssp. *wyomingensis*. Finally, the lack of response to our seeding treatments may be limited to the species used in our study, and an alternative species composition from the perennial grasses and shrubs in our seed mix may have produced more favorable recruitment outcomes.

Environmental Gradients and Recruitment Outcomes (Q3)

We found that climatic, topographic and edaphic gradients identified from the first two axes of the principal component analysis had a significant influence on recruitment outcomes (Q3). For all

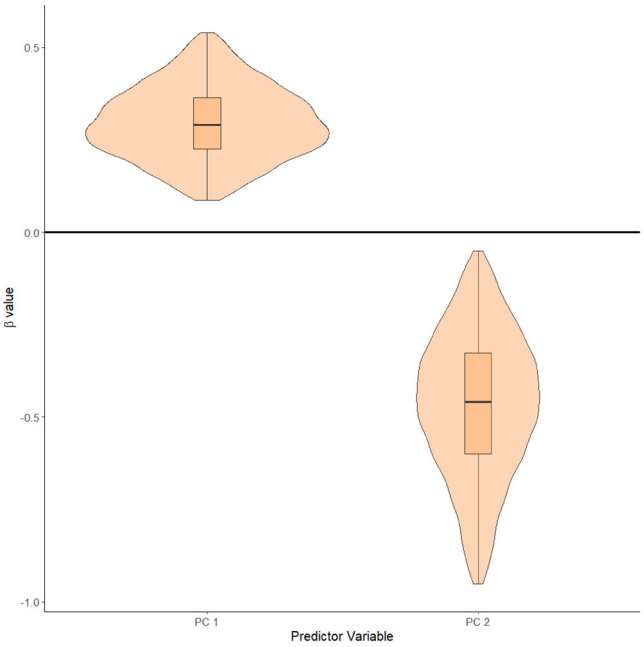

Figure 6. Effect of environmental variable principal components on seedling counts on seeded perennial grasses (*Elymus elymoides* and *Poa secunda*) from the negative binomial multiple linear regression models that include PC1, PC2 and seeding treatment/year observed as predictor variables, with overdispersion varying by seeding treatment/year observed. Violin plots represent less than 97.5% and greater than 2.5% of the posterior distribution effect of PC1 and PC2.

functional groups, we found that recruitment benefited from increasing annual precipitation and decreasing annual temperatures that are associated with higher elevations but were mediated by soil texture and soil surface characteristics for all seeded species, seeded perennial forbs and L. argenteus. The results for these two functional groups regarding the interaction between precipitation, temperature, and soil texture align with the inverse texture hypothesis which suggests that coarse textured soils benefit plant productivity when precipitation is relatively low and when evaporative soil water losses are high due to increased filtration of water to deeper soil layers (Noy-Meir 1973). Studies have tested this hypothesis using responses of plant productivity (Lane et al. 1998; Terry & Adler 2024) and other studies have looked at the singular effect of soil texture on arid plant recruitment (Lesica et al. 2007; Boyd & Davies 2012), but this study is the first to directly investigate the interactive effect of precipitation, temperature, and soil texture on plant recruitment in an arid environment. However, soil texture was strongly correlated with soil surface grain size, and there may be interactive dynamics between these two soil characteristics that may have influenced recruitment in this experiment. Soil surface grain sizes have been shown to influence seed entrapment rates and germination events (Chambers et al. 1991; Chambers 2000) and while we were not able to experimentally test the relative effects of soil texture and soil surface grain sizes, further studies may disentangle the relative importance of each variable on seed-based restoration outcomes.

Impacts on Invasive Species and Application for Management (Q4)

The use of a high seeding rate and repeated annual seeding is an expensive proposition to replace current post-fire seeding practices at scale (Shackelford et al. 2021). Both would require substantially more seed to be used, and often the availability and cost of seed, especially for native forbs, is one of the primary limitations in native plant restoration (Shaw et al. 2005). Alternatively, these methods could be used in smaller, high priority areas in conjunction with restoration techniques such as applied nucleation or connectivity modifiers to promote resilient native-dominated restoration islands (Hulvey et al. 2017; Young et al. 2025). When there are areas with high priority for restoration, such as areas that support endangered species, where fires are likely to impact human populations (i.e., Wildland Urban Interface), or areas with high cultural value, a combination of these strategies have the potential to increase the overall long-term success of restoration projects.

If management objectives are to decrease non-native annual grass cover with the longer-term goal of promoting native-dominated plant community trajectories, we found there was no effect from these seeding treatments at the relatively short timescale (3 years) of this study (Q4). The 3-year period may not be enough time for seedlings established from seeding to compete with non-native annual species. Indeed, Pyke et al. (2013) found that aerial seeding in arid and semiarid shrublands and grasslands had no effect or increased invasive plant species cover within 3 years, but found decreases in invasive plant species cover over longer time scales and with higher levels of seeded species establishment. Therefore, the effect of seeding on decreasing non-native annual grass cover in this study may manifest in subsequent years when seedlings have had enough time to grow and compete with non-native annual grasses. Alternatively, the observed results may be due to the lack of establishment of perennial grasses to compete with non-native annual grasses. Decreases in non-native annual grass cover in post-fire sagebrush steppe at similar time frames have been attributed to increases in seeded native perennial grasses establishment (Schantz et al. 2019), for which we did not find significant differences between seeding treatments. Alternative seeding methods such as drill seeding have been shown to be more successful at establishing native perennial grasses in short time scales (Kluender & Germino 2023), and this seeding technique could have led to significant decreases in non-native annual grass cover in our study.

The use of native forbs in seeding projects, particularly in the Great Basin, has seen a steady increase over the last few decades (Pilliod et al. 2017). Native forbs play an important role in habitat quality for greater sage grouse (*Centrocercus urophasianus*), an endangered bird species that has driven efforts to restore Great Basin sagebrush steppe habitat (Connelly et al. 2000). However, traditional practices of seeding native forbs has generally not been successful in increasing cover of the functional group in post-fire seeding projects (Knutson et al. 2014), but this trend may be due to a small number of studies. Increasing use of native forbs may better elucidate the success of seeding native forbs with traditional seeding practices

(Pilliod et al. 2017). Regardless, the increased recruitment of native forbs from higher seeding rates and repeated annual seeding in this study shows promise in increasing native forb cover to aid in the recovery of sagebrush steppe habitat.

Overall, we found that repeated annual seeding and higher seeding rates are promising strategies to increase the overall likelihood of successful seeding outcomes, specifically with the native perennial forbs and nitrogen-fixing perennial forbs used in this study, in response to the unpredictable climatic variability of semiarid dryland ecosystems. While potentially infeasible at broad scales, this strategy can be used in situations where seed availability is high and repeated seeding over multiple years is logistically possible. Our results also suggest that the use of a relatively low seeding rate may not be enough to distinguish seeding from not seeding at all, even during years with favorable climate conditions. Increasing seeding rates, even marginally, may ensure greater success when climate conditions are favorable. The lack of positive outcomes from commonly used seed rates alternatively points to looking at alternate strategies for restoration of degraded post-fire ecosystems, such as planting nursery grown seedlings (Pyke et al. 2020), a strategy that has not been fully explored in the Great Basin.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Posterior predictive check indexes and Bayesian *p*-values.
Table S2. Posterior predictive check indexes, Bayesian *p*-values, deviance information criteria (DIC) values, and effective number of parameters.
Table S3. Seeding rate used for each species in kg seed/0.1 ha.
Figure S1. Factorial seeding treatment combination design within each site.
Figure S2. Seedling counts of *Artemisia tridentata* ssp. *wyomingensis* and *Purshia tridentate*.
Figure S3. Violin plot of the <97.5% and >2.5% posterior distribution effect size.
Figure S4. 2024 seedling counts.
Supplement S1. Details of methods and results.

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