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Rethinking seed selection based on climate matching during restoration: Geography, soils and climate explain species-specific mortality

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Research Article

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Abstract

Implicit in the construction of seed transfer zones (STZs) are the assumptions that plant populations are adapted to their home climates and that transferring native seed across climate gradients risks maladaptation and poor performance. However, plants are adapted to multiple aspects of their environments that are often excluded from STZ development. Here, we used models integrating geographic distance, climate distance and soil metrics to predict plant mortality in an experimental garden for three restoration-relevant species in the southwestern United States: *Bouteloua curtipendula*, *Heterotheca villosa* and *Sporobolus cryptandrus*. Overall, climate distance explained mortality better than geographic distance, but increasing climate distance was not consistently associated with higher mortality. In contrast, mortality always increased with geographic distance. Species responded idiosyncratically to environmental gradients such as soil texture and pH, indicating that incorporating site-specific variables beyond climate can improve predictions of survival. Finally, seed sources of *H. villosa* from hotter, drier climates exhibited improved survival during abnormally hot, dry conditions at the experimental site, whereas no consistent pattern emerged for the two grass species. Collectively, our results suggest that seeding strategies extending beyond climate matching alone may better support restoration outcomes when species-specific guidance is unavailable.

Impact Statements

Restoration professionals often rely on tools for sourcing plant materials (e.g., native seed) to bolster restoration outcomes. Common tools include seed transfer zones, which delimit areas of climate similarity, and web-based applications, which calculate climate distances between seed sources and restoration sites. These tools assume restoration success increases as climate distance decreases. This assumption, rarely tested during or after restoration treatments, is based on abundant research supporting the evolutionary process of local adaptation. Our analyses of mortality patterns across three plant species, each represented by 10–18 wildland seed sources collected at varying climate distances from an experimental garden, indicate that predictors of mortality vary among species. Specifically, our results indicate that: (1) many facets of environmental variation influence species, including climate, soils and unknown aspects correlated with geographic distance; (2) species respond to suites of environmental variation uniquely, impeding generalizations; (3) while a model can be constructed to explain mortality across species, mortality was positively correlated with climate distance for only one species; (4) for each species, the climatically closest population to the experimental garden did not have the lowest mortality – however, averaging mortality rates across seed sources with similar climates always resulted in lower overall mortality. Further, we assessed patterns of mortality in the context of abnormally hot and dry weather at our experimental garden compared with average climates and demonstrated that seed sources from hotter and drier climates relative to the garden had lower mortality in only one species. Our results highlight a potential strategy for restoration in drylands: if multiple intraspecific, genetically appropriate, and climatically approximate seed sources are available, a regional admixture provenancing strategy may increase the probability that plants can establish and persist.

Introduction

Decisions about the geographic origin of native plant seed directly influence restoration outcomes, affecting plant survival, ecosystem function and long-term resilience in degraded landscapes. To promote successful management outcomes, practitioners must balance a myriad of considerations during seed selection, including population-level suitability (Davidson and Germino, 2020), climate suitability, site conditions (McKay et al., 2005; Havens et al., 2015)

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and logistical constraints, including cost, seed availability and project mandates (Cortina-Segarra et al., 2021; McCormick et al., 2021; Shriver et al., 2025). Given that adaptation to the home environment is a well-illustrated phenomenon in plants (Baughman et al., 2019), practitioners often leverage tools that incorporate known or assumed adaptive patterns, such as seed transfer zones (STZs), to guide the selection and movement of native seed.

STZs are models that link plant evolutionary processes to environmental conditions. As a result, they inform seed selection and support genetically and ecologically appropriate restoration (Plant Conservation Alliance [PCA], 2015). They are informed by the assumption that plants are adapted to their local climates, such that grouping geographic areas with similar climates (i.e., areas where climate distance is minimized) can help mitigate the risk of maladaptation (McKay et al., 2005). Provisional STZs utilize climate variables such as winter minimum temperature and aridity, which are generally assumed to influence adaptation across species (Bower et al., 2014), while empirical STZs incorporate climate gradients correlated with a species' morphological traits or allele frequencies (St. Clair et al., 2013; Shryock et al., 2024). STZs are largely based on climate normals, or 30-year averages of weather variables, that represent a baseline for yearly weather variability and long-term climate change; in North America, these are typically represented by either WorldClim v2.1 (Fick and Hijmans, 2017) or ClimateNA (Wang et al., 2016). However, shifting regional climate patterns may make the utility of climate-based STZs obsolete (Koehn et al., 2021; McKinnon et al., 2021).

At the same time that current climate trajectories are mismatched with climate normals (Seager et al., 2007), many landscapes are experiencing weather events that are exposing plants to conditions outside their optimal climate envelopes (Smith, 2011; Stott, 2016). In the context of restoration efforts, extreme or unusually timed weather events are decreasing restoration success (Hagger et al., 2018). For example, novel timing of weather events, such as late freezes or early soil warming, inhibits the establishment of native seed sources not adapted to these environmental pressures (Farnsworth et al., 1995; Ishioka et al., 2013; Wheeler et al., 2014). When weather filters establishment at early life stages (James et al., 2011; Copeland et al., 2021), opportunities may exist to use species or populations adapted to alternative environmental conditions (e.g., hotter and drier conditions; Klein and Mitchell, 2024).

Despite the primary emphasis on climate and the increasing importance of extreme weather in seed sourcing guidance (Hardegree et al., 2018), other biotic and abiotic factors exert selective pressures and influence the adaptation of a species to its local environment. Biotic influences include exposure and response to herbivory (Karban and Myers, 1989; Diaz et al., 2007), soil microbial communities (Lau and Lennon, 2012) and pollinators (Brooker, 2006; Aslan et al., 2025). Non-native species also impose selective pressures on native plant communities by shifting competitive dynamics and community composition (Brown et al. 2008). Plants may also exhibit context-dependent responses to abiotic attributes, such as solar radiation and nutrients (Tilman, 1984; Lavorel and Garnier, 2002; Piedallu and Gégout, 2008; Gates, 2012). Moreover, soil has been shown to drive local adaptation in plants (Raabová et al., 2011; Sherrard et al., 2015; Gibson et al., 2019). Soil characteristics, including compaction, nutrients, texture and pH, impact plant distribution and performance metrics, such as survivorship and reproduction (Mod et al., 2016; Soong et al., 2020; Shaheb et al., 2021). Extreme soil environments can exert strong selective pressure, resulting in genetic differentiation within species (Andrade et al., 2022), endemism (Rajakaruna, 2004) and speciation. Despite the importance of soil for the performance, distribution and diversity of plants, edaphic characteristics are underutilized in species distribution modeling, niche modeling and the development of STZs (Mod et al., 2016; Velazco et al., 2017; Gibson et al., 2019). Layered on top of this milieu is the disturbance event that precipitates the need for revegetation, which may have altered the site so that it falls outside a target species' preferred suite of abiotic environmental attributes despite an otherwise suitable climate (Shinoda and Akasaka, 2019).

In the context of long-term climate averages, contemporary weather and the additional selective pressures imposed by environmental variation such as soil characteristics, we leveraged mortality data from a 5-year, multispecies experimental garden to model relationships between plant performance (i.e., mortality in the experimental garden after 4 years) and climate distance (i.e., the similarity between the climate of seed source locations and the planting location). We predicted that minimizing climate distance can help reduce mortality, which represents the prevailing assumption of restoration using STZs. However, given the abundance of research supporting plant species' complex biotic and abiotic interactions within their environments, we predicted that more complex models, including additional environmental factors, would explain mortality patterns more effectively. First, we constructed a null model to investigate whether climate distance or geographic distance more accurately predicted mortality. Second, we increased model complexity to test the prediction that many environmental factors influence plant performance (i.e., factors that are not typically included in STZs) and quantified model improvement. Specifically, we included soil texture and pH, as both factors play an important role in determining plant community composition (Renne et al., 2019; Barlow et al., 2020). Third, we investigated whether species' mortality responses were influenced by parameters in similar ways or if responses were species-specific. Finally, we assessed whether populations from hotter and drier locations compared to the experimental garden survived better during abnormally hot, dry weather conditions. Overall, by shedding light on species-specific responses to geographic, climatic and environmental variation, our goal was to illuminate genetically and ecologically appropriate restoration strategies that foster successful outcomes given unpredictable weather and climate patterns.

Methods

We used data from three widely distributed perennial species important for restoration in the southwestern United States, including two C4 grasses, *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama; Poaceae) and *Sporobolus cryptandrus* (Torr.) A. Gray (sand dropseed; Poaceae) and the C3 forb *Heterotheca villosa* (Pursh) Shinners (hairy false goldenaster; Asteraceae). These species are commonly included in post-disturbance and rehabilitation seedings on public lands because they establish reliably across broad environmental gradients and provide key ecosystem functions, including forage for wildlife and livestock (*B. curtipendula*, *S. cryptandrus*) and nectar resources for native pollinators (*H. villosa*). Seeds from 10 populations of *B. curtipendula*, 18 populations of *H. villosa* and 14 populations of *S. cryptandrus* were collected from New Mexico, Arizona, southern Utah and southern Colorado (Figure 1 and Supplementary Table S1) in accordance with the Bureau of Land Management's Seeds of Success protocol (Haidet and Olwell, 2015).

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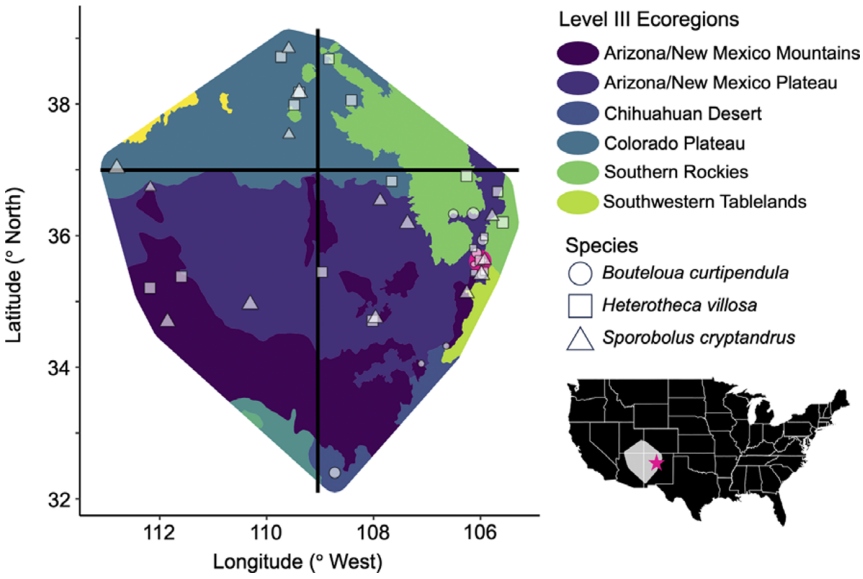


Figure 1. Collection locations of *B. curtipendula* (circles), *H. villosa* (squares) and *S. cryptandrus* (triangles) within the Four Corners region of the western United States. Background colors reflect Omernik Level III Ecoregions (Omernik and Griffith, 2014). Larger symbols reflect higher mortality in 2023. The large pink circle indicates the common garden location in Santa Fe, New Mexico. The garden location is also indicated as a pink star in the map inset showing the polygon location relative to the contiguous United States.

Plant propagation and garden establishment

Methods for plant propagation and garden establishment at the New Mexico Land Conservancy's Petchesky Conservation Center, located in Santa Fe, New Mexico (35.6126, −106.0045), are detailed in Samuel et al. (2024). Briefly, in March 2019, seeds were sown in a greenhouse to obtain 50 plants per population. Plants were grown for approximately 110 days before outplanting in the experimental garden (90–170 days for *S. cryptandrus* due to poor germination in some populations). Outplanting occurred after the onset of monsoon precipitation in July 2019. Plants received supplemental watering in the summer and fall of 2019 to counteract transplant shock, and again in summer 2020 due to historically low precipitation and high temperatures (Supplementary Figure S1). Plants were monitored in October 2019 and annually thereafter in spring or summer, and plants that displayed any green tissue were designated as living. Small interannual decreases in mortality (i.e., plants recorded as dead in previous surveys but later observed alive) were attributed to dormancy. Plants without green tissue were left *in situ* and not destructively harvested.

Fifty individuals from each population of *H. villosa* and *B. curtipendula* were outplanted. The number of replicates of *S. cryptandrus* varied and ranged from 15 to 68 individuals, as germination was variable and generally low among populations. Source locations represented twelve Bower et al. (2014) seed zones (Supplementary Table S1) and five Omernik Level III Ecoregions (Omernik and Griffith, 2014). Twenty-two source locations share the same seed zone as the garden (Bower et al., 2014). Across species, geographic distance between source locations and the garden ranges from 1.56 km to 630 km (Supplementary Table S1). The proportion of dead plants after four years ranged from 0.42–0.94 with a mean of 0.62 for *B. curtipendula*, 0.50–1.00 with a mean of 0.84 for *H. villosa* and 0.58–0.98 with a mean of 0.81 for *S. cryptandrus*. Garden mean annual temperature and mean annual precipitation are 10.9 °C and 358 mm, respectively. Mean annual temperature and mean annual precipitation of source locations range from 9.8–16.2 °C and 302–392 mm for *B. curtipendula*; 3.3–12.7 °C and 273–769 mm for *H. villosa* and 9.1–17 °C and 193–508 mm for *S. cryptandrus* (Supplementary Table S1).

Calculating geographic distance and climate distance

Because our goal was not to investigate specific climate drivers influencing species survival, but rather to quantify relationships between climate distance and survival, we chose to collapse climate variation across the study area into orthogonal axes using principal component analysis. We used WorldClim v2 bioclimatic data (Supplementary Table S2; Fick and Hijmans, 2017) to represent climate space and performed PCA using the *raster* package (Hijmans, 2023) in R v4.4.1 (Foundation for Statistical Computing, 2023). Specifically, we calculated the Euclidean climate distance between the experimental garden and each seed source location using the first three PC axes, which accounted for 87% of climate variation (Supplementary Table S2). To calculate geographic distance in kilometers, we used the *distm* function from the *geosphere* package (Hijmans, 2022).

Model selection and statistical analyses

Ultimately, mortality was high across populations for each species (Supplementary Table S1). Thus, we decided to focus on mortality, rather than survival data. We modeled mortality patterns within and across populations for each species. We used mortality data collected in 2023 (i.e., four years after garden establishment) for model-building purposes. We did not include a plot-level random effect since plants were randomized across plots, and individual-level data were summarized as the proportion of population mortality. Because our data are proportions, we modeled mortality using a beta distribution (Geissinger et al., 2022). Furthermore, because 99.99% mortality is functionally the same as 100% mortality in a biological sense, we adjusted the four populations that displayed 100% mortality downward by 0.00001% to facilitate model fit (Supplementary Table S1). We note that zero–one-

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inflated beta regression provides an alternative framework for proportional data with boundary values; however, given the small number of populations exhibiting complete mortality and the biological equivalence of near-complete and complete mortality for our questions, we retained a standard beta regression approach. We modeled data using the *betareg* package and function (Cribari-Neto and Zeileis, 2010) and evaluated model assumptions graphically. During model selection, we retained factors that reduced the Akaike Information Criterion (hereafter, AIC) value by at least 4, which represents strong evidence of model difference (Burnham and Anderson, 2004). While a reduction of 2 in AIC is usually regarded as enough to opt for greater complexity and additional parameters (Richards, 2005), we used a difference of 4 to be more conservative in selecting parameters whenever AIC was used to compare models, and followed the principle that, in the case of a difference of <4, the model with fewer parameters was the preferred one.

Question 1. Do geographic distance, climate distance, or both predict mortality?

We evaluated climate and geographic distance for correlation. We began with two simple models, Proportion Dead ~ Climate Distance and Proportion Dead ~ Geographic Distance, and compared them using AIC. Next, the Proportion Dead model, including both distance metrics, was evaluated with AIC against the single-predictor models.

Question 2. Do environmental factors represented by soil metrics improve model predictions?

We obtained soil data from 100-m CONUS SoilGrids (Ramcharan et al., 2018). In general, soils with higher sand content are expected to result in less water availability and lower nutrient retention, while soil pH influences nutrient availability and solubility in a variety of nonlinear ways (Brady and Weil, 2016; Penn and Camberato, 2019). We extracted soil pH and percent sand at 0, 5, 15 and 30 cm depth for the seed source and garden locations, then averaged these values to create a profile for the most biologically active layer of soil that hosts most herbaceous plant roots and microbial biomass (Brady and Weil, 2016). All predictive variables (distance metrics and soil variables) were checked for correlations before including them in the model-building process. Soil variables were added first individually, then together, to the model with the lowest AIC generated in Question 1.

Question 3. Is mortality equally sensitive across species to all factors?

After determining the best model in Question 2, we added species identity as an interaction term with each predictor variable in a stepwise manner and evaluated predictive power against the simpler version of the model using AIC. All models from Questions 1–3 were ranked by their AIC weights, which give the probability that a model is correct, assuming the correct model is included in the full set (Burnham and Anderson, 2004).

Question 4. Do populations from hotter and drier source locations establish and persist better at our garden in abnormally hot, dry conditions?

The 2019 and 2020 growing seasons (defined as June–September) were abnormal with respect to temperature and precipitation relative to 30-year averages (Supplementary Figure S1), which provided an opportunity to explore survivorship in an extreme weather context adjacent to our formal modeling goals (see above). For each source location, we extracted mean annual temperature (WorldClim Bio1) and mean annual precipitation (WorldClim Bio12) as indices of climatic origin. We graphed interannual mortality of each population, ranked by their source location mean annual temperature and mean annual precipitation values, to evaluate whether populations sourced from hotter, drier locations exhibited lower mortality by the final monitoring year. Furthermore, for each species, we tested the significance of correlations between the response variable (proportion of individuals dead in each population in 2023) and each predictor variable (either mean annual temperature or mean annual precipitation) using a beta regression model. These models were constructed separately from the modeling efforts described in Questions 1–3.

Results

We evaluated four questions regarding how geographic distance, climate distance and additional environmental factors influence plant mortality and present four findings. Regarding Question 1, climate distance explained mortality better than geographic distance, with limited improvement when both predictors were included. For Question 2, incorporating soil texture and pH substantially improved model performance, indicating that environmental factors beyond climate contribute to mortality. For Question 3, species-specific responses to climate and edaphic variables were evident, although mortality increased consistently with geographic distance for all species. Finally, populations from hotter and drier environments exhibited improved survival under abnormally hot and dry conditions in only one species. We detail results for each question in turn (Findings 1–4).

Finding 1. In a simple model, climate distance was the primary predictor of mortality across species, whereas geographic distance contributed little additional explanatory power

Climate distance and geographic distance were moderately correlated (adjusted $R^2 = 0.46$). Assumptions of normality for geographic and climatic distance were violated due to two outlying collection locations of *H. villosa* that were geographically close yet climatically distant, likely due to their high elevations relative to the garden. However, we opted not to transform the data. In models where climate distance and geographic distance were each considered as the sole predictors of mortality, climate distance was a better predictor of mortality than geographic distance (pseudo-R^2 of 0.33 and 0.04, respectively, $\Delta AIC = 21.33$; Supplementary Table S3). The model Proportion Dead ~ Geographic Distance + Climate Distance resulted in a ΔAIC of 1.94 compared to Proportion Dead ~ Climate Distance, indicating that climate distance is the primary driver of predictive strength.

Finding 2. Soil characteristics were important for explaining mortality patterns in all species

Although soil pH and percent sand were moderately correlated (adjusted $R^2 = 0.53$), each variable independently improved model performance. When added individually to the model Proportion Dead ~ Geographic Distance + Climate Distance, either pH or percent sand reduced the AIC by 3.74 (Supplementary Table S3).

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Including both soil variables further improved model fit, decreasing the AIC by an additional 2.64 relative to models containing only one soil predictor. These results indicate that soil texture and pH each contribute independent explanatory power beyond geographic distance and climatic distance.

Finding 3. Species responded uniquely to climate and edaphic variables, but mortality was always positively correlated with geographic distance

Using the model with the lowest AIC from Question 2 (Proportion Dead ~ Geographic Distance + Climate Distance + pH + Percent Sand), we found that including species-specific responses to climate distance, pH and percent sand – but not geographic distance – resulted in a model with the lowest AIC (Table 1 and Supplementary Table S3).

Species-specific responses to climate distance, pH and percent sand varied in both strength and direction (Figure 2; Supplementary Table S4). For example, *B. curtipendula* exhibited a significant negative relationship between percent sand and mortality, whereas *S. cryptandrus* and *H. villosa* showed significant positive relationships. Only *H. villosa* had a significant relationship between pH and mortality. Responses to climate distance also differed: *S. cryptandrus* showed no significant association, while *B. curtipendula* and *H. villosa* exhibited significant relationships in opposite directions.

All species had a positive relationship between mortality and geographic distance between the garden and source locations (Figure 3 and Supplementary Table S4). Geographic distance alone was a weak predictor of mortality, but its inclusion alongside climate distance and soil variables consistently improved model fit, indicating that it captures additional, unmeasured environmental or biotic variation relevant to survival. Estimated phi values indicated substantial dispersion in mortality among populations, consistent with heterogeneous biological responses to environmental gradients and suggesting caution when extrapolating predictions beyond the sampled populations (Supplementary Table S4).

Table 1. Akaike Information Criterion (AIC, a metric for the relative performance of a model on a given dataset) values of the five top-performing models predicting mortality of the three study species

Highest performing predictive models	df	AIC	AIC weight
Proportion Dead ~ pH * Species + Percent Sand * Species + Geographic Distance + Climate Distance * Species	14	−112.47	0.740
Proportion Dead ~ pH * Species + Percent Sand * Species + Geographic Distance * Species + Climate Distance * Species	16	−110.30	0.249
Proportion Dead ~ pH * Species + Percent Sand * Species + Geographic Distance	11	−101.10	0.003
Proportion Dead ~ pH * Species	7	−101.10	0.002
Proportion Dead ~ pH * Species + Percent Sand * Species	10	−100.93	0.002

Note: The first model satisfies the requirement that it uses fewer parameters than the second-best-performing model and has a ΔAIC >4 relative to the next-best model that uses fewer parameters. The degrees of freedom (df) are associated with the log-likelihood of the given model. AIC weights are interpreted as the probability that a given model is the best model, assuming the correct model is in the model set. For a full accounting of the models tested, please see Supplementary Table S3.

Finding 4. Populations sourced from hotter and drier climates survived better in only one species during the experiment

Across species, mortality responses to climatic origin differed among species (Figure 4; Table 2). In *H. villosa*, populations sourced from locations with higher mean annual temperature and lower mean annual precipitation experienced significantly lower mortality over 4 years than populations from cooler, wetter origins. In contrast, we found no evidence that populations from hotter, drier source environments had improved survival in *B. curtipendula* or *S. cryptandrus* (Figure 4; Table 2).

Discussion

Successful restoration depends on plant materials, usually in the form of native seed, that can establish and survive following disturbances or management actions. Given the ubiquitous process of climate-based local adaptation in plants (Leimu and Fischer, 2008), we often assume that tools such as STZs facilitate plant survival (Bower et al., 2014). However, in the context of adaptively important environmental variation not included in STZs (e.g., most provisional and empirical STZs are based solely on climate averages) and interannual weather variation, we may question whether STZs accurately predict native seed source performance (e.g., Nolan et al., 2023). Field-based experiments that incorporate wild-collected native seed from across species' environmental distributions are opportunities to test these hypotheses. By leveraging wild-sourced seed from at least 10 populations of three species important for restoration across the southwestern United States, we show that climate matching alone does not best predict empirical patterns of mortality. Instead, species respond to environmental variation in complex and individualistic ways.

After four years in an experimental garden with minimal management, *B. curtipendula, S. cryptandrus* and *H. villosa* experienced high levels of mortality across all seed sources (Figure 4). High mortality, despite supplemental watering in 2019 and 2020, reflects the difficulties restoration practitioners face in establishing plants in drylands worldwide (Shackelford et al., 2021). Our model that explained the most variation in mortality was one of the most complex, including all variables with species interaction terms except for geographic distance. Geographic distance was the only variable to which all species responded consistently, though geographic distance by itself was a poor predictor of performance. Despite a moderate correlation between geographic and climate distance, geographic distance increased our best model's predictive power, indicating that it encapsulates environmental or biotic factors relevant to species survival beyond climate and the soil variables included here. For example, geographic distance may capture other interactions known to influence plant performance, such as with mycorrhizae (Bahram et al., 2015), soil biota (Vandegehuchte et al., 2012; Sherrard et al., 2015), pathogens (Crémieux et al., 2008; Rúa et al., 2016), or other interactions between the abiotic and biotic environment (López-Goldar and Agrawal, 2021).

Species' mortality responded inconsistently in both direction and strength to percent sand, soil pH and climate distance (Figure 2), reflecting the importance of interaction terms in our best model. Species-specific responses to edaphic characteristics are well demonstrated within the literature (Rajakaruna, 2004). Within species, differences in pH and nutrient levels can result in adaptive trait differentiation among populations (Raabová et al., 2011) and soil texture influences aridity experienced by plants by how they retain water and how available that water is to plants (Jensen et al.,

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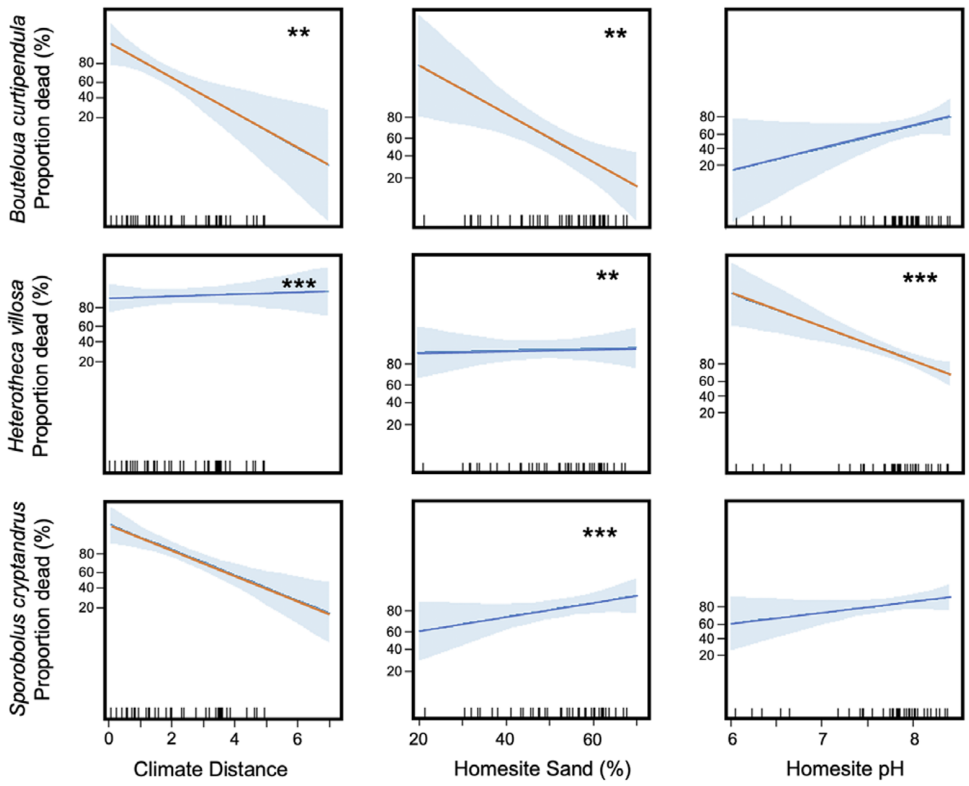


Figure 2. Estimated mortality effects based on the best predictive model (Proportion Dead ~ pH * Species + Percent Sand * Species + Geographic Distance + Climate Distance * Species). Species showed species-specific responses to climate distance between collection sites and the garden (first column), percent sand (second column) and pH (third column). Black stars indicate a significant effect, orange lines signify a negative relationship between the predictor and mortality and blue lines indicate a positive relationship between the predictor and mortality. Confidence intervals are represented by blue shading around the trend lines. Tick marks on the x-axis indicate data points.

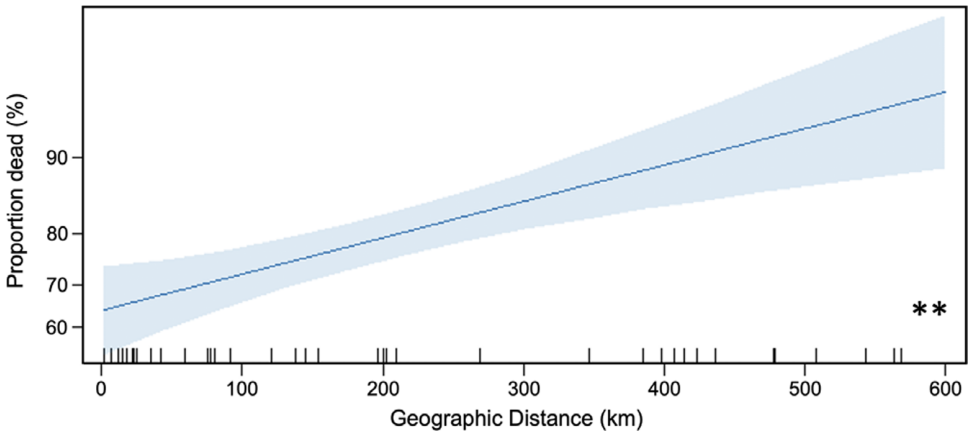


Figure 3. Estimated mortality effects based on the best predictive model (Proportion Dead ~ pH * Species + Percent Sand * Species + Geographic Distance + Climate Distance * Species) as predicted by geographic distance (km) between the garden and collection locations. All species responded uniformly to geographic distance based on the AIC comparison to models with a Geographic Distance * Species term. The farther away the plants were sourced, the higher the percent mortality. Confidence intervals are represented by blue shading around the trend line. Black stars indicate a significant effect, and tick marks on the x-axis represent data points.

1998). In our study, mortality was significantly affected by percent sand across species, while species' responses to pH were idiosyncratic (Rupprecht et al., 2021), which demonstrates the importance of evaluating all species prioritized for restoration and rehabilitation efforts, including those known to have strong local adaptation to edaphic factors or that inhabit edaphically distinct environments (Rajakaruna, 2017). We acknowledge the difficulty of finding soil data at fine enough resolution or across broad spatial extents (though see Nauman et al., 2024; Ramcharan et al., 2018). However, pH and soil texture may be readily obtained for restoration sites with either rough measurements in the field or in partnership with a local expert.

While species-specific responses to edaphic characteristics were expected, the unique responses of species to climate distance were unexpected. Indeed, the implicit assumption in many management efforts is that minimizing climate distance, as facilitated by tools such as STZs, supports successful restoration outcomes (Bower et al., 2014). Within our study species, *B. curtipendula* seed sources

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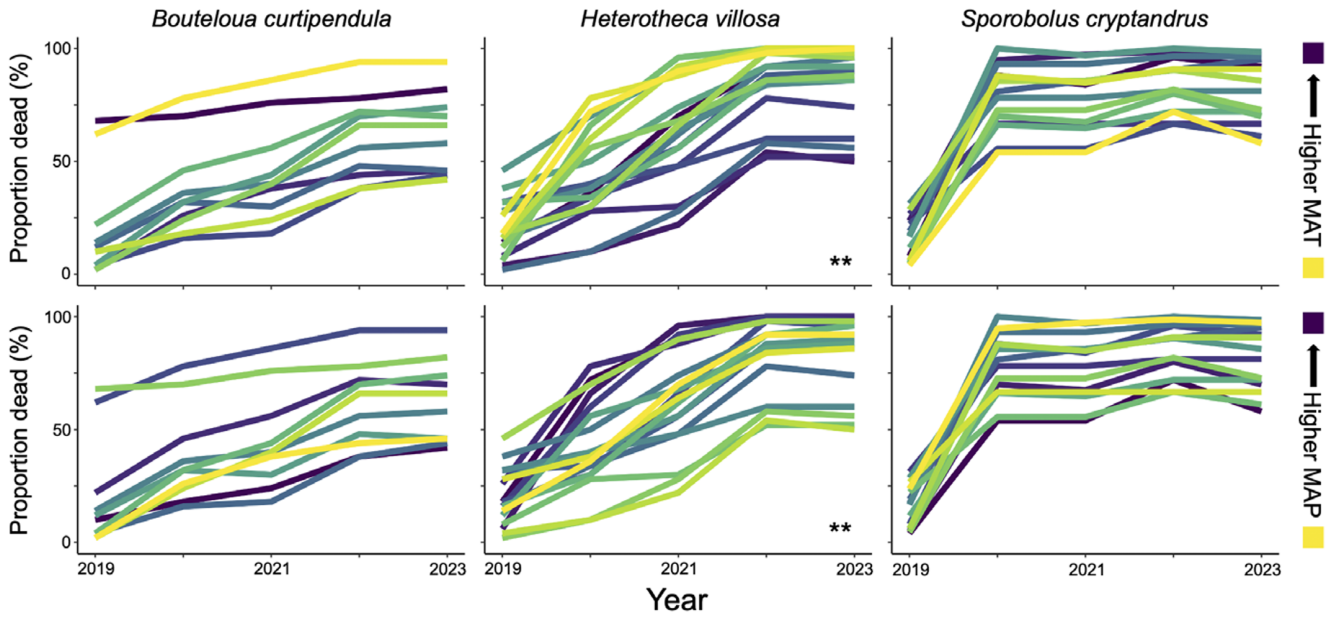


Figure 4. Proportion of plants recorded dead for each population across 4 years of monitoring. Species-specific results are arranged in columns. Rows represent the mean annual temperature (MAT) and mean annual precipitation (MAP). Line colors indicate populations ranked relative to one another, with darker colors representing higher mean annual temperature and precipitation at seed source locations. Decreases in mortality are attributed to dormancy, as plants were not removed from the soil to confirm mortality. Stars indicate a significant relationship between the proportion dead in 2023 and either MAT or MAP; detailed results of the beta regression models are provided in Table 2.

Table 2. Species-specific parameter estimates of the beta regression models for proportion dead per population in 2023 (response variable) and the predictor variables, mean annual temperature (MAT) or mean annual precipitation (MAP)

Species	Predictor variable	Estimate	Std error	Z value	Pr (> |Z|)
Bouteloua curtipendula	MAT	0.007	0.129	0.058	0.954
B. curtipendula	MAP	−0.012	0.009	−1.321	0.186
Heterotheca villosa	MAT	−0.460	0.143	−3.217	0.001
H. villosa	MAP	0.007	0.002	3.250	0.001
Sporobolus cryptandrus	MAT	0.117	0.113	1.036	0.300
S. cryptandrus	MAP	−0.003	0.003	−1.297	0.195

Note: Estimates indicate the change in the response variable associated with a one-unit change in the predictor.

from climates more similar to the experimental garden performed substantially worse, and the strength of the relationship (i.e., the slope in Figure 2) was also strong. *H. villosa* seed sources from similar climates performed substantially better, though the strength of the relationship was weak, and *S. cryptandrus* performance was not correlated with climate distance. These results corroborate patterns identified in Baughman et al. (2019), wherein a literature review of local adaptation experiments across the western United States demonstrated that, while local adaptation may be a pervasive evolutionary response by plants across the region, there are many instances of mixed or negative performance outcomes (i.e., see their Figure 4c). While our data do not help us identify the mechanism by which the hypothesized climate-adaptation relationship breaks down, the inclusion of geographic distance and soil properties in our best model indicates that climate distance alone may not support management practices. We also note that we did not test whether species-specific, empirical STZs may result in lower mortality when selecting seed sources based on climate matching, as these products were not available for our focal species during our study.

Our findings highlight the usefulness of long-term monitoring in experimental gardens (Aradottir and Hagen, 2013; Moffet et al., 2019). We did not begin to observe a consistent leveling out of mortality until 2022, three years after plugs were planted in the experimental garden. Moreover, species experienced mortality at different rates throughout the study (Figure 4). For example, mortality in *S. cryptandrus* occurred most rapidly between 2019 and 2020 across all populations, whereas *H. villosa* experienced greater variability among populations in mortality rates, and *B. curtipendula* was more consistent throughout. These trends parallel those reported by Germino et al. (2018), wherein *Artemisia tridentata* establishment was monitored over a 25-year period in an experimental garden. Mortality in this long-lived shrub took approximately 17 years to stabilize, and the rate of mortality varied among populations. Within a restoration treatment, differences between populations with rapid mortality versus gradual mortality may influence outcomes; plants persisting after relatively high mortality may reproduce opportunistically during wet years, thereby potentially overcoming initially poor performance. Further, it is possible that some populations may have increased

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reproductive output earlier in establishment at the expense of survival (Sheth and Angert, 2018). Whether such a demographic trade-off can effectively rescue declining populations remains unclear (Sheth and Angert, 2018).

Contemporary, interannual weather variability can present a challenge to land management practices that use tools based on long-term climate averages, as unpredictable short-term weather patterns, extreme weather events (Williams et al., 2022) and the velocity of climate change (Loarie et al., 2009) introduce variation outside what is represented by climate values averaged over past decades. Plants experienced years with high temperatures and low precipitation relative to the long-term average conditions at the experimental site. Considering these weather patterns, we tested whether mortality in 2023 was significantly correlated with seed source mean annual temperature or precipitation. While no discernible patterns were evident in *B. curtipendula* or *S. cryptandrus*, *H. villosa* seed sources from populations with the highest mean annual temperature had the lowest mortality (Table 2). While not a ubiquitous pattern across species, for those species in which predictive provenancing – or selecting seed sources according to the climate expected to prevail at a restoration site (Bucharova et al., 2019) – may support higher performance, climate-matching tools incorporating future climate variation can support the selection of seed sources during landscape management activities (Shryock et al., 2018; St. Clair et al. 2022). However, we note that our field-based experiment started with greenhouse-grown plants, and we bypassed selective factors that may influence survival resulting from a species' regeneration niche (Poorter, 2007). Furthermore, we did not track fecundity over the timeframe of this study (see Samuel et al., 2024), which may be more important for the persistence of a restored population than an individual plant's long-term survival (Pywell et al., 2003).

For species where climate distance does not predict performance, mixed-source provenancing strategies may support more successful restoration outcomes compared to predictive provenancing or climate matching (also known as local provenancing). Mixed-source provenancing strategies, for example, admixture and composite provenancing, focus less on climate matching and more on increasing overall genetic diversity, under the assumption that higher genetic diversity allows selection of the best genotypes at a particular site (see Breed et al., 2013; Prober et al., 2015; Bucharova et al., 2019 for in-depth discussions and references). Here, we do not test whether genotypic diversity may be correlated with population performance, but we quantify that, at least for *B. curtipendula* and *S. cryptandrus*, mortality is not tied to climate distance. However, for every species, mortality averaged across seed sources with a climate distance <2 (relative to the experimental garden, based on principal components analysis) was lower than the mortality rate of the climatically closest seed source to the experimental garden (Supplementary Table S1). As such, our results indicate that a regional admixture provenancing strategy (Bucharova et al., 2019) may represent a bet-hedging approach, for example, by providing population variability that can buffer interannual weather conditions and/or microsite variability (Nolan et al., 2023), which may increase overall survival in a restoration treatment. To the extent that interannual variation influences the performance of seed sources, an additional approach may be to seed restoration sites over multiple years, contrary to standard practice (Kulpa et al., 2012; Pyke et al., 2013).

In the event that restoration professionals can include multiple intraspecific seed sources in a seed mix designed for a restoration site, care should be taken to avoid mixing incompatible seed sources for outcrossing species, either within the seed mix or between the seed mix and conspecifics at the restoration site. Incompatibility can manifest as reduced fecundity when individuals established from seed sources pollinate other intraspecific seed sources or pre-existing conspecifics, or as lower competitive ability of seedlings resulting from such outcrossing events. Incompatibility results from genomic differences that accumulate within a species through processes such as genome duplication (e.g., polyploidy or aneuploidy; Kramer et al., 2018), inversions (Kirkpatrick and Barton, 2006), local adaptation (McKay et al. 2005), or genetic drift over a species' history (Frankham et al., 2011). Without pre-existing knowledge of the genetic patterns within a species, practitioners can reduce the probability of mixing seed sources that are too differentiated by limiting the geographic distances across which seed sources are collected (Massatti et al., 2020). However, quantifying spatial patterns of genetic differentiation resulting from historical processes (e.g., Massatti and Winkler, 2022) would provide the most actionable guidance for seed source mixing, as genetically defined groups are generally considered cohesive units due to recent or ongoing gene flow (Waples and Gaggiotti, 2006).

In conclusion, by using mortality patterns of three plant species established in an experimental garden, we were able to quantify the complexity of species' responses to environmental gradients. Specifically, our results indicate that (1) in a simple model, climate distance performed better than geographic distance in predicting mortality; (2) soil characteristics, including texture and pH, were important for explaining mortality patterns across the study species; (3) species responded to climate and edaphic variables uniquely, but mortality was always positively correlated with geographic distance; (4) when we assessed mortality patterns in the context of abnormally hot, dry weather at our experimental garden relative to average climates, we found that seed sources from hotter and drier climates relative to the garden had lower mortality in only one species. Further, for each species, averaging mortality rates across seed sources with roughly similar but not identical climates relative to the experimental garden resulted in lower mortality than the most climatically similar seed source. Our results indicate that, if species-specific resources are not available, restoration in drylands may benefit from a regional admixture provenancing strategy.

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Data availability statement. The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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Author contribution. R.M. conceived of the analysis, C.M.R. conducted the analysis, C.M.R. and R.M. wrote the manuscript, E.M.S. conducted the field work and generated the data, and all authors provided manuscript edits.

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References

Andrade LRM, Aquino FG, Echevarria G, Oliveira JS, Pereira CD, Malaquias JV, Souza KS, Montargès-Pelletier E, Faleiro FG, Reis Junior FB, Miranda ZG, Sano EE and do Amaral LIV (2022) Edaphic factors as genetic selection agents and adaptation drivers of native plant species in harsh environments of the Brazilian savanna. *Plant and Soil* **479**(1–2), 301–323.

Aradottir AL and Hagen D (2013) Ecological restoration. *Advances in Agronomy* **120**, 173–222.

Aslan CE, Grady K and Haubensak K (2025) Pollination networks and plant local adaptation: The importance of serving the pollinator community in restoration. *Restoration Ecology* **33**(4), e70027.

Bahram M, Peay KG and Tedersoo L (2015) Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi. *New Phytologist* **205**(4), 1454–1463.

Barlow KM, Mortensen DA and Drohan PJ (2020) Soil pH influences patterns of plant community composition after restoration with native-based seed mixes. *Restoration Ecology* **28**(4), 869–879.

Baughman OW, Agneray AC, Forister ML, Kilkenny FF, Espeland EK, Fiegener R, Horning ME, Johnson RC, Kaye TN, Ott J, St. Clair JB and Leger EA (2019) Strong patterns of intraspecific variation and local adaptation in Great Basin plants revealed through a review of 75 years of experiments. *Ecology and Evolution* **9**(11), 6259–6275.

Bower AD, Clair JBS and Erickson V (2014) Generalized provisional seed zones for native plants. *Ecological Applications* **24**(5), 913–919.

Brady N and Weil R (2016) *Nature and Properties of Soils*, 15th Edn. Boston, MA: Pearson Education 375–376.

Breed MF, Stead MG, Ottewell KM, Gardner MG and Lowe AJ (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* **14**(1), 1–10.

Brooker RW (2006) Plant–plant interactions and environmental change. *New Phytologist* **171**(2), 271–284.

Brown CS, Anderson VJ, Claassen VP, Stannard ME, Wilson LM, Atkinson SY, Bromberg JE, Grant TA and Munis MD (2008) Restoration ecology and invasive plants in the semiarid west. *Invasive Plant Science and Management* **1**(4), 399–413.

Bucharova A, Bossdorf O, Hölzel N, Kollmann J, Prasse R and Durka W (2019) Mix and match: Regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. *Conservation Genetics* **20**(1), 7–17.

Burnham KP and Anderson DR (2004) Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* **33**(2), 261–304.

Copeland SM, Baughman OW, Boyd CS, Davies KW, Kerby J, Kildisheva OA and Svejcar T (2021) Improving restoration success through a precision restoration framework. *Restoration Ecology* **29**(2) ,e13348.

Cortina-Segarra J, García-Sánchez I, Grace M, Andrés P, Baker S, Bullock C, Decleer K, Dicks LV, Fisher JL, Frouz J, Klimkowska A, Kyriazopoulos AP, Moreno-Mateos D, Rodríguez-González PM, Sarkki S and Ventocilla JL (2021) Barriers to ecological restoration in Europe: Expert perspectives. *Restoration Ecology* **29**(4), e13346.

Crémieux L, Bischoff A, Šmilauerová M, Lawson CS, Mortimer SR, Doležal J, Lanta V, Edwards AR, Brook AJ, Tscheulin T, Macel M, Lepš J, Müller-Schärer H and Steinger T (2008) Potential contribution of natural enemies to patterns of local adaptation in plants. *New Phytologist* **180**(2), 524–533.

Cribari-Neto F and Zeileis A (2010) Beta regression in R. *Journal of Statistical Software* **34**(2), 1–24.

Davidson BE and Germino MJ (2020) Spatial grain of adaptation is much finer than ecoregional-scale common gardens reveal. *Ecology and Evolution* **10**(18), 9920–9931.

Diaz S, Lavorel S, McIntire S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg G, Noy-Meir I, Landsberg J, Zhang W, Clark H and Campbell BD (2007) Plant trait responses to grazing – a global synthesis. *Global Change Biology* **13**(2), 313–341.

Farnsworth EJ, Nunez-Farfan J, Careaga SA and Bazzaz FA (1995) Phenology and growth of three temperate forest life forms in response to artificial soil warming. *The Journal of Ecology* **83**(6), 967.

Fick SE and Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**(12), 4302–4315.

Foundation for Statistical Computing (2023) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Frankham R, Ballou JD, Eldridge MD, Lacy RC, Ralls K, Dudash MR and Fenster CB (2011) Predicting the probability of outbreeding depression. *Conservation Biology* **25**(3), 465–475.

Gates DM (2012) *Biophysical Ecology*. New York, NY: Springer Science and Business Media.

Geissinger EA, Khoo CLL, Richmond IC, Faulkner SJM and Schneider DC (2022) A case for beta regression in the natural sciences. *Ecosphere* **13**(2), e3940.

Germino MJ, Moser AM and Sands AR (2018) Adaptive variation, including local adaptation, requires decades to become evident in common gardens. *Ecological Applications* **29**(2), e01842.

Gibson A, Nelson CR, Rinehart S, Archer V and Eramian A (2019) Importance of considering soils in seed transfer zone development: Evidence from a study of the native *Bromus marginatus*. *Ecological Applications* **29**(2), e01835.

Hagger V, Dwyer J, Shoo L and Wilson K (2018) Use of seasonal forecasting to manage weather risk in ecological restoration. *Ecological Applications* **28**(7), 1797–1807.

Haidet M and Olwell P (2015) Seeds of success: A national seed banking program working to achieve long-term conservation goals. *Natural Areas Journal* **35**(1), 165–173.

Hardegree SP, Abatzoglou JT, Brunson MW, Germino MJ, Hegewisch KC, Moffet CA, Pilliod DS, Roundy BA, Boehm AR and Meredith GR (2018) Weather-centric rangeland revegetation planning. *Rangeland Ecology and Management* **71**(1), 1–11.

Havens K, Vitt P, Still S, Kramer AT, Fant JB and Schatz K (2015) Seed sourcing for restoration in an era of climate change. *Natural Areas Journal* **35**(1), 122–133.

Hijmans RJ (2022) geosphere: Spherical Trigonometry. R package version 1.5–18, https://cran.r-project.org/src/contrib/Archive/geosphere/

Hijmans R (2023) raster: Geographic Data Analysis and Modeling. R package version 3.6–20, https://CRAN.R-project.org/package=raster.

Ishioka R, Muller O, Hiura T and Kudo G (2013) Responses of leafing phenology and photosynthesis to soil warming in forest-floor plants. *Acta Oecologica* **51**, 34–41.

James JJ, Svejcar TJ and Rinella MJ (2011) Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* **48**(4), 961–969.

Jensen CR, Mogensen VO, Poulsen HH, Henson IE, Aagot S, Hansen E, Ali M and Wollenweber B (1998) Soil water matric potential rather than water content determines drought responses in field-grown lupin (Lupinus angustifolius). *Functional Plant Biology* **25**(3), 353–363.

Karban R and Myers JH (1989) Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* **20**(1), 331–348.

Kirkpatrick M and Barton N (2006) Chromosome inversions, local adaptation and speciation. *Genetics* **173**(1), 419–434.

Klein Z and Mitchell RM (2024) Seed source environment predicts response to water availability in Plantago patagonica. *Restoration Ecology* **32**(2), e14002.

Koehn CR, Petrie MD, Bradford JB, Litvak ME and Strachan S (2021) Seasonal Precipitation and Soil Moisture Relationships Across Forests and Woodlands in the Southwestern United States. *Journal of Geophysical Research: Biogeosciences* **126**(4), e2020JG005986.

Kramer AT, Wood TE, Frischie S and Havens K (2018) Considering ploidy when producing and using mixed-source native plant materials for restoration. *Restoration Ecology* **26**(1), 13–19.

Kulpa SM, Leger EA, Espeland EK and Goergen EM (2012) Postfire seeding and plant community recovery in the Great Basin. *Rangeland Ecology & Management* **65**(2), 171–181.

Lau JA and Lennon JT (2012) Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proceedings of the National Academy of Sciences* **109**(35), 14058–14062.

Lavorel S and Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology* **16**(5), 545–556.

Leimu R and Fischer M (2008) A meta-analysis of local adaptation in plants. *PLoS One* **3**(12), e4010.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB and Ackerly DD (2009) The velocity of climate change. *Nature* **462**(7276), 1052–1055.

López-Goldar X and Agrawal AA (2021) Ecological interactions, environmental gradients, and gene flow in local adaptation. *Trends in Plant Science* **26**(8), 796–809.

Massatti R, Shriver RK, Winkler DE, Richardson BA and Bradford JB (2020) Assessment of population genetics and climatic variability can refine climate-informed seed transfer guidelines. *Restoration Ecology* **28**(3), 485–493.

Massatti R and Winkler DE (2022) Spatially explicit management of genetic diversity using ancestry probability surfaces. *Methods in Ecology and Evolution* **13**(12), 2668–2681.

McCormick ML, Carr AN, Massatti R, Winkler DE, De Angelis P and Olwell P (2021) How to increase the supply of native seed to improve restoration success: The US native seed development process. *Restoration Ecology* **29**(8), e13499.

McKay JK, Christian CE, Harrison S and Rice KJ (2005) 'How local is local?' - A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* **13**(3), 432–440.

McKinnon KA, Poppick A and Simpson IR (2021) Hot extremes have become drier in the United States Southwest. *Nature Climate Change* **11**(7), 598–604.

Mod HK, Scherrer D, Luoto M and Guisan A (2016) What we use is not what we know: Environmental predictors in plant distribution models. *Journal of Vegetation Science* **27**(6), 1308–1322.

Moffet CA, Hardegree SP, Abatzoglou JT, Hegewisch KC, Reuter RR, Sheley RL, Brunson MW, Flerchinger GN and Boehm AR (2019) Weather tools for retrospective assessment of restoration outcomes. *Rangeland Ecology & Management* **72**(2), 225–229.

Nauman TW, Kienast-Brown S, Roecker SM, Brungard C, White D, Philippe J and Thomson JA (2024) Soil Landscapes of the United States (SOLUS): Developing predictive soil property maps of the conterminous United States using hybrid training sets. *Soil Science Society of America Journal* **88**(6), 2046–2065.

Nolan MP, Luong JC, Valliere JM, Mazer SJ and D'Antonio CM (2023) Rethinking local seed sourcing for the restoration of a foundational grass species in California. *Restoration Ecology* **31**(8), e13992.

Omernik JM and Griffith GE (2014) Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. *Environmental Management* **54**(6), 1249–1266.

Penn CJ and Camberato JJ (2019) A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. *Agriculture* **9**(6), 120.

Piedallu C and Gégout J (2008) Efficient assessment of topographic solar radiation to improve plant distribution models. *Agricultural and Forest Meteorology* **148**(11), 1696–1706.

Plant Conservation Alliance [PCA] (2015) *National Seed Strategy for Rehabilitation and Restoration 2015–2020*. Washington, DC, Department of the Interior Bureau of Land Management, p. 50. https://www.blm.gov/programs/natural-resources/native-plant-communities/national-seed-strategy (accessed 11 January 2025).

Poorter L (2007) Are Species Adapted to Their Regeneration Niche, Adult Niche, or Both?. *Comparative Study* **169**(4), 433–442. https://doi.org/10.1086/512045.

Prober SM, Byrne M, McLean EH, Steane DA, Potts BM, Vaillancourt RE and Stock WD (2015) Climate-adjusted provenancing: A strategy for climate-resilient ecological restoration. *Frontiers in Ecology and Evolution* **3**(65), 1–5.

Pyke DA, Wirth TA and Beyers JL (2013) Does seeding after wildfires in rangelands reduce erosion or invasive species? *Restoration Ecology* **21**(4), 415–421.

Pywell RF, Bullock JM, Roy DB, Warman L, Walker KJ and Rothery P (2003) Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* **40**(1), 65–77.

Raabová J, Münzbergová Z and Fischer M (2011) The role of spatial scale and soil for local adaptation in Inula hirta. *Basic and Applied Ecology* **12**(2), 152–160.

Rajakaruna N (2004) The edaphic factor in the origin of plant species. *International Geology Review* **46**(5), 471–478.

Rajakaruna N (2017) Lessons on evolution from the study of edaphic specialization. *The Botanical Review* **84**(1), 39–78.

Ramcharan A, Hengl T, Nauman T, Brungard C, Waltman S, Wills S and Thompson J (2018) Soil property and class maps of the conterminous United States at 100-meter spatial resolution. *Soil Science Society of America Journal* **82**(1), 186–201.

Renne RR, Bradford JB, Burke IC and Lauenroth WK (2019) Soil texture and precipitation seasonality influence plant community structure in North American temperate shrub steppe. *Ecology* **100**(11), e02824.

Richards SA (2005) Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology* **86**(10), 2805–2814.

Rúa MA, Antoninka A, Antunes PM, Chaudhary VB, Gehring C, Lamit LJ, Piculell BJ, Bever JD, Zabinski C, Meadow JF, Lajeunesse MJ, Milligan BG, Karst J and Hoeksema JD (2016) Home-field advantage? evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. *BMC Evolutionary Biology* **16**(1), 122.

Rupprecht D, Hölzel N and Bucharova A (2021) Is there local adaptation in plant species to soil reaction? A lesson from a multispecies experiment. *Restoration Ecology* **29**(5), e13393.

Samuel EM, Mitchell RM, Winkler DE, Davidson ZM, Lencioni S and Massatti R (2024) Intraspecific trait variability in wild plant populations predicts neither variability nor performance in a common garden. *Restoration Ecology* **33**(6), e14322.

Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang HP, Harnik N, Leetmaa A, Lau NC, Li C, Velez J and Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* **316**(5828), 1181–1184.

Shackelford N, Paterno GB, Winkler DE, Erickson TE, Leger EA, Svejcar LN, Breed MF, Faist AM, Harrison PA, Curran MF, Guo Q, Kirmer A, Law DJ, Mganga KZ, Munson SM, Porensky LM, Quiroga RE, Török P, Wainwright CE, Abdullahi A, Bahm MA, Ballenger EA, Barger N, Baughman OW, Becker C, Lucas-Borja ME, Boyd CS, Burton CM, Burton PJ, Calleja E, Carrick PJ, Caruana A, Clements CD, Davies KW, Deák B, Drake J, Dullau S, Eldridge J, Espeland E, Farrell HL, Fick SE, Garbowski M, de la Riva EG, Golos PJ, Grey PA, Heydenrych B, Holmes PM, James JJ, Jonas-Bratten J, Kiss R, Kramer AT, Larson JE, Lorite J, Mayence CE, Merino-Martín L, Miglécz T, Milton SJ, Monaco TA, Montalvo AM, Navarro-Cano JA, Paschke MW, Peri PL, Pokorny ML, Rinella MJ, Saayman N, Schantz MC, Parkhurst T, Seabloom EW, Stuble KL, Uselman SM, Valkó O, Veblen K, Wilson S, Wong M, Xu Z and Suding KL (2021) Drivers of seedling establishment success in dryland restoration efforts. *Nature Ecology and Evolution* **5**(9), 1283–1290.

Shaheb MR, Venkatesh R and Shearer SA (2021) A review on the effect of soil compaction and its management for sustainable crop p roduction. *Journal of Biosystems Engineering* **46**(4), 417–439.

Sherrard ME, Joers LC, Carr CM and Cambardella CA (2015) Soil type and species diversity influence selection on physiology in Panicum virgatum. *Evolutionary Ecology* **29**(5), 679–702.

Sheth SN and Angert AL (2018) Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences* **115**(10), 2413–2418.

Shinoda Y and Akasaka M (2019) Species turnover differentiates diversity–disturbance relationships between aboveground vegetation and soil seedbank. *Plant Ecology* **220**(6), 595–603.

Shriver LC, Jordan SE, Massatti R and Munson SM (2025) Bridging theory and practice to inform seed selection for restoration. *Restoration Ecology* **33**(8), e70174.

Shryock DF, DeFalco LA and Esque TC (2018) Spatial decision-support tools to guide restoration and seed-sourcing in the Desert Southwest. *Ecosphere* **9**(10), e02453.

Shryock DF, Nila L, DeFalco LA and Esque TC (2024) Concordant signal of genetic variation across marker densities in the desert annual Chylismia

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brevipes is linked with timing of winter precipitation. *Evolutionary Applications* **17**(12), e70046.

Smith MD (2011) An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology* **99**(3), 656–663.

Soong JL, **Janssens IA**, **Grau O**, **Margalef O**, **Stahl C**, **Van Langenhove L**, **Urbina I**, **Chave J**, **Dourdain A**, **Ferry B**, **Freycon V**, **Herault B**, **Sardans J**, **Peñuelas J and Verbruggen E** (2020) Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. *Scientific Reports* **10**(1), 1–13.

St. Clair BJ, **Kilkenny FF**, **Johnson RC**, **Shaw NL and Weaver G** (2013) Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. *Evolutionary Applications* **6**(6), 933–948.

St. Clair JB, **Richardson BA**, **Stevenson-Molnar N**, **Howe GT**, **Bower AD**, **Erickson VJ**, **Ward B**, **Bachelet D**, **Kilkenny FF**, **Wang T** (2022) Seedlot Selection Tool and Climate-Smart Restoration Tool: web-based tools for sourcing seed adapted to future climates. *Ecosphere* **13**(5), e4089.

Stott P (2016) How climate change affects extreme weather events. *Science* **352**(6293), 1517–1518.

Tilman GD (1984) Plant dominance along an experimental nutrient gradient. *Ecology* **65**(5), 1445–1453.

Vandegehuchte ML, **De La Peña E**, **Breyne P and Bonte D** (2012) Non-local genotypes of a resident grass species reduce invertebrate species richness. *Insect Conservation and Diversity* **5**(6), 453–460.

Velazco SJE, **Galvão F**, **Villalobos F and De Marco P** (2017) Using worldwide edaphic data to model plant species niches: An assessment at a continental extent. *PLoS One* **12**(10), e0186025.

Wang T, **Hamann A**, **Spittlehouse D and Carroll C** (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One* **11**(6), e0156720.

Waples RS and Gaggiotti O (2006) INVITED REVIEW: What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology* **15**(6), 1419–1439.

Wheeler JA, **Hoch G**, **Cortés AJ**, **Sedlacek J**, **Wipf S and Rixen C** (2014) Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia* **175**(1), 219–229.

Williams AP, **Cook BI and Smerdon JE** (2022) Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. *Nature Climate Change* **12**(3), 232–234.

https://doi.org/10.1017/dry.2026.10031 Published online by Cambridge University Press