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RESEARCH ARTICLE

Can surface treatments and climate matching enhance restoration success in the Sonoran Desert?

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Abstract

Introduction: Restoring native plant communities in arid ecosystems through seeding is a critical yet often unsuccessful strategy due to severe environmental stressors, including degraded soils, low and variable rainfall, and seed predation.

Objectives: To improve restoration outcomes, we examined the influence of seed mix types and soil surface treatments on seeded and unseeded plant establishment across three Sonoran Desert sites, Arizona, United States.

Methods: Using a factorial design, we tested two seed mix types (cool versus warm adapted species) and four soil surface treatments (pits, mulch, connectivity modifiers or ConMods, and controls) on plant establishment. We examined if patterns of plant establishment could be predicted by whether the climate envelope of species in the seed mix types was similar to the site climate where they were seeded (climate matching). We monitored seeded and unseeded species establishment for 3 years and analyzed these effects using generalized linear mixed models and Tukey-adjusted multiple comparisons.

Results: Pit treatments significantly enhanced seeded species density by nearly 3× and cover by 2× compared with ConMods and increased unseeded plant density by 2× to 4× times during post-drought springs. During these same seasons, species suited to cooler temperatures (e.g. *Salvia columbariae* and *Lupinus sparsiflorus*) had higher cover at the site receiving the highest precipitation, and species suited to warmer temperatures (e.g. *Sphaeralcea ambigua* and *Senna covesii*) established better at the drier two sites.

Conclusions: In arid systems, surface treatments like pits that retain soil moisture were most promising for supporting seed-based restoration, and matching species that have high temperature tolerance with hotter, drier sites may enhance restoration success.

Implications for Practice: In arid environments, seeding success and native plant recruitment can be bolstered by surface modifications that increase water and litter capture, such as pits. Mulch also appeared to help seedling establishment but was highly variable; measures to ensure it stays in place may improve success. Managers may consider matching species climate envelopes of seed mixes with site climate, particularly for sites with extreme climates. Ultimately, site conditions, climatic uncertainty, and plant species traits should be integrated together into dryland restoration planning.

Key words: climate adaptation, climate matching, connectivity modifiers or ConMods, mulch, pits, seeding, Sonoran Desert

Introduction

Restoration in dryland ecosystems is particularly challenging due to high aridity and soils with low organic matter (Hardegee et al. 2016). Seed-based restoration is a commonly used approach for reintroducing plant species to a disturbed site (Bainbridge 2007). However, seeding often fails, either with no establishment or declines in seeded species over time in dryland regions (Shackelford et al. 2021). Seeds may not germinate or survive early establishment due to low rainfall, high temperatures, or soils with low nutrient availability and water-holding capacity (Anaya-Romero et al. 2015; Muñoz-Rojas et al. 2016). Two basic strategies may improve plant establishment in extreme environments, such as in the Sonoran Desert: climate matching seeded species with the site environment and modifying the environment to increase soil moisture retention and organic matter.

Author contributions: SL wrote the first draft, led the data analyses, and designed figures with JB and HIR; SMM designed the experiment; HIR, MF managed overall field treatments and sites; MF, JXB, DL, SF installed sites and data management; all authors revised and approved the final version of the manuscript.

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Using seeds adapted to local climates is recognized as a best practice to avoid maladaptation to local site conditions and seeds typically survive and perform better under historical climatic conditions (Keller et al. 2000; McKay et al. 2005; O'Brien et al. 2007). However, the traditional strategy of relying on local adaptation to select seed species may no longer be sufficient in the face of climate change. In response, the concept of “preadaptation” proposes incorporating climate-resilient genotypes or species suitable to future climate, which may create more resilient communities in the long term (Butterfield et al. 2017). Indeed, matching species' climate envelopes, or the range of climate conditions where a species occurs, with the climate at the site where it is seeded (climate matching) led to higher establishment success in the Colorado Plateau, United States (Balazs et al. 2020). As climate in the Southwest is expected to become warmer and more arid (Seager et al. 2007), increasing the use of species that have high heat and drought tolerance in seed mixes may help promote future plant establishment (Butterfield & Munson 2016).

A variety of soil surface treatments can improve outcomes in dryland restoration, including pits, mulch, and connectivity modifiers (ConMods). Pits are designed to increase soil moisture and microplot stability (Kabore & Reij 2004; Laushman et al. 2022; Farrell et al. 2023) and have been shown to enhance seedling emergence by up to three times compared to untreated controls, especially when cumulative precipitation post-seeding is high (Farrell et al. 2023). Pits are a traditional dryland agricultural practice used by the Native Americans of the Sonoran Desert, including the Hohokam culture (Hodgson 2001). Similar practices occur in other places in the world, for example, in West Africa where Zai pits have been shown to effectively increase agricultural yields in Burkina Faso, Niger, and Kenya, especially in conjunction with organic and inorganic amendments (Kabore & Reij 2004). Mulch increases soil moisture and provides seed and seedling protection (Kader et al. 2019) and facilitates seedling recruitment in dryland ecosystems like pit treatments (Hueso-González et al. 2017).

ConMods are small physical barriers made from wire hardware cloth that mimic nurse plants and are designed to retain litter, nutrients, and seeds as well as provide a favorable microclimate for seedlings (Okin et al. 2015). ConMods have been shown to increase the emergence of seedlings, especially when precipitation timing is favorable (Huxman et al. 2008; Fick et al. 2016). However, recent research results have revealed a lack of strong recruitment response with ConMods (Havrilla et al. 2020), while other studies have shown positive effects of ConMods on seedling recruitment in drylands (Okin et al. 2015; Fick et al. 2016). These differences indicate that site-level factors may be influential, such as whether there is a depositional environment for the ConMods to trap seed and litter. Treatment effectiveness for all restoration treatments may also depend on site characteristics like soil texture, exotic species competition, and precipitation timing (Farrell et al. 2023), indicating the need for site-specific restoration strategies. Surface treatments can increase the success of seeded species, but they may also promote natural recruitment of both native and non-native species from the seedbank and surrounding undisturbed plant community.

In 2018, 18 partnering organizations developed a distributed and coordinated restoration field trial network of 21 dryland sites—RestoreNet—that systematically tests soil surface treatments and seed mixes based on the climate tolerances of species (Havrilla et al. 2020; Farrell et al. 2023). We selected three Sonoran Desert RestoreNet sites, which represent the most extreme climate (Farrell et al. 2023) and likely the most challenging conditions in the network for restoration to collect additional data, allowing us to conduct new analyses of climate matching and soil surface treatment success for this region. The three sites represent a range of climate conditions and elevation within the northern Sonoran Desert. Unlike the overall RestoreNet network, treatments at our three Sonoran Desert sites were applied in the same season and used a consistent set of 16 species. This allowed us to directly compare how individual species responded to surface treatments under varying site conditions and test whether the individual species' climate envelopes predicted their performance. For species' climate envelopes, we employed MAT95 values, which are calculated based on the 95th percentile of mean annual temperature across a species' distribution (Havrilla et al. 2020). Species were then grouped into cool (locally adapted to historical climate) and warm (pre-adapted to warmer climate expected in the future) seed mix types based on their MAT95 values.

In particular, we had the following objectives and hypotheses: (1) *Seed mix types and soil surface treatments*: Compare the success of two 8-species seed mix types (locally adapted “cool” or pre-adapted “warm,” based on MAT95 values) and soil surface treatment on seedling establishment. Although this objective overlaps with the analysis conducted on the whole network (Farrell et al. 2023), we wanted to test whether the trends held at this extreme subset of sites. We hypothesized that seed establishment would be highest in the pit treatments due to water and litter catchment (H1). We expected that, at warmer sites, the warm seed mix with species adapted to warmer climates would establish better, and the cooler seed mix would establish better at cooler sites (H2). (2) *Climate matching*: Evaluate whether the performance of individual species is predicted by matching the species-specific climate envelope to the long-term average climate conditions of the sites. Since we used the same species across these three sites, we were able to conduct a new analysis of individual species based on their unique MAT95 values. We hypothesized that individual seeded species with higher MAT95 values would perform better across all sites and especially at the hotter, drier sites compared to the species with cooler MAT95 values (H3). (3) *Soil surface treatment effects on unseeded plant community*: Assess the response of the overall plant community recovery over time to soil surface treatments. We collected data on unseeded species at the whole-plot level that allowed us to assess treatment effects at a larger scale. As with seeded species establishment, we hypothesized that using pits as a surface treatment would have a greater effect on the overall plant community recovery than the other treatments (H4).

Methods

Study Sites

We selected three RestoreNet sites (Fig. 1E) that represent a gradient in climate and elevation in the Sonoran Desert, Arizona, United

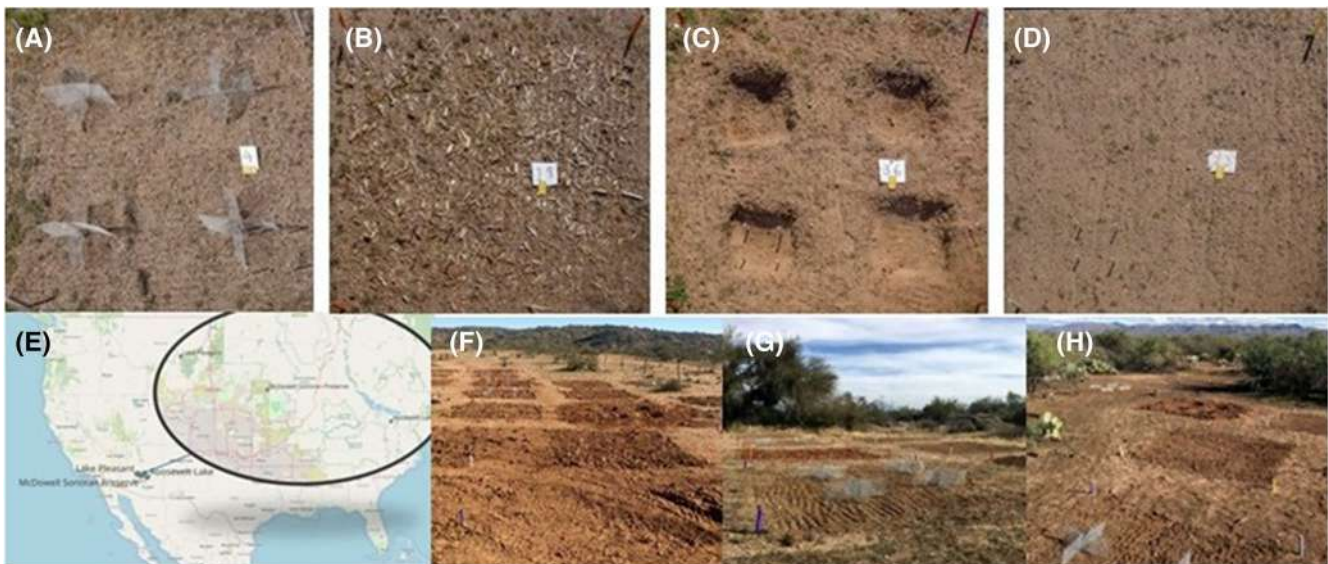


Figure 1. RestoreNet surface treatments and sites. Surface treatments include seeding with (A) connectivity modifiers (ConMods), (B) mulch, (C) pits, and (D) seed only control (photos taken 1/31/2020 by Jane Brady and Debbie Langefeld). Site locations in the northern Sonoran Desert, Arizona, United States, are shown on a (E) map (basemap from <https://www.openstreetmap.org>) and with photos of the three site installations at (F) Lake Pleasant on 12/19/2019, (G) McDowell Sonoran Preserve on 25 November 2019, and (H) Roosevelt Lake on 22 November 2019 (photo credit: Mary Fastiggi).

States (Table S1). Site mean annual precipitation (MAP) ranges from 286 to 401 mm; mean annual temperature (MAT) ranges from 20.1 to 21.8°C (1991–2020; PRISM Climate Group 2021, Oregon State University, <https://prism.oregonstate.edu>); and elevation ranges from 532 to 793 m above sea level (Table S1). Sites receive between 25.8 and 30.2% of their annual precipitation from the warm season (July–September) North American Monsoon (monsoon). All sites were potential desert scrub plant communities (based on a compilation of Landfire terrestrial vegetation subclasses [<https://landfire.gov/evt.php>] and observations of nearby undisturbed sites). The soil texture of all three sites is sandy loam (United States Department of Agriculture classification) at 0–10 cm depth. RestoreNet sites were initially disturbed by wildfire (Roosevelt Lake) or vehicle/ft traffic (Preserve and Lake Pleasant). The soil series are Typic Haplargids, Ustic Haplocambids, and Ustic Calcicargids, warm thermic basins and fan remnants in the Roosevelt Lake site; Gran-Wickenburg-Rock outcrop complex, 10–65% slopes at McDowell Sonoran Preserve; and Continental gravelly sandy loam, 2–15% slopes at Lake Pleasant. Despite having different disturbance types, disturbances had a similar degree of severity and influence on the initial conditions across sites in that they all had low initial native perennial plant cover (<5%), intact soil horizons and surface integrity, and the potential to support a perennial native plant community. We acknowledge that differences in initial site disturbance might have influenced restoration outcomes in ways that we were not otherwise able to control. To homogenize initial plant and soil conditions across sites, we removed all existing vegetation from treatment plots using hand tools prior to site installation (Laushman et al. 2022). To further minimize the potential for differences among initial site conditions, we installed each site on a flat area (<1% slope) and raked each plot into a homogenous soil surface prior to applying a treatment.

The annual precipitation in 2020 at all three sites was below the 30-year average from 1991 to 2020 (Table S2). Annual precipitation at Lake Roosevelt remained below normal in 2021. Winter precipitation across these sites was lowest in 2020 and has been gradually recovering since, though it has not yet returned to 2019 winter levels. Monsoon precipitation showed the same trend in 2020 as winter precipitation, but in the following year, 2021, it exceeded monsoon normal levels at all three sites.

Experimental Design and Treatments

Restoration treatments were applied in late 2019 to three sites using the same installation protocol as the RestoreNet network (Laushman et al. 2022). A factorial experimental design was implemented to evaluate the effects of restoration surface treatments and seed mix types on plant establishment. The four surface treatments included (Fig. 1): (1) no surface treatment (control); (2) ConMods; (3) mulch spread to loosely cover over the soil surface (mulch); and (4) four pits dug 10 cm deep and 40 × 40 cm wide, one in each quadrant equidistant from each other (pits) (Laushman et al. 2022).

Each surface treatment was applied in combination with two different seed mix types, resulting in eight unique treatment combinations. These 8-species seed mix types (warm, cool) were composed of species native to the region and listed on the flora list of the McDowell Sonoran Preserve, except *Bouteloua barbata* var. *rothrockii*, which was found nearby (SEINet 2025). The MAP and MAT of the Preserve are close to the mean MAP and MAT of the three sites. The selected 16 species, which included grasses, forbs, and shrubs, were divided into warm or cool seed mix types based on the species'

climate envelope (the 95th percentile of MAT across a species' global distribution, MAT95) obtained from occurrence records (Butterfield et al. 2017; Havrilla et al. 2020) (Table 1). The climate envelope (MAT95) of the cool seed mix ranged from 21.7 to 22.9°C, and the warm season mix climate envelope ranged from 23.5 to 24.9°C (Table 1). The MAT of the sites all fell below or within the range of the cool season mix climate envelope range; thus, this mix represents species adapted for current/historic conditions. The range of the warm season mix climate envelope is above the site MAT; thus, this mix represents species adapted for hotter conditions. Therefore, the warm seed mix, with a hotter temperature niche, was expected to perform better in a slightly warmer and drier climate than the historical site climate and at the hotter sites (Lake Pleasant and the McDowell Sonoran Preserve).

Plots were seeded at a seeding rate recommended by the seed company for each species (Table 1). Seeds were purchased from Armenta Seed Company (Gilbert, AZ, U.S.A.), and any recommended pre-treatments to break dormancy were applied. The seed was broadcast by hand following the installation of the soil surface treatment. Four replicate plots were established for each surface treatment × seed mix combination, yielding a total of 32 plots within the factorial design. In addition to the factorial combinations, four control plots that received no seeding or other treatment were included to serve as a baseline for

comparison with the unseeded plant community. In total, the experimental setup comprised 36–2 m × 2 m permanently marked plots per site. In each plot, a 25 cm × 25 cm permanently marked subplot was established using a standardized protocol (Laushman et al. 2022). This smaller monitoring subplot area was designated to closely track plant emergence and growth, which would have been difficult within the much larger plot area.

Data Collection

Following treatment installation, we monitored seedling recruitment at each RestoreNet site twice annually from spring 2020 to spring 2022, both within each subplot and at the whole-plot scale, except for fall 2020, which followed a dry monsoon season and little to no plants emergence in the plots. For each subplot, we measured density as the count of seedlings (first season) or seedlings or plants (after the first season) of each species that appeared above the soil surface at each monitoring visit at each site. To calculate native and non-native unseeded plant density, we summed plant densities for individual species according to their native status. At the whole-plot scale, we estimated (1) plant cover for each individual seeded species, using 10 cover classes (Peet et al. 1998) and converted to midpoints of the cover classes for analysis; and (2) total plant cover (including both

Table 1. RestoreNet seeded species name and seed mix type, common name with plant lifespan (abbreviations in bold: Annual, Perennial), and growth form (Forb, Grass, Shrub, Legume), flowering season, 95th percentile of mean annual temperature across a species' distribution (MAT95), seeding rate, and sum of seedlings across subplots for each monitoring period. (Butterfield et al. 2017; Havrilla et al. 2020). Seeding rate was obtained from seed vendors and internet research (upper threshold), then adjusted for purity and the size of the 4 m² plot. Flowering season indicates months of peak flowering (forbs, <http://southwestdesertflora.com>). Seeding numbers in bold represent species that were fewer than 10 seedlings and were not included in the analysis for that season.

Species name	Common name (lifespan, and growth form)	Flowering season	MAT95	Seeding rate (g/plot)	Sum seedlings		
					First spring season 2020	Post-drought fall season 2021	Post-drought spring seasons 2021–2022
Cool seed mix							
<i>Salvia columbariae</i>	Chia (A-F)	Mar–May	21.66	1.84	219	2	70
<i>Lupinus sparsiflorus</i>	Coulter's lupine (P-F)	Jan/Feb–May	21.75	5.93	100	0	32
<i>Baileya multiradiata</i>	Desert marigold (P-F)	Mar–Nov	21.8	0.90	31	0	1
<i>Digitaria californica</i>	Arizona cottontop (P-G)	Mar–Nov	22.87	2.36	17	0	26
<i>Sphaeralcea</i> <i>ambigua</i> subsp. <i>ambigua</i>	Apricot globemallow (P-S)	Jan–Dec	22.94	1.92	2	2	9
<i>Sporobolus cryptandrus</i>	Sand dropseed (P-G)	May–Nov	19.65	0.91	0	0	0
<i>Muhlenbergia porteri</i>	Bush muhly (P-G)	Apr–May	20.86	1.41	0	0	0
<i>Ambrosia deltoidea</i>	Triangle-leaf bursage (P-S)	Apr/May–Nov/Dec	22.89	2.27	0	0	0
Warm seed mix							
<i>Aristida purpurea</i> var. <i>purpurea</i>	Purple threeawn (P-G)	Apr–Oct	23.46	2.95	10	0	1
<i>Plantago ovata</i>	Desert indianwheat (A-F)	Jan–May	23.5	4.57	326	0	32
<i>Senna covesii</i>	Coues' senna (A-L)	Apr–Oct	23.83	6.29	6	13	8
<i>Bouteloua barbata</i> var. <i>rothrockii</i>	Rothrock Grama (P-G)	May–Sep	24.2	0.95	0	58	0
<i>B. aristoides</i>	Needle grama (P-G)	Jan–Dec	24.88	1.37	0	13	0
<i>B. curtipendula</i>	Sideoats grama (P-G)	Jun–Nov	23.06	4.19	0	0	0
<i>Encelia farinosa</i> var. <i>farinosa</i>	Brittlebush (P-S)	Feb–May; Aug–Sep	23.41	1.05	0	0	0
<i>Calliandra eriophylla</i>	Fairyduster (P-L)	Feb–April/May; Sep; Oct	23.97	2.25	0	0	0

seeded and unseeded species) estimated as a single percentage. The integrity of the soil surface treatments was noted for each plot at each monitoring visit (e.g. % mulch remaining) but was not amended.

Data Analysis and Preparation

Modeling and Statistical Analysis. To address the three research questions, separate generalized linear mixed models (GLMM) were created to assess the effects of seeds and surface treatments on seeded and unseeded plant species establishment across our three study sites over the 3 years of the study (specific models described below). To best understand the results at different stages of establishment and stages of the study, we separated the analysis into the first and post-drought seasons, due to the extreme drought period in summer/fall 2020. We further separated the post-drought spring and fall seasons because of the different species composition seen in our plots in these seasons. As a result, we analyzed datasets separately for the first season germination and emergence (spring 2020), post-drought spring seasons (spring 2021 and spring 2022), and post-drought-fall (fall season 2021).

Spatial environmental variables (elevation, soil texture, MAP, and MAT) and temporal environmental variables (cumulative precipitation since seeding and since the last sampling event, and total precipitation) were collected as potential covariates for analysis. All environmental data were extracted from PRISM (Prism Climate Group 2021, Oregon State University, <https://prism.oregonstate.edu>). These variables were selected to comprehensively capture influences on seedling establishment, growth, and survival across spatial and temporal gradients. Predictor variables for the models' fixed effects were selected based on univariate analyses and Akaike Information Criterion (AIC) rankings for the first season. Each predictor was looped through the univariate GLMM independently, and the best-performing variables (with relatively lower AIC value) were incorporated into models. Since the dataset was analyzed separately for spring and fall in the post-drought seasons, univariate analyses were also conducted separately for spring and fall to ensure that the selected predictor variables were season-specific.

Q1. Seed Mix Types and Soil Surface Treatments. We analyzed the density count data using a GLMM with a negative binomial distribution and log link function to account for overdispersion with three fixed factors: site (three levels: Lake Pleasant, Preserve, and Roosevelt), surface treatment (four levels: ConMod, mulch, pits, and seed only), and seed mix (two levels: cool and warm). Post-drought spring models also included year as fixed effects. All fixed effect interactions were included in all models but removed if not significant. We included site and plot nested within site as a random effect. The GLMM explicitly accounts for spatial dependencies of the random effects included in each model by modeling the variability between and within each site by estimating a random intercept for each site and covariance between the plot measurements. A zero-inflated

negative binomial distribution was used in the subplot seeded species density model for the post-drought fall season to correct for overdispersion and excess zeros in the density count data. All fixed effect interactions were included in all models but removed if not significant. Post hoc comparisons were conducted using Tukey-adjusted multiple comparisons.

Q2. Climate Matching Analysis. Species with fewer than 10 seedlings were removed from the data used for the plant cover models for the season in which they were below the threshold (Table 1). The analyzed dataset included only species that emerged in their expected/seeded plots. The species-specific model was the same as above, except instead of seed mix, we included the species climate envelope (MAT95) as a continuous fixed effect. Random effects in the model were site and plot nested in site, except for the pre-drought season plant cover model, in which the random effect was plot nested in site.

Q3. Soil Surface Treatment Effects on Unseeded Plant Community. The same modeling procedure was followed to assess the effect of surface treatment on the unseeded plant community, except that fixed factors only included site, surface treatments, and in the post-drought spring model, year was also included. The zero-inflated negative binomial distribution was applied except in the subplot native seedling density model of post-drought fall season and the whole-plot total plant cover models of all seasons. Random effects were site and plot.

All analyses were performed in R (version 4.4.0; R Core Team 2024). Data preparation and filtering were performed using the dplyr and tidyverse packages (Wickham et al. 2023). GLMM was performed using the glmmTMB package (McGillucuddy et al. 2025), while ggplot2 (Wickham 2016) and sjPlot (Lüdtke et al. 2024) were employed for model visualization and statistical summaries to identify the best-fit models. The car package was used to perform analysis of variance to assess the significance of model terms and provide statistical support for model comparisons. Post hoc pairwise comparisons were performed by the emmeans package, and Tukey-adjusted multiple comparisons were performed by the multcomp package.

Results

Q1. Seed Mix Types and Soil Surface Treatments

Surface Treatments (H1). In the post-drought spring seasons, the pit surface treatment improved seeded plant density and cover, compared to ConMod and seed only controls (Table 2, Fig. 2C & 2D). The pairwise comparisons of surface treatments of seeded plant density, averaged over year, are as follows (a ratio of 2.88 means that the numerator is 2.88 times more than the denominator): Pits/ConMod, ratio = 2.88, $p = 0.002$; Pits/Seed only, ratio = 1.99, $p = 0.042$ (for all ratio comparisons, refer to Table S3). The pairwise comparisons for plant cover are: Pits/ConMod, ratio = 1.76, $p = 0.037$; Pits/Seed only, ratio = 1.90, $p = 0.018$ (Table S4). For the first and post-drought spring seasons, we did not detect a difference in

Table 2. Results of generalized linear mixed models (GLMMs) analyses on a full factorial model of site (Lake Pleasant, Preserve, and Roosevelt), seed mix (cool and warm), surface treatments (ConMod, mulch, pits, and seed only), and year (post-drought spring seasons only) and their interactions on seeded plant density and cover. Models were run separately for three time periods: first spring season (spring 2020), post-drought fall season (fall 2021), and post-drought spring seasons (spring 2021 and spring 2022). Random effects in the model were site and plot nested within site. Bold font highlights significant effects; dash indicates that the factor was not included in the model; no results indicate interactions that were removed from models because they were not significant. *df*, degrees of freedom.

Response variables	Fixed factors									
	Site (df = 2)		Seed (df = 1)		Surface (df = 3)		Year (df = 1)		Interactions: Site × seed (df = 2)	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
First season										
Seeded species density	4.06	0.131	15.95	<0.001	1.50	0.683	—			
Seeded species cover	4.34	0.114	34.20	<0.001	0.29	0.961	—			
Post-drought fall season										
Seeded species density	28.73	<0.001	0.56	0.453	6.26	0.099	—	7.30	0.026	
Seeded species cover	40.26	<0.001	7.29	0.007	3.87	0.276	—			
Post-drought spring seasons										
Seeded species density	3.03	0.219	22.11	<0.001	15.71	0.001	21.33	<0.001		
Seeded species cover	3.88	0.144	17.69	<0.001	11.50	0.009	11.22	<0.001		

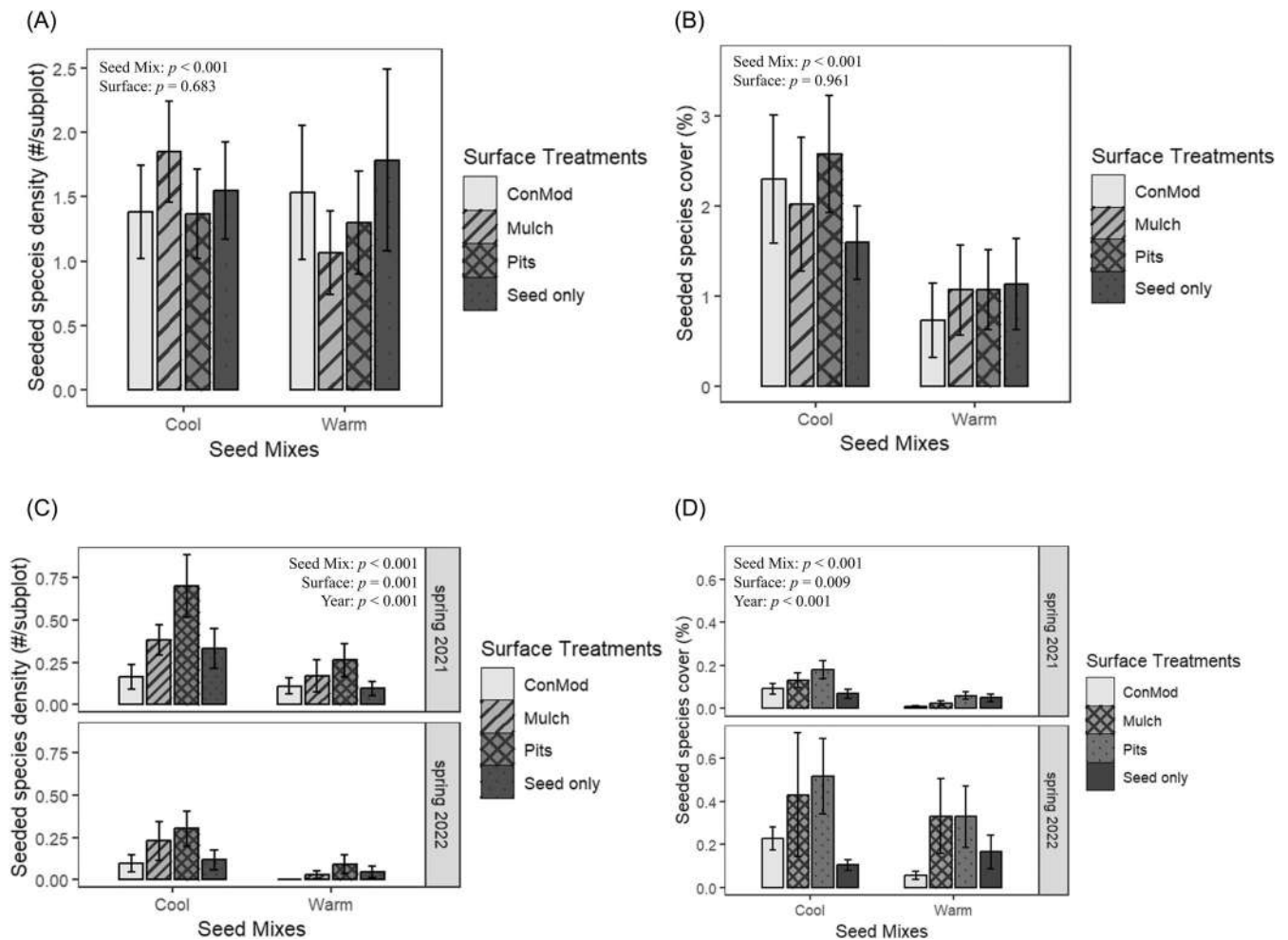


Figure 2. Mean plant density (A) and cover (B) of seeded species with cool and warm seed mix types in the first season and mean plant density (C) and cover (D) of seeded species with cool and warm seed mix types and surface treatments in the post-drought spring seasons (spring 2021 and spring 2022). Bars represent ± 1 SE of the mean. Only *p* values for the treatments included in the figures are shown; for full model output see Table 2. (A, B) Spring season 2020. (C, D) Post-drought spring seasons.

plant density or cover among surface treatments (Table 2; Fig. 2).

Seed Mix Types (H2). Seeded plant density and cover differed between seed mix types in all seasons, but the effects on plant density depended on site in the post-drought fall season (Table 2). In the first and post-drought spring seasons, the cool seed mix resulted in higher seeded plant density and cover than the warm seed mix (Table S5–S8; Fig. 2). By contrast, in the post-drought fall season, the warm seed mix had 1.57 times more plant cover than the cool seed mix (Table S9, warm/cool, ratio = 1.57, $p = 0.007$).

In the post-drought fall season, the effect of seed mix type on seeded plant density depended on its interaction with site (Table 2, $\chi^2 = 7.29$, $p = 0.026$). Both warm and cool seed mix types had the highest seeded plant density in Preserve (Table S10). At Lake Pleasant, the warm seed mix resulted in the lowest plant density, but there were no differences detected between the sites for the cool seed mix (Table S10).

Q2. Climate Matching (H3)

Plant Density. The species' climate envelope (MAT95) significantly influenced seeded species density in all seasons, with effects depending on site for the first season and post-drought fall season (Table 3). In the first season, seeded species with higher MAT95 (e.g. *Plantago ovata*) had higher density than lower MAT95 species at the Lake Pleasant and Roosevelt sites, but seeded species with low MAT95 (e.g. *Salvia columbariae*) had higher density than high MAT95 species (e.g. *P. ovata*) at the Preserve site (interaction effect, Table 3; Fig. 3A). In the post-drought fall season, seeded species with high MAT95 (e.g. *Bouteloua barbata* var. *rothrockii*, *B. aristoides*, and *Senna covesii*) had higher density than low MAT95 species at the Preserve and

Roosevelt sites (Table 3; Fig. 3C). In the post-drought spring seasons, species with low MAT95 had higher density than those with high MAT95 (Table 3; Fig. 3E).

Plant Cover. In the first season, seeded species with low MAT95 had higher cover than those with high MAT95 (Table 3; Fig. 3B), reflecting the finding that the cool seed mix did better than the warm mix (Fig. 2A & 2B). In the post-drought fall season, seeded plant cover was much higher at the Preserve site than the other sites, largely driven by high *B. barbata* var. *rothrockii* cover (Table S11; Fig. 3D; Preserve/Pleasant, ratio = 5.95, $p < 0.0001$; Preserve/Roosevelt, ratio = 2.61, $p = 0.001$). In the post-drought spring seasons, the effect of species climate envelope (MAT95) on plant cover depended on site (Table 3). Species with high MAT95 (e.g. *Sphaeralcea ambigua* and *S. covesii*) established better at Lake Pleasant and Roosevelt, and species with low MAT95 (e.g. *Lupinus sparsiflorus*) established better at the Preserve site (Fig. 3F).

Across all seasons, of the three species with the highest density and cover, two had the lowest MAT95 values (*Salvia columbariae* and *L. sparsiflorus*), and one had the highest MAT95 values (*P. ovata*) of the seed mix species (Fig. 3).

Q3. Soil Surface Treatment Effects on Unseeded Plant Community (H4)

Native Plant Community (Unseeded). During the first season, ConMods had significantly higher unseeded native plant density than pits, but not compared with seed only controls (ConMod/Pits, ratio = 2.79, $p = 0.013$; ConMod/Seed only, ratio = 1.75, $p = 0.589$; Table S12; Fig. 4A); the rest of the surface treatment pairwise comparisons were not significantly different. In the post-drought spring seasons, the Preserve site exhibited significantly higher unseeded native plant density compared to the other

Table 3. Results of generalized linear mixed models analyses on a full factorial model of site (Lake Pleasant, Preserve, and Roosevelt), surface treatments (Con-Mod, mulch, pits, and seed only), MAT95 (95th percentile of mean annual temperature across a species' distribution), and their interactions on subplot seeded species density and seeded species whole-plot cover. Interactions were removed if they were not significant. Models were run separately for three time periods: first spring season (spring 2020), post-drought fall season (fall 2021), and post-drought spring seasons (spring 2021 and spring 2022). Random effects in the model were site and plot nested in site, except the pre-drought season seeded species whole-plot cover model only included plot nested in site as a random effect. Bold font highlights significant effects; dash indicates that the factor was not included in the model; no results indicate interactions that were removed from models because they were not significant. *df*, degrees of freedom.

Response variables	Fixed factors							
	Site (df = 2)		Surface (df = 3)		MAT95 (df = 1)		Interaction: Site × MAT95 (df = 2)	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p
First season								
Seeded species density	16.15	<0.001	2.24	0.524	6.41	0.011	15.63	<0.001
Seeded species cover	7.33	0.026	0.48	0.924	27.14	<0.001		
Post-drought fall season								
Seeded species density	7.97	0.019	4.39	0.222	0.02	0.896	8.95	0.011
Seeded species cover	34.02	<0.001	1.16	0.764	7.65	0.006		
Post-drought spring seasons								
Seeded species density	0.52	0.771	10.19	0.017	13.71	<0.001	0.61	0.737
Seeded species cover	8.31	0.016	9.42	0.024	0.31	0.575	8.35	0.015

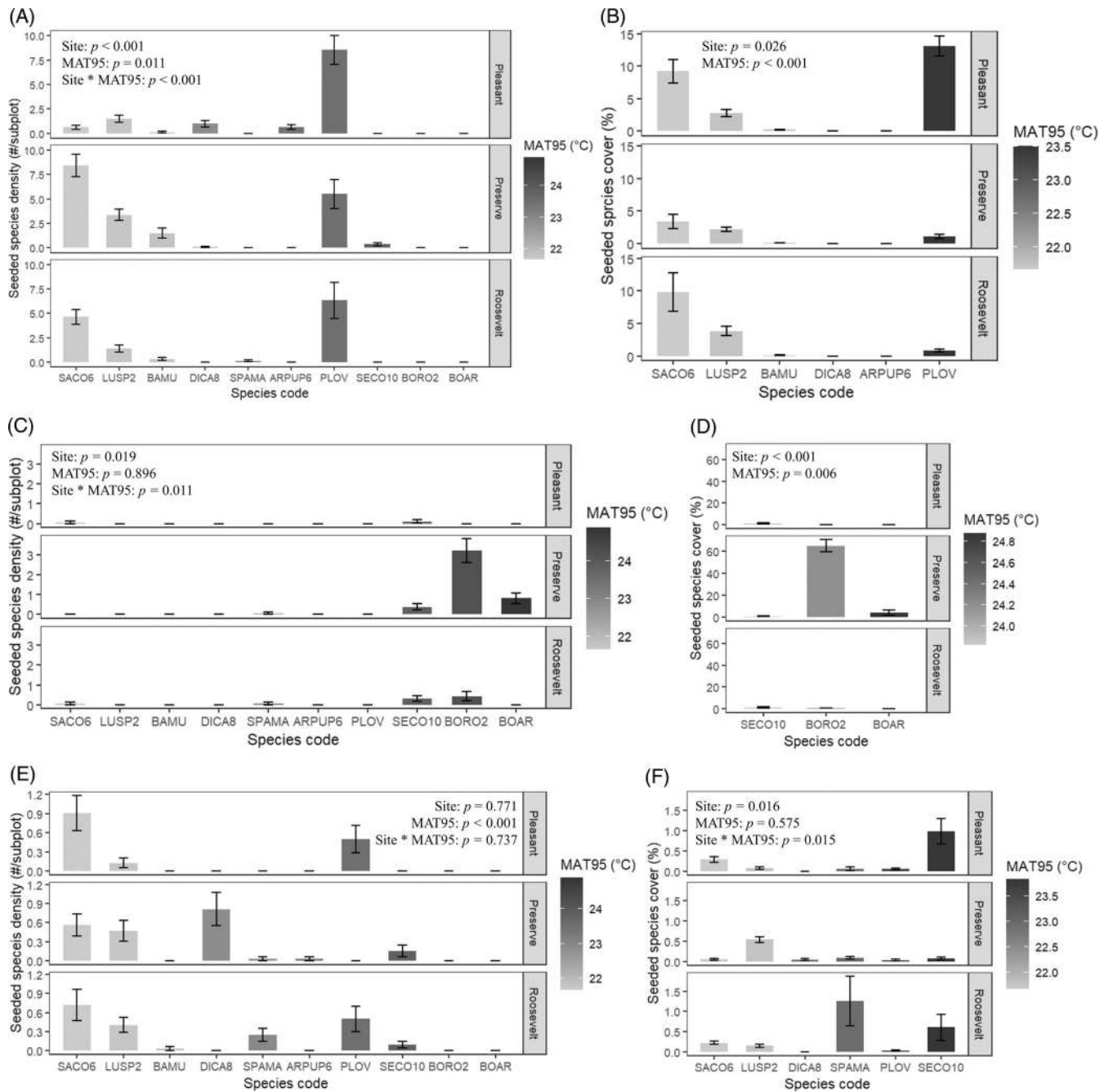


Figure 3. Mean plant density and cover of seeded species at each study site in the first spring season 2020; (A, B), post-drought fall season (C, D), and the post-drought spring seasons (E, F) by MAT95 (95th percent). The species order and sites are arranged from lowest (Lake Roosevelt) to highest site MAT (Lake Pleasant). Note that species were not included in the analysis as individual species, but represented by their climate envelope (MAT95) as a continuous variable represented by the grey to black color gradient in the figure. We include species names to correspond with the MAT95 as follows: *Salvia columbariae* (SACO6), *Lupinus sparsiflorus* (LUSP2), *Baileya multiradiata* (BAMU), *Digitaria californica* (DICA8), *Sphaeralcea ambigua* (SPAMA), *Aristida purpurea* (ARPUP6), *Plantago ovata* (PLOV), *Senna covesii* (SECO10), *Bouteloua barbata* var. *rothrockii* (BORO2), *B. aristoides* (BOAR). Bars represent ± 1 SE of the mean. Only p values for the treatments included in the figures are shown; for the full model output see Table 3.

two sites, depending on the surface treatment (site \times surface treatment interaction: Tables 4 & S13; Fig. 4E). Pairwise comparisons indicated that surface treatment ConMod, mulch, seed only, and control had the highest native plant density in the Preserve

site, compared to the other two sites (Table S13; Fig. 4E). In the pit treatments, native plant density in the Preserve site was 2.1 times higher than the Lake Pleasant site (Table S13; Fig. 4E; Preserve/Pleasant, ratio = 2.14, $p = 0.003$), but there was no

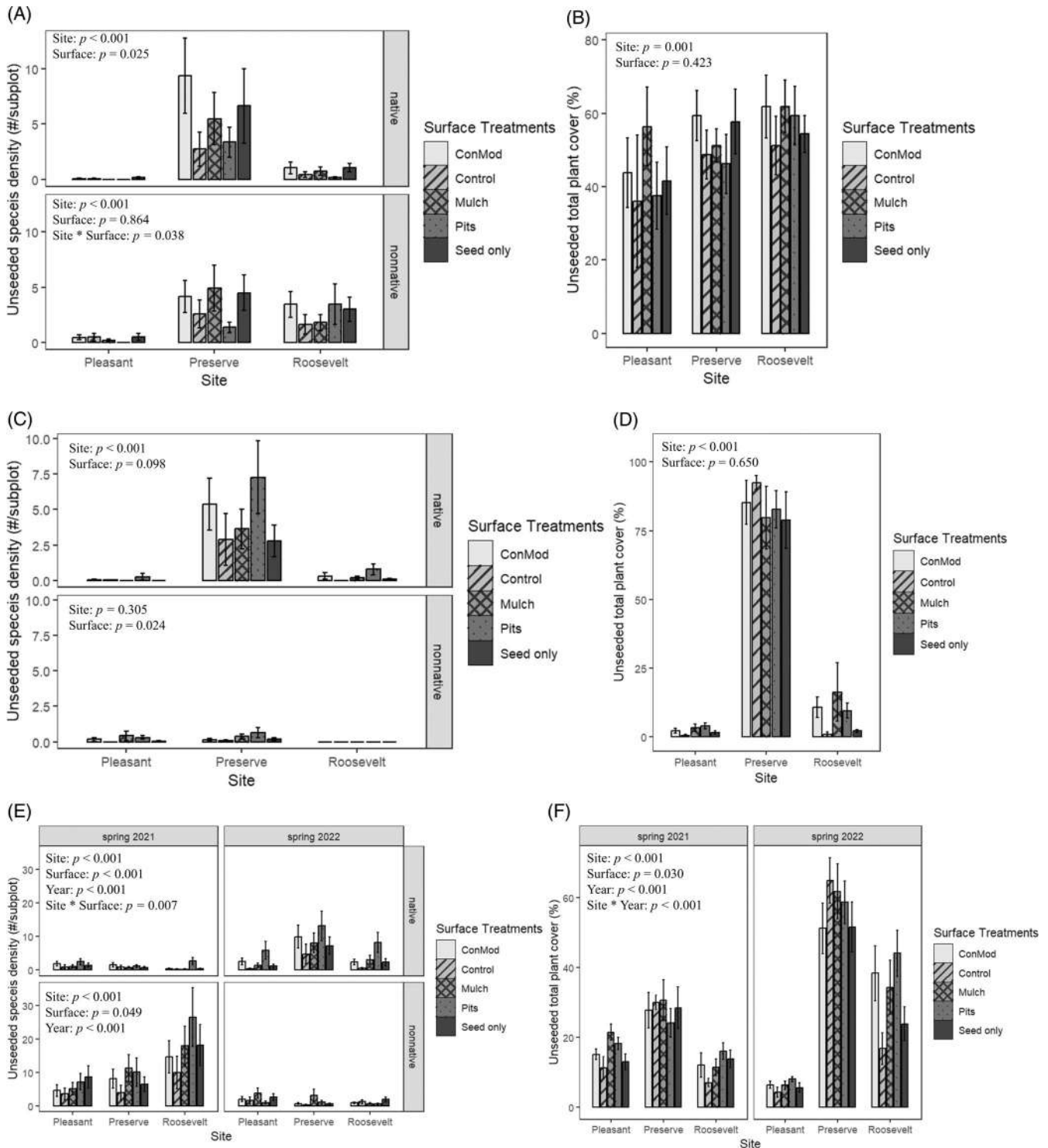


Figure 4. Unseeded total plant density and total plant cover by site and surface treatment in the first spring season 2020 (A, B); the post-drought fall season 2021 (C, D), and post-drought spring seasons 2021 and 2022 (E, F). Bars represent ± 1 SE of the mean. Only p values for the treatments included in the figures are shown; for full model output see Table 4.

significant difference between the Preserve and Roosevelt sites (Table S13; Fig. 4E; Preserve/Roosevelt, $p = 0.352$). When averaged over site, unseeded native plant density was highest

in pits compared with all the other surface treatments (Tables 4 & S14). Pits had 2.0 times higher unseeded native plant density than ConMod (Table S14; Pits/ConMod,

Table 4. Results of generalized linear mixed models on a full factorial model of site (Lake Pleasant, Preserve, and Roosevelt), surface treatments (ConMod, mulch, pits, seed only control, and unseeded control), and their interactions on unseeded native and non-native plant density and total plant cover. Interactions were removed if they were not significant. Models were run separately for three time periods: first spring season (spring 2020), post-drought fall season (fall 2021), and post-drought spring seasons (spring 2021 and spring 2022). Random effects in the model were site and plot. Bold font highlights significant effects; dash indicates that the factor was not included in the model; no results indicate interactions that were removed from models because they were not significant. *df*, degrees of freedom.

Response variables	Fixed factors									
	Site (df = 2)		Surface (df = 4)		Year (df = 1)		Interaction: Site × surface/year			
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	df	
First season										
Native seedling density	83.60	<0.001	11.15	0.025	—	—	—	—	—	—
Non-native seedling density	14.34	<0.001	1.28	0.864	—	—	Surface: 16.33	0.038	8	8
Total plant cover	13.69	0.001	3.88	0.423	—	—	—	—	—	—
Post-drought fall season										
Native seedling density	24.73	<0.001	7.82	0.098	—	—	—	—	—	—
Non-native seedling density	2.38	0.305	11.25	0.024	—	—	—	—	—	—
Total plant cover	301.41	<0.001	2.47	0.650	—	—	—	—	—	—
Post-drought spring seasons										
Native seedling density	25.43	<0.001	19.38	<0.001	136.79	<0.001	Surface: 21.12	0.007	8	8
Non-native seedling density	104.36	<0.001	9.55	0.049	244.82	<0.001	—	—	—	—
Total plant cover	48.67	<0.001	10.70	0.030	33.56	<0.001	Year: 102.89	<0.001	2	2

ratio = 2.00, $p = 0.0002$), 2.48 times higher than mulch (Table S14; Pits/Mulch, ratio = 2.48, $p < 0.0001$), 2.75 higher than seed only control and 4.31 times higher than control (Table S14; Pits/Seed only, ratio = 2.75, $p < 0.0001$; Pits/control, ratio = 4.31, $p < 0.0001$).

Non-Native Plant Community. For the first season, the differences in non-native plant establishment depended on the interaction between site and surface treatment. In the mulch treatment, non-native plant density was highest at the Preserve compared to the other two sites (Tables 4 & S15; Fig. 4A; Mulch: Preserve/Pleasant, ratio = 18.12, $p = 0.0002$; Preserve/Roosevelt, ratio = 2.62, $p = 0.005$), but non-native plant density with pit treatments was highest in the Roosevelt compared to the Preserve site (Tables 4 & S15; Fig. 4A; Pits: Roosevelt/Preserve, ratio = 2.44, $p = 0.028$). In the post-drought fall season, non-native seedling density was significantly different among surface treatments (significant main effect); however, the effect was not strong enough to be detected in Tukey's post hoc comparisons (Tables 4 & S16).

In the post-drought spring seasons, pits supported a higher unseeded non-native plant density than ConMod, but not seed only controls (Table S17; Fig. 4E; Pits/ConMod, ratio = 1.45, $p = 0.019$; Pits/Seed only, ratio = 1.21, $p = 0.473$), with no significant difference among other treatments. In the fall season, although there was a significant surface treatment main effect for total plant cover (Table 4), the post hoc comparisons were not significant (Table S18).

Discussion

Our study showed that the establishment of seeded and unseeded species at disturbed sites in the Sonoran Desert was affected by restoration surface treatments, seed mix

types, site-specific factors, and seasonality. These findings answer our three research questions and four hypotheses: (1) pits significantly improved seeded species density and cover in post-drought spring seasons, particularly in cooler and wetter settings, supporting H1. Generally, the cool seed mix established better, except in the fall season, disproving H2 that the warmer seed mix would perform better, especially at warmer sites. These results align with RestoreNet's broader findings on microtopography effects and success with locally adapted cool seed mixes (Farrell et al. 2023); (2) species' climate envelopes (MAT95) partly predicted performance: in the first season, species with warmer climate envelopes had higher subplot density at the warmest site, Lake Pleasant (support for H3). However, in the post-drought seasons, this general trend did not persist. Instead, the phenology and other attributes of the individual species may better explain the trends among seasons and sites; and (3) the unseeded plant community also increased with the Pit treatment (support for H4), with the Preserve site consistently supporting the highest native plant productivity. Together, these results emphasize the importance of aligning treatment strategies and plant species attributes with site-specific and seasonal conditions in arid land restoration, and offer partial support for the use of species' climate envelopes as a trait that can be used to match to site climate for predicting establishment success.

Surface Treatments

Among all surface treatments, pits most improved seeded species density and cover, and the unseeded native and non-native subplot plant density, by the end of the study (post-drought spring seasons). This benefit was most significant when compared to ConMods and Seed only treatments. Pits likely enhanced establishment by capturing moisture and protecting

seeds from environmental stress (Rader et al. 2022), which is especially advantageous in arid lands. Recruitment of non-native species also increased with the pit treatments, but this may not be expected because conditions that promote native plants can also support non-native plants (Stohlgren et al. 2003).

Other surface treatments had mixed results; for instance, mulch performed similarly well to pits for all sites in the post-drought spring season, but was not distinct in effectiveness compared with ConMods, due to high variance in success. The high variability in seedling establishment in the mulch treatment was likely exacerbated by the mulch becoming depleted over time (Havrilla et al. 2020; Farrell et al. 2023). In the Sonoran Desert, others have found mulch to be effective for increasing plant cover, soil moisture, and decreasing soil temperature in the form of straw (Fehmi & Kong 2012), and mesquite branches (Leger et al. 2022). However, woodchips applied on the surface, similar to our study, did not affect plant cover but did increase soil organic carbon (Espinosa et al. 2020). ConMods, though effective in earlier RestoreNet studies, showed weaker or inconsistent effects in our subset analysis. ConMods had a high unseeded native seedling emergence in the first monitoring season. This may be explained by initial treatment disturbance in which the seed bank was removed from the pits, but not the area under the ConMods. Favorable rainfall in winter 2019 preceding the first sampling season may have fostered reestablishment of the unseeded plant community in less disturbed plots. ConMods were designed to help capture litter and seed (Fick et al. 2016; Havrilla et al. 2020) and provide shade that may reduce evaporation. However, these effects were not enough to foster establishment of the seed mixes, particularly in the drier periods of the study. A prior RestoreNet analysis of a subset of seven Arizona sites, not including ours (Havrilla et al. 2020), also reported poor recruitment response with ConMods, even with above-average precipitation (Havrilla et al. 2020). The contrast of these findings with earlier studies demonstrating the success of ConMods may indicate that effects increase in depositional environments, in which sediment, litter, and seed are brought into the site by wind or water and trapped by the wire mesh. These surface treatment results are broadly consistent with prior analysis of the full RestoreNet network, including our sites (Farrell et al. 2023), indicating that the best-performing treatment, pits, consistently perform well for promoting seedling and plant community establishment.

Seedlings at the Preserve site established particularly well with all surface treatments, especially in pits, and were generally the most productive site overall for the recovery of the unseeded native plant community in plots by the end of the study. Although the Roosevelt site is generally the wettest site, according to the 30-year normal, the Preserve had the highest monsoon and winter rains, prior to the fall 2021 and spring 2022 sampling periods, which may help explain site differences seen in this study.

Seed Mix and Climate Matching

Seed mix effects varied by season and site. The cool seed mix consistently outperformed the warm seed mix in spring across

all locations, while the warm seed mix showed modest success in plant cover in the post-drought fall season. This reflects the trend found in the analysis of the full RestoreNet site network, in which the cool seed mix, adapted to current conditions, established best (Farrell et al. 2023), even though all species in this study were local to the region. However, the analysis of establishment by individual species' climate envelopes (MAT95) did not yield clear results. The pattern that we found in the first season in which species with higher MAT95 climate envelopes established best at the warmest site and species with lower MAT95 established better at the cooler sites did not continue in the last two spring seasons for seeded species density or cover. However, we did find a pattern in which species with lower MAT95 values established best in the post-drought spring seasons for the site that received the most precipitation during that time (Preserve) and the higher MAT95 species did best at the other two sites. These patterns suggest that climate-matching species with higher MAT95 values in seed mixes at hotter and drier sites may deserve additional investigation.

In the fall season, the warmer MAT95 species performed better than cooler MAT95 species at the Preserve and Roosevelt sites, with low overall emergence at Lake Pleasant. These patterns may be partially explained by differential species phenology. Two of the three species (*Bouteloua barbata* var. *rothrockii* and *B. aristidoides*) that emerged in the fall season were warm season (C4) grasses and only appeared in the fall. Two other C4 grasses with cooler MAT95 (*Digitaria californica* and *Aristida purpurea*) established, but only in the spring. Only one species, *Senna covesii*, which blooms from April to October, appeared in both seasons.

Furthermore, while MAT95 may still offer one metric for matching species to site conditions, it fails to account for critical traits such as germination requirements, water-use efficiency, and bet-hedging. In the face of unpredictable environmental variation, seeds produced from a single plant can use bet-hedging to germinate at different times and years to spread out the chances of successful establishment (Adonakis & Venable 2004; Gremer et al. 2016). In this study, species that emerged successfully may have possessed germination traits such as dormancy or delayed emergence that allowed them to take advantage of post-drought rainfall, consistent with functional trait-based frameworks (Donohue et al. 2010; Huang et al. 2016). These findings match with prior work in desert systems showing that interannual variation in precipitation and species-level physiological strategies—rather than average climate itself—drive establishment outcomes (Venable 2007; Gremer & Venable 2014; Butterfield et al. 2023). Recent observations show a decline in monsoon reliability in parts of the Southwest, which affects the recruitment success of warm season, drought-intolerant species (Dalglish et al. 2011; Gremer & Venable 2014).

Interannual and Seasonal Variability

Temporal dynamics before and after the 2020 drought year (monsoon 2020 and winter 2020–2021) revealed contrasting emergence patterns. Seeded species density peaked in spring

2021, immediately after the drought, suggesting that the moisture from winter rains following the drought may have triggered a delayed but strong recruitment event (Schultz et al. 2014). Seeded species density in the subplots declined in spring 2022 from spring 2021, despite wetter winter conditions than the previous year. However, seeded species increased in cover at the whole-plot level compared to spring 2021, indicating that the seeded species may be propagating across the larger plots (Li et al. 2013). Species that emerged post-drought may have possessed physiological mechanisms like drought-priming capacity that enabled them to delay germination and high water-use efficiency, enabling them to withstand subsequent climatic stress (Huang et al. 2016; Liu et al. 2017). These results indicate that the positive effects of seeding in dryland restoration may be delayed and the full effect of restoration efforts may not manifest immediately after they are implemented. Still, these strategies are not without limitations: species with low water-use efficiency or narrow germination windows may perform poorly under ongoing drought stress (Huxman et al. 2008; Dalglish et al. 2011). Compared to broader RestoreNet studies that pool data across sites and years (Havrilla et al. 2020; Farrell et al. 2023), our focused multi-season comparison clearly shows that site-level climate characteristics can override general treatment effects and alter the establishment of plants. (Havrilla et al. 2020; Farrell et al. 2023).

The unseeded plant community had opposite trends for native and non-native plants. The unseeded native plant community remained very low in the first spring after the drought (2021) but increased markedly by spring 2022. However, non-native plants had the highest cover in the drier post-drought spring (2021) compared to spring 2022. Since the non-native plants were mainly annuals, this may reflect the superior ability of annual invasive plants to respond opportunistically to moisture pulses (Horn et al. 2015).

Scale and Consistency of Treatment Effects

To assess whether the treatment effects observed at the subplot scale extend to broader vegetation patterns, we examined the agreement between subplot density measures and whole-plot cover. For seeded species, both seed mix and surface treatments produce consistent effects across scales—treatments that enhanced emergence at the subplot level also led to increased cover at the whole-plot level. This agreement suggests that microsite-level mechanisms, such as improved moisture retention, produced large enough effects to be observed at a broader scale. However, we found no significant effect of species climate envelope on whole-plot cover, indicating that species-specific responses observed in subplots did not scale up to shape total plot-level vegetation patterns. Similarly, for the unseeded plant community, surface treatments that appeared effective at the subplot level did not result in significant effects on the whole-plot scale. These results highlight which subplot-scale treatment effects may be most promising for landscape-scale restoration. Our findings suggest that for successful dryland restoration outcomes, pits as a soil surface treatment can improve outcomes. While

metrics like climate envelopes may offer valuable guidance for seed selection, they must be balanced with other species' functional traits. In arid environments, seeding success can be bolstered PR by surface modifications and matching species climate tolerances, but these effects vary depending on site conditions and traits of the species in the seed mix. Ultimately, dryland restoration actions must be flexible, responsive to site conditions, and resilient to climatic uncertainty that is inherent in arid settings.

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Supporting Information

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

Table S1. RestoreNet site name, state, ecoregion, potential plant community, MAP, MAT, the percent (%) of annual precipitation that occurs during the North American Monsoon.

Table S2. RestoreNet site precipitation and temperature normal and means during the study period.

Table S3. Results of Q1's Tukey-adjusted multiple comparisons on surface treatments of the seeded species density model in post-drought spring seasons.

Table S4. Results of Q1's Tukey-adjusted multiple comparisons on surface treatments of the seeded species plant cover model in post-drought spring seasons.

Table S5. Results of Q1's post hoc pairwise comparisons on seed treatments of the seeded species density model in the first season.

Table S6. Results of Q1's post hoc pairwise comparisons on seed treatments of the seeded species plant cover model in the first season.

Table S7. Results of Q1's post hoc pairwise comparisons on seed treatments of the seeded species density model in the post-drought spring seasons.

Table S8. Results of Q1's post hoc pairwise comparisons on seed treatments of the seeded species plant cover model in the post-drought spring seasons.

Table S9. Results of Q1's post hoc pairwise comparisons on seed treatments of the seeded species plant cover model in the post-drought fall season.

Table S10. Results of Q1's Tukey-adjusted multiple comparisons on interactions (site \times seed treatments) of the seeded species density model in the post-drought fall season.

Table S11. Results of Q2's Tukey-adjusted multiple comparisons on the site effect of the seeded species plant cover model in the post-drought fall season.

Table S12. Results of Q3's Tukey-adjusted multiple comparisons on the surface treatments of the native seedling density model in the first season.

Table S13. Results of Q3's Tukey-adjusted multiple comparisons on the interactions (site \times surface treatments) of the native seedling density model in the post-drought spring seasons.

Table S14. Results of Q3's Tukey-adjusted multiple comparisons on the surface treatments of the native seedling density model in the post-drought spring seasons.

Table S15. Results of Q3's Tukey-adjusted multiple comparisons on the interactions (site \times surface treatments) of the non-native seedling density model in the first season.

Table S16. Results of Q3's Tukey-adjusted multiple comparisons on the surface treatments of the non-native seedling density model in the post-drought fall season.

Table S17. Results of Q3's Tukey-adjusted multiple comparisons on the surface treatments of the non-native seedling density model in the post-drought spring seasons.

Table S18. Results of Q3's Tukey-adjusted multiple comparisons on the surface treatments of the total plant cover model in the post-drought spring seasons.

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