

THESIS

IMPLICATIONS OF FACILITATION AND HETEROGENEITY FOR PLANT
COMMUNITY RESTORATION IN THE ROCKY MOUNTAIN REGION

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ABSTRACT

IMPLICATIONS OF FACILITATION AND HETEROGENEITY FOR PLANT COMMUNITY RESTORATION IN THE ROCKY MOUNTAIN REGION

Seeding is the most widespread and viable method to revegetate degraded dryland ecosystems. Despite its prevalence, efforts to establish plants through seeding frequently fail. Variable weather conditions, competition with dominant and invasive species and herbivory pose barriers to the establishment of seeded plants. As a result, there is a great need and demand for innovative restoration practices that can aid revegetation efforts.

Pit, mound and slash pile treatments create spatial and resource heterogeneity and thus can provide niches for different plants to find suitable habitat. I completed a four-year study that tested the impacts of seeding in conjunction with heterogeneity treatments on measures of plant community structure and cover compared to untreated but seeded plots and unseeded controls. Research sites were located in California Park, Colorado USA, a 11,000-ha *Artemisia cana* (silver sagebrush) meadow in the Medicine Bow Routt National Forest. In 2018, replicated test plots containing four treatments (unseeded control, seeded only, seeded plus soil pits and mounds, and seeded plus slash) were established at degraded sites in California Park. Seeded plots received a high diversity native seed mix (39 species) at a high rate (1496 Pure Live Seed [PLS] / m²). I monitored seeded species density and total plant species cover in the summers of 2019 through 2022. I analyzed treatment effects on plant Shannon

Wiener diversity (H), richness, seeded abundance (plants / m²), Pielou's evenness (J) and percent cover with linear mixed-effects models.

Plots that received the seeded only and seeded plus soil pits and mounds treatments contained higher seeded species diversity than control plots in 2019 and 2022. While seeded plus slash pile treatment plots increased seeded species diversity in the first year of monitoring, this effect diminished after 2019. It is important to note, no seeded diversity differences emerged between heterogeneity treatment plots and untreated but seeded plots in any year. Findings suggest that seed application can increase the diversity of desirable seeded species and may be a useful tool to shift plant community composition.

Shrub subcanopies accumulate moisture and nutrients in a manner that can facilitate understory plants. Consequently, seeding beneath shrubs may improve seedling establishment and survival in dryland ecosystems where harsh environmental conditions are present. I set up a study to evaluate whether seeded shrub islands had higher seeded species abundance and richness compared to seeded interspaces and unseeded controls. Study sites were located outside of Grand Junction, Colorado in Dominguez Escalante and McInnis Canyons National Conservation Areas (NCA) (Figure 2.1). Six sites were established in fall of 2020, three within sagebrush and three within salt desert shrublands. Five seeded shrub islands, five seeded interspaces, five unseeded shrub island controls and five unseeded interspace controls were established at each site. In addition, I evaluated if the impacts of these treatments were different between sagebrush and salt desert shrublands. Furthermore, I assessed whether plant functional groups and soil chemical properties were impacted by treatment type. I

analyzed treatment effects on seeded species richness, seeded species abundance, cover by plant functional group, surface soil moisture, temperature and chemical properties with separate linear mixed-effects models.

While sub canopy microsites were on average nutrient enriched and cooler than interspace plots, they did not facilitate seeded species establishment. In contrast to expectations, seeded interspaces contained higher seeded species richness than all other plot types. Lower richness in seeded shrub islands may be due to sodic, saline and or saline-sodic soil conditions found beneath shrubs within the salt desert. In addition, high cover of introduced perennial grasses beneath shrub islands may prevent seedling establishment at sagebrush sites. Results suggest that interspaces provide more favorable conditions for seeded plant establishment than shrub islands in both systems.

Land managers are interested in leveraging positive plant-plant interactions (i.e., facilitation) and heterogeneity to improve seeded plant establishment and plant community restoration outcomes. I investigated whether applying a native seed mix either beneath shrub islands, or in tandem with heterogeneity treatments, increased seeded plant establishment and diversity respectively. I hope this research can contribute to improving plant community restoration outcomes in degraded dryland ecosystems.

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CHAPTER I IMPLICATIONS OF HETROGENEITY TREATMENTS AND SEEDING FOR SPECIES DIVERSITY AT A DEGRADED, SILVER SAGEBRUSH MEADOW

Introduction

Restoration practitioners recognize the importance of maintaining and restoring native plant diversity in degraded areas (Jordan et al. 1987, Rey Benayas et al. 2009). Plant diversity is valued as a restoration goal due to its implications for ecosystem resilience, productivity and recovery (Lesage et al. 2018). High diversity sites tend to be more resistant to invasion and restoring plant diversity is shown to increase ecosystem resilience to extreme climate events and disturbances (Chapin et al. 1997, Peterson et al. 1998, Kennedy et al. 2002, Isbell et al. 2015). These effects extend to higher trophic levels and plant diversity is associated with the stability of entire food webs (Haddad et al. 2010). However, environmental barriers often exist to achieving this outcome.

Seeding is one of the most widespread and viable methods to increase cover and diversity of native plant species, but seedling establishment failure is common in arid and semi-arid (“dryland”) ecosystems (Shackelford et al. 2021). Variable weather conditions, competition with dominant and invasive species and herbivory make achieving diversity outcomes through seeding difficult (Cumberland et al. 2017, Shriver et al. 2018, Shackelford et al. 2021). As sagebrush steppe systems face the impacts of climate change, it is important to establish a diverse native plant community that will be resilient to extreme weather events, disturbances and invasive species (Chapin et al. 1997, Peterson et al. 1998, Kennedy et al. 2002, Isbell et al. 2015) and provide habitat for sensitive species such as *Centrocercus urophasianus* (Greater sage grouse).

The heterogeneity-diversity hypothesis proposes that environmental heterogeneity, drives plant species diversity (Levins 1979, Ricklefs 1977). Heterogenous environments can promote species diversity by expanding niche availability, providing refugia and enabling resources to be partitioned in a manner that facilitates coexistence (Levins 1979, Chesson 2000). Specifically, treatments that create variable soil resources or microsite conditions may increase the ability of plants with different traits or ecological strategies to establish and coexist (Ricklefs 1977, Biederman and Whisenant 2011, Williams and Houseman 2014, Bergholz et al. 2017, Stover and Henry 2020). It is uncertain whether creating heterogeneity and sowing a native seed mix in degraded sites will increase species diversity. This study was designed to evaluate the impact of applying seed, in conjunction with the creation of soil pits and mounds or the creation of slash piles, on metrics of plant community structure and cover compared to unseeded controls and seeded only plots.

Pit and mound treatments are used in dryland and grassland ecosystems to promote seedling establishment (Chambers 2000, Biederman and Whisenant 2011, Havrilla et al. 2020, Farrell et al. 2023). They create resource heterogeneity by generating variable site conditions including nutrient concentrations and soil moisture gradients (Biederman and Whisenant, 2011). Pit and mound treatments are rooted in indigenous arid land farming techniques, such as waffle gardens, that promote water retention and create microclimates for plants to establish (Salmón 2012, Nabhan 2013). Both human created pits and mounds as well as holes formed by digging and burrowing animals capture seeds and provide beneficial microsites and soil water conditions for seedling establishment (Reichman 1984, Eckert et al. 1986, Chambers 2000) The

combination of seeding and pit treatments has been shown to increase seeded densities threefold compared to unseeded controls and increase seeded density over seeding alone (Havrilla et al. 2020, Farrell et al. 2023).

Slash additions are also applied during restoration to promote plant establishment by trapping seeds, decreasing soil movement and promoting water and nutrient holding capacity, especially in semiarid woodlands (Jacobs and Gatewood 1999, Stoddard et al. 2008, Brown and Naeth 2014). In degraded sagebrush shrublands, adding woody debris from *A. tridentata* is also associated with faster recovery of *A. tridentata*. (Johnston 2019).

For the past 30 years land managers at California Park, a high elevation *Artemisia cana* (silver sagebrush) parkland in the Medicine Bow Routt National Forest, Colorado, aimed to develop plant communities that contain a high diversity, density and cover of desirable native vegetation (USDA Forest Service 2003). They strived to achieve these metrics to prevent soil loss and increase wildlife habitat quality in the region (USDA Forest Service 2003). These goals reflect larger scale management objectives in the imperiled sagebrush steppe ecosystem (Pyke 2015). However, restoration treatments to increase native plant diversity have largely been unsuccessful (USDA Forest Service 2003, Maxwell et al. 2021).

The objectives of this study were to 1. Determine if soil pits and mounds increase metrics of plant diversity at seeded treatment plots within California Park. 2. Determine if slash piles increase metrics of plant diversity at seeded treatment plots within California Park and 3. Identify if plant diversity, richness, cover and seeded species abundance (plants / m²) differ between site types within seeded plots. I expected that

creating heterogeneity, via soil pits and mounds and slash piles, along with the application of a high diversity seed mix, would increase plant diversity, richness, evenness, cover and seeded species abundance compared to controls and seeding alone in study plots within California Park. I expected that site type would influence species diversity, richness, evenness, seeded abundance and percent cover in seeded plots. These findings provide insight into whether seeding in tandem with heterogeneity treatments may set these degraded sites on desirable plant community trajectories.

Methods

Study Site Description

Research sites were established in California Park, Colorado USA, a 11,000-ha *Artemisia cana* (silver sagebrush) park in the Medicine Bow Routt National Forest managed by the USDA Forest Service, Hahn's Peaks- Bears Ears Ranger District (Figure 1.1). California Park is designated as a Special Interest Area due to its diversity, cultural heritage, archeological and geologic significance (USDA Forest Service 2003). California Park is a hotspot for wildlife diversity and contains the greatest richness of sensitive species in Routt National Forest (USDA Forest Service 2003).

The sites are at approximately 2,479m. Between 1991 and 2020 the study sites' mean annual precipitation (MAP) was 793 mm (PRISM Climate Group, 1991-2020 climate normals, Appendix Table 1). California Park experienced higher than average MAP in 2019 (Appendix Table 1). However, in the following two years the region experienced drought conditions. Mean annual precipitation was 37% lower than the 30-year average in 2020 (Appendix Table 4). Drought conditions extended into the summer of 2021 and became more severe (U.S Drought Monitor 2023). In 2021, the study

region received 11% less annual precipitation and experienced an average annual temperature that was 1.7°C higher than the 30-year average. In 2022, MAP was 7% lower than 30-year averages (Appendix Table 1). Between 1991 and 2020, mean annual temperature (MAT) at the study sites was 4.4°C (PRISM climate group, 1991-2020 climate normals, Appendix Table 1). While MAT was 0.4°C lower compared to normal in 2019, MAT was 0.3°C and 1.7°C higher than normal in 2020 and 2021 respectively (Appendix Table 1).

Study plots were located on soils within the Jodokowski series, which are characterized by smectitic clays that exhibit shrink-swell cracking (Soil Survey Staff, 2006). California Park geology consists predominantly of landslide deposits and residuum from sedimentary rocks including the Lance Formation and Lewis shale. Soils derived from Lewis shale pose management concerns due to their, high erodibility and susceptibility to landslides and earth flows (USDA Forest Service 2003).

In the late 1800s, tens of thousands of cattle passed through the range in California Park as part of the stock drive route known as the Beef Trail (Maxwell et al. 2021). While cattle numbers in the park dropped after the passage of the Taylor Grazing Act in 1934, overgrazing and subsequent denudation of vegetation compacted the fine-grained clay soils and led to degraded range conditions (USDA Forest Service 2003).

In the 1950s, the Forest Service took actions to improve degraded range conditions with a focus on improving forage. Non-native pasture grass species such as *Bromus inermis* (smooth brome), *Phleum pratense* (Timothy), *Poa pratensis* (Kentucky bluegrass), and *Dactylis gomerata* (orchardgrass) were planted (Grant-Hoffman et al., 2018; Kachergis et al., 2014). Between the 1950s and 1980s, the broadleaf herbicide

2-4-D was sprayed over large areas of California Park (USDA Forest Service 2003). Herbicides were sprayed to reduce the cover of *Artemisia* (*spp.*) and *Wyethia amplexicaulis* (mule-ears) a native forb that can form large monocultures after heavy grazing (Kachergis et al., 2012, 2014). More recently, the Forest Service has shifted its goals to improving wildlife habitat, and increasing the diversity and cover of native plant species (USDA Forest Service 2003). Managers have tried to achieve these objectives through fertilization, subsoil ripping, tilling and seeding with little success (USDA Forest Service 2003).

Research plots were located throughout three degraded plant communities that the Forest Service is interested in restoring (Figure 1.1). One degradation state, termed “Timothy” is dominated by *P. pratense* and other non-native pasture grasses (Kachergis et al., 2012, 2014). Another degradation state is dominated by bare ground and the perennial forb *Lomatium leptocarpum* (gumbo lomatium). These sites are termed “Scab” (USDA Forest Service 2003). The third degradation state, termed “Wyethia,” is dominated by *W. amplexicaulis*. (Kachergis et al., 2012, 2014). These three degraded, sloping upland areas all consist of low vegetative cover or vegetation such as *Wyethia* that senesces rapidly leaving relatively bare soils for a portion of the year (USDA Forest Service 2003). I will refer to these degraded plant communities as “site types” throughout the chapter.

Restoration Treatments and Experimental Design

In fall of 2018, ninety plots were established to examine the effect of heterogeneity treatments on seedling establishment. Within each degraded plant community (i.e., Scab, Timothy and Wyethia) three blocks were established for a total of

nine blocks. Each block was divided into two sub-blocks (10- by 10-m) that were randomly assigned either a fencing treatment or no fencing treatment (Figure 1.2). Sub blocks were located at least 3 m apart to reduce edaphic and environmental differences. Exclosures were constructed around the randomly assigned sub block. Exclosures were approximately 1.25m tall and constructed of wooden posts and top-rails. Woven wire extended from the top rail to the soil surface. Grazing exclosures were unable to remove the presence of all livestock and herbivores and thus their effects are not discussed in this thesis. However, fencing was still included in the model. Before seeding treatments began, USDA Forest Service personnel applied a broad-spectrum herbicide (glyphosate) in each sub-block at a rate of 32 fl oz/ac (2338 ml/ha) using an All-Terrain Vehicle (ATV) mounted spray rig. Herbicide was applied to reduce the competitive effect of existing vegetation on seeded species. We then prepared the seedbed by rototilling each subplot to a depth of 10 cm.

Four plots (2- by 2-m) were established within each sub block (Figure 1.2). Each plot received one of four treatments: soil pits and mounds plus seeding, slash plus seeding, seeding only and a control. Soil pits and mounds were created by digging 30- x 30-cm holes and placing the removed soil in a mound next to the pit. We placed slash of *Artemisia tridentata* (big sagebrush) in one plot within each sub-block. Slash piles were 0.5 m in height and covered approximately 50% of the soil surface. After creating the heterogeneity treatments, we broadcast a diverse native mix of seed (39 species) at a rate of 1496 PLS m⁻² in all plots except controls. (Table 1.1). We then lightly raked plots to incorporate seed, applied wood straw as mulch and pulled a seedbed roller across the plots to improve seed surface soil contact.

Vegetation Sampling

Monitoring efforts tracked the density of seeded plant species and cover of unseeded and seeded plant species. Vegetation sampling was conducted in early June and July in 2019, and between late June and early August during the summers of 2020, 2021 and 2022. In this thesis I focus on summer season data, and thus will not discuss data collected in early June of 2019 (see Schroeder 2020).

Data collected in 2019, 2020, 2021 and 2022 included density counts and cover estimates of seeded plant species, and cover estimates of unseeded plant species. This data allowed for the comparison between treatments on seeded species richness, diversity, evenness and abundance (plants m⁻²) and overall species diversity, richness, evenness and cover. Unseeded plant species were identified to the finest taxonomical level possible. Nomenclature for all plant species follows the USDA NRCS PLANTS Database (2019). Voucher specimens were collected for unknown species for identity verification.

I used a quadrat sampling method for vegetation sampling (Figure 1.3). Four 0.25- x 0.75-m sampling frames were placed in each plot with a 0.25-m buffer. Within each quadrat, we recorded the number of individual plants of each seeded species rooted inside the frame. A modified Daubenmire (1959) method was used in July of 2019, 2020 and 2021 to collect aerial vegetation cover estimates for all species in each frame. The modification of the Daubenmire cover classes included an additional “Trace” cover class for the occurrence of items with <1% cover. Ground cover was also collected for each frame in 2019, 2020 2021 and 2022. Ground cover classes included bare ground, wood straw, litter and scat.

Statistical Analyses

The impact of treatments and site type on vegetation response variables, including Shannon-Wiener diversity (H), species richness, plant abundance and Pielou's evenness (J) were analyzed with linear mixed-effects models from the lme4 package (Bates et al. 2015) in R 4.1.2 (R Core Team 2021). Fixed effects incorporated in the model included site type, fence type, plot level treatments and their interactions. Block and the interaction of block and fence type are included in the model as random effects.

Analyses were run separately by year so that I could examine the statistical conclusions from data collected in different years. Response variables were log, square or cube root transformed if necessary to meet normality assumptions. When significant main or interactive effects were found, I used post hoc tests to evaluate differences between pairwise means ($\alpha = 0.05$) with the emmeans package in R (Lenth et al. 2019). If variance of random effects in the model was greater than zero, the degrees of freedom was reduced from normal model degrees of freedom to account for the error of random variables. Before beginning statistical analyses on density data, species density counts were converted to plants m^{-2} for each frame sampled. H and species richness were calculated using the diversity and specnumber functions in the vegan package in R (Oksanen et al. 2019). Total seeded species abundance was determined by summing all species abundances for each plot. J was determined by dividing H values by the log of species richness.

Results

While 31 out of 39 seeded species (80%) were present in the study plots across California Park in 2019, this number declined to 15 out of 39 species (39%) by 2022

(Appendix Tables 3a-3d). The largest decrease in seeded species present was seen between 2019 and 2020. In 2020, 48% less seeded species were present in the study plots than in 2019 (Appendix Tables 3a and 3b). After this year, seeded species richness stayed relatively stable throughout the rest of study, with 16 seeded species found in 2020 and 2021 (Appendix Tables 3b and 3c).

In July of 2019, sampling of both seeded and unseeded species cover found 64 species present within the study plots in California Park (Appendix Table 3a). Thirty-one were unseeded species. Conversely, approximately half, or 48%, were seeded species. The total number of plant species found within study plots declined and we found 49 species present in 2022 (Appendix Table 3d). Thirty-four of the species were unseeded. Consequently, 31% of species found in study plots were seeded species in 2022.

Certain seeded species such as *Melica spectabilis* (purple oniongrass), *Perideridia gairdneri* (Gardner's yampah), *Festuca idahoensis* (Idaho fescue), *Pascopyrum smithii* (western wheatgrass), *Rosa woodsii* (Wood's rose), and *Potentilla* sp. (cinquefoil) were found in unseeded control plots. I attribute this phenomenon to either potential seed movement, resprouting roots of perennial plants or emergence of species from the soil seed bank (Appendix Tables 3a-3d).

Effects of Heterogeneity Treatments on Seeded Species

(a) Seeded Species Shannon Wiener Diversity and Pielou's Evenness

In the first year of the study, heterogeneity treatment plots had higher seeded species diversity and evenness than control plots (Appendix Table 2a, Figures 1.4 and 1.5). However, differences were not found between heterogeneity treatment plots and seeded only treatment plots for seeded species diversity (Figure 1.4 and 1.5). In the

following two years, 2020 and 2021, there were no seeded species diversity or evenness differences between heterogeneity treatment plots and seeded only or control plots (Figures 1.4 and 1.5). This trend persisted until 2022, when plots that received the seeding plus soil pits and mounds treatment again had higher diversity than control plots (Figure 1.4). Similar to 2019, there were no seeded diversity differences between seeded soil pits and mounds treatment plots and seeded only treatment plots (Figure 1.4).

(b) Seeded Species Richness

In the first year of the study, heterogeneity treatment plots had higher seeded species richness than control plots (Figure 1.6). However, I did not find any seeded species richness differences between heterogeneity treatment plots and seeded only treatment plots in the same year (Figure 1.6). Seeded species richness differences also emerged between the two heterogeneity treatments. In 2021, seeded plus soil pits and mounds treatment plots had higher seeded species richness than seeded plus slash pile plots (Figure 1.6). There were no seeded species richness differences between heterogeneity treatment plots and seeded only or control plots in 2020, 2021 and 2022 (Figure 1.6). There were no seeded species richness differences between any plot type in 2020 and 2022 (Figure 1.6).

(c) Seeded Species Abundance

Seeded species abundance did not differ between heterogeneity treatment plots and control plots in any year (Figure 1.7). In contrast, seeded species abundance was significantly higher in seeded only plots compared to controls in 2019 (Figure 1.7). However, there were distinctions between treatment plot types (Appendix Table 2a). In

2019 and 2020 seeded species abundance was higher in plots that received the seeding plus soil pits and mounds treatment compared to the seeding plus slash piles treatment (Figure 1.7). In 2019 and 2021, plots that received the seeding plus slash piles treatment had lower seeded species abundance than plots that received the seeding only treatment (Figure 1.7). In 2022, there were no significant differences in seeded species abundance between any plot type (Figure 1.7).

Effects of Heterogeneity Treatments on Total Plant Species

(a) Total Species Richness

Heterogeneity treatment plots contained higher overall species richness than control plots in 2019 (Figure 1.8). However, there were no overall species richness differences between heterogeneity treatment plots and seeded only treatment plots in the same year. This trend diminished after 2019 and in 2020, 2021 and 2022 there were no differences between heterogeneity treatment plots and control plots in terms of total species richness. There were also cases when total species richness differed between treatment types. In 2020, overall species richness was lower in seeded plus slash pile treatment plots compared to seeded only and seeded plus pits and mounds treatment plots (Figure 1.8).

(b) Total Species Shannon Wiener Diversity and Pielou's Evenness

Overall species diversity and evenness were not strongly impacted by treatment type (Appendix Table 2b). In 2019 there was a two-way interaction between site type and treatment (Appendix Table 2b). Within Scab sites, seeded plus pits and mounds and seeded only treatment plots (0.49 ± 0.06) contained lower species evenness than seeded plus slash pile treatment plots (0.65 ± 0.07). Furthermore, in 2022, there was a

3-way interaction between treatment, site and fence type for total plant diversity and evenness values (Appendix Table 2c). However, upon analyzing pairwise comparisons using emmeans, no ecologically relevant comparisons could be found. There were no impacts of treatments on overall plant diversity or evenness in any other year (Appendix Table 2c).

Effects of Heterogeneity Treatments on Species Cover

In 2019, total and unseeded percent plant cover in seeded plus slash pile treatment plots was lower than in control plots (Figures 1.11 and 1.12). Total percent plant cover was also lower in both heterogeneity treatment plots compared to seeded only treatment plots in 2019 (Figure 1.11). In 2021, unseeded percent plant cover was again lower in slash treatment plots compared to control plots (Figure 1.12). Treatment differences in terms of unseeded or total plant species cover were not found in 2020 or 2022 (Appendix Table 2c).

Effects of Site Type

(a) Seeded Species Shannon Wiener Diversity, Richness, Abundance and Pielou's Evenness

Site type had an impact on response variables of seeded species density and diversity in all four years of the study (Appendix Table 2a). Differences arose predominantly between Scab site types and Wyethia and Timothy site types. Site type had an impact on seeded species richness, and diversity in 2019, 2021 and 2022 (Table 1.2). Specifically, plots in scab sites had lower richness and diversity than plots located in Wyethia and Timothy sites (Table 1.2). Plots in Scab sites had lower seeded species abundance than plots located in Timothy sites in 2021 and 2022 (Table 1.2). In terms of seeded species evenness, site type had an impact in 2020, 2021 and 2022 (Table 1.2).

Plots in scab sites had lower seeded species evenness than plots located in Wyethia and Timothy site types (Table 1.2).

(b) Total Species Shannon Wiener Diversity, Richness and Pielou's Evenness

In 2020, Scab sites had lower diversity than Wyethia and Timothy sites (Table 1.3). There was no impact of site type on diversity in 2019, 2021 and 2022 (Table 1.3, Appendix Table 2b). While there was a 3-way interaction between treatment, site and fence type for total plant diversity and evenness values in 2022, upon analyzing pairwise comparisons using emmeans, no ecologically relevant comparisons could be found (Appendix Table 2c).

Site had an impact on total species richness in all four years of the study (Table 1.3, Appendix Table 2b). In 2019, 2021 and 2022 plots located in Scab sites had lower total species richness than plots located in Timothy and Wyethia sites (Table 1.3). Despite the statistical significance of site in 2020, no pairwise differences were evaluated with emmeans. Site type had an impact on evenness in 2020 and 2019 (Appendix Table 2b). In 2019, there was a two-way interaction between treatment and site type and mounds and seeded only treatment plots (0.49 ± 0.06) had lower evenness than slash treatment plots (0.65 ± 0.07) within Scab sites (Appendix Table 2b). In 2020 Wyethia had lower overall species evenness than Scab and Timothy sites (Table 1.3).

(c) Species Cover

Site type had an impact on unseeded and total percent cover in 2019, 2020 and 2022 (Table 1.3). In 2019, 2020 and 2022 plots in both Scab and Timothy sites had lower unseeded percent cover than plots in Wyethia sites (Table 1.3). In 2019 and

2022, both Scab and Timothy had lower total percent cover than Wyethia (Table 1.3). In 2020, only Scab sites had lower total percent cover than Wyethia. Site type had an impact on seeded percent cover in 2019 and 2022 (Appendix 2c). Scab sites had lower seeded cover than Timothy in 2019 and 2022 (Table 1.3).

Discussion

There is a strong need for restoration practices that can effectively increase native plant diversity in degraded sagebrush systems (Jordan et al. 1987, Rey Benayas et al. 2009). A diverse seed mix (39 species) was applied at a high rate (1496 PLS m⁻²) with and without heterogeneity treatments (i.e. soil pits and mounds and slash piles) at three degraded site types within California Park, Colorado to determine if heterogeneity treatments can increase plant diversity compared to controls and seeding alone.

Impacts of Heterogeneity Treatments

Seed application, both in tandem with heterogeneity treatments and alone, increased seeded species diversity compared to control plots in 2019 and 2022. Treatment impacts were greatest in 2019 when seeded only, seeded pits and mounds and seeded slash pile treatment plots had higher seeded species diversity and seeded and total species richness compared to control plots. In the following two years, 2020 and 2021, there were no differences in terms of seeded or total species richness and diversity between treatment and control plots. In 2022, seeded only and seeded plus soil pits and mounds treatment plots again had higher seeded species diversity than control plots. However, it is important to note, no ecologically significant differences could be found between plot types in terms of overall plant diversity in any year of the study. Furthermore, I found no evidence that heterogeneity treatments increased

seeded species diversity compared to untreated but seeded areas. Consequently, while seeding can increase the diversity of desirable seeded species, it may not dramatically impact overall species diversity. Seeding alone proved to be just as effective as seeding in tandem with heterogeneity treatments.

Although the application of slash piles has been shown to increase seeded species establishment in arid woodlands (Jacobs and Gatewood 1999, Stoddard et al. 2008), this treatment did not produce a similar result in the sagebrush steppe at California Park. Seeded slash pile treatment plots contained higher seeded species diversity compared to controls in 2019, however the treatment did not have an impact on seeded species diversity in any other year. Furthermore, in 2019, 2020 and 2022, slash pile treatment plots had lower seeded species abundance than either or both seeded only and seeded plus soil pits and mounds treatment plots. In addition, I observed lower unseeded species cover in slash piles compared to controls in 2019 and 2021.

The creation of slash or branch piles at restoration sites may have unintended consequences. Piles can attract wildlife, such as rodents, and increase seed predation (García-Morote et al. 2017). In fact, pocket gophers were observed in several slash pile plots during the first year of the study (Schroeder 2020). Slash piles may also limit plant emergence through physical obstruction (García-Morote et al. 2017).

Obstacles to Restoration Success

Harsh conditions in 2020 and 2021 may have contributed to the lack of treatment effect on diversity during those years. In the summer of 2020, California Park experienced a grasshopper outbreak (USDA-APHIS 2023, Figures 1.14 and 1.15) and

moderate drought conditions (PRISM 2023, U.S Drought Monitor 2023). Drought conditions extended until the summer of 2021 (US Drought Monitor 2023). Low precipitation and drought can impede native plant establishment and subsequent restoration efforts (James et al. 2019, Garbowski et al. 2021). Furthermore, since soil pit and mound treatments increase water retention during pulse events, they may be more effective at improving plant establishment during a wet year (Havrilla et al. 2020). High densities of grasshopper also reduce the total biomass of restoration plants and can damage rangelands (Branson et al. 2006, Cumberland et al. 2017). One grasshopper species identified at the site, *Melanoplus bivittatus*, tends to consume the reproductive parts of agricultural plants, which can inhibit regeneration (Olfert and Slinkard 1999).

The compound impacts of a grasshopper outbreak and drought were reflected in total plant cover and the number of species found at study plots. In 2019 plant cover averaged 84%, but by 2020 average plant cover was only 25%. While 64 species were recorded in the study plots in 2019, only 41 species were recorded in 2020. Average total plant cover remained low, at 28%, in 2021. In 2022, the region received average MAT and MAP values, and this return to normality was reflected in metrics of plant cover and structure. Average total cover was 47% and 49 species were recorded. Furthermore, seeded only and seeded plus soil pits and mounds treatment plots again had higher seeded species diversity than control plots. While these trends indicate that the grasshopper outbreak and drought conditions may have altered plant community recovery trajectories, they also demonstrate the resilience of treatment effects after disturbance events.

Impact of Site Type:

Site type had a consistent impact on seeded species richness and diversity. Plots located in Scab sites had lower overall species richness than Timothy and Wyethia sites in all four years of the study. Plots located in Scab sites had lower seeded species richness and diversity than plots located in Timothy and Wyethia sites in 2019, 2021 and 2022. These findings align with historic challenges to restore Scab sites by the Forest Service. The soils in Scab sites tend to dry out and exhibit soil cracking earlier than the soils located in other site types. Wyethia sites had higher cover of unseeded species than Timothy and Scab sites in 2019, 2020 and 2022 and lower evenness than Timothy and Scab sites in 2020. High cover of unseeded species and lower evenness indicate that Wyethia sites may experience periodic problems with dominance by *W. amplexicaulis*.

Conclusions and Management Recommendations

Applying seed in tandem with heterogeneity treatments showed promise for increasing seeded species diversity in study plots during the first and last year of the study. However, I found no evidence that heterogeneity treatments increased seeded species diversity compared to untreated but seeded areas. As a result, seeding a native seed mix appears to be just as effective as seeding plus the addition of soil pits and mounds in the high elevation sagebrush meadows characteristic of California Park. This finding has important implications for the level of resource inputs and subsequent expenditure required by land managers.

In 2020 and 2021, there were no treatment effects on plant diversity. A drought and a grasshopper outbreak hampered restoration efforts and may have altered plant

community trajectories by eliminating plant species from the site (Olfert and Slinkard 1999, James et al. 2019, Garbowski et al. 2021). As a result, I recommend that land managers use fall adult surveys and grasshopper hazard maps by USDA APHIS and drought predictions from NOAA National Weather Service (NWS) Climate Prediction Center (CPC) to inform timing of seeding events (Bradford et al. 2018). When the ability to predict weather and grasshopper densities is limited, adaptive and repeated seeding may be necessary to overcome seeding establishment failures (Shriver et al. 2018). Despite disturbance events, seeding effectively increased seeded species diversity four years post application. This study suggests that application of a native seed mix can increase the diversity of desirable seeded species and may be a useful tool to shift plant community composition onto more desirable trajectories.

TABLES AND FIGURES

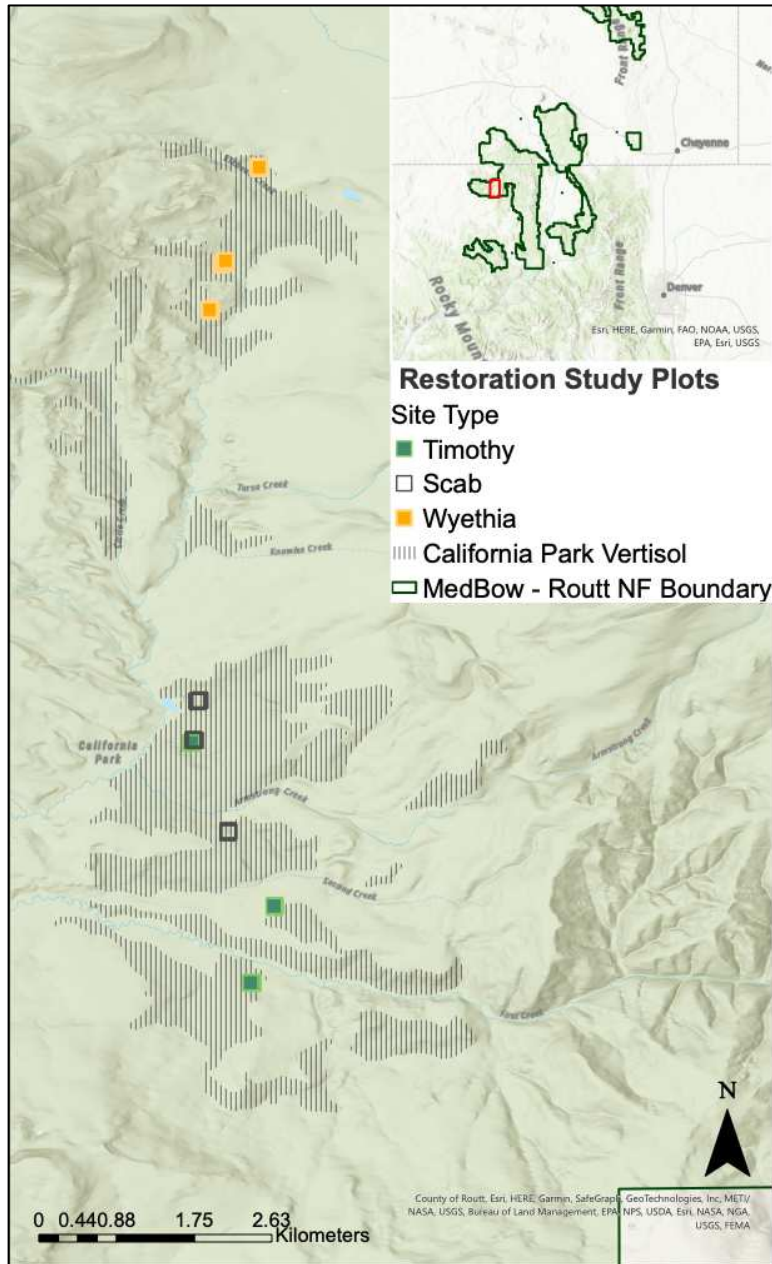


Figure 1.1: Locations of nine study blocks in California Park. Timothy sites were dominated by introduced *Phleum pratense* (Timothy) and other non-native pasture grasses. Scab sites were dominated by bare ground and the native perennial forb *Lomatium leptocarpum* (gumbo lomatium). Wyethia sites are dominated by *Wyethia amplexicaulis* (mule-ears), a native annual forb that can form large monocultures after heavy grazing. All sites are located on smectitic clays within the Jodokowski series.

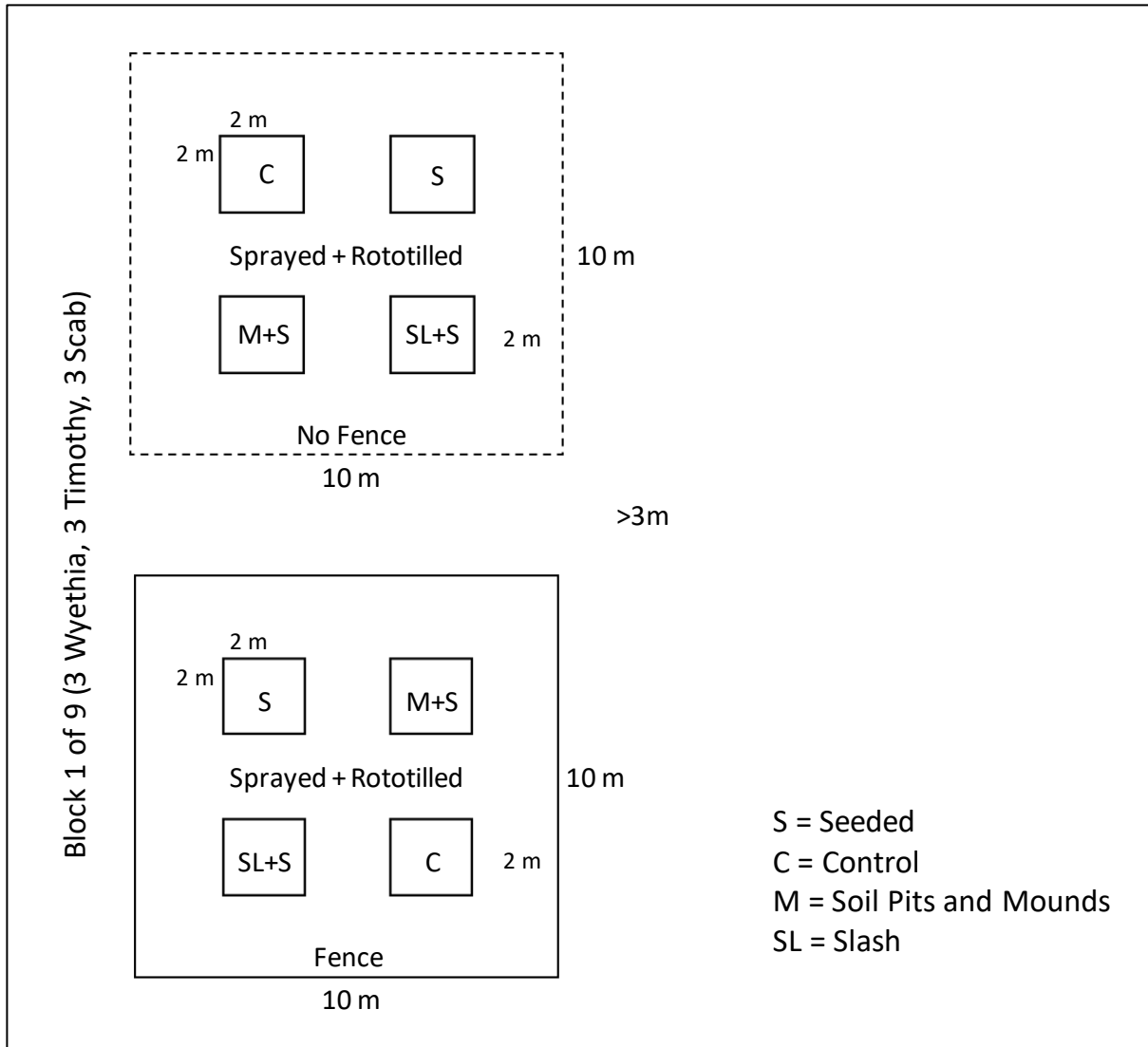


Figure 1.2: Diagram of one of the nine revegetation study blocks established in California Park in 2018. In each block, one sub block had a livestock exclusion fence installed around the 10- x 10- m area, and the other sub block was not fenced.

Table 1.1: Native species included in the seed mix applied on restoration study plots in California Park. Including 19 native forbs, 12 native grasses, and 7 native shrubs at a seeding rate of 1496 Pure Live Seed (PLS) m⁻² (USDA NRCS PLANTS Database, 2019). Plants highlighted in gray were present during the study period.

Common name	Genus	Species	var	PLS m ⁻²
Forbs:				
Yarrow	<i>Achillia</i>	<i>millifolium</i>		45
nettelleaf hyssop	<i>Agastache</i>	<i>urticifolia</i>		45
western pearly everlasting	<i>Anaphalis</i>	<i>margaritacea</i>		38
arrowleaf balsamroot	<i>Balsamorhiza</i>	<i>sagittata</i>		45
Indian paintbrush	<i>Castilleja</i>	<i>spp.</i>		89
fireweed	<i>Chamerion</i>	<i>angustifolium</i>		75
old man's whiskers	<i>Geum</i>	<i>triflorum</i>		3
fivenerve helianthella	<i>Helianthella</i>	<i>quinquenervis</i>		3
oneflower helianthella	<i>Helianthella</i>	<i>uniflora</i>		15
showy goldeneye	<i>Heliomeris</i>	<i>multiflora</i>		83
hairy false goldenaster	<i>Heterotheca</i>	<i>villosa</i>		38
Porter's licorice-root	<i>Lingusticum</i>	<i>porterii</i>		38
flax	<i>Linum</i>	<i>lewisii</i>		8
biscuitroot	<i>Lomatium</i>	<i>dissectum</i>		45
silverleaf lupine	<i>Lupinus</i>	<i>argenteus</i>		45
silky lupine	<i>Lupinus</i>	<i>sericeus</i>		45
Rocky Mtn Penstemon	<i>Penstemon</i>	<i>strictus</i>	Bandera	45
Yampah	<i>Perideridia</i>	<i>gairdneri</i>		75
cinquefoil	<i>Potentilla</i>	<i>spp.</i>		83
spreadfruit goldenbanner	<i>Thermopsis</i>	<i>divaricarpa</i>		2
Grasses:				
mountain brome	<i>Bromus</i>	<i>marginatus</i>		30
tufted hairgrass	<i>Deschampsia</i>	<i>caespitosa</i>		15
bottlebrush squirreltail	<i>Elymus</i>	<i>elymoides</i>		30
Idaho fescue	<i>Festuca</i>	<i>idahoensis</i>		45
needle and thread	<i>Hesperostipa</i>	<i>comtata</i>		3
prairie Junegrass	<i>Koeleria</i>	<i>macrantha</i>		30
spike fescue	<i>Leucopoa</i>	<i>kingii</i>		30
purple oniongrass	<i>Melica</i>	<i>spectabilis</i>		30
green needlegrass	<i>Nasella</i>	<i>viridula</i>		30
western wheatgrass	<i>Pascopyrum</i>	<i>smithii</i>	Rosana	15

Table 1.1 Continued:

muttongrass	<i>Poa</i>	<i>fendleriana</i>	Ruin Canyon	15
bluebunch wheatgrass	<i>Pseudoroegneria</i>	<i>spicata</i>		30

Shrubs:

mountain big sagebrush	<i>Artemisia</i>	<i>Tridentata</i>	vaseyana	90
snowbrush ceanothus	<i>Ceanothus</i>	<i>velutinus</i>		1
winterfat	<i>Krascheninnikovia</i>	<i>lanata</i>		45
chokecherry	<i>Prunus</i>	<i>virginiana</i>		75
woods rose	<i>Rosa</i>	<i>woodsii</i>		46
thimbleberry	<i>Rubus</i>	<i>parviflorus</i>		38
Greene's mountain ash	<i>Sorbus</i>	<i>scopolina</i>		38

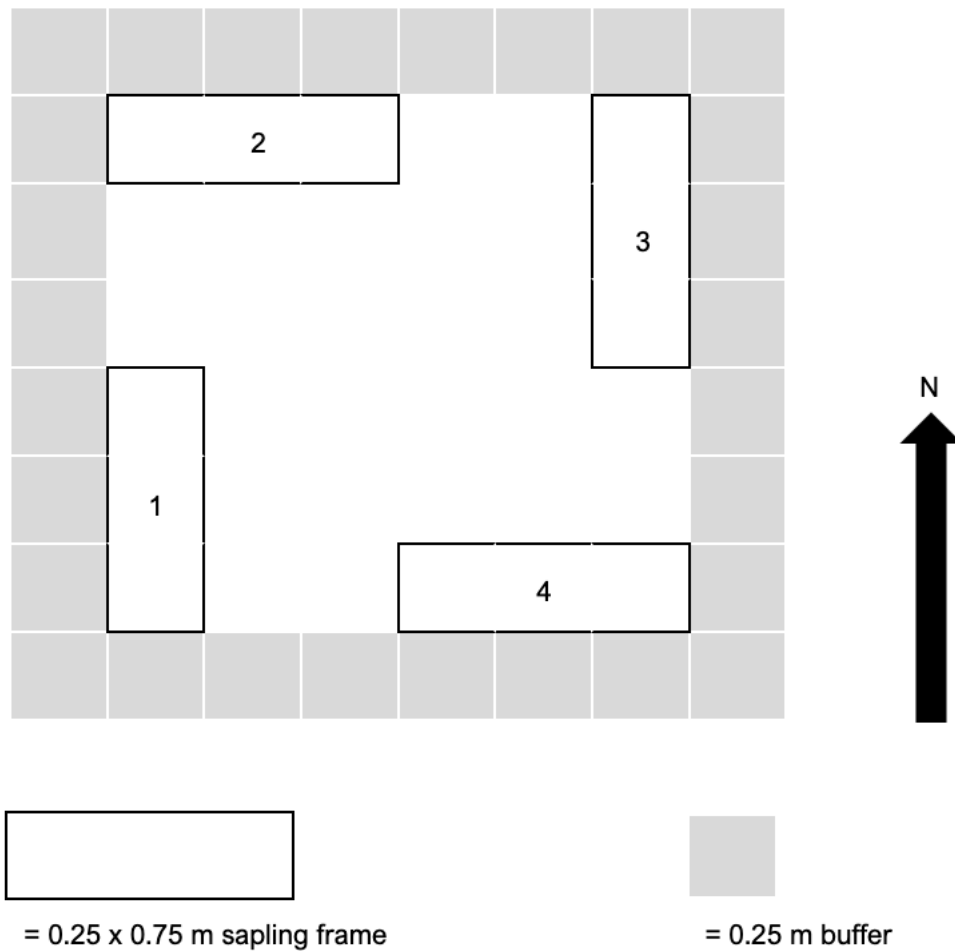


Figure 1.3: Layout of the four sampling frames (0.25 x 0.75-m in each 2- x 2-m study plot, allowing for a 0.25-m buffer).

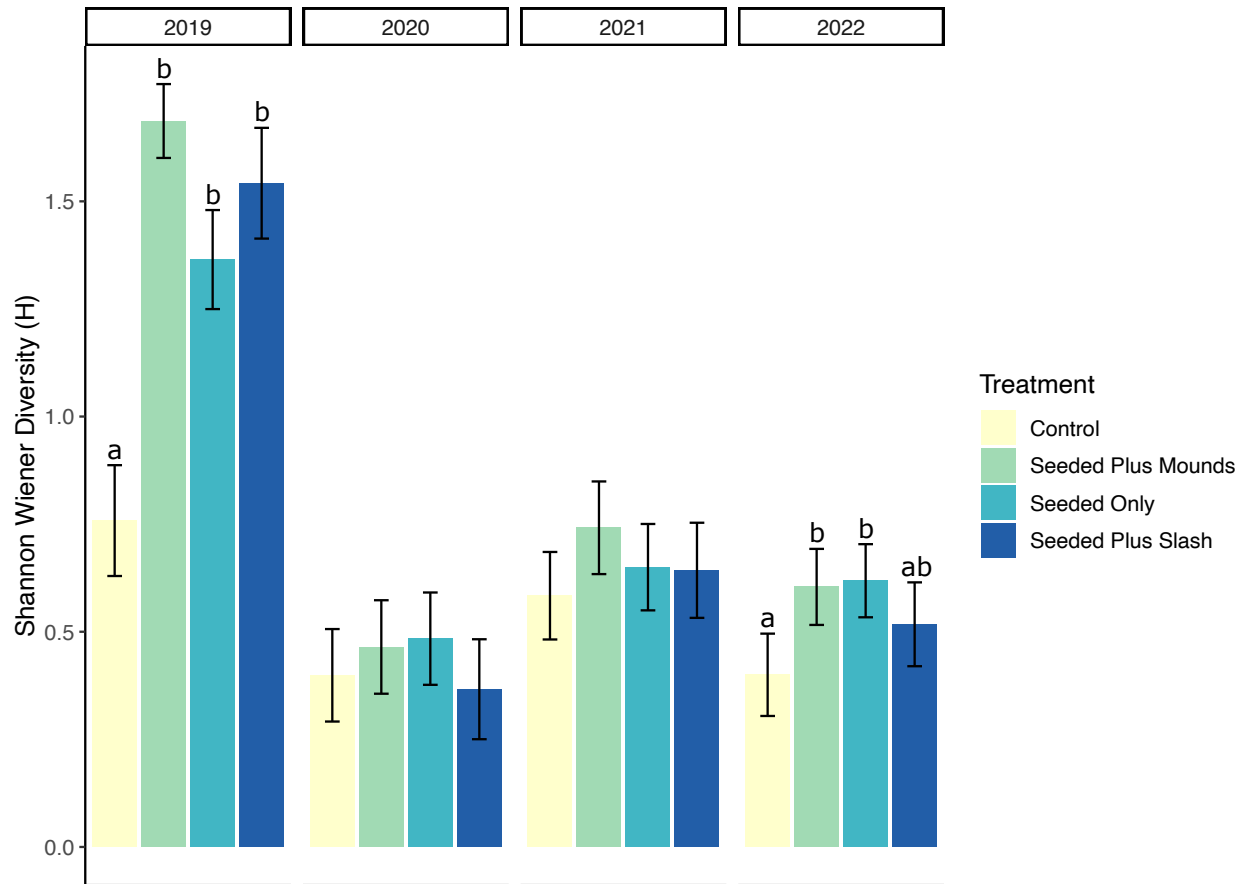


Figure 1.4: Shannon Wiener diversity (H) of seeded species in restoration treatment plots and controls in California Park. Graph includes data from all four years of the study. Year was not included in the model. Treatment was significant in 2019 and 2020 ($p\text{-adj} < 0.05$). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

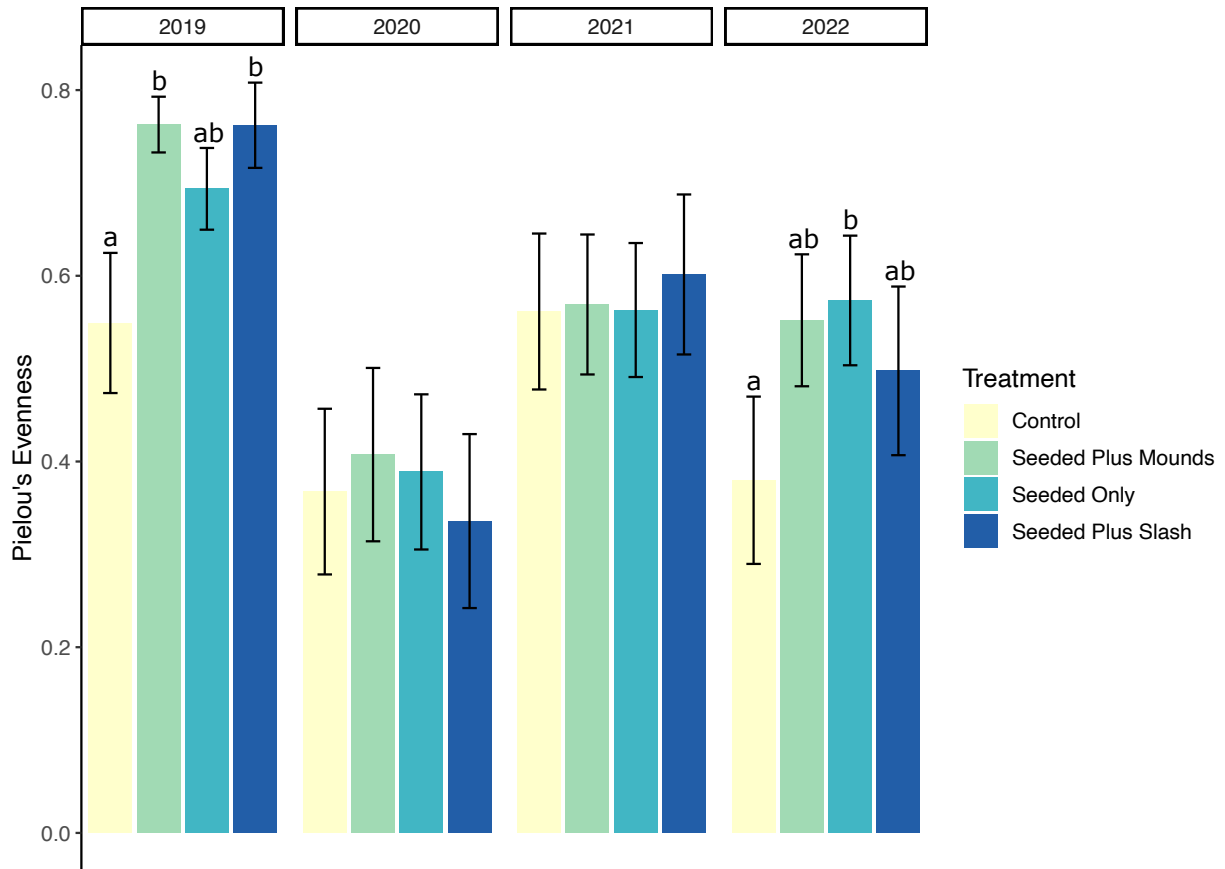


Figure 1.5: Pielou's evenness of seeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was significant in 2019 and 2022 (p -adj < 0.05). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

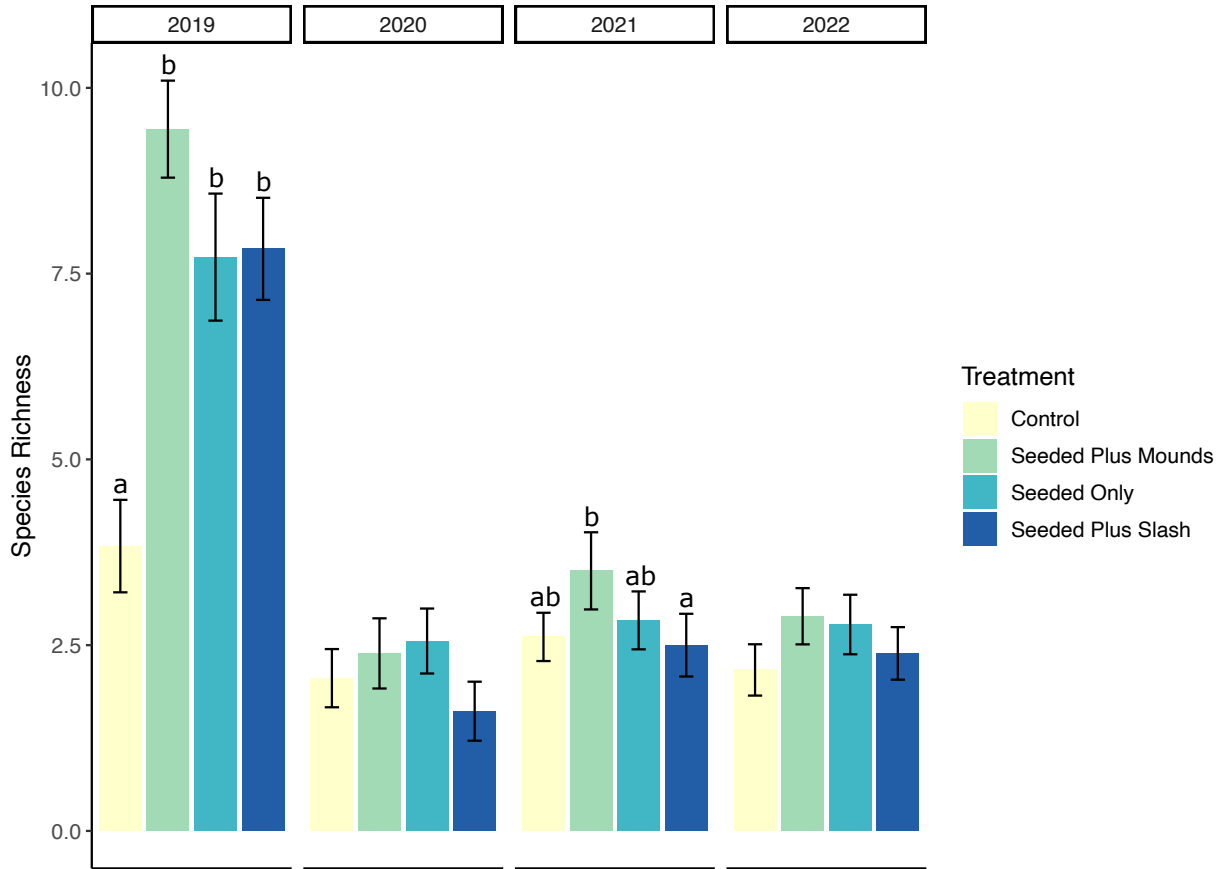


Figure 1.6: Species richness of seeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was significant in 2019 and 2021 ($p\text{-adj} < 0.05$). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

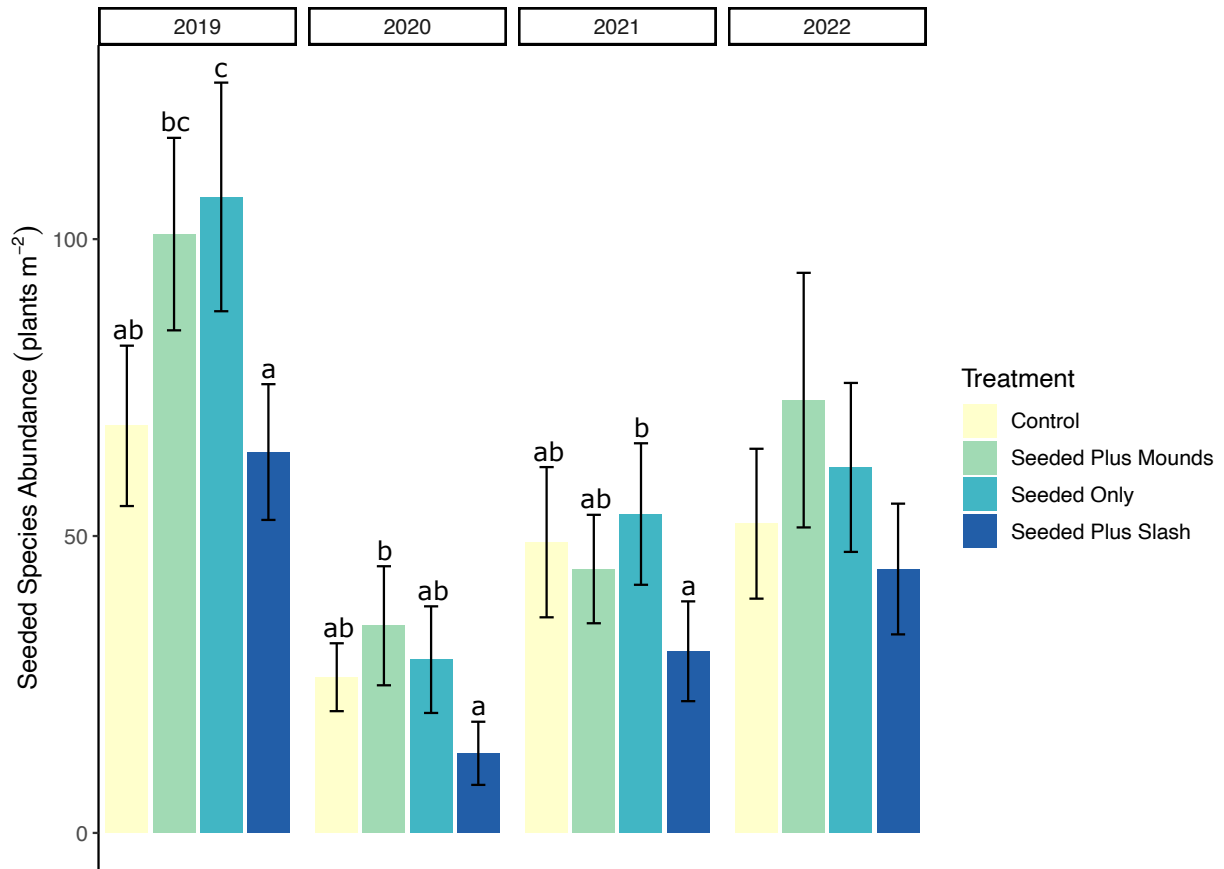


Figure 1.7: Abundance of seeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was significant in 2019, 2020 and 2021 ($p\text{-adj} < 0.05$). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

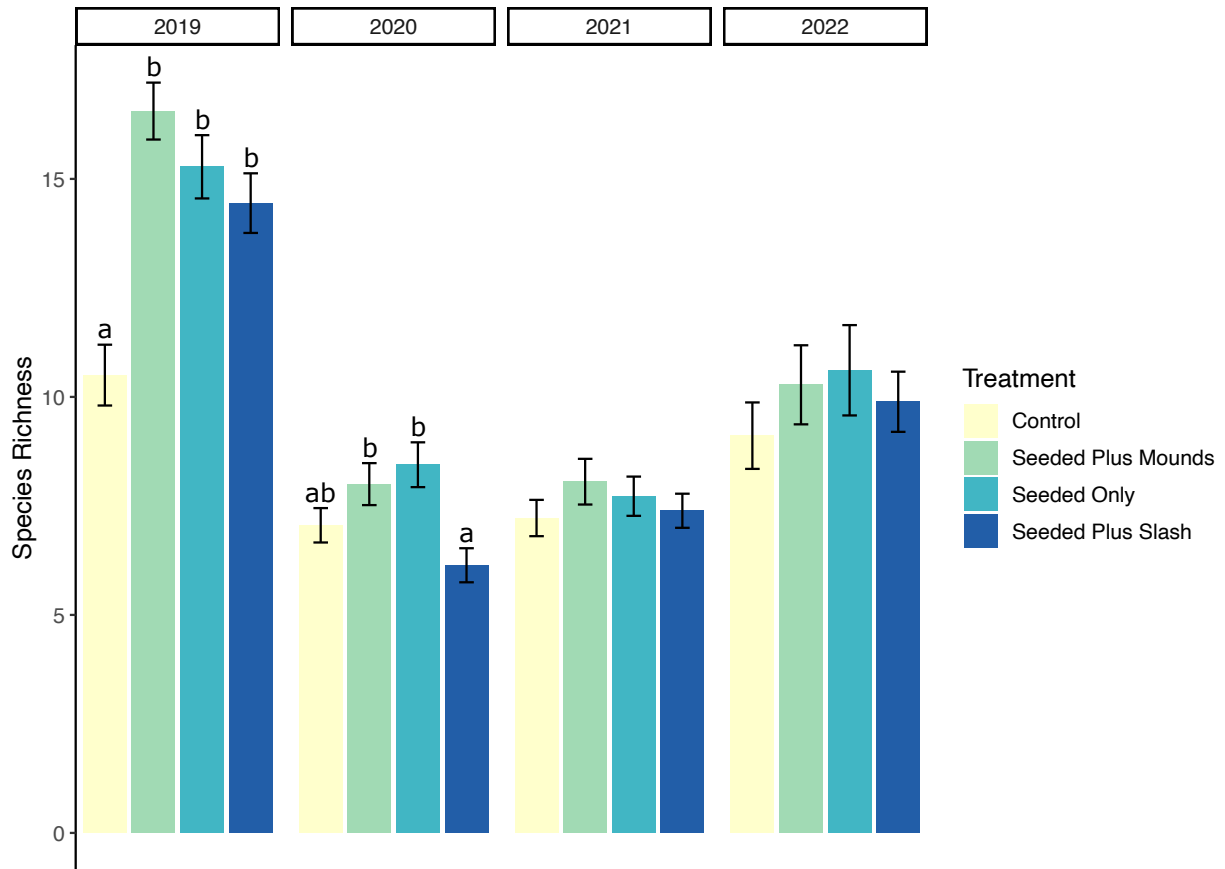


Figure 1.8: Species richness of unseeded and seeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was significant in 2019 and 2020 ($p\text{-adj} < 0.05$). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

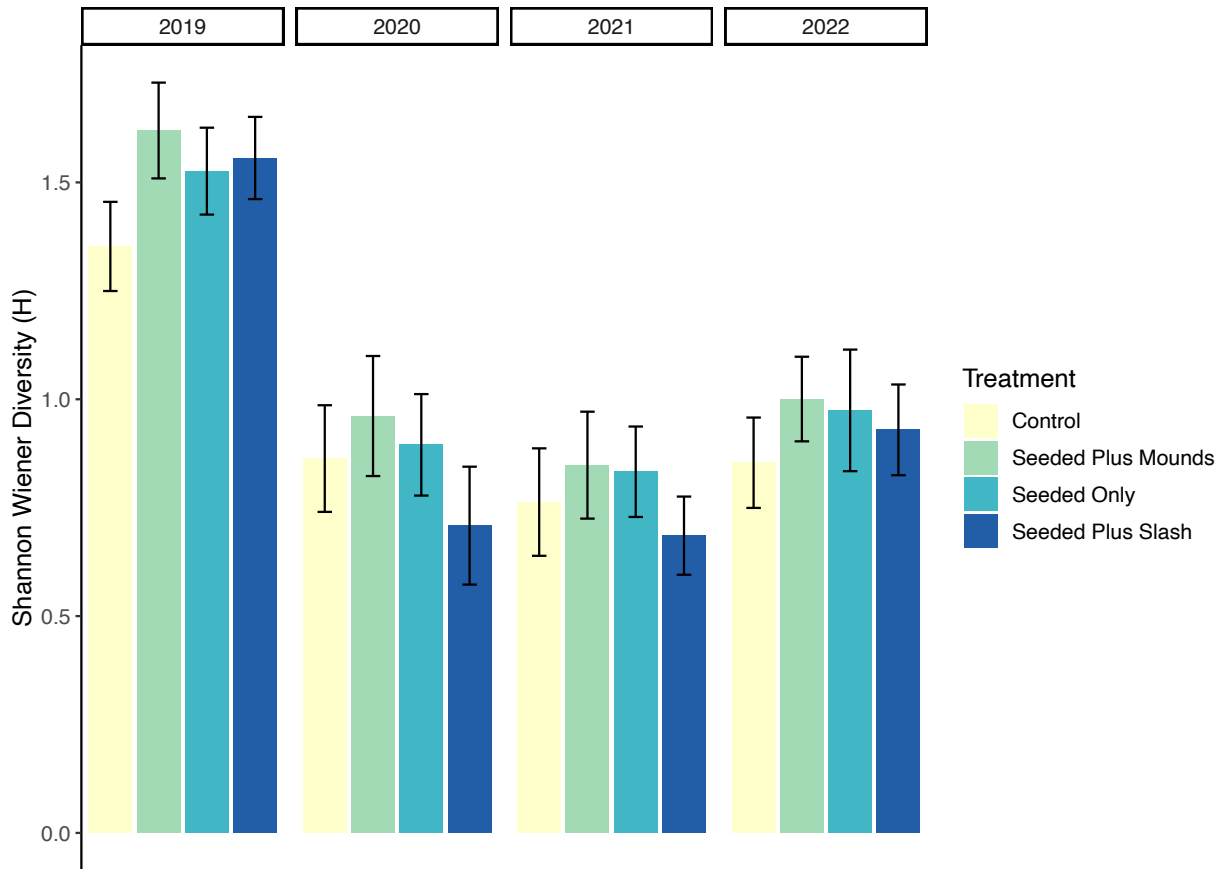


Figure 1.9: Shannon Wiener Diversity (H) of unseeded and seeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was not significant in any year ($p\text{-adj} < 0.05$). Error bars = SE.

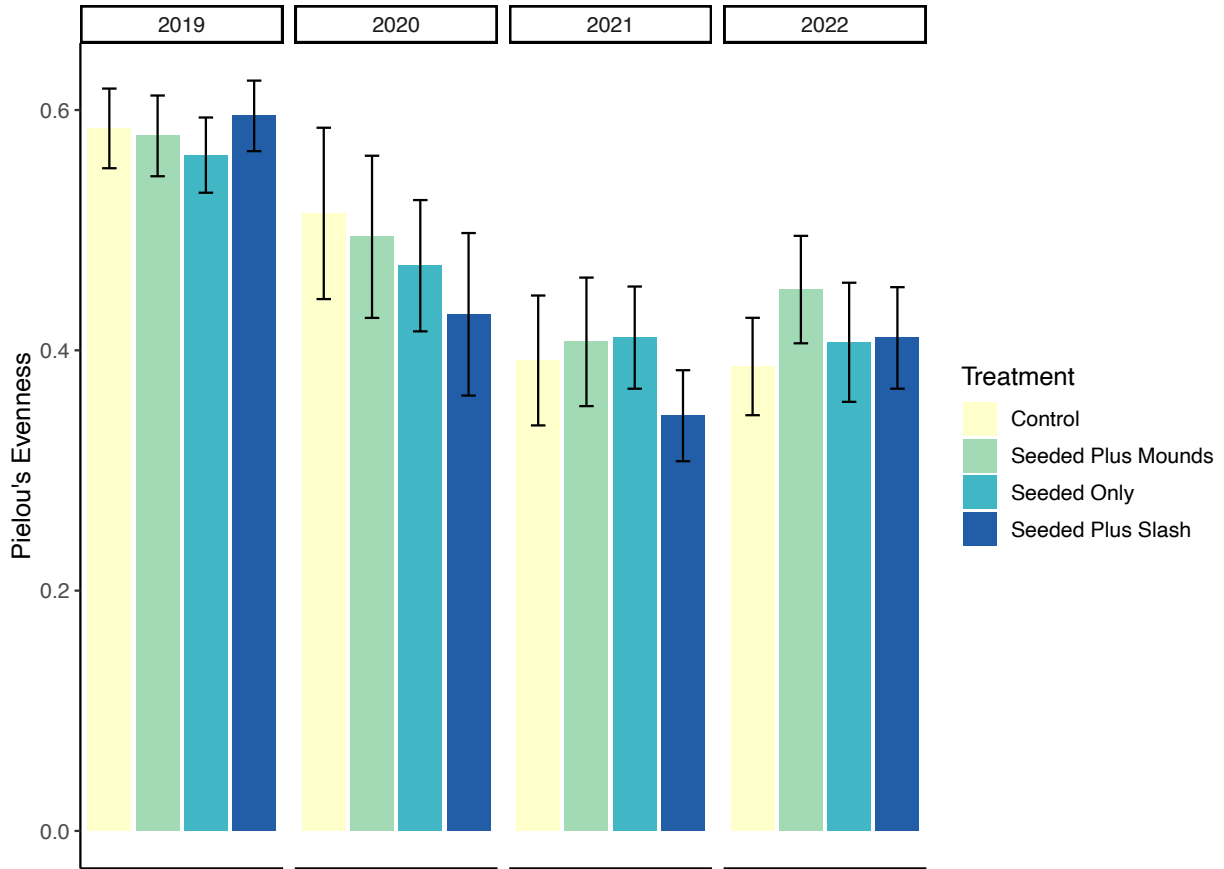


Figure 1.10: Pielou's evenness of seeded and unseeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

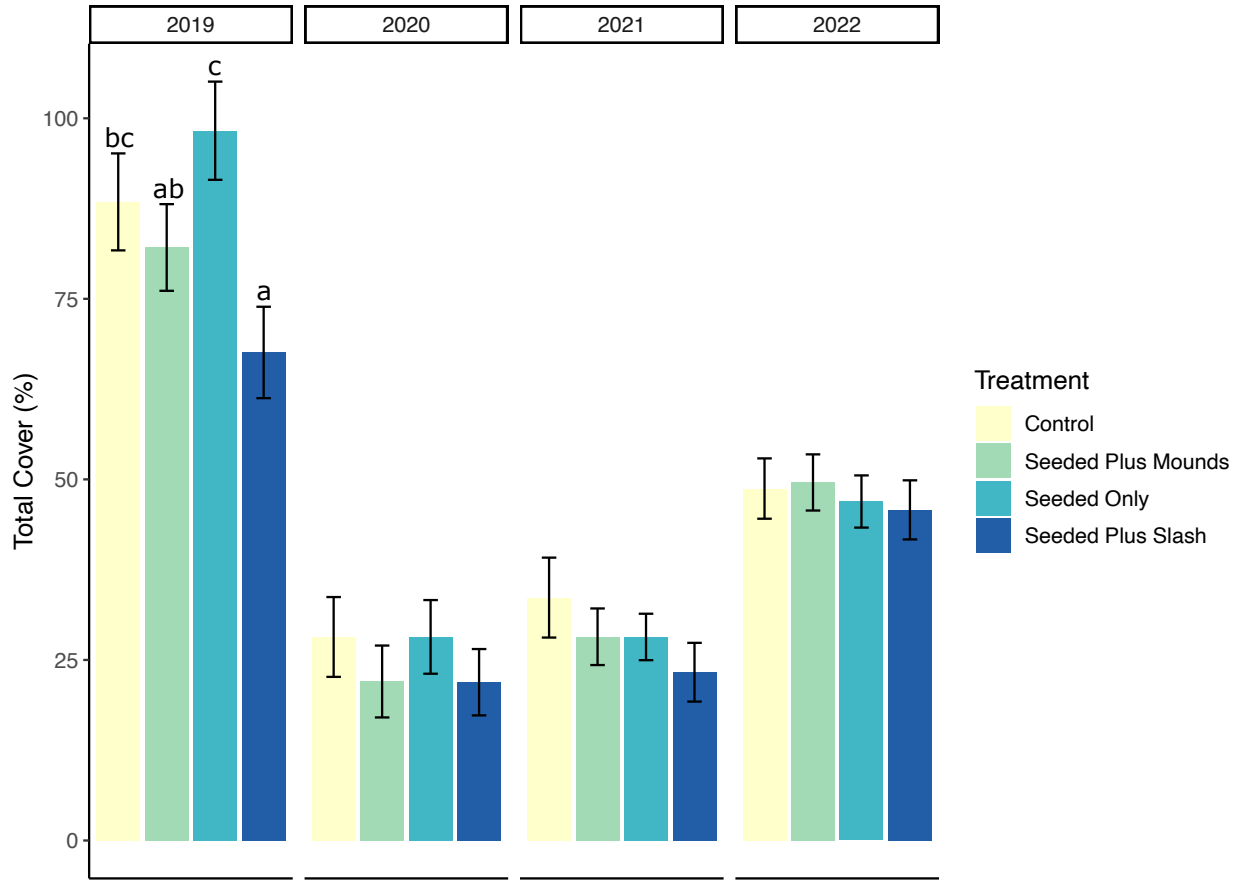


Figure 1.11: Percent cover of total species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was significant in 2019 ($p\text{-adj} < 0.05$). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

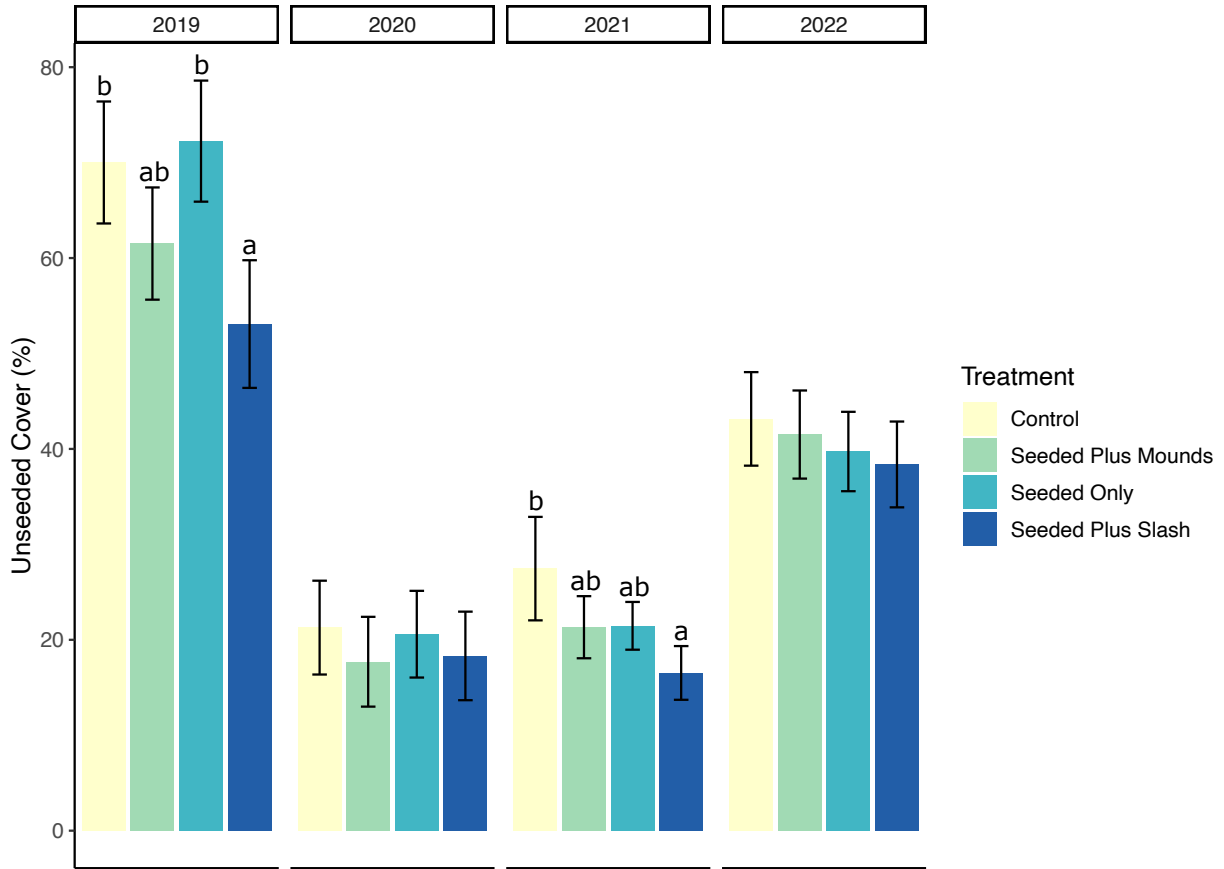


Figure 1.12: Percent cover of unseeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was significant in 2019 and 2021 (p -adj < 0.05). Error bars = SE. Letters indicate Tukey's HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

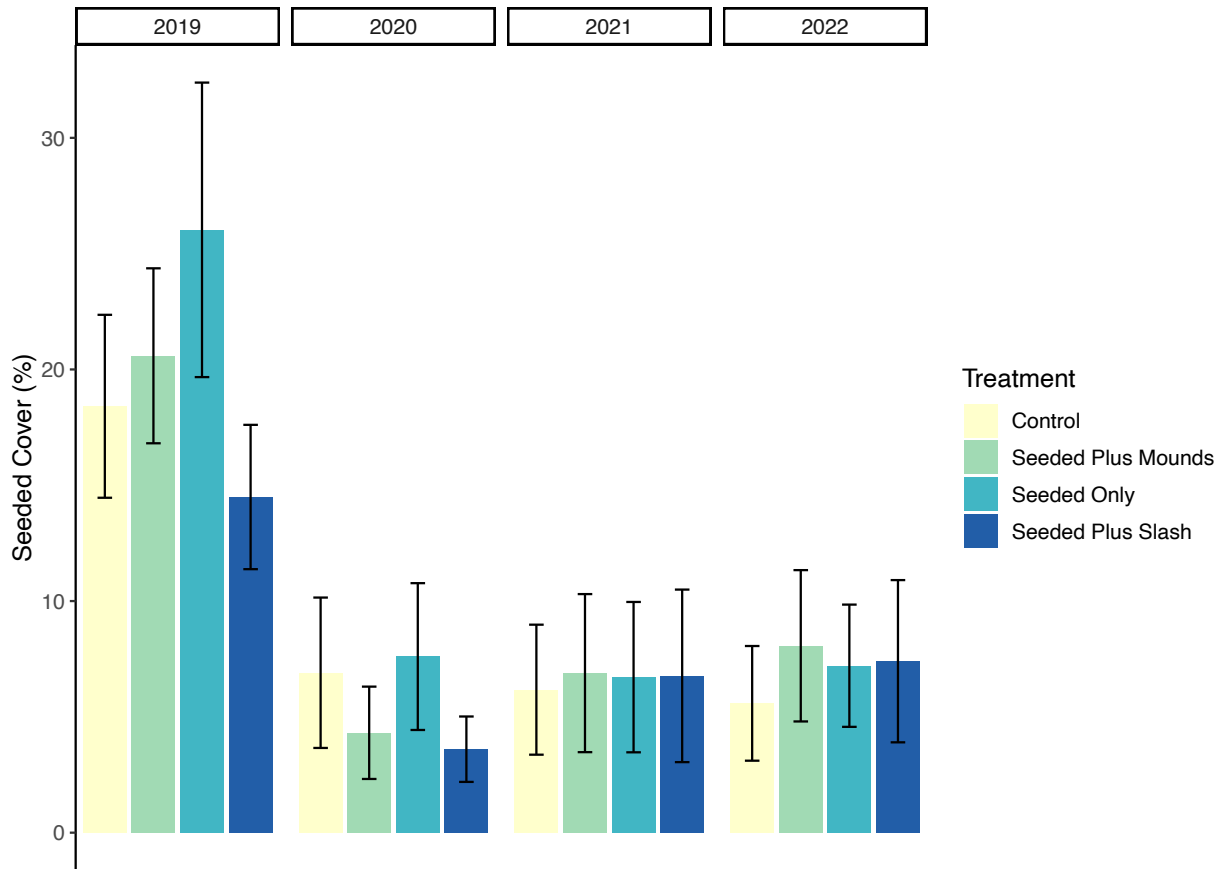


Figure 1.13: Percent cover of seeded species in restoration treatments and controls in California Park. Although the graph includes data from all four years of the study, year was not included in the model. Treatment was not significant in any year due to high variability. Error bars = SE. Letters indicate Tukey’s HSD calculated post-hoc with multcomp cld at $\alpha = 0.05$.

Table 1.2: Seeded species Pielou’s evenness, Shannon Wiener Diversity (H), richness and seeded abundance by site type. Letters indicate Tukey’s HSD calculated post hoc with multcomp cld at $\alpha = 0.05$.

Year	Response	Scab		Timothy		Wyethia	
		Mean	SE	Mean	SE	Mean	SE
2019	Evenness	0.65	0.07	0.66	0.04	0.76	0.02
	H	1.04	0.14 a	1.32	0.11 ab	1.66	0.09 b
	Richness	4.75	0.52 a	7.42	0.67 b	9.46	0.68 b
	Seeded Species Abundance	37.60	5.45	119.00	14.80	99.00	13.00
2020	Evenness	0.17	0.07 a	0.50	0.08 b	0.45	0.06 b
	H	0.15	0.06	0.57	0.10	0.56	0.09
	Richness	0.96	0.21	2.42	0.33	3.08	0.40
	Seeded Species Abundance	6.39	2.18	39.80	8.67	31.60	6.00
2021	Evenness	0.34	0.09 a	0.71	0.03 b	0.67	0.04 b
	H	0.26	0.07 a	0.84	0.05 b	0.86	0.08 b
	Richness	1.21	0.20 a	3.54	0.25 b	3.83	0.36 b
	Seeded Species Abundance	12.80	2.96 a	76.30	10.90 b	44.20	6.82 ab
2022	Evenness	0.19	0.07 a	0.65	0.05 b	0.67	0.05 b
	H	0.15	0.05 a	0.73	0.06 b	0.72	0.06 b
	Richness	1.12	0.18 a	3.21	0.26 b	3.33	0.28 b
	Seeded Species Abundance	18.80	3.65 a	100.00	18.10 b	54.30	7.18 ab

Table 1.3: Total species Pielou’s evenness (J), Shannon Wiener Diversity (H), richness, seeded, unseeded and total percent cover by site type. Letters indicate Tukey’s HSD calculated post hoc with multcomp cld at $\alpha = 0.05$.

Year	Response	Scab		Timothy		Wyethia	
		Mean	SE	Mean	SE	Mean	SE
2019	Evenness	0.54	0.03	0.66	0.02	0.54	0.02
	H	1.26	0.09	1.76	0.07	1.52	0.08
	Richness	10.83	0.54 a	14.46	0.56 ab	17.29	0.58 b
	Seeded Cover (%)	7.41	0.93 a	31.08	4.80 b	21.16	3.23 ab
	Unseeded Cover (%)	58.88	4.76 ab	48.12	4.82 a	85.65	4.25 b
	Total Cover (%)	66.29	4.73 a	79.20	5.36 ab	106.81	4.55 b
2020	Evenness	0.57	0.05 b	0.63	0.04 b	0.23	0.04 a
	H	0.89	0.09 ab	1.24	0.09 b	0.44	0.09 a
	Richness	4.88	0.39 a	7.29	0.43 a	7.29	0.59 a
	Seeded Cover (%)	1.88	0.63	12.94	3.28	1.99	0.65
	Unseeded Cover (%)	6.26	0.98 a	12.09	1.99 a	40.05	4.01 b
	Total Cover (%)	8.14	1.42 a	25.04	3.75 ab	42.05	4.12 b
2021	Evenness	0.39	0.04	0.50	0.04	0.28	0.03
	H	0.64	0.08	1.09	0.10	0.62	0.08
	Richness	5.00	0.30 a	8.96	0.41 b	8.83	0.48 b
	Seeded Cover (%)	0.53	0.11	17.57	4.04	1.81	0.44
	Unseeded Cover (%)	15.99	2.27	17.49	2.73	31.59	3.60
	Total Cover (%)	16.52	2.28	35.06	3.82	33.41	3.63
2022	Evenness	0.39	0.04	0.55	0.03	0.31	0.03
	H	0.74	0.08	1.29	0.08	0.79	0.09
	Richness	6.63	0.34 a	10.75	0.53 b	12.54	0.70 b
	Seeded Cover (%)	1.23	0.31 a	17.46	3.54 b	2.49	0.55 ab
	Unseeded Cover (%)	37.26	2.37 ab	24.61	2.29 a	60.18	2.70 b
	Total Cover (%)	38.49	2.31 a	42.10	2.85 ab	62.67	2.56 b



Figures 1.14 and 1.15: A picture demonstrating the grasshopper outbreak at California Park in the summer of 2020 (top). Photo of *Melanoplus bivittatus* specimen in a study plot in the summer of 2020 (bottom). Both photos used courtesy of Dr. Jayne Jonas.

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CHAPTER II: SHRUB ISLANDS OF OPPORTUNITY FOR DRYLAND RESTORATION

Introduction

There is growing interest in the potential for positive plant interactions, or facilitation, to ameliorate harsh environmental conditions and improve seedling establishment in dryland ecosystems (Huber-Sannwald and Pyke 2005, Holthuijzen and Veblen 2015, Hulvey et al. 2017). In the western United States (US), dryland ecosystems, including sagebrush (*Artemisia* spp.) and saltbush (*Atriplex* spp.) dominated habitats, occupy millions of hectares of land (Blaisdell and Holmgren 1984, Jonas et al. 2018). Livestock grazing, disturbances from human development and climate change have dramatically shifted plant community composition, creating a significant need for restoration and native plant revegetation in these areas (Bainbridge 2007, Duniway et al. 2018, Jonas et al. 2018).

Harsh environmental conditions such as low rainfall and high temperatures make seedling recruitment and subsequent restoration efforts difficult in dryland ecosystems (Bainbridge 2007, Shriver et al. 2018). Natural recruitment is episodic and related to precipitation (Blaisdell and Holmgren 1984). Because natural recruitment is slow, seeding is the most common method of vegetation re-establishment (Merritt and Dixon 2011, Kildisheva et al. 2016). However, attempts to revegetate salt desert and sagebrush shrublands through seeding often fail (Grant-Hoffman et al. 2015, Kildisheva et al. 2016, Svejcar et al. 2017, Shriver et al. 2018, Shackelford et al. 2021). Plant establishment success after seeding is low, with only 2-7% of species persisting past the seedling stage (Chambers 2000, James et al. 2011, Larson et al. 2015). The

majority of plant mortality occurs in the seedling stage due to desiccation. For many species, establishment depends on weather patterns that can provide adequate soil moisture (Blaisdell and Holmgren 1984, Pyke 1990, Jonas et al. 2018).

Levering beneficial relationships between existing and seeded plants can be useful for improving restoration outcomes in high stress environments (Padilla and Pugnaire 2006). In dryland ecosystems, facilitation is performed by ‘nurse plants’ that mitigate the harsh environmental conditions and provide favorable subcanopy sites for seedling establishment (Brown and Porembski 1998, Padilla and Pugnaire 2006). This positive relationship between an adult and immature plant is termed the “nurse plant syndrome”(Niering et al. 1963). Shrubs act as islands of fertility and nurse plants by forming sub canopy microsites where surface soils are nutrient-enriched, cooler and contain higher soil water content compared to interspaces (Moro et al. 1997, Chambers 2001, Davies et al. 2007). *Artemisia tridentata*, the dominant shrub within sagebrush habitats, reduces evapotranspiration, mediates soil temperatures and increases nutrient concentrations and soil water content beneath its canopy (Callaway et al. 1996, Chambers 2001, Davies et al. 2007, Cardon et al. 2013). Furthermore, *Artemisia tridentata* can move water from deep to shallow soil depths via a process called hydraulic lift (Caldwell and Richards 1989). This process benefits neighboring plants, (Caldwell et al. 1998) and studies demonstrate that *Artemisia tridentata* can facilitate perennial grass species (Huber-Sannwald and Pyke 2005, Boyd and Davies 2010, 2012, Holthuijzen and Veblen 2015, Swanson et al. 2021).

The Stress Gradient Hypothesis predicts that facilitation, including the nurse plant syndrome, will increase in environments under high physical stress or high

consumer pressure (Bertness and Callaway 1994). In contrast, competition will be more prevalent in benign environments (Bertness and Callaway 1994). While syntheses generally support this hypothesis (Gómez-Aparicio 2009, He et al. 2013), exceptions exist. For instance, nurse plants may switch to competing with subcanopy plants when resources become limiting (Tielbörger and Kadmon 2000). Furthermore, under extremely stressful conditions facilitation can collapse as the benefits of nurse plants are left ineffective (Michalet et al. 2006, Maestre et al. 2009, Chaieb et al. 2021). Finally, nurse plant sub canopy microsites may prove unsuccessful at facilitating seeded plants if they increase the abundance or biomass of competitive, introduced species (Griffith 2010, Lortie et al. 2021).

Despite this caveat, a growing body of studies demonstrate that seeding and planting beneath shrubs can improve plant establishment in a restoration context (Castro et al. 2002, Huber-Sannwald and Pyke 2005, Michalet et al. 2006, Gómez-Aparicio 2009, Boyd and Davies 2010, 2012). Since establishment and survival of seedlings in dryland systems depends on weather patterns that provide sufficient soil moisture, seeding underneath shrub 'islands of fertility' can increase seedling establishment and survival when harsh environmental conditions are present (Hulvey et al. 2017).

There is growing interest in leveraging facilitation to establish native plant species and improve management efficiency (Hulvey et al. 2017). While there is mounting evidence of the facilitative effect of shrubs on sub canopy plants, studies have not taken place within salt desert shrubland communities. Existing research in sagebrush habitats focuses predominantly on the relationship between a few perennial grass species and

nurse shrubs (Huber-Sannwald and Pyke 2005, Boyd and Davies 2010, 2012, Holthuijzen and Veblen 2015, Swanson et al. 2021). In the study, I seeded a diverse native seed mix consisting of forbs, grasses and shrubs in interspace and subcanopy sites within sagebrush and salt desert shrublands. Increasing the diversity and cover of native forb, grass and shrub species is important due to their role in supporting species such as the *Centrocercus minimus* (Gunnison sage grouse) (Crawford et al. 2004). A diverse native plant community, with a significant forb component, is also an element of preferred habitat for the *Antilocapra americana* (pronghorn) and *Odocoileus hemionus* (mule deer) that use these systems for winter range (Watkins et al. 2007, Grant-Hoffman 2012, Yoakum et al. 2012). Plant functional groups play a significant role in determining the outcome of plant-plant interactions (Soliveres 2012). Consequently, forbs and shrubs may respond differently to shrub canopy compared to perennial grasses.

The objectives of this study were to 1) Determine if seeded native plant establishment differs between subcanopy microsites and interspaces 2) If there is an effect of either treatment on plant establishment, determine if it differs between sagebrush and salt desert shrublands. 3) Identify plant functional groups that beneficially respond to either shrub island or interspace treatments. 4). Identify if surface soil moisture, electrical conductivity, total N, total C, sodium adsorption ratio (SAR), cation exchange capacity (CEC), organic matter and pH differ between interspace and shrub island plots. This information can elucidate potential abiotic mechanisms that contribute to the relationship between shrubs and seeded understory plants. I hypothesized that shrubs would facilitate increased establishment of seeded

plant species compared to interspaces as evidenced by higher seeded species abundance and richness. I expected that this effect would be different between sagebrush and salt desert shrublands. I also anticipated that soil chemical properties would differ between shrub island and interspace plots.

Methods

Study Site Description

Study sites were located outside of Grand Junction, Colorado in Dominguez Escalante and McInnis Canyons National Conservation Areas (NCAs) (Figure 2.1). The two NCAs were formed in 2009 by Omnibus Public Lands Management Act to conserve, protect and restore their outstanding cultural and ecological resources. The NCAs are part of the Colorado Plateau, one of North America's five major deserts centered on the Four Corners of the southwest US. Within the NCAs salt desert shrublands are found at lower elevations and sagebrush shrublands occur at higher elevations (Grant-Hoffman et al. 2012). The sites range in elevation from approximately 1,583 to 2,088m. Between 1991 and 2020 mean annual temperature (MAT) and precipitation (MAP) in Grand Junction were 11.9°C and 232 mm, respectively (PRISM climate group, 1991-2020 climate normals). In 2020, Grand Junction experienced precipitation that was 42% lower than normal and a mean average temperature that was approximately 0.8° C higher than normal (Appendix Table 4). Mean annual precipitation was 6% and 10% greater than normal in 2021 and 2022. Mean annual temperatures were 1.2 and 0.6 ° C higher than normal in 2021 and 2022 respectively.

Soils are derived from sandstone, shale, and mixed alluvium. While soil textures vary, they include sandy loam, loam, silty clay, and silty loam (Grant-Hoffman et al. 2012). Biological soil crusts (BSCs) or communities of living organisms on the soil surface, play a role in increasing soil stability, enhancing moisture, and nutrient retention (Belnap and Gardner 1993). However, they are also vulnerable to degradation by trampling and physical disturbance (Belnap and Gardner 1993, Duniway et al. 2018).

Heavy grazing by livestock since the 1880s has broken up biological soil crusts (BSCs) and caused shifts in plant community composition within the NCAs (Blaisdell and Holmgren 1984, Duniway et al. 2018, Jonas et al. 2018). Starting around 1915, large flocks of sheep were also brought to the area and persistent grazing led to losses in vegetation cover. The Taylor Grazing Act of 1934 limited grazing to some extent, however, heavy use continued until 1957 when the stock driveway closed (Lusby 1979).

Soil disturbance is prevalent today in the form of human development. Energy and transportation infrastructure, mining and recreation disturb the soil and enable the introduction of non-native propagules (Blaisdell and Holmgren 1984, Stier 2012, Jonas et al. 2018). Invasive species present within the study areas include *Halogeton glomeratus* (halogeton), *Eremopyrum triticeum* (annual wheatgrass), *Salsola tragus* (prickly Russian thistle) and *Bromus tectorum* (cheatgrass (Grant-Hoffman 2012, Jonas et al. 2018, Winkler et al. 2018). *Agropyron cristatum* (crested wheatgrass), a non-native seeded pasture grass is also a component of plant communities within sagebrush habitats (Grant-Hoffman et al. 2018).

(a) *Salt Desert Shrublands*

Salt deserts are characterized by their saline or alkaline soils. At our study sites, these conditions can be found on soils underlain or derived from Mancos shale (Lusby 1963, Blaisdell and Holmgren 1984, Duniway et al. 2018). Salinity and alkalinity of surface soils varies spatially and temporally and can depend on precipitation, parent material, vegetation and management (Lusby et al. 1963, Roundy et al. 1984, Jonas et al. 2018).

Salt deserts are considered “cold deserts” with warm to hot summers and cold winters. The frost-free period usually lasts from May to August or September, during which high daytime temperatures and low relative humidity result in high evapotranspiration rates (Lusby 1963, Jonas et al. 2018). Consequently, the time favorable for plant growth can be shorter than the frost-free period (Turner 1971, Blaisdell and Holmgren 1984, Jonas et al. 2018). As a result, plants that live in salt deserts are adapted to some degree of salinity and aridity.

The sparse mosaic of plants is dominated by halotolerant shrub species, primarily of the genus *Atriplex*, and other plants in the Chenopode family. Perennial bunch grasses are patchily distributed and include *Pleuraphis jamesii* (James galleta) (Blaisdell and Holmgren 1984, Duniway et al. 2018, Jonas et al. 2018). Perennial forbs and native annuals can be locally abundant when soil moisture is high (Blaisdell and Holmgren 1984, Jonas et al. 2018). Overall plant cover is sparse, typically less than 20%, and BSCs play a significant role in plant interspaces in intact systems (West 1983, Jonas et al. 2018).

(b) *Sagebrush Shrublands*

Sagebrush shrublands within the study area differ from lower elevation salt desert systems in that they receive on average slightly more precipitation. In contrast to the sagebrush steppe, sagebrush shrublands in the NCA contain less understory herbaceous production, more bare ground, and biological crusts are often present (Boyle and Reeder, 2005). Vegetation is dominated by *Artemisia spp.* including *Artemisia tridentata spp. wyomingensis* (Wyoming big sage). Understory species include grasses such as *Hesperostipa comata (needle and thread)*, *P. jamesii* and *Elymus elymoides* (bottlebrush squirreltail). Forbs include *Achillea millefolium* (yarrow) and *Sphaeralcea coccinea* (scarlet globemallow).

Disturbances such as fire, grazing, extended drought and herbivory play a role in shaping the dynamics of these sagebrush shrublands. Recovery periods after disturbance are typically slow, making restoration difficult in this system (West 1983). Prolonged droughts are common, with forb cover responding to precipitation conditions (Passey et.al. 1982). Habitat for *Centrocercus minimus* (Gunnison sage grouse) is found along the southeast edge of the McInnis Canyons NCA and it is a goal of the Grand Junction Field Office to improve sage grouse habitat in this region (Grant-Hoffman 2012).

Restoration Treatments and Experimental Design

In November of 2020, six study sites containing intact shrub islands were identified in Delta and Mesa County within the Grand Junction Field Office and within or adjacent to McInnis Canyons NCA and Dominguez Escalante NCA (Figure 2.1). In this study, the term shrub island refers to a cluster of shrubs made up of two or more

individuals. Half of the study sites were located within salt desert shrublands and half were located within sagebrush shrublands. At one of the salt desert shrubland sites, the intact shrub islands consisted of *Atriplex confertifolia* (shadscale). At two of the salt desert shrubland sites, the intact shrub islands consisted of *Sarcobatus vermiculatus* (greasewood). In sagebrush shrubland sites, intact shrub islands consisted of *Artemisia tridentata* (big sagebrush).

The study uses a randomized complete block design with three experimental units: site, plot and block. Within each study site, five seeded shrub islands, five seeded interspaces and five unseeded shrub island controls were established. In September of 2022, five additional unseeded interspace plots were added within each study site. Within each block four 1- x 1-m plots were established, two underneath shrub islands and two within adjacent interspaces. Each plot was located at least one meter apart. Seeding treatments were randomly assigned to plots. Within each block, one shrub island and one adjacent interspace were seeded. The unseeded shrub island acted as a control for the seeded shrub island. The unseeded interspace acted as a control for the seeded interspace.

A high diversity seed mix consisting of native annual and perennial forbs, grasses and woody shrubs was selected for seeded shrub island and adjacent seeded interspace plots. Seeds were divided into two seed mixes, one for application at salt desert sites and one for application at sagebrush sites, with 34 and 35 species respectively. Species were seeded at 2,000 pure live seed (PLS) per m² in the fall of 2020 (Table 2.1). Seeded plots were lightly raked before seeding to prepare a seedbed

and again after seeding to incorporate the seed. Each seeded plot was then firmed by tamping. Wood straw mulch was applied at a rate to achieve 50% ground cover.

Vegetation Sampling

Vegetative sampling was conducted in May of 2021 and May and September of 2022 to align with the growing season in Grand Junction, Colorado. Plant establishment of seeded species in May of 2021 was low, and no patterns were identified based on treatment. As a result, I will focus on vegetation data collected in May and September of 2022. In May 2022, density counts of seeded species, percent cover by plant functional group, the species identify of the shrub, ground and canopy cover were assessed in 90 plots. In September of 2022, this was expanded to 120 plots due to the addition of unseeded interspace plots to the study.

To account for variability in seeded plant density between sagebrush and salt desert sites, vegetation sampling occurred at two scales. I collected data at both the full plot, or 1- by 1-m scale, and at the quadrat scale. For quadrat sampling, four 20- by 30-cm sampling frames were placed in each plot in a manner that allowed a 10-cm buffer around the edge of the plot (Figure 2.2). Within each quadrat, I recorded the number of individual seedlings of each seeded species rooted inside the frame. If plant counts of any seeded species were above 50, then the number of individuals was counted solely within the four 20- by 30-cm frames. Because establishment rates are low in dryland systems, I also collected density counts of seeded species for the full 1- by 1-m frame.

Seeded species were identified to species using USDA nomenclature. A modified Daubenmire (1959) method was used to collect cover by plant functional group in each frame and within the 1- by 1- m plot. Plant functional groups included 1. Native

perennial forb 2. Native perennial graminoid 3. Native annual forb 4. Native annual graminoid 5. Introduced perennial forb 6. Introduced perennial graminoid 7. Introduced annual forb 8. Introduced annual graminoid 9. Succulent. The modification of the Daubenmire cover classes included an additional "Trace" cover class for the occurrence of items with <1% cover. Ground cover, and shrub canopy cover were also collected within each frame and within the 1- by 1-m plot using the modified Daubenmire cover classes (1959). Ground cover classes included bare ground, moss, litter, wood straw, rock, biological soil crust and cow scat.

Soil Sampling

In May of 2021, soil temperature was measured within each plot using an UEI INF215 Scout III Infrared Thermometer. Temperatures (°C) were collected within each of the four sampling frames and averaged. In May of 2021, I also collected a soil core in the northwest quadrant of each sampling frame using a soil probe. The four cores from each plot were combined in a tray and transferred into a whirl pak bag. Soil samples were analyzed for gravimetric soil water content (i.e., soil moisture) in the lab. In September and November of 2021, I returned to each plot to collect additional soil samples. In September, I collected a soil core to a depth of 5 cm from the four corners of each plot, sifted the soil through a sieve into a bucket and then transferred the soil into a Ziplock bag. Soil was analyzed for soil moisture in the lab. In addition, the soil was sent to Ward Labs for analysis of pH (0.1 M CaCl), organic matter (LOI %), sum of cations (CEC) (me/100g), Potassium (K), Calcium (Ca), Magnesium (Mg) and Sodium (NA) ppm. I calculated Sodium Adsorption Ratio by converting the concentration of magnesium, calcium and sodium to meq/100g and then plugging variables into the

equation $SAR = [Na]/\left(\frac{[Ca]+[Mg]}{2}\right)^{1/2}$. In November of 2021, I returned to each plot and collected a soil core up to 5 cm in the corner of each plot, in a spot adjacent to the former sampling site. Similar to May of 2021, the four cores were combined in a tray and transferred into a whirl park bag. Soil samples were analyzed for soil moisture in the lab. To reduce the impacts of soil collection on study plots, in May of 2022 soil samples were collected from beneath approximately 6 random interspaces and 6 random shrub islands within each study site. Since I sampled shrubs that were not already included in the study, collection numbers differed slightly between sites depending on shrub availability. Per previous methods, at least 5 soil cores, up to 5 cm, were collected within each interspace and shrub island. The soil was combined in a tray and transferred into a whirl pak bag. Soil samples were analyzed for soil moisture in the lab and sent to Colorado State University EcoCore Analytical facility for analysis of total N % and total C % and the Soil, Water and Plant Testing Lab at Colorado State University for analysis of electrical conductivity (EC) (mmho/cm).

Statistical Analyses

A linear mixed- effects modelling approach was used to analyze the effect of treatments on response variables using the package lme4 (Bates et al. 2015) in R 4.1.2 (R Core Team 2021). Separate models were run for each response variable including seeded species abundance, richness, vegetative cover by plant functional groups and measures of surface soil chemical properties, temperature and moisture.

A linear mixed effects modelling approach was used to analyze the effect of treatments on seeded species abundance and richness using the package lme4 (Bates et al. 2015). This modeling approach incorporated the effect of ecosystem type

(i.e., sagebrush or salt desert) treatment (i.e., interspace control, seeded interspace, shrub island control, seeded shrub island) and their interaction as fixed effects, and the block and site as random effects. I will refer to ecosystem type as “system.” Density counts of seeded species were converted to plants m^{-2} for each frame sampled, and the mean of the four quadrats calculated to give a mean plants m^{-2} . Since establishment levels were low, counts of individuals not contained within the frames, but that occurred in the 1- by 1-m plot, were included in analyses. Plant abundance values and species richness were calculated for each plot using the `specnumber` function in the `vegan` package in R (Oksanen et al. 2019). Seeded plant species abundance of each species was summed for each plot to give the total seeded species plant abundance. Response variables were square root or log transformed if necessary to meet assumptions of normality. Models were run separately for May and September data due to the addition of unseeded interspace control plots to the study in September. In May of 2022, I used Dunnett’s comparisons to assess differences between seeded shrub island treatments and the seeded interspace and unseeded shrub island treatments for plant density data. I used pairwise comparisons to compare all treatments using plant density data from September 2022. An $\alpha = 0.05$ was used for significance testing as a threshold for assigning statistical differences. When significant main or interaction effects were found I assessed differences using `emmeans` multiple comparison tests (Lenth 2019).

A linear mixed-effects modelling approach was also used to analyze the effect of treatments on vegetative cover by plant functional group (i.e., annual forb, annual grass, introduced annual forb, introduced annual grass, perennial forb, perennial grass, succulent and shrub) using the package `lme4` (Bates et al. 2015). This modeling

approach incorporated the effect of system, treatment and their interactions as fixed effects, and the block and site as random effects. Percent cover of plant functional groups was assessed by taking the average cover of the four quadrats sampled. When analyzing percent vegetative cover data from May 2022, I used Dunnett's comparisons to assess differences between seeded shrub island treatments and seeded interspace and unseeded shrub island treatments. When analyzing percent vegetative cover data from September 2022, I used pairwise comparisons to compare all treatments to each other. Response variables were square root, cube root or log transformed if necessary to meet assumptions of normality. It should be mentioned that when running linear mixed effects models, not all functional groups met assumptions of normality. This is due in part to a high number of zeros for several plant functional groups in the salt desert system.

A linear mixed- effects modelling approach was also used to analyze the effect of treatments on surface soil moisture, temperature, pH, CEC, EC, SAR, total N, total C and organic matter using the package lme4 (Bates et al. 2015). This modeling approach incorporated the effect of system, treatment and their interactions as fixed effects, and the block and site as random effects. Response variables were log or square root transformed if necessary to meet assumptions of normality. Analyses for electrical conductivity, total N and total C contain unbalanced sample sizes due to collection limitations. I used pairwise comparisons to compare surface soil chemical properties between interspace and shrub treatments. An $\alpha = 0.05$ was used for significance testing

as a threshold for assigning statistical differences. When significant main or interaction effects were found I assessed differences using emmeans multiple comparison tests (Lenth 2019).

Results

Seeded Species Establishment in Subcanopy Microsites versus Interspaces

In May of 2022, the interaction between treatment and system significantly impacted both seeded species richness and seeded species abundance (Appendix Table 5). In salt desert shrubland sites, seeded interspace plots had greater seeded species richness and seeded species abundance than seeded shrub island plots (Figures 2.3 and 2.4). In contrast, in sagebrush shrubland sites, there was not a significant difference between seeded shrub island and seeded interspace plots in terms of seeded species richness or abundance (Figures 2.3 and 2.4). However, seeded shrub island plots demonstrated higher seeded species richness than unseeded shrub island control plots in May (Figure 2.3). This indicates that there was an initial effect of seeding in sagebrush sites.

In September 2022, there was no longer a two-way interaction between treatment and system on seeded species richness and abundance. Instead, treatment had a significant effect on seeded species richness but not seeded species abundance (Appendix Table 5). Seeded interspace plots had higher species richness than all other plot types (Figure 2.5). In contrast to results from May, there were no discernable differences between treatment plots in terms of seeded species abundance in either system (Figure 2.6).

Native Plant Establishment Differences between Sagebrush and Salt Desert Systems

In May and September of 2022 seeding beneath shrub islands did not improve seeded species richness or abundance compared to seeding in interspaces. In salt desert shrubland sites, seeded interspaces contained higher species richness than seeded shrub islands in May and September. This pattern was observed in sagebrush sites in September. Consequently, seeding in interspaces was consistently effective at increasing native plant establishment in the salt desert.

Findings indicate that species richness and abundance tend to be higher in sagebrush sites compared to salt desert sites, regardless of seeding efforts. The interaction between treatment and system impacted seeded species richness and abundance in May and system impacted seeded species richness and abundance in September (Appendix Table 5). In May, seeded treatment plots within sagebrush sites had higher species richness than shrub island plots within salt desert sites (Figure 2.3). Furthermore, seeded treatment plots in sagebrush shrubland sites had higher seeded species abundances than seeded shrub island plots in the salt desert (Figure 2.4). Overall, seeded species abundance and richness were higher in sagebrush shrublands than in salt desert shrublands in September of 2022 (Figures 2.5 and 2.6).

Plant Functional Group Responses to Treatment Type

(a) May 2022

After running the linear mixed effects model, the interaction between treatment and system significantly impacted perennial grass ($p=0.010$), introduced perennial grass ($p=0.010$), introduced annual forb ($p=0.037$) and native annual forb ($p=0.006$) cover. Perennial grass cover was higher in seeded interspaces than seeded shrub

islands plots within salt desert shrublands (Table 2.2). Native annual forb cover was higher in seeded interspace plots compared to seeded shrub islands within sagebrush sites (Table 2.2). There was no cover of annual forbs within shrub island plots in the salt desert. Consequently, seeded interspaces contained higher native annual forb cover than both shrub island plots (Table 2.2). Introduced perennial grass cover was higher in seeded shrub islands than seeded interspaces in sagebrush habitats (Table 2.2). There was no cover of introduced perennial grasses in the salt desert. No ecologically relevant pairwise comparisons were found for introduced annual forb cover. No other plant cover types were impacted by treatment or the interaction between treatment and system. Perennial forb ($p=0.018$) cover was significantly impacted by system and was higher in sagebrush shrublands (1.46 ± 0.39) compared to salt desert shrublands (0.02 ± 0.02).

(a) September 2022

The interaction between treatment and system was significant for introduced perennial grass ($p < 0.001$), introduced annual grass ($p=0.043$), perennial forb ($p=0.001$) and native annual forb cover ($p=0.010$) in September of 2022. Shrub island treatment and control plots contained higher cover of introduced perennial grass compared to interspace treatment and control plots within sagebrush habitats (Table 2.3). Since cover of introduced perennial grasses was zero in salt desert sites, there were no differences between shrub island treatment and control plots in terms of introduced perennial grass cover. For perennial forbs, seeded and unseeded interspaces had higher cover than seeded and unseeded shrub island plots in sagebrush shrubland sites (Table 2.3). Perennial forb cover was only found in sagebrush habitats in September of 2022. Interspace control plots contained higher

cover of annual forbs than shrub island control and treatment plots at sagebrush sites (Table 2.3). There was no annual forb cover found in salt desert sites. While the interaction between treatment and system was significant for introduced annual grass cover, no differences were found when running pairwise comparisons in emmeans (Table 2.3). In addition, while treatment was found to have a significant impact on perennial grass cover, there were no ecologically relevant pairwise comparisons (Table 2.3). No other plant cover types were impacted by treatment, system or the interaction between treatment and system.

Seeded Species Responses to Treatment Type

Sampling conducted in May of 2022 found 17 out of 40 species (43%) located across study plots within the NCAs (Table 2.4). Only three of the 34 species (9%) seeded in the salt desert system were found in salt desert plots (Table 2.4). In contrast, 16 out of the 35 species (46%) seeded in the sagebrush system were located in plots within this system (Table 2.4). Sampling conducted in September of 2022 found 9 out of 40 species (23%) located across restoration lots (Table 2.5) Only two of the 34 species (6%) seeded in the salt desert were located in salt desert plots (Table 2.5).

In contrast, seven out of 35 species (20%) seeded in the sagebrush system were found within sagebrush plots (Table 2.5).

Many of the species in the seed mix were also found in control plots. For instance, *B. gracilis* and *V. octoflora* were found in control plots (Tables 2.4 and 2.5). However, certain species such as *A. millefolium*, *D. reptans*, *C. lutea*, *I. aggregate*, *L. lewisii*, *S. parvifolia*, *L. argenteus*, *G. viscosissimum*, and *H. multiflora* were only found in seeded plots. (Table 2.4 and 2.5). *D. reptans*, *H. multiflora*, *I. aggregata*, *L. argenteus*,

and *S.parvifolia* were only found in seeded interspace plots (Tables 2.4 and 2.5). In contrast, *G. viscosissimum* was the only seeded species to be found solely in seeded shrub island plots (Table 2.4). *A.millefolium*, *C. lutea* and *L. lewisii* were found in both seeded interspace and seeded shrub island plots (Tables 2.4 and 2.5).

Surface Soil Differences Between Treatment Types

After running the linear mixed effects models, treatment was found to have a significant effect on average soil surface temperature ($p < 0.001$), but not soil moisture ($p = 0.982$). Shrub island plots were 6.6°C cooler on average than interspace plots. The mean soil moisture in interspaces was 5.46% (± 0.53) and the mean soil moisture in shrub islands was 5.57% (± 0.56).

There was a two-way interaction between treatment and system when running linear mixed models for response variables including SAR ($p = 0.001$), EC ($p < 0.001$), total N ($p = 0.005$), total C ($p < 0.001$), CEC ($p = 0.020$), organic matter ($p = 0.035$) and pH ($p = 0.002$) (Table 2.6). Across all study plots, surface soil SAR ranged from 0.03 to 24.23 meq/L with a mean of 2.75 meq/L. Shrub Island plots within the salt desert had higher surface soil SAR values than interspace plots in the salt desert. In addition, surface soils beneath shrub island plots in the salt desert had higher SAR values than interspace and shrub island plots with sagebrush sites (Table 2.6). Across all study plots, EC values were variable and ranged from 0.68 to 12.20. Electrical conductivity followed a similar pattern to SAR values and shrub island plots within the salt desert had higher surface soil EC values than interspace plots in the salt desert (Table 2.6). In addition, EC values in salt desert shrub island plots were greater than both interspace and shrub island plots in the sagebrush (Table 2.6).

Surface soil samples collected within sagebrush habitats had lower pH levels compared to samples collected in salt desert habitats (p -value=0.005). Within salt desert sites, shrub island treatment plot pH levels were more alkaline than interspace plots (Table 2.6). Cation exchange capacity followed a similar pattern and soil samples collected in sagebrush habitats had generally lower CEC values than soil samples collected in the salt desert (p -value = <0.001). Within salt desert sites, shrub island treatment plots had higher CEC values than interspace plots (Table 2.6). Cation exchange capacity was not different between surface soils in interspaces compared to surface soils beneath shrub islands in sagebrush habitats (Table 2.6).

In both salt desert and sagebrush sites, total N and total C were higher in soil samples collected beneath shrub islands than soil samples collected in interspaces (Table 2.6). Shrub island plots in the salt desert contained higher total C than all other plot types (Table 2.6). Similar to trends in total N and C, plots that received the shrub island treatment had higher organic matter in both sagebrush and salt desert habitats compared to plots that received the interspace treatment (Table 2.6).

Discussion

There is a strong need for restoration practices that ameliorate harsh environmental conditions and improve seeding success rates in dryland ecosystems. I evaluated whether seeding beneath shrub islands can facilitate seedling establishment in sagebrush and salt desert habitats, and if these habitats responded differently to the treatments. In addition, I explored what plant functional groups benefited from these treatments and how soil chemical properties differed between treatment types.

Effects of Treatments in Salt Desert Shrublands

In the salt desert, negligible seeded species establishment occurred in shrub island plots. Soil analyses indicate that this may be due to sodic and saline conditions within these microsites. The study sites lie on top of Mancos shale, a geologic formation which contains a high concentration of mineral salts and can promote saline, or alkaline soil conditions. (Lusby 1963, Duniway et al. 2018, Jonas et al. 2018). *Atriplex* spp. can lead to increased zones of surface salinity by redistributing salts from deeper to shallower soils (Roundy et al. 1984, Ungar 1984, Jonas et al. 2018). Furthermore, soils beneath *S. vermiculatus* can be higher in exchangeable Na⁺ percentage compared to interspaces due to senescence of plant parts (Ungar et al. 1984). As a result, it is not surprising that I observed higher average SAR and EC values in salt desert shrub island plots compared to salt desert interspace plots.

Additional analyses demonstrated that whether plots reached sodic or saline thresholds depended on the shrub species present (Appendix Table 6). When shrub islands consisted of *S. vermiculatus*, SAR values were greater than when shrub island plots consisted of other shrub species. The mean soil surface SAR beneath *S. vermiculatus* was 11.55 meq/L and ranged up to 24 meq/L. In addition, underneath the canopy of *S. vermiculatus*, mean surface soil pH equaled 9.9. Sodic soils are characterized by a pH over 8.5 and SAR above 13.

Soils with an SAR above 13 can pose problems for plant emergence and growth due to effects on water uptake by plants, nutrient availability and impermeability of soils (Donahue et al. 1983, Stavi et al. 2021). Problems with sodicity can emerge earlier depending on soil type, drainage conditions and when plants are young. Furthermore,

pH values over 8.5 can create alkaline conditions that are be toxic for plants (Stavi et al. 2021). While the mean SAR value was close to meeting the threshold for sodic soils in shrub island plots with *S. vermiculatus* cover, since I measured plant establishment, effects may be prominent even at lower levels. In addition, pH values exceeded the threshold for sodic soils. Consequently, in shrub island plots with *S. vermiculatus* cover, seeded species may be particularly at-risk of low emergence due to SAR and pH values indicative of sodic soils (Donahue et al. 1983). In shrub island plots with *S. vermiculatus* cover, mean EC values equaled 4.76 mmho.cm, which meets the criteria for saline soils. As a result, there may be compounding issues of sodicity and salinity in these plots.

The results support evidence that there is high spatial variability of salinity and sodicity found in salt desert surface soils (Jonas et al. 2018). Saline, sodic and sodic-saline soils were more prevalent in shrub island sub canopy plots due to the influence of overstory shrubs (Ungar et al. 1984). However, certain shrub species may have a stronger influence on salinity and sodicity, and I found higher levels of SAR under *S. vermiculatus* compared to *A. confertifolia*. As a result, *S. vermiculatus* subcanopies contain challenging conditions for seedling emergence and establishment. In contrast, interspace sites did not meet criteria for sodic or saline soils and thus may be more hospitable for seedling establishment in salt desert habitats.

Across both treatment types, plant establishment was generally low in the salt desert. By September of 2022, seeded species established in only 20% of salt desert plots. While I seeded native halotolerant plant species, including *A. canascens*, *A. confertifolia* and *S. vermiculatus*, very few of these species established. The majority of

seed was obtained from commercial sources due to barriers acquiring locally collected seed. Locally sourced populations generally experience higher survival and fitness than non-locally sourced populations (Baughman et al. 2019). For instance, transplanted seedlings of a local *A. canescens* ecotype experienced a 67% survival rate. The literature indicates that locally adapted seed and transplants may be better suited for soil conditions found in salt desert shrubland restoration sites.

Effects of Treatments in Sagebrush Shrublands

In the sagebrush system, species richness in shrub island plots was equivalent to interspace plots in May and lower than interspace plots in September. Seeded species abundance did not differ between treatment plots in either month. Shrub islands may not act as nurse plants for seedling establishment due to the indirect competitive effects of introduced perennial grass cover. The most ubiquitous introduced perennial grass at the sites was *A. cristatum*. Cover of *A. cristatum* is shown to competitively interfere with and impede efforts to establish native plant species through seeding (Gunnell et al. 2010, Knutson et al. 2014, McAdoo et al. 2017). In addition, studies demonstrate that *A. cristatum* can be facilitated by *Artemisia* canopy, which may explain its higher cover in shrub island subcanopies compared to interspaces (Boyd and Davies 2010). Seed banks and cover of *A. cristatum* may need to be reduced, or avoided when initiating seeding efforts.

Functional Plant Group Responses to Treatment Type

Treatment type significantly impacted percent cover of certain plant functional groups. Annual forb cover was consistently higher in interspace plots compared to shrub island plots in the sagebrush system. Annual forbs are frequently light

demanding, ruderal species that exhibit traits associated with rapid resource acquisition (Ning et al 2022). Plants with high resource consumption rates are associated with sensitivity to competition with neighboring plants (Liancourt et al. 2005). As a result, annual forbs may perform worse underneath a shaded shrub canopy. In contrast to previous studies in sagebrush systems, perennial grass species were not facilitated in seeded shrub microsites when compared to seeded interspace plots (Boyd and Davies 2010, Holthuijzen and Veblen 2015). It is worth mentioning that other studies selectively chose sites without high cover of introduced and invasive grass species (Holthuijzen and Veblen 2015). As noted previously, introduced perennial grass cover was higher in shrub island plots, which may be a relic of past facilitation.

Seed Mix Species Selection

Seeding efforts were effective at introducing new native species to the salt desert and sagebrush restoration sites. The perennial forb species *L. lewisii* and *S. parvifolia* were found solely in seeded treatment plots. In addition, these two species were observed in both May and September monitoring efforts. Specifically, *L. lewisii* was found in both seeded treatment plot types and both systems. In contrast, certain species such as the annual grass *V. octoflora* and perennial grasses *P. jamesii* and *B. gracilis* were found in substantial densities within control plots. This suggests that these grass species are establishing without assistance from seeding efforts. Within salt desert shrubland sites, few species were successful at establishing within seeded plots. Successful species included *P. jamesii*, *L. lewissii* and *P. secunda*. It should be noted that *P. jamesii* occurred in both seeded and control plots and may not have been introduced by seeding efforts.

Conclusions and Management Implications

In contrast to expectations, seeding in interspaces improved plant establishment compared to applying these practices beneath shrub islands. This effect was more consistent in salt desert habitats and was observed in both May and September. In sagebrush sites this effect was only observed in September. These findings are important because they indicate managers can target interspaces for seeding efforts where seeding equipment is less likely to damage existing shrub islands.

In the salt desert, sodic and saline soils underneath shrub islands may prevent establishment of seeded species. Species found within salt desert study plots can initiate plant soil feedbacks which make it more difficult for less halotolerant species to establish (Ungar 1998). Specifically, I found evidence that salinity and sodicity issues are stronger under *S. vermiculatus* canopies. Consequently, seeding efforts underneath the canopy of *S. vermiculatus* should be avoided.

Overall, seeded plant establishment in the salt desert was low and additional studies should analyze the efficacy of applying locally adapted seed or transplants. While acquisition of locally adapted seed is difficult (Johnson et al. 2010), it may be advantageous to include seed that is collected within close geographic proximity to the restoration site within similar environmental conditions (Johnson et al. 2010, Baughman et al. 2019). Seed transfer zones have been developed for the Colorado Plateau to identify areas with similar climates where seed can be transferred and still well adapted to the site. However, seed transfer zones should be applied judiciously in salt desert shrublands since these indices do not include measures of soil properties (Shryock et al. 2018). If surface soils experience salinity or sodicity, the use of locally adapted

transplants may also be useful in achieving revegetation goals due to their more developed root systems (McFarland et al. 1990).

For physical, non-resource stresses such as salinity, reviews have found that biotic interactions are positive at low stress and grow increasingly positive with more stress (He et al 2013). However, there is evidence facilitation may collapse at high levels of stress (Michalet et al. 2006). While salt desert shrubland sites shrub island plots contained a wide range of sodicity and salinity levels, facilitation was not evident. Further research on how plant interactions are impacted along gradients of salinity and sodicity within dryland ecosystems may be useful for restoration in salt desert shrublands.

At sagebrush sites, cover of *A. cristatum* may be impeding establishment by native seeded species in seeded shrub island treatment plots. Before application of seed, it is recommended to reduce cover of and seeds of *A. cristatum* in the seed bank. Frequently this is done through the application of glyphosate (McAdoo et al. 2017). In the study *A. cristatum* cover was primarily in shrub island plots. Since glyphosate is a non-selective herbicide, it could cause overstory shrub mortality, which is not desired. Consequently, it may be advantageous to target seeding in interspace or intermediate areas without cover of *A.cristatum*.

Seeding in intermediate zones, or areas between canopy dripline and up to 1 m away from shrub canopy, may enable seedlings to benefit from shrub island islands of fertility while avoiding competitive effects of shrubs and associated introduced perennial grasses (Huber-sannwald and Pyke 2005). In both sagebrush and salt desert systems, plots located beneath shrub canopy contained higher total N %, total C% and organic

matter and buffered soil temperatures. However, shrubs can potentially influence nutrients, such as N concentrations, up to 0.89 m away from shrub center (Mudrak et al. 2014). Further studies are needed in sagebrush systems to determine if seeding in intermediate zones may prove beneficial for seedling establishment under harsh environmental conditions.

In dryland systems, seed establishment is promoted by weather patterns that can increase soil moisture. Advances in climate forecasting may allow managers to align seeding efforts with periods of higher precipitation, and thus water availability for emerging plants. Periodic climate oscillations, such as El Niño Southern Oscillation (ENSO) are associated with higher precipitation from April to October on the Colorado Plateau and in the Great Basin (Ropelewski and Halpert 1987). Currently ENSO can be forecasted between 6 months and 1 year ahead of time (Tang et al. 2018). If managers utilize ENSO forecasting to align seeding efforts with periods of predicted higher precipitation, restoration outcomes may be improved in dryland ecosystems (Bradford et al. 2018).

Certain plant species in the study may be valuable in future seed mixes. A few species were successful at establishing in salt desert shrublands. Successful species included *P. jamesii*, *L. lewissi* and *P. secunda*. Consequently, it may be advantageous to include these species in future seed mixes for the salt desert. Since land managers are interested in increasing forb cover in sagebrush shrublands due to its implications for wildlife habitat (Grant-Hoffman 2012), successful forb species such as *L. lewisii* and *S. parvifolia* would be beneficial to include in seed mixes for sagebrush habitats within the NCAs.

Across restoration sites, identifying key barriers to seedling establishment, such as sodicity, salinity and introduced species, and effectively targeting barriers to restoration efforts can improve restoration success (Copeland et al. 2021). Results suggest that interspaces are more favorable for seeded plant establishment, where competitive effects of introduced perennial grasses are lower in sagebrush shrublands and salt desert soils are more hospitable for plant establishment.

TABLES AND FIGURES

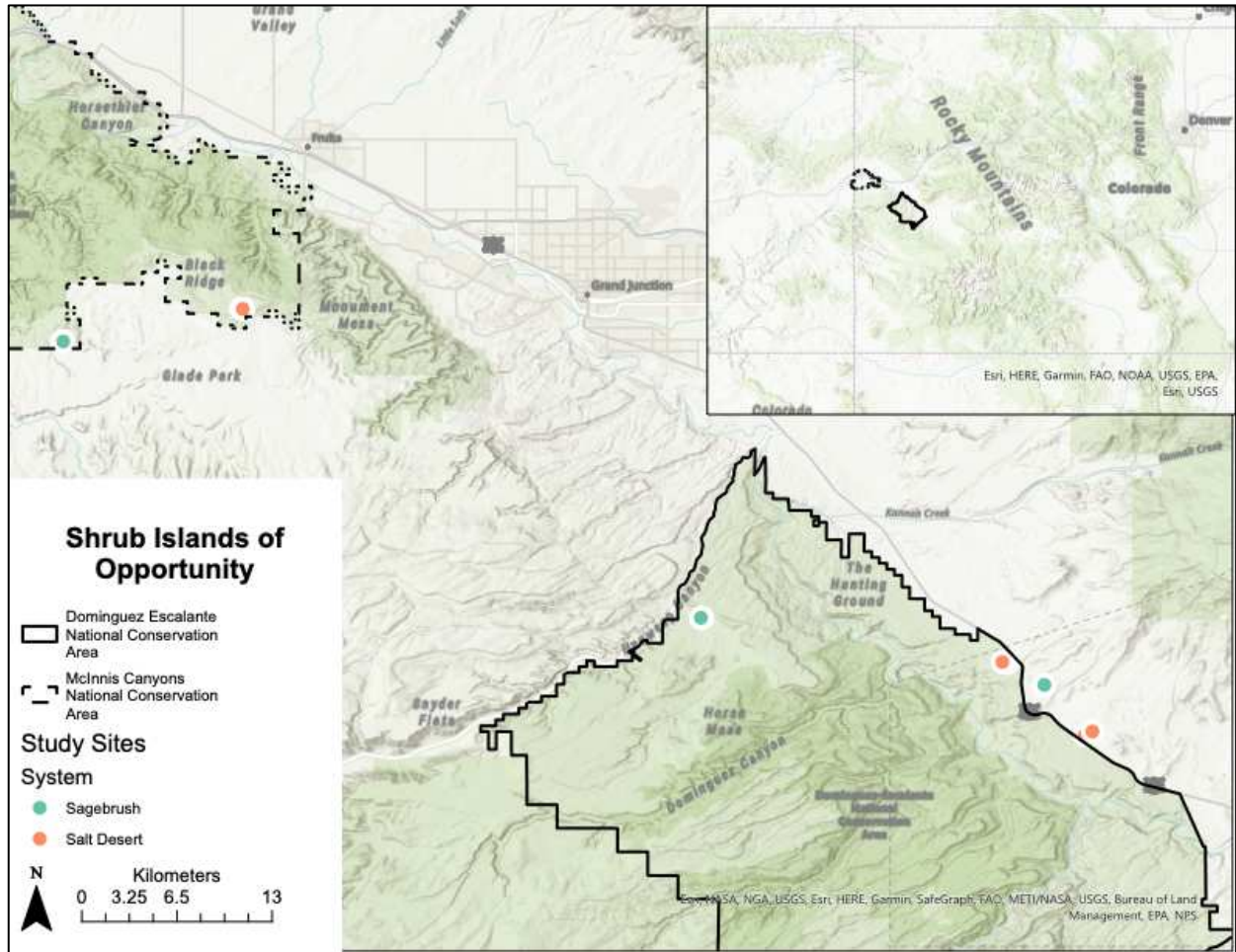


Figure 2.1: Map of six study sites, 3 were in salt desert shrublands and 3 were in sagebrush shrublands. All sites were within or adjacent to Dominguez Escalante and McInnis Canyons National Conservation Areas.

Table 2.1: A list of the native herbaceous and woody species included in the seed mix and pure live seeds (PLS) applied per 1-m² plot. Plant names and functional groups follow USDA (2020)¹. Seed sources included commercial sources, the Upper Colorado Environmental Plant Center (UCEPC) and the Germplasm Resources Information Network (GRIN) managed by the Agricultural Research Service of the United States Department of Agriculture (USDA).

Species	Plant Functional Group	Source	System	Salt Desert PLS/m ²	Sagebrush PLS/m ²
<i>Achillea millefolium</i>	Perennial Forb	Commercial sources	Both	40	40
<i>Artemisia frigida</i>	Perennial Shrub	Commercial sources	Both	100	100
<i>Astragalus convallarius</i>	Perennial Forb	Commercial sources	Both	60	60
<i>Astrida purpurea</i>	Annual/Perennial Grass	Commercial sources	Both	40	40
<i>Atriplex canescens</i>	Perennial Shrub	Commercial sources	Both	80	80
<i>Atriplex confertifolia</i>	Perennial Shrub	Commercial sources	Both	80	80
<i>Bouteloua gracilis</i>	Perennial Grass	Commercial sources	Both	40	40
<i>Chaenactis douglasii</i>	Biennial/Perennial Forb	Commercial sources	Both	20	20
<i>Cleome lutea</i>	Annual Forb	Commercial sources	Both	60	40
<i>Draba reptans</i>	Annual Forb	Commercial sources	Both	40	40
<i>Elymus elymoides</i>	Perennial Grass	Commercial sources	Both	40	40
<i>Elymus elymoides elymoides</i>	Perennial Grass	UCEPC	Both	40	40
<i>Ericameria nauseosa</i>	Perennial Shrub	Commercial sources	Both	100	100
<i>Eriogonum umbellatum</i>	Perennial Forb	Commercial sources	Both	100	100
<i>Ipomopsis aggregata</i>	Biennial/Perennial Forb	Commercial sources	Both	71	60
<i>Linanthus pungens</i>	Perennial Forb	Commercial sources	Both	80	80
<i>Linum lewisii</i>	Perennial Forb	Commercial sources	Both	40	40
<i>Oenothera pallida</i>	Biennial/Perennial Forb	Commercial sources	Both	80	40
<i>Penstemon comarrhenus</i>	Perennial Forb	Commercial sources	Both	80	80
<i>Phacelia crenulata</i>	Annual Forb	Commercial sources	Both	60	40
<i>Pleuraphis jamesii</i>	Perennial Grass	Commercial sources	Both	40	40

Table 2.1 Continued

<i>Poa fendleriana</i>	Perennial Grass	Commercial sources	Both	40	20
<i>Poa secunda</i>	Perennial Grass	UCEPC	Both	40	20
<i>Pseudoroegneria spicata</i>	Perennial Grass	Commercial sources	Both	40	40
<i>Sarcobatus vermiculatus</i>	Perennial Shrub	Commercial sources	Both	80	80
<i>Sphaeralcea parvifolia</i>	Perennial Forb	Commercial sources	Both	80	80
<i>Sporobolus airoides</i>	Perennial Grass	Commercial sources	Both	40	40
<i>Sporobolus cryptandrus</i>	Perennial Grass	Commercial sources	Both	60	60
<i>Vulpia octoflora</i>	Annual Grass	Commercial sources	Both	80	40
<i>Artemisia tridentata</i> ssp. <i>tridentata</i>	Perennial Shrub	Commercial sources	Sagebrush		100
<i>Castilleja linariifolia</i>	Perennial Forb	Commercial sources	Sagebrush		60
<i>Geranium viscosissimum</i>	Perennial Forb	Commercial sources	Sagebrush		40
<i>Heliomeris multiflora</i>	Perennial Forb	Commercial sources	Sagebrush		40
<i>Leymus cinereus</i>	Perennial Grass	Commercial sources	Sagebrush		40
<i>Lupinus argenteus</i>	Perennial Forb	Commercial sources	Sagebrush		40
<i>Atriplex corrugata</i>	Perennial Shrub	Commercial sources	Salt Desert	100	
<i>Atriplex obovata</i>	Perennial Shrub	GRIN	Salt Desert	3	
<i>Chaetopappa ericoides</i>	Perennial Forb	GRIN	Salt Desert	3	
<i>Lepidium montanum</i>	Biennial/Perennial Forb	GRIN	Salt Desert	3	
<i>Leymus salinus</i>	Perennial Grass	UCEPC	Salt Desert	40	
Total				2000	2000

¹ USDA, NRCS. 2020. The PLANTS Database (<http://plants.usda.gov>, 10 December 2020). National Plant Data Team, Greensboro, NC 27401-4901 USA.

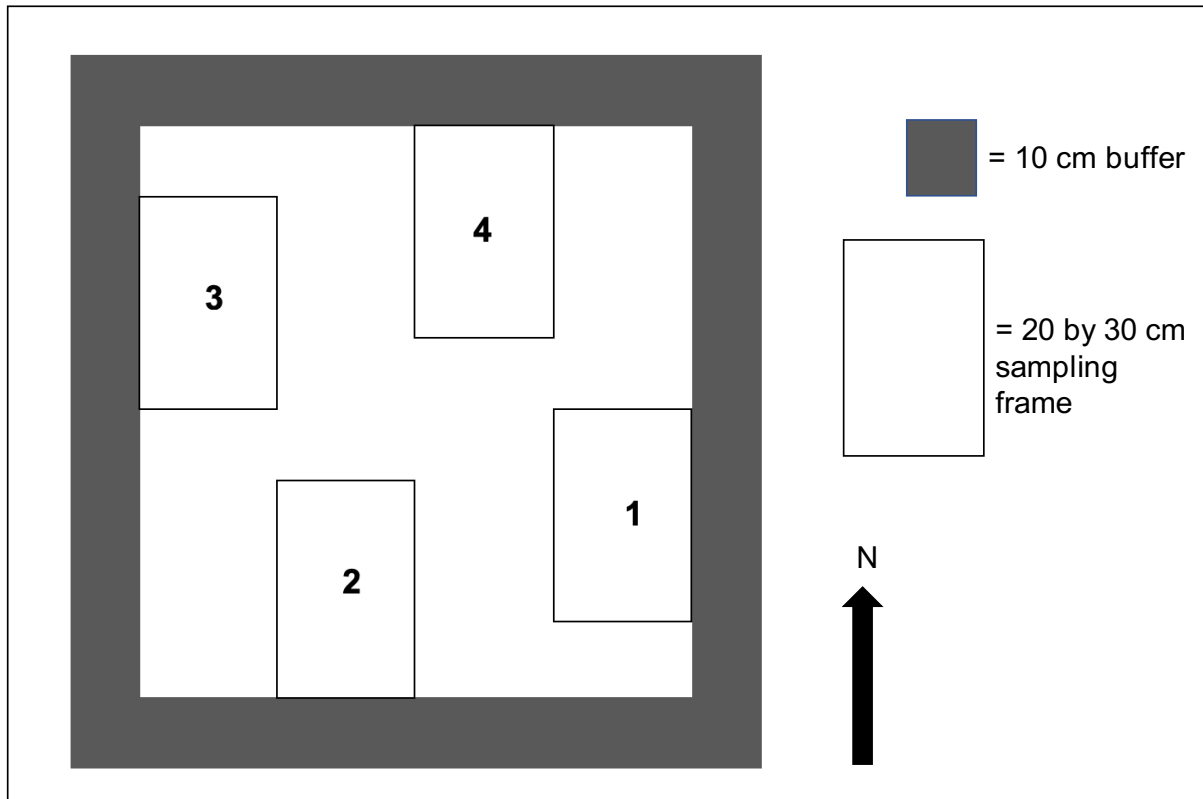


Figure 2.2: Layout of sampling frames within 1- by 1- m plots. Sampling frames were laid out in a manner that allowed a 10-cm buffer around the edge of the plot. Plant density data, ground cover, canopy cover, and percent cover by functional group were measured within each of the four sampling frames. Note that these measurements were also assessed at the 1-by-1 meter scale due to low density counts and cover within dryland ecosystems.

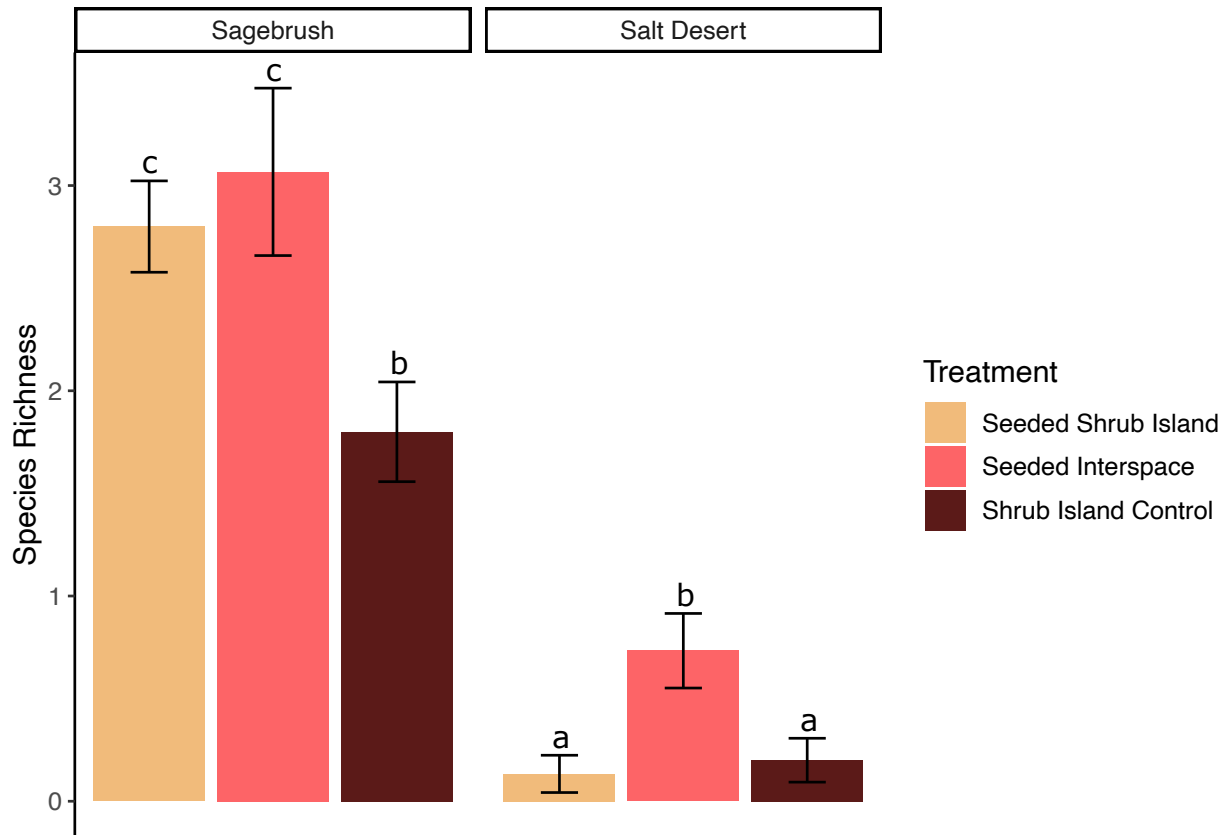


Figure 2.3: Seeded Species richness in May 2022 across treatments and controls. The interaction between treatment and system was significant in May 2022 ($p\text{-adj} < 0.05$). Seeded interspace plots contained higher species richness than seeded shrub island plots in both the salt desert and sagebrush systems. Error bars = SE. Letters indicate Dunnett's test for multiple comparisons calculated post-hoc with multcomp cld at $\alpha = 0.05$. Seeded interspaces and shrub island controls were both compared to seeded shrub islands.

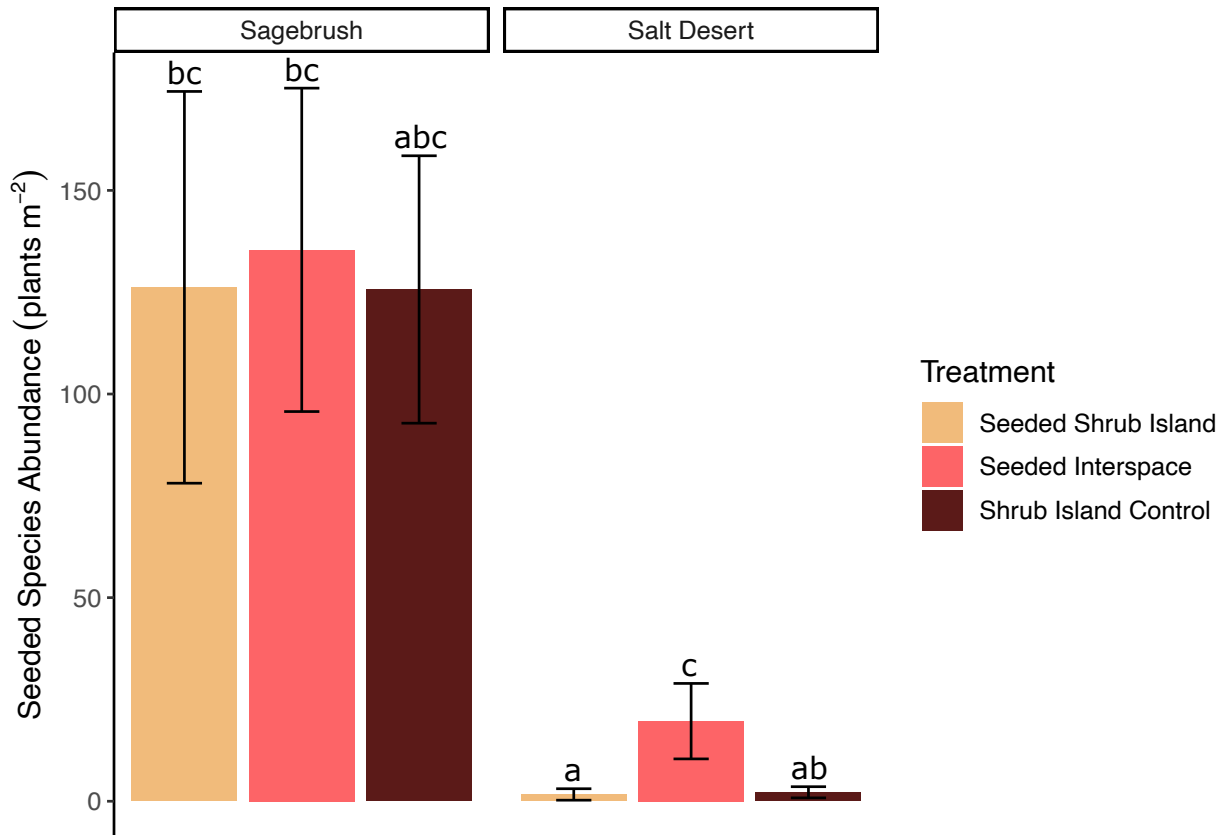


Figure 2.4: Seeded species abundance in May 2022 across treatments and controls. The interaction between treatment and system was significant ($p\text{-adj} < 0.05$). Seeded interspace plots contained higher seeded species abundance than seeded shrub island plots in the salt desert. Error bars = SE. Letters indicate Dunnett's test for multiple comparisons calculated post-hoc with multcomp cld at $\alpha = 0.05$. Seeded interspaces and shrub island controls were both compared to seeded shrub islands.

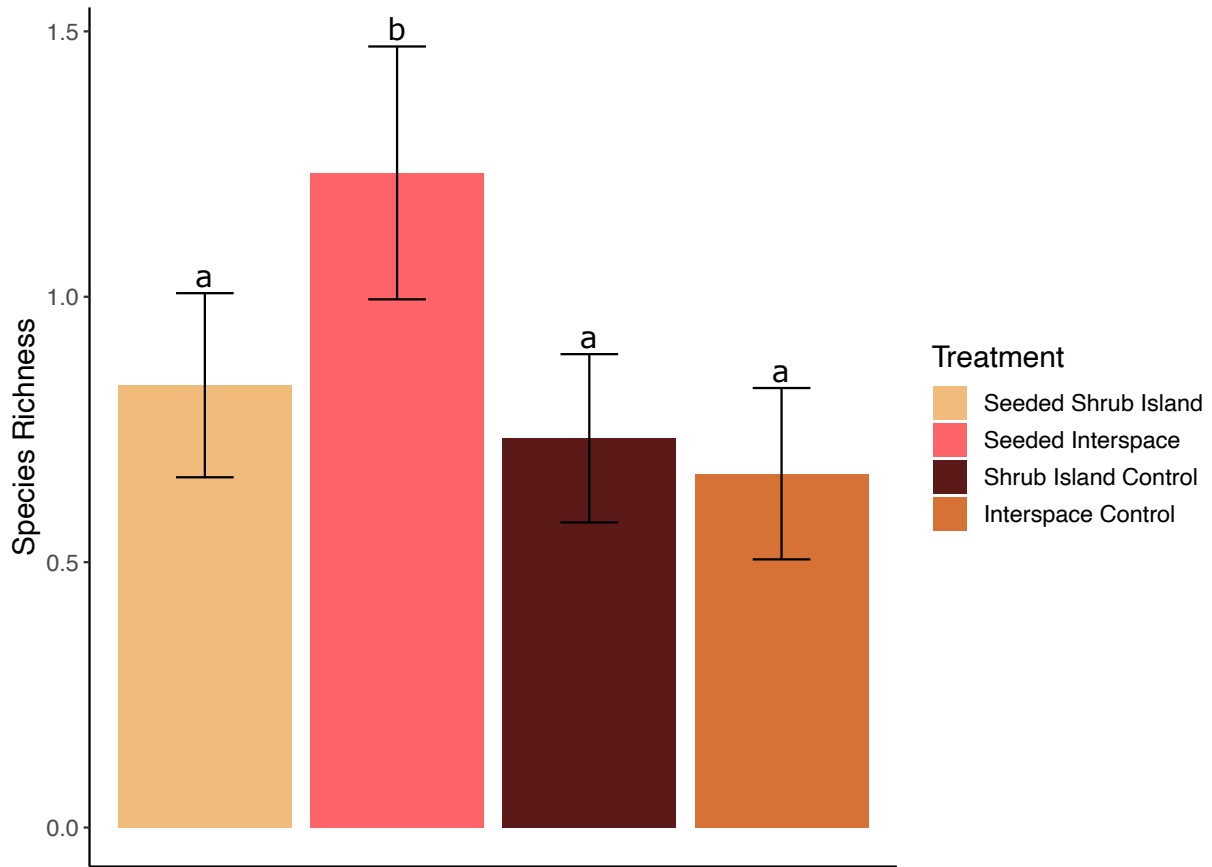


Figure 2.5: Seeded species richness in September 2022 across treatments and controls. Treatment was significant ($p\text{-adj} < 0.05$). Seeded interspace plots contained higher species richness than other treatment plots and control plots. Error bars = SE. Letters indicate Tukey's HSD for multiple comparisons calculated post-hoc with `multcomp cld` at $\alpha = 0.05$.

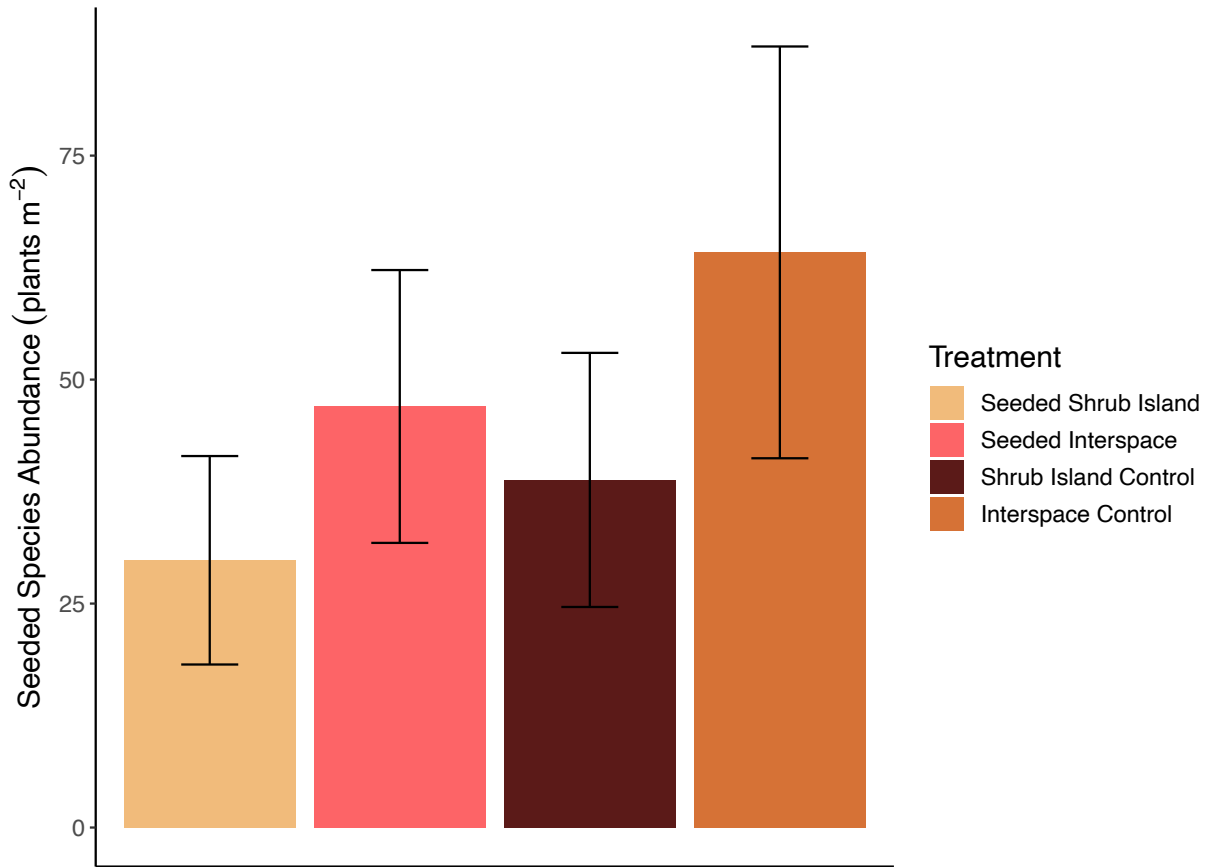


Figure 2.6: Seeded species abundance in September 2022 across treatments and controls. Treatment did not have a significant effect ($p\text{-adj} < 0.05$). Error bars = SE.

Table 2.2: Mean and standard error (SE) for percent cover by functional plant group in May 2022. Letter indicate Dunnett’s test for multiple comparisons using multcomp cld at $\alpha = 0.05$. Cover was measured using Daubenmire cover classes and averaged across frames. Seeded interspaces and shrub island controls were both compared to seeded shrub islands.

System	Cover Type	Seeded Interspace		Shrub Island Control		Seeded Shrub Island	
		Mean	SE	Mean	SE	Mean	SE
Sagebrush	Annual Forb	0.30	0.07 b	0.10	0.05 a	0.03	0.03 a
	Annual Grass	1.55	0.61	0.71	0.17	0.69	0.19
	Introduced Annual Forb	1.51	0.45 ab	1.75	0.64 ab	1.03	0.40 ab
	Introduced Annual Grass	0.75	0.46	0.47	0.20	0.75	0.45
	Introduced Perennial Grass	0.95	0.26 a	8.19	2.85 b	7.69	1.56 b
	Perennial Forb	1.55	0.43	1.88	1.04	0.95	0.37
	Perennial Grass	1.53	0.43 ab	2.62	1.04 ab	3.86	1.20 ab
	Succulent	<0.01	<0.01	0.03	0.03	2.17	1.36
Salt Desert	Shrub	1.69	0.99	0.20	0.17	0.96	0.92
	Annual Forb	0.03	0.03				
	Introduced Annual Forb	2.23	0.84 b	0.27	0.17 a	1.69	1.08 ab
	Introduced Annual Grass	0.13	0.06	0.03	0.03	0.07	0.05
	Perennial Forb	0.07	0.05				
	Perennial Grass	2.18	1.02 b	0.35	0.27 a	1.03	1.00 a
	Succulent	2.50	2.50	0.17	0.17	0.07	0.05
	Shrub	1.00	1.00	<0.01	<0.01	3.00	2.51

Table 2.3: Mean and standard error (SE) for percent cover by functional plant group in September 2022. Letters indicate Tukey’s HSD for multiple comparisons using multcomp cld at $\alpha = 0.05$. Cover was measured using Daubenmire cover classes and averaged across frames.

System	Cover Type	Interspace Control		Seeded Interspace		Shrub Island Control		Seeded Shrub Island	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sagebrush	Annual Forb	7.69	3.21 b	2.91	1.20 ab	2.60	1.11 a	1.05	0.42 a
	Annual Grass	0.85	0.37	0.47	0.14	0.61	0.33	0.51	0.30
	Introduced Annual Forb	0.05	0.04	0.07	0.04	0.13	0.07	0.01	0.01
	Introduced Annual Grass	0.07	0.03 a	0.23	0.10 a	0.16	0.07 a	0.31	0.15 a
	Introduced Perennial Grass	1.55	0.58 a	1.55	1.00 a	7.99	2.66 b	6.49	1.34 b
	Perennial Forb	1.18	0.60 b	0.98	0.39 b	0.18	0.06 a	0.08	0.04 a
	Perennial Grass	2.85	0.84	1.83	0.50	0.60	0.18	1.49	0.45
	Succulent	1.33	1.01			0.07	0.05	0.42	0.22
	Shrub	2.75	1.05	1.40	0.94	1.05	0.59	1.24	0.64
Salt Desert	Introduced Annual Forb	1.57	0.68	0.46	0.14	0.51	0.23	0.63	0.41
	Introduced Annual Grass	1.19	0.82 a	0.06	0.04 a				
	Perennial Grass	0.63	0.63	1.73	0.82	0.72	0.62	0.29	0.29
	Succulent	1.46	1.29	0.25	0.25	0.25	0.18	0.33	0.23
	Shrub	0.07	0.05	0.64	0.64	0.05	0.05	0.50	0.50

Table 2.4: Mean and standard error (SE) for seeded species plant density data in May of 2022. Data is divided by treatment, month and system. Plant names follow USDA nomenclature (2020).

System	Species	Seeded Shrub Island		Shrub Island Control		Seeded Interspace	
		Mean	SE	Mean	SE	Mean	SE
Sagebrush	<i>Achillea millefolium</i>	0.27	0.27			0.8	0.58
	<i>Artemisia tridentata</i>	0.53	0.53	0.07	0.07		
	<i>Astragalus convallarius</i>	2.8	2.8	1.93	1.93		
	<i>Bouteloua gracilis</i>			0.27	0.27	0.73	0.4
	<i>Cleome lutea</i>	0.27	0.27			0.27	0.27
	<i>Draba reptans</i>					0.27	0.27
	<i>Elymus elymoides</i>	3.07	1.57	1.93	1		
	<i>Geranium viscosissimum</i>	0.27	0.27				
	<i>Heliomeris multiflora</i>					0.07	0.07
	<i>Ipomopsis aggregata</i>					0.8	0.43
	<i>Linum lewisii</i>	1.87	0.62			1.2	0.47
	<i>Lupinus argenteus</i>					0.33	0.27
	<i>Pleuraphis jamesii</i>	1.4	0.63	1.4	1.15	16.13	7.83
	<i>Poa secunda</i>	8.87	3.2	9.33	3.56	0.53	0.29
	<i>Sphaeralcea parvifolia</i>					0.93	0.43
		<i>Vulpia octoflora</i>	106.9	48.33	110.7	33.75	113.3
Salt Desert	<i>Linum lewisii</i>					0.07	0.07
	<i>Pleuraphis jamesii</i>	1.67	1.41	2	1.38	18.67	9.34
	<i>Poa secunda</i>					0.93	0.86
	<i>Sarcobatus vermiculatus</i>			0.2	0.2		

Table 2.5: Mean and standard error (SE) for seeded species plant density data in September of 2022. Data is divided by treatment, month and system. Plant names follow USDA nomenclature (2020).

System	Species	Interspace Control		Seeded Interspace		Seeded Shrub Island		Shrub Island Control	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sagebrush	<i>Bouteloua gracilis</i>	30.60	14.36	11.00	6.10	0.27	0.27	0.60	0.60
	<i>Elymus elymoides</i>					4.20	2.85	0.60	0.34
	<i>Linum lewisii</i>			0.47	0.27	0.40	0.27		
	<i>Poa secunda</i>	1.47	0.90	0.60	0.36	12.53	4.52	3.47	1.75
	<i>Sphaeralcea parvifolia</i>			2.07	0.99				
	<i>Sporobolus cryptandrus</i>	0.27	0.27	2.53	2.53				
	<i>Vulpia octoflora</i>	93.87	30.01	67.60	24.05	41.40	21.39	68.20	24.97
Salt Desert	<i>Pleuraphis jamesii</i>	2.20	2.20	9.73	5.52	0.87	0.87	3.87	2.82
	<i>Sarcobatus</i>							0.87	0.87
	<i>vermiculatus</i>								

Table 2.6: Mean and standard errors (SE) for cation exchange capacity, electrical conductivity, organic matter, pH, sodium adsorption ratio (SAR), Total C and Total N. Letters indicate Tukey's HSD for multiple comparisons calculated post-hoc with multcomp cld at $\alpha = 0.05$.

System	Response Variables	Interspace		Shrub	
		Mean	SE	Mean	SE
Sagebrush	Cation Exchange Capacity (me/100g)	10.55	0.74 a	11.16	1.08 a
	Electrical Conductivity (mmho/cm)	0.06	0.005 a	0.12	0.03 a 0.16
	Organic Matter (LOI %)	1.71	0.09 a	2.24	bc
	pH (0.1 M CaCl)	6.74	0.11 a	6.87	0.11 a
	Sodium Adsorption Ratio (meq/L)	0.05	<0.01 a	0.05	0.01 a
	Total C (%)	0.78	0.06 a	1.65	0.11 b 0.03
	Total N (%)	0.10	0.005 a	0.17	bc
Salt Desert	Cation Exchange Capacity (me/100g)	28.55	1.20 b	33.09	2.02 c
	Electrical Conductivity (mmho/cm)	1.04	0.32 a	3.51	0.78 b
	Organic Matter (LOI %)	2.05	0.11ab	3.49	0.33 c
	pH	8.29	0.08 b	8.81	0.14 c
	Sodium Adsorption Ratio (meq/L)	2.59	0.90 a	8.32	2.14 b
	Total C (%)	2.68	0.18 ab 0.008	4.51	0.35 c
	Total N (%)	0.10	ab	0.26	0.02 c

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APPENDIX: SUPPLEMENTAL INFORMATION & DATA

Appendix Table 1: PRISM Climate Data for California Park, Colorado. Thirty- year climate averages presented for 1991-2020 and yearly precipitation and temperature for each year of monitoring (2019-2022). From PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>.

California Park, Colorado (40.7431°N 107.1281°W)										
Month	1991-2020		2019		2020		2021		2022	
	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)
January	88.9	-6.9	97.2	-6.7	80.1	-7.2	53.5	-5.3	61.2	-5.8
February	78.7	-5.4	80.3	-6.9	83.3	-8.3	93.1	-5.7	34.7	-7.6
March	69.8	-1.1	118.9	-2.5	61.8	-0.6	65.7	-0.8	71.1	-1.7
April	84.8	2.6	66.3	3.9	53.2	1.9	22.7	2.9	61.3	2.2
May	70.3	7.7	106.1	5.6	31.4	9.0	44.0	9.5	73.4	6.8
June	39.7	13.3	91.0	11.7	24.8	13.6	18.5	16.5	19.8	13.6
July	33.8	17.2	15.7	17.7	15.7	17.4	23.3	19.1	63.9	18.2
August	39.2	16.4	13.3	17.4	11.7	19.5	42.7	16.7	32.3	17.8
September	53.0	12.2	22.2	13.3	15.8	12.4	64.8	14.7	43.6	14.9
October	66.8	5.2	45.8	0.8	25.0	5.8	81.4	5.9	55.2	5.6
November	81.2	-1.5	63.2	-0.9	38.3	-0.4	48.7	2.8	74.3	-3.3
December	87.0	-6.6	84.5	-6.0	61.9	-6.2	150.4	-3.5	146.8	-6.4
Annual	793.2	4.4	804.2	4.0	502.7	4.7	708.5	6.1	737.6	4.5

Appendix Table 2a: Results of mixed effects analyses for seeded species density data across all four years of the study. Models reported include those for Shannon Wiener Diversity (H), seeded species richness, seeded species abundance (plants per m⁻²) and Pielou's evenness. Columns include the year, source of variance, numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), the F statistic (F) and the probability of the F statistic (p). Variable names were abbreviated including treatment (T), site (S) and fence type (F). Values shaded in gray are significant ($\alpha <$).

Year	Source of Variance	Shannon Wiener Diversity (H)				Richness				Seeded Species Abundance				Pielou's Evenness			
		N	D	F	p	N	D	F	p	N	D	F	p	N	D	F	p
		D	D			D	D			D	D			D	D		
		F	F			F	F			F	F			F	F		
2019	Site Type (S)	2	6	5.71	0.041	2	6	14.5	0.005	2	6	2.96	0.13	2	6	0.73	0.519
	Fence Type (F)	1	6	0.76	0.418	1	6	0.49	0.511	1	6	0.1	0.76	1	6	0.01	0.913
	Treatment (T)	3	36	20.4	<0.001	3	36	20.2	<0.001	3	36	5.5	0.003	3	3	5.68	0.003
	S*F	2	6	0.53	0.612	2	6	0.27	0.775	2	6	0.17	0.84	2	6	0.62	0.571
	S*T	6	36	0.57	0.754	6	36	0.2	0.976	6	36	0.53	0.78	6	3	1.14	0.358
	F*T	3	36	0.89	0.454	3	36	2.16	0.11	3	36	0.65	0.59	3	3	0.27	0.85
	S*F*T	6	36	0.54	0.772	6	36	0.49	0.81	6	36	0.4	0.87	6	3	0.84	0.548
															6		
2020	Site Type (S)	2	6	4.62	0.061	2	6	2.64	0.151	2	6	1.43	0.31	2	6	7.4	0.024
	Fence Type (F)	1	6	7.23	0.036	1	6	5.22	0.062	1	6	0.49	0.51	1	6	5.27	0.061
	Treatment (T)	3	36	0.42	0.737	3	36	2.03	0.127	3	36	3.08	0.04	3	3	0.21	0.888
	S*F	2	6	0.09	0.919	2	6	0.04	0.963	2	6	0.46	0.65	2	6	0.01	0.989
	S*T	6	36	0.51	0.795	6	36	0.98	0.452	6	36	1.38	0.25	6	3	0.57	0.754
	F*T	3	36	0.44	0.723	3	36	0.61	0.613	3	36	0.79	0.51	3	3	0.5	0.686
	S*F*T	6	36	0.63	0.704	6	36	0.48	0.816	6	36	0.99	0.45	6	3	0.82	0.563
															6		

Appendix Table 2a Continued:

2021	Site Type (S)	2	6	10.3	0.011	2	6	12.5	.001	2	6	6.35	0.03	2	6	12.6	0.007
	Fence Type (F)	1	6	2.69	0.152	1	6	1.69	0.218	1	6	1.68	0.24	1	6	1.44	0.236
	Treatment (T)	3	36	0.76	0.526	3	36	3.04	0.042	3	36	3.97	0.02	3	3	0.05	0.987
	S*F	2	6	0	1	2	6	0.21	0.812	2	6	0.21	0.82	2	6	0.61	0.549
	S*T	6	36	0.11	0.995	6	36	1.04	0.417	6	36	1.07	0.4	6	3	0.39	0.881
	F*T	3	36	1.2	0.326	3	36	0.79	0.505	3	36	0.06	0.98	3	3	2.37	0.084
	S*F*T	6	36	1.19	0.333	6	36	0.99	0.445	6	36	1.08	0.39	6	3	1.61	0.168
2022	Site Type (S)	2	6	10.8	0.01	2	6	7.55	0.023	2	6	5.16	0.05	2	6	30.5	0.001
	Fence Type (F)	1	6	9.52	0.022	1	6	1.72	0.238	1	6	0.05	0.83	1	6	3.4	0.115
	Treatment (T)	3	36	3.8	0.018	3	36	2.23	0.102	3	36	0.99	0.41	3	3	3.15	0.037
	S*F	2	6	1.43	0.31	2	6	1.22	0.361	2	6	0.06	0.94	2	6	0.11	0.9
	S*T	6	36	0.83	0.552	6	36	0.23	0.964	6	36	0.12	0.99	6	3	2.05	0.084
	F*T	3	36	2.35	0.089	3	36	1.19	0.326	3	36	0.6	0.62	3	3	2.59	0.068
	S*F*T	6	36	1.2	0.33	6	36	0.92	0.495	6	36	1.3	0.28	6	3	2.06	0.083

Appendix Table 2b: Results of mixed effects analyses for total species density data across all four years of the study. Models reported include those for Shannon Wiener Diversity (H), seeded species richness and Pielou's evenness. Columns include the year, source of variance (SOV), numerator degrees of freedom (NumDF), denominator degrees of freedom (DenDF), the F statistic (F) and the probability of the F statistic (p). Variable names were abbreviated including treatment (T), site type (S) and fence type (F). Values shaded in gray are significant ($\alpha < .05$).

Year	Source of Variance	Shannon Wiener Diversity (H)				Richness				Pielou's Evenness			
		NumDF	DenDF	F	p	NumDF	DenDF	F	p	NumDF	DenDF	F	p
2019	Site (S)	2	6	3.965	0.079	2	6	12.419	0.007	2	6	3.062	0.121
	Fence Type (F)	1	6	3.191	0.124	1	6	0.692	0.437	1	6	2.061	0.201
	Treatment (T)	3	36	2.502	0.075	3	36	13.581	<0.001	3	36	0.420	0.740
	S*F	2	6	0.575	0.591	2	6	1.172	0.372	2	6	0.057	0.950
	S*T	6	36	1.615	0.171	6	36	0.326	0.919	6	36	2.625	0.033
	F*T	3	36	1.261	0.302	3	36	0.788	0.508	3	36	1.235	0.311
	S*F*T	6	36	0.854	0.537	6	36	0.365	0.896	6	36	0.758	0.607
2020	Site (S)	2	6	8.388	0.018	2	6	5.400	0.046	2	6	9.571	0.014
	Fence Type (F)	1	6	1.797	0.229	1	6	4.175	0.087	1	6	1.428	0.277
	Treatment (T)	3	36	2.041	0.125	3	36	4.754	0.007	3	36	0.735	0.538
	S*F	2	6	0.515	0.622	2	6	0.539	0.609	2	6	1.021	0.415
	S*T	6	36	0.339	0.912	6	36	1.396	0.243	6	36	0.447	0.842
	F*T	3	36	0.314	0.815	3	36	0.143	0.934	3	36	0.767	0.520
	S*F*T	6	36	1.605	0.174	6	36	0.318	0.923	6	36	1.648	0.162
2021	Site (S)	2	6	3.713	0.089	2	6	14.461	0.001	2	6	3.503	0.098
	Fence Type (F)	1	6	6.293	0.046	1	6	1.205	0.294	1	6	7.512	0.034

Appendix Table 2b Continued:

	Treatment (T)	3	36	1.085	0.368	3	36	0.816	0.494	3	36	0.892	0.455
	S*F	2	6	1.518	0.293	2	6	0.481	0.630	2	6	1.456	0.305
	S*T	6	36	1.109	0.376	6	36	0.484	0.816	6	36	1.315	0.276
	F*T	3	36	0.193	0.900	3	36	0.398	0.755	3	36	0.585	0.629
	S*F*T	6	36	1.582	0.181	6	36	1.273	0.294	6	36	1.649	0.162
2022	Site (S)	2	6	4.310	0.069	2	6	14.318	0.005	2	6	2.809	0.138
	Fence Type (F)	1	6	3.968	0.093	1	6	3.496	0.111	1	6	2.896	0.140
	Treatment (T)	3	36	0.929	0.437	3	36	1.412	0.255	3	36	0.895	0.453
	S*F	2	6	0.898	0.456	2	6	1.37	0.323	2	6	0.519	0.619
	S*T	6	36	1.098	0.383	6	36	0.845	0.544	6	36	1.451	0.223
	F*T	3	36	0.160	0.923	3	36	1.025	0.393	3	36	0.742	0.534
	S*F*T	6	36	3.232	0.012	6	36	0.709	0.645	6	36	3.205	0.013

Appendix Table 2c: Results of mixed effects analyses for total species density data across all four years of the study. Models reported include those for seeded cover %, unseeded cover % and total cover %. Columns include the year, source of variance (SOV), numerator degrees of freedom (NumDF), denominator degrees of freedom (DenDF), the F statistic (F) and the probability of the F statistic (p). Variable names were abbreviated including treatment (T), site type (S) and fence type (F). Values shaded in gray are significant ($\alpha < .05$).

Year	Source of Variance	Seeded Cover (%)				Unseeded Cover (%)				Total Cover (%)			
		NumDF	DenDF	F	p	NumDF	DenDF	F	p	NumDF	DenDF	F	p
2019	Site (S)	2	6	5.284	0.047	2	6	7.168	0.026	2	6	9.458	0.014
	Fence Type (F)	1	6	0.068	0.803	1	6	6.826	0.040	1	6	4.714	0.073
	Treatment (T)	3	36	2.150	0.111	3	36	4.180	0.012	3	36	9.273	<0.001
	S*F	2	6	0.406	0.683	2	6	1.455	0.305	2	6	1.125	0.385
	S*T	6	36	0.474	0.823	6	36	0.589	0.737	6	36	0.491	0.811
	F*T	3	36	1.174	0.333	3	36	0.631	0.600	3	36	0.748	0.530
	S*F*T	6	36	0.377	0.889	6	36	1.108	0.377	6	36	1.595	0.177
2020	Site (S)	2	6	1.954	0.222	2	6	20.637	0.002	2	6	5.267	0.048
	Fence Type (F)	1	6	0.370	0.565	1	6	0.202	0.669	1	6	2.273	0.182
	Treatment (T)	3	36	1.538	0.221	3	36	0.283	0.837	3	36	1.550	0.218
	S*F	2	6	1.876	0.233	2	6	0.693	0.536	2	6	3.443	0.101
	S*T	6	36	1.148	0.356	6	36	0.891	0.512	6	36	1.045	0.413
	F*T	3	36	1.029	0.391	3	36	0.934	0.434	3	36	0.614	0.610
	S*F*T	6	36	0.750	0.614	6	36	0.583	0.742	6	36	0.749	0.614
2021	Site (S)	2	6	3.707	0.089	2	6	2.801	0.138	2	6	1.99	0.217
	Fence Type (F)	1	6	0.314	0.596	1	6	1.674	0.243	1	6	2.492	0.166

Appendix Table 2c Continued:

	Treatment (T)	3	36	1.457	0.242	3	36	2.984	0.044	3	36	2.672	0.062
	S*F	2	6	0.267	0.774	2	6	1.451	0.306	2	6	2.445	0.167
	S*T	6	36	0.692	0.658	6	36	1.505	0.204	6	36	2.05	0.084
	F*T	3	36	0.810	0.497	3	36	0.191	0.902	3	36	0.409	0.748
	S*F*T	6	36	0.905	0.503	6	36	1.554	0.189	6	36	1.923	0.104
2022	Site (S)	2	6	6.892	0.028	2	6	12.236	0.008	2	6	5.811	0.039
	Fence Type (F)	1	6	0.493	0.509	1	6	0.437	0.533	1	6	2.116	0.196
	Treatment (T)	3	36	1.413	0.255	3	36	0.810	0.497	3	36	0.441	0.725
	S*F	2	6	1.277	0.345	2	6	3.431	0.101	2	6	2.203	0.192
	S*T	6	36	0.256	0.954	6	36	0.830	0.555	6	36	1.242	0.309
	F*T	3	36	0.780	0.513	3	36	0.939	0.432	3	36	0.951	0.427
	S*F*T	6	36	1.776	0.132	6	36	0.464	0.830	6	36	0.878	0.520

Appendix Table 3a: Species list from 2019 including mean and standard error (SE) for percent cover data for both seeded and unseeded plant species. Percent cover data was collected using Daubenmire cover classes. Data is divided by treatment. Plant codes follow USDA nomenclature (2019).

USDA Species Code	Control		Mounds		Seeded		Slash	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ACMI2	2.82	0.96	3.60	0.85	4.72	1.95	2.60	0.80
ACNE9	0.01	0.01	0.07	0.07	0.26	0.21	0.56	0.56
AGGL			0.07	0.05				
ALLIU	1.36	0.69	1.10	0.65	2.49	1.16	1.71	0.78
ANMA	0.03	0.03						
ARFE3	0.01	0.01	0.08	0.05	0.01	0.01	0.01	0.01
ARTR							0.03	0.03
ASTER			0.11	0.08	0.07	0.07	0.19	0.09
ASTRA	2.43	1.25	1.91	0.80	3.13	1.46	2.33	1.02
BASA3			0.03	0.03	0.21	0.21		
BRIN2							0.07	0.07
BRMA4			0.03	0.03	0.03	0.03	0.03	0.03
CANU3	0.01	0.01	0.04	0.04				
CASTI2			0.03	0.03	0.01	0.01		
CEAR4	4.74	2.22	3.28	1.14	2.07	0.97	3.55	1.40
CEVE			0.01	0.01			0.01	0.01
CHAN9			0.03	0.03				
COLI2	2.10	1.12	1.30	0.39	1.80	0.96	1.02	0.46
DENU2	0.07	0.07	0.10	0.08	0.06	0.04	0.14	0.11
ELEL5	1.18	0.92	0.64	0.45	0.25	0.21	0.13	0.08
ELTR7	0.24	0.24	0.12	0.08	0.24	0.24	0.03	0.03
EPBR3	0.35	0.15	0.68	0.49	0.22	0.11	0.23	0.12
ERIGE2	1.01	0.78	0.52	0.49	1.39	0.89	0.21	0.11
ERUM	0.63	0.63			0.03	0.03	0.07	0.05
FEID	1.26	0.71	1.01	0.52	2.76	1.55	0.56	0.24
GABO2	0.03	0.03	0.03	0.03				
GEVI2	1.18	0.85	0.24	0.21	0.28	0.28	0.08	0.07
HEMU3	0.66	0.55	0.35	0.13	0.29	0.13	0.26	0.14
HEQU2	1.01	0.97	0.42	0.26	0.14	0.10	0.42	0.23
HEUN	0.03	0.03	0.99	0.24	0.30	0.11	0.60	0.23
HEVI4			0.15	0.05	0.24	0.09	0.08	0.07
HYCA4	0.01	0.01					0.03	0.03
LASE	0.10	0.06	0.10	0.07	0.27	0.11	0.08	0.05
LILE3			0.01	0.01	0.05	0.04		
LIPO	0.01	0.01	0.17	0.06	0.20	0.09	0.25	0.10
LODI							0.08	0.07
LOLE2	22.40	5.90	20.56	5.18	23.58	6.12	11.94	3.64

Appendix Table 3a Continued:

LUAR3	0.28	0.28	1.92	0.39	2.96	1.18	0.92	0.15
LUSE4	0.01	0.01	0.01	0.01	0.14	0.10		
MAGL2	0.25	0.12	0.40	0.19	0.53	0.26	0.49	0.26
MERTE	0.07	0.05	0.03	0.03	0.01	0.01		
MESP	1.77	0.56	1.37	0.46	1.83	0.78	0.90	0.46
NAVI4	0.13	0.06	0.19	0.08	0.23	0.09	0.53	0.24
PASM	3.19	1.14	2.56	1.04	3.60	1.33	1.58	0.68
PEGA3	1.47	0.62	1.53	0.70	2.10	1.25	0.85	0.38
PEST2	0.59	0.45	0.44	0.26	0.94	0.64	0.47	0.45
PHPR3	5.92	2.60	5.16	2.03	6.26	2.38	3.87	1.60
POBI6	0.10	0.08	0.18	0.11	0.17	0.08	0.26	0.25
PODO4	3.45	0.96	4.68	1.24	5.13	1.83	5.42	1.32
POFE	0.05	0.04	0.16	0.11	0.05	0.04	0.04	0.04
POTEN	3.65	2.30	4.39	2.49	4.67	3.59	3.60	2.51
PRVI			0.11	0.08	0.08	0.05	0.22	0.07
PSSP6							0.03	0.03
RAGL	0.01	0.01	0.23	0.15	0.04	0.04	0.06	0.04
ROWO	0.28	0.28	0.34	0.10	0.23	0.07	0.29	0.10
RUPA			0.04	0.04	0.01	0.01	0.02	0.02
SYRO	0.03	0.03			0.52	0.52		
TAOF	0.91	0.48	0.73	0.45	0.73	0.32	0.68	0.24
THDI4			0.03	0.03			0.01	0.01
VIPR3	0.15	0.14	0.14	0.11	0.18	0.14	0.07	0.07
WYAM	22.47	7.91	19.65	7.17	22.78	7.51	20.00	7.08

Appendix Table 3b: Species list from 2020 including mean and standard error (SE) for percent cover data for both seeded and unseeded plant species. Percent cover data was collected using Daubenmire cover classes. Data is divided by treatment. Plant codes follow USDA nomenclature (2019).

USDA Species Code	Control		Mounds		Seeded		Slash	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ACMI2	0.46	0.21	0.95	0.42	1.64	0.76	1.01	0.62
ACNE9					0.04	0.04		
ALAL3					<0.01	<0.01		
ALLIU	0.04	0.04	<0.01	<0.01	0.07	0.07	<0.01	<0.01
ARTR	<0.01	<0.01						
ASTRA	0.73	0.39	1.77	1.10	0.94	0.51	0.90	0.54
BRMA4	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		
CANU3			<0.01	<0.01				
CEAR4	0.29	0.13	0.53	0.34	0.32	0.24	0.67	0.34
COLI2	<0.01	<0.01	0.01	<0.01	0.04	0.03	<0.01	<0.01
ELEL5							<0.01	<0.01
ELTR7	0.38	0.28	0.25	0.15	0.31	0.16	0.21	0.14
EPBR3	0.07	0.05	0.21	0.14	0.14	0.14	0.07	0.07
ERIGE2	0.73	0.50	0.53	0.45	0.63	0.40	<0.01	<0.01
FEID	0.63	0.48	0.45	0.45	0.80	0.54		
GABO2			0.24	0.24				
GEVI2	0.45	0.45	<0.01	<0.01	0.87	0.66	0.45	0.45
HEQU2					0.03	0.03		
HEUN	0.35	0.35	0.04	0.03	<0.01	<0.01	0.18	0.11
LASE	<0.01	<0.01			0.04	0.03	<0.01	<0.01
LEPID					<0.01	<0.01		
LODI	0.28	0.28	0.31	0.31	0.28	0.28	0.49	0.49
LOLE2	2.33	1.47	1.32	0.45	2.57	1.14	1.88	0.84
LUAR3					0.04	0.04		
LUSE4	0.52	0.52	0.04	0.03	1.22	1.14		
MAGL2	0.25	0.10	0.39	0.15	0.42	0.22	0.66	0.38
MESP	0.32	0.22	0.08	0.05	0.01	<0.01	0.01	<0.01
NAVI4	0.04	0.03	0.04	0.04	0.56	0.38	0.08	0.07
PASM	0.14	0.10	0.07	0.07	0.28	0.28	0.14	0.10
PEGA3	0.07	0.05	0.10	0.10	0.07	0.05	<0.01	<0.01
PHPR3	2.26	1.54	1.12	0.52	0.42	0.18	0.70	0.49
PODO4	0.43	0.23	0.57	0.33	0.71	0.46	1.82	1.07
POFE			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
POTEN	2.40	1.63	2.15	1.21	2.68	1.91	1.39	0.80
PRVI			0.03	0.03				
ROWO	0.24	0.24	0.03	0.03				
SOSC2					<0.01	<0.01		

Appendix Table 3b Continued:

SYRO					0.21	0.21		
TAOF							<0.01	<0.01
TRDU2					<0.01	<0.01		
WYAM	14.76	4.97	10.76	4.69	12.85	4.61	11.25	4.59

Appendix Table 3c: Species list from 2021 including mean and standard error (SE) for percent cover data for both seeded and unseeded plant species. Percent cover data was collected using Daubenmire cover classes. Data is divided by treatment. Plant codes follow USDA nomenclature (2019).

USDA Species Code	Control		Mounds		Seeded		Slash	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ACMI2	0.55	0.25	1.13	0.53	0.88	0.40	0.92	0.50
AGGL	0.01	0.01			0.01	0.01		
ALLIU	0.10	0.07	0.06	0.03	0.05	0.03	0.09	0.04
ARTR							0.01	0.01
ASTRA	1.81	1.13	0.32	0.12	0.78	0.36	0.60	0.45
BRMA4			0.02	0.01				
CAGU	0.01	0.01						
CALOC	0.01	0.01						
CANU3			0.01	0.01	0.01	0.01	0.01	0.01
CEAR4			0.01	0.01	0.01	0.01		
CHAN9							0.01	0.01
COLI2	0.36	0.24	0.79	0.63	0.33	0.24	0.10	0.05
EPBR3	0.15	0.06	0.26	0.09	0.12	0.04	0.26	0.09
ERIGE2	0.43	0.31	0.51	0.48	0.17	0.11	0.08	0.04
FEID	0.28	0.28	0.27	0.24	0.79	0.77	0.01	0.01
FRVI							0.01	0.01
GABI	0.01	0.01					0.01	0.01
GABO2			0.03	0.03				
GEVI2	0.61	0.59			0.45	0.42	0.53	0.36
HEMU3	0.42	0.42	0.09	0.06	0.06	0.04	0.07	0.04
HEQU2	0.01	0.01	0.02	0.01	0.02	0.02		
HEUN	0.04	0.04	0.02	0.02			0.03	0.03
LASE					0.01	0.01	0.01	0.01
LODI	0.13	0.11	0.03	0.02	0.02	0.01	0.03	0.02
LOLE2	8.77	3.16	8.20	2.62	8.93	2.50	6.82	2.48
LUAR3	0.51	0.48	0.31	0.24	0.68	0.49	0.03	0.02
LUSE4			0.04	0.04	0.01	0.01		
MESP	0.16	0.07	0.13	0.05	0.14	0.05	0.10	0.04
NAVI4	0.05	0.04	0.09	0.07	0.35	0.25	0.05	0.03
PASM	0.22	0.07	0.19	0.06	0.44	0.26	0.19	0.09
PEGA3	0.01	0.01	0.03	0.01	0.02	0.02	0.01	0.01
PHPR3	0.85	0.77	0.20	0.11	0.71	0.62	0.38	0.28
POBI6	0.03	0.02	0.16	0.10	0.01	0.01	0.03	0.02
PODO4	0.33	0.06	0.89	0.56	0.32	0.05	0.26	0.05
POTEN	3.56	2.47	4.51	2.86	3.31	2.35	5.28	3.54
ROWO	0.22	0.22					0.01	0.01
STELL	0.16	0.09	0.15	0.07	0.11	0.05	0.09	0.04

Appendix Table 3c Continued:

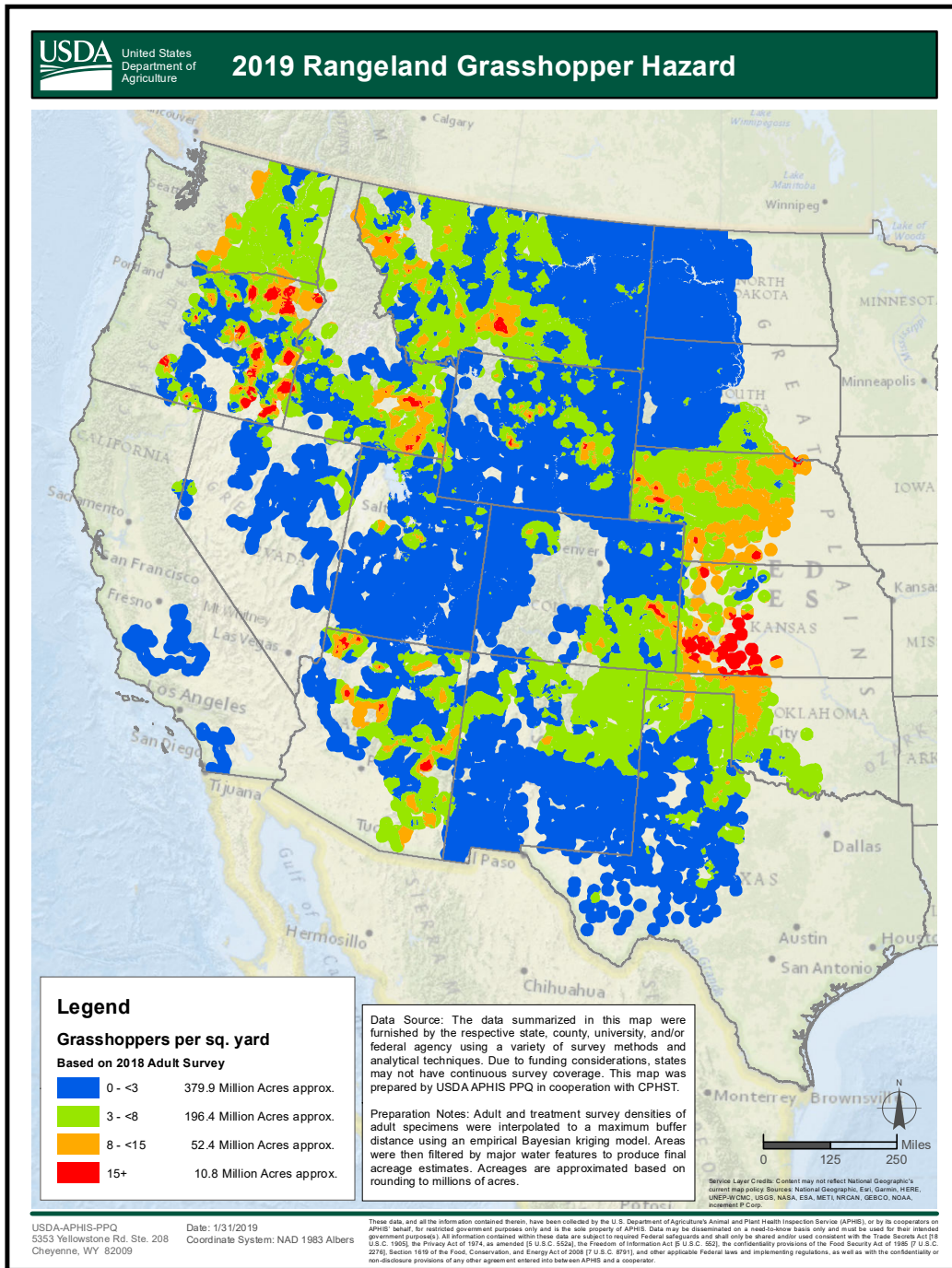
SYRO			0.03	0.03	0.21	0.21		
TAOF	0.09	0.06	0.03	0.03	0.08	0.05	0.02	0.01
VIAM					0.01	0.01	0.01	0.01
VIPR3	0.01	0.01	0.01	0.01	0.08	0.06		
WYAM	13.72	5.73	9.65	3.64	9.08	3.13	7.23	3.01

Appendix Table 3d: Species list from 2022 including mean and standard error (SE) for percent cover data for both seeded and unseeded plant species. Percent cover data was collected using Daubenmire cover classes. Data is divided by treatment. Plant codes follow USDA nomenclature (2019).

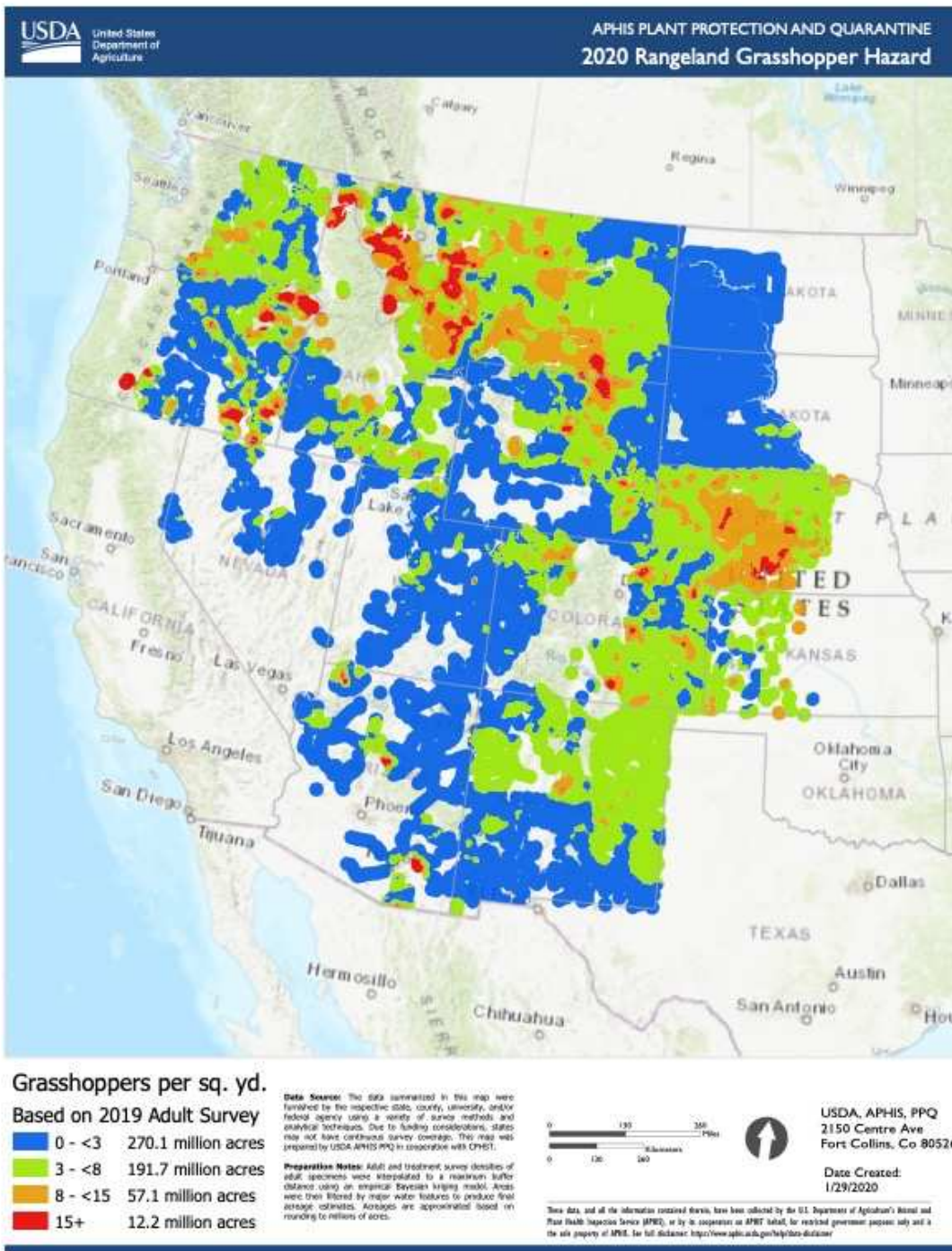
USDA Species Code	Control		Mounds		Seeded		Slash	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ACMI2	0.83	0.49	2.40	1.09	1.76	0.66	1.53	0.75
ALAC4	0.38	0.17	0.35	0.16	0.38	0.26	0.42	0.15
ALTE	0.19	0.15	0.21	0.13	0.15	0.07	0.04	0.02
ARFE3					0.03	0.03		
ARTR							0.03	0.03
ASMI9	1.43	0.71	1.08	0.56	0.86	0.50	0.86	0.41
BOECHERA			0.01	0.01	0.01	0.01	0.01	0.01
CEAR4	1.53	0.67	1.47	0.83	0.51	0.29	1.25	0.60
COLI2	0.79	0.29	2.53	1.43	0.88	0.46	1.33	0.78
CYMOP							0.21	0.21
DENU2	0.13	0.05	0.13	0.05	0.24	0.11	0.15	0.08
ELTR7	0.13	0.11	0.06	0.05			0.04	0.04
EPBR3							0.01	0.01
ERIGE2	1.01	0.62	0.78	0.59	0.52	0.30	0.59	0.42
ERUM	0.21	0.21			0.24	0.24		
FEID	0.13	0.10	0.28	0.14	0.33	0.18	0.14	0.10
FRVI			0.01	0.01			0.03	0.03
GABI	0.03	0.02	0.03	0.02	0.30	0.28	0.68	0.66
GABO2			0.01	0.01				
GETR							0.01	0.01
GEVI2	0.97	0.78	0.04	0.04	0.46	0.45	0.26	0.24
HEMU3					0.08	0.05	0.21	0.21
HEUN	0.01	0.01	0.03	0.03				
LASE	0.08	0.06	0.05	0.04	0.04	0.03	0.17	0.12
LEPID	0.06	0.04	0.05	0.02	0.02	0.02	0.06	0.04
LIPO							0.01	0.01
LOLE2	16.18	4.20	12.92	3.78	14.17	3.62	13.13	3.23
LUAR3	0.11	0.11	0.07	0.05	0.12	0.08	0.03	0.03
LUSE4	0.06	0.05	0.49	0.32	1.47	1.16	0.12	0.05
MESP	0.19	0.07	0.31	0.10	0.26	0.10	0.19	0.08
NEBR	0.08	0.08	0.10	0.10	0.01	0.01		
ORUN	0.23	0.11	0.09	0.05	0.15	0.08	0.15	0.07
PASM	0.84	0.50	0.39	0.19	0.22	0.07	0.40	0.25
PEGA3	0.26	0.11	0.26	0.12	0.33	0.17	0.46	0.28
PF02	0.01	0.01						

Appendix Table 3d Continued:

PF08	0.04	0.04						
PHPR3	0.49	0.29	1.17	0.84	0.90	0.42	1.10	0.84
POBI6	0.04	0.03	0.12	0.08	0.13	0.08	0.07	0.07
PODO4	0.37	0.08	0.77	0.31	0.59	0.22	0.62	0.22
POFE			0.01	0.01				
POTEN	3.13	2.28	3.78	2.23	2.68	2.14	4.49	3.25
ROWO	0.04	0.04	0.03	0.03				
SEIN2	0.08	0.04	0.08	0.05	0.19	0.08	0.08	0.05
SYRO			0.03	0.03	0.21	0.21		
TAOF	0.10	0.06	0.17	0.09	0.43	0.25	0.60	0.41
TRLO					0.01	0.01		
VIAM	0.21	0.21			0.04	0.04	0.03	0.03
VIOLA	0.22	0.14	0.23	0.09	0.28	0.13	0.27	0.13
WYAM	18.16	6.45	19.03	6.07	17.92	5.76	15.97	5.69



Appendix Figure 1: Rangeland grasshopper hazard maps from 2019. Anticipated risk or hazard for the year specified is based on the previous year's grasshopper densities. It is important to note that the number of eggs laid by grasshoppers during the summer and weather conditions in the winter and spring are not included in forecasting despite their importance for grasshopper densities. Field surveys of grasshopper densities and mapping were done by USDA-APHIS-PPQ Western Region.



Appendix Figure 2: Rangeland grasshopper hazard maps from 2020. Anticipated risk or hazard for the year specified is based on the previous year's grasshopper densities. It is important to note that the number of eggs laid by grasshoppers during the summer and weather conditions in the winter and spring are not included in forecasting despite their importance for grasshopper densities. Field surveys of grasshopper densities and mapping were done by USDA-APHIS-PPQ Western Region.

Appendix Table 4: PRISM Climate Data for Grand Junction, Colorado. Thirty- year climate averages presented for 1991-2020 and yearly precipitation and temperature for each year of monitoring (2019-2022). From PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>.

Grand Junction, Colorado (39.0734° N, 108.5373° W)								
Month	1991-2020		2020		2021		2022	
	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)	ppt (mm)	tmean (°C)
January	15.4	-1.9	11.2	-2.8	11.0	-1.5	12.9	-1.6
February	13.4	2.0	1.8	0.7	6.9	2.0	6.8	0.4
March	18.8	7.3	34.8	8.4	12.0	7.2	15.1	6.9
April	24.4	11.2	5.5	11.6	8.6	12.2	6.9	11.9
May	22.3	16.6	2.0	19.4	12.7	18.2	11.2	17.1
June	11.6	22.4	14.1	23.6	5.1	25.8	6.5	24.0
July	17.8	25.8	1.8	26.6	26.1	28.2	21.2	27.4
August	22.9	24.4	0.1	27.7	25.9	25.3	20.5	26.0
September	28.7	19.4	29.5	19.8	46.7	21.4	38.0	22.4
October	26.0	12.1	22.9	12.8	38.2	11.6	64.3	12.8
November	16.6	4.8	2.6	6.4	4.9	7.2	22.7	3.5
December	14.4	-1.4	8.6	-2.1	49.1	-0.7	31.9	-0.6
Annual	232.0	11.9	134.5	12.7	247.1	13.1	257.9	12.5

Appendix Table 5: Results of mixed effects analyses for seeded species density data in May and September of 2022. Models reported include those for seeded species richness and seeded species abundance (plants per m⁻²). Columns include the year, source of variance, numerator degrees of freedom (Num DF), denominator degrees of freedom (Den DF), the F statistic (F) and the probability of the F statistic (p). Variable names were abbreviated including treatment (T) and System (S). Values shaded in gray are significant ($\alpha < .05$).

Month	Source of Variance	Seeded Species Richness				Seeded Species Abundance			
		NumDF	DenDF	F	p	NumDF	DenDF	F	p
May	System (S)	1	4	45.774	0.002	1	4	15.033	0.018
	Treatment (T)	2	56	10.337	<0.001	2	56	3.756	0.029
	S*T	2	56	3.826	0.028	2	56	3.208	0.048
September	System (S)	1	4	14.286	0.019	1	4	8.157	0.046
	Treatment (T)	3	84	4.961	0.003	3	84	1.364	0.259
	S*T	3	84	2.110	0.105	3	84	1.880	0.139

Appendix Table 6: The impact of shrub species on soil chemical properties including electrical conductivity (mmho/cm), pH (0.1 M CaCl) and sodium adsorption ratio (meq/L), were analyzed using linear mixed effects models. This table includes the means and standard errors (SE) for each soil chemical property and shrub combination. Letters indicate Tukey's HSD for multiple comparisons calculated post-hoc with multcomp cld at $\alpha = 0.05$.

Shrub Species	Treatment	Electrical conductivity		pH		Sodium Adsorption Ratio	
		Mean	SE	Mean	SE	Mean	SE
<i>Artemisia tridentata</i>	Interspace	0.06	0.01 a	6.74	0.11 a	0.05	<0.01 a
	Shrub	0.12	0.03 a	6.87	0.11 a	0.05	0.01 ab
<i>Atriplex confertifolia</i>	Interspace	0.28	0.02 a	8.02	0.04 ab	0.53	0.156 ac
	Shrub	1.02	0.14 ab	8.26	0.05 ab	1.86	0.26 bd
<i>Sarcobatus vermiculatus</i>	Interspace	1.41	0.44 a	8.42	0.09 a	3.62	1.24 cd
	Shrub	4.76	0.99 b	9.09	0.15 b	11.55	2.67 e