

BIOTIC AND ABIOTIC BARRIERS TO DRYLAND RESTORATION

by

CLAIRE CURRY KARBAN

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Committee Members:

Dr. Nichole N. Barger

Dr. Laura E. Dee

Dr. Michael C. Duniway

Dr. Nancy C. Emery

Dr. Katharine N. Suding

## ABSTRACT

Karban, Claire Curry (Ph.D., Ecology and Evolutionary Biology)

Biotic and Abiotic Barriers to Dryland Restoration

Thesis directed by Professor Nichole N. Barger

Drylands cover ~45% of Earth's land surface and up to 20% of drylands are severely degraded. Land degradation results in the long-term loss of important ecosystem services and functions such as grazing and cropland, soil fertility, soil stabilization, erosion prevention, primary productivity, and biodiversity. Once degraded, recovery often either does not occur, or occurs too slowly to be relevant for management. In these cases, active restoration is required to restore ecosystem services and functions. Despite the tremendous need for dryland restoration, success is elusive. About 17% of seedings failing to establish any plants and over 90% of seeds used in restoration fail to recruit.

My dissertation looks at biotic (propagule scarcity, granivory, competition) and abiotic (harsh climate, destabilized soils) barriers to restoration in severely degraded drylands. My first chapter investigates the role of granivory in limiting seeded restoration. I find that harvester ants can remove up to 80% of seeds, significantly reducing the number of native seeds in the seedbank. However, foraging behavior occurs primarily in late spring through early fall. Increasing seed germination during the first growing season would protect seeds from ant granivory. In the second chapter, I test several methods to create microsites and stabilize soils while maintaining active grazing. The shifting nature of restoration barriers meant that we were not successful in setting the site on a positive trajectory towards recovery. This project highlights the importance of adaptive management and the need to be realistic when it comes to restoration

outcomes under a changing climate. My third chapter investigates microsite limitation in dryland restoration by creating microsites with soil pitting, biochar, and seed pellets. I find that soil pitting and biochar increase native plants, but they also contribute to even larger increases in non-native vegetation. The barriers presented by dryland restoration remain clear throughout this work, as does the importance of continuing to improve our practical understanding of dryland restoration.

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# CHAPTER I

## INTRODUCTION

Dryland ecosystems cover about 45% of Earth's land surface and support the livelihoods of over 2 billion people (Právělie, 2016; Reynolds et al., 2007). As global population grows, land use on drylands intensifies. Today drylands are more heavily used – for grazing, cropland, and energy production – than ever before. In addition to these provisioning ecosystem services, drylands also provide crucial regulating, supporting, and cultural ecosystem services. These include native plant diversity, net primary productivity, soil fertility, erosion control, recreation, aesthetic services, and spiritual services. All these ecosystem services depend on the functioning of dryland ecosystems. However, land over-use as well as aridification contribute to the loss of ecosystem services and functions, defined as land degradation. Estimates vary but it's likely that at least 20% of dryland ecosystems are currently degraded, including about 20% of rangeland in the western U.S.

Severe degradation can lead to persistent changes in ecosystem structure and function. These persistent new states, or alternative stable states, are particularly common in dryland systems. There are several well-established feedbacks that can maintain persistently degraded states, such as a feedback between invasive annual grasses and fire, or a feedback between soil degradation and declining vegetation cover. These feedbacks can be difficult to overcome, and once a state change has occurred, natural recovery of ecosystem structure and functions does not occur in a timeframe that is relevant to management.

The challenge of restoring ecosystem services and functions to severely degraded dryland ecosystems is to overcome biotic and abiotic barriers that maintain the site in a degraded state. While there is not always a restoration target to hit, the goal of many land managers is to set the

site on a trajectory towards recovering ecosystem services and functions. The business-as-usual approach to dryland restoration is to add native seeds, commonly through broadcast methods or drillseeding. However, seeding has a very low success rate in dryland restoration, with about 17% of seedlings failing to establish any plants (Shackelford et al., 2021) and over 90% of seeds used in restoration failing to recruit (Kildisheva et al., 2016). To improve dryland restoration outcomes, there is growing consensus that a whole systems approach, tackling multiple barriers present at a given site, is necessary (Copeland et al., 2021; James et al., 2013). There is also relative consensus that harsh conditions (i.e. low soil moisture, high vapor pressure deficit) often limit the success of seeded restoration (Shackelford et al. 2020), and that many drylands will experience increased aridification in the future (Reynolds et al., 2007).

Soil destabilization and erosion are well-known to be important drivers of degradation in dryland systems (Okin et al., 2009; Ravi et al., 2010), making them crucial to address in restoration. Methods that slow the movement of wind and water across the soil surface, such as straw checkerboards and small metal fences ('ConMods'), trap fine soil particles and increase seedling germination and herbaceous cover on sandy, destabilized soils (Li et al., 2006; Miao et al., 2015; Okin et al., 2015; Rachal et al., 2015). Stabilizing soils is particularly important for restoring soils and maintaining native propagules in an area.

One of the main contributors to soil stability and nutrient cycling in many intact dryland soils is biological soil crust, or 'biocrust.' These communities of cyanobacteria, lichens, and mosses stabilize soil surfaces against erosion, facilitating soil formation (Chaudhary et al., 2009). Biocrusts are highly susceptible to disturbances such as trampling, and once crushed, biocrusts lose their stabilizing function (Zaady et al., 2016). This makes biocrusts an important functional component to restore in degraded drylands. As the functional importance of biocrust becomes

more widely known, new biocrust restoration techniques are being developed (Antoninka et al., 2020b), including propagating biocrust in greenhouses and farms for restoration material. However, biocrust restoration is still challenging. Remaining barriers to biocrust restoration likely include destabilized soils and harsh, desiccating conditions.

Similarly, harsh conditions are the main driver of low plant recruitment in dryland restoration (Shackelford et al., 2021). The early life stages, from germination to seedling emergence, are the most challenging. Up to 80% of seeds used for dryland restoration exhibit some form of seed dormancy, limiting germination (Kildisheva et al., 2019). The germination requirements vary between species and populations, but environmental cues such as moisture and temperature are important drivers of dormancy loss (Baskin and Baskin, 2014). When germination does occur, failure to emerge can be common, leading to mortality (James et al., 2019, 2011; Larson et al., 2015). This failure can also be driven by soil moisture and temperature (Butterfield and Munson, 2016; James et al., 2019; Larson et al., 2021). Restoration under increasing aridity requires creative approaches and adaptive responses to overcome the many barriers present in dryland restoration.

## **Overview of Chapters**

My dissertation looks at biotic (propagule scarcity, granivory, competition) and abiotic (harsh climate, destabilized soils) barriers to restoration in severely degraded drylands with the aim to improve both our understanding of these barriers and our ability to overcome them through management.

In Chapter 2, I investigate the role of granivores, such as rodents and harvester ants, in limiting seeded restoration. Granivores are known to influence soil seed banks, community

structure, and ecosystem functioning in drylands, and yet their impact on restoration is not well understood. I find that harvester ants can remove up to 80% of seeds during the summer periods of high foraging activity, translating into a 20% reduction in restoration seeds remaining in the seed bank. However, foraging behavior occurs primarily in late spring through early fall, creating a window of opportunity. Seeding that occurs in the late fall for a spring germination are likely to avoid seasonal ant granivory pressure. Seedlings with high rates of seed dormancy are likely to face granivore pressure and addressing this barrier may be necessary.

In Chapter 3, I evaluate restoration strategies to stabilize soils and increase native vegetation while maintaining cattle grazing. Livestock grazing is the largest land use on drylands globally, and overgrazing represents a major degradation pathway. At the same time, domestic livestock grazing provides critical ecosystem services to support human livelihoods, so understanding tradeoffs between grazing ecosystem services and other ecosystem services is crucial in dryland ecosystems. We applied three restoration treatments: 1) restoration of the seedbank by a business-as-usual drillseeding approach, 2) soil stabilization and safe site creation with artificial barriers (“ConMods”) plus hand seeding, 3) drillseeding treatment plus application of an organic soil stabilizer (psyllium) in combination with inoculation of biological soil crusts and compared them to 4) untreated controls. Half of the treatment plots were rested from grazing for the entire experiment. Cattle were reintroduced to half of the restoration treatment plots after a two-year rest period. The shifting nature of restoration barriers meant that we were not successful in setting the site on a positive trajectory towards recovery. Given that, there were not large tradeoffs between cattle grazing and other ecosystem services. This project highlights the importance of adaptive management and the need to be realistic when it comes to restoration outcomes under a changing climate.

In Chapter 4, I investigate microsite limitation in dryland restoration by creating microsites with soil pitting, biochar, and seed pellets. I find that soil pitting and biochar increase native plant density and biomass, and in this study, these microsites were required for native plant germination. There was basically zero native plant germination outside of the soil pits. However, microsite creation came with a cost - they increased non-native vegetation by about 100-fold. Seed pellets did not have an effect in this study.

The barriers presented by dryland restoration remain clear throughout this work, as does the importance of continuing to improve our practical understanding of dryland restoration.

## CHAPTER II

### Seasonal effects of granivory on broadcast seeding in a degraded semi-arid grassland

Claire C. Karban & Nichole N. Barger

#### **Abstract**

Granivores such as rodents and harvester ants are common in dryland systems. Their effects on soil seed banks, plant community structure, and ecosystem functioning are well established for intact dryland ecosystems. However, the effects of granivores on dryland restoration have received much less attention. In this study we evaluated the seasonality of seed removal by harvester ants, seed preference, and the soil seed bank after harvester ant and rodent exclosure. We found that harvester ants foraging behavior was highly seasonal, removing no seeds during winter months, and up to 80% of seeds during high activity in the summer. This seasonal foraging behavior translating into measurable differences in the soil seed bank. There was no difference in the seed bank when ants were excluded over the winter. However, ants reduced the number of seeds in the seed bank by approximately 20% over the summer months. These findings have implications for management. Business-as-usual seeding practices are to seed in the late fall. If seeds germinate in the first growing season, ant granivory is unlikely to occur. However, if seeds remain dormant during the first year as is common in many dryland species, seeds are vulnerable to ant granivory.

#### **Introduction**

Restoring degraded landscapes is one of the central challenges of the twenty first century. Drylands cover approximately 40% of terrestrial surface area and are estimated to be degraded across more than 50% of their range (UNDP/UNSO, 1997). Following degradation, active

restoration is often required to restore ecological function (Miguel et al., 2020). Seeding, increasingly with native species, is the most widely used active restoration technique because it is relatively inexpensive and is logistically feasible in most landscapes (Miguel et al., 2020). Unfortunately, fewer than 10% of seeds used in dryland restoration successfully recruit (Kildisheva et al., 2016). Improving recruitment in dryland restoration remains an active topic of research. Research on seeded restoration has focused primarily on seed-mix selection, seed sourcing, and seed technologies like priming or coating (e.g. Barga et al., 2020; Funk et al., 2008; Svejcar et al., n.d.). Biotic effects such as granivory have received far less consideration, despite the potential of granivores to remove a huge number of seeds.

Granivores, predominantly harvester ants and rodents, are known to strongly influence soil seed banks, plant community structure, and ecosystem functioning in drylands (Bricker et al., 2010; Brown et al., 1979; Gurney et al., 2015; Hulme, 1998; MacMahon et al., 2000). These influences are important considerations for dryland restoration outcomes, particularly for seeded restorations that aim to replenish the soil seed bank. Harvester ants from the *Pogonomyrmex* genus are central-place foragers, and seeds make up the primary food source for most species. There is no evidence of myrmecochory – or seed dispersal – for *Pogonomyrmex spp.*, and the majority of seeds that are removed by *Pogonomyrmex spp.* do not recruit (reviewed in MacMahon et al., 2000). Most studies estimate that ants remove <10% of total seed rain in intact desert ecosystems (e.g. MacMahon et al., 2000, 2000; Whitford, 1978). However, harvester ants prefer some species over others and may remove preferred species at much higher rates, sometimes up to 100% (Crist and MacMahon, 1992; Reichman, 1979). Seed preference is influenced by seed size, caloric content, morphology, viability, and relative abundance (Hansen, 1978; MacMahon et al., 2000; Whitford, 1978), and these factors vary by ant species and across

season and years. Harvester ants forage for seeds only at the soil surface (Reichman, 1979), such as those applied via broadcast and aerial methods in restoration.

In addition to harvester ants, there are many species of granivorous mammals in drylands. Several of the most important genera in southwestern North America are kangaroo rats (*Dipodomys spp.*) and pocket mice (*Perognathus spp.*), which eat exclusively or primarily seeds (Brown et al., 1979). Seed predation by rodents is known to be an important biotic filter in community assembly processes (Lucero and Callaway, 2018; Maron et al., 2012; Orrock et al., 2009). Unlike ants, rodents will collect seeds both at the surface and buried up to 14 cm in the soil (Reichman, 1979) and have been found to reduce plant establishment by over 50% (Orrock et al., 2009). Rodents show preferences for heavier seeds, as these maximize caloric gain for foraging effort (Brown et al., 1979; Inouye et al., 1980; Maron et al., 2012). There is limited evidence that reducing rodent granivory can lead to increased recruitment in restoration (Pearson et al., 2019).

Granivory in drylands is influenced by land degradation. Overgrazing is the dominant degradation pathway in many drylands. Soil and vegetation patterns are altered by overgrazing, and these are important controls over ant and rodent density and distribution. Indirect effects of grazing on soil texture and type are the most important drivers of ant and rodent granivory (Crist and Wiens, 1996). Ant density is influenced by soil texture, and ant foraging is decreased by disturbances such as soil erosion or livestock trampling that divert foraging energy to nest maintenance. Given the importance of granivory in shaping dryland community assembly, a better understanding of granivore-seed interactions on degraded land is crucial for restoration outcomes. Studies that consider granivores as a biotic filter to restoration consistently find significant influences of both ants and rodents (Elliott et al., 2021; Fick et al., 2016; Gurney et

al., 2015; Pearson et al., 2019; Suazo et al., 2013). However, our understanding of granivore-seed relations in degraded rangelands is still lacking.

In this study, we evaluate the effect of granivory on broadcast seeding in a highly degraded rangeland on the Colorado Plateau. Our first objective was to quantify seed removal by harvester ants across season and years. Season and annual variation in seed removal by harvester ants influences the effects of granivory on restoration outcomes. Our second objective was to evaluate harvester ant preference for native species commonly used in rangeland restoration. We predicted that seed mass and seed morphology would determine preference, as foragers balance caloric gain with ease of handling. Our final objective was to evaluate the influence of rodents and ants on the abundance of broadcast seeds in the seedbank. Highly degraded rangelands are often targeted for restoration seeding. However, our understanding of how granivory may influence the success of broadcast seeding methods is incomplete. This understanding will inform and hopefully improve broadcast seeding methods in future rangeland restoration.

## **Methods**

### *Site description*

We conducted our study at four sites at the Canyonlands Research Center, on the Colorado Plateau in southeastern Utah. The sites are located at about 1627m above sea level, and have a cool desert climate with a mean annual temperature of 15° C and a mean annual precipitation of 197mm (Urban, 2017). Precipitation falls bimodally, with convective monsoonal events in the summer and snow and rain in the winter. The sites span several ecosites, with predominantly well-drained, sandy loam soils and reference state dominant vegetation including perennial bunch grasses such as Indian ricegrass (*Achnatherum hymenoides*) and James' galleta grass (*Pleuraphis jamesii*). The reference state shrub canopy is dominated by four-wing saltbush

(*Atriplex canescens*) or Greasewood (*Sarcobatus vermiculatus*). All sites have experienced cattle grazing over the last century and are currently moderately to severely degraded. The “Bromus” site (38.0684059°, -109.5671036°) is dominated by cheatgrass (*Bromus tectorum*) but still contains an assemblage of native vegetation as well as intact, well-developed biocrusts. The “Rocky” site (38.1081613°, -109.6006833°) has rockier soils, native vegetation, well-developed biocrust, and few invasive species. The “Invaded” (38.10800000°, -109.60244444°) and “Invaded\_Fenced” (38.10866667°, -109.60227778°) are severely degraded and contain no biocrust. These sites are dominated by invasive species, including mouse barley (*Hordeum murinum*), annual wheatgrass (*Eremopyrum triticeum*), Russian thistle (*Salsola tragus*), and redstem filaree (*Erodium cicutarium*). The Invaded\_Fenced site has been within a fence excluding cattle grazing since 2017. Two species of harvester ants, the western harvester ant (*Pogonomyrmex occidentalis*) and the desert harvester ant (*Pogonomyrmex rugosus*) were present in the area. *P. rugosus* were found at the Invaded\_Fenced and Invaded sites. *P. occidentalis* were found at the Bromus site. Both species of ants were found at the Rocky site but only the *P. occidentalis* ant nests were used in this study.

For this study we selected seeds from native species that are representative of nearby intact plant communities (Table 2-1). We sourced seeds from regional seed suppliers commonly used to supply large-scale restoration projects. A dry mass for each seed species was calculated as the average of 50 dried seeds. The seeds purchased for restoration had some morphological differences from wild seeds, including smaller or less prominent awns.

**Table 2-1.** Seed species used in experiments.

Species (ABBR.)	Func. group	Seed mass (mg)	Awn	Seed removal	Seed preference	Seedbank exclosure
<i>Achnatherum hymenoides</i> (ACHY)	C3 grass	4.085	No	X	X	X
<i>Atriplex canescens</i> (ATCA)	shrub	6.440	No	X	X	X
<i>Cleome lutea</i> (CLLU)	annual forb	4.015	No		X	X
<i>Elymus lanceolatus</i> (ELLA)	C3 grass	3.105	Yes		X	
<i>Helianthus annuus</i> (HEAN)	annual forb	7.390	No		X	
<i>Leymus cinereus</i> (LECI)	C3 grass	3.285	Yes		X	X
<i>Machaeranthera canescens</i> (MACA)	perennial forb	0.320	No		Only 2018	
<i>Pleuraphis jamesii</i> (PLJA)	C4 grass	3.400	Yes		X	X
<i>Sporobolus cryptandrus</i> (SPCR)	C4 grass	0.120	No		Only 2018	
<i>Sphaeralcea grossulariifolia</i> (SPGR)	perennial forb	1.180	No		Only 2018	

### *Seed removal by harvester ants*

Sixteen *P. occidentalis* nests and 26 *P. rugosus* nests across all four sites were marked in June 2018. To compare seed removal rates in different seasons, seed removal trials were set up in summer (late June/early July), fall (late October/early November) and spring (mid-late April) from summer 2018 – spring 2020. Seeds from two dominant native plant species – *A. hymenoides* and *A. canescens* were placed 1m from the most prominent nest entrance hole. At each nest, we systematically placed the seeds 1m from the hole in one of the four cardinal directions, irrespective of existing paths of ant travel. Twenty of each seed species was left for 1hr during a period when ants were observed to be active. The timing of activity changed seasonally, as ants are most active between 30° to 45°C. Any seeds remaining after 1hr were counted, and the percent removed was calculated.

The same seasonal time points (summer 2018 – spring 2020) and the same 42 ant nests used in the removal rate experiment were used for the preference experiment (Figure S1-1). To test whether ants showed a preference for removing some species of seeds over others, we drew a grid in the soil directly outside of the most prominent nest entrance hole to ensure discovery.

Two seeds of each species were placed in each grid cell, and the arrangement of the seed species was systematically varied for each nest. During the first year, ten species of seeds were used in the preference trials (Table 2-1). Three of those species were dropped for the second and third year of the preference experiments due to limited availability (*Machaeranthera canescens* and *Sphaeralcea grossulariifolia*) and difficulty handling small seeds in the field (*Sporobolus cryptandrus*). Data for all the species used is reported.

#### *Influence of harvester ants and rodents on seeded species in the seedbank*

To examine the effects of granivores on the community composition of the seedbank, we conducted two manipulative experiments (Figure S1-2). These experiments were done at the two most degraded sites (“Invaded” and “Invaded\_Fenced”) where the vegetation is dominated by non-native invasive species. First, we used plastic containers (11.7 cm diameter x 4.3 cm tall) coated in Fluon to exclude ants from a section of the soil seed bank. Identical containers with ant access holes (1.5 cm wide x 3 cm tall) cut into the sides were used as a control. Ten *P. rugosus* mounds in the Fence site were marked, and four plastic containers were placed 1m from the ant nest hole in the four cardinal directions. Cardinal direction was randomly assigned to ant enclosure treatments. In November 2019, 50 total native seeds (10 PLJA, 10 ATCA, 10 ACHY, 10 LECI, 10 CLLU) were placed into each plastic container. Although these species are present at nearby intact reference sites, none were present at Fence in its degraded state, so it is highly likely that any recovered seeds of these species are related to the experiment. Approximately 6 months later (April 2020), the plastic containers were monitored. Any seeds of these species that had germinated were recorded to account for the fate of those seeds. The top 1 cm of soil from the area inside the plastic containers was then collected. The 1cm soil cores were sieved to 2

mm, which was small enough to capture any of the seed species that we had added. Seeds of the five added species were removed and counted.

To assess the effect of granivores during the late spring-early fall, we repeated the exclosure experiment between April 2021-November 2021 (Figure S1-2). Twenty ant nests in Fence were used for this experiment. We noticed burrows in the site that suggested there was rodent activity, most likely granivorous *Dipodomys spp.* To account for this, we added a treatment excluding rodents using 25 cm x 25 cm cages made of chicken wire (1" hexagonal gaps). These cages allowed ants but not rodents to pass through. At each nest, we set up one replicate of each of the four treatments (– ants and rodents, – ants + rodents, + ants – rodents, and + ants and rodents). The exclosure treatment was randomly assigned to one of four cardinal directions and placed 1m from the nest entrance hole. We added the same mix of native seeds (10 PLJA, 10 ATCA, 10 ACHY, 10 LECI, 10 CLLU) in April 2021. In November 2021 we recorded any seeded species that had germinated, and then collected the top 1 cm of soil from inside the plastic containers. The 1 cm soil cores were sieved to 2 mm, which was small enough to capture any of the seed species that we had added. Seeds of the five added species were removed and counted.

### *Statistical Analysis*

#### Removal Experiment

We tested whether the percentage of seeds removed varied significantly between seasons (spring, summer, fall) and across years (2018-2020). We had data from six time points from ant nests that were repeatedly sampled. We fit a repeated measures linear mixed effects model with season, year, and their interaction, as well as a random term for the repeatedly sampled ant nests and site. The model was fit using the 'lmer' function in the lme4 package (Bates et al., 2015)

with the “contr.sum” contrast matrix to account for the unbalanced design. The significance of the predictor variables was evaluated using a Wald Type III F test from the ‘Anova’ function in the car package (Fox et al., 2022). The ‘emmeans’ function in the emmeans package was used to explore contrasts in group means within levels (Lenth et al., 2022).

### Preference Experiment

We calculated selection ratios for each species of seed for each ant species. The selection ratio was calculated for each trial as:

$$\frac{\text{\# seeds of species}_i \text{ removed}}{(\text{\# species}_i \text{ seeds available}) * (\text{sum of all added seeds removed})}$$

following (Gurney et al., 2015). A selection ratio >1 indicates that the species was preferred, while a selection ratio <1 indicates the species was avoided. 95% confidence intervals were also calculated to determine the probability of the selection ratio overlapping 1.

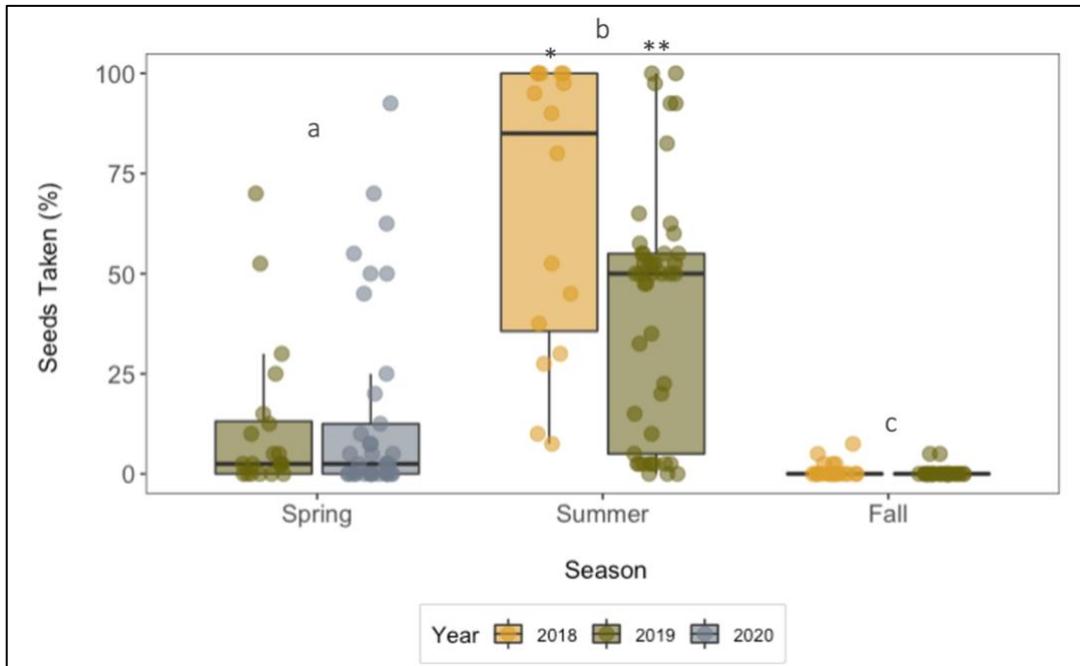
### Granivore Exclosure Experiment

In the exclosure experiment there were two replicates of ant access and ant exclusion at each of ten nests, for twenty total replicates. This issue of pseudo replication of nests is addressed in the statistical model. We used linear mixed-effects models to test whether excluding ants and rodents influenced the restoration seedbank. Models were fit using the ‘lmer’ function in the LME4 package. Seeds were modeled by exclosure treatment, with ant mound included as a random effect. We obtained a Type III Analysis of Variance Table with Satterthwaite’s method using the LmerTest package (Kuznetsova et al., 2020), and marginal and conditional  $R^2$  values

using the MuMIn package (Bartoń, 2022). The ‘emmeans’ function in the emmeans package was used to explore contrasts in group means within levels.

## Results

### Removal Experiment



**Figure 2-1.** Percentage of seeds removed from experimental trials in Summer 2018 – Spring 2020. Boxes show median with the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, as well as the data points. Lower case letters indicate significant ( $p < 0.05$ ) differences between Seasons and asterisks indicate a significant difference between year within a season.

We surveyed seed removal by harvester ants across four sites at three time-points: April, late June – early July, and October, corresponding to spring, summer, and fall seasons. Seed removal varied seasonally ( $F = 19.071$ ,  $p < 0.001$ ; Table 2-2 and Figure 2-1). Ants removed the highest percentage of seeds in the summer (emmeans  $p = 0.0042$ ; 56% *P. rugosus*, 26% *P. occidentalis*), followed by spring (6% *P. rugosus*, 20% *P. occidentalis*) and then fall (1% *P. rugosus*, 0% *P. occidentalis*). This is consistent with patterns of ant foraging activity. Seed removal also varied across years ( $F = 11.306$ ,  $p < 0.001$ ; Table 2-2 and Figure 2-1). Seed removal

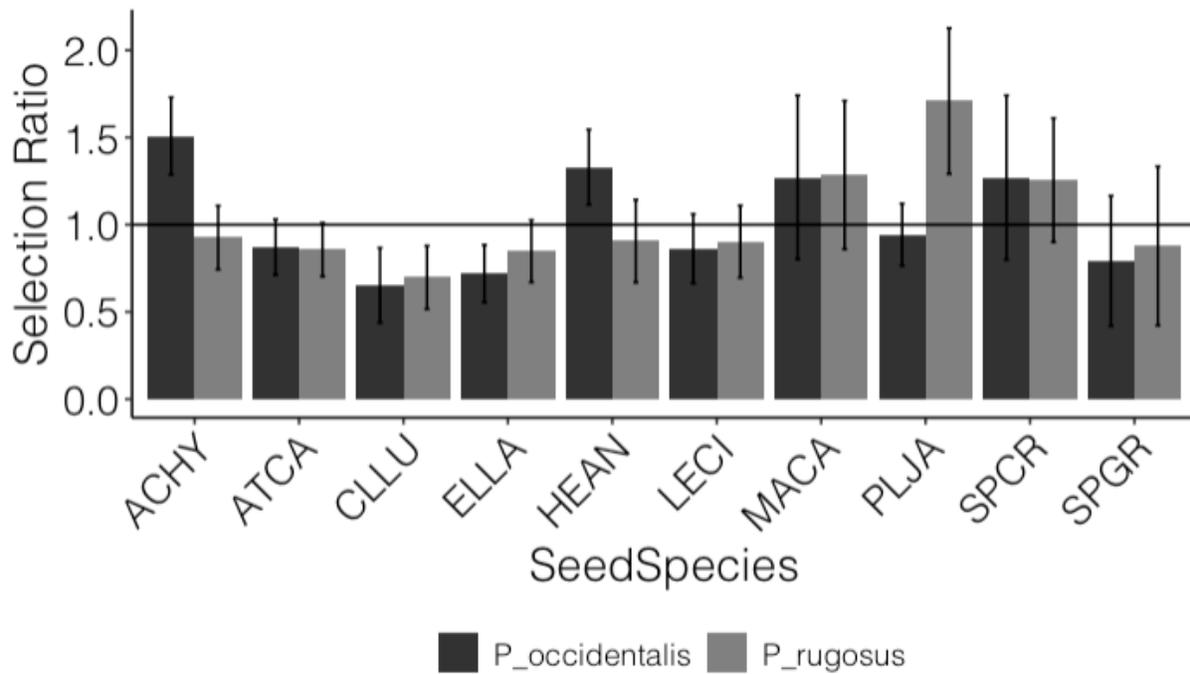
in the summer varied by year ( $F= 13.423$ ,  $p=0.006$ ; Table 2-2 and Figure 2-1), whereas the pattern was consistent across years in the spring and fall. 2018 was a historically dry year with low seed availability, while 2019 was an extremely wet year with abundant seed resources. In summer of 2018, 67% of seeds were removed on average, compared to only 34% in summer of 2019. Both species responded similarly to year and season effects.

**Table 2-2.** Relationships between the percentage of seeds removed by ants, year, season. Mound and site were included as random effects in the model. The coefficients for the repeat measures linear mixed-effects model were calculated using a Wald Type III F test. The marginal and conditional  $R^2$  values indicate the proportion of variance explained by fixed and random effects.

	df	F	p-value	R2m	R2c
Seeds taken ~ Year + Season + Year * Season + (1   mound) + (1   site)				0.4727899	0.479116
Year	2	11.306	<0.001		
Season	2	19.071	<0.001		
Year * Season	1	13.423	<0.001		

### *Preference Experiment*

Seed preferences varied by ant species. *P. occidentalis* preferred *Achnatherum hymenoides* (ACHY) and *Helianthus annuus* (HEAN) and avoided *Cleome lutea* (CLLU) and *Elymus lanceolatus* (ELLA) (Figure 2-2). *P. rugosus* preferred *Pleuraphis jamesii* (PLJA), although this preference only observed in the spring (Figure 2-2). *P. rugosus* did not show a significant preference for any species during the summer months when foraging activity was high. Like *P. occidentalis*, *P. rugosus* avoided *Cleome lutea* (CLLU) (Figure 2-2).



**Figure 2-2.** Seed preferences for each ant species. Selection ratios with 95% confidence intervals are graphed. A ratio of 1 = no preference, >1 indicates preference, and <1 indicates avoidance.

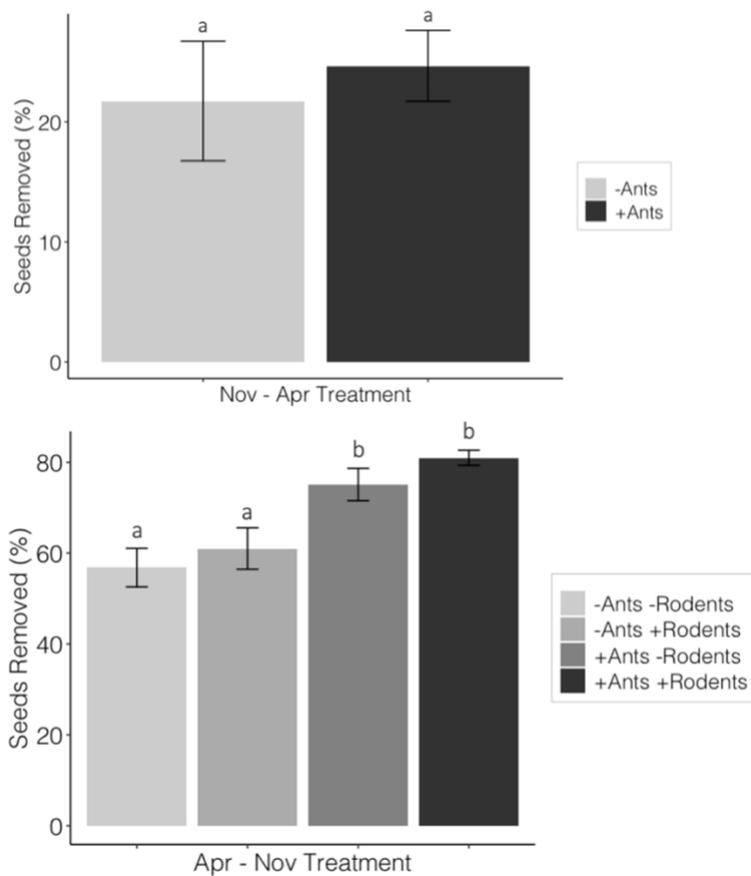
### *Exclosure Experiment*

Excluding ants from the seedbank during the winter months (November – April) had no effect on the seedbank (Table 2-3 & Figure 2-3). This is consistent with fall and spring seed removal patterns (Figure 2-1). However, this pattern changed when ants were excluded from the seedbank during the warmer months with higher ant foraging activity (April – November).

Excluding ants from the seedbank during spring-late fall significantly increased the percentage of seeds from seeded species in the seedbank ( $F=9.803$ ,  $p<0.001$ ; Table 2-3 & Figure 2-3) by about 20%. Excluding rodents from the seedbank did not have a significant effect on the percentage of seeds from seeded species in the seedbank (Figure 2-3).

**Table 2-3.** Relationships between the number of seeds remaining in the seedbank and exclosure treatment for the two seasons when the experiment was run (November – April and April – November). Mound was included as a random effects in the model. The coefficients for the linear mixed-effects models were calculated using Type III analysis of variance table with Satterthwaite’s method. The marginal and conditional R<sup>2</sup> values indicate the proportion of variance explained by fixed and random effects.

Season		df	F	p-value	R2m	R2c
November - April	Seeds ~ Treatment + (1 mound)				0.008573081	0.008573081
	Treatment	1	0.2767	0.6026		
April - November	Seeds ~ Treatment + (1 mound)				0.2681078	0.279796
	Treatment	3	9.803	<0.001		



**Figure 2-3.** Effects of ants and rodents on the percentage of seeds removed from the seedbank. Bars show means values ±1 standard error. Top: the percent of seeds removed after a five-month period from late fall into early spring. Bottom: the percent of seeds removed after a six-month period from spring into late fall. Bars with different lowercase letters indicate significant (p<0.05) differences in means.

## Discussion

Our results show that harvester ants can remove a large percentage of native seeds from at the soil surface. This seed removal corresponds seasonally to ant foraging activity, with much more seed removal in the warmer half of the year. These experiments were conducted in degraded grasslands where seeded restoration was underway to increase native vegetation. Adding seeds is among the most common active restoration strategies in dryland restoration (Shackelford et al., 2021) because it is well-suited to large scales and variable terrain. Seeding as a restoration treatment has increased in the southwestern U.S in recent decades with efforts to combat invasive species and increase native cover (Copeland et al., 2018) and is a significant part of restoration budgets (Munson et al., 2020), particularly if the seedmix includes high diversity or less common species. On the Colorado Plateau, seeding is recommended to occur in the late fall so that seeds can take advantage of winter precipitation. We find that ant granivory is low during this time. This finding suggests that if seeds germinate the first season after being applied in a restoration treatment, they should avoid high rates of ant granivory. If, however, seeds remain dormant, they may be consumed by ants rather than replenishing the soil seedbank.

### *Seasonal and annual variation in seed removal*

The high seasonality of seed removal that we observed is in line with known patterns of ant foraging behavior. Soil temperature is the best predictor of seed foraging across ant taxa (Pol and de Casenave, 2004; Porter and Tschinkel, 1987; Whitford and Ettershank, 1975), particularly at high and low temperatures (Pol and de Casenave, 2004). While cold temperatures more often constrain foraging than high temperatures, *Pogonomyrmex spp.* are known to forage diurnally during the hottest parts of the day in the hot season (Bailey and Polis, 1987; Pol and de

Casenave, 2004). We found these same foraging patterns at our sites in Utah – ant colonies were inactive during the coldest winter months, and ants foraged diurnally on the hottest summer days.

In addition to soil temperature patterns, seed availability also fluctuates with season, influencing foraging behavior (Pol et al., 2011; Porter and Tschinkel, 1987; Suazo et al., 2013). In environments that are governed by spatially and temporally patchy resources, harvester ants specialize their foraging activity (Crist and Haefner, 1994; Pol et al., 2011) and their diet preferences (Crist and MacMahon, 1992; Wilby and Shachak, 2000) to take advantage of seed availability. Grasslands on the Colorado Plateau typically experience two pulses of seeds during the growing season – one in the spring and another in the summer. The increased removal of seeds that we measured during the summer corresponds to the season when seed availability is expected to be highest at our sites.

The results of our study are applicable to seeding treatments, but likely less applicable to natural seed dispersal events. Restoration treatments often provide a large pulse of seed resources at unseasonable times. Seed set naturally occurs in the spring and summer, whereas restoration seeding is typically done in late fall. Additionally, the experimental treatments used in this study provided caches of the same two species throughout the year, and so our results may be influenced by changing seasonal preferences in addition to seasonal foraging activity. It is also possible that the high-density caches of seeds that were used to estimate seed removal % inflate removal due to seed density effects. *P. rugosus* and *P. occidentalis* are known to be group foragers, meaning they increase foraging efficiency to dense patches of resources by working as a group rather than foraging individually (Davidson, 1977; Reichman, 1979). While the rates reported here are comparable to many other experiments that estimate percent seed removal, the removal percentage may not be generalizable for naturally, more sparsely-distributed seedfall.

Food availability and satiation also influence seed foraging behavior (Whitford and Ettershank, 1975). Optimal foraging theory predicts that as ants become satiated, they should forage closer to the nest and remove fewer seeds. Studies have confirmed this, finding that foraging activity is very high in drought years when there is little seed available, and all but stops after ants fill up nest caches during years with abundant seeds (Whitford and Ettershank, 1975). A study manipulating ant satiation found that satiated ants removed 22% of seeds compared to 58% removed by controls and 69% removed by food-deprived colonies (Bailey and Polis, 1987).

The results of this study are limited in their ability to evaluate the impact of granivory on an entire area of restoration. Foraging distance influences seed removal rate, and so the density of ant nests at a site will be important in determining the overall effects of harvester ants on the seedbank. Published nest densities range from 20 to 150 colonies per hectare (reviewed in MacMahon et al., 2000). We estimate that nest density was around 40 colonies per hectare at our sites, but it is a little tricky to estimate as density varied by location, and nests can be over 1 m in diameter and can have multiple entrance holes (reviewed in MacMahon et al., 2000). Foraging rates decrease exponentially with distance from the ant nest (reviewed in MacMahon et al., 2000). This means that our caches of seed placed 1m from ant nests likely experienced higher rates of seed removal than seed located a greater distance from an ant nest. One caveat to that is that seeds located along trunk-trail foraging paths are likely to experience higher seed removal. Many *Pogonomyrmex* spp., including *P. occidentalis* and *P. rugosus*, forage along trunk-trails, so seeds easily encountered from those trails are more likely to be removed. The location and relative activity of trunk-trails varies with seed availability, vegetation structure, and interactions with neighboring ant colonies (reviewed in MacMahon et al., 2000).

### *Seed preference*

Harvester ants eat a wide range of seed species, but they can show strong preferences for some species. In our experiments, *P. rugosus* did not show clear preferences. *P. jamesii* was a preferred seed species in the spring but this preference disappeared in the summer when removal is higher. While we can't know for sure, it is possible that some of the *P. jamesii* seeds were lost in the wind rather than removed by ants as the seeds have large, fluffy awns. Both species of ants avoided *C. lutea* seeds. These seeds are small and may therefore provide a smaller reward, but they are not the lightest seeds included in the study, so mass is not a good predictor of preference here. *P. occidentalis* showed a more consistent preference for both *A. hymenoides* and *H. annuus* seeds. These seeds are among the heaviest, but seed mass does not provide a complete explanation of *P. occidentalis* preference. Compared to other granivores, harvester ants specialize on smaller seeds, limited by the size of their mandibles (Crist and MacMahon, 1992; Davidson, 1993).

In addition to seed size, other factors that can influence seed preference include relative abundance, caloric content, morphology, and viability (reviewed in MacMahon et al., 2000). The *A. hymenoides* and *H. annuus* seeds preferred by *P. occidentalis* are morphologically very similar, with smooth, awnless seed coats. The influence of morphology on preference is debated. Studies have found that *Pogonomyrmex spp.* prefer awned seeds, perhaps because they are easier to grasp during transport (Pulliam and Brand, 1975). Other studies show the opposite – that ants prefer smooth seeds and may find large awns cumbersome for transport (Crist and MacMahon, 1992). Seeds with robust seed coats may be the most resistant to desiccation. Although seeds were stored in cool, dry conditions during the experiment, we did not procure fresh seeds each year and it is possible that the quality of the seeds deteriorated and influenced ant preferences.

Foraging distance and seed density can also influence seed preferences. Some studies find that ants show very strong preferences, removing up to 100% of preferred species (Crist and MacMahon, 1992). However, selective exploitation is limited to greater distances (>10m) from the nest and no strong preferences are found within a short distance (5m) to their nest (Crist and MacMahon, 1992). Harvester ants selectively forage for and remove seeds that are closer to their nests, so strong preferences at greater distances may not be consequential at a plant community level when nest density is relatively high. Our experiment placed the seeds directly outside the nest entrance hole (<1m) to ensure rapid discovery, and this may have influenced our preference results.

### *Seedbank*

As a result of selective foraging, granivores can change the seedbank and ultimately the distribution and relative abundance of plants (reviewed in MacMahon et al., 2000). In our experiment, we evaluated the effect of granivore exclusion on the seedbank of seeds that are typically used in restoration of degraded grasslands in this region. Our seedbank sampling areas were 1 m from the ant nest, which is on the short end of published mean foraging distances, so the sampling areas are expected to experience high seed removal, possibly with low seed species selectivity (reviewed in MacMahon et al., 2000). We found that excluding ants significantly altered the seedbank across the warm season of high ant activity, but not over the cool season when seed removal is negligible. This reduction in seeds will likely result in lower emergence and recruitment in restoration. In one experiment, workers found that ants reduced seed densities of a desert annual, decreasing plant competition and reproductive output (Harmon and Stamp, 1992).

There was no significant effect of rodent enclosure on the seedbank in the warm season, but there does appear to be a small, non-significant decrease in number of seeds in the seedbank as a result of rodents. The plastic containers that were used to exclude ants did not prevent rodents from accessing seeds, but it is possible that they acted as a deterrent. We placed seeds at the soil surface to mimic broadcast seeding methods, and it is possible this may have favored ant granivory over rodent granivory. Other studies have found higher rates of rodent granivory when seeds are buried to mimic drillseeding methods (Gurney et al., 2015).

### *Management Implications*

In this experiment, we mimicked broadcast seeding methods by scattering seeds at the soil surface. Broadcast seeding is a common method in restoration because it can be done at a large scale, it is relatively inexpensive, and it does not create any additional disturbance such as soil destabilization caused by drillseeding. However, broadcast seeding spreads seeds indiscriminately on the soil surface where they are exposed to desiccation, redistribution, and granivory, and are unlikely to germinate unless they find their way into a more favorable site. Methods that protect against these shortcomings should be optimized for large-scale distribution, given the large areas of land that are currently degraded and in need of restoration. There are several promising solutions to reduce ant granivory in broadcast seeding restorations.

Physical deterrents may be effective against ant granivory. Harvester ants do not forage for seeds that are buried under the soil surface, and lightly raking seeds has been shown to decrease ant activity and increase recruitment (Fick et al., 2016). This practice has the additional benefit of increasing seed soil contact. However, similarly to drillseeding, raking seeds has the potential to increase soil destabilization and does not protect seeds from rodent granivory.

Depending on site-specific soil conditions and granivory threats, this may or may not improve restoration outcomes. Glue or mucilage to stick seeds to the soil may be another important physical deterrent, reducing ant granivory in seeds where it occurs naturally (Fuller and Hay, 1983; Pan et al., 2021). Wetting seeds to activate mucilage or adding a glue to seeds that do not produce a mucilage are potentially interesting strategies to reduce granivory, however they have not yet been evaluated for restoration.

Timing of seeding is an important management consideration to reduce granivory during restoration. Current best practices on the Colorado Plateau typically recommend seeding in late fall so that seeds can take advantage of winter moisture, and to help break dormancy for some species. Our research supports this timeline, finding low seed-removal rates in the fall and spring. If seeds are applied during the fall and germinate that year, ant granivory should be minimal. However, seed dormancy in dry systems is very high. One study estimates that over 80% of seeds commonly used in restoration in the Great Basin may have some level of dormancy (Kildisheva et al., 2019). While seed dormancy may be a good trait in intact plant communities experiencing variable dryland conditions, it is also likely very costly in a restoration context. If seeds do not germinate in year one of a restoration project, they may be susceptible to high levels of granivory during the spring and summer when ants are actively removing seeds.

Methods to break seed dormancy may reduce seed loss to granivory by ensuring that seeds germinate before ant activity increases. There are many methods to break dormancy, including seed priming with water, salicylic acid, fungicides or gibberellic acid (Pedrini et al., 2020).

Results of priming are variable and species-specific. However, temperature may be the most limiting factor to germination in many species (Kildisheva et al., 2019). Additionally, breaking dormancy is only likely to increase plant establishment under certain abiotic conditions (i.e.,

enough moisture for seedling survival). Tools that predict soil moisture, such as the ecological drought forecast tool from the USGS (Bradford and Andrews, n.d.) should be coupled with dormancy manipulations to maximize plant recruitment in restoration treatments. Another option is to seed over multiple years to bet hedge against climate conditions that do not break seed dormancy (Shriver et al., 2018).

## CHAPTER III

### Ecosystem service restoration in a severely degraded semi-arid grassland

Claire C. Karban, Rebecca Mann, Michael Duniway, Akasha Faist, David Hoover, Nichole N. Barger

#### **Abstract**

Domestic livestock grazing provides ecosystem services to support human livelihoods around the globe. However, historic and current livestock overgrazing is a major degradation pathway in dry rangeland ecosystems. Degradation can trigger a shift to an alternative stable state, which is often accompanied by a reduction or change in the portfolio of ecosystem services provided by the land. Decisions regarding restoration and management of degraded land are complicated by how to maximize ecosystem services under a changing climate. In this study, we evaluate restoration strategies to stabilize soils and increase native vegetation while maintaining cattle grazing. This study was conducted over four years at a semiarid grassland in SE Utah that was converted to a degraded, alternative stable state. We applied three restoration treatments: 1) restoration of the seedbank by a business-as-usual drillseeding approach, 2) soil stabilization and safe site creation with artificial barriers (“ConMods”) plus hand seeding, 3) drillseeding treatment plus application of an organic soil stabilizer (psyllium) in combination with inoculation of biological soil crusts and compared them to 4) untreated controls. Half of the treatment plots were rested from grazing for the entire experiment. Cattle were reintroduced to half of the restoration treatment plots after a two-year rest period.

We found that soil stability was increased in the psyllium plus biocrust treatment. None of the treatments were effective at establishing native vegetation, and changes in plant cover

were driven by inter-annual climate variability and not restoration treatments. Reintroducing cattle grazing after a two-year rest period reduced total plant density and in an extremely dry year, grazing significantly increased total plant cover. The increase in cover was primarily driven by non-seeded, weedy or invasive species rather than native species. Grazing-derived ecosystem services can often trade-off with other ecosystem services. We found that there was no tradeoff with soil stability, but grazing did increase wind-borne sediment fluxes. Overall, the restoration barriers in drylands are numerous and change over time and space. Under a changing climate, strategies that manage for ecosystem services and functions, rather than strategies that restore to a previous intact state, are likely to be most successful.

## **Introduction**

Dryland ecosystems cover about 40% of earth's land area and support the livelihoods of over two billion people through ecosystem services (Millennium Ecosystem Assessment, 2005). Over half of the world's livestock live on drylands, making livestock grazing the dominant land use (Allen-Diaz, 1996). However, drylands also provide supporting, regulating, and cultural ecosystem services including native plant diversity, net primary productivity, soil fertility, erosion control, recreation, and aesthetic and spiritual services. The continued supply of ecosystem services from drylands is threatened by overuse, such as overgrazing by livestock, coupled with increasing aridification in dry regions (Millennium Ecosystem Assessment, 2005; Reynolds et al., 2007; Seager et al., 2007). Ten to 20% of global drylands are currently degraded (Millennium Ecosystem Assessment, 2005), with about 12 hectares added each year (Brauch and Oswald, 2009).

Severe degradation can lead to persistent changes in ecosystem structure and function (Beisner et al., 2003), altering the ecosystem services provided (Folke et al., 2004). These

alternative stable states are particularly common in drylands, where precipitation is low and variable (Reynolds et al., 2007; Schlesinger et al., 1990). Published examples of state changes in drylands include a shift from perennial plants to invasive annual grasses (D'Antonio and Vitousek, 1992; Okin et al., 2009) and feedbacks between soil degradation and declining vegetation (Okin et al., 2009; van de Koppel et al., 1997). These state shifts can result in losses of palatable forage for livestock, decreases in soil stability, increases in soil erosion, loss of native plant diversity, loss of soil fertility, and loss of soil water-holding capacity (Miller et al., 2011). Once a state change has occurred, natural recovery of ecosystem services does not occur in a management-relevant time frame (Miller et al., 2011; Suding et al., 2004).

Restoration of ecosystem services on highly degraded rangelands is extremely challenging and there are often tradeoffs between services (James et al., 2011; Miller et al., 2011). For example, livestock provisioning services often come at the cost of net primary productivity, so restoration strategies may vary depending on management objectives (Petz et al., 2014). Barriers to restoration include a lack of native plant propagules, a lack of safe sites for plant germination and establishment, and destabilized, eroding soils (Allen, 1996; Suding et al., 2004). Business-as-usual restoration focuses solely on replenishing native seed (Hobbs and Norton, 2013), which is a relatively inexpensive intervention that can be implemented at a large scale. However seeding has very low success rates in dryland restoration, with about 17% of seedlings failing to establish any plants, and over half of species used in seed mixes failing to establish (Shackelford et al., 2021). A business-as-usual seeding strategy addresses the barrier of native propagule scarcity, but it overlooks the additional restoration barriers of safe site limitation and soil destabilization. At sites where soils are destabilized or prone to erosion, stabilizing soils and providing seed safe sites are essential for ecosystem service recovery.

Soil destabilization and erosion are well-known to be important drivers of degradation in dryland systems (Okin et al., 2009; Ravi et al., 2010), making them crucial to address in restoration. Several methods to obstruct or slow the movement of wind and water across the surface of degraded drylands have been successful in restoration. For example, straw checkerboards trap fine soil particles, increasing soil fertility and herbaceous cover in restoration on sandy soils (Li et al., 2006; Miao et al., 2015). Woody debris piles increase plant establishment (Visser et al., 2007). More recently, wire mesh barriers called ‘connectivity modifiers’ (‘ConMods’) have been used to capture sediment and litter (Okin et al., 2015; Rachal et al., 2015), and create safe sites, increasing seed germination (Fick et al., 2016). More work is needed to understand the potential of ConMods, particularly in combination with active grazing pressure.

One of the main contributions to soil stability and nutrient cycling in dryland soils is biological soil crust, or ‘biocrust.’ These communities of cyanobacteria, lichens, and mosses stabilize soil surfaces against erosion, facilitating soil formation (Chaudhary et al., 2009; Weber et al., 2022). Biocrusts are highly susceptible to disturbances such as trampling, and once crushed, biocrusts lose their stabilizing function (Zaady et al., 2016). As the functional importance of biocrust becomes more widely known, new biocrust restoration techniques are being developed, however there are still barriers to restoring biocrusts (Antoninka et al., 2020b). Barriers for biocrust restoration include a lack of propagules at degraded sites, as well as destabilized soils that prevent establishment. Our ability to grow biocrust in greenhouses has greatly improved in recent years, but successfully establishing biocrust in a field setting remains a significant obstacle to successful restoration (Antoninka et al., 2020b), particularly when coupled with active grazing.

In this study, we test ConMods and biocrust inoculation – two novel restoration strategies – at a severely degraded rangeland in southeastern Utah. We provide a field test of a new biocrust restoration method: greenhouse-grown biocrust inoculum (Velasco Ayuso et al., 2017), applied with psyllium, a biodegradable polymer soil stabilizer to promote establishment (Fick et al., 2020b). Our restoration strategies were targeted to address specific barriers to restoration: a lack of native plant and biological soil crust propagules, a lack of safe sites for plant germination and establishment, and destabilized, eroding soils. Our overarching goal was to evaluate the efficacy of these strategies for restoring regulating (erosion control) and supporting (net primary productivity, soil formation) ecosystem services, while maintaining provisioning services provided by livestock grazing. Drillseeding is a business-as-usual restoration strategy that addresses only the plant propagule scarcity restoration barrier. We hope that by creating safe sites and stabilizing soils through novel restoration strategies, we will be able to increase the regulating and supporting ecosystem services compared to drillseeding and no active restoration. We expect that regulating and supporting ecosystem services, such as erosion control, soil stability, and net primary productivity, may trade off with provisioning ecosystem services when grazing is reintroduced.

## **Methods**

### *Study Site*

We established restoration plots at a former pasture in SE Utah (38.1094 N latitude, 109.6017 W longitude, 1568 m elevation) on the Colorado Plateau physiographic province. The site is semi-arid cool desert with an average annual temperature of 15° C and an average annual precipitation of 197 mm (Urban, 2017). The soils at the site are classified as loam (45.5% sand, 17.8% clay, 36.8% silt; data from control plots in 2021) in the Mivida series, which are linked to

the semidesert fourwing saltbush sandy loam NRCS Ecological Site (R035XY215UT, Jornada EDIT, n.d.). This site is typically dominated by C3 and C4 perennial bunch grasses including Indian ricegrass, sand dropseed, and James' galleta grass, interspersed with four wing saltbush shrubs. For reference, intact sites in the area have around 46% cover of vascular plants, including exotic species, and 34% biocrust cover, dominated by cyanobacteria, with mosses and lichens (Miller et al., 2011). The site selected for this study has been grazed by cattle for over 100 years and used as irrigated pasture for some portion of that time. It is in a severely degraded state, with extensive patches of bare ground, essentially no biocrust cover, and vegetation dominated by annual wheat grass, wall barley, and Russian thistle.

### *Experimental Design*

In October 2017 we applied glyphosate herbicide with an adjuvant at a rate of 48 oz/ac to reduce the high density of invasive vegetation. The experimental area was fenced in December 2017 to exclude cattle. 25m x 25m plots were established with four restoration treatment levels: 1) drillseed (Drill), 2) connectivity modifiers (ConMod), 3) drillseed plus biocrust inoculation and soil stabilizer (BSC + psyllium), and 4) an untreated control. These four treatments were replicated 6 times in a complete block design.

In seeded plots, we seeded an eleven-species seed mix (Table 3-1) at a rate of 7.59 PLS lb./ac. Prior to seeding, globemallow seeds were dipped in boiling water for 60secs prior to seeding to help break dormancy. The Drill plots were based on current business-as-usual restoration approaches for the area. Drill seeding was performed for six of the species in the seedmix using a rangeland drill, with a disk spacing of 12", a furrow depth of 2", and steel drag chains following the seed drop to loosely cover the seed with soil. This resulted in a final planting depth of approximately ½" within furrows. The remaining five species in the seedmix

were either small-seeded or fluffy; these species were broadcast by hand to achieve a shallower planting depth as recommended in NRCS planting guides. Furthermore, due to mechanical complications, not all seeds were released from the rangeland drill after a full pass of all plots; all remaining seeds were recovered from the rangeland drill and broadcast by hand throughout all drillseed plots. After broadcast seeding, drill-seeded plots were raked by hand using garden rakes to improve seed to soil contact and burial.

In each ConMod plot, we installed 289 wire mesh ‘ConMod’ barriers (32 cm x 32 cm), regularly spaced at 1.5 m intervals, and covering 4.7% of the total area in the 625 m<sup>2</sup> plot. The 0.1024 m<sup>2</sup> area under each ConMod was seeded with the same seed mix and seeding rate as the drillseeded areas, although seeds were planted by hand at optimal depths for each species.

The plots receiving the BSC + psyllium treatments were first seeded using the same methods as the drill-seeded plots. After seeding, a biodegradable, psyllium husk-based soil stabilizer (M-Binder by Ecology Controls) was sprinkled over the entire plot area at a rate of 60 g/m<sup>2</sup>. We gently raked it in following distribution. In the same plots, we inoculated 26 0.5m x 5m strips (32.5 m<sup>2</sup>, or 10.4% of the whole plot area) with a biological soil crust and psyllium mixture. Thirteen of the 26 strips were inoculated in February 2018 using an 8.5% biocrust delivery rate, and the other thirteen strips were inoculated in November 2018 using a 20% biocrust delivery rate. The biological soil crust used for inoculation was collected near the study area and then bulked up in a greenhouse. The greenhouse-produced biocrust was gently crumbled to retain chunks up to 1” in diameter, and then mixed with 60g/m<sup>2</sup> of psyllium. For field delivery, the strips to be inoculated were watered to saturation, sprinkled with the inoculum + psyllium mixture, and then watered to saturation again.

In April 2020, following 2+ years of cattle exclusion, we reintroduced 8 calf-cow pairs (16 total cows) to 3 of the 6 experimental blocks. Three bulls were added to encourage movement after we observed that the cows were standing around more than actively grazing. Grazing was conducted as a flash grazing to target abundant annual grasses prior to seed set. Stubble height in the grazed plots was reduced to an average of 7.7 cm (+/- 2 cm; Fig. S2-1). To reach this stubble height target, animal-hours in each plot varied from 1.58 – 48 due to differences in movement and eating rates. Before the April grazing, we reseeded half of each plot, excluding controls. We broadcast seeded each plot (excluding the no-treatment controls) at 19.92 PLS lb./ac with a modified seedmix (*Sporobolus cryptandrus*, *Sporobolus airoides*, *Achnatherum hymenoides*, *Atriplex canescens*, *Sphaeralcea grossulariifolia*, *Cleome lutea*, and *Helianthus annuus*).

**Table 3-1.** Native seedmix used to seed the plots in Fall 2017.

Species	Scientific name	Functional group	% of mix	Seeding depth
Indian ricegrass	<i>Achnatherum hymenoides</i>	C3 grass	16.2	½” (drill); 2” (ConMod)
Sand dropseed	<i>Sporobolus cryptandrus</i>	C4 grass	16.2	surface
Basin wildrye	<i>Leymus cinereus</i>	C3 grass	16.2	½”
Thickspike wheatgrass	<i>Elymus lanceolatus</i>	C3 grass	6.1	½”
James’ galleta	<i>Pleuraphis jamesii</i>	C4 grass	16.2	surface (drill); ½” (ConMod)
Yellow beeplant	<i>Cleome lutea</i>	Annual forb	1.8	½”
Gooseberry globemallow	<i>Sphaeralcea grossulariifolia</i>	Perennial forb	3.2	surface
Pale evening primrose	<i>Oenothera pallida</i>	Perennial forb	3.2	surface
Hoary tansyaster	<i>Machaeranthera canescens</i>	Perennial forb	3.2	surface
Annual sunflower	<i>Helianthus annuus</i>	Annual forb	1.5	½”
Fourwing saltbush	<i>Atriplex canescens</i>	Shrub	16.2	½”

### Soil Sampling

All soil retention variables were collected at sampling locations along plot transects. Control, Drill, and ConMod plots had 4 transects each, and BSC + psyllium plots had 5 transects. Sampling was done at fixed locations along each transect and the number of samples collected

varied by plot treatment. For Control, Drill, and ConMod plots, we collected 18 samples per plot for each of the soil variables: soil stability, chlorophyll a, and EPS. For the BSC + psyllium plots we collected samples at 36 locations per plot. Biocrust cover was sampled 20 times per Control and Drill plot, 40 times per ConMod plot, and 50 times per BSC + psyllium plot. The increased number of sampling points in the ConMod and BSC + psyllium plots were to capture increased variability because of the patchy distribution of conmods and biocrust inoculation.

Soil stability samples were tested for soil stability in the field, using a field aggregate stability test (Seybold & Herrick 2001). At each sampling location, we collected separate 1 cm x 8 mm soil peds for chlorophyll a and for EPS. Loose litter was gently brushed away from the soil prior to sampling. Soils were kept in the dark, air-dried, frozen, and transported back to the lab for analysis. Chlorophyll a was extracted with acetone (supplemental S2-1), and values were calculated based on the equations in Ritchie (2006). We extracted loosely-bound, tightly-bound, and glyocalyx fractions of EPS with a phenol-sulfuric acid, modified from Chock et al. (2019; supplemental S2-2).

#### *Aeolian sediment flux monitoring*

Aeolian sediment fluxes were captured in free-rotating Big Springs Number Eight (BSNE) dust samplers (Fryrear, 1986). Three dust samplers were located in a triangle arrangement in the center of each plot. Sediment was captured in a 0.001 m<sup>2</sup> opening at 15 cm +/- 2 cm above the ground. Sediment was collected monthly, dried at 60°C for 24 hours, weighed, and converted to flux values by dividing grams collected by days of collection, by area of the sampler opener (g/m<sup>2</sup>/day; Fryear 1986).

#### *Cover and biomass monitoring*

Plant cover was estimated every meter along each transect using a line-point intercept method (Herrick, 2005). Line-point intercept includes a soil surface cover measurement, but to better capture the variability of the soil surface, soil surface cover was estimated using a  $0.20 \times 0.20$ -m pin-frame with a grid of sampling intersections. We recorded 20 soil surface cover points per plot following classes described in Herrick et al. (2005), with modifications used by the National Wind Erosion Research Network (Webb et al., 2016).

Aboveground biomass was sampled in four  $0.5\text{m}^2$  quadrats per plot each spring and fall to capture the two peaks in the growing season. The ConMod plots had 4 additional paired plots to include samples both in ConMods and in ConMod interspaces. The quadrat location changed every season to avoid resampling the sample location. Aboveground biomass was sorted by species, dried at  $60^\circ\text{C}$  for 48 hours, and weighed.

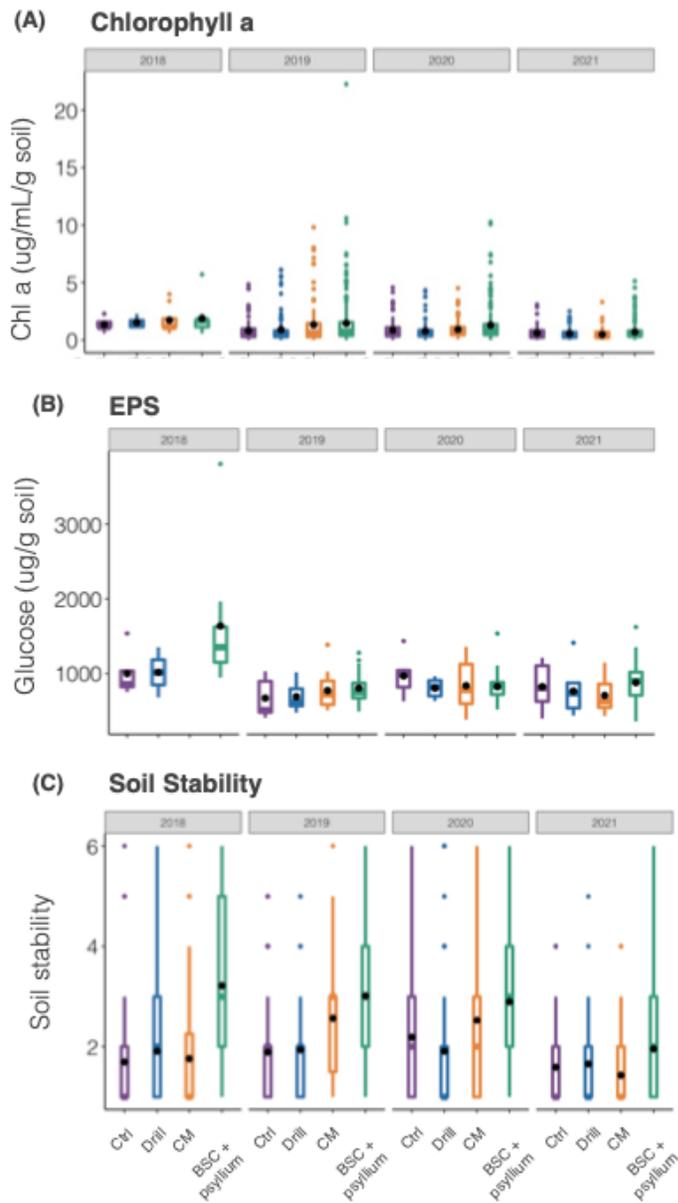
### *Statistical Analysis*

To compare variables across restoration treatment and grazing treatments, we fit linear mixed effects models using the lme4 package. Response variables were transformed to approximate a normal distribution if necessary. We fit separate models for data collected pre-grazing (2018-2019) and post-grazing (2020-2021) to look at the effects of grazing. Year was included as a fixed effect in all models. We also included a nested random effect of transect within plot within block for the plant models to account for non-independence in sampling. Since the BSNE data was not collected along transects, we included just the random effect of plot nested within block. Additionally, we took a subset of the 2018-2019 BSNE data to analyze only the highest flux collection period (June) as this flux period was the largest and likely most impactful over the study period. Fixed effects were examined with Wald Type II  $X^2$  test (Anova

function in the car package ; Fox et al., 2022). Finally, we conducted post hoc contrast testing within our fixed effects using the emmeans package (Lenth et al., 2022). We evaluated the LMM models by examining the normality and homogeneity of variance of the residuals.

## Results

**Figure 3-1.** Soil retention variables by restoration treatments, 2018-2021. The black dot indicates mean; the box shows median with 1<sup>st</sup> and 3<sup>rd</sup> quartiles.



### *Treatment effects on soil retention*

Soil retention was largely unaffected by restoration treatments (Fig. 3-1). There was a significant effect of restoration treatment on chlorophyll a and soil stability (Table 3-2). However, the magnitude of differences between treatments was too small in the case of the chlorophyll a to translate into biologically meaningful differences in ecosystem service provisioning. Biocrust inoculation significantly increased soil stability to 2.8 from an average of 1.9 in the control (Table S2-1). Soil stability is measured on a scale from 1 to 6, so soils with a stability of 2.8 are still on the less-stable end of the scale. There was no measurable effect of restoration treatments on EPS. Similarly, there was no effect of grazing on any soil retention variables, suggesting that at these very low values, there is no tradeoff in ecosystem service provisioning to reintroducing grazing after a two-year rest period (Table 3-2). Biocrust cover is not reported because it remained very low across nearly all sampling locations, indicating that the inoculation treatment was not effective.

**Table 3-2.** Summary of fixed and random effects for linear mixed effects models testing effects of restoration and grazing treatments on soil retention variables. For the fixed effects, results of the Wald Type II  $X^2$  test are shown. Estimates are reported on the transformed scale. Stars indicate significance ( $p < 0.05^*$ ,  $p < 0.01^{**}$ ,  $p < 0.001^{***}$ ).

log(chlorophyll a) ~ Restoration + Year + (1 Block/Plot/Transect)				
Fixed effects	Chisq	df	Pr(>Chisq)	
Restoration treatment	18.03	3	0.0004	***
Year	85.37	3	<0.0001	***
Random effects	Variance	Std. Dev		
Transect	0.01	0.09		
Plot	0.00	0.01		
Block	0.00	0.05		
residual	0.15	0.39		
$R^2_m$ : 0.066	$n_{obs} = 1597$			
$R^2_c$ : 0.124				

sqrt(eps) ~ Restoration + Year + (1 Block/Plot/Transect)			
Fixed effects	Chisq	df	Pr(>Chisq)
Restoration treatment	3.13	3	0.37
Year	6.75	1	0.01 **
Random effects	Variance	Std. Dev	
Transect	0.00	0.00	
Plot	0.09	0.30	
Block	0.00	0.00	
residual	50.08	7.01	
R <sup>2</sup> <sub>m</sub> : 0.02	n <sub>obs</sub> = 485		
R <sup>2</sup> <sub>c</sub> : 0.02			

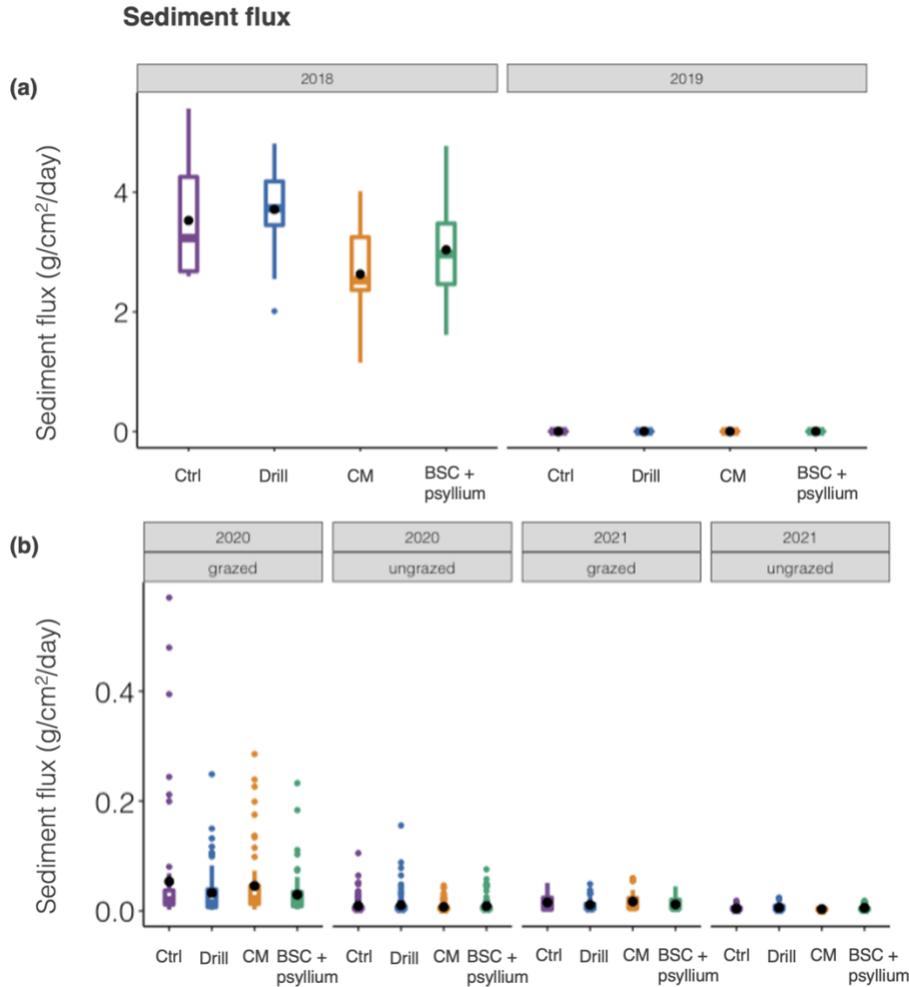
log(soil stability) ~ Restoration + Year + (1 Block/Plot)			
Fixed effects	Chisq	df	Pr(>Chisq)
Restoration treatment	42.19	3	<0.0001 ***
Year	74.70	1	<0.0001 ***
Random effects	Variance	Std. Dev	
Plot	0.02	0.14	
Block	0.01	0.10	
residual	0.29	0.54	
R <sup>2</sup> <sub>m</sub> : 0.11	n <sub>obs</sub> = 2122		
R <sup>2</sup> <sub>c</sub> : 0.18			

### *Treatment effects on erosion*

In the first two years of the experiment, the ConMod treatment reduced sediment flux by 34% in 2018 and by 21% in 2019 compared to untreated controls during peak flux in early summer (Figure 3-2; Table 3-3). Sediment flux fell from 3.528 g/cm<sup>2</sup>/day in the control plots to 2.630 g/cm<sup>2</sup>/day in 2018, and from 0.0021 g/cm<sup>2</sup>/day to 0.0018 g/cm<sup>2</sup>/day in 2019. The grazing treatment was added in April 2020. In the second two years of the experiment, grazing increased sediment flux 38-fold. However, the total amount of sediment transported during all three years following 2018 remained low compared to the spike measured in 2018 (Table 3-3). The grazed plots had an average sediment flux of 0.03 g/cm<sup>2</sup>/day in 2020-2021, compared to just 0.01

g/cm<sup>2</sup>/day on ungrazed plots. For comparison, sediment fluxes from the plots peaked in 2018 following the restoration experiment. In 2018 the average sediment flux for the drillseeded plots was 2.02 g/cm<sup>2</sup>/day, about 14% higher than the control at 1.77 g/cm<sup>2</sup>/day. In 2018, the ConMod treatment had the lowest sediment flux of 1.62 g/cm<sup>2</sup>/day.

**Figure 3-2.** Sediment flux. The black dot indicates mean; the box shows median, 1<sup>st</sup> and 3<sup>rd</sup> quartiles. (a) June sediment flux by restoration treatment, showing only one month of data (collected July 1 for 2018 and 2019) coinciding with peak summer winds. (b) Sediment flux by restoration treatment and grazing treatment. Sediment flux was collected monthly and averaged by year. Grazing was implemented in April 2020.



**Table 3-3.** Summary of fixed and random effects for linear mixed effects models testing effects of restoration treatment and grazing on sediment flux. Results of the Wald Type II  $X^2$  test are shown for fixed effects first. The estimates from the mixed effects model are shown below. In the 2018-2019 model, the levels of Treatment are compared to the control. In the 2020-2021 model, the ungrazed level is compared to the grazed, and 2021 is compared to 2020. Estimates for the 2020-2021 model are reported on the log scale. Stars indicate significance ( $p < 0.05^*$ ,  $p < 0.01^{**}$ ,  $p < 0.001^{***}$ ).

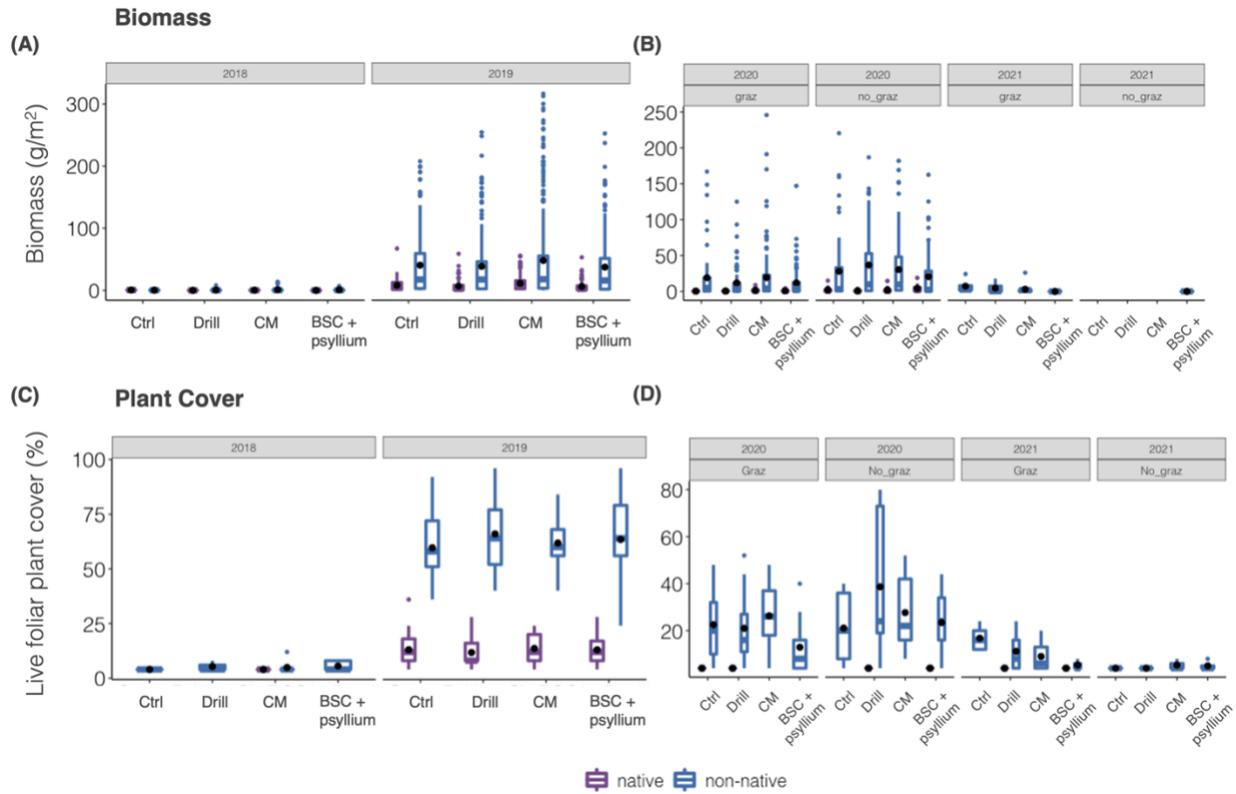
July bsne flux 2018-2019 ~ RestorationTreatment + Year + (1 Block/Plot)					
Fixed effects	Chisq	df	Pr(>Chisq)		
Restoration treatment	14.163	3	0.002692 **		
Time	1281.945	1	<0.0001 ***		
Fixed effects	Estimate	Std. Error	df	t value	Pr(>t)
Intercept	160.3	4.431	115	36.17	<0.0001 ***
Treatment ConMod	-0.45	0.16	14.75	-2.87	0.0119 *
Treatment Drillseed	0.07	0.16	14.75	0.44	0.6662
Treatment BSC	-0.27	0.16	15.04	-1.72	0.1053
Year	-0.01	0.00	114.6	-35.80	<0.0001 ***
Random effects	Variance	Std. Dev			
Plot	0.03	0.16			
Block	0.09	0.30			
residual	0.25	0.53			
$R^2_m$ : 0.87	$n_{obs} = 139$				
$R^2_c$ : 0.91					
Log(bsne flux 2020-2021 ~ RestorationTreatment + Grazing + Year + (1 Block/Plot/Location)					
Fixed effects	Chisq	df	Pr(>Chisq)		
Restoration treatment	0.28	3	0.96		
Grazing treatment	229.31	1	<0.0001 ***		
Year	109.32	1	<0.0001 ***		
Fixed effects	Estimate	Std. Error	df	t value	Pr(>t)
Grazing: ungrazed	-1.59	0.10	262.41	-15.14	<0.0001 ***
Year: 2021	-0.75	0.07	949.15	-10.49	<0.0001 ***
Random effects	Variance	Std. Dev			
Location	0.00	0.00			
Plot	0.06	0.24			
Block	0.07	0.26			
residual	0.98	0.99			
$R^2_m$ : 0.370	$n_{obs} = 970$				
$R^2_c$ : 0.442					

### *Treatment effects on vegetation*

Biomass and plant cover both varied considerably between years, most likely in response to abiotic variables such as soil moisture (Figure 3-3). Over the first two years of the experiment in particular, the site experienced an exception drought followed by an exceptionally wet year. Over those two years, year explained 65% of remaining variance in the biomass model and 93% of remaining variation in the plant cover model (Table 3-4). The climatic differences between 2020 and 2021 were less dramatic, but year still explained 22% of variation in the biomass model and 32% of variation in the plant cover model (Table 3-4). After controlling for year and the blocked sampling of the experiment, restoration treatment significantly influenced native biomass but not non-native biomass over the first two years of the experiment (Table 3-4). However, none of the treatments differed significantly from the control plot which was not seeded (Table S2-2). Over the second two years of the study, restoration treatment and grazing both had significant effects on biomass (Table 3-4). Ungrazed ConMod plots had significantly more non-native biomass than the ungrazed biocrust plots (Table S2-2).

There were no effects of restoration treatment on plant cover over the four years of the study (Figure 3-3; Table 3-4). There was a significant interaction between native\_status and grazing. The goal of the grazing treatment was to reduce cover of non-native species to increase native plant establishment. The significant interaction reveals that the grazing treatment did significantly reduce non-native cover from 24% to 18%, but that reduction did not lead to an increase in native cover.

**Figure 3-3.** Biomass (A, B) and live foliar plant cover (C, D) by restoration grazing treatments 2018-2021. Data is separated into before grazing (2018-2019) and after grazing (2020-2021). Native and non-native vegetation are shown with separate-colored bars. The black dot indicates mean; the box shows median with 1<sup>st</sup> and 3<sup>rd</sup> quartiles.



**Table 3-4.** Summary of fixed and random effects for linear mixed effects models testing effects of restoration treatment and native status on biomass and cover. For the fixed effects, results of the Wald Type II  $X^2$  test are shown. Estimates are reported on the log scale. Stars indicate significance ( $p < 0.1$ ,  $p < 0.05^*$ ,  $p < 0.01^{**}$ ,  $p < 0.001^{***}$ ).

$\log(\text{biomass } 2018-2019) \sim \text{Restoration} * \text{Native\_status} + \text{Year} + (1|\text{Block/Plot/Location})$

Fixed effects	Chisq	df	$Pr(>Chisq)$	
Restoration treatment	12.83	3	0.005012	**
Native status of biomass	105.12	1	<0.0001	***
Restoration * Native status	11.28	3	0.010285	*
Year	888.22	1	<0.0001	***
Random effects	Variance	Std. Dev		
Transect	0.00	0.00		
Plot	0.02	0.15		
Block	0.02	0.16		
residual	3.96	1.99		

$R^2_m: 0.39$

$n_{\text{obs}} = 1572$

$R^2_c: 0.39$

$\log(\text{biomass } 2020-2021) \sim \text{Restoration} * \text{Native\_status} * \text{Grazing} + \text{Year} + (1|\text{Block/Plot/Location})$

<b>Fixed effects</b>	<b>Chisq</b>	<b>df</b>	<b>Pr(&gt;Chisq)</b>	
Restoration treatment	14.72	3	0.0021	**
Native status of biomass	99.33	1	<0.0001	***
Grazing treatment	6.87	1	0.0087	**
Year	17.09	1	<0.0001	***
Restoration * Native status	6.38	3	0.0946	.
Restoration * Grazing	2.73	3	0.4355	
Native status * Grazing	0.00	1	0.9740	
Restoration * Native status * Grazing	8.09	3	0.0442	*

<b>Random effects</b>	<b>Variance</b>	<b>Std. Dev</b>
Transect	0.00	0.00
Plot	0.00	0.00
Block	0.04	0.19
residual	4.83	2.20

R<sup>2</sup><sub>m</sub>: 0.15      n<sub>obs</sub> = 849  
R<sup>2</sup><sub>c</sub>: 0.16

log(cover 2018-2019) ~ Restoration + Native\_status + Year + (1|Block/Plot/Transect)

<b>Fixed effects</b>	<b>Chisq</b>	<b>df</b>	<b>Pr(&gt;Chisq)</b>	
Restoration treatment	1.20	3	0.75	
Native status of biomass	667.89	1	<0.0001	***
Year	551.20	1	<0.0001	***

<b>Random effects</b>	<b>Variance</b>	<b>Std. Dev</b>
Transect	0.00	0.00
Plot	0.00	0.00
Block	0.00	0.04
residual	0.18	0.42

R<sup>2</sup><sub>m</sub>: 0.823      n<sub>obs</sub> = 213  
R<sup>2</sup><sub>c</sub>: 0.825

log(cover 2020-2021) ~ Restoration \* Native\_status \* Grazing + Year + (1|Block/Plot/Transect)

<b>Fixed effects</b>	<b>Chisq</b>	<b>df</b>	<b>Pr(&gt;Chisq)</b>	
Restoration Treatment	3.34	3	0.34	
Native status of biomass	23.35	1	<0.0001	***
Grazing Treatment	0.13	1	0.72	
Year	32.91	1	<0.0001	***
Restoration * Native status	6.06	2	0.0484	*
Restoration * Grazing	4.31	3	0.23	
Native status * Grazing	10.94	1	0.0009	***
Treatment * Native status * Grazing	0.13	1	0.72	

Random effects	Variance	Std. Dev
Transect	0.00	0.00
Plot	0.12	0.34
Block	0.13	0.36
residual	0.35	0.59
$R^2_m$ : 0.310	$n_{obs} = 135$	
$R^2_c$ : 0.595		

## Discussion

### *Loss of ecosystem services remained largely persistent*

Restoration treatments targeted at soil stabilization and biocrust regeneration did not increase soil retention variables as intended. There are many reasons why restoration treatments can fail to work as expected, and we think it is helpful here to differentiate between a failure of the treatment to be installed correctly versus a failure of the treatment to function as expected once in place. Our biocrust + psyllium treatment likely failed during the installation process. Our chlorophyll a and EPS values fell far below any baseline measures for intact sites (Jech, unpublished data), suggesting that our biocrust restoration efforts failed to establish biocrust at the site. Additionally, we did not see decreased sediment yields with biocrust inoculation, which could be due to the very low cover of biocrust on our plots. Our biocrust treatment had just 2.2% biocrust cover in ungrazed plots and 0.6% cover in grazed plots, compared to an average biocrust cover of 34% across comparable, intact sites (Miller et al., 2011). Biocrust cover is a good indicator of sediment yields, mediated by soil stability (Fick et al., 2020a). Inoculating with biocrust and psyllium did increase soil stability to an average of 2.8 on a scale of 6. This is still well below soil stability levels of 5.5 for intact reference sites, and even below soil stability levels measured for other similar, persistently degraded sites (Miller et al., 2011). Soil stability is associated with improved water infiltration (Chamizo et al., 2016; Fick et al., 2019), as well as

decreased sediment yields (Le Bissonnais, 2016). Our results highlight the risk associated with biocrust inoculation as a restoration treatment, rather than providing insight as to whether increased biocrust restores soil retention ecosystem services.

In contrast to the biocrust + psyllium treatment, both the drillseeding treatment and the ConMod treatment are less risky to install and were put in place as anticipated. However, none of our restoration treatments increased native plant cover or biomass over our study period due to extremely low seedling emergence. We did observe some emergence in the first year of monitoring, particularly Indian ricegrass seedlings, but these seedlings died before they could become established. Natural recruitment from seed is a somewhat rare event in drylands, and up to 80% of seeds used in restoration exhibit some form of dormancy (Kildisheva et al., 2019). We also know that many individual plants germinate but fail to emerge in dryland restoration settings. We did not track seed and seedling transitions so we cannot pinpoint the life stage or cause of plant establishment failures in our study. Propagule pressure from invasive species remained high through the experiment, evidenced by the high cover and biomass of these species. In 2017, the year that we installed the experiment, the region was experiencing an extreme drought. Drought and high invasive propagule pressure also likely contributed to the very low native plant recruitment.

Climate conditions in the first year of a restoration project can be important in determining the restoration outcomes through priority effects (e.g. Groves et al., 2020; MacDougall et al., 2008). In our four-year experiment we experienced an exceptional drought immediately after seeding and throughout year one, an exceptionally wet year in year 2, an average year, and finally another exceptional drought. The entire region is considered to be in a mega-drought since the early 2000s (Williams et al., 2022). In addition to impacting plant

responses, these harsh abiotic conditions may have contributed to the biocrust restoration failure. Recent work has found that shading and watering biocrust following field inoculation can increase biocrust cover (Antoninka et al., 2020a; Fick et al., 2020b). Shading and watering are likely impractical at large scales; however, this work suggests that microsite limitation may affect biocrust establishment similarly to plant establishment.

### *Trade-offs with grazing*

Approximately 90% of the Colorado Plateau is grazed by cattle, making the provisioning of food a major ecosystem service currently being provided by rangelands in the region (Schwinning et al., 2008). Although livestock production on rangelands is increasing globally as demand for meat increases (Herrero and Thornton, 2013), livestock production on rangelands in the U.S., including the Colorado Plateau, has been steadily declining in recent decades (Copeland et al., 2017; Havstad et al., 2007). As it declines, the ecosystem services provided by rangelands are shifting from livestock production to regulating and supporting services (Havstad et al., 2007). This shift in land use is in line with international targets such as those set out by the Convention on Biological Diversity, aiming to restore biodiversity and ecosystem services (Larigauderie et al., 2012; Mace et al., 2010).

In this paper, we aimed to restore regulating and supporting services while maintaining provisioning services associated with cattle grazing. On rangelands globally, plant biomass is 4% lower on grazed lands, and high-intensity grazing is associated with a 10% increase in erosion compared to low-intensity grazing (Petz et al., 2014). Tradeoffs vary significantly by site, but sites nearby to our experiment have experienced up to 40% increases in sediment flux as a result of disturbance, including grazing (Belnap et al., 2009), which can lead to decreased silt, soil C and soil N, even 3 decades after grazing pressure is removed (Neff et al., 2005). We did not find

a significant effect of grazing on soil retention (chlorophyll a, EPS, and soil stability), but this is likely because we did not meaningfully restore soil retention through our treatments. Grazing did increase sediment flux by about 88-fold compared to the ungrazed plots, however the total flux was still relatively low compared to other reported rates (e.g. [Belnap et al., 2009](#)). The increase in sediment flux from grazing was also much lower than the sediment fluxes measured in the first year after installing the restoration (2018). That year was extremely dry, and other studies have reported large inter-annual differences in fluxes on degraded lands, likely driven by climate (Belnap et al., 2009). Another contributing factor could be the installation of the restoration project itself. Business-as-usual methods, such as drillseeding, disturb the soil and can increase sediment flux in erosion-prone areas (Duniway et al., 2019) such as the Colorado Plateau.

Grazing reduced standing biomass but did not reduce cover when we looked at data from both 2020 and 2021. In the very dry year of 2021, cover was higher in grazed plots than in ungrazed, and was almost entirely absent from ungrazed areas. This was a surprising result and is likely due to the increased seed-soil contact and microsite creation provided by the cattle stomping and pooping. Although we reseeded native seeds prior to grazing, most of the cover in 2021 was non-native and indicative of the highly invaded seed bank at the site. Overall, we measured very low levels of regulating and supporting ecosystem services as a result of our restoration treatments, and mixed effects of adding provisioning services (grazing) to the land. There was a tradeoff between grazing and sediment flux, but there was an even larger tradeoff between restoration installation and sediment flux. Given these findings, maintaining low levels of grazing at the site may be the best option for maximizing ecosystem services on an already severely degraded rangeland. This calculation would be different if the site was less degraded and was providing more regulating and supporting services that were at risk of being lost.

### *Where do we go from here*

Ecosystem transformations are characterized by persistent, irreversible changes in the structure and function of an ecosystem as compared to a reference or historical state (Lynch et al., 2021; Noss, 1990). These transformations are occurring in many biomes around the world, often driven by climate change (Lynch et al., 2021). The southwestern U.S. is predicted to see a 4-8° C increase in mean annual temperature under high emissions scenarios by 2100 (Christensen et al., 2007). Most climate models predict a 5-10% decrease in annual precipitation by 2100 (Christensen et al., 2007). These extreme abiotic conditions make the restoration of dryland ecosystem services much more difficult.

Dryland restoration faces barriers to success that include a lack of propagules, microsite limitation, and destabilized soils, all of which our study attempted to overcome. However, our results highlight the shifting nature of restoration barriers, particularly as climatic variability increases. The first year of our restoration was an extreme drought, so the major hurdles were likely related to moisture availability. However, in the second year of our experiment, there was abundant moisture. Unfortunately, pressure from invasive species in the seedbank resulted in high cover and biomass of non-native species. In year two the barrier to restoration likely shifted to competition and native seed limitation. Native seeds were outnumbered by invasive seeds to begin with, and we do not know how many native seeds had already flushed out of the system by germinating and then dying during year 1. Additionally, the high sediment fluxes in 2018 (Fig. 3-2) created mounds on the ConMods, likely burying any remaining seeds too deeply to germinate. By year 3 of the experiment, we reseeded (with little effect) but we never reinoculated biocrust after the low success rates during year 1 and it's likely that a lot of the inoculum was redistributed out of the site area with the high rates of sediment flux during that first year.

Anecdotally, this study demonstrates the shifting nature of restoration barriers and illustrates why dryland restoration is so challenging.

One way to approach shifting restoration barriers is through adaptive management, a strategy of adapting restoration actions to deal with uncertainty (Walters and Hilborn, 1978). In our study, we timed our grazing treatment to target annual grasses early in the growing season in the hopes of reducing competition for later-germinating and slower-growing native species, which has been effective in similar studies (e.g. Porensky et al., 2021). We also added a second, unplanned seeding prior to grazing to ensure there were native propagules available. However, these actions were not enough to overcome barriers. Our restoration actions failed to line up well with climate fluctuations and we did not adapt any of our treatments during year two of our study to take advantage of the wet conditions. Additionally, we did not repeat herbicide application nor biocrust inoculation treatments. In part, grant funding structures often constrain timing of restoration applications. However, lack of information can also be limiting. For example, if you delay implementing a restoration treatment in a given year, there is no guarantee that conditions the following year will be better. Recent advances in short-term climate predictions are likely to be helpful here; tools such as the ecological drought forecast tool from the USGS provide short-term drought forecasting to aid in decision-making (Bradford and Andrews, n.d.)

Finally, as ecosystem transformations become more common, there will be difficult decisions about how to best invest resources. Formalized decision-making approaches, such as the Resist-Accept-Direct (RAD) framework, are being developed to guide practice (Lynch et al., 2021). The RAD framework offers a strategy for managing ecosystems undergoing transformation, where a resist approach is consistent with traditional restoration actions to resist change and restore to established baselines. However, the framework recognizes that there are

thresholds beyond which resisting change is unrealistic, and accepting and learning to manage a novel ecosystem is required (Lynch et al., 2021). Given the level of degradation at our study system, it is possible that a strategy such as maintaining low levels of grazing on an invaded grassland community – an accept strategy – may be more successful than attempting to reverse the state change and restore regulating and supporting ecosystem services that are provided at intact sites.

## CHAPTER IV

Microsite creation and biochar amendments benefit native and non-native seedlings

Claire C. Karban, Sierra Jech, Nichole N. Barger

### **Abstract**

Degradation on drylands is widespread, yet our ability to restore native plant communities is nearly non-existent. Recruitment from seed is often <10%, due to high rates of dormancy, harsh conditions that lead to high rates of mortality, and competition with invasive species. In this experiment we test several restoration treatments designed to relieve harsh conditions. We experimentally tested pits to increase water capture, a biochar soil amendment to increase water holding capacity of the soil, and a seed pellet with clay to increase moisture directly around the seed. We conducted this experiment in a highly degraded semi-arid grassland. Invasive species made up most of the standing vegetation. We tested broadcast seeding, seed pellets, and no seeding in three types of plots: controls, pits, and pits with biochar. We measured seedling biomass and seedling density for both native and non-native species. Seeding alone, with or without a seed pellet, did not result in seedlings in the control plots. Both the pits and the pits with biochar increase native plant biomass and density. Native biomass and density was higher in the pits with biochar. There was no effect of seed pellets, and in most cases, they performed slightly worse than bare seeds. The pit and pit with biochar treatments also increased density and biomass of non-native species. Total density of non-native species was about 100 times greater than density of native species in the pits and pits with biochar. While this is a large increase, our results cover only two years of study, and the dynamics between native and non-native plants will likely take years to stabilize.

## **Introduction**

Dryland ecosystems are more heavily used now than ever before, providing livestock grazing, cropland, and energy production to a growing global population (Herrick et al., 2012). Global change, particularly altered patterns of temperature and precipitation, as well as widespread biological invasions, threaten dryland ecosystem structure, function, and processes, including their continued provisioning of ecosystem services (Bradford et al., 2019; Glick et al., 2011; Huang et al., 2017). Over-use and global change have already led to significant degradation on drylands, with few successful methods for restoring native vegetation (DiTomaso, 2000; Herrick et al., 2010; Kildisheva et al., 2016).

Harsh conditions are the major driver of low plant recruitment in dryland restoration (Shackelford et al., 2021). Recruitment rates in seeded dryland restoration are commonly <10% (Kildisheva et al., 2016). In desert systems, up to 80% of seeds exhibit some form of seed dormancy, limiting germination (Kildisheva et al., 2019). Germination requirements vary between species and populations, but environmental cues such as moisture and temperature are important drivers of dormancy loss (Baskin and Baskin, 2014). With the harsh conditions present in many degraded drylands, dormancy is often not broken, and recruitment from seed does not naturally occur every year. When germination does occur, the transition between germination and emergence is a vulnerable stage with high mortality in dryland restoration (James et al., 2019, 2011; Larson et al., 2015), and this transition can also be limited by soil moisture (Larson et al., 2021) and by temperature (Butterfield and Munson, 2016; James et al., 2019). As aridity increases in drylands, new methods are needed to overcome environmental barriers and increase plant recruitment in restoration.

In addition to increasing aridity in drylands, invasive species pose a major challenge to restoration efforts. Across the western U.S., 21 percent of rangelands show moderate degradation, characterized by declining native plant cover and invasion by annual grasses and forbs (Herrick et al., 2010), and invasive species alone cost the U.S. an estimated \$2 billion of losses annually (DiTomaso, 2000). Invasive annual species often grow at higher densities than native plants and compete with natives for scarce water resources (Brown and Rice, 2000; Dyer and Rice, 1999). For example, invasive annual grasses can meaningfully reduce available soil moisture, even more than the measured effects of decreased precipitation (Garbowski et al., 2021). Invasive species also tend to germinate earlier in the growing season than native species, giving them a head start, and they are more efficient at using limited resources such as water quickly, before native species green up or germinate (Funk and Vitousek, 2007). The prevalence of invasive species in degraded drylands increases competition for already limited soil moisture. Additionally, the replacement of perennial vegetation with annual vegetation can reduce soil moisture (D'Odorico et al., 2007). Perennial plants hold water beneath the plant canopy, increasing soil moisture and facilitating (both native and non-native) plant establishment (Caylor et al., 2006).

The current challenges for dryland restoration require methods that can increase soil moisture and native seed germination in systems that are invaded by annuals. There are several restoration techniques aimed at alleviating harsh conditions and facilitating native plant recruitment. Increasing water capture by increasing surface roughness, such as through the creation of pits, has been found to increase soil moisture (Havrilla et al., 2020; Li et al., 2014; Stroosnijder et al., 2012), increase seedling emergence (Chambers, 2000), and increase seedling density (Havrilla et al., 2020). Soil amendments, such as biochar, are another strategy to increase

soil moisture available to plants, by increasing the water holding capacity of degraded soils (Fehmi et al., 2020). However, microsites with higher soil moisture may be higher-competition environments as abiotic filters (i.e. harsh conditions) are relaxed (Keddy, 1992). Thus, there is a risk that increasing water capture and/or adding biochar could benefit invasive species when implemented in invaded systems, particularly in the short-term before native plants are able to get established. An alternative restoration strategy is to concentrate the microsite effects around only the desired seeds, using seed technologies (Madsen et al., 2016). Seed pelleting is a form of seed technology where seeds are coated in substances (e.g. clay, manure, chili powder) to improve seed germination, increase growth, and reduce granivory (Gornish et al., 2019). So far the published literature shows mixed results for the efficacy of seed pellets and more work is needed to understand their potential in dryland restoration (Gornish et al., 2019).

In this study, we tested several restoration strategies to improve seedling recruitment in a severely degraded shrubland in southeastern Utah. Our restoration strategies were selected based on known barriers to plant establishment in degraded drylands: soil moisture limitation and competition with invasive species. We created pits to increase soil moisture capture, and tilled biochar into a subset of the pits to further increase soil water holding capacity (“microsite” treatments). We expected both pit treatments to increase native plant recruitment, but we also predicted that invasive species at the site would benefit from the additional moisture. These pit treatments were compared to plots where no microsite modifications were made. We seeded the plots with a mix of native grasses and forbs applied via two seeding methods. We tested seed pellets designed to increase germination, increase growth, and protect the seeds from granivory. Seed pellets were compared to a standard broadcast seeding method, and a control where no

seeds were added. We predicted that seed pellets would increase native species recruitment without increasing non-seeded species.

## Methods

We implemented restoration treatments in a severely degraded semidesert sandy loam site ( R035XY215UT, NRCS, n.d.) in southeastern Utah (38.07, -109.57; 1655m). The site is semi-arid, receiving an average of 197 mm of annual precipitation (Urban, 2017). About 30% of the annual precipitation falls as summer monsoon thunderstorms, and the remainder falls as snow and rain during the winter. The site has been irrigated and overgrazed in the past century, leading to degraded, bare soils and very little plant cover. Soils were sandy to about 10cm, where a calcium carbonate layer had formed. Active livestock grazing occurred until the start of the study, but utilization was low due to very low forage availability. We fenced the area to exclude livestock in September 2020.

**Table 4-1.** Native seedmix used for seeding the experiment.

Species	Scientific name	Functional group	% of mix
Indian ricegrass	<i>Achnaetherum hymenoides</i>	C3 grass	20
Needle-And-Thread	<i>Hesperostipa comata</i>	C3 grass	16
Sandberg Bluegrass	<i>Poa secunda</i>	C3 grass	12
Sand dropseed	<i>Sporobolus cryptandrus</i>	C4 grass	16
James' galleta	<i>Pleuraphis jamesii</i>	C4 grass	16
Yellow beeplant	<i>Cleome lutea</i>	Forb	10
Gooseberry globemallow	<i>Sphaeralcea grossulariifolia</i>	Forb	10

Vegetation at the site at the start of the experiment was dominated by invasive Russian thistle (*Salsola tragus*), as well as other non-native forbs: western stickseed (*Lappula occidentalis*), Halogeton (*Halogeton glomeratus*), and western tansymustard (*Descurainia pinnata*). Native perennial bunch grasses would be the dominant vegetation for a comparable

intact site. Fourwing saltbush (*Atriplex canescens*) should be the dominant native shrub for this ecosite, and the site did contain several remnant fourwing saltbush individuals. We chose native grass and forb species to seed based on nearby intact communities as well as anticipated climate and recent restoration experience in the area. Our seedmix (Table 4-1) was sourced from regional seed providers, and contained cool season perennial grasses, warm season perennial grasses, and forbs.

### *Experimental Design*

We manipulated microsites in 20 cm x 20 cm plots. We had three levels of pit treatment: control where we did nothing, pit where we removed the top 10cm of soil, and a pit + biochar where we removed the top 10cm of soil and then tilled 80 g of biochar into the pit. Control and pit treatments were replicated 60 times each, and the pit + biochar treatment was replicated 30 times. Pit treatments were installed in October 2020.

To monitor the microsite effects of the treatments, we installed 12 soil moisture probes into the plots (Decagon Em5B), randomly stratified by treatment. Soil moisture data was collected as an average of the top 10cm of the soil profile and logged every 60 min. We also installed 6 temperature and relative humidity sensors (iButton Hygrochron), randomly stratified by treatment. These sensors captured air conditions at the soil surface every 60 min. The temperature and relative humidity sensors were placed in tubes covered in reflective tape to shield them from direct solar radiation. Soil moisture probes collected data continuously throughout the study period. Temperature and relative humidity data was collected only during the spring growing season to avoid damaging the sensors in harsh conditions.

We seeded the microsites at three levels: control where no seeds were added, a broadcast seeding with bare seeds, and a seed pellet seeding. The bare seed and seed pellet levels received

the same seeding rate of 21.23 PLS lb/a. This amounted to approximately 100 seeds per plot, but calculations were based on weight so the actual number of seeds varied by plot. Prior to seeding, the gooseberry globemallow seeds were submerged in boiling water for 10 seconds to help break physical dormancy. Seed pellets were coated with clay and steer manure to increase water retention and nutrient availability, habanero powder to deter granivory, and poly-selvol alcohol to bind materials together. Seeds were spun in a salad spinner with pellet ingredients and water to form irregular seed balls and then air dried. Pellets ranged in diameter from 0.8 cm to 1.4 cm. Seed pellets were added to the microsites by weight, with each plot receiving 1.5 g -1.6 g of pellet. This amounted to 2-3 pellets per plot depending on size. The seeding treatments were replicated equally within each pit treatment (20 reps. each for the control and pit treatments, and 10 reps. for the pit + biochar treatment). Seeding occurred in November 2020.

### *Seedling measurements*

We surveyed the density of seedlings, identified by species, in April 2021, November 2021, and April 2022. Biomass was collected after the final seedling surveys in April 2022. We gently removed seedlings from the ground, brushed off excess soil, and placed them in paper bags labeled by species by plot. In the lab, seedlings were washed in ultra-pure DI water to remove remaining soil. Seedlings were clipped to separate root and shoot material and oven-dried at 60° C for 48 hrs before weighing. Seedling density and biomass values have been converted from the plot area to m<sup>2</sup>.

### *Statistical analysis*

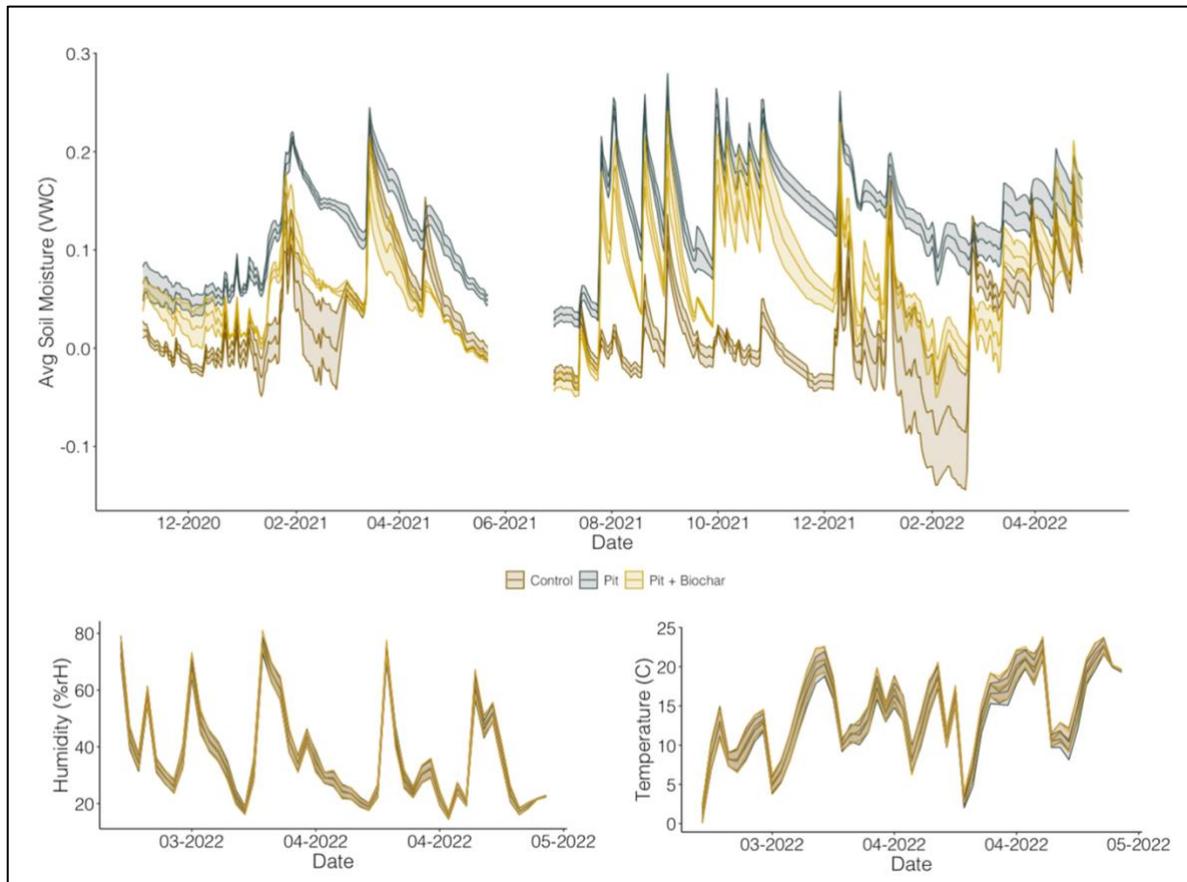
To compare abiotic variables in the microsite, we fit repeated measures anovas using the nlme package in R. Each abiotic variable was modeled as a function of pit treatment and time, with plot included as a random effect. We used the glht function from the multcomp package to look at Tukey comparisons using the Bonferroni contrasts.

To compare biomass across microsite and seeding treatments we fit linear models using the lme4 package. Response variables were transformed to approximate a normal distribution. Fixed effects were examined with Wald Type II  $X^2$  test (Anova function in the car package, Fox et al., 2022). Finally, we conducted post hoc contrast testing within our fixed effects using the emmeans package (Lenth et al., 2022).

To compare seedling counts across microsite and seeding treatments we fit generalized linear models with a negative binomial distribution using the glm.nb function in the mass package (Ripley et al., 2022). Fixed effects were examined with Wald Type II  $X^2$  test (Anova function in the car package, Fox et al., 2022). Finally, we conducted post hoc contrast testing within our fixed effects using the emmeans package (Lenth et al., 2022). We evaluated the GLMM models by examining the normality and homogeneity of variance of the residuals.

## **Results**

Pit treatments significantly influenced the soil moisture in the top 10 cm of the soil profile (F-value = 41.05822, p-value = 0.0001; Figure 4-1). The pit treatment had the highest soil moisture – a six-fold increase over the control ( $p < 0.001$ ) and nearly double that of the pit + biochar ( $p < 0.001$ ). The pit + biochar treatment had 3-fold more soil moisture than the control ( $p = 0.0066$ ). There was no measurable difference in relative humidity or temperature across the pit treatments.

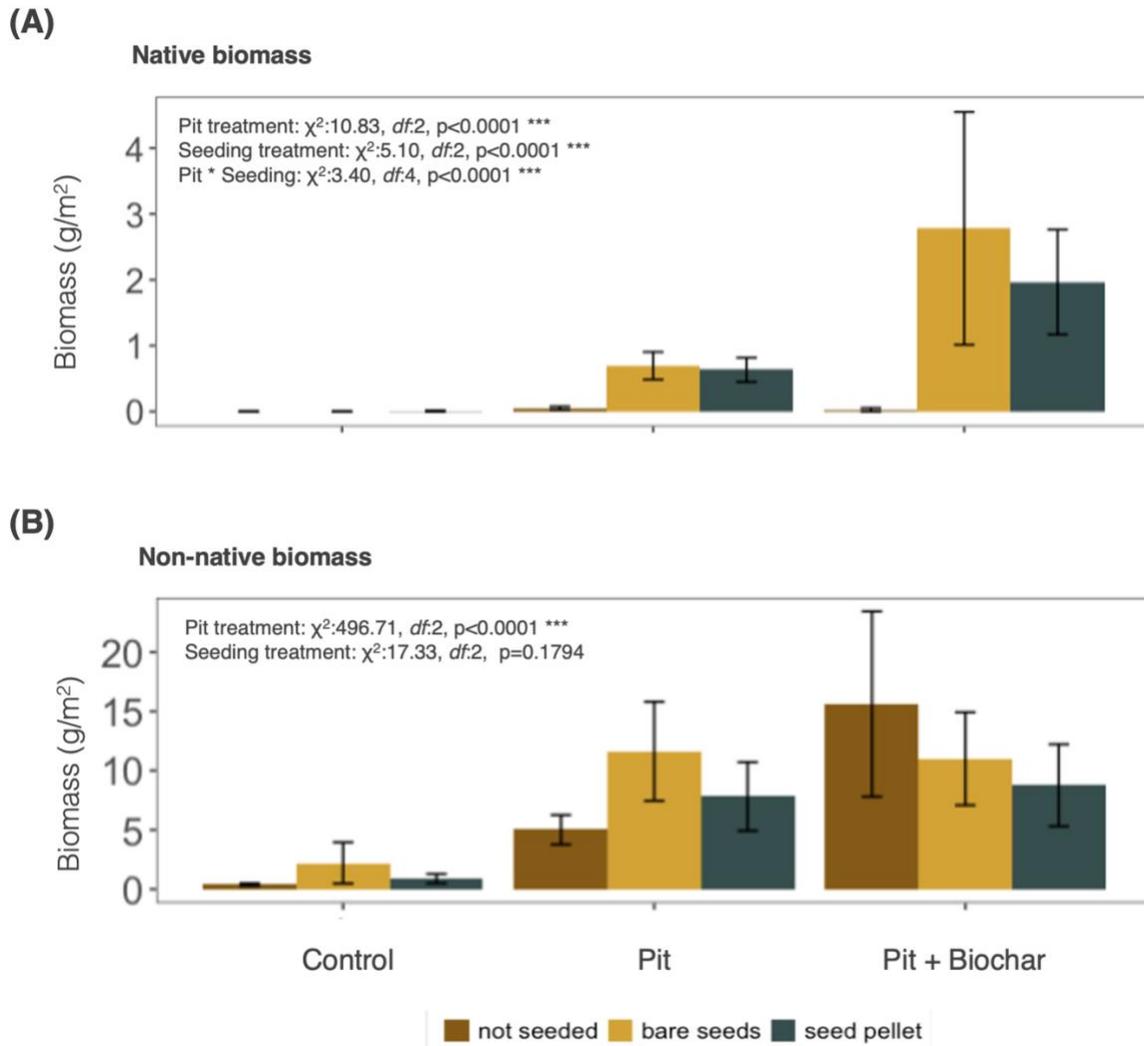


**Figure 4-1.** Soil moisture (VWC), relative humidity (%rH), and temperature (C) data for each of the pit treatments are graphed as solid lines, with standard error shading. Soil moisture data was collected continuously from November 2020 – April 2022, except for an approximately 1-month gap in May 2021. Relative humidity and temperature data are shown for the spring 2022 germination period only.

### *Biomass*

The pit treatments and seeding treatments significantly increased biomass of native seeded species, as we predicted. The pit treatment explained more variance than the seeding treatment (Figure S3-1), in line with our prediction that microsites with higher moisture are likely limiting for native plant establishment. The pit treatments resulted in ~100-fold increase in native biomass over the microsite control. Adding biochar to the pits had an even stronger effect, more than tripling the amount of native biomass compared to the pit treatment alone. Both bare seeds and seed pelles seeding treatments increased native biomass compared to unseeded plots

(Table 4-2). However, there was no added benefit of the seed pellet compared to the bare seeds (Table 4-2). Additionally, seeding alone was not sufficient to increase native biomass. Only when seeding was coupled with a pit treatment was there an increase in biomass.



**Figure 4-2.** Native and non-native seedling biomass across microsite and seeding treatments. Data is from April 2022. Bars represent means  $\pm$  1 s.e. Results for the main effects of linear mixed models are included. Pit and seeding treatment were both significant for native biomass, as was the interaction term. Only pit treatment was significant for non-native biomass.

The pit treatments also had positive effects on non-native biomass. (Figure 4-2). The pit treatment resulted in a 6-fold increase in non-seeded biomass, while the pit + biochar treatment

increased biomass nearly 10-fold over the control (Figure 4-2). There was no significant difference in non-native biomass between the pit and the pit + biochar (Table 4-2). The total biomass for non-native species was much greater than the total biomass for the seeded species, however the percent increase of biomass as a result of the pit treatment was smaller for non-native species than for seeded species. As expected, the seeding treatment did not influence the non-seeded species biomass.

**Table 4-2.** Pairwise contrasts for means of main effects in the seedling biomass LM. Results for Holms-adjusted Tukey’s HSD tests showing comparisons of group means for significant categorical fixed effects with associated standard error and p-values. Results are given on the log scale. (p<0.05\*, p<0.01\*\*, p<0.001\*\*\*)

<b>log(Non-native seedling biomass) ~ microsite tmt + seed tmt</b>					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>t value</b>	<b>P value</b>	
Pit Treatment					
control – pit	-3.41	0.40	-8.60	<0.0001	***
control – pit + biochar	-3.98	0.48	-8.25	<0.0001	***
pit – pit + biochar	-0.58	0.48	-1.21	0.4487	
<b>log(Native seedling biomass) ~ microsite tmt * seed tmt</b>					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>t value</b>	<b>P value</b>	
Pit Treatment					
control – pit	-0.42	0.05	-7.77	<0.0001	***
control – pit + biochar	-0.59	0.06	-9.30	<0.0001	***
pit – pit + biochar	-0.17	0.06	-2.77	0.00170	*
Seeding Treatment					
control – bare seeds	-0.45	0.06	-7.44	<0.0001	***
control – seed pellet	-0.42	0.06	-6.74	<0.0001	***
bare seeds – seed pellet	0.03	0.06	0.59	0.8247	
Pit Treatment: control					
control – bare seeds	0.00	0.10	0.00	1.0000	
control – seed pellet	-0.02	0.10	-0.25	0.9655	
bare seeds – seed pellet	-0.02	0.10	-0.25	0.9655	
Pit Treatment: pit					
control – bare seeds	-0.51	0.09	-5.67	<0.0001	***
control – seed pellet	-0.44	0.09	-4.85	<0.0001	***
bare seeds – seed pellet	0.07	0.09	0.82	0.6938	
Pit Treatment: pit + biochar					
control – bare seeds	-0.84	0.12	-6.79	<0.0001	***
control – seed pellet	-0.78	0.13	-6.10	<0.0001	***
bare seeds – seed pellet	0.06	0.11	0.50	0.8718	

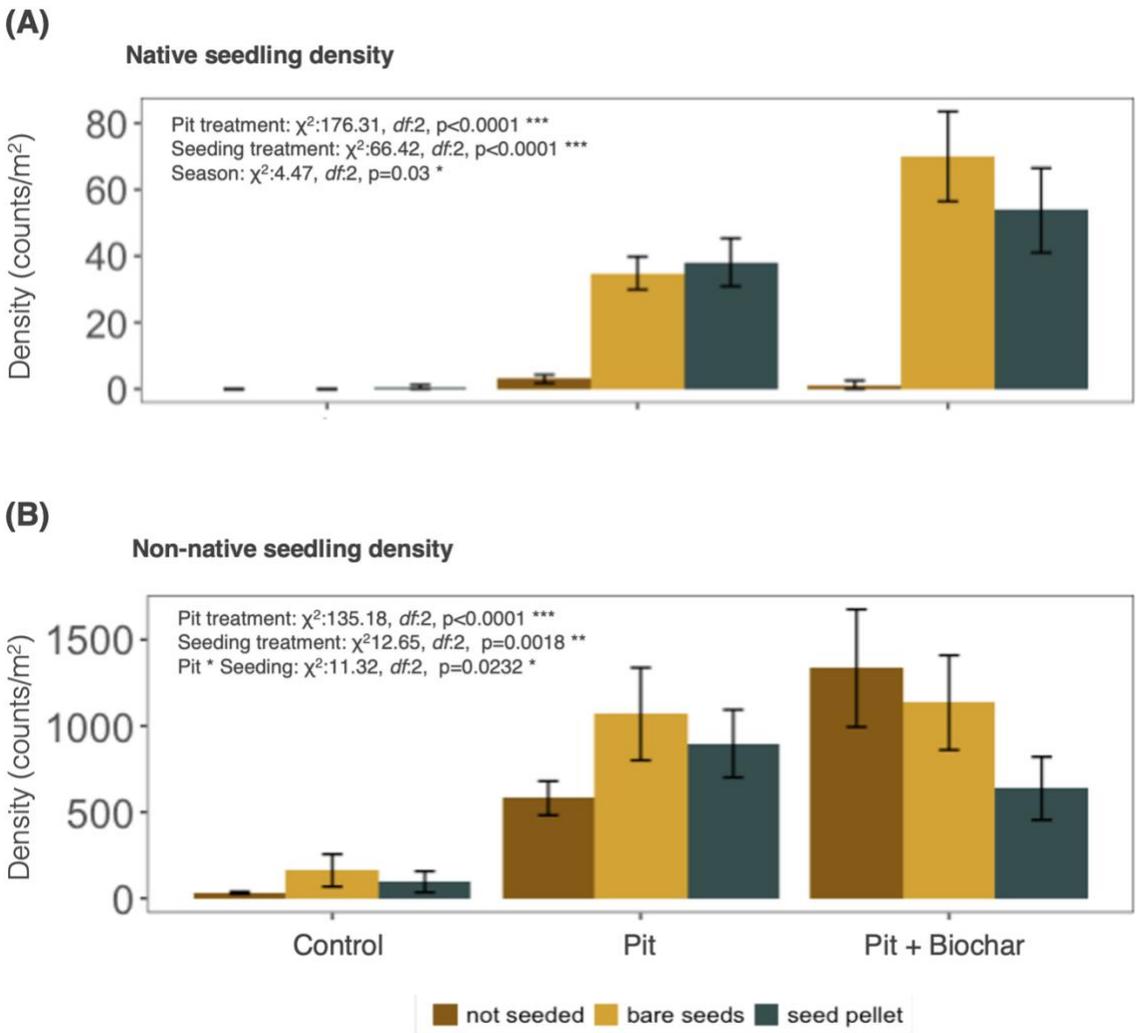
**Table 4-3.** Pairwise contrasts for means of main effects in the seedling density *GLM* models. Results for Holms-adjusted Tukey’s HSD tests showing comparisons of group means for significant categorical fixed effects with associated standard error and p-values. Results are given on the log scale. (p<0.1., p<0.05\*, p<0.01\*\*, p<0.001\*\*\*)

<b>Non-native species density ~ microsite_tmt * seed_tmt + season</b>					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>z value</b>	<b>P value</b>	
<b>Pit Treatment</b>					
control – pit	-2.35	0.23	-9.33	<0.0001	***
control – pit + biochar	-2.53	0.29	-8.26	<0.0001	***
pit – pit + biochar	-0.18	0.29	-0.64	0.80	
<b>Seeding Treatment</b>					
control – bare seeds	0.71	0.26	2.73	0.0175	*
control – seed pellet	0.40	0.36	1.52	0.2796	
bare seeds – seed pellet	-0.32	0.36	-1.21	0.4498	
<b>Pit Treatment: control</b>					
control – bare seeds	1.67	0.39	4.25	0.0001	***
control – seed pellet	0.42	0.39	1.07	0.5331	
bare seeds – seed pellet	-1.25	0.39	-3.18	0.0042	**
<b>Pit Treatment: pit</b>					
control – bare seeds	0.60	0.93	1.52	0.2828	
control – seed pellet	0.16	0.39	0.41	0.9104	
bare seeds – seed pellet	-0.44	0.40	-1.10	0.5160	
<b>Pit Treatment: pit + biochar</b>					
control – bare seeds	-0.13	0.56	-0.23	0.9723	
control – seed pellet	0.61	0.56	1.10	0.5115	
bare seeds – seed pellet	0.74	0.56	1.33	0.3785	
<b>Native seedling density ~ microsite_tmt + seed_tmt + season</b>					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>z value</b>	<b>P value</b>	
<b>Pit Treatment</b>					
control – pit	-5.44	0.43	-12.58	<0.0001	***
control – pit + biochar	-5.57	0.48	-11.51	<0.0001	***
pit – pit + biochar	-0.13	0.38	-0.33	0.9412	
<b>Seeding Treatment</b>					
control – bare seeds	-2.62	0.42	-6.26	<0.0001	***
control – seed pellet	-3.27	0.41	-7.91	<0.0001	***
bare seeds – seed pellet	-0.66	0.38	-1.74	0.1897	
<b>Season</b>					
fall-spring	-0.70	0.32	-2.11	0.0345	*

*Density*

The pit treatment had the largest influence on native seedling density (Figure 4-3). Seeding and season were also significant predictors of native seedling density (Figure 4-3). The pit and the pit + biochar both significantly increased native seedling density by about 9-fold

compared to the control. There was no significant advantage with the addition of biochar to the pit (Table 4-3). Seeding with both bare seeds and seed pellets significantly increased native seedling density compared to unseeded plots, but there was no difference between bare and pelleted seeds (Table 4-3). Finally, native seedling density was slightly higher in the spring compared to the fall (Table 4-5).



**Figure 4-3.** Native (A) and non-native (B) species seedling density across pit and seeding treatments. Data includes density counts from November 2021 and April 2022. Bars represent means  $\pm$  1 s.e. Results for the main effects in linear mixed models are shown. Pit, seeding treatment, and season were significant predictors of native seedling density. Pit, seeding treatment, and their interaction were significant predictors of non-native seedling density.

The pit treatments had a strong positive influence on non-native seedling density, as predicted (Figure 4-3). There was also a significant effect of seeding and an interaction between seeding and pit treatment (Figure 4-3). This could suggest competition as seedling density got high in the pit treatments. There was no difference between the pit and pit + biochar treatment for non-native density, but both significantly increased seedling density, by 8.8-fold and 10.7-fold respectively, compared to the control (Table 4-3).

## **Discussion**

Rates of plant recruitment in degraded drylands are often extremely low, presenting a challenge for maintaining important ecosystem services as climate change and land use intensify (Kildisheva et al., 2016; Shackelford et al., 2021). Soil moisture is often the most important control on plant outcomes in drylands (Shackelford et al., 2021), but granivory (Suazo et al., 2013) and competition with invasive species (Funk and Vitousek, 2007) can also limit success. Despite the often-low rates of seedling recruitment in dryland restoration, the microsite and seeding treatments that we tested successfully increased native plant density and biomass.

### *Effects of restoration treatments on native seeded species*

Our microsite pit treatments were designed to increase moisture capture, creating a microenvironment where seed germination would be increased. Using soil moisture probes, we found that the pits increased soil moisture 6-fold over the controls and about 2-fold over the pit + biochar. The soil moisture differences between the pit and the pit + biochar were greatest in the winter (Feb. – March 2021 and Dec. – Feb. 2022). We didn't test for a direct relationship between moisture and plant outcomes but the measured soil moisture in the pit treatments could

be the reason for the observed pattern of increased native seedling density and biomass compared to the control plots.

Our site experienced significant precipitation between August and October, which triggered late fall germination in the pits, particularly for C4 grasses. C3 grass germination was higher in the spring, consistent with dormancy traits in our main C3 grass, Indian ricegrass. The varied response of C3 and C4 grasses highlights the importance of having a diversity of response traits present in restoration. Increasing the response traits present in a community increases the likelihood that a seed will be able to respond to the unpredictable conditions that often characterize dryland systems. Further, C3 grasses on the Colorado Plateau have been declining in recent years in response to climate variability (Munson et al., 2011). One of the predicted outcomes of climate change in this region is increased variability and altered timing of precipitation, underscoring the need for diversity in restoration seed mixes.

Biochar as a soil amendment holds moisture in the soil for longer, increasing the benefits of increased moisture capture in the pit (Blanco-Canqui, 2017). The soil moisture probes showed that the biochar increased soil moisture over the control, but significantly less than the pits without biochar. The biggest differences in soil moisture between the pit and the pit with biochar are during the winter months rather than during the fall and spring when plants are recruiting. It's also possible that the beneficial effects of biochar were due to chemical or microbial changes in the soil rather than moisture. Biochar has been found to increase nutrient holding capacity of the soil, (Gebhardt et al., 2017), as well as the abundance and diversity of the soil microbial community (Lehmann et al., 2011). Biochar effects on plants are more mixed, with some studies finding increased biomass (Gebhardt et al., 2017), other studies have finding decreased plant growth (Haider et al., 2017) or no effect (Fehmi et al., 2020). Whatever the mechanism, the

addition of biochar to the pits increased both density and biomass of native plants compared to the pits alone and compared to the controls. The strength of the increase associated with biochar was less than the increase gained just by creating the pits, so decisions about whether to add biochar may depend on restoration budgets. A deeper understanding of the mechanisms promoting biomass and seedling density in the pits with biochar would also help with decision making.

Seeding significantly increased native plant density when coupled with pit treatments, but seeding alone was insufficient for native plant recruitment. The pits were necessary for seed germination and emergence. During the first season of the experiment, ambient precipitation at the site was low, and there was zero native plant recruitment in any of the treatments. This highlights the fact that the effects of most restoration efforts aren't observed in the first season and may take multiple years. Our seed pellets did not increase seed recruitment. Results on the effectiveness of seed pellets for dryland have been mixed (Gornish et al., 2019) and in this study they appeared to offer no benefit compared to broadcasting bare seeds. This is particularly surprising given that seeds didn't germinate in the first year after we seeded, so we expected that bare seeds would have been more vulnerable to granivory or damage during this time (Chapter II).

While germination and emergence are important bottlenecks for restoration, the long-term recruitment of native plants is the goal of most restoration projects. While the pitting plus seeding treatments in our study overcame the barriers to germination and emergence, most (but not all) of the native seedlings had not yet reached reproductive maturity by the time of our last sampling (approximately 1.5 years after installation). Longer term studies are needed to evaluate the long-term viability of the pitting treatments.

### *Restoration effects on non-natives*

While the pitting treatment was the most effective at increasing native density and biomass, it also resulted in the largest increase in non-native and invasive species density and biomass. This was a predicted outcome, as the conditions that facilitate the native species (i.e. increased soil moisture) are also favorable conditions for other species, and this pattern has been observed in other dryland restoration studies that modify microsite (Abella and Chiquoine, 2019; Havrilla et al., 2020). We saw little-to-no native plant recruitment in the control plots, suggesting that during our study period, microsite modification was necessary for native species recruitment. This tradeoff presents a conundrum for decision making. While some studies have found that pitting increases native cover close to that of invasive species (Havrilla et al., 2020), in our pits the density of invasive species was about 7 times higher than seeded species density. We had hoped that the seed pellets might offer microsite effects that were more locally targeted to our seeded species, but the pellets did not provide detectable effects in any pit treatment. Our seeding rate was on the high end of seeding rates typical of dryland restoration on federal land, but increasing the seeding rate or the number of seeding events are strategies to increase performance against invasives (Mazzola et al., 2011) because seed limitation is an important determinant of competitive interactions in microsites (Aicher et al., 2011). Although increasing seeding rate would increase the costs of the restoration intervention, it may be warranted.

The competitive interactions between native and non-native plants will take longer to stabilize than the time frame presented in this study. We seeded native perennials, while the invasives at this site are annuals. There is mixed evidence for how these longer-term competitive interactions will play out. Perennial grasses, which composed the majority of the seed mix used

in this study, are not as competitive as annual grasses at the seedling stage, but may become more competitive at later life stages (Dyer and Rice, 1999; Lulow, 2006). In some cases, established perennials are able to outcompete invasive annuals over longer periods of time (Corbin and D'Antonio, 2004). However, other studies find that while established perennial plants can benefit native species by acting as nurse plants, they more often benefit invasive annuals (Abella and Chiquoine, 2019). Longer-term studies are necessary to understand the implications of increasing non-native species along with desired native species.

### *Scaling up*

Treatments like microsite modification, such as the pits tested in this study, are proving to be effective strategies for increasing native plant recruitment in dryland restoration (Fick et al., 2016; Havrilla et al., 2020; Rachal et al., 2015). However, microsite creation is a time- and labor-intensive treatment compared to a seeding-only approach. We estimate that creating pits by hand prior to seeding increased our labor by more than 10-fold. One solution is to use drillseeder machines that have been modified to create pits and deliver seeds into them (Shaw et al., 2020). This method has similar downsides as drillseeding: it is not an option in rocky soils, in some cases seeds must be modified to ensure they pass through the drillseeder, and there is a high level of surface disturbance that can lead to soil destabilization and erosion. In light of these downsides, we propose that microsite modification treatments such as pit creation may be most suitable for a restoration island approach (Hulvey et al., 2017). Restoration islands concentrate restoration resources into patches where the chances of success are higher, with the hope that plants will establish in the patches and then spread naturally over time (Hulvey et al., 2017). Given the high labor inputs associated with digging pits, and even higher resource inputs

associated with integrating biochar, the most effective way to use these treatments might be to concentrate them in high priority areas. By creating restoration islands, practitioners increase diversity at a landscape scale and maintain a source for native seed propagules on the landscape. Maintenance of native propagules is particularly important in drylands where the conditions for recruitment don't occur every year and it is difficult to time restoration to line up with favorable recruitment conditions (Kolden et al., 2012). Dryland restoration is currently needed at a large scale and the demand is increasing as climate change and land use intensify. Meeting this demand requires new techniques that can be deployed widely and provide higher rates of successful recruitment than standard restoration techniques.

### *Conclusions*

As land-use and climate change intensify, the need for restoration of ecosystem services also increases. Low restoration success rates in drylands calls for new restoration methods that can increase native plant recruitment under these challenges. We show that microsite creation, specifically pitting and adding a biochar amendment, in combination with seeding, can boost native seedling biomass and density. However, these methods also increased the density and biomass of non-native species, presenting a challenge for practitioners. Coupling the pit treatment with additional methods such as targeted grazing or herbicide would be an interesting next step. Additionally, understanding the mechanisms behind biochar effects may provide some solutions.

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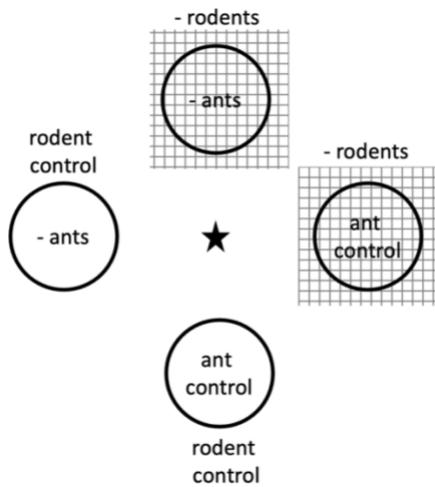
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*APPENDIX I:  
Supplemental Materials for Chapter II*



**Figure S1-1.** The seed preference experiment. The grid of seeds is on the left and offers a choice of seven species of native seeds (Table 2-1). It has been placed just outside of the ant nest entrance hole in the lower right of the image.



**Figure S1-2.** Enclosure experiment schematic. We placed four plastic containers 1 m away from each ant nest entrance, represented by the star. Two of the plastic containers had holes cut in the sides to allow ants to enter (ant control) and two of the plastic containers excluded ants. Seeds were placed within the plastic containers. In the second trial (April 2020 – November 2020), we added a rodent exclusion treatment by placing metal cages over the plastic containers.

*APPENDIX II:  
Supplemental Materials for Chapter III*

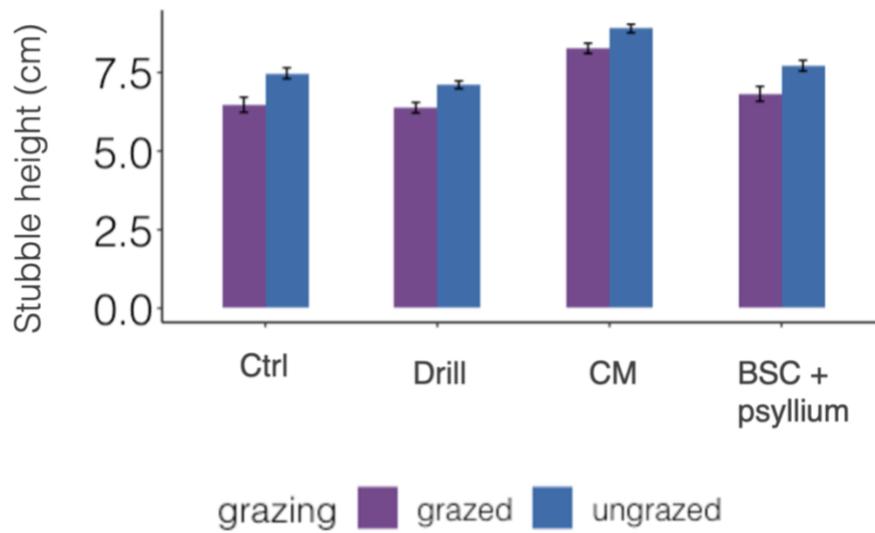
S2-1. Supplemental methods for Chl *a* extraction

To extract chlorophyll *a*, 1 g of soil was ground with a mortar and pestle in 3 mL of 90% acetone for 3 min. 90% acetone was added to bring the sample and solvent volume up to 10 mL. Samples were vortexed for 2 min and incubated at 4° C for 24 hours in the dark. Samples were then centrifuged (12 min, 4000xg, 15° C). Finally, we measured absorbance of the supernatant with a spectrophotometer (Ocean Optics CHEMUSB4-VIS-NIR Spectrophotometer, 400-950 nm). We calculated chlorophyll *a* content from absorbance values using the calculations in Ritchie (2006).

S2-2. Supplemental methods for EPS extraction

We extracted loosely-bound, tightly-bound, and glycocalyx fractions of EPS with slight modifications to the protocol in Chock et al. (2019). First, 50 mg of homogenized soil was shaken with 400 µL DI water for 15 minutes (orbital shaker, 700 rpm) to extract loosely-bound EPS. The sample was centrifuged (5 minutes, 6000xg) and the supernatant was saved. Next, 500 µL of 0.1 M Na<sub>2</sub>EDTA was added to the remaining pellet and shaken (orbital shaker, 700 rpm) for 16 hours in the dark. The sample was centrifuged (5 minutes, 6000xg) and the supernatant was removed and saved as the tightly-bound EPS fraction. Finally, 500 µL of DI water was added to the remaining pellet and incubated at 80° C for 1 hour. The sample was centrifuged (5 minutes, 6000xg), and the supernatant was saved as the glycocalyx fraction. All three supernatants were analyzed using a phenol-sulfuric assay by adding 1 mL of concentrated H<sub>2</sub>SO<sub>4</sub> and 200 µL of phenol to 200 µL of each sample. The mixture cooled for one hour and

then 200  $\mu\text{L}$  were analyzed with a monochromatic microplate spectrophotometer (BioTek EL800, Winooski, VT) using 490 nm for EPS, 660 nm to check for ruptured cells, and 750 nm to correct for turbidity. A ten-point calibration curve of D-glucose in DI water was used to quantify EPS concentration (0-200 mg/L), and then the weight of each sample was used to determine the final concentration of EPS ( $\mu\text{g}$  glucose per gram of dry soil). Total EPS was calculated as the sum of each fraction for a given sample.



**Figure S2-1.** Average annual wheat grass stubble height (+/- SE) by treatment after grazing, April 2020.

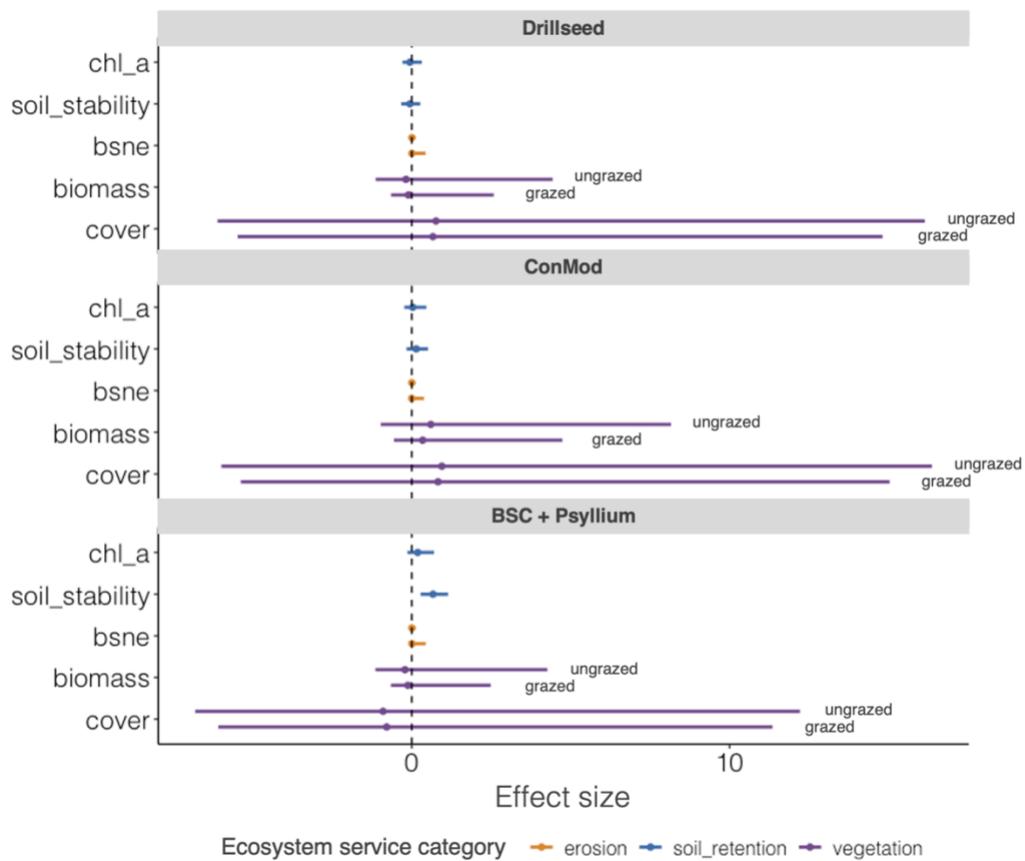
**Table S2-1.** Pairwise contrasts for means of main effects in the soil retention linear models. Results for Holms-adjusted Tukey’s HSD tests showing comparisons of group means for significant categorical fixed effects with associated standard error and p-values. Results are given on the transformation scale. Stars indicate significance (p<0.05\*, p<0.01\*\*, p<0.001\*\*\*).

log10(chlorophyll a) ~ Treatment + Year + (1 Block/Plot/Transect)					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>df</b>	<b>t value</b>	<b>p value</b>
<i>Restoration Treatment</i>					
control – drillseed	0.04	0.04	20.2	0.98	0.76
control – conmod	-0.02	0.04	19.7	-0.47	0.97
control – BSC + psyllium	-0.11	0.04	13.4	-2.88	0.05 .
drillseed – conmod	-0.06	0.04	19.5	-1.45	0.48
drillseed – BSC + psyllium	-0.14	0.04	13.3	-3.97	0.01 *
conmod – BSC + psyllium	-0.09	0.04	13.2	-2.36	0.13
log(soil stability) ~ Treatment +  Year + (1 Block/Plot)					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>df</b>	<b>t value</b>	<b>p value</b>
<i>Restoration Treatment</i>					
control – drillseed	0.04	0.07	36.7	0.58	0.94
control – conmod	-0.08	0.07	35.4	-1.15	0.66
control – BSC + psyllium	-0.34	0.07	30.5	-5.15	0.0001 ***
drillseed – conmod	-0.12	0.07	36.2	-1.75	0.32
drillseed – BSC + psyllium	-0.38	0.07	31.0	-5.83	<0.0001 ***
conmod – BSC + psyllium	-0.26	0.07	30.1	-3.96	0.0023 **

**Table S2-2.** Pairwise contrasts for means of main effects in the productivity and cover linear models. Results for Holms-adjusted Tukey’s HSD tests showing comparisons of group means for significant categorical fixed effects with associated standard error and p-values. Results are given on the log scale. Stars indicate significance (p<0.1., p<0.05\*, p<0.01\*\*, p<0.001\*\*\*).

log(biomass 2018-2019) ~ Restoration * Native_status + (1 Year) + (1 Block/Plot/Location)					
Group comparison	Mean difference	Std. Error	df	t value	p value
<i>Native biomass</i>					
control – drillseed	2.04	0.61	142.8	2.38	0.08 .
control – conmod	0.77	0.21	107.2	-0.94	0.78
control – BSC + psyllium	2.11	0.62	135.3	2.55	0.06 .
drillseed – conmod	0.38	0.10	90.4	-3.67	0.00 **
drillseed – BSC + psyllium	1.03	0.29	115.9	0.12	1.00
conmod – BSC + psyllium	2.74	0.71	82.8	3.91	0.00 ***
<i>Non-native biomass</i>					
control – drillseed	0.95	0.20	34.8	-0.24	1.00
control – conmod	0.74	0.14	25.1	-1.57	0.41
control – BSC + psyllium	0.99	0.20	31.9	-0.08	1.00
drillseed – conmod	0.78	0.15	22.8	-1.34	0.55
drillseed – BSC + psyllium	1.04	0.21	29.5	0.17	1.00
conmod – BSC + psyllium	1.33	0.24	20.5	1.56	0.42
log(biomass 2020-2021) ~ Restoration * Native_status * Grazing + (1 Year) + (1 Block/Plot/Location)					
Group comparison	Mean difference	Std. Error	df	t value	p value
<i>Native biomass, Grazed</i>					
control – drillseed	0.79	0.57	275.82	-0.33	0.99
control – conmod	0.30	0.19	197.45	-1.86	0.25
control – BSC + psyllium	0.52	0.35	233.57	-0.97	0.77
drillseed – conmod	0.38	0.25	205.69	-1.47	0.46
drillseed – BSC + psyllium	0.65	0.45	235.66	-0.61	0.93
conmod – BSC + psyllium	1.70	1.04	161.25	0.88	0.82
<i>Native biomass, Ungrazed</i>					
control – drillseed	2.99	2.21	254.24	1.48	0.45
control – conmod	1.25	0.85	205.89	0.33	0.99
control – BSC + psyllium	0.50	0.43	289.14	-0.80	0.85
drillseed – conmod	0.42	0.27	190.68	-1.34	0.54
drillseed – BSC + psyllium	0.17	0.14	315.67	-2.10	0.15
conmod – BSC + psyllium	0.40	0.32	260.69	-1.16	0.65
<i>Non-native biomass, Grazed</i>					
control – drillseed	1.84	0.68	19.18	1.65	0.38
control – conmod	0.98	0.33	12.79	-0.05	1.00
control – BSC + psyllium	2.08	0.76	20.09	2.00	0.22
drillseed – conmod	0.53	0.16	9.83	-2.10	0.22
drillseed – BSC + psyllium	1.13	0.38	15.09	0.37	0.98
conmod – BSC + psyllium	2.12	0.63	10.43	2.52	0.11
<i>Non-native biomass, Ungrazed</i>					
control – drillseed	0.44	0.19	41.15	-1.94	0.23
control – conmod	0.41	0.15	24.71	-2.43	0.10
control – BSC + psyllium	1.11	0.43	27.18	0.27	0.99
drillseed – conmod	0.93	0.35	25.84	-0.21	1.00
drillseed – BSC + psyllium	2.51	0.99	27.93	2.34	0.11
conmod – BSC + psyllium	2.72	0.91	15.22	2.98	0.04 *
log(cover 2018-2019) ~ Restoration + Native_status + (1 Year) + (1 Block/Plot/Location)					

<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>df</b>	<b>t value</b>	<b>p value</b>
native – non-native	0.21	0.01	128	-25.75	<0.0001 ***
log(cover 2020-2021) ~ Restoration * Native_status * Grazing + (1 Year) + (1 Block/Plot/Location)					
<b>Group comparison</b>	<b>Mean difference</b>	<b>Std. Error</b>	<b>df</b>	<b>t value</b>	<b>p value</b>
<i>Non-native biomass</i>					
Grazed - ungrazed	0.84	0.29	4.02	-0.51	0.64



**Figure S2-2.** Summary of the effect sizes (with 95% CI) of the three restoration treatments on ecosystem service variables. The effect size of the control has been subtracted. Ecosystem services are colored by category: erosion, soil retention, vegetation. Data spans 2018-2021.

*APPENDIX III:  
Supplemental Materials for Chapter IV*

**Table S3-1.** Summary of fixed effects for linear models testing effects of pit treatments and seeding treatments on seedling biomass. Each treatment level is shown compared to the control. Estimates are reported on the log scale. ( $p < 0.1$ .,  $p < 0.05$ \*,  $p < 0.01$ \*\* ,  $p < 0.001$ \*\*\*)

<b>log(Non-native seedling biomass) ~ microsite_tmt + seed_tmt</b>				
<b>Fixed effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	-0.81	0.38	-5.614	<0.0001 ***
microsite pit	1.82	0.40	8.60	<0.0001 ***
microsite pit + biochar	2.28	0.48	8.25	<0.0001 ***
seeding bare seeds	-0.78	0.43	-1.81	0.0719 .
seeding seed pellet	-0.21	0.43	-0.48	0.6309
<b>Multiple R<sup>2</sup></b>	0.40			
<b>log(Native seedling biomass) ~ microsite_tmt * seed_tmt</b>				
<b>Fixed effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	0.04	0.07	0.67	0.5030
microsite pit	0.11	0.10	1.14	0.2580
microsite pit + biochar	0.06	0.12	0.50	0.6171
seeding bare seeds	0.00	0.10	0.00	1.0000
seeding seed pellet	0.02	0.10	0.25	0.8010
pit * bare seeds	0.51	0.13	3.85	0.0002 ***
pit + biochar * bare seeds	0.84	0.16	5.32	<0.0001 ***
pit * seed pellet	0.42	0.13	3.13	0.0021 **
pit + biochar * seed pellet	0.76	0.16	4.70	<0.0001 ***
<b>Multiple R<sup>2</sup></b>	0.57			

**Table S3-2.** Summary of fixed effects for generalized linear model (GLM) testing effects of pit treatments and seeding treatments on seedling density. The density model is based on a negative binomial error distribution, and model results are given on a log scale. Each treatment level is shown compared to the control. (p<0.1., p<0.05\*, p<0.01\*\*, p<0.001\*\*\*)

**Non-native seedling density** ~ microsite\_tmt \* seed\_tmt + season

Family: negative binomial, link = log

<b>Fixed effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>z value</b>	<b>Pr(&gt; z )</b>	
(Intercept)	4.86	0.30	16.43	<0.0001	***
Microsite pit	-1.67	0.39	-4.25	<0.0001	***
Microsite pit + biochar	-0.42	0.39	-1.07	0.2849	
Seeding bare seeds	1.91	0.39	4.91	<0.0001	***
Seeding seed pellet	1.99	0.48	4.14	<0.0001	***
Season Spring	0.38	0.20	1.88	0.0604	
Bare seeds * pit	1.08	0.56	1.94	0.0530	.
Seed pellet * pit	0.26	0.55	0.47	0.6375	.
Bare seeds * pit + biochar	1.80	0.68	2.64	0.0082	***
Seed pellet * pit + biochar	-0.19	0.68	-0.28	0.7770	

**Native seedling density** ~ microsite\_tmt + seed\_tmt + season

Family: negative binomial, link = log

<b>Fixed effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>z value</b>	<b>Pr(&gt; z )</b>	
(Intercept)	-4.90	0.54	-9.15	<0.0001	***
Microsite pit	2.62	0.42	6.26	<0.0001	***
Microsite pit + biochar	3.27	0.41	7.91	<0.0001	***
Seeding bare seeds	5.44	0.43	12.58	<0.0001	***
Seeding seed pellet	5.57	0.48	11.51	<0.0001	***
Season spring	0.68	0.32	2.11	0.0345	*