DISSERTATION

OVERCOMING ECOLOGICAL BARRIERS TO DRYLAND RESTORATION: INNOVATIVE TECHNIQUES AND COMMUNITY-ENGAGED APPROACHES ACROSS SPATIAL SCALES AND ENVIRONMENTAL GRADIENTS

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ABSTRACT

OVERCOMING ECOLOGICAL BARRIERS TO DRYLAND RESTORATION: INNOVATIVE TECHNIQUES AND COMMUNITY-ENGAGED APPROACHES ACROSS SPATIAL SCALES AND ENVIRONMENTAL GRADIENTS

Drylands are arid and semi-arid ecosystems characterized by water limitation. These landscapes are often overlooked, yet cover over 40% of the global terrestrial surface, support billions of people, and face high rates of degradation. Under anthropogenic climate change, drylands are expected to expand and increase in aridity. Restoration of plant communities in these water-limited systems is inherently challenging but identifying effective strategies to enhance restoration success is increasingly urgent. Given the large spatial extent of dryland areas in need of revegetation and associated cost constraints, seed-based restoration approaches are the most common. However, many restoration projects in drylands result in little or no establishment of desirable species. Major barriers to emergence include abiotic stress, invasive species dominance, degraded soils, and interannual climate variability.

This dissertation evaluates how active restoration interventions targeting dispersal limitation, harsh abiotic conditions, and biotic interactions influence restoration outcomes across dryland systems in the western United States. The experiments included in the four chapters of this dissertation range in scale from a greenhouse study to a multi-site networked trial, and each uses a precision restoration framework, designed to address site-specific ecological barriers to restoration that vary across space and time. A further unifying theme is the use of community-engaged approaches throughout to develop and frame each study and to provide actionable insights to our research partners and the broader restoration community.

Across these studies, climatic variability and competitive pressure constrained seed-based restoration outcomes. However, even small gains in the emergence and establishment of desirable species can have meaningful ecological impacts in degraded drylands. Key findings include, increasing propagule

availability through active seeding led to increases in desirable species. Microsite climate modification strategies designed to retain moisture and, in some cases, reduce soil surface temperatures, showed promise when paired with sufficient precipitation. However, many of our more intensive restoration interventions, including soil inoculation, targeted livestock treatment, and seed pellets, had limited or context dependent effects, particularly under persistent drought conditions. We also found using herbicide as a restoration tool to control invasive species resulted in both target and non-target impacts, emphasizing the importance of careful consideration of site history, existing community composition, and the potential for secondary invasion following the removal of a target species. Pairing preemergent herbicide application with seed pellets made with activated carbon showed promise as a strategy to reseed desirable species under reduced competitive pressure.

Ultimately, restoration outcomes are constrained by interacting ecological filters, including propagule availability, biotic, and abiotic constraints. Strategies to address these filters can lead to gains in restoration success but are often mediated by climatic conditions at the time of intervention and during early plant life stages. Successful restoration of drylands under climate change will depend on aligning interventions targeting site-specific ecological barriers with favorable episodic climatic conditions, using adaptive and iterative invasive species management, and continuing to test novel interventions.

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INTRODUCTION

As the climate changes and land degradation impacts our world now and into the future, effective ecological restoration becomes an ever more pressing need (Abhilash, 2021; Simonson et al., 2021; United Nations General Assembly, 2019). Restoration presents an opportunity to reverse ecosystem degradation, support biodiversity, build resilience, and ensure humans are able to thrive (Abhilash, 2021; Gann et al., 2019; Suding, 2011). Plants in drylands, arid or semi-arid ecosystems, already exist under conditions of water limitation, and under climate change, conditions across many of these areas are projected to become even more arid (Bradford et al., 2020; Hoover et al., 2020; Munson et al., 2013). These changes could trigger the crossing of ecological thresholds where ecosystem responses become non-linear with potentially catastrophic consequences (Berdugo et al., 2020; Munson et al., 2013). Covering approximately 41% of the Earth's terrestrial surface, supporting billions of people and degraded in as much as 50% of their range, drylands are understudied compared to many other terrestrial biomes (Hoover et al., 2020; Shackelford et al., 2021). Understanding these often-forgotten systems and improving our ability to restore them is essential to support global ecological functioning, the provisioning of ecosystem services, and human wellbeing (Copeland et al., 2021; Kildisheva et al., 2016; Svejcar & Kildisheva, 2017). Active restoration—defined as human intervention when the potential for natural recovery is low or absent (Gann et al., 2019)—is often necessary in these degraded drylands as they are unlikely to recover on their own (Shackelford et al., 2021).

Dryland restoration efforts often employ a seed-based restoration (SBR) approach due to the large spatial extent of areas in need of restoration and related cost limitations (Copeland et al., 2021; Shackelford et al., 2021). However, most dryland SBR projects result in little or no establishment of desirable seeded species (James et al., 2011; Shackelford et al., 2021; Stapleton et al., 2024). SBR in drylands faces many major barriers to success, including abiotic limitations (e.g., water limitation, extreme heat) (Duniway et al., 2022; Shackelford et al., 2021), seed predation (Gornish et al., 2019; Pearson et al., 2019), invasive

species prevalence and associated legacy effects (James et al., 2011; Ravi et al., 2022; Shackelford et al., 2021; Zhang et al., 2019), and degraded soils (Duell et al., 2023; Larson et al., 2015). These factors often lead to low establishment rates of desired species (James et al., 2011; Shackelford et al., 2021; Stapleton et al., 2024). Under a changing climate, many of these already existing challenges are expected to be further amplified, and the incorporation of anticipatory actions to build climate resilience into restoration approaches will be necessary (Coleman et al., 2020; Simonson et al., 2021; Winkler et al., 2020). Given these constraints, we need innovative, science-based strategies to overcome barriers to revegetation and support positive SBR outcomes in drylands under increasingly extreme and variable climatic conditions.

Each of the four chapters in my dissertation investigates active restoration interventions aimed at overcoming one or more ecological barriers in drylands (Fig. 1), including propagule availability, abiotic limitations, and both competitive and facilitative biotic factors (Hulvey & Aigner, 2014; Kraft et al., 2015; Pearson et al., 2018). Throughout, I apply a precision restoration approach, where interventions are designed to overcome site-specific barriers that vary across space and time (Copeland et al., 2021). Collectively, this work helps advance our understanding of how and when targeted interventions, applied alone or in combination, can improve restoration outcomes in drylands. The work presented in this dissertation spans scales ranging from greenhouse studies to networked, regional restoration trials. In addition to building knowledge on ecological restoration approaches, I use a lens of community-engaged scholarship (Fig. 2) throughout, aimed at generating actionable science to support communities and science informed decision making (Suding, 2011). All these dissertation chapters showcase research developed with feedback and collaboration from a diverse group of research partners spanning academics, ranching communities, city, state, and federal agencies, and the Ute Mountain Ute Tribe. Each of these projects and their scales are mapped onto ecological barriers in a conceptual figure, providing a visual representation of this dissertation research (Fig. 1).

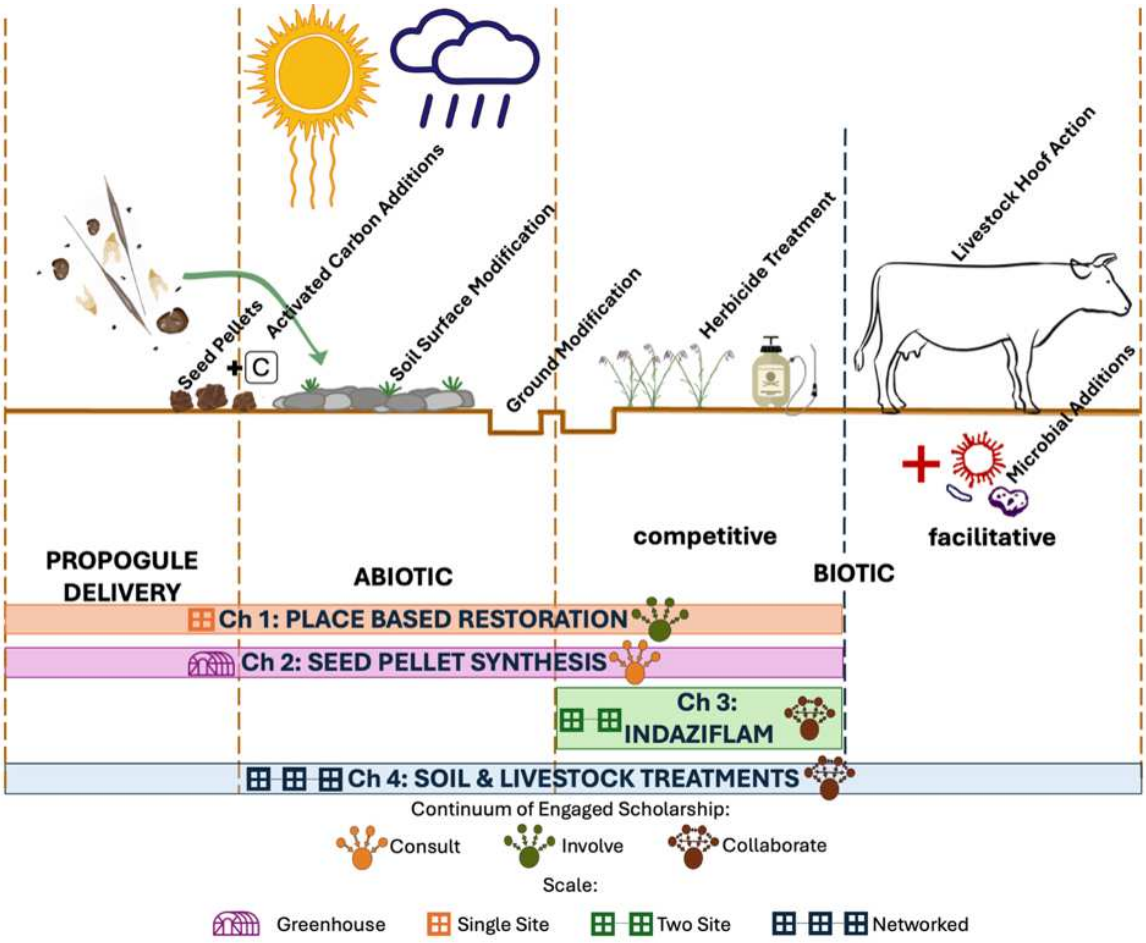

Figure 1: Conceptual figure illustrating barriers to restoration success, treatments explored in this dissertation, and the alignment of each of the four chapters with specific restoration barriers. The diagram maps each chapter to relevant ecological barriers (e.g., abiotic factors such as climate, biotic interactions like competition) and depicts the scale and level of engagement according to the "Continuum of Engaged Scholarship" (Figure 2). This framework highlights how each chapter addresses distinct challenges in restoration ecology, aiming to enhance native plant establishment through various strategies.

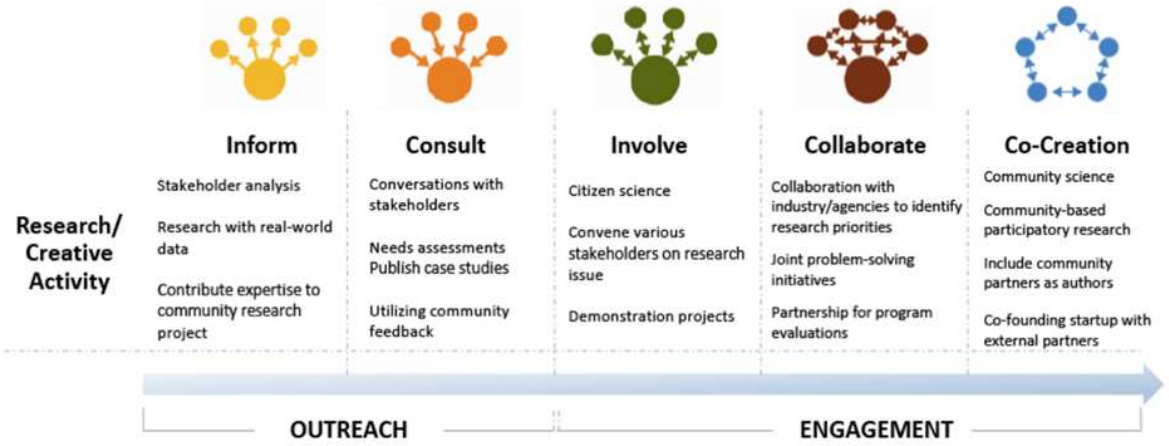

Figure 2: Colorado State University – Continuum of Engaged Scholarship. Adapted from: https://engagement.colostate.edu/wp-content/uploads/2019/09/Continuum-of-Engaged-Scholarship-REV-9-16-19.pdf

Chapter 1 of my dissertation focuses on climate-adaptive, place-based restoration approaches in collaboration with the Ute Mountain Ute Tribe. This project tests hyperlocal and culturally relevant restoration strategies crossed with herbicide treatment to reduce competitive pressure from invasive species at a single culturally significant location in Mancos Canyon near Towaoc, CO on Ute Mountain Ute Tribal lands. Due to low seeded species density, we were unable to quantify treatment differences using statistical models. However, we observed higher mean seeded species density (not significant) in treatments designed to retain moisture. Overall, my treatments were likely insufficient to overcome competitive pressure from introduced species and challenging climate conditions. These findings reflect many SBR outcomes in drylands (Shackelford et al., 2021; Stapleton et al., 2024) and emphasize the need for continued development of novel approaches. I also observed secondary invasion (O'Loughlin & Green, 2017; Pearson et al., 2016), in which other introduced species establish following suppression of a target invader. This pattern was a key driver of low desirable species emergence and emphasizes the need for continued work on the effective management of multi-species invasions (Brandt et al., 2023).

Chapter 2 builds upon challenges from the field experiment in Chapter 1 and tests strategies to improve seed pellet treatments, a seed enhancement technology, designed to protect seeds from predation, harsh conditions, and provide targeted amendment delivery within the seed pellet ensuring good contact with seeds, (Brown et al., 2021; Gornish et al., 2019). In a controlled greenhouse experiment we explored the influence of seed pellet composition, and investigated using activated carbon additions in seed pellets to protect desirable seeds from herbicide residuals, leveraging low-tech and accessible approaches (Davies et al., 2024; Madsen et al., 2014). We found limited effects of pellet composition on seedling emergence under relatively high-water conditions, suggesting that optimal seed pellet formulations are likely context dependent and vary with site conditions. Incorporating activated carbon into seed pellets offers a potential improved approach to seeding shortly following preemergent herbicide treatment, allowing desirable species to establish under conditions of reduced competitive pressure from introduced species.

Chapter 3, in collaboration with the City of Boulder, investigates the impacts of indaziflam, a relatively new nonselective pre-emergent herbicide, on plant community composition. I examine the efficacy of using indaziflam to control introduced perennial species that depend on seed for reproduction, using a novel target species, *Arrhenatherum elatius* (tall oat grass), as a study system (Wilson & Clark, 2001). I investigate the target and non-target impacts of indaziflam treatment on the target species, and other native and introduced species post-herbicide application at two sites with different land use histories and ecological contexts over three years. In this study, I found that indaziflam had multiyear impacts on plant community composition which varied between sites with differing conditions. Although indaziflam is designed to prevent seed germination and emergence without impacting established species (Clark et al., 2019; Courkamp et al., 2022), we observed significant aboveground mortality at one site, which largely drove differences in our target species cover. We found that any potential use of indaziflam on perennial species dependent on seed for reproduction would need to be paired with control of established individuals. Finally, I demonstrated that indaziflam continued to suppress germination from the seed bank in samples collected two and a half years post-application, highlighting its long residual activity (Dombro et al., 2025b; Sebastian et al., 2025). Given this extended control period, pre-existing desirable vegetation is critical to recovery because recruitment from the seed bank remains limited.

Chapter 4 explores how ground modification (pitting) and using seed pellets in combination with live soil inoculation and targeted livestock treatments impact SBR outcomes at four sites across an aridity gradient in Arizona. The study leverages RestoreNet, a large restoration field trial network spanning the Southwest U.S. and co-produced with a variety of local, state, federal, and tribal research partners (Havrilla et al., 2020; Laushman et al., 2022) working on dryland restoration. Overall, I found limited effects of these treatments, likely because seeded species density was constrained by persistent drought conditions across sites for much of the study period. Ground modification through pitting shows promise for increasing seeded species density in systems characterized by pulse precipitation regimes, areas with variable precipitation event sizes. However, many of our more intensive restoration interventions, including soil

inoculation, targeted livestock treatment, and seed pellets, had limited or context dependent effects. Collectively, these results indicate that dryland restoration outcomes can be constrained by climatic conditions and investing in more intensive restoration interventions may not be effective unless aligned with episodic conditions favorable for plant recruitment.

This dissertation helps advance our understanding of how and when active restoration interventions can overcome key ecological barriers including propagule availability, biotic and abiotic limitations, in dryland systems. By evaluating restoration strategies across spatial scales, environmental gradients and social contexts, this work highlights the need for flexible, and context aware approaches designed to overcome site-specific constraints (Copeland et al., 2021). This work affirms the dominant role of climatic conditions at the time of restoration interventions and during early plant life stages in mediating dryland restoration outcomes (Farrell et al., 2023; Shriver et al., 2018) and emphasizes the need for continued development of novel approaches to overcome these challenges, which are expected to amplify under climate change (Hoover et al., 2020). This research helps provide actionable insights to improve SBR outcomes in drylands.

CHAPTER 1: INVASION DYNAMICS LIMIT DRYLAND RESTORATION OUTCOMES IN SOUTHWEST COLORADO

SUMMARY

Climate change and other anthropogenic pressures have resulted in widespread degradation across dryland ecosystems globally, with over 50% of their range already degraded. Additionally, Indigenous communities are disproportionately impacted by climate change, with significant consequences for ecosystem health, human well-being, and cultural practices, making restoration on Indigenous lands a priority. Ute Mountain Ute Tribal lands cover arid and semi-arid areas on the Colorado Plateau, and restoration is a Tribal priority. We collaboratively tested place-based, climate-adapted approaches with the goal of improving seed-based restoration outcomes. This research tested novel strategies designed to overcome local barriers to revegetation, including competitive pressure from introduced species, an introduced-dominated seed bank, low precipitation, and high temperatures, at a culturally important location. We investigated the impact of treatments designed to overcome multiple ecological barriers, including propagule availability, biotic, and abiotic constraints. We tested active seeding combined with low-tech rock structures, media lunas, to retain water, and coarse woody debris, which was locally available, to cool the soil surface, retain moisture and create heterogeneity. We also evaluated an alternative seeding method, seed pellets, designed to protect seeds from harsh conditions. Each of these treatments was crossed with targeted herbicide application to reduce the primary invasive species of concern, *Acroptilon repens* (Russian Knapweed). Results showed limited seeded species recruitment, likely constrained by climatic conditions and intense competitive pressure with invasive species. Although not statistically significant, we anecdotally observed higher mean seedling densities in treatments designed to modify the soil surface microclimate (media lunas and coarse woody debris), potentially suggesting that these strategies may be effective under favorable climatic conditions and less competitive pressure. While herbicide treatment successfully reduced the target invasive species, we observed secondary invasion,

where other invasive species increased following targeted treatment of *A. repens.* This subsequent invasion emphasizes the need for iterative and adaptive weed management when restoration sites are facing multi-species invasions. A supplemental seed bank assay confirmed dominance by introduced species, emphasizing the need for active seeding approaches combined with strategies to overcome ecological barriers at this degraded dryland location.

INTRODUCTION

Restoration under a changing climate is facing new challenges, including critical decisions about the state to which ecosystems should be restored, to ensure resilience under future conditions. Historically, restoration outcomes typically sought to replicate a pre-disturbance plant community from some prior time point when the system was considered "healthy" (Coleman et al., 2020; Higgs et al., 2014; Hobbs et al., 2009; Martin, 2017). However, the environmental conditions that supported those healthy communities may no longer exist—or may not exist in the future. Reframing restoration goals to include anticipatory actions that proactively increase resilience and the adaptive capacity of ecosystems is critical for effective restoration under climate change (Coleman et al., 2020; Winkler et al., 2020). Additionally, restoration is also recognized as an essential component of climate change adaptation and as a mitigation strategy including through increasing the uptake and storage of carbon in restored systems compared to their former degraded state (Morecroft et al., 2019). Climate adapted plant restoration outcomes might include developing novel communities that prioritize ecosystem structure, processes, and function rather than a specific species composition (Higgs et al., 2014; Hobbs et al., 2009; Simonson et al., 2021).

Drylands, or water limited ecosystems, characterized by low precipitation relative to potential evapotranspiration, cover roughly 40% of the earth's terrestrial surface and support about 40% of the global population through agriculture and critical ecosystems services (Duniway et al., 2022; Hoover et al., 2020; Shackelford et al., 2021). Drylands have both cultural and economic importance, about half the population living in drylands depends directly on the local ecosystem for food and fiber and drylands play a critical role in global livestock production (Hoover et al., 2020). Under a changing climate and increased

anthropogenic pressure, drylands are generally expected to expand, get warmer, have changes in seasonal precipitation regimes, experience increased frequency of extreme events (e.g., drought), and become more arid than current conditions (Bradford et al., 2020; Hoover et al., 2020; Maestre et al., 2016). Despite a clear need for restoration given the economic and cultural significance of drylands, seed-based restoration (SBR) of these systems is challenging and often fails, making the need for novel strategies to improve revegetation outcomes essential (Shackelford et al., 2021).

Indigenous communities in the United States are disproportionately impacted by land degradation and climate change, and systemic policy, funding, and governance barriers limit implementation of climate adapted restoration approaches critical to ensuring ecosystem resiliency, supporting human health and wellbeing and the ability to maintain critical cultural practices (Farrell et al., 2021; Jennings et al., 2025; McNeeley, 2017). Place-based approaches to ecological restoration recognize the unique attributes of a landscape and their human connections. Wickham et al. (2022) define place-based values-led restoration as efforts with clear objectives informed by local knowledge that aim to preserve or improve ecosystem biodiversity and productivity. Collaboration and place-based restoration can also be a powerful tool for building local or regional restoration and climate change adaptation approaches (Jennings et al., 2025). Importantly, place-based restoration is often, but not always, Indigenous-led and integrates Traditional Ecological Knowledge (TEK) and western scientific approaches (Wickham et al., 2022). Tribal climate adaptation planning and strategies often are grounded in place-based approaches and center the preservation of cultural resources (Bliska et al., 2024; Hepler & Kronk Warner, 2019). The Ute Mountain Ute territory in Southwestern Colorado spans a semi-arid area of the four corners region of the Colorado Plateau and is facing numerous challenges as a result of climate change including warming trends, changes in precipitation regimes, and increased extreme weather including heatwaves and drought impacting local ecosystems, livelihoods, health and cultural practices (Ute Mountain Ute Tribe, 2020). These impacts are expected to continue and intensify, making it critical to identify effective local and culturally relevant restoration strategies (Copeland et al., 2021; Ute Mountain Ute Tribe, 2020).

Drylands, including Ute Mountain Ute Tribal lands, are characterized by water limitation and episodic favorable conditions for plant germination and establishment (Copeland et al., 2021; Shackelford et al., 2021). In addition to low moisture availability, there are numerous abiotic and biotic barriers that must be overcome for plant community restoration of these landscapes to be successful (Shackelford et al., 2021). Key biotic barriers include invasion by introduced species, some of which are better able to capitalize on interannual variability in precipitation to outcompete native species (Garbowski et al., 2021; Ravi et al., 2022) and can have legacy effects that persist even following removal (Duell et al., 2023; Zhang et al., 2019). Abiotic barriers include extreme temperatures, the interaction of temperature and moisture influencing plant available water (Farrell et al., 2023; Shriver et al., 2018; Stapleton et al., 2024), and low soil fertility (Duell et al., 2023; Stapleton et al., 2024; Zhang et al., 2019). Early demographic processes including germination and emergence are particularly sensitive to challenging abiotic conditions. Seedling survival through these early stages largely explains eventual establishment rates and is a significant bottleneck in dryland restoration efforts (James et al., 2011; Larson et al., 2015).

Restoring ecosystem function under a changing climate has been identified as a priority by Tribal leadership in the Núchíú Ute Mountain Ute Tribe Climate Action Plan (2020), which integrates TEK with Western science. However, there is limited information on strategies specifically effective on Ute Mountain Ute Tribal lands, so research is needed to test novel strategies designed to overcome local barriers to revegetation using a precision restoration approach (Copeland et al., 2021). Site specific challenges include a lack of desirable propagules, extreme environmental conditions including low and variable precipitation and high temperatures, and extreme introduced species dominance (Hulvey & Aigner, 2014). In 2021 a RestoreNet site was installed in the Mancos Canyon, RestoreNet is a large networked dryland restoration trial across the southwest that tests standardized and local questions codeveloped with the community (Farrell et al., 2023; Havrilla et al., 2020; Laushman et al., 2022). Following this installation, interest grew in testing even more site-specific, local material-focused, and culturally relevant restoration strategies. Co-creating knowledge needed to support restoration decision-making and practice for working-land managers

including ranchers, restoration practitioners, and community members from the Ute Mountain Ute Tribe in Southwestern Colorado was the underlying goal of this research.

We aimed to assess the effectiveness of climate-adaptive restoration treatments in overcoming barriers limiting ecosystem recovery and promoting healthy, resilient rangelands in the face of climate change. Restoration needs on Ute Mountain Ute Tribal lands include previously riparian areas that no longer have the abiotic conditions needed to support returning to a riparian state and an interest in active transformation to climate resilient upland plant communities. In response to the barriers present at the site, we conducted a field experiment to evaluate the effectiveness of place-based restoration treatments including targeted invasive species control with the goal of increasing SBR success co-developed with the Tribe (Hulvey & Aigner, 2014). Using a plot-based approach, we tested the effects of soil surface modifications aimed at improving microclimatic conditions (Kildisheva et al., 2016), invasive species management using herbicide, and an alternative seeding method on seedling emergence, establishment, and resulting community composition. We hypothesized:

(H1): Seeded species cover was expected to increase in actively seeded treatments due to propagule availability, and these increases will vary by treatment:

(H1a): We expected the highest seeded species emergence in the two soil surface modification treatments of coarse woody debris (CWD) and media luna rock structures, where increased soil moisture (Martyn et al., 2022) and cooler temperatures were expected to mitigate abiotic barriers (e.g., limited soil moisture, high surface temperature).

(H1b): Seed pellet treatments, an alternative seeding method, were expected to protect seeds from predation, desiccation, and harsh conditions addressing biotic and abiotic barriers to emergence (Gornish et al., 2019).

(H2): Herbicide application was expected to reduce the abundance of the main introduced species of concern, *Acroptilon repens* (Russian knapweed), thereby reducing competitive pressure and facilitating higher recruitment of seeded species.

(H3): We expected divergence in community composition between herbicide treated and untreated plots driven by reductions in *A. repens* and the resulting changes in competitive pressure. Additionally, we anticipated differences in composition between actively seeded and control plots driven by higher densities of desirable species in actively seeded plots due to propagule availability.

METHODS

Experimental design

We conducted a fully crossed restoration field experiment to evaluate the effects of place-based restoration treatments on vegetation in the Mancos Canyon near Towaoc, Colorado, from 2022-2024 in collaboration with the Ute Mountain Ute Tribe Environmental Programs Department. Using a plot-based approach we tested the effects of treatments designed to change the soil surface microclimate and an alternative seeding method to protect seeds from harsh environmental conditions paired with and without targeted weed management using an herbicide, on seedling density and community composition. Each plot measured 4 m^2 and was placed on level ground within a small, fenced restoration area. The exact experimental location is confidential to protect cultural resources.

Five treatments were tested (Fig. 1.1): (1) an unseeded control; (2) broadcast seeding (our business-as-usual treatment); (3) seed pellets; (4) broadcast seeding into media luna rock structures (Fig. 1.2a), and (5) broadcast seeding into coarse woody debris (CWD) (Fig. 1.2b). Treatment details are included below. We established four replicates of the five treatments, with and without herbicide application, resulting in 40 experimental plots. Plots were established in November 2022, and during plot establishment half of them were randomly selected and treated with Milestone™ (aminopyralid) herbicide. All plots were then seeded in March 2023 and subsequently monitored in May and September of 2023 and 2024, allowing us to observe vegetation responses over two growing seasons.

Figure 1.1: Experimental treatment design: unseeded control, broadcast (business as usual) seeding, broadcast seeding into coarse woody debris (CWD), broadcast seeding into media luna rock structures and seed pellets, each treatment has four replicates.

Study site

Our experimental site is a unique location on Ute Mountain Ute Tribal lands, along the Mancos River. Parts of the area contain legacy cottonwood galleries, but due to prolonged drought and upstream water diversion, the water table has dropped, limiting the recruitment of young riparian species (Ute Mountain Ute Tribe, 2020). This location is used for cultural harvest practices and is important to the local community. Our experimental location was selected after unsuccessful attempts to revegetate the roughly 0.4-hectare area with riparian seedlings in previous years, prompting recognition that an active transformation of this previously riparian area to a novel upland species community was likely needed to meet Tribal climate adaptation goals. Following *Tamarix sp.* (salt cedar) removal in 2021 and the installation of a livestock exclusion fence, the site quickly became dominated by *A. repens* (Russian knapweed), along with smaller populations of *Bromus tectorum* (cheatgrass) and *Cardaria draba* (whitetop). *A. repens* is a list B invasive species in Colorado due to its tendency to form dense monocultures: it reproduces by both seed and adventitious buds making it difficult to control (*Noxious Weed Species in Colorado*, n.d.). Additionally, allelopathic chemicals produced in the roots and leaves along with its

extensive root system that competes for water and nutrients allows populations of *A. repens* to exclude other species (Beck, 2025; Grant et al., 2003; Jacobs & Denny, 2006).

Seed mix

We designed a diverse seed mix of 19 native plant species, comprised of warm and cool season grasses, forbs, and shrubs (Appendix 1, Table 1). The mix was selected based on a seed mix designed by scientists and restoration practitioners engaged in the U.S. Geological Survey (USGS) RestoreNet project (Laushman et al., 2022) for the Colorado Plateau ecoregion and informed by additional input and species selection from the Tribal community including culturally important species. The seeding rates we used were the high end of the recommendations provided by seed suppliers. We then adjusted the seeding rate by Pure Live Seed (PLS) to ensure the high recommended seeding rate was fully comprised of viable seed applying a total of 14,254 PLS per square meter (Appendix 1, Table 1).

Herbicide treatment

Herbicide was applied roughly three months prior to seeding. Prior to herbicide application, we cleared all plots of vegetation and debris. A one-time herbicide treatment of Milestone™, with active ingredient aminopyralid, was applied to control our target species *A. repens* (Russian knapweed) on half of the experimental plots (n=20). The herbicide was applied at the recommended rate of 142.2 grams active ingredient per hectare (5 fluid ounces per acre) with a non-ionic surfactant at 0.25% of total volume (Corteva Agriscience, 2023). Milestone™ was applied on November 16, 2022, using an Ortho Manual Pump Backpack Sprayer fitted with a wide flat fan nozzle. The sprayer was calibrated to deliver 187 liters per hectare prior to use (Ozkan, 2018).

Seeding and surface modification treatments

Seeding and surface modification treatments were installed on March 16-17, 2023. We attempted to not disturb any vegetation that had emerged since clearing and applying herbicide to the plots the previous November. We implemented five seeding treatments: (1) an unseeded control, (2) broadcast

seeding, (3) seed pellets, (4) laying coarse woody debris (CWD) across the plot, and (5) media luna rock structures (Fig. 1.1). Broadcast seeding reflects a standard SBR approach in drylands and served as our business-as-usual treatment. Seeds were scattered across the designated plots by hand. Seed pellets are an alternative seeding method where seeds are encased in clay and amendments. Seed pellets were produced using a low-tech "Bicycle-Powered Seed Pelletizer" and followed the recommended ratio of 2 parts seed to 1-part tackifier/amendment (EZ Weed Free Straw) to 3 parts clay (Red Art Clay) (Gornish et al., 2018). The pellets produced using this method were variable in size and shape, ranging from 2 to 4 cm in size and roughly spherical or oblong in shape. We made the seed pellets two to three weeks in advance and allowed them to fully dry in ambient indoor conditions prior to being deployed. In the field, seed pellets were scattered across the plot by hand. Our CWD treatment utilized readily available on-site materials left over from cultural harvest practices. We collected already downed cottonwood branches, ranging in diameter from 2cm to 10cm, and laid it across relevant plots at a depth of roughly 20-25cm (Fig. 1.2a). Seed was then broadcast into the CWD plots. CWD was designed as a cross between mulch and creating artificial nurse plants to retain moisture and cool the soil surface through shading (Dhar et al., 2022; Neilly et al., 2025). Media lunas are half-moon shaped low-tech rock structures (Sponholtz & Anderson, 2010). We constructed media lunas to span the entire plot width and we oriented them to intercept, slow and spread sheet flows across the site particularly during large precipitation events. While the plots were roughly level, there was a slight 1% to 2% slope, to the whole site (Fig. 1.2b). The top of the rock structure was 1-3cm above ground level (Fig. 1.2b). Media lunas aim to increase soil moisture and create a favorable microsite between the rocks (Martyn et al., 2022; Norman et al., 2021). Seed was then broadcast over the whole plot.

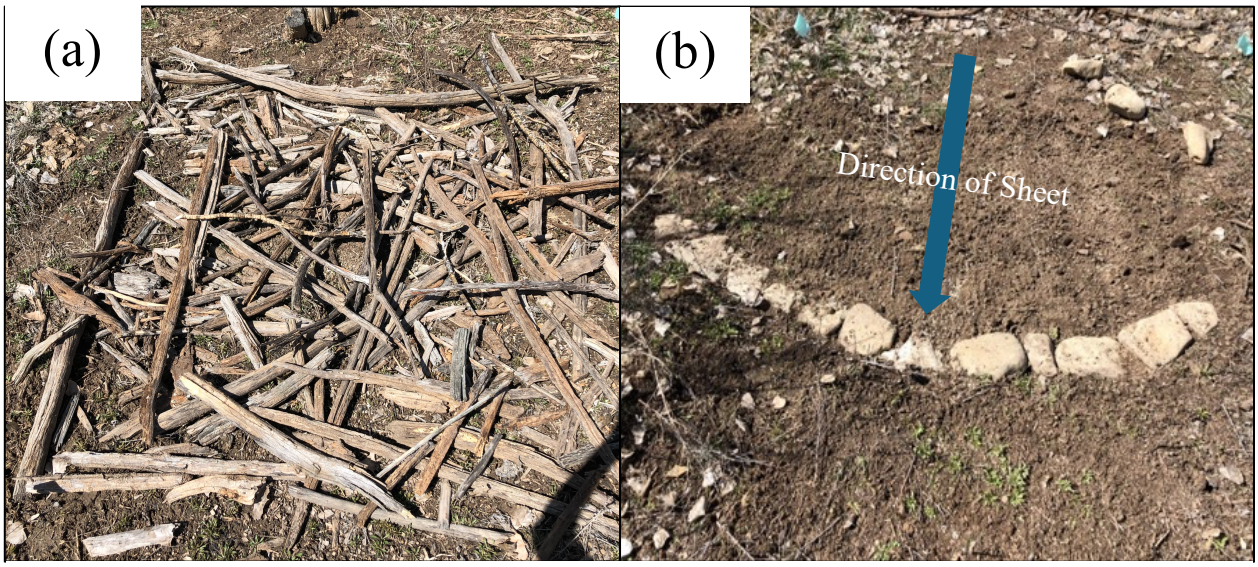

Figure 1.2: Photos showing **(a)** a coarse woody debris (CWD) treatment and **(b)** a recently installed media luna rock structure.

Soil temperature and moisture sensors

To understand how the soil surface treatments influenced microclimates, soil moisture and temperature sensors were installed at the center of each plot prior to seeding. Soil microclimate data was collected using custom built dataloggers based on an Adafruit Feather 328P microcontroller (3.3 V, 8MHz) paired with an Adafruit FeatherWing providing a battery backed real time clock and microSD card storage. Each sensor was powered using a 3.7V 10Ah lithium-ion battery. Sensors were housed in 177 ml storage jar (Nalgene), with sensor cables sealed using caulk to prevent moisture intrusion. Our dataloggers were programmed to read every 30 minutes

Soil temperature was measured using a DS18B20 digital temperature probe encased in a stainless-steel housing (HiLetgo). A SoilWatch10 soil moisture sensor (Pino-Tech) was used to measure relative water content. Both probes were placed at a depth of 5cm. The soil moisture readings were calibrated using minimum values measured in dry air and maximum values taken from fully submerged SoilWatch10 probes. These calibration values were used to rescale sensor output relative to a 0-100 soil moisture index. Due to difficult soil conditions and widespread sensor failure, soil microclimate data were only available

during the spring season of each year. Data collected between March 21 and May 15 were available for 2023 and 2024 and represent the sensor data used in subsequent analyses.

Data collection

We monitored plots bi-annually (in May and September) for two growing seasons (2023 and 2024). Within each plot, four subplots were established in standard locations across each plot each measuring 10 cm by 30 cm, to capture potential spatial variability within treatments (Appendix 1, Fig. 1). Plant density was recorded by counting each individual plant within the subplots. We also recorded the average height (mm) of each species present in the subplots. The presence of species seen within the full experimental plot but not captured within the subplots were noted. Additionally, visual estimates of percent canopy cover for seeded species, as well as native and unseeded forbs, shrubs, grasses were recorded.

Seed bank assay

In addition to our field experiment, we conducted a seed bank assay using soil samples from our experimental site collected during the dormant winter season on March 9, 2024, one year post seeding. Four 500 cm^3 soil seed bank samples were collected in a 100 cm area at a depth of 5 cm from each control and broadcast seeded plot that was untreated with herbicide, representing the natural seed bank and a seed bank with actively added propagules. We then randomly selected pairs of subsamples, homogenized them, and stored them at ambient conditions in paper bags to dry out. We used mesocosms at the Colorado State University Plant Growth Facility in Fort Collins, CO, USA to grow out our soil seed bank samples starting on June 24, 2024, and grew the seed bank out for 150 days. Our mesocosms consisted of 13.25-liter plastic tubs filled with field soil purchased locally, that was steam pasteurized to eliminate any viable seeds (Arancibia, 2020), as our growing medium. Soil seedbank samples were screened of large vegetative material and spread evenly across each mesocosm tub. Two mesocosms were seeded with the subsamples from each plot, one of the two mesocosms was randomly assigned to be treated with a different herbicide mixture than the pre-emergent aminopyralid used in the field to target *A. repens* to test if an herbicide mixture would effectively control of a greater array of introduced species present at the experimental site.

Selected mesocosms were sprayed with aminopyralid (Milestone) at a higher rate of 199.1 grams active ingredient per hectare (7 fluid ounces per acre) than we used at our field site (Corteva Agriscience, 2023), mixed with imazipic (Plateau) at a rate of 132.3 grams active ingredient per hectare (8 fluid ounces per acre) (BASF Corporation, 2023), with a non-ionic surfactant at 0.25% of total volume. The herbicide mix was applied using a Generation 4 Research Track Sprayer (DeVries Manufacturing, Hollandale, MN) at 2.65 km per hour and at a shelf height of 41 cm from the nozzle. The herbicide solution was sprayed onto lightly damp soil. Each mesocosm was divided in half, on one side individuals were counted and removed as soon as they could be identified with location marked to prevent counting resprouts, on the other side the community was allowed to develop and canopy cover of seeded, native and introduced species were recorded. Mesocosms were watered to field capacity every four days, and monitoring occurred weekly starting as soon as the first seedling could be identified.

Statistical analysis

All analyses were performed in R Statistical Software, version 4.5.2 (R Core Team, 2025). Prior to analysis, seedling density data collected at the species level from the field experiment was aggregated into three groups: seeded species, introduced species, and *A. repens* (Russian knapweed) reflecting the response variables of interest. Zeros were added as needed for plots where that group of species were not observed to reflect true absences. Unseeded native species were not analyzed because there were only two observations, reflecting the same individual across time. Due to limited emergence, plant density (seeded species, introduced species, and *A. repens*) was summed across subplots prior to analysis.

We initially intended to model each of our response variables of interest using generalized linear mixed effects models (GLMMs). However, seeded species density was low, with 82% of observations equal to zero, and several treatment–monitoring event combinations had no seeded species emergence (Appendix 1, Table 2). These groups contained only zero values and no within-group variation, leading to low power, model convergence failures and complete separation that precluded reliable model fitting. Consequently,

seeded species density was not modeled and we cannot infer differences; however important patterns still emerged which we present using descriptive statistics.

To model introduced species and *A. repens* (Russian knapweed) density, we used GLMMs with the glmmTMB package (Brooks et al., 2017). Since our density response variables were count data that exhibited overdispersion, we used a negative binomial error distribution with a log link function. Herbicide, monitoring event and treatment, along with all two-way interactions, were included as fixed effects for both response variables. To account for repeat measures, a unique identifier for each plot was included as a random effect. Post-hoc pairwise comparisons were conducted using the emmeans package (Lenth, 2024) with p-values adjusted using a false discovery rate (FDR) correction to control for multiple comparisons. A significance cutoff of a=0.05 was used throughout to balance sensitivity and control for Type I error.

To quantify plant community composition, we used permutational multivariate analysis of variance (PERMANOVA) using a Bray-Curtis dissimilarity matrix of vegetation in Fall 2024 (our last monitoring event) as the response variable, testing the effects of treatment and herbicide application. PERMANOVA tests were conducted using the vegan package (Oksanen et al., 2025), and pairwise comparisons were calculated using the pairwise.perm.manova() function in the RVAideMemoire package with a FDR adjustment for multiple comparisons (Herve, 2025).

To assess the effect of experimental treatments on the soil surface microclimate, we fit separate linear mixed effects models for daily mean soil temperature (°C) and volumetric soil moisture (%) using Gaussian error distributions with treatment, year and their interaction as fixed effects. A unique identifier for each plot and sampling date were included as random effects to account for repeat measures and shared day to day environmental variation.

RESULTS

Higher mean seeded species density (not significant) observed in moisture retention treatments

Because low and variable seeded species density precluded reliable statistical analysis, we report only observed qualitative patterns and make no inferences about pairwise differences among treatments. Visual inspection of seeded species density showed no consistent pattern associated with herbicide treatment, and substantial variability among treatments was observed (Appendix 1, Fig. 2). When averaged across herbicide treatment, some descriptive patterns (not significant) among treatments emerged (Fig. 1.3a). Across all four monitoring events, media lunas consistently had some seeded species recruitment. Higher mean recruitment in media luna treatments coincided with periods when precipitation in the months before monitoring was average or above average, including instances when the immediately preceding month had below-average precipitation. In 2024, seeded species were also consistently observed in CWD treatments. Seed pellets consistently had lower mean seeded species observed than in media lunas and, in 2024, also had lower density than CWD. Seeded species density across all treatments was lower in Fall 2023 following a period of lower-than-average precipitation and above-average temperatures (Fig. 1.3). In contrast, the highest mean seeded species density observed was in broadcast seeded plots in Fall 2024, following above-average summer precipitation in the months prior to monitoring (Fig. 1.3b); however, as this was the final monitoring event we could not assess subsequent seedling survival. Out of a total of 19 possible seeded species, 10 were observed at least once during the experiment (Appendix 1, Table 1). When seeded species were present, two species dominated 2m by 2m plot level presence/absence observations, *Linum lewisii* (blue flax) and *Krascheninnikovia lanata* (winterfat) with 32 and 28 total observations, respectively.

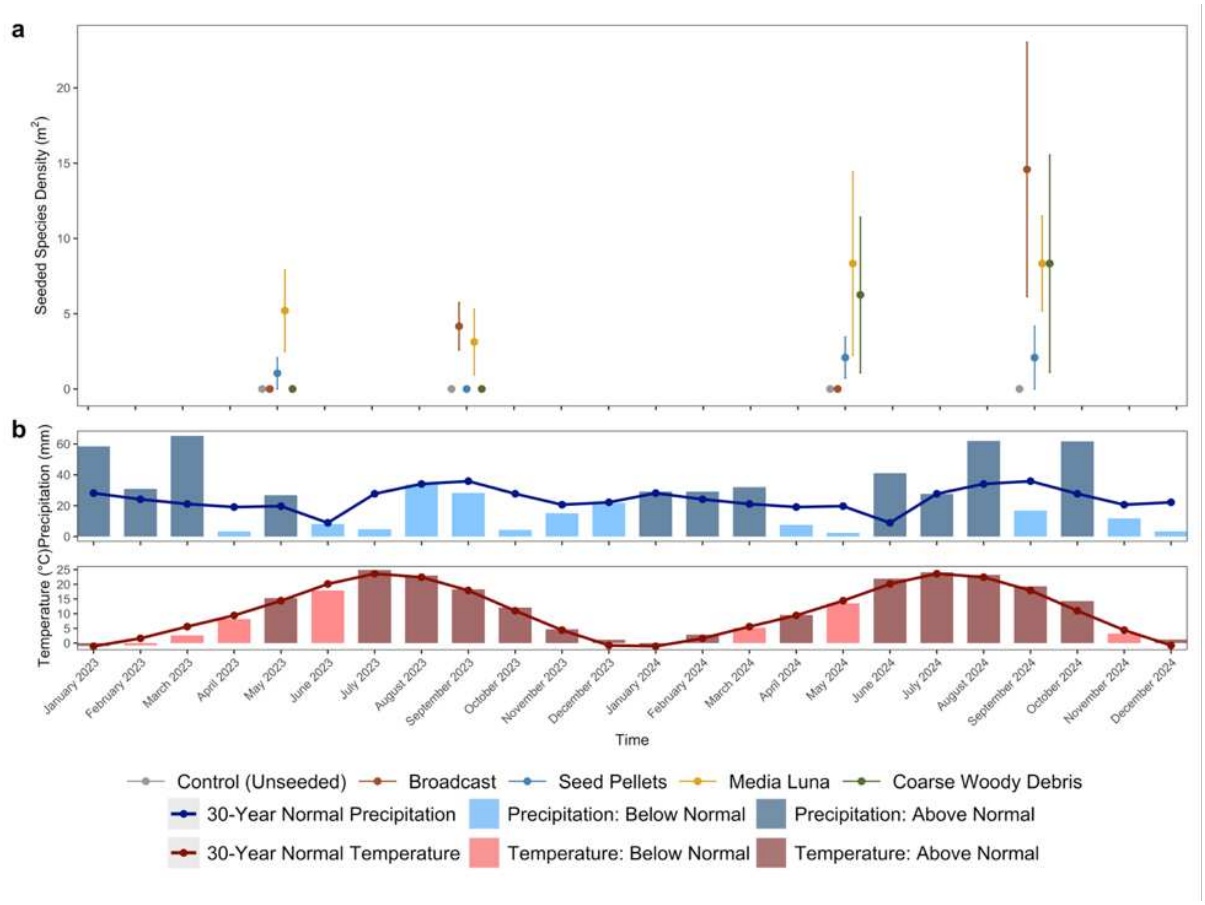

Figure 1.3: Plot showing **(a)** observed mean seeded species density (± standard error) by treatment over time, averaged across herbicide application, **(b)** monthly climate conditions for 2023–2024, where bars show observed precipitation and temperature; darker bars indicate above-average conditions and lighter bars indicate below-average conditions relative to the 30-year normals. Lines represent the 30-year climate normals (1991–2020). Climate data were obtained from PRISM.

Herbicide application reduced A. repens but did not reduce overall introduced species density

Overall, the density of introduced species was greater than any seeded species that emerged. As expected, herbicide treatment targeting *A. repens* (Russian knapweed) significantly reduced *A. repens* density during most monitoring periods (Fig. 1.4a; Appendix 1, Table 3). Herbicide treatment reduced *A. repens* density by 93% on average, holding all other factors constant ($p<0.001$; Appendix 1, Table 3). Some significant interactions between monitoring event and herbicide treatment indicated herbicide influence on *A. repens* density was modified by seasonal and annual variation, potentially reflecting climate variability (Appendix 1, Table 3). The clear exception to density differences occurred in Fall 2023, when the only significant difference in *A. repens* density was in our CWD treatment following below-average precipitation

and above-average temperatures. However, despite the lack of consistent density differences in Fall 2023, herbicide still influenced *A. repens.* Herbicide application significantly reduced average plant height, with mean height declining from 167 mm in untreated plots to 12 mm in treated plots (Welch's t-test, $p<0.001$) indicating suppression of plant height.

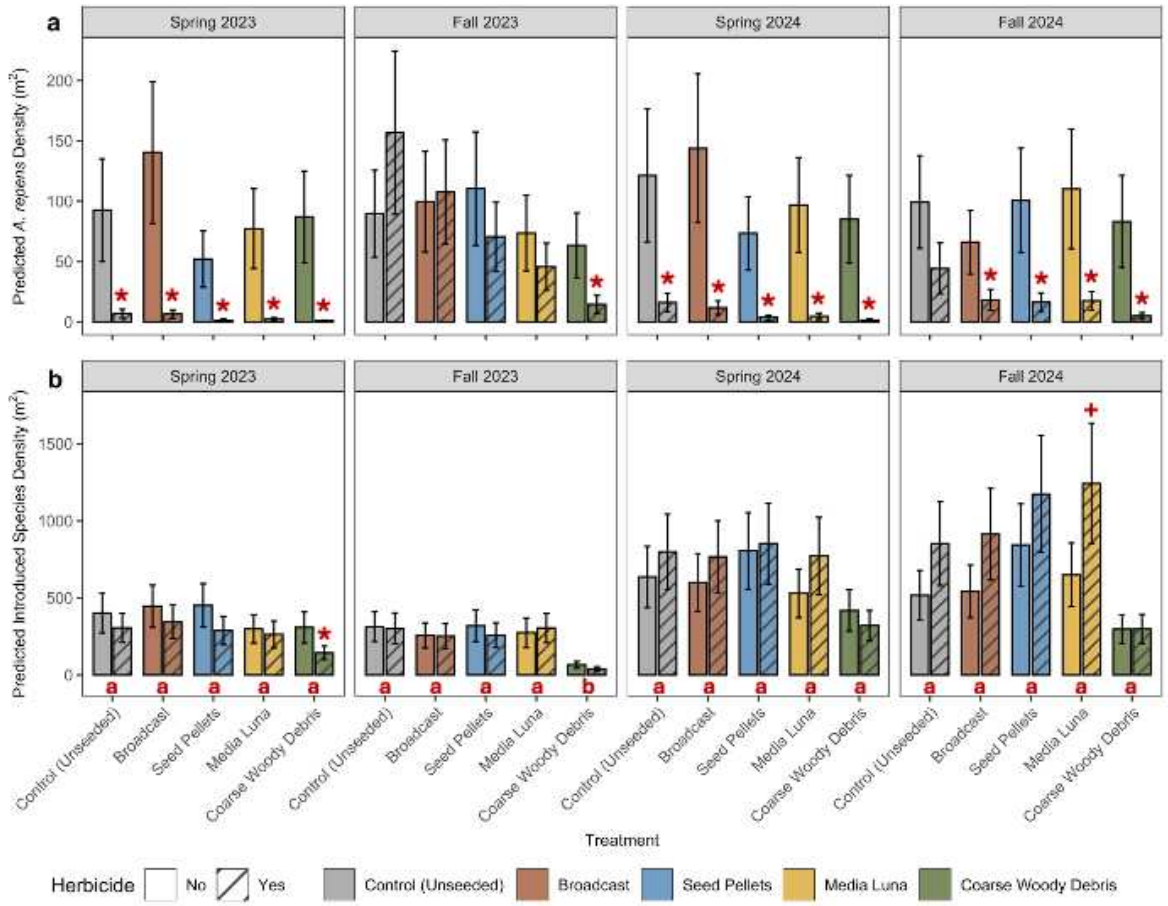

Figure 1.4: Predicted mean (± standard error) seedling density of **(a)** *A. repens* and **(b)** all introduced species (including *A. repens*) across treatments and monitoring events. Patterned bars indicate herbicide application. Within each monitoring event and treatment, asterisks (*) denote significant herbicide effects ($p<0.05$), and plus signs (+) indicate marginal herbicide effects ($p<0.1$) (Appendix 1, Tables 4 and 6). For **(b)** introduced species density, lowercase letters indicate treatments that differ significantly from the unseeded control within a monitoring event, averaged across herbicide treatment. Herbicide did not significantly influence total introduced species density in most treatments and years (Appendix 1, Table 5).

Despite reductions in *A. repens,* we largely did not observe significant changes in introduced species density, including *A. repens*, more broadly following herbicide treatment (Fig. 1.4b, Appendix 1, Table 5). We did not detect any significant main effect of herbicide, treatment or monitoring event on

introduced species density (Appendix 1, Table 6). While there was no significant main effect of CWD detected, there were differences when compared to other treatments. We observed a pattern of lower introduced density in CWD plots under both herbicide and untreated conditions, with significantly lower densities of introduced species detected in Fall 2023 ($p<0.001$; Fig. 1.4b; Appendix 1, Table 7)

No evidence of differences in community composition among actively seeded and control plots with and without herbicide two and a half years post herbicide application

Since we detected no significant differences in community composition between our experimental treatments (Appendix 1, Table 8), treatments were collapsed into two groups: actively seeded (broadcast, seed pellets, media lunas and CWD) and control. Using these simplified groups, we did not see evidence of our hypothesized divergence in community composition between herbicide treated and untreated plots in Fall 2024, two and a half years post herbicide treatment suggesting herbicide effectiveness may be declining as the soil residual decays (Fig. 1.5; Table 1.1). Similarly, there were no significant differences in plant community between our actively seeded treatments, where we hypothesized greater propagule availability would drive increases, and our control plots likely driven by low overall seeded species density.

Table 1.1: Pairwise PERMANOVA contrasts among seeding treatment (yes/no) and herbicide application (yes/no) groups. Values are FDR adjusted p-values; no contrasts are significant.

	No Herbicide Control	**No Herbicide Seeded**	**Herbicide Control**
No Herbicide Seeded	0.41	-	-
Herbicide Control	0.64	0.41	-
Herbicide Seeded	0.14	0.14	0.97

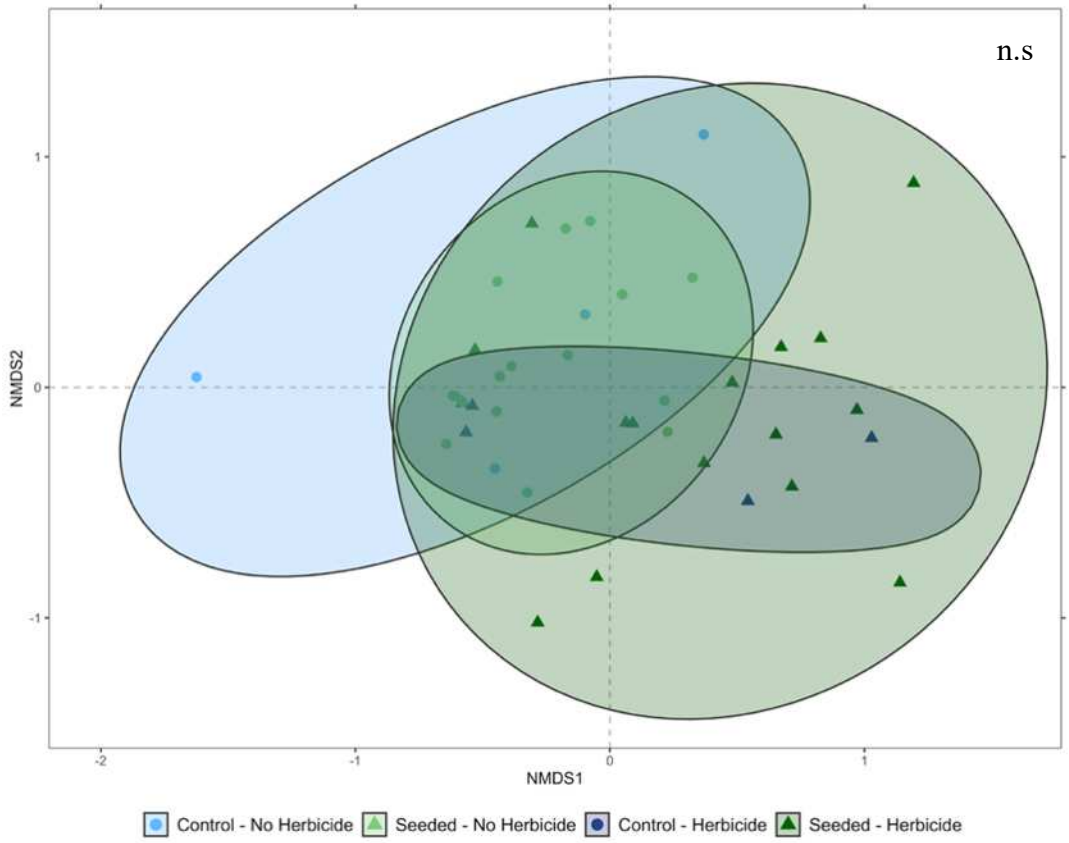

Figure 1.5: Non-metric multidimensional scaling (NMDS) ordination of plant community composition in September 2024 using Bray-Curtis dissimilarity. Points represent individual plots, shapes and colors indicate seeding treatment (active seeding or control) and herbicide application (no herbicide or herbicide). Ellipses visually represent groups based on seeding treatment and herbicide. PERMANOVA results show no significant differences in community composition between groups ($p>0.05$).

Experimental treatments modified soil microclimate during spring growing season

Soil temperature (Appendix 1, Table 9) and moisture (Appendix 1, Table 10) varied strongly by date and between years, with comparatively limited differences among experimental treatments during the spring growing season. As expected, soil temperature (°C) increased over the course of the spring growing season (Fig. 1.6a), while soil moisture (%) decreased (Fig. 1.6b). Our two treatments hypothesized to modify the soil surface microclimate, media lunas and CWD, had variable effects. In both years, media luna treated plots were significantly warmer than broadcast plots (2023: $p= 0.005$; 2024: $p<0.001$) while CWD plots were significantly cooler (2023: $p<0.001$; 2024: $p= 0.016$, Appendix 1, Table 11) during the spring. In

2023, media lunas averaged 5.5% higher soil moisture than broadcast seeded plots (p=0.083), while CWD plots averaged 5.7% lower average soil moisture (p=0.083), both differences are marginally significant after a false discovery rate (FDR) correction (Appendix 1, Table 12). In 2024, no treatments had soil moisture significantly different from broadcast plots during the spring (Fig. 1.6; Appendix 1, Table 12). However, sensors capture point level measurements and may not fully capture fine scale spatial heterogeneity associated with ground modification.

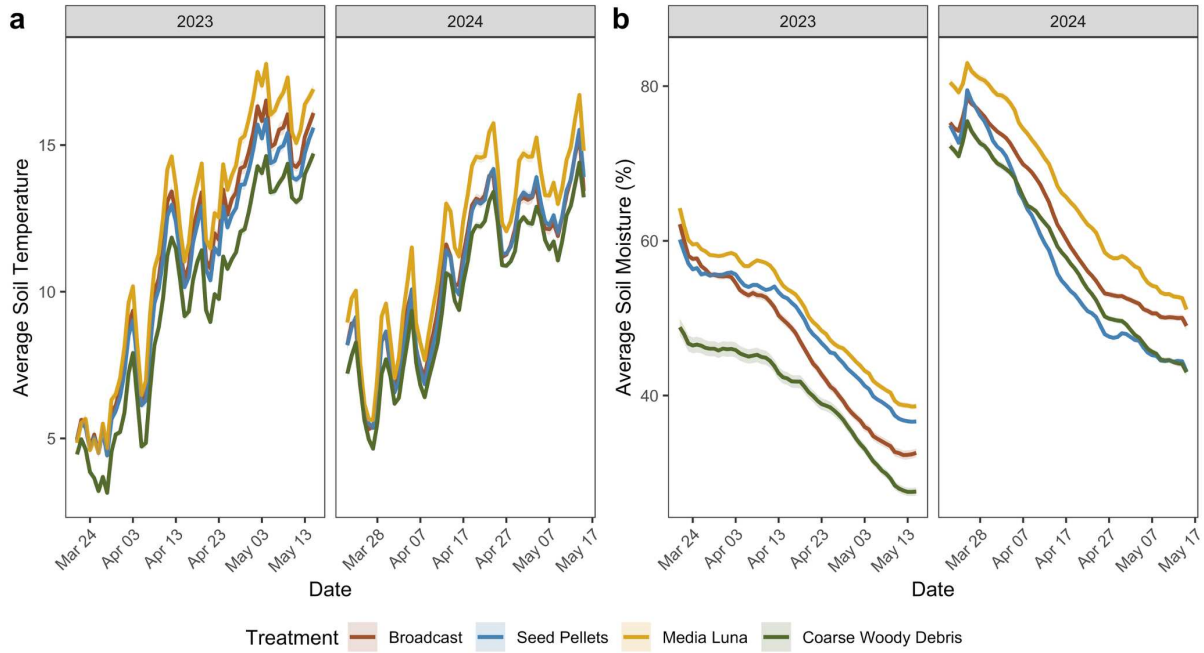

Figure 1.6: Mean **(a)** soil temperature (°C) and **(b)** soil moisture (%) measured during the spring season (between March 21 and May 15) in 2023 and 2024. Lines represent treatment-level means, with shading showing ± standard error. Control plots were removed due to sensor failures.

Limited recruitment of seeded species and minimal emergence under alternative herbicide mixture in seed bank assay

Our seed bank assay findings largely reflected our field experiment where introduced species dominated and only one seeded species, *Sporobolus cryptandrus* (sand dropseed), emerged from our untreated mesocosms (Fig. 1.7). Our herbicide application that included aminopyralid at a higher rate than used in the field mixed with imazipic suppressed emergence across all species under greenhouse conditions, with mean emergence near zero (Fig. 1.7).

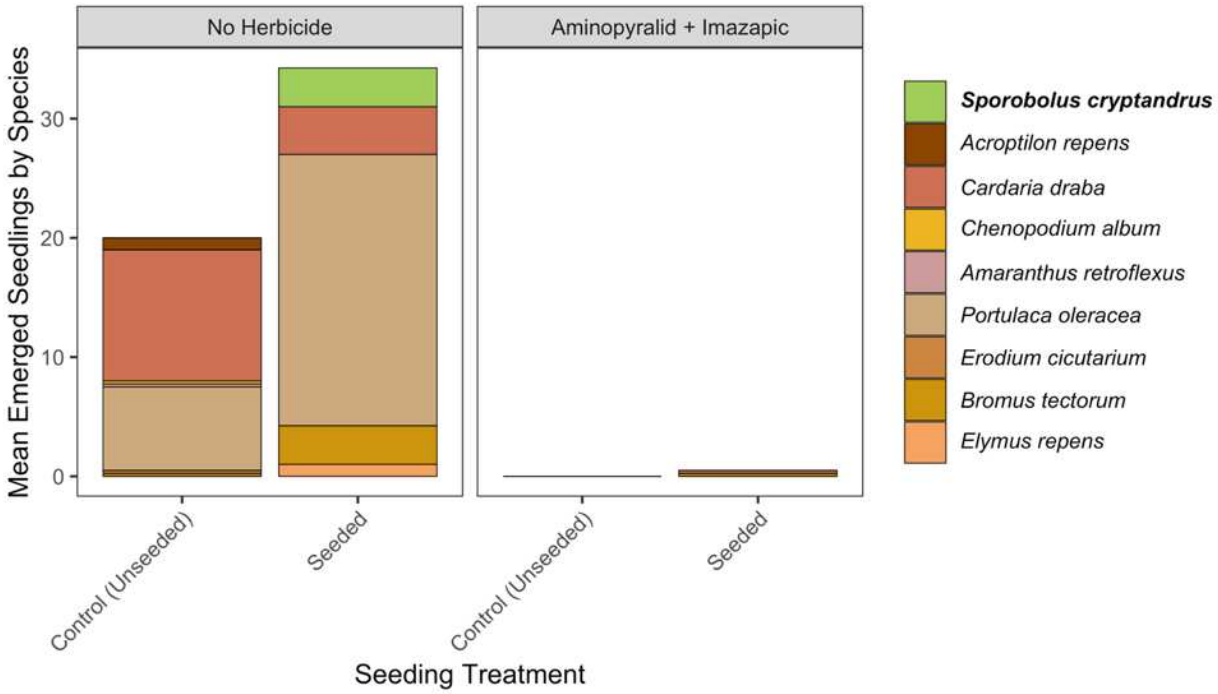

Figure 1.7: Mean number of seedlings by species emerged per half mesocosm (individual side where seedlings were removed after identification) from the seed bank assay. Control seed bank samples were collected from unseeded control plots while seeded samples were collected from broadcast seeded plots in Spring 2024 at our experimental site, all samples were collected from plots not treated with herbicide in Fall 2022. The left panel shows emergence with no herbicide application, while the right panel shows emergence after seed bank samples were treated with a tank mix of aminopyralid and imazapic.

DISCUSSION

The limited emergence and establishment of seeded species in this experiment (scaled mean density = 3.9 plants/m^2) is consistent with patterns reported in many dryland restoration efforts, where successful establishment following reseeding may be as low as 1% (Hulvey et al., 2017; James et al., 2013; Shackelford et al., 2021). Dryland systems, including our experimental site, face large abiotic and biotic barriers that must be addressed to successfully establish native seedlings (Hulvey & Aigner, 2014; Shackelford et al., 2021; Stapleton et al., 2024). A key goal of this restoration research was to inform a climate-adapted transition from riparian to a novel upland species assemblage as our experimental site has changed under drier and warmer conditions and the water table has dropped due to upstream diversion (Ute Mountain Ute Tribe, 2020). However, even these dryland adapted species struggled to emerge and establish

because of overwhelming ecological barriers. Hulvey and Aigner (2014) propose filter-based community assembly models as a framework to guide restoration interventions. They and others suggest that management actions that simultaneously manage dispersal, abiotic, and biotic filters are more likely to result in successful revegetation (Hulvey & Aigner, 2014; Rader et al., 2022; Shackelford et al., 2021; Stapleton et al., 2024).

Managing multiple ecological filters did not overcome establishment barriers

Our experimental design targeted multiple establishment filters simultaneously, including dispersal (active seeding), abiotic constraints (soil surface modification), and biotic interactions (livestock exclusion and targeted herbicide treatment), yet seeded species density remained limited under the environmental and competitive conditions present throughout our experiment and we were unable to reliably fit statistical models limiting our inference abilities. We actively seeded in all but our control plots to increase desirable propagule availability, recognizing that the naturally occurring seed bank was dominated by introduced species, as confirmed by our seed bank assay. We applied herbicide to target *A. repens* (Russian knapweed) to reduce competitive pressure, a key biotic barrier. Although *A. repens* declined following treatment, overall introduced species density was not reduced. We tried seed pellets to protect seeds from desiccation and granivory and to increase soil seed contact within the pellet (Gornish et al., 2019). We implemented soil surface modifications (media lunas and CWD) to alleviate harsh environmental abiotic conditions with the goal of increasing moisture availability (Kildisheva et al., 2016; Martyn et al., 2022) with CWD additionally reducing soil surface temperatures through shading (Dhar et al., 2022; Neilly et al., 2025). We observed a pattern of higher mean seeded species density in these moisture retention treatments but could not quantify differences. While treatments produced some measurable differences in the soil microclimate (Fig 1.6), these were detected using point-based sensors that may not have fully captured fine-scale heterogeneity within plots. Given the low density of desirable species, the magnitude of treatment-induced changes was likely insufficient to overcome the challenging climatic and competitive conditions, and more intensive restoration actions or better alignment with favorable climatic windows are likely needed.

Although restoration challenges can be site-specific, our results highlight the difficulty of overcoming multiple interacting filters in highly degraded dryland systems, particularly under a changing climate, emphasizing the need for continued research into novel approaches and better integration of weather forecasting (Copeland et al., 2021; Siegmund et al., 2026; Stapleton et al., 2024).

Limited seed bank constrained recovery

A key barrier in many dryland restoration contexts is a lack of a desirable seed bank (Kushbokov et al., 2025), making active seeding approaches common and necessary (Shackelford et al., 2021). Our seed bank assay indicated dominance by introduced species, suggesting that passive recovery to a native plant community at this site is likely impossible without intervention given the lack of desirable propagules and the vast reserves of introduced species. The very limited emergence of seeded species from seed bank samples (Fig. 1.7) in actively seeded plots suggests that the additional desirable propagules we added a year prior may no longer be viable, may have germinated into conditions unfavorable to survival, or may have been lost to granivory (Ooi, 2012; Pearson et al., 2019; Shriver et al., 2018). Further evidence of a limited desirable seed bank comes from the lack of significant differences in community composition between actively seeded and control plots during our last monitoring event in September 2024 (Fig. 1.5).

Secondary invasion and competitive pressure were key barriers

Seed bank dynamics help create the biotic dominant barrier at this site resulting from high competitive pressure exerted by introduced species including *A. repens* (Russian knapweed). While we saw significant reductions in our target species, *A. repens*, following herbicide application, reductions in *A. repens* did not correspond to our hypothesized increase in seeded species density. Introduced species and/or efforts to control them can have significant legacy effects even after removal including from changes in the microbial community, altered soil properties and herbicide residues with non-target effects (Duell et al., 2023; Gutiérrez et al., 2014; McManamen et al., 2018; Pearson et al., 2016). *A. repens* is a particularly problematic species due to its intense competitive ability, allelopathic properties and resulting legacy effects (Beck, 2025; Pearson et al., 2016). Native species responses to *A. repens* are likely species specific with

some species exhibiting greater sensitivity than others (Grant et al., 2003). Grant et al. (2003) showed that the presence of both *A. repens* roots and litter reduced survival of some native species including two used in our seed mix, *Bouteloua gracilis* (blue grama) and *S. cryptandrus* (sand dropseed), and may impact other species not included in that experiment.

We also observed a pattern consistent with secondary invasion, where the density of a target species, *A. repens*, declined but overall introduced density was unimpacted by our herbicide treatment (Pearson et al., 2016). Approaches to weed management often default to removing a novel disturbance thought to cause and/or allow for the persistence of the species of concern paired with direct control of a single target species (Brandt et al., 2023; Firn et al., 2010). Our approach followed this paradigm – fences were constructed to exclude cattle thought to be a primary disturbance, and an herbicide was selected to target the most dominant introduced species, *A. repens*. However, this approach, though logical and often the most feasible, can have unintended consequences including secondary invasion, where non-target invasive species increase following efforts to control the dominant or species of highest concern (Bennion et al., 2020; Firn et al., 2010; O'Loughlin & Green, 2017; Pearson et al., 2016). Where introduced species are present and problematic there are often numerous species with complex interactions, which influence their combined impacts including the potential for invaders to change the properties of the system (Brandt et al., 2023; O'Loughlin & Green, 2017; Pearson et al., 2016). In these multiple invader contexts, restoration interventions need to move beyond targeting single species of concern to more integrated, adaptive and iterative approaches to weed management to effectively reduce competition to levels where native species may be able to establish (Brandt et al., 2023; Pearson et al., 2016).

Climatic conditions influence seedling emergence and establishment

Within the restoration ecology field, there is increasing recognition that successful restoration in drylands often requires more than a single seeding intervention since abiotic conditions allowing for successful germination, emergence, and establishment are episodic (Copeland et al., 2025; Farrell et al., 2023; Shriver et al., 2018; Svejcar et al., 2023). Many plants in arid ecosystems require adequate soil

moisture paired with suitable temperatures to emerge, and need favorable conditions to persist long enough for seedlings to establish (James et al., 2011; Shriver et al., 2018). While our seeding timing during above average precipitation in Spring 2023 may have encouraged germination, the following summer months into fall were characterized by below average precipitation and above average temperatures (Fig. 1.3b), conditions that likely limited seedling survival, since environmental conditions have particularly strong effects during the vulnerable early establishment and growth phases (Copeland et al., 2025; Farrell et al., 2023; James et al., 2011; Shriver et al., 2018). Further, changes in precipitation timing and snow versus rain patterns can have implications for soil moisture (McNeeley, 2017; Shriver et al., 2018). More precipitation on Ute Mountain Ute lands is falling as rain rather than snow and this shift is likely impacting soil moisture conditions through potential lower infiltration from rain events than slowly melting snow and impacting germination, emergence, and establishment of species (Hammond et al., 2019; Ute Mountain Ute Tribe, 2020). Our experiment was limited to two growing seasons and in drylands with variable interannual conditions two years may be an insufficient amount of time to see responses to restoration interventions although we observed higher mean seeded species density (not significant) following periods of higher precipitation. In arid ecosystems, eight or more years is often required to achieve a relatively stable cover of restoration species (Gornish & dos Santos, 2016).

Soil microclimate modifications show context dependent effects

Despite limited recruitment of desirable species, we did observe patterns (not significant) in seeded species density between our experimental treatments, we observed higher mean seeded species density with soil surface modifications (Fig. 1.3). We also observed small differences in the soil microclimate due to these surface modifications (Fig. 1.6). Further exploration of these treatments, especially media luna rock structures and coarse woody debris (CWD) in areas with lower competitive pressure from introduced species may result in more pronounced effects. For example, Martyn et al. (2022) demonstrated increased total spring emergence of seedlings, both seeded and unseeded, within much larger media luna structures and higher species richness even under drought conditions in Southern Arizona suggesting that reducing

abiotic barriers even without active seeding can also have a positive effect (Rader et al., 2022). However, they note that they found no differences in established plant cover (Martyn et al., 2022). Additionally, media lunas and similar simple rock structures have been shown to increase soil moisture and improve infiltration in arid and semi-arid systems often a key limiting factor in plant recruitment (Martyn et al., 2022; Norman et al., 2021; Shriver et al., 2018). CWD as a restoration tool has been shown to increase vegetation cover, species richness, biomass production and reduce soil surface temperatures (Dhar et al., 2022; Mangani et al., 2022; Neilly et al., 2025). Importantly, techniques (e.g. size and density) of CWD installation vary across studies suggesting more research is needed to optimize this potential tool under variable environmental contexts. Contrary to most findings, we observed a marginal decrease in soil moisture in CWD plots in 2023 and no differences in 2024, potentially driven by the CWD acting as a barrier to moisture reaching the ground surface as has been shown in some limited contexts (Dhar et al., 2022; Neilly et al., 2025). Although, we observed a promising reduction of introduced species in CWD plots during portions of our experiment (Fig 1.4b), Nielly et al. (2025) note that the potential favorable microclimates created by CWD may also lead to unintended increases in introduced species. Notably, these studies were all conducted under lower introduced species pressure than observed at our site, suggesting that treatment effectiveness is context dependent. These approaches should continue to be explored to improve SBR outcomes in dryland systems with lower competitive pressure under variable climatic conditions.

Bet hedging strategies to improve SBR outcomes, opportunities for further research

Continued testing of novel restoration approaches emphasizing climate adaptation may improve revegetation outcomes in drylands, a pressing need given the global importance of these systems and widespread degradation (Shackelford et al., 2021; Stapleton et al., 2024). Tribal lands that are disproportionately impacted by climate change should continue to be prioritized for novel restoration approaches (Farrell et al., 2021). Continued research to design seed mixes targeting various biotic and abiotic factors would be valuable, including using functional trait-based approaches to select species most likely able to compete with introduced species (Funk et al., 2008; Hulvey & Aigner, 2014) and/or selecting

species with variable climate responses as a bet hedging strategy against poor conditions for germination and emergence (Copeland et al., 2025; Dalziell et al., 2022; Larson & Funk, 2016; Lewandrowski et al., 2021). Novel approaches, including seed enhancement technologies to overcome specific biotic and abiotic barriers, may result in increased recruitment of seeded species (Brown et al., 2021; Jarrar et al., 2023; Swartz et al., 2026, Chapter 2 of this dissertation). Seeding outcomes could also be improved by leveraging short to long term weather forecasting to time seeding efforts to match favorable conditions (Farrell et al., 2023; Siegmund et al., 2026). Experiments that seed multiple times, use forecasting of near-term weather to plan seeding efforts, employ long term post-seeding monitoring, and adaptive management approaches including potential reseeding efforts and continued invasive species management, will be essential given the interannual variability and episodic conditions that characterize drylands (Genova et al., 2025; Shriver et al., 2018; Svejcar et al., 2023). While seed based restoration of dryland systems is inherently challenging, even small gains in the establishment of desirable species can have large impacts (Davies et al., 2024; Madsen et al., 2016) emphasizing the importance of continued research on novel methods to improve revegetation outcomes under a changing climate.

CHAPTER 2: SEED PELLETS CONTAINING ACTIVATED CARBON INCREASE EMERGENCE OF NATIVE PLANT SPECIES USED IN DRYLAND RESTORATION FOLLOWING HERBICIDE APPLICATION[1]

SUMMARY

Introduction

Over half of dryland ecosystems worldwide are degraded, making restoration a priority. Most dryland restoration efforts use seed-based approaches, which often result in limited establishment of desirable species. The dual challenges of abiotic stressors and invasive species dominance are key barriers to native plant community reestablishment in degraded drylands. Innovative seeding approaches that help overcome these barriers are needed.

Objectives

We tested seed pellets, a seed enhancement technology, with varying compositions and activated carbon amendments, both for herbicide protection and in the absence of herbicide.

Methods

We conducted two greenhouse mesocosm experiments. The first experiment tested the protective effect of activated carbon in seed pellets, produced using a low-tech "Bicycle-Powered Seed Pelletizer," after aminopyralid herbicide (Milestone™) application on diverse seedling emergence. The second experiment examined how seed pellet composition, including variable clay ratios and activated carbon additions in the absence of herbicide, affected seedling recruitment.

[1] Swartz, E. H., Caldwell, B., & Havrilla, C. A. (2026). Seed pellets containing activated carbon increase emergence of native plant species used in dryland restoration following herbicide application. *Restoration Ecology*, e70316. https://doi.org/10.1111/rec.70316

Results

Seed pellets improved seedling emergence in both experiments, with 136% and 56% higher odds of emergence from seed pellets compared to broadcast seeding in the first and second experiments, respectively. Composition and activated carbon additions without herbicide treatment had limited effects. Following aminopyralid herbicide treatment, we found significantly higher emergence from seed pellets containing activated carbon.

Conclusions

Seed pellets with activated carbon may be an effective seeding method in dryland ecosystems where herbicide treatment and reseeding are needed. Varying clay content and activated carbon additions had limited impacts without herbicide treatment.

Implications for Practice

Low-tech seed pellets made using a "Bicycle-Powered Seed Pelletizer," should be considered in dryland restoration since pellets improved seedling emergence across all treatments compared to broadcast seeding. Pellet composition had limited effects on emergence under greenhouse conditions, though differences may be more pronounced under low-water field conditions. When invasive species management and seeding are needed simultaneously, seed pellets containing activated carbon provide herbicide protection and offer a low-tech restoration strategy using widely available materials. Without herbicide, activated carbon amendments did not improve emergence. Abiotic stressors and invasion are common challenges; hence, the need for revegetation extends beyond dryland systems. These approaches may be relevant in other degraded systems.

INTRODUCTION

Drylands, defined as hyper-arid, arid, and/or semiarid ecosystems, cover more than 40% of the Earth's terrestrial surface and support approximately 39% of the human population (Duniway et al., 2022; Hoover et al., 2020; Shackelford et al., 2021). The global extent of dryland ecosystems is expected to

increase because of climate change and aridification (Hoover et al., 2020). Drylands are susceptible to land degradation, biodiversity loss, reduced ecosystem functioning, and lower resilience as a result of land use change, overgrazing, and invasion by introduced species, among other anthropogenic drivers (Hoover et al., 2020; Shackelford et al., 2021). Already, over half of drylands are degraded, driven by global change and anthropogenic disturbances, making restoration a critical priority (Abhilash, 2021; Shackelford et al., 2021). With significant biotic and abiotic barriers to success, these landscapes are unlikely to recover without active intervention (Gann et al., 2019; Shackelford et al., 2021). Active restoration—defined as human intervention when the potential for natural recovery is low or absent (Gann et al., 2019)— is often necessary in these denuded drylands (Shackelford et al. 2021).

Active dryland restoration interventions often include herbicide treatments and/or seed-based restoration (SBR) approaches. These are the most practical methods given the large areas in need of treatment and cost limitations; however, most dryland SBR projects result in little or no establishment of desirable species (Copeland et al., 2021; Havrilla et al., 2020; Shackelford et al., 2021). SBR in drylands faces many major barriers to success, including abiotic limitations (e.g., water limitation, extreme heat) (Shackelford et al., 2021), seed predation (Gornish et al., 2019), invasive species prevalence (James et al., 2011; Shackelford et al., 2021) , and degraded soils (Larson et al., 2015). Precision restoration is a proposed framework that applies specific restoration techniques that address ecological barriers to recruitment, focused on the limitations of the desired restoration site (Copeland et al., 2021; Madsen et al., 2016). Innovative, science-based restoration strategies are needed to improve precision restoration tools and overcome ecological barriers to support positive SBR outcomes in drylands in the context of climate change (Svejcar et al., 2023).

Invasive species dominance is a common and difficult barrier to overcome when using SBR efforts in drylands. Invasive species can be problematic because they often modify soil nutrients, change competitive dynamics for limited resources including soil moisture, change the vegetation structure of a community, and some release allelopathic compounds, all resulting in reduced germination and

establishment of desirable species (Brown et al., 2021; Garbowski et al., 2021; Svejcar et al., 2022). Further, management or removal of these species can open the possibility of secondary invasion or management-mediated invasion, resulting in further challenges (O'Loughlin & Green, 2017; Pearson et al., 2016; Shackelford et al., 2021). Overcoming initial and secondary invasion often requires targeted weed treatments, often in the form of preemergent herbicides that provide effective control over a longer period, in combination with revegetation (Lazarus & Germino, 2022; Pearson et al., 2016). Preemergent herbicides, however, can also impact non-target species by damaging seeds and seedlings, making it difficult to establish desirable species before inevitable competition from secondary invasive species becomes an issue again (Davies et al., 2014; Madsen et al., 2014). Protecting desirable seeds from herbicide impacts allows restoration practitioners to establish native species in the window where herbicide is suppressing weeds effectively, reducing competition in the critical early establishment stage.

Various seed enhancement technologies, defined as techniques that protect seeds, allow for precision seeding and/or improve germination and establishment have been documented in dryland restoration projects (Brown et al., 2021). Examples of seed enhancement technologies include seed coating, priming, flash flaming to remove appendages, and seed agglomeration (Brown et al., 2021; Pedrini et al., 2020). However, many come with high costs and specialized equipment needs, making these techniques inaccessible to many land managers (Brown et al., 2021; Iftekhar et al., 2017). This work aims to identify relatively low-tech seed enhancement techniques using technology built with widely available materials and ingredients to improve restoration outcomes.

Seed pellets (also referred to as seed balls, seed bombs, seed pillows, and pods in the literature) are a type of low-tech seed enhancement technology. Seed pellets are an agglomeration of seed, clay, amendments, and water that aim to protect seeds, improve germination and establishment, allow for precision delivery of amendments, and ease of deployment across the landscape (Gatherum, 1951; Gornish et al., 2019; Madsen et al., 2016). Primary reasons for using seed pellets in dryland restoration are to protect seeds from granivory (Pearson et al., 2019), harsh conditions, and to prevent seed movement off the

restoration site until conditions are suitable for germination such as a large precipitation event (Gornish et al., 2019; Teichroew & Rew, 2024). While research into seed pellet technology is increasing, several critical knowledge gaps remain, including uncertainty in best practices for seed pellet composition such as determining the amount of clay used to bind the pellet together under site specific environmental conditions, considering appropriate amendments based on site characteristics and desired outcomes, and synthesis methods (e.g., making seed pellets by hand or using a "Bicycle-Powdered Seed Pelletizer" or other methods) (Berto et al., 2024; Gornish et al., 2018, 2019).

Activated carbon is one potential seed pellet amendment that could be beneficial for addressing multiple biotic and abiotic barriers to seed emergence. Activated carbon has been shown to be effective at neutralizing the impacts of various herbicides due to its large surface area and absorptive capacity (Davies et al., 2024) and can be used to protect desirable seeds, and may also influence emergence in the absence of herbicide (Clenet et al., 2019; Davies et al., 2017; Svejcar et al., 2022). Previous work (e.g., Clenet et al. 2019; Davies et al. 2017; Madsen et al. 2014) has shown that including activated carbon protected desirable seeds when used as a seed coating or in Herbicide Protection Pods (HPPs) (Davies et al., 2024). HPPs, a type of extruded seed pellet, as described by Madsen et al. (2014, 2016) are constructed using specialized equipment used in the restaurant industry for pasta making, resulting in uniform 8mm-thick, 16mm-long, and 16mm-wide pods containing seeds. These studies have demonstrated effectiveness when used with preemergent herbicides used to target exotic annual grass species (Davies et al., 2017; Madsen et al., 2014). Most studies to date use preemergent herbicides in contexts where annual grasses are the invasive species of concern and use relatively low diversity seed mixes for revegetation efforts ranging from a single grass species (e.g., Davies et al. 2017; Madsen et al. 2014), to more diverse seed mixes (Clenet et al., 2020). The diverse mixes are mostly grass dominated but also include at least one forb and/or shrub species (e.g. (Clenet et al., 2020; Davies, 2018; Munro et al., 2023; Svejcar et al., 2024a, 2024b). A significant benefit of using activated carbon to neutralize herbicide is it may allow for single-entry restoration approaches where seeding and invasive species control happen simultaneously rather than requiring a phased approach,

where herbicide is applied and seeding occurs months to years later, which is more resource intensive (Davies et al., 2017; Madsen et al., 2014; Sheley et al., 2012). Challenges in using activated carbon include determining the quantity of activated carbon needed to neutralize the herbicide utilized and understanding the germination responses of various species and functional groups to the inclusion of activated carbon both in combination with herbicide and in the absence of chemical weed management (Svejcar et al., 2022).

To address these knowledge gaps, we conducted two greenhouse experiments to test how seed pellet composition, including variable clay ratios and carbon additions, affects seedling recruitment and to explore the protective effect of activated carbon after Milestone™ (active ingredient: aminopyralid) herbicide treatment. We tested three main hypotheses: (H1) seed pellets increase seedling emergence relative to broadcast seeding because of increased water and nutrient holding capacity of the clay used in seed pellets; (H2) within seed pellet treatments, seedling recruitment varies depending on seed pellet composition (i.e., clay content, carbon additions) because of impacts on seed pellet physical characteristics, including rate of pellet disintegration and changes in nutrient dynamics; and (H3) under herbicide treatment, carbon addition will increase seedling emergence due to the ability of activated carbon to neutralize herbicide. While further field testing will be needed, the greenhouse setting allows for closer monitoring and proof of concept under a highly controlled environment.

METHODS

Experimental design

Two greenhouse experiments were conducted at the Plant Growth Facility at Colorado State University in Fort Collins, Colorado, USA, in the Spring-Summer of 2023. Both experiments used a mesocosm approach. Each mesocosm consisted of a 13.25-L plastic bin with drainage holes, lined with weed cloth to prevent spillage, and filled with 9 cm of play sand as the growing medium. Mesocosm placement on greenhouse benches was fully randomized.

Experiment 1: Activated Carbon × Herbicide

To test potential protective effects of activated carbon in seed pellets following herbicide treatment, we conducted a fully crossed experiment testing seedling emergence under two seeding methods (broadcast seeding or seed pellets), with and without activated carbon (+/- carbon), and with and without herbicide (+/- herbicide) (Fig. 2.1). This resulted in eight treatment combinations with four replicates of each, for a total of 32 experimental mesocosms.

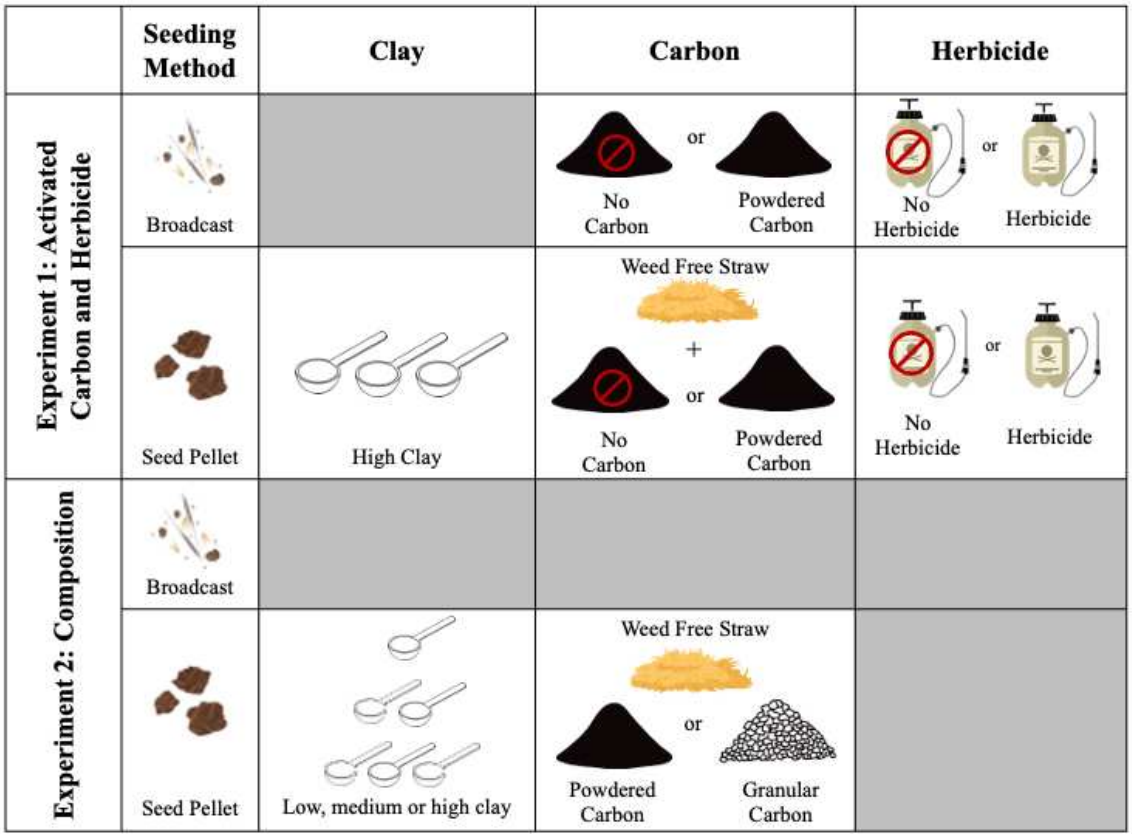

Figure 2.1: Diagram showing treatment structure for both experiments. In Experiment 1: Activated Carbon and Herbicide, seeding method (broadcast or seed pellet), activated carbon (no carbon or powdered carbon), and herbicide (no herbicide or herbicide) were fully crossed. In Experiment 2: Composition, broadcast seeding served as a control, while seed pellets with varying clay content (low, medium, or high) were crossed with activated carbon treatments (none, powdered carbon, or granular carbon).

Experiment 2: Seed pellet composition

Separately, to test the effect of seed pellet composition and activated carbon amendments on seedling emergence, we conducted a partially crossed experiment to test seedling emergence under four seeding methods: broadcast seeding and seed pellets with low, medium, or high clay ratios. The seed pellet treatments were further crossed with three activated carbon treatments—no carbon (where straw was used as the amendment), powdered activated carbon, and granular activated carbon. This resulted in 10 treatment combinations, each replicated four times, for a total of 40 mesocosm units (Fig. 2.1).

Seed mix

All mesocosms were seeded with a seed mix consisting of species native to and commonly used in dryland restoration projects in the Colorado Plateau Ecoregion and both include a mixture of warm- and cool-season species (Laushman et al., 2022). The seed mix varied by experiment. In both experiments, five seeds of each species were used per mesocosm. Seeds were sourced primarily from Southwest Seed Inc. (www.southwestseed.com) with three species from Granite Seed (https://nativeseedgroup.com). Both companies provided germination and purity information. For Experiment 1 (Activated Carbon × Herbicide), the functionally diverse seed mix consisted of 19 species (Appendix 2, Table 1): eight forbs, eight grasses, and three shrubs. For Experiment 2 (Seed pellet composition) (Appendix 2, Table 2), we used a 12 species seed mix including four forb species, seven grasses, and one subshrub species.

Seed pellet treatments

Seed pellets were created using a custom-made, tabletop seed pellet hand crank (Appendix 2, Fig 1), a modified tabletop version of a "Bicycle-Powdered Seed Pelletizer" (Gornish et al. 2018). Using this method, the resulting seed pellets were heterogeneous and less compacted than if made by hand. The recipes used for seed pellets were modified from the "A Bicycle-Powdered Seed Pelletizer for Use in Gardening and Restoration" guide (Gornish et al., 2018). The hand crank seed pellets ranged from 1 cm to 4 cm and were roughly spherical or oblong. Seed pellets are generally made from seed, clay, and amendment. In Experiment 1 (Activated Carbon × Herbicide), activated carbon was added in addition to the seed, clay, and

amendment (straw). In Experiment 2 (Composition), activated carbon was used as the amendment, and the amount of amendment was manipulated to change the clay-to-amendment ratio. All recipes are included in Appendix 1, Table 3.

Herbicide treatment

In Experiment 1 (Activated Carbon × Herbicide), herbicide treatments were applied to designated mesocosms to assess the impacts of herbicide on both seeding methods (broadcast and seed pellets) which were fully crossed with activated carbon additions. Milestone™, a Corteva Agriscience product with active ingredient aminopyralid, was selected based on site conditions at a related field experiment where a similar native seed mix was deployed and *Acroptilon repens* (Russian knapweed) is the dominant invasive species of concern. Milestone™ acts as both a pre- and post-emergent broadleaf selective herbicide and is advertised to provide season-long residual control (Corteva Agriscience, 2023). Milestone™ herbicide was applied at the recommended rate of 142.2 g active ingredient per hectare (5 fluid ounces per acre) with a non-ionic surfactant at 0.25% of total volume (Corteva Agriscience, 2023). Milestone™ was applied using an HDX multiuse pump sprayer fitted with the standard included cone spray nozzle and calibrated to deliver 25 gal/acre. Calibration accuracy was verified prior to application by collecting spray output over a defined area in three replicate trials and adjusting walking speed (using a metronome) to maintain the target delivery rate (Ozkan, 2018). Groups of five mesocosms were sprayed at a time, and the sprayer was repressurized between groups. Herbicide was applied to designated mesocosms 25 days prior to seeding. The average soil half-life for Milestone™ is 103 days, so this lag time allowed its concentration to decrease to approximately 85% of the initial application strength (Aminopyralid: Roadside Vegetation Management Herbicide Fact Sheet, 2017). Herbicide treatment was not a component of the composition study (Experiment 2).

Activated carbon treatments

Activated carbon treatments were included in both experiments. In Experiment 1 (Activated Carbon × Herbicide), powdered Nuchar SA-20 (Nuchar AG, MWV, Richmond, VA) activated carbon was included in the designated treatments at a rate of 10 times the average seed weight, selected based on previous work

(e.g., Brown et al., 2021; Clenet et al., 2019; Davies et al., 2017; Madsen et al., 2014; Munro et al., 2023). Powdered activated carbon was either broadcast onto the substrate or incorporated as an additional ingredient to the base pellet recipe including seed, clay and amendment (weed free straw) depending on seeding method treatment. The activated carbon is a very fine material, and when broadcast onto the soil surface, much of it aerosolized during the initial watering, so how much remained in the substrate is uncertain.

For Experiment 2 (Composition), activated carbon was included as the amendment component in the seed pellets assigned to carbon treatments, using either powdered (Nuchar SA-20, Nuchar AG, MWV, Richmond, VA) or granular (Granular food-grade activated carbon, Lab Alley, Austin, TX) forms to explore how carbon treatments affected recruitment outcomes.

Watering protocol

Since precipitation and freeze-thaw cycles are likely main drivers of seed pellet disintegration under field conditions, our watering protocols mimicked rainfall (Davies et al. 2024). Our mesocosms did not experience freeze-thaw conditions, so pellet breakdown does not fully reflect common conditions experienced in the field. We used a custom-made watering device, which consisted of a sprinkler mounted on a frame with a flow regulator to maintain a consistent water application rate (Appendix 2, Fig. 2). The watering device calibration was checked biweekly to ensure consistency. For Experiment 1 (Activated Carbon × Herbicide), each mesocosm received 6 mm of water every two days for an average of 20 mm per week to ensure the bins dried out between watering events, although the level of drying varied based on ambient greenhouse conditions. In Experiment 2 (Composition), we used a larger, less frequent precipitation pulse approach, mimicking monsoonal patterns present in some drylands. Each mesocosm received 50 mm of water every four days.

Data collection

For both experiments, we monitored plant emergence for all plant species, which were then analyzed by functional group (i.e., grasses and forbs/shrubs). In Experiment 1 (Activated Carbon × Herbicide), we monitored every two days for a total of 30 sampling events. We began monitoring after the first seedling emergence. In Experiment 2 (Composition), we monitored twice weekly for a total of 11 sampling events. Monitoring began two days after seeding with the first seedling emergence.

Statistical analyses

All data analyses were conducted in R, version 4.3.0 (R Core Team, 2025). Since the response variables in both experiments are a proportion of emerged seedlings, a beta regression approach was used (Geissinger et al., 2022). Beta regression was chosen because it appropriately models proportional data bounded between 0 and 1 and accounts for non-normal residual structures common in such data (Geissinger et al., 2022). To test our hypotheses, we used the glmmTMB package (Brooks et al., 2017) to fit mixed-effects beta regression models with a logit link function. Seedling emergence (as a proportion) was the response variable in all models. To account for repeated measures and spatial variability, we included unique identifiers for each mesocosm and greenhouse bench location as random effects in all models. For all models, we conducted post hoc pairwise comparisons using the emmeans package (Lenth, 2024), applying a false discovery rate (FDR) adjustment to control for multiple comparisons. An alpha level of 0.05 was used throughout as the significance cutoff to balance the risk of type I error with statistical sensitivity.

To evaluate the effects of herbicide treatment, seeding method, activated carbon addition and functional group on seedling emergence in Experiment 1 (Activated Carbon × Herbicide), we utilized a single mixed-effect beta regression model with all treatment factors and their interactions. Herbicide treatment (presence/absence), seeding method (broadcast/seed pellet), activated carbon addition (presence/absence) and functional group (grass vs. forb/shrub) were included as fixed effects. The model

included the same random effects structure to account for repeat measures and spatial variability, as well as the same post hoc testing approach described above.

To compare seedling emergence proportion by seeding method in the composition experiment, we used seeding method (broadcast vs. seed pellets, averaged over all levels of clay-to-amendment ratios) as a fixed effect. The model included the same random effects structure to account for repeat measures and spatial variability, as well as the same post hoc testing approach described above. To test the effects of clay-to-amendment ratios and carbon additions on seedling emergence in seed pellet treatments, we used a mixed-effects beta regression model. Fixed effects included seeding method (seed pellets with low, medium, and high clay-to-amendment ratios) and carbon type (no carbon, powdered carbon, or granular carbon). The same random effects structure and post hoc testing methods were applied.

RESULTS

Experiment 1: Activated Carbon × Herbicide

Impact of herbicide on seedling emergence by functional group

Herbicide treatment (Milestone™) significantly reduced the odds of emergence by 57% across all functional groups compared to mesocosms not treated with herbicide ($p < 0.0001$; Fig. 2.2; Table 2.1). Herbicide treatment likely had a stronger suppressive effect on forb and shrub emergence due to its broadleaf selectivity; forbs and shrubs had 33% lower odds of emergence than grasses under herbicide treatment ($p=0.016$; Fig. 2.2; Table 2.1; Appendix 1, Table 4).

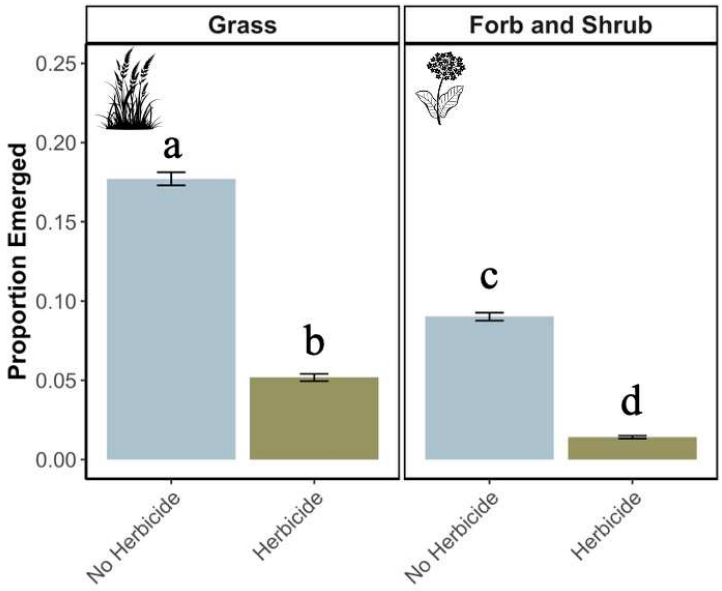

Figure 2.2: Mean proportion (± standard error) of seedlings emerged by functional group (grass vs. forb/shrub) both with and without herbicide treatment averaged across seeding method and carbon addition. Herbicide application significantly reduced emergence across both functional groups ($p < 0.0001$).

Impact of seeding method on seedling emergence

Seed pellet treatments resulted in 136% higher odds of seedling emergence compared to broadcast seeding holding herbicide treatment constant ($p=0.0003$; Fig. 2.3; Table 2.1), supporting our first hypothesis that seed pellets would result in greater recruitment than broadcast seeding. There was no significant difference in emergence between seed pellet and broadcast seeding under herbicide treatment (Fig. 2.3; Appendix 2, Table 5).

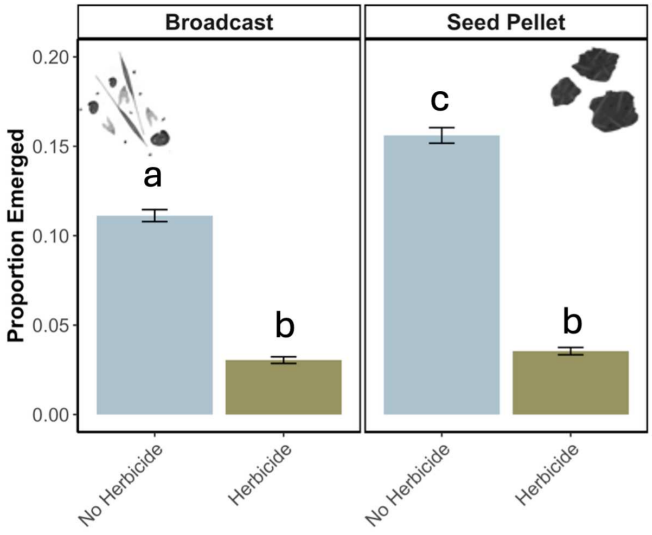

Figure 2.3: Mean proportion (± standard error) of seedlings emerged by seeding method (broadcast vs. seed pellet) with and without herbicide treatment averaged across carbon addition and functional group. Herbicide application significantly reduced emergence across both seeding methods ($p < 0.0001$). Seed pellets had significantly higher emergence than broadcast seeding in the absence of herbicide treatment ($p=0.0003$), but there was no significant difference in emergence between seed pellets and broadcast seeding under herbicide treatment.

Effects of herbicide, carbon, seed pellets, and their interactions on seedling emergence

We found significant interactive effects of seeding method, herbicide treatment, and carbon addition, indicating that the treatment factors do not interact in predictable ways, but outcomes depend on the treatment components interacting in complex ways. There was a significant interaction among herbicide, seeding method, and carbon addition, showing a strong positive effect of seed pellets containing activated carbon on seedling emergence under herbicide treatment ($p < 0.0001$; Fig. 2.4; Table 2.1; Appendix 2, Table 6). This result supports our third hypothesis that the inclusion of activated carbon in seed pellets would increase emergence because of the ability of activated carbon to neutralize herbicide residues.

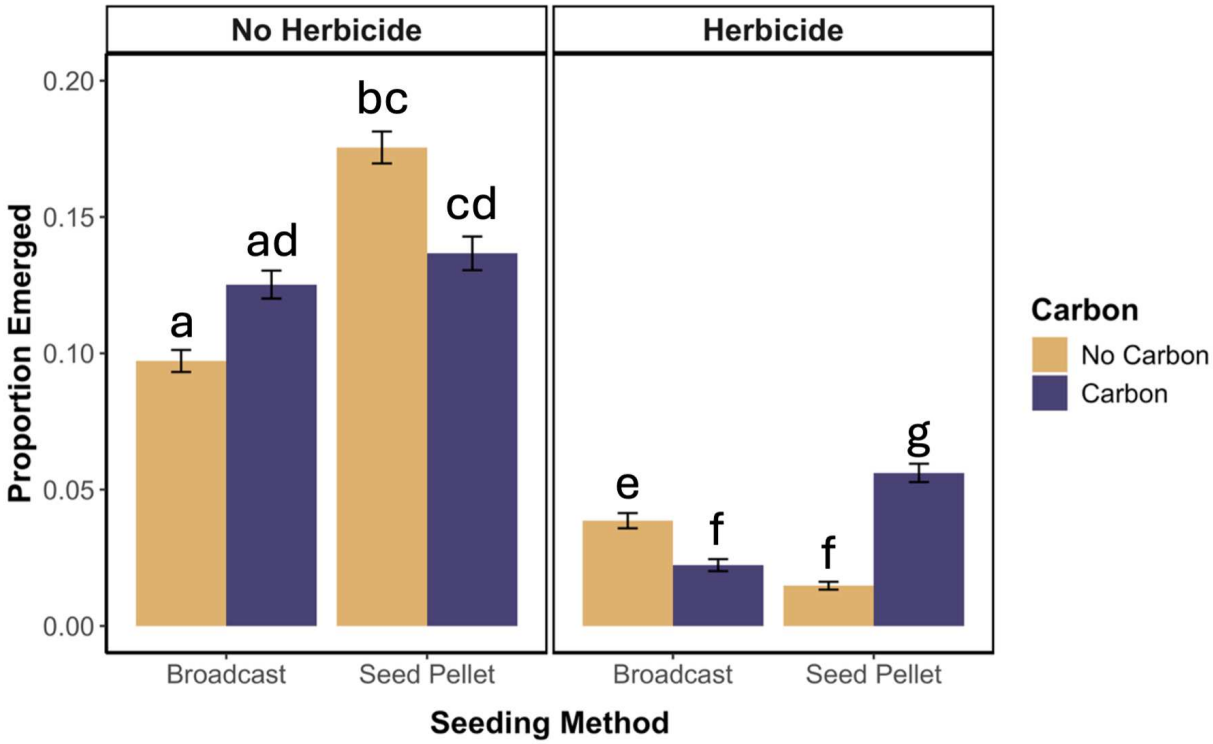

Figure 2.4: Mean proportion (± standard error) of seedlings emerged by herbicide treatment (presence/absence), compared by seeding method (broadcast vs. seed pellet) and carbon addition (presence/absence). Herbicide application significantly reduced emergence across both seeding methods ($p < 0.001$). Lowercase letters indicate significant differences ($p < 0.05$) using a mixed effects beta regression model.

Table 2.1: Results of a mixed-effects beta regression model evaluating the effects seeding method (broadcast vs. seed pellet), herbicide treatment (presence/absence), activated carbon additions (presence absence) and functional group (grass vs. forb/shrub) and their interactions on seedling emergence proportion. The model includes random effects to account for repeat measures and spatial variability in greenhouse bench location. Estimates are on the odds scale.

	Response Variable: Emergence Proportion			
Predictor	**Estimate (b)**	**Standard Error**	**z value**	**Pr(>|z|)**
Intercept	0.120	0.016	-15.55	< 0.0001
Herbicide	0.428	0.083	-4.35	< 0.0001
Seed Pellet	2.363	0.438	4.65	< 0.0001
Carbon	1.273	0.240	1.28	0.2000
Functional Group – Forb/Shrub	0.674	0.073	-3.66	0.0003
Herbicide:Seed Pellet	0.200	0.055	-5.85	< 0.0001
Herbicide:Carbon	0.470	0.131	-2.72	0.0066
Seed Pellet:Carbon	0.659	0.172	-1.60	0.1099
Herbicide:Functional Group – Forb/Shrub	0.669	0.112	-2.40	0.0164
Seed Pellet: Functional Group – Forb/Shrub	0.678	0.096	-2.73	0.0063
Carbon:Functional Group – Forb/Shrub	0.863	0.131	-0.97	0.3335
Herbicide:Seed Pellet:Carbon	11.113	4.304	6.22	< 0.0001
Herbicide: Seed Pellet:Functional Group – Forb/Shrub	2.552	0.595	4.02	< 0.0001
Herbicide: Carbon:Functional Group – Forb/Shrub	1.470	0.357	1.59	0.1126
Seed Pellet: Carbon:Functional Group – Forb/Shrub	0.986	0.201	-0.07	0.9436
Herbicide:Seed Pellet:Carbon:Functional Group-Forb/Shrub	0.270	0.089	-3.96	< 0.0001

Experiment 2: Composition

Seed pellet effects on emergence

Overall, seed pellets increased emergence relative to broadcast seeding. Seedling emergence in the seed pellet treatment had 56% higher odds compared to the broadcast treatments (p=0.072; Fig. 2.5; Table 2.2; Appendix 2, Table 7), providing additional marginal evidence that seed pellets increase seedling emergence, further confirming hypothesis one.

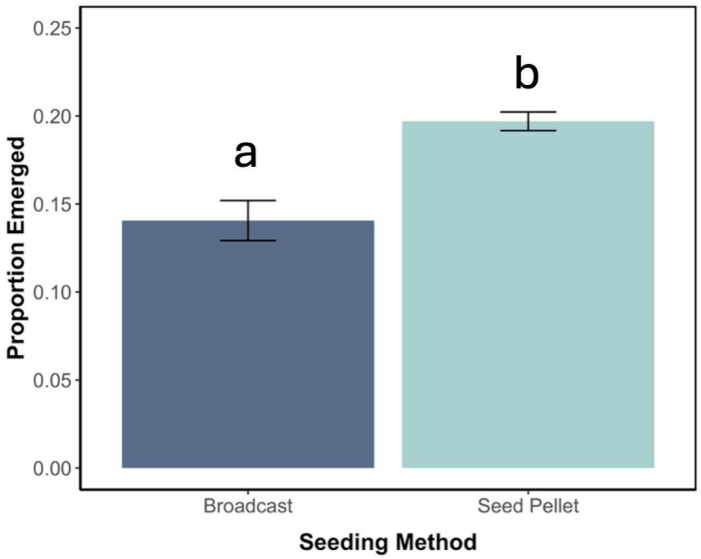

Figure 2.5: Mean proportion (± standard error) of seedlings emerged by seeding method (broadcast vs seed pellet, averaged across all clay to amendment ratios). Seedling emergence was marginally significantly higher in seed pellet treatments compared to broadcast seeding (p= 0.072).

Table 2.2: Results of a mixed effects beta regression model evaluating the effect of seeding method (broadcast vs. seed pellet, averaged across all clay to amendment ratios) on seeding emergence proportion. The model includes random effects to account for repeat measures and spatial variability in greenhouse bench location. Seed pellet treatment shows a marginally significant increase in seedling emergence proportion compared to broadcast seeding (p=0.072). Estimates are on the odds scale.

	Response Variable: Emergence Proportion			
Predictor	**Estimate (b)**	**Standard Error**	**z value**	**Pr(>|z|)**
Intercept (Broadcast)	0.13	0.032	-8.25	< 0.001
Seed Pellets	1.55	0.39	1.80	0.072

Interactive impacts of clay: amendment ratio and activated carbon amendments on seedling emergence

There was no effect of percent clay on seedling emergence from seed pellets (all p>0.05; Fig. 2.6; Table 2.3; Appendix 2, Table 8). However, seedling emergence did vary with carbon addition treatments, with the addition of powdered carbon resulting in approximately twice the odds of seedling emergence compared to those without powdered carbon, holding all other factors constant (p=0.015; Fig. 2.6; Table 2.3). There was also a weak interaction between seed pellet clay content and carbon addition type: powdered carbon as an amendment and medium clay to amendment ratio seed pellets (p=0.083; Fig. 2.6; Table 2.3), indicating the effect of powdered carbon on emergence may depend on the clay to amendment ratio in seed

pellets. These results provide limited support of our second hypothesis that emergence would vary based on composition and amendments; however, we did not observe the stronger effects we hypothesized.

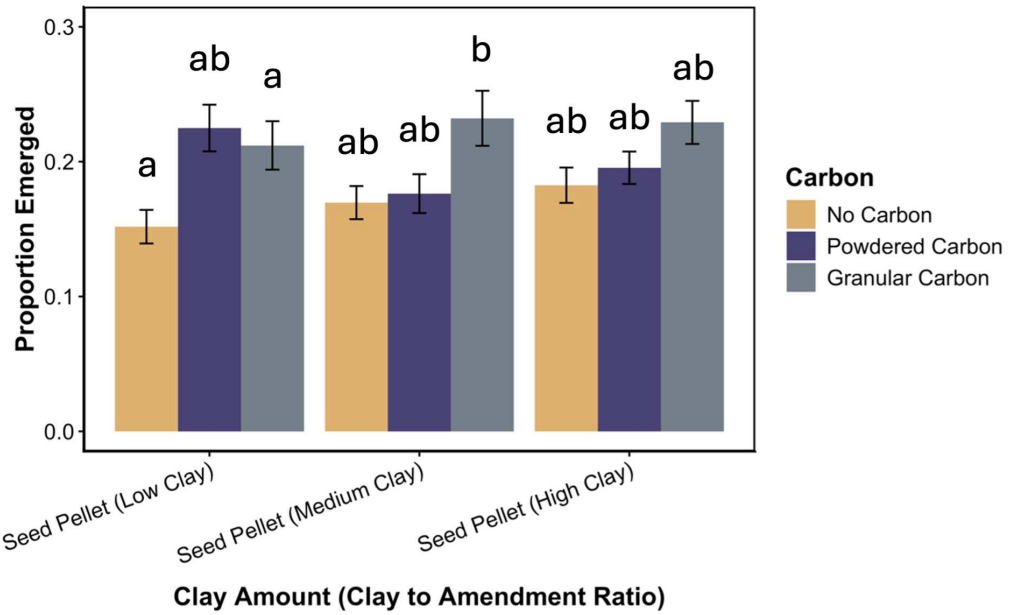

Figure 2.6: Mean proportion (± standard error) of seedlings emerged from seed pellets with variable clay to amendment ratios colored by carbon amendments (no carbon, powdered carbon, granular carbon). Lowercase letters indicate significant differences ($p < 0.05$) from a beta regression mixed effects model with seeding method (including clay to amendment ratio) and carbon amendment and their interaction as fixed effects.

Table 2.3: Results of a mixed-effects beta regression model evaluating the effects of clay-to-amendment ratios within seed pellets**,** activated carbon amendments**,** and their interaction on seedling emergence proportion. The model includes random effects to account for repeat measures and spatial variability in greenhouse bench location. Powdered carbon, when used as the amendment in the seed pellets, significantly increased seedling emergence (p=0.0145). A marginally significant interaction was observed between seed pellets with a medium clay to amendment ratio and powdered carbon (p=0.0833). Estimates are on the odds scale.

	Response Variable: Emergence Proportion			
Predictor	**Estimate (b)**	**Standard Error**	**z value**	**Pr(>|z|)**
Intercept	0.138	0.03	-9.15	< 0.0001
Seed Pellet – Medium Clay	1.312	0.38	0.94	0.3494
Seed Pellet – High Clay	1.341	0.39	1.02	0.3090
Carbon – Powder	2.018	0.58	2.45	0.0145
Carbon – Granular	1.018	0.30	0.06	0.9523
Seed Pellet – Medium Clay:Carbon - Powder	0.500	0.20	-1.73	0.0833
Seed Pellet – High Clay:Carbon - Powder	0.663	0.26	-1.03	0.3016
Seed Pellet – Medium Clay:Carbon - Granular	1.793	0.72	1.46	0.1449
Seed Pellet – High Clay:Carbon - Granular	1.425	0.56	0.90	0.3708

DISCUSSION

Seed-based restoration (SBR) in drylands faces many major biotic and abiotic barriers to success and often results in low establishment of desirable seeded species (Havrilla et al., 2020; Shackelford et al., 2021). To improve SBR outcomes in drylands, restoration techniques that can be precisely deployed to address ecological barriers to establishment that vary across space and time, both within and across sites, are needed (Copeland et al., 2021). Seed pellets are a seed enhancement technology that target several barriers to establishment, including protecting seeds from desiccation, granivory, and, with activated carbon additions, damage from herbicide used to control invasive species (Davies et al., 2024; Gornish et al., 2019).

Our findings suggest that seed pellets, and, specifically, seed pellets with activated carbon following herbicide treatment, have the potential to improve native seedling emergence by neutralizing herbicide residues, a significant bottleneck in dryland restoration supporting our first and third hypotheses (James et al., 2011; Larson et al., 2015; Shackelford et al., 2021). Seed pellets produced using mechanical synthesis methods (e.g., seed pellet bike or a tabletop hand crank version) (Gornish et al., 2018), are a relatively low-tech seed enhancement technology that can improve emergence in dryland ecosystems by increasing water-holding capacity, decreasing evaporative losses, lowering temperatures, and providing thermal stability to seeds (Gornish et al., 2019). Our findings contribute to understanding best practices for seed pellet synthesis.

Supporting some previous work, we found that seed pellets increased seedling establishment compared to broadcast seeding methods in both our composition and activated carbon and herbicide studies (Berto et al., 2024; Gornish et al., 2018; Teichroew & Rew, 2024). While seed pellets are often shown to increase seedling emergence, there are examples of cases where seed pellets have negative effects, inhibiting the emergence and establishment of all or some species tested (Baughman et al., 2021; Brown et al., 2023; Gornish et al., 2019). These declines in emergence from seed pellets may be partially attributable to differences in pellet size (Baughman et al., 2021), seed position within the pellet (Brown et al., 2023), and variable seed pellet recipes including amendment additions including activated carbon (Svejcar et al.,

2024b). Similarly to Teichroew & Rew (2024), we found minimal differences in emergence across clay-to-amendment ratios. This is contrary to our second hypothesis but may be due to the relatively high watering rates used in our study. Under more limited water conditions, composition and related seed pellet breakdown may have a larger impact on seedling emergence since breakdown with insufficient moisture may result in seed predation and movement off the restoration site, while seed pellets that fail to disintegrate under high moisture conditions may affect emergence. In the composition study (Experiment 2), where herbicide was not used, we found limited impacts of activated carbon additions. Given the expense of activated carbon (Davies et al., 2024; Madsen et al., 2016), we recommend only incorporating activated carbon into seed pellets when deployed in tandem with herbicide.

Activated carbon additions to seed pellets deployed shortly after herbicide treatment increased seedling emergence, suggesting this treatment provided some protection to the encased seeds supporting our third hypothesis. Our synthesis method uses readily available materials to build a simple "Bicycle-Powered Seed Pelletizer" (Gornish et al., 2018), and easy to source base ingredients for seed pellets (seed, clay and weed-free straw). Previous work using activated carbon to protect from herbicide residues has been in either extruded pellets or as a seed coating, both of which require specialized equipment and ingredients (e.g., Clenet et al., 2019; Davies et al., 2017; Munro et al., 2023). Much of the existing literature is focused on herbicides used to control invasive annual species (Davies et al., 2024), while this work uses a broadleaf selective herbicide, with a long soil half-life, indicating wider applications for using activated carbon to neutralize herbicides and protect seeds (Madsen et al., 2014; Munro et al., 2023; Svejcar et al., 2024a). This research supports the use of seed pellets as a potential restoration approach in drylands, and the use of activated carbon to protect seeds from recently applied herbicide residues. Using this technology for a single restoration intervention rather than a phased approach is a key benefit of seed pellets containing activated carbon (Davies et al., 2014; Sheley et al., 2001, 2012).

Seed pellets containing activated carbon show promise as a dryland restoration strategy, as they can protect seeds following herbicide application and increase seedling recruitment. While pelletizing seeds

adds additional effort and inputs compared to broadcast seeding, the resulting potential for small increases in establishment can have large impacts, particularly in areas where more traditional revegetation attempts have failed (Davies et al., 2024). Simultaneous control of invasive species and seeding allows for single entry restoration that requires fewer resources than a multi-entry approach (Davies et al., 2024; Sheley et al., 2001, 2012). Our approach using a "Bicycle-Powered Seed Pelletizer" offers a low-tech approach to making seed pellets containing activated carbon and requires less specialized equipment than approaches that utilize an extruder, making it more accessible than previous pelletizing and seed coating methods. In addition to using seed pellets with activated carbon, our findings provide support of the continued use of seed pellets in dryland restoration to improve the emergence of desirable seeds compared to broadcast seeding methods. We did not find significant differences in emergence when testing different seed pellet compositions, which did not support our second hypothesis that emergence would vary based on composition. We did find limited evidence of differences in emergence with carbon amendments in the absence of herbicide; however, these effects were not as strong as we expected. The ideal seed pellet recipe likely varies based on specific local abiotic conditions (e.g., water availability, seasonal precipitation patterns, freeze-thaw cycles) and if chemical weed management is required, so we recommend local testing prior to widespread implementation (Davies et al., 2024).

Limitations and future directions

Further research is needed to verify these effects in the field under variable conditions; however, this greenhouse study provides a proof of concept for using bicycle made seed pellets as a relatively low-tech approach to improve SBR in dryland systems after herbicide application. We concur with Davies et al. (2024) that future studies should explore these effects under field conditions and across a range of precipitation conditions. Low water conditions are especially critical to study since water is the key limiting resource in drylands and precipitation impacts seed pellet breakdown which is likely influenced by clay quantity. As herbicide residues bind to soil particles the strength and length of effective control varies by soil type (Smernik & Kookana, 2015; Stevenson, 1972), further investigation into how well and for how

long activated carbon protects seeds in seed pellets across soil types is also needed. While activated carbon has been shown to be effective at neutralizing at least five herbicides (Davies et al., 2024) and, in this study, a sixth broadleaf selective preemergent, this protective effect will need to be tested for additional herbicides using other methods of action. We also do not expect that all species or functional groups will respond similarly to being encased in a seed pellet due to differences in seed traits and emergence requirements, as has been shown in other research (Baughman et al., 2021; Brown et al., 2023; Lieurance et al., 2024). However, we did not have a large enough sample to be able to test the effects for individual species or functional groups in this study. Future research could further investigate species-level or trait responses to seed pellets and clay and activated carbon additions to seed pellets, building on existing research (e.g., Baughman et al. 2021; Brown et al. 2023; Lieurance et al. 2024), to help optimize restoration seed mixes and pellet synthesis. While much of the research on seed pelletizing, including herbicide protection using activated carbon, has been focused on dryland systems (Davies et al., 2024; Gornish et al., 2019), the need for innovative seeding approaches to improve SBR outcomes extends far beyond drylands. Single entry restoration approaches that allow for herbicide treatment and simultaneous reseeding efforts could be applicable in any system experiencing invasion and requiring revegetation. Further, pelletizing could be considered in any system where SBR approaches, including broadcast and drill seeding, have been unsuccessful in ameliorating specific abiotic and biotic barriers to emergence. Appropriate amendment inclusions in seed pellets will depend on site-specific concerns. These technologies could be applicable in grasslands, postindustrial sites, and other areas, so further research is needed to optimize seed pellet synthesis in other degraded systems.

CHAPTER 3: REDUCING COMPETITIVE PRESSURE FROM AN INTRODUCED PERENNIAL GRASS: INDAZIFLAM AS A POTENTIAL TOOL FOR NATIVE PLANT COMMUNITY RESTORATION

SUMMARY

Invasion by introduced species is a widespread challenge across drylands, resulting in significant impacts on biodiversity, ecosystem functioning, and fire regimes. Indaziflam (marketed as Rejuvra by Envu) is a broad spectrum, pre-emergent herbicide that has been shown to effectively control invasive annual grasses in rangelands without impacting established plants. Introduced perennial species are also a concern, and we investigated whether indaziflam may be a useful management tool for perennial species that depend on seed for reproduction, using *Arrhenatherum elatius* (tall oatgrass) invaded areas on the Colorado Front Range as a study system. We evaluated both target and nontarget effects on the plant community. We conducted a field experiment in Boulder County, Colorado supplemented by a seed bank assay. We compared plant species cover and community composition in plots treated with a one-time application of indaziflam versus untreated controls at two sites invaded by *A. elatius*: one post-agricultural site dominated by introduced species, and one foothills site with higher native plant cover, over a three-year period. We also grew out seed bank samples taken from treated and control plots roughly two and a half years post treatment to assess indaziflam treatment effects on seed germination. Our results show that indaziflam behaved differently across our two study sites, causing unexpected aboveground mortality at the post-agricultural site, emphasizing the need for more research on the influence of site history and soil characteristics on outcomes following indaziflam application. Where indaziflam behaved as expected, and did not impact established plants, we saw limited decreases in *A. elatius.* Indaziflam treatment likely prevented the recruitment of new individuals from seed as supported by our seed bank assay where we saw almost no recruitment of any species from seed, suggesting management of perennial species will likely need to be paired with control of established individuals. We

observed a decline in other problematic introduced species. In our seed bank assay, nearly all seed germination was suppressed, providing further evidence of a long biologically relevant soil residual that may render reseeding efforts ineffective. Where native species were present and established, we anecdotally observed higher mean native canopy cover in our treated plots compared to control plots over time, but these differences were not significant. Overall, our results suggest that indaziflam may be a tool to help control introduced perennial species when paired with other management techniques in some contexts.

INTRODUCTION

Invasion by introduced species is a widespread challenge across arid ecosystems in the western United States, resulting in significant direct and indirect impacts on biodiversity and ecosystem functioning (Gutiérrez et al., 2014; James et al., 2011; Shackelford et al., 2021). Invasive annual grasses including *Bromus tectorum* (cheatgrass), have invaded millions of acres, resulting in declines in native plant diversity, disruption of historic grazing regimes, and heightened risk of wildfire due to increased fine fuel loads (Fusco et al., 2022; Gutiérrez et al., 2014; Sebastian et al., 2017a). Managing invasive species is challenging and can lead to unintended consequences, including non-target impacts of herbicide application, secondary invasion, and limited recovery of native species following removal; therefore, expanding the range of management strategies is necessary (Donaldson & Germino, 2022; Kettenring & Adams, 2011; Pearson et al., 2016)

Indaziflam (currently marketed as Rejuvra by Envu) is a non-selective pre-emergent herbicide that was approved in 2020 for use on rangelands and natural areas to control invasive plant species (US EPA, 2020). Indaziflam is a group 29 herbicide that inhibits cellulose–biosynthesis; it works by limiting the production of cellulose, an essential structural component of plant cell walls (Brabham et al., 2014; *Rejuvra Pesticide Registration*, 2020; Sebastian et al., 2017a). Indaziflam binds tightly to soil organic matter particles and typically has little mobility in the soil profile, staying near the soil surface after application (Courkamp et al., 2022; Jeffries & Gannon, 2016). Under most conditions, due to its lack of mobility in the

soil, indaziflam selectively impacts plants forming roots from seed at or near the soil surface, while established species with deeper roots are typically unaffected (Sebastian et al., 2017a; Clark et al., 2019; Courkamp et al., 2022). Indaziflam has been shown to reduce or eliminate cover of target invasive annual grasses such as *B. tectorum* (Clark et al., 2019; Meyer-Morey et al., 2021; Sebastian et al., 2017a). Where established native species are present, following indaziflam treatment and the associated decline of the species targeted by indaziflam, native species released from competitive pressure have been shown in some studies to increase in cover, richness and biomass (Bradbury et al., 2024; Clark et al., 2019; Sebastian et al., 2025). Other studies document declines in in annual forb species richness that recruit from the seed bank each growing season with more limited impacts on perennial species although recruitment from seed was still impacted (Meyer-Morey et al., 2021).

While much less common than *B. tectorum, Arrhenatherum elatius* (tall oatgrass), a perennial cool-season bunchgrass that depends on seed for reproduction (Clark & Wilson, 1997; Pfitzenmeyer, 1962), is an introduced plant species found in grassland ecosystems across North America that can result in many similar negative effects on ecosystem functioning and diversity (MacMillan & Lee, 2025). Introduced in the early 1800s as a pasture grass and used for revegetation, *A. elatius* is now considered naturalized in much of the United States (*Tall Oatgrass*, n.d.; Tanphiphat & Appleby, 1990) and is threatening grassland ecosystems. Issues posed by *A. elatius* include threats to local biodiversity (Clark & Wilson, 1997) and ecosystem function (Clark & Wilson, 1997; Maret & Wilson, 2005), as well as a greater presence of fine fuels and increased fuel continuity, which can lead to increased fire risk. Given these characteristics and impacts, we used *A. elatius* invaded areas on the Colorado Front Range as a study system.

The City of Boulder Open Space and Mountain Parks (Boulder OSMP) has identified *A. elatius* as a key management concern since the invasion continues to grow and threaten the diverse grasslands that OSMP manages (Aulabaugh, 2025; *Tall Oatgrass Ecological Study*, 2018). It is found on OSMP properties on the plains and in the foothills near Boulder Colorado (*Tall Oatgrass Ecological Study*, 2018). OSMP staff expressed interest in testing the pre-emergent herbicide with the active ingredient indaziflam to control

A. elatius. However, the effectiveness of indaziflam at controlling *A. elatius* and similar perennial grass species that rely heavily on seed-based reproduction and its impacts on non-target species that co-occur with introduced grasses have not been evaluated.

To understand if indaziflam may be an effective management tool for perennial species that depend on seed for reproduction, we conducted a field-based experiment using *A. elatius* invaded systems on the Colorado Front Range as a study system supplemented by a greenhouse seed bank assay. We hypothesized:

(H1) Indaziflam treatment would reduce the canopy cover of *A. elatius* and other introduced species by inhibiting recruitment of new individuals. Further, we hypothesized that indaziflam treatment would not impact established individuals, since indaziflam acts selectively near the soil surface rather than throughout the root zone of mature plants.

(H2) Where native species were already well established, we hypothesized native species cover would increase because of a release from competition with controlled *A. elatius* and other introduced species, though we did not anticipate substantial recruitment from seed of any species following indaziflam treatment.

(H3) Given indaziflam's cellulose biosynthesis inhibition, soil profile selectivity, and long residual activity, we hypothesized much lower seedling emergence from the seed bank in treated plots than in control plots, using soil samples collected roughly two and a half years after herbicide application.

METHODS

Study species

A. elatius (tall oatgrass) is a cool season species that germinates before many native species, primarily grows in the spring, sets seed and then senesces during dry summer months, allowing it to outcompete many native species over time (Clark & Wilson, 1997; *Tall Oatgrass Ecological Study*, 2018). Seeds are produced starting the first year after emergence; the resulting seeds have no dormancy

characteristics and do not appear to form a persistent seed bank (Clark & Wilson, 1997; Pfitzenmeyer, 1962). There are two varieties of *A. elatius* found in the United States, there is a bulbous variety (*Arrhenatherum elatius subsp. bulbosum)* that depends on vegetative reproduction (Clark & Wilson, 1997; Pfitzenmeyer, 1962), but this variety has not been observed in Colorado (Ackerfield, 2022; SEINet – Arizona–New Mexico Chapter, n.d.). *Arrhenatherum elatius subsp. elatius*, the much more widespread non-bulbous variety (SEINet – Arizona–New Mexico Chapter, n.d.), is thought to depend almost exclusively on seed for reproduction (Clark & Wilson, 1997; Pfitzenmeyer, 1962). In Colorado, *A. elatius* is listed as a "watch list species" by the Colorado Department of Agriculture, indicating that more information is needed to assess the potential threat of these species and if further listing is warranted (*Noxious Weed Species in Colorado*, n.d.). Historically, *A. elatius* has been controlled through livestock grazing by Boulder OSMP (Aulabaugh, 2025; *Tall Oatgrass Ecological Study*, 2018). Significant expansions of *A. elatius* were observed when formerly grazed properties were purchased by the City of Boulder and grazing ceased. While grazing is used by OSMP to control *A. elatius* in some areas, this is not feasible everywhere that has been invaded (*Tall Oatgrass Ecological Study*, 2018) leading to a desire to test indaziflam as a potential management tool.

Field study

To test the impacts of indaziflam treatment on introduced and native plant species, we selected two sites for their contrasting characteristics (Table 3.1). Both sites are owned and managed by the City of Boulder, Open Space and Mountain Parks department (OSMP). The first site is a post-agricultural (Post-Ag) located on the plains and urban periphery of Boulder, Colorado, USA. *A. elatius* (tall oatgrass) is the dominant species at this site, with some other introduced species present including but not limited to *Convolvulus arvensis* (field bindweed) and *Rumex crispus* (curly dock). Very few native species are represented at the study site. This site is in the High Plains level three ecoregion, which is higher and drier than much of the Great Plains (Chapman et al., 2006; U.S. Environmental Protection Agency, 2013). The

potential natural vegetation in these systems is characterized by *Bouteloua* species (grama grasses) *and Buchloë dactyloides* (buffalo grass) (Chapman et al., 2006; U.S. Environmental Protection Agency, 2013).

The second site is in the foothills west of Boulder and is a much more diverse site with a well-established native plant community intermixed with introduced species including *A. elatius, Phleum pratense* (timothy), and *Bromus inermis* (smooth brome). The community is grass-dominated but no single species dominates, intermixed with the grasses are a diverse mix of forbs and sub-shrubs. This site borders the High Plains and Southern Rockies level three ecoregions as it transitions from grasslands to forested vegetation communities (Chapman et al., 2006).

Table 3.1: Basic site information and soil characteristics for each of the two study sites. Climate data was sourced from PRISM, and soil characteristics are from Web Soil Survey or from physical samples collected during the summer of 2025 and tested at the Colorado State University Soil, Water and Plant Testing Laboratory.

Site	**Post-Agricultural**		**Foothills**	
Coordinates	40.048368 ° N, 105.232059 ° W		39.967074 ° N, 105.277611° W	
Elevation (m)	1608		1867	
Mean Annual Temperature (°C) (1990-2020 30-year normal)	10.5		10	
Mean Annual Precipitation (mm) (1990-2020 30-year normal)	447		546	
Level Four Ecoregion	25l: Front Range Fans		Border between 25l: Front Range Fans and 21c: Crystalline Mid-Elevation Forests	
Soil Type (Web Soil Survey)	Valmont clay loam, 1 to 3 percent slopes		Boulder, bouldery-Sylvandale complex, 9 to 45 percent slopes	
Indaziflam Application Date (Rejuvra)	9/20/2022		8/1/2022	
Soil Characteristics	**Control**	**Indaziflam Treated**	**Control**	**Indaziflam Treated**
pH	7.7	7.8	5.5	5.5
Organic Matter (%)	5.26	5.16	13.68	11.25
Cation Exchange Capacity meq/100g	27.2	30.1	45.3	16.7
Sand (%)	55	50	54	51
Silt (%)	17	19	21	22
Clay (%)	28	31	26	27
Soil Class	Sandy Clay Loam	Sandy Clay Loam	Sandy Clay Loam	Sandy Clay Loam

Ten, 16 m^2 plots were established at each site during the summer of 2022; five plots per site were randomly selected and treated with herbicide, five were untreated controls. A rate of 350.3 g/hectare (5 oz/acre) of Rejuvra (with active ingredient indaziflam) was used; this is equivalent to 66.7 g of active ingredient/hectare. Herbicide was applied by pesticide applicator licensed OSMP staff to the designated plots using a calibrated battery-operated backpack sprayer (My4Sons M4) fitted with a four-boom sprayer wand (My4Sons Big Boomer) using flat fan nozzles. Sprayers were calibrated by collecting spray output over a known area with three replicate trials (Ozkan, 2018). Within each 16 m^2 plot, four 4 m^2 subplots were established to monitor different aspects of treatment impacts. Subplots were designated for microbial community sampling, vegetation monitoring, and destructive biomass harvest, and the final quadrant was reserved for any additional questions of interest that arose during the study period. The data used in this analysis is from the subplot designated for vegetation monitoring.

Annually in mid-July following treatment, each plot was monitored. We used the quadrat-point-intercept method for vegetation monitoring (Pellant et al., 2005), where up to four canopy layers were recorded at 100 points within a 1 m^2 quadrat. Visual *A. elatius* canopy cover across the entire plot was also recorded. Soil microbial samples were collected at the same time in a separate designated subplot. Physical soil samples were collected from each plot at a depth of 10 cm in 2025 and pooled by site and treatment (n=4).

Field experiment data analysis

All data analyses were conducted in R, version 5.2.0 (R Core Team, 2025). Canopy cover was rescaled to a zero-to-one proportion using our quadrat-point intercept data, which recorded up to four canopy layers per point. As such, generalized linear mixed effects models (GLMM) were used to analyze the canopy cover data using a beta regression since our response variables are all proportions constrained between zero and one. A beta regression approach was used since it accounts for the error structure associated with proportional data (Geissinger et al., 2022). We used three canopy cover proportion response variables aligned with our research questions: cover of *A. elatius* (tall oatgrass), cover of all introduced

species including *A. elatius*, and cover of native species. However, at the Post-Ag site native species were only observed in three observations out of a total of 30 plot and year combinations, so a site-specific model for the Foothills site was used and native species at the Post-Ag site were not modeled. Since the beta distribution excludes values exactly equal to zero and one, the small number of introduced species cover observations exactly equal to one (n= 2) were adjusted prior to fitting our models by subtracting 1e-6 from those observations. To test our hypotheses, we used the glmmTMB package (Brooks et al., 2017) to fit mixed-effects beta regression models with a logit link function for each response variable. We used the same random effects structure across all our models; a unique plot identifier was used to account for repeat measures over time, and an observer effect was used to account for variability between observers. We conducted post hoc pairwise comparisons using the emmeans package (Lenth, 2024), applying a false discovery rate (FDR) adjustment to control for multiple comparisons. An alpha level of 0.05 was used throughout as the significance cutoff. Treatment (+/- indaziflam), site (Foothills or Post-Ag; except in the Native Foothills only model) and year (2023, 2024, 2025) were used as fixed effects in all models. All interactions were initially included; however, non-significant interactions were removed to improve ease of interpretation (Appendix 3, Table 1).

To quantify community plant community composition, we used permutational multivariate analysis of variance (PERMANOVA) using a Bray-Curtis dissimilarity matrix of vegetation as the response variable, testing the effects of site, treatment, and year. PERMANOVA tests were conducted using the vegan package, with unique plot identifiers to constrain permutations to account for repeat measures (Oksanen et al., 2025). Pairwise comparisons were conducted using the pairwise.perm.manova() function in the RVAideMemoire package with a FDR adjustment for multiple comparisons (Herve, 2025).

Seed bank assay

In addition to the field-based experiment, we also conducted a seedbank assay roughly two and a half years post-treatment. On March 25, 2025, we collected soil samples during the dormant winter season from each of our treated and control plots. Four 500 cm^3 soil samples were collected in a 10cm-by-10cm

area at a depth of 5 cm in each plot. These four subsamples were then homogenized and stored in paper bags at ambient indoor conditions. The seedbank assay began on June 11, 2025, at the Colorado State University Plant Growth Facility in Fort Collins, CO, USA. Mesocosms were set up to grow out each homogenized plot sample, 13.25-liter plastic tubs were filled with 13 cm of field soil purchased locally. The field soil growing medium was autoclaved in small batches using a gravity cycle at 121 C (at 15 psig) for 60 minutes to eliminate any viable seeds (Steris, AMSCO 630LS, Model LS-136H). The seedbank soil samples collected from our field site were screened of any large vegetative material and spread in an even layer across the growing medium. Each mesocosm was watered every four days to field capacity. The top two inches of the mesocosms were typically dry prior to the next watering; however, this varied slightly with ambient greenhouse conditions. Monitoring occurred once a week after the first plants could be confidently identified. Any plants that could be identified were carefully removed by clipping the biomass off below the soil surface; these locations were marked and any resprouts were removed without recounting. The experiment ran for 15 weeks; any remaining plants that could not be identified were carefully transplanted to continue growing until identification was possible.

Seedbank assay data analysis

To test the effects of site and treatment on seedling emergence in our seed bank assay, we used generalized linear mixed effect models. Three response variables were used: total emergence, native emergence, and introduced emergence. Since our data were overdispersed, each response was modeled as a count using a negative binomial error distribution with a log link function. Models were fitted using the glmmTMB package (Brooks et al., 2017), with site (Foothills or Post-Ag) and Treatment (+/- indaziflam) as fixed effects, and greenhouse bench location included as a random effect to account for differences in ambient conditions. The emmeans package (Lenth, 2024) was used to conduct post-hoc pairwise comparisons with a false discovery rate (FDR) adjustment.

RESULTS

Community composition varied between sites and indaziflam treatment

Unsurprisingly, we found significant differences between the plant communities at our two sites given their selection for contrasting characteristics (p=0.001, Fig. 3.1). In addition to differences between sites, we also found that community composition varied between our control and indaziflam treated plots within sites, with significantly different composition at the Post-Ag site (p=0.006, Fig. 3.1). These differences are likely attributable to unexpected significant herbicide damage and mortality to established *A. elatius* individuals shortly following treatment since indaziflam typically does not impact established vegetation (Courkamp et al., 2022). While not as pronounced, we still found marginally significant differences between treated and control plots at the Foothills site (p=0.086, Fig. 3.1). At this location, we observed minimal herbicide injury to aboveground vegetation following indaziflam treatment following the expected behavior of indaziflam not impacting established individuals with deep root systems (Courkamp et al., 2022).

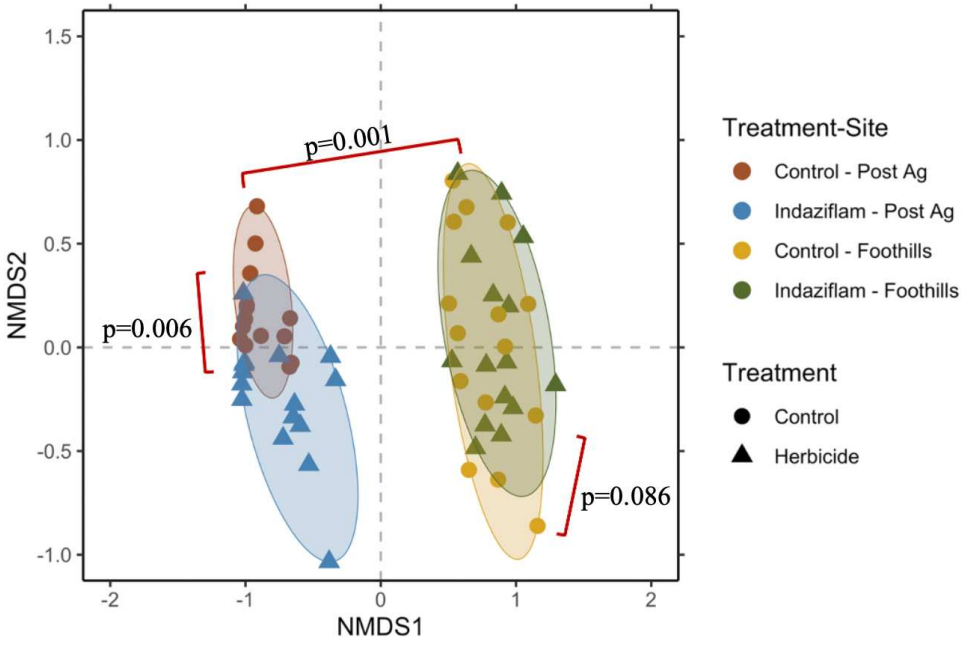

Figure 3.1: Non-metric multidimensional scaling (NMDS) ordination of plant community composition using Bray-Curtis dissimilarity. Points represent individual plots, colored by treatment and site. Ellipses indicate groups based on site and treatment. p-values shown reflect pairwise comparisons with an FDR correction.

A. elatius (tall oatgrass) declined at one site driven by unexpected aboveground mortality

A. elatius canopy cover varied among sites, years and indaziflam treatment, with treatment responses differing across sites and over time (Appendix 3, Table 2). At the Post-Ag site, indaziflam treatment significantly reduced the odds of *A. elatius* canopy cover for all three study years (Fig. 3.2a, Table 3.2). Predicted cover in treated plots was 29.2% lower than control plots in 2023; this effect was stronger in subsequent years, with 63.7% and 61.4% lower cover in 2024 and 2025, respectively (Fig. 3.2a, Table 3.2). The decline in *A. elatius* at the post agricultural site was driven in large part by unexpected aboveground damage and mortality of existing individuals shortly following indaziflam treatment in 2022. In contrast, at the Foothills site, where the cover of *A. elatius* was lower overall prior to treatment, we did not detect significant differences in predicted cover between our control plots and indaziflam-treated plots in any of the years monitored (Fig. 3.2a, Table 3.2). We also did not observe obvious herbicide injury or mortality of established individuals following treatment.

Table 3.2: Predicted *Arrhenatherum elatius* canopy cover by indaziflam treatment, site and year. Odds ratios and the FDR adjusted p-values indicate the effect of indaziflam treatment on *A. elatius* canopy cover compared to untreated control plots. Odds ratios above one indicates higher odds of *A. elatius* cover in control plots compared to indaziflam-treated plots.

Response Variable: *Arrhenatherum elatius* Canopy Cover (Proportion)					
Site	**Year**	**Treatment**	**Predicted Cover**	**Odds Ratio (Control/Indaziflam Treatment)**	**p-value (Control/Indaziflam Treatment)**
Post-Ag	2023	Control	0.521		
	2023	Indaziflam Treatment	0.229	3.66	0.010
	2024	Control	0.773		
	2024	Indaziflam Treatment	0.136	21.62	<0.001
	2025	Control	0.886		
	2025	Indaziflam Treatment	0.272	20.72	<0.001
Foothills	2023	Control	0.211		
	2023	Indaziflam Treatment	0.176	1.25	0.679
	2024	Control	0.143		
	2024	Indaziflam Treatment	0.099	1.52	0.449
	2025	Control	0.133		
	2025	Indaziflam Treatment	0.133	1.01	0.991

Introduced species decline after indaziflam treatment

Introduced species canopy cover, including *A. elatius* (tall oatgrass), declined at both sites following indaziflam treatment, although the magnitude and timing of the responses differed between locations (Fig. 3.2b; Table 3.3; Appendix 3, Table 3). At the Post-Ag site, introduced species cover was significantly lower in indaziflam treated plots in all three years, with predicted cover 26.2%, 45.7%, and 20.5% lower in treated plots than control plots in 2023, 2024 and 2025, respectively (Fig. 3.3b; Table 3.3). Pre-study introduced species cover was lower at the Foothills site compared to the Post-Ag location. In 2023, at the Foothills site, there was no significant difference between introduced species cover in control versus treated plots (p=0.753; Fig. 3.2b; Table 3.3). By 2024, we observed a marginally significant decline in introduced species, with 12.3% lower cover in treated plots (p=0.082; Fig. 3.2b; Table 3.3). This effect became significant in 2025, when introduced species cover was predicted to be to be 17.9% lower in treated plots relative to the controls (p=0.041; Fig. 3.2b; Table 3.3).

Table 3.3: Predicted introduced species canopy cover by indaziflam treatment, site and year. Odds ratios and the FDR adjusted p-values indicate the effect of indaziflam treatment on introduced species canopy cover compared to untreated control plots. Odds ratios above one indicates higher odds of introduced species cover in control plots compared to indaziflam treated plots.

Response Variable: Introduced Species Canopy Cover (Proportion)					
Site	**Year**	**Treatment**	**Predicted Cover**	**Odds Ratio (Control/Indaziflam Treatment)**	**p-value (Control/Indaziflam Treatment)**
Post-Ag	2023	Control	0.700		
	2023	Indaziflam Treatment	0.438	3.00	0.0191
	2024	Control	0.827		
	2024	Indaziflam Treatment	0.370	8.17	<0.0001
	2025	Control	0.968		
	2025	Indaziflam Treatment	0.763	9.55	<0.0001
Foothills	2023	Control	0.317		
	2023	Indaziflam Treatment	0.350	0.86	0.7534
	2024	Control	0.243		
	2024	Indaziflam Treatment	0.120	2.35	0.0824
	2025	Control	0.332		
	2025	Indaziflam Treatment	0.153	2.75	0.0409

At the Foothills site indaziflam treatment had no effect on native species cover

Out of 30 plot sampling events (10 plot-level observations per year), native species were observed at only three sampling events at the Post-Ag site. As such, native species cover was not modeled for this site (Appendix 3, Table 4). We did not detect significant differences in native species canopy cover (Fig. 3.2c; Table 3.4) at the Foothills site. While not statistically significant, our model predicted higher native species cover in treated than control plots all three years. The differences were predicted to be 4.5%, 16.1%, and 12.9% higher native species cover under indaziflam treatment than in control plots in 2023, 2024 and 2025, respectively; however, these differences are not statistically significant (Fig. 3.2c; Table 3.4).

Table 3.4: Predicted native species canopy cover at the Foothills site by indaziflam treatment and year. Odds ratios and the FDR adjusted p-values indicate the effect of indaziflam treatment on native species canopy cover compared to untreated control plots. Odds ratios above one indicate higher odds of native species cover in control plots compared to indaziflam treated plots.

Response Variable: Native Species Canopy Cover (Proportion)					
Site	**Year**	**Treatment**	**Predicted Cover**	**Odds Ratio (Control/Indaziflam Treatment)**	**p-value (Control/Indaziflam Treatment)**
Foothills	2023	Control	0.435		
	2023	Indaziflam Treatment	0.480	0.84	0.686
	2024	Control	0.347		
	2024	Indaziflam Treatment	0.508	0.514	0.133
	2025	Control	0.629		
	2025	Indaziflam Treatment	0.758	0.541	0.172

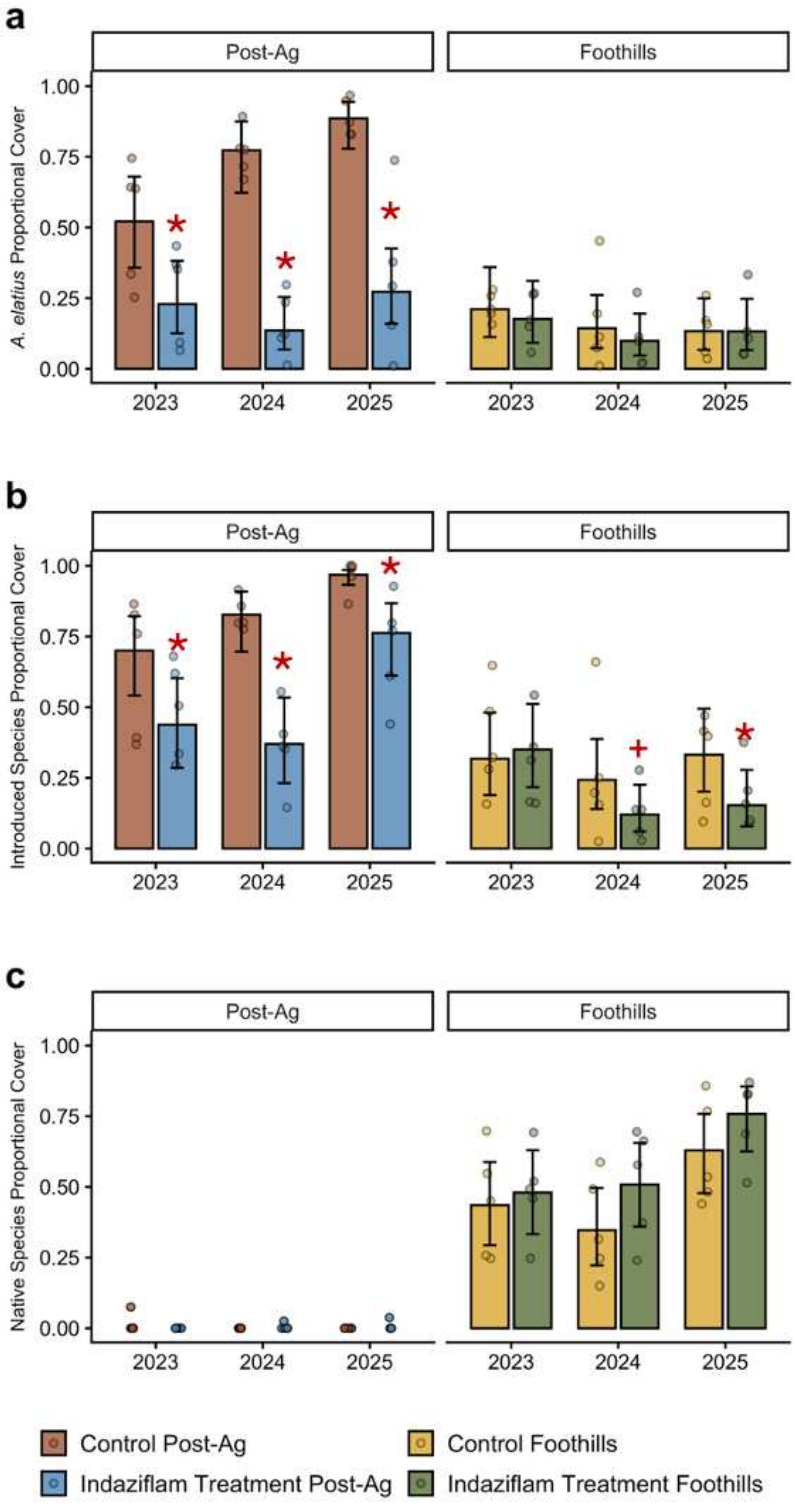

Figure 3.2: Bars show mean predicted canopy cover proportion of **(a)** *A. elatius*, **(b)** introduced species and **(c)** native species. Error bars show the 95% confidence interval. Asterisks (*) indicate significant differences ($p<0.05$), plus signs (+) indicate marginally significant differences ($p<0.1$) between mean predicted values within site and year using a mixed effects beta regression model. Points show observed canopy cover proportion.

Indaziflam treatment suppresses all seed germination

Indaziflam treatment significantly reduced emergence from seed of all species when seed bank samples were collected roughly two and a half years post-treatment. Predicted total emergence at both sites averaged 42-43 seedlings in control mesocosms compared to 5-7 seedlings in treated mesocosms (Fig. 3.3; Table 3.5). Total emergence was predicted to be 7.92 times and 6.1 times higher in controls than mesocosms with treated samples at the Post-Ag and Foothills site, respectively ($p<0.001$; Fig. 3.3; Table 3.5). The trend of significantly lower emergence from treated samples held for introduced species as well ($p<0.001$; Fig. 3.3; Table 3.5). Native species emergence was only modeled for the Foothills site due to no native emergence at the Post-Ag site. In general, native emergence was lower than introduced emergence, but the trend of suppressed emergence under indaziflam treatment held ($p=0.023$; Fig. 3.3; Table 3.5).

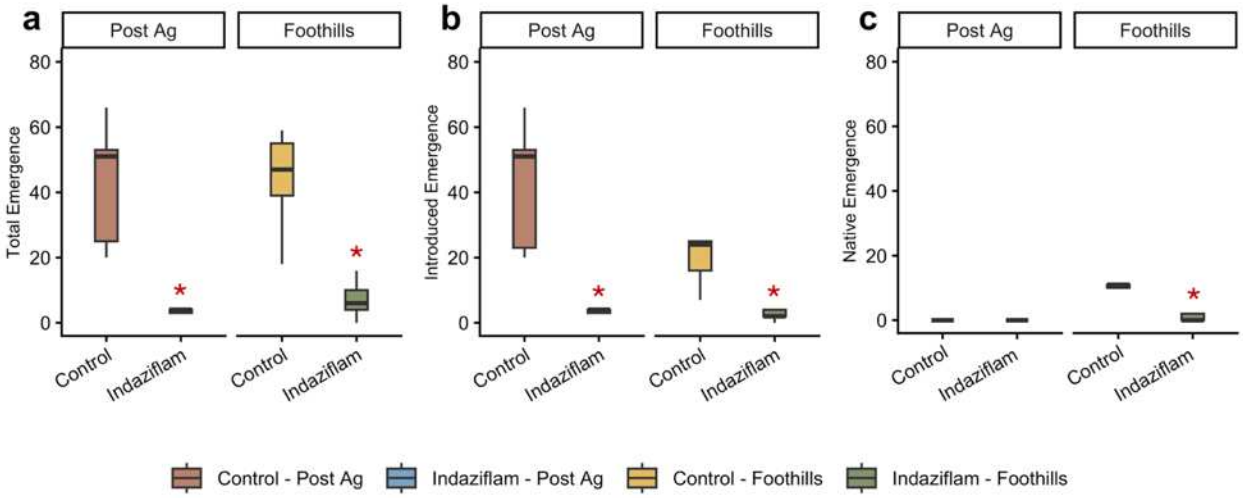

Figure 3.3: Box and whisker plots showing observed (a) total, (b) introduced, and (c) total emergence from seed bank assay mesocosms. Asterisks (*) indicate significant differences ($p<0.05$) in predicted emergence within site between mesocosms sampled from control and treated plots in March 2025. Each response variable was modeled using a mixed effects negative binomial distribution. There was no emergence of native species at the Post-Ag site and so this was not modeled.

Table 3.5: Predicted emergence from seed bank mesocosms by site and indaziflam treatment. Ratios and the FDR adjusted p-values indicate the effect of indaziflam treatment on emergence from seed bank samples collected from indaziflam treated plots compared to untreated control plots. Ratios greater than one indicate a multiplicative increase in expected seedling emergence in control mesocosms compared to those that were treated with indaziflam in 2022.

Seed Bank Assay					
Site	**Response Variable**	**Treatment**	**Predicted Emergence**	**Ratio (Control/Indaziflam Treatment)**	**p-value (Control/Indaziflam Treatment)**
Post-Ag	Total Emergence	Control	42.3		
		Indaziflam Treatment	5.4	7.92	<0.001
	Introduced Emergence	Control	42.4		
		Indaziflam Treatment	4.8	8.83	<0.001
Foothills	Total Emergence	Control	43.7		
		Indaziflam Treatment	7.2	6.10	<0.001
	Introduced Emergence	Control	23.0		
		Indaziflam Treatment	2.4	9.58	<0.001
	Native Emergence	Control	6.5		
		Indaziflam Treatment	1.1	5.65	0.023

DISCUSSION

Managing invasive grasses in rangelands is a persistent challenge with significant implications for ecosystem functioning, wildfire potential, and biodiversity (Gutiérrez et al., 2014; James et al., 2011; Shackelford et al., 2021). While indaziflam has been shown to be an effective management tool for introduced annual grasses (Bradbury et al., 2024; Sebastian et al., 2025), with limited effects on native communities, its efficacy to control perennial species that rely on seed-based reproduction is largely unknown. In this study, we tested if indaziflam may be an effective tool to control introduced perennial species dependent upon seed for reproduction using *A. elatius* (tall oatgrass) invaded rangelands on the Colorado Front Range as a study system. We also investigated the non-target impacts on other introduced species, and the native plant community and seed bank. We found that indaziflam application had multiyear impacts on plant community composition and dynamics. Indaziflam showed potential as a management tool for controlling *A. elatius* and other perennial species dependent on seed for reproduction. However,

our results were mixed reflecting the complexity of managing ecological systems. Its potential effectiveness may be partially explained by the overlapping phenology and reproductive characteristics of *A. elatius* to many annual invasive grasses effectively controlled by indaziflam (e.g., *B. tectorum*; Bradbury et al., 2024; Dombro et al., 2025a; Sebastian et al., 2017a), including early germination, growth, reproduction and senescence, the reliance on seed-based reproduction rather than vegetative reproduction and relatively short seed bank viability (Clark & Wilson, 1997; Pfitzenmeyer, 1962; *Tall Oatgrass Ecological Study*, 2018). Indaziflam had vastly different impacts on established existing vegetation at our two sites indicating that more research is needed on how indaziflam responds to different land use history and site conditions to prevent unexpected injury to established plants. Overall, indaziflam suppressed introduced species and where a native community was established prior to indaziflam treatment, at the Foothills site, there was a delayed effect on introduced species and native species cover was not statistically different in treated and control plots. Finally, we found nearly complete control of all seed germination in a seed bank assay using samples collected roughly two and a half years post indaziflam application adding to the evidence that biologically relevant soil activity persists for a long period of time (Sebastian et al., 2025).

Indaziflam effects on established species varied between sites with differing conditions

Established species including *A. elatius* (tall oatgrass) responded to indaziflam treatment differently at the two study sites. At the Post-Ag site, we saw unexpected herbicide injury and mortality of most aboveground biomass shortly following treatment, while we observed little herbicide injury and no mortality at the Foothills site. This phenomenon did not support our hypothesis that indaziflam treatment would not impact established mature individuals with deep roots. However, with different land use histories and soil characteristics across sites, this difference in response to indaziflam treatment is not entirely surprising given documented differences in indaziflam efficacy, bioavailability, and sorption with variable soil characteristics. Soil organic matter (SOM) has been identified as the most important soil characteristic influencing the fate of indaziflam (Alonso et al., 2011; Jeffries & Gannon, 2016; Sebastian et al., 2017).

At the Post-Ag site there is a history of tillage and much lower SOM than the Foothills site. Average SOM at the Post-Ag site is 5.21% while the Foothills site averages 12.47% (Table 3.1). The Rejuvra herbicide label, with active ingredient indaziflam, notes the potential for perennial grass injury in areas where soil has been disturbed including previously agricultural fields (*Rejuvra Pesticide Registration*, 2020). While most studies report no injury to existing individuals (Clark et al., 2019; Dombro et al., 2025b; Sebastian et al., 2017a), injury to established species has been documented following indaziflam treatment under both field and greenhouse conditions (González-Delgado et al., 2015; Jones et al., 2013; Schneider et al., 2015). Injury has been shown to be related to low SOM conditions that favor increased indaziflam-soil bioavailability including at depths up to 7.5cm (Jeffries & Gannon, 2016; Jones et al., 2013; Schneider et al., 2015). While indaziflam has been shown to be present in greater concentrations near the soil surface, it also has been shown to move through the soil profile and is detectable at greater depths possibly increasing injury potential (González-Delgado & Shukla, 2020; Jeffries & Gannon, 2016; Jones et al., 2013). Liquid chromatography mass spectrometry indaziflam residual analysis conducted on the same study plots in 2024, showed concentrations roughly triple in magnitude at the Foothills site than the Post-Ag site in the top centimeter of soil and roughly double in deeper soils (1-5cm below the soil surface) (Myers, 2025). The lower concentration of indaziflam detected at the Post-Ag site paired with the lower SOM and a soil disturbance history likely indicates lower sorption potential, greater bioavailability and potential leaching in the soil profile which may help explain the damage and mortality to established vegetation, largely *A. elatius*, observed following treatment at the Post-Ag site but not at the Foothills site. However, this study was not designed to assess the behavior of indaziflam across land use histories and soil characteristics so further research would be required understand the mechanisms behind the damage and mortality observed at the Post-Ag site shortly following indaziflam application. While the reductions in *A. elatius* in our field study likely were confounded by aboveground mortality, we did find clear evidence that indaziflam effectively suppresses *A. elatius* emergence in our seed bank assay with no germination in any mesocosms with treated seed bank samples. Since these samples were collected roughly two and a half years post

indaziflam application, this indicates the suppressive effect is persistent, reflecting long residual activity (Bradbury et al., 2024; Sebastian et al., 2025).

Introduced species declined following indaziflam treatment

Our hypothesis that we would see a reduction in introduced species, including *A. elatius*, due indaziflam's broad spectrum activity was partially supported at both sites. The reduction in introduced species was largely driven by the loss of *A. elatius* (tall oatgrass) at the Post-Ag site since prior to treatment and in the untreated control plots it was largely an *A. elatius* monoculture. At the Foothills site, we did not detect differences in introduced species cover the first year following indaziflam application ($p=0.753$; Fig. 3.2b; Table 3.3), but marginally lower introduced species cover the second year ($p=0.082$; Fig. 3.2b; Table 3.3) and significantly lower cover the third year ($p=0.041$; Fig. 3.2b; Table 3.3) potentially reflecting a depletion of the seedbank of annual introduced species as has been observed following indaziflam use to control *B. tectorum* (S. L. Clark et al., 2019; Courkamp et al., 2022). Indaziflam application may have prevented recruitment of new introduced individuals from seed reducing cover and thus limiting competitive pressure to existing established individuals. This strengthening effect over time provides additional evidence for the long residual and effective control of emergence from seed offered by indaziflam (Clark et al., 2019; Dombro et al., 2025a; Sebastian et al., 2025). Our seed bank assay further supported this hypothesis with minimal introduced species emergence from treated mesocosms ($p<0.001$; Fig. 3.3; Table 3.5).

Where native species were established prior to indaziflam treatment, native canopy cover was not different between indaziflam treated and control plots

We were able to model native species cover only at our Foothills site due to a lack of native species at the Post-Ag site. Our hypothesis anticipating an increase in native species cover where an established native community was present was not supported across all years (Fig. 3.2c; Table 3.4), however we did see greater native species cover over time but these within year differences between control and treated plots were not significant. Since our experimental design did not remove or manage established introduced

species, including *A. elatius* (tall oatgrass), following indaziflam treatment, shifts in competitive dynamics at the Foothills site likely depended on indaziflam's suppression of recruitment of introduced species from seed. The plant community is dominated by both introduced and native established perennial species which appeared to be largely unaffected by indaziflam treatment, so while new recruitment was likely suppressed, the competition with established introduced species remained. As a result, we did not see the expected release from competition, as shown in other studies, that would allow native species cover to increase (Bradbury et al., 2024; Clark et al., 2019; Sebastian et al., 2017b). Studies that have shown increases in native species cover following indaziflam treatment all had annual species of concern and observed major declines in the cover of those target species (Clark et al., 2019; Courkamp et al., 2022; Sebastian et al., 2025). We suspect that if established *A. elatius* individuals were removed in conjunction with indaziflam treatment we may detect an effect on native species cover.

Indaziflam treatment resulted in long lasting suppression of emergence from seed across all species

Indaziflam significantly reduced emergence from the seedbank across functional groups and species origins (Fig. 3.3; Table 3.5) when growing out seedbank samples collected two and a half years post herbicide treatment. These significant reductions in seedling emergence add support to other seed bank assays that found similar reductions in emergence two to three growing seasons post indaziflam treatment using similar rates of indaziflam (Courkamp et al., 2022; Dombro et al., 2025b). These findings also reflect field studies that found reduced recruitment of annual species and seeded perennials following indaziflam treatment, however studies have shown that deeper seeding depths can ameliorate some of reduction in emergence for some grass species (Davies et al., 2025; Shriver et al., 2024).

Indaziflam may be an effective management tool for perennial species in some contexts

While we found significant reduction in *A. elatius* (tall oatgrass) at the Post-Ag site following indaziflam treatment, this decline was driven by unexpected herbicide injury. As a result we did not find clear evidence for or against the use of indaziflam to control *A. elatius* (tall oatgrass) on the Colorado Front Range. However, we deepened our understanding of aspects of target and non-target effects that have

management implications. For indaziflam to be an effective tool on perennial species, that depend on seed for reproduction, in addition to using indaziflam to limit recruitment from seed, its effect on already established individuals needs to be considered. Potential options for control of established *A. elatius* individuals are grazing and/or mowing which has been shown to be effective at reducing *A. elatius* and could be combined with indaziflam treatment in future studies (Clark & Wilson, 1997; *Tall Oatgrass Ecological Study*, 2018; Wilson & Clark, 2001). Additionally, indaziflam is likely not a good choice of herbicide in areas without remnant native plant communities since all seed germination, native and introduced, is effectively disrupted (Courkamp et al., 2022; Dombro et al., 2025b; Shriver et al., 2024). Using indaziflam on a monoculture in areas with low soil organic matter and a history of agriculture likely will result in significant areas of bare ground if there is not an existing community that can be released from competition. Future research could consider the use of restoration islands prior to indaziflam application in areas with a monoculture of introduced species but without soil disturbance history. By planting nursery grown seedlings, this would be a pre-restoration approach through precision planting of restoration islands, essentially creating a remnant native community, with enough time for those seedlings to become well established prior to indaziflam treatment (Copeland et al., 2021; Hulvey et al., 2017). Finally, given the unexpected aboveground herbicide injury and mortality observed at our Post-Ag site shortly following indaziflam treatment, ensuring a good understanding of site history and soil characteristics is essential. We recommend testing indaziflam in a small area prior to widespread use at any site with agricultural history and low SOM.

Opportunities for future research

While this study provides valuable information on using indaziflam to control *A. elatius* (tall oatgrass), our study was limited in several ways and future research is needed to continue to expand our understanding of the effect of indaziflam application on introduced perennial species of concern reliant upon seed for reproduction and non-target species. Due to practical and permitting constraints, we used small plot sizes (16 m^2) further subdivided for various research questions, applying herbicide consistently

across small areas using a backpack sprayer despite careful calibration is challenging. We recommend larger plot sizes for future research including sprayed buffers around the plot where possible. As discussed above, significant herbicide injury and mortality of aboveground biomass unexpectedly occurred at the Post-Ag site. Greater replication across sites with variable land use histories would be beneficial in future studies. At a minimum, we recommend spraying a small area prior to selecting experimental sites to screen for these unintended consequences or using an experimental design that addresses the mechanisms behind aboveground injury. An additional limitation of our experiment design is the inherent challenge of testing a pre-emergent herbicide targeting a perennial species, since we did not remove established *A. elatius* individuals prior to the experiment. The lack of differences in cover at the Foothills site, where indaziflam did not result in damage to established species, may be a result of already established individuals persisting. Integrating approaches to reduce established *A. elatius* such as mowing or grazing (Clark & Wilson, 1997; Wilson & Clark, 2001) with indaziflam treatment would likely provide a greater understanding of indaziflam as a potential management tool in these invaded systems. Finally, this experiment used a single herbicide rate (66.7 g of active ingredient/hectare). However, one greenhouse study showed effective control of *A. elatius* recruiting from seed using much lower rates (Myers, 2025), field testing various rates of indaziflam would be beneficial and may also allow some desirable species to establish from the seedbank (Dombro et al., 2025b; Myers, 2025; Shriver et al., 2024).

CHAPTER 4: INTENSIFYING RESTORATION INTERVENTIONS INCLUDING TARGETED LIVESTOCK TREATMENT AND SOIL INOCULATION PROVIDE LIMITED BENEFITS UNDER DROUGHT CONDITIONS

SUMMARY

Soil health, typically quantified by metrics representing physical, biological, chemical properties of soil, is often overlooked in dryland restoration, but improving edaphic conditions may enhance plant restoration outcomes. Drylands, or water-limited ecosystems, cover a large portion of the globe, are degraded in much of their range, are expected to expand under climate change, and are unlikely to recover without active intervention. Despite their ecological and social importance, seed-based restoration often results in little or no recruitment of desirable species. Using RestoreNet, a networked dryland restoration trial, we evaluated the effects of active seeding, ground modification treatments (i.e., pitting), and seed pellets on plant emergence across four sites in Arizona spanning environmental and disturbance gradients. We also tested these treatments in combination with live soil inoculation from nearby reference sites to address underlying edaphic barriers to revegetation. Recognizing that many degraded drylands are rangelands and removing grazing livestock permanently is often unfeasible, we also crossed our treatments with a short duration targeted livestock treatment designed to increase soil surface heterogeneity and improve soil seed contact. Like many dryland restoration efforts, we observed limited seeded species emergence, which was likely constrained by persistent drought conditions across all four sites. Despite limited emergence of seeded species, we found that treatments had context dependent effects. Across sites, active seeding significantly improved seeded species density. Ground modification (pitting) improved seeded species density at sites characterized by more pulsed precipitation regimes, where there is high variability in precipitation event size. In contrast, our other treatments largely resulted in neutral effects on seeded species density, and any possible effects were likely masked by drought conditions. Collectively, these results emphasize the importance of aligning seed-based restoration efforts to favorable episodic

climate conditions using short- to long-range climate forecasts, which may be more effective than intensifying restoration interventions during droughts.

INTRODUCTION

Drylands, or water-limited ecosystems, are among the most extensive globally, covering roughly 40% of the earth's terrestrial surface, and already at least 50% of these areas are degraded due to anthropogenic activities including land use change, overgrazing, desertification, and resource extraction (Maestre et al., 2016; Shackelford et al., 2021; Stapleton et al., 2024). Restoration of drylands is inherently difficult due to water limitation, extreme temperatures, invasive species, and infertile soils (Hoover et al., 2020; Shackelford et al., 2021). Despite these challenges, effective restoration is a priority as drylands support nearly 40% of the global population and provide critical ecosystem services (Copeland et al., 2025; Hoover et al., 2020; Shackelford et al., 2021). Under climate change, the global extent of drylands is expanding and these already dry systems are projected to increase in aridity and experience more extreme temperatures, see shifts in precipitation timing and intensity, and more frequent and extreme drought conditions (Duniway et al., 2022; Hoover et al., 2020; Maestre et al., 2016; Shackelford et al., 2021).

Large biotic and abiotic barriers limit restoration success and make passive restoration unlikely to succeed, necessitating more active or intensive restoration interventions (Gann et al., 2019; Kildisheva et al., 2016; Shackelford et al., 2021; Suding, 2011). Key biotic barriers on degraded drylands in need of restoration include competition with introduced species (Garbowski et al., 2021), intensive livestock grazing (Shriver et al., 2018), and altered soil microbial communities (Duell et al., 2023; Marasco et al., 2023). Abiotic barriers include water limitation and high temperatures (Maestre et al., 2016; Muñoz-Rojas et al., 2016; Shackelford et al., 2021), limited windows of precipitation for plant germination and establishment (Shriver et al., 2018), and low soil fertility (Hoover et al., 2020; James et al., 2013; Muñoz-Rojas et al., 2016), all of which can further hinder restoration success. Seed-based restoration (SBR) is the most common approach used to restore dryland plant communities due to its large-scale efficiency compared to more intensive planting of nursery grown plants (outplanting) (Shackelford et al., 2021).

However, these seed-based approaches often fail to overcome biotic and abiotic barriers and regularly result in no or low establishment of desirable plant species (James et al., 2013; Shackelford et al., 2021; Stapleton et al., 2024). Due to the low success of many dryland restoration efforts, it is clear that novel approaches that directly target propagule availability as well as biotic and abiotic barriers are needed to improve revegetation outcomes (Copeland et al., 2021; Hulvey & Aigner, 2014; Kildisheva et al., 2016).

Soil health is often overlooked in SBR efforts, yet improving edaphic conditions may improve aboveground revegetation success (Kimmell et al., 2023; Muñoz-Rojas et al., 2016). Healthy soils can buffer against the effects of drought and other stressors on productivity by increasing water and nutrient availability and providing protection from erosion (Barrios, 2007; Boeddinghaus et al., 2019; Bünemann et al., 2018). Living communities in the soil play critical roles in soil processes including decomposition, nutrient cycling, and soil structure development, but these communities are easily disturbed, limiting the capacity to support desirable, late-successional plant species (Barrios, 2007; Coleine et al., 2024; Duell et al., 2023; Zhang et al., 2019). Degraded soils often lack desirable propagules in the seed bank, beneficial soil microbes, adequate nutrients, high water-holding capacity, and soil stability, all of which make it difficult for seedlings to establish and survive (Kildisheva et al., 2016; Muñoz-Rojas et al., 2016; Vallejo et al., 2012). Through plant-soil feedback, changes in the soil microbiome can exert positive or negative effects on plant establishment and biomass, influencing community assembly and restoration trajectories (Coleine et al., 2024; van der Putten et al., 2016). Therefore, incorporating soil health into restoration efforts may help promote feedbacks that support both above- and below-ground communities (Brown & Herrick, 2016; Duell et al., 2023; Kimmell et al., 2023).

Many rangeland improvement guides recommend removing livestock or implementing long rest periods to recover from overgrazing during the restoration process, which may be economically infeasible and overlooks the potential for incorporating livestock into restoration efforts (Briske et al., 2011; Filazzola et al., 2020; Fynn et al., 2017; Porensky et al., 2018). One potential approach is the application of a short duration targeted cattle treatment during active seeding efforts. The hoof action from this targeted livestock

treatment can increase soil surface heterogeneity and improve soil seed contact ultimately improving seedling emergence (Driessen et al., 2011; Eichberg & Donath, 2018; Isselin-Nondedeu & Bédécarrats, 2007; Norton et al., 2009). Additionally, hoof action may resemble smaller scale pitting that has been shown to increase seedling emergence (Farrell et al., 2023; Havrilla et al., 2020) and allow for localized water capture during precipitation events. Additionally, targeted livestock treatment may increase nutrient availability through urine, excrement and trampling of hay into the soil (Driessen et al., 2011; Norton et al., 2009)

This work leverages a subset of four RestoreNet sites, a networked dryland restoration trial in the Southwest United States that utilizes a co-production framework, across Arizona (Havrilla et al., 2020; Laushman et al., 2022). Benefits of using a multi-site networked approach across abiotic gradients include the ability to compare treatments across a range of environmental conditions allowing for inference to new areas, and increased collaboration between land managers, decision makers and scientists (Gellie et al., 2018; Havrilla et al., 2020; Ladouceur et al., 2022). This research examines the effects of active seeding, soil surface modification through pitting, seed pellets and soil inoculum additions with and without targeted livestock treatment on plant density across environmental and disturbance gradients. We hypothesized:

(H1): Restoration treatments will improve seeded species density relative to controls through direct treatment effects (specific hypotheses are outlined in Table 4.1)

(H2): Layering restoration interventions will lead to larger improvements in desirable plant density by strengthening direct treatment effects (Table 4.1) and addressing multiple barriers to dryland restoration (Copeland et al., 2021; Hulvey & Aigner, 2014).

Table 4.1: Hypothesized effect and justification for each treatment used in the experiment.

Treatment	Hypothesized Effect
 Broadcast Seeding	Application of high-priority native seed mixes developed for RestoreNet sites (Laushman et al., 2022) is intended to mitigate the lack of desirable propagules present in the natural seed bank and increase seeded species density (Shackelford et al., 2021).
	Seed pellets encase multiple seeds in clay and amendments that are designed to improve seed-soil contact, protect seeds from predation and harsh environmental conditions, wind movement, and decrease desiccation enhancing seed viability and increasing seedling density (Gornish et al., 2019).
	Pitting of the soil surface is an ancient technology designed to improve microclimatic conditions at the soil surface by increasing soil moisture, both quantity and duration of available moisture, and helps prevent wind movement of seeds (Farrell et al., 2023; Havrilla et al., 2020; Johnston & Mann, 2024), leading to higher densities of seeded, naturally occurring native, and introduced species. This was demonstrated to be the most effective treatment in earlier RestoreNet trials (Farrell et al., 2023; Havrilla et al., 2020).
 Soil Inoculum	Live soil inoculum containing soil microbes is intended to improve soil health (Kimmell et al., 2023), reduce invasive species reestablishment (Duell et al., 2023) and enhance establishment of late successional grassland plants (Koziol et al., 2022)
	Utilization of short duration targeted livestock just after seeding and treatment installation is designed to increase soil surface heterogeneity and improve soil-seed contact increasing seedling emergence (Driessen et al., 2011; Eichberg & Donath, 2018; Isselin-Nondedeu & Bédécarrats, 2007; Norton et al., 2009). Additionally, targeted livestock treatment increases nutrient availability through urine, excrement and trampling of hay into the soil (Driessen et al., 2011; Norton et al., 2009)

METHODS

Experimental design

This research tested treatments to improve seed-based restoration outcomes in degraded rangelands (Fig. 4.1; Table 4.1). The strategies we employed are technologically simple and seek to ameliorate specific challenges of revegetating dry and drought-prone regions (Table 4.1). Our partially crossed experimental treatments were tested with and without targeted livestock treatment across climate and soil gradients across four sites in Arizona (Table 4.2). Two seeding methods (broadcast or seed pellet) were crossed with live or

pasteurized soil inoculum treatments. However, the volume of inoculum varied by seeding treatment: broadcast seeded plots received 13,600 g of inoculum spread across the 1 m^2 plot while seed pellet plots had 1,530 g of inoculum incorporated directly into the pellet. We further crossed seeding and inoculum treatments with the presence or absence of ground modification (pits), resulting in ten treatments with four replicates each, for a total of 40 experimental plots at each site (Fig. 4.1). These 40 plots, each 1 m^2, were replicated twice at each site, with one set exposed to a single targeted livestock treatment directly after seeding, followed by livestock exclusion; and the other set excluded from livestock entirely. Treatments at all sites were implemented in late Spring and Summer 2024. Summer seeding timing was intended as a monsoon seeding, were seeding occurred before the normal onset of summer monsoon rains typical at the two more southern Arizona sites.

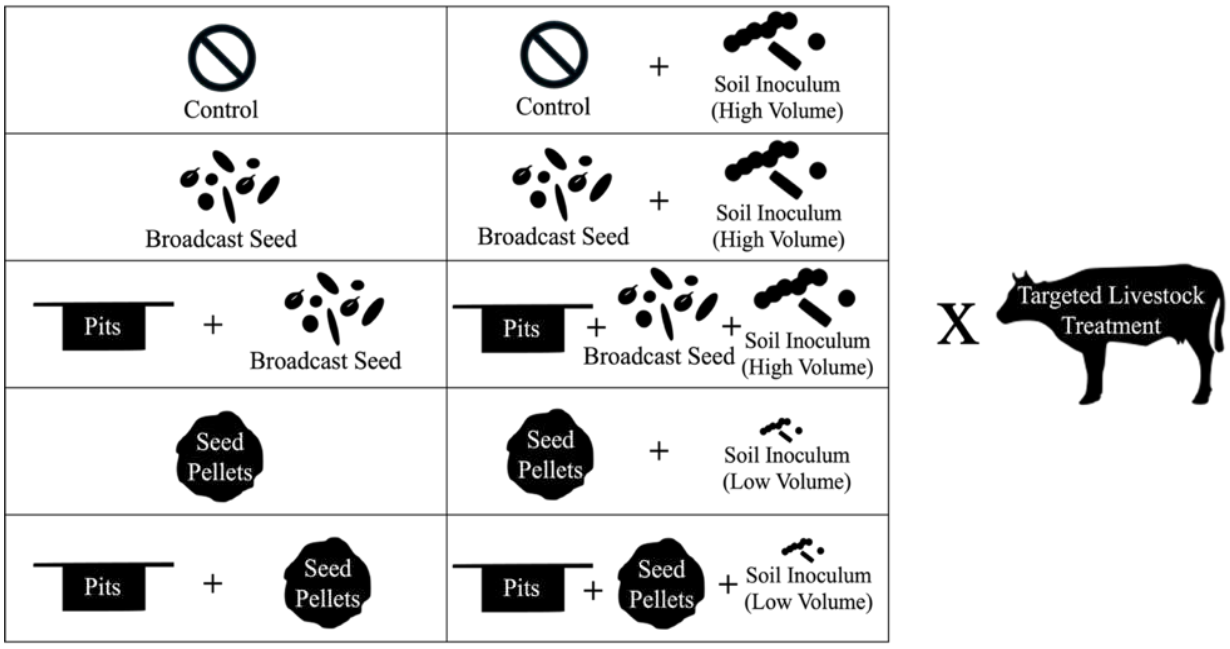

Figure 4.1: Schematic showing experimental treatments, each treatment was replicated four times for a total of 40 experimental plots. The 40 plots were replicated twice at each site with one set receiving a targeted livestock treatment at installation.

Table 4.2: Site information organized from the most arid site to the most mesic including location, ecoregion, elevation, ownership, mean annual temperature (°C), mean annual precipitation (mm) and soil type. Mean annual temperature and precipitation are 30-year normals (1991-2020) from the PRISM climate group. Aridity index values (lower values = higher aridity) were obtained from the Global Aridity and Potential Evapotranspiration Databased published by the CGIAR Consortium for Spatial Information. Soil type information was retrieved from the Natural Resource Conservation Service Web Soil Survey.

Site	Ecoregion	Coordinates	Elevation (m)	Ownership	Mean Annual Temperature (C) (PRISM)	Mean Annual Precipitation (mm) (PRISM)	Aridity Index (CGIAR)	Soil Type (Web Soil Survey)
Roosevelt	Sonoran Basin	33.611153°N, 111.039686°W	762	U.S. Forest Service/ Private	20.1	401	0.204	Typic Haplargids, Ustic Haplocambids, and Ustic Calciardgids; warm thermic basin and fan remnants
BarTBar	Arizona & New Mexico Plateau	34.889439°N, 111.06063°W	1176	Private	11.3	300	0.2356	Winona gravelly loam, 0 to 8 percent slopes
Santa Rita Experimental Range (SRER)	Madrean Archipelago	31.786117°N, 110.823944°W	1324	University of Arizona	18.1	455	0.2726	Comoro soils, 0 to 5 percent slopes
Flying M	Arizona & New Mexico Mountains	34.835766°N, 111.111596°W	1854	Private	10.9	356	0.2727	Paymaster-Lynx association, gently sloping

Seed mix

A common seed mix was used across the four sites and was based upon mixes designed for the original RestoreNet experiment (Laushman et al., 2022). A diverse mix of native forbs, cool and warm season grasses, and shrub species was included in the 17 species mix (Appendix 4, Table 1). Seeding rates used reflected the high end of the recommended rate for each species provided by the seed companies. A total of 7,710 pure live seeds (PLS) were spread on each 1 m^2 plot.

Soil surface treatments (pits)

For this experiment, a single pit, or small depression, was dug in the center of the designated plots. Each pit was 40cm by 40cm with a depth of 10cm, pits were dug to be flat across the bottom with nearly vertical sides creating a level basin (Laushman et al., 2022). Topsoil from the area where the pit was dug was preserved and returned to the bottom of the pit after it was dug out. The other soil removed in the pit digging process was spread evenly across the rest of the 1m-by-1m experimental plot.

Soil inoculum

Soil inoculum was prepared for each site using soils collected from areas that had more intact native perennial vegetation and had experienced less historical disturbance near each experimental restoration site (Chaudhary et al., 2020). These reference site soils were then conditioned in a greenhouse before being applied directly to the relevant experimental plots or incorporated into seed pellets. Reference soil samples were collected in the Fall of 2023. At each reference site 50m transects were established and soil was collected every five meters at a depth of 10cm after surface litter had been cleared. Where possible, these collections were taken from the base of a nearby perennial plant. Three to five transects were needed at each site to collect the 190 liters of needed reference soil.

Collected soil was conditioned in the greenhouse (Markovchick et al., 2024) using a ratio of one part reference soil to two parts sand (Sakrete multipurpose sand) (Ndoye et al., 2024). Greenhouse conditioning began in early spring 2024, with conditioning timed with our intended installation date for

each site. Soils were conditioned using plastic growing bins where reference soil and sand was layered in each bin and planted with our restoration seed mix as well as with two additional species (Appendix 4, Table 2) known to be highly mycotrophic or known to discourage common greenhouse pests (Hooks et al., 2010; Plenchette et al., 1983; Tenzin et al., 2022). These bins were allowed to grow for nine weeks then watering was ceased ten days prior to harvest to allow the inoculum to dry down. Aboveground biomass was removed, but root biomass remained in the inoculum. Half of the bins per site were randomly selected to be pasteurized. Selected bins were wetted and then pasteurized in an Electric Soil Sterilizer (Pro-Grow Supply Model SST-30) over two twelve-hour cycles at 93 °C, with an hour of off-gassing between cycles.

Conditioned pasteurized or live inoculum was either spread across the soil surface of designated plots or incorporated directly into seed pellets that were then spread across the relevant plots. 10 liters of inoculum (pasteurized or live) was spread across our control + inoculum, broadcast seed + inoculum, and broadcast seed + pit + inoculum treatments to depth of approximately 1 cm (Remke et al., 2022). Half of the conditioned inoculum was applied, then seeds were broadcast across the plot then the remaining inoculum was applied sandwiching the seeds between layers of inoculum. During the entire conditioning and application process, all tools and equipment were sterilized throughout to ensure no contamination between sites and/or pasteurized and live inoculum.

Seed pellets

Seed pellets were made using a low-tech "Bicycle Powered Seed Pelletizer" which produced heterogeneous seed pellets that range in size and shape (Gornish et al., 2018). Two batches of seed pellets were produced for each site with one batch containing live inoculum and the other pasteurized inoculum. Seed pellets were made using 170g of seed, 1530g of live or pasteurized inoculum and 1190g of clay (Lincoln 60 Fire Clay). This is equivalent to a ratio of 1 part seed to 9 parts inoculum to 7 parts clay. After seed pellets were formed using the "Bicycle Powered Seed Pelletizer", they were allowed to dry completely in ambient greenhouse conditions then were divided equally, by weight, to be applied to the relevant plots. On average, each plot received 10-15 total seed pellets. During plot installation, seed pellets were scattered

across each plot and gently tamped into the plot surface to reduce rolling off the plot.

Targeted livestock treatment

The targeted livestock treatment occurred a single time per site directly following the installation of the other treatments (ground modification, inoculum and seeding) in an enclosure containing half the experimental plots (n=40) and lasted 5.5 to 6.5 hours. Cattle used in grazing were provided supplemental feed (Weed Free Timothy), equally distributed in the center of each plot to encourage hoof action across the whole enclosure (Fig. 4.2). To standardize grazing pressure, the number and type of cattle (animal units) and grazing time were manipulated to match the size of each enclosure.

Figure 4.2: Example of targeted livestock treatment with weed-free hay placed in the center of each plot to encourage hoof action across the entire enclosure.

Data collection

Each site was monitored biannually in the spring and fall; exact monitoring timing varied by site to account for differences in growing season and precipitation patterns. Monitoring data from Fall 2024 and Fall/Spring 2025 are included in this analysis. A permanent 0.5 m by 0.5 m subplot was established in the center of each plot. Plant density and height information was collected by counting each individual plant

present in the subplot at the species level and recording an average height (mm) for each species. At the larger 1m x 1m plot level, we also took visual estimates for seeded species, unseeded native and introduced forbs, grasses and shrubs as well as noted any seeded species present not observed in the subplot.

Data analysis

All analyses were performed in R Statistical Software, version 4.5.2 (R Core Team, 2025). Seedling density data captured at the species level was aggregated by seeded species, unseeded native species, and introduced species prior to analysis. Zeros were added for each group as needed to reflect true absence.

We used generalized linear mixed effects models (GLMMs) implemented in the glmmTMB package (Brooks et al., 2017) to test our hypotheses, with plant density (seeded, unseeded native, and unseeded introduced) measured at the subplot scale as our response variable. Since all our response variables are count data and exhibited overdispersion, a negative binomial error distribution was used in all models. For cross-site analysis, models included experimental treatment, grazing, site, monitoring event and the interaction between experimental treatment and grazing as fixed effects. A unique identifier for each plot was used as a random effect to account for repeat measures (Appendix 4, Table 3). Due to limited data within sites, we fit fully additive site-specific models that included experimental treatment, grazing and monitoring event as fixed effects with a plot identifier included as a random effect (Appendix 4, Table 3). We additionally fit pooled models to isolate the effects of individual treatment components (seed pellets, ground modification/pits, targeted livestock treatments, and soil inoculum). For each pooled analysis, models included a three-way interaction between the pooled treatment of interest, site, and livestock treatment. When livestock treatment was the focal treatment, the model instead included only the two-way interaction between livestock treatment and site. A unique identifier for each plot was used as a random effect to account for repeat measures (Appendix 4, Table 3).

Post hoc comparisons were conducted using the emmeans package (Lenth, 2024), with p-values adjusted using the false discovery rate (FDR) correction. Post hoc tests were restricted to hypothesis driven contrasts with α=0.05 used throughout as our significance threshold.

RESULTS

Post-treatment characterized by drought and windy conditions

Each of the four study sites experienced drought conditions for most of the study period, with all sites classified as abnormally dry during and immediately following seeding (Fig. 4.3). All sites experienced periods of moderate drought, and Roosevelt and SRER also experienced periods of severe and extreme drought conditions. Precipitation during the study period was relatively infrequent and occurred in discrete events punctuated by extended dry spells (Appendix 4, Table 4). Roosevelt and Flying M had the greatest variability in precipitation event size, consistent with more strongly pulsed precipitation patterns. In addition to these dry conditions, these sites also were exposed and windy. Mean daily maximum 10-meter wind gusts ranged from 10.9 to 12.2 m s^{-1} with guests as high as 23.3-26.5 m s^{-1} during 2024 and 2025 at all sites (Appendix 4, Table 5).

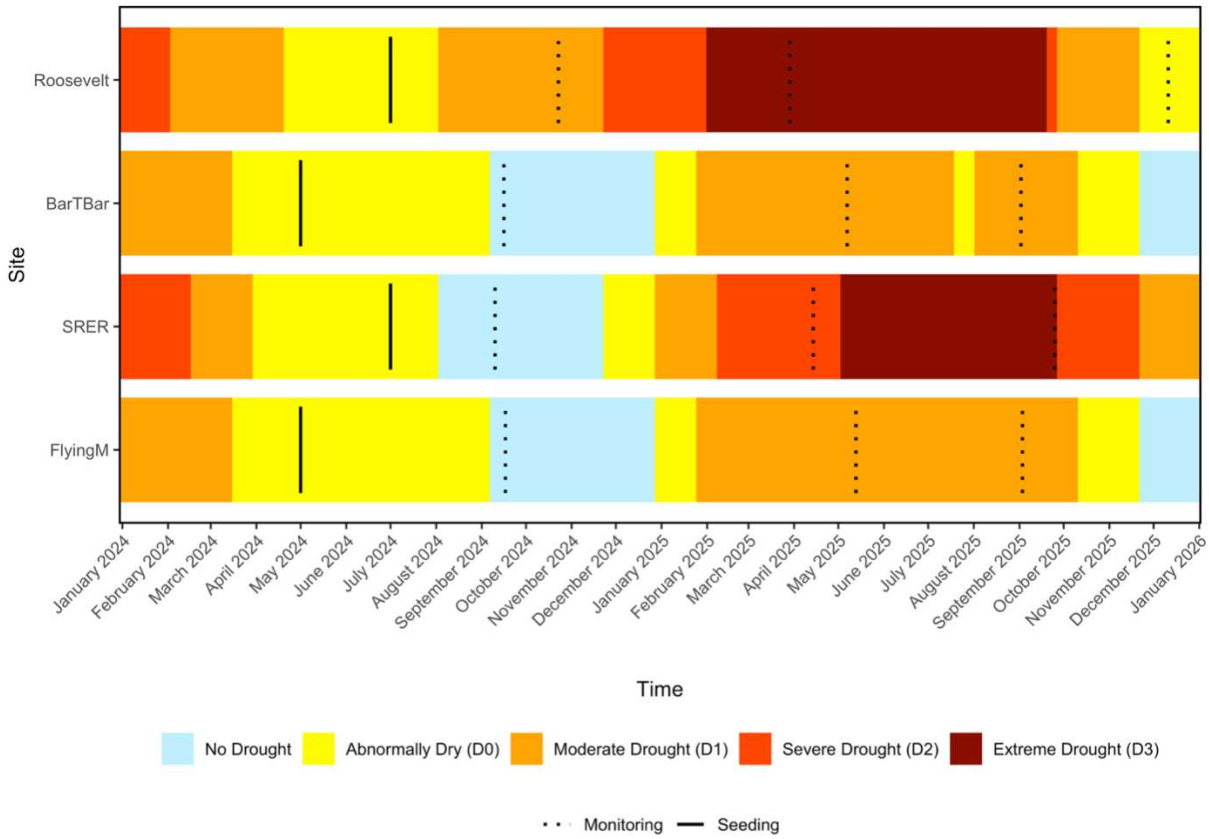

Figure 4.3: Weekly United States Drought Monitor weekly drought classifications for each study site in 2024 and 2025. Sites are ordered from the most arid at the top to the most mesic at the bottom. Solid vertical lines indicate seeding dates, and dotted vertical lines show monitoring events.

Desirable Species Increased with Seeding

Using a cross-site model, all actively seeded treatments significantly increased seeded species density relative to the control pasteurized inoculum experimental treatment, which served as the reference, averaged across livestock treatment, and monitoring event ($p<0.05$; Fig. 4.4; Appendix 4, Table 6). Relative to the control pasteurized treatment, seeded species density was approximately 4- to 13-fold higher in actively seeded treatments. However, all site main effects were significant ($p<0.05$; Appendix 4, Table 7), indicating differences in seeded species density among locations and associated environmental conditions.

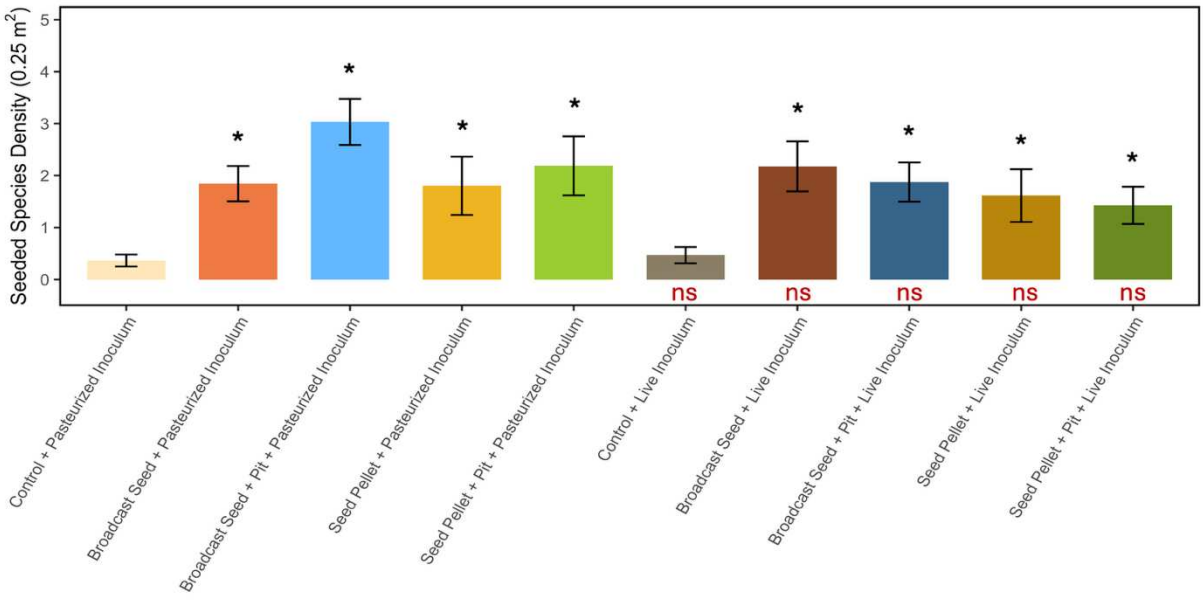

Figure 4.4: Mean observed seeded species density (± standard error) by experimental treatment averaged across site, targeted livestock treatment and monitoring event. Black asterisks (*) above bars indicate significant differences ($p<0.05$) from the Control Pasteurized Inoculum treatment using FDR adjusted comparisons (Appendix 4, Table 6). Red symbols beneath live inoculum treatments indicate contrasts comparing live and pasteurized inoculum within treatment using FDR-adjusted comparisons (Appendix 4, Table 19), treatments share a common color with darker shades indicating live inoculum. Dagger symbol (‡) denotes $p< 0.05$ and ns denotes non-significant differences.

At the most arid site, Roosevelt, all actively seeded treatments had higher emergence compared to our control ($p<0.05$; Fig. 4.5; Appendix 4, Table 8). Seeded species density was approximately 3 to 6 times higher in actively seeded plots than in control pasteurized plots. Responses to active seeding were less consistent at the remaining sites (Fig. 4.5). At BarTBar, only three experimental treatments resulted in

significantly higher densities of seeded species compared to control pasteurized: broadcast seeding with pasteurized inoculum (~8 fold increase; $p=0.017$), broadcast seeding with live inoculum (~6 fold increase; $p=0.023$) and broadcast seeding into pits with pasteurized inoculum (~7 fold increase; $p=0.019$; Fig. 4.5; Appendix 4, Table 9). We also observed a marginally significant increase in seeded species density in the live inoculum seed pellet treatment ($p=0.099$; Fig. 4.5; Appendix 4, Table 9). At the SRER site in Southern Arizona, no actively seeded treatments significantly improved seeded species density. However, both broadcast seeding with pasteurized inoculum and seeding into pits with pasteurized inoculum marginally increased density ($p<0.1$; Fig. 4.5; Appendix 4, Table 10). At our most mesic site, Flying M, there was no emergence of seeded species from the control pasteurized treatment, so the control live inoculum treatment was used as the reference. At this site, most treatments improved seeded species density relative to the reference, with increases ranging from 5- to 35-fold relative to the control, except for seed pellets with pasteurized inoculum and broadcasting seeding into pits with live inoculum (Fig. 4.5; Appendix 4, Table 11). Seed pellets with live inoculum crossed with pits resulted in only a marginal increase in seeded species density ($p=0.055$; Fig. 4.5; Appendix 4, Table 11).

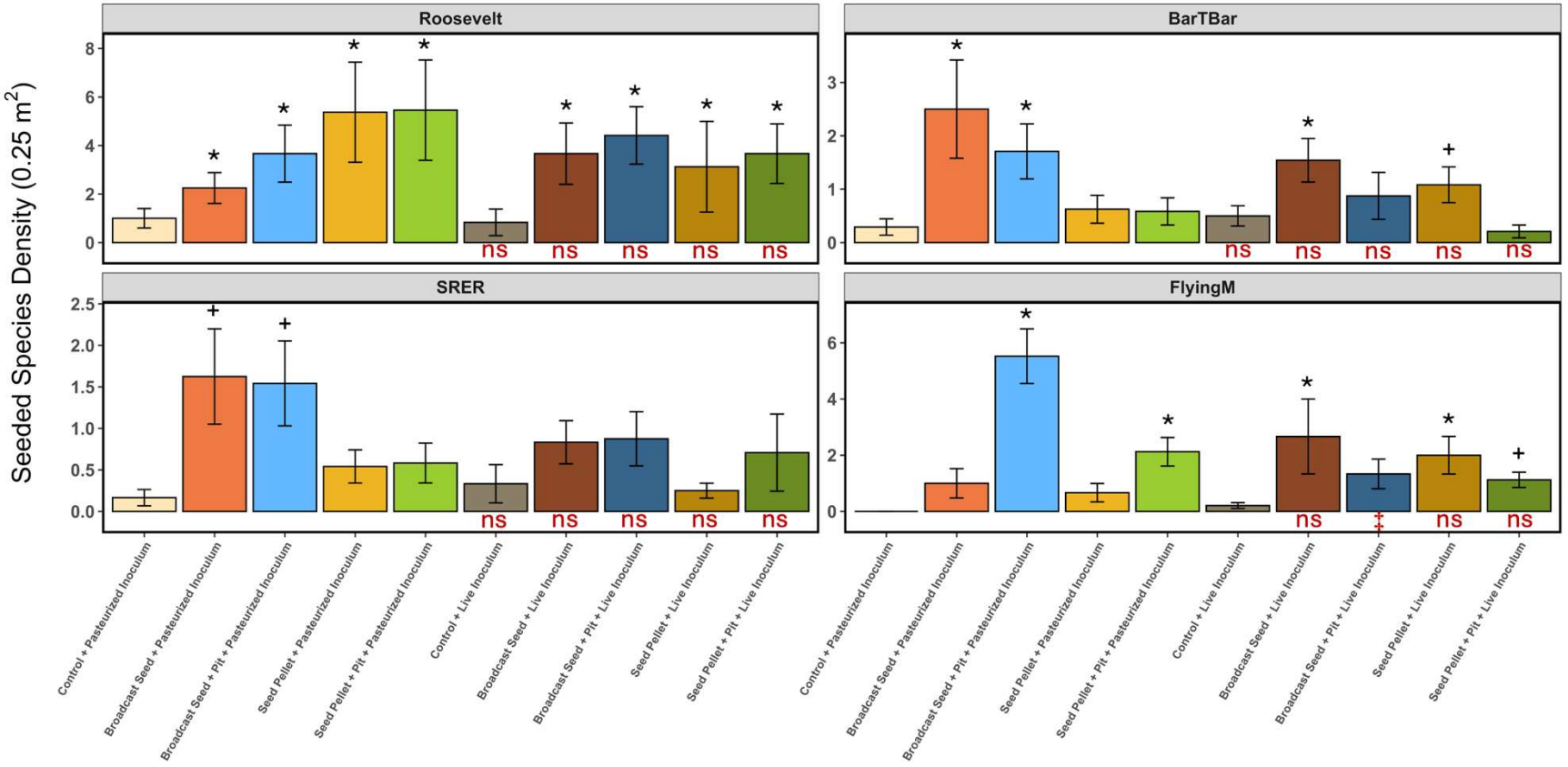

Figure 4.5: Mean observed seeded species density (± standard error) by experimental treatment and site, averaged across targeted livestock treatment and monitoring event. Black asterisks (*) above bars indicate significant differences ($p<0.05$), black plus signs (+) indicate marginal differences ($p<0.1$) relative to the Control Pasteurized Inoculum treatment using FDR adjusted comparisons within each site (Appendix 4, Table 8 - 11). At Flying M, no seeded species emerged from the Control Pasteurized Inoculum treatment, therefore, the Control Live Inoculum treatment was used as the reference level for treatment-control contrasts. Red symbols beneath live inoculum treatments indicate contrasts comparing live and pasteurized inoculum within treatment and site using FDR-adjusted comparisons (Appendix 4, Table 20 - 23), treatments share a common color with darker shades indicating live inoculum. Dagger symbol (‡) denotes $p< 0.05$, and ns denotes non-significant differences. The live–pasteurized inoculum contrast for control treatments at Flying M was not estimable due to zero emergence in the Control Pasteurized Inoculum treatment.

Seed pellets and ground modification (pits) had limited effects

Using pooled models, we did not observe a consistent increase in seeded species density consistently across sites in the seed pellet (Fig. 4.6a) or pitting treatments (Fig. 4.6b). For seed pellets, there was no difference between treatments that used pelleted seeds and broadcast seeded treatments at three sites (Fig. 4.6a; Appendix 4, Table 12). In contrast, at the BarTBar site seed pellets had 54% lower seeded species density than treatments without seed pellets, contrary to our hypothesis ($p= 0.011$; Fig. 4.6a; Appendix 4, Table 12).

Ground modification via pits also showed variable effects on seeded species density across sites. No differences were detected between pitted and unmodified treatments at both BarTBar and SRER (Fig. 4.6b, Appendix 4, Table 13). However, pitting resulted in a 3-fold increase in seeded species density at Flying M ($p=0.001$) and a marginal 1.6-fold increase at Roosevelt ($p=0.097$; Fig. 4.6b; Appendix 4, Table 13), providing partial support for our hypothesis. Pits may provide greater benefits at sites characterized by more pulsed precipitation regimes (i.e., larger and less frequent precipitation events). Roosevelt (CV = 1.53) and Flying M (CV = 1.14) exhibited the greatest variability in precipitation event size among our study sites (Appendix 4, Table 4), and these sites also showed the strongest responses to pitting.

We also anticipated similar effects on unseeded native and introduced species due to increased moisture. Averaged across sites, we observed that all pitting treatments resulted in higher unseeded native species density than our control pasteurized treatment, with increases ranging from ~1.6 to 2-fold (Appendix 4, Fig. 1; Appendix 4, Table 14). No other experimental treatments resulted in significantly different non-seeded native species density from our pasteurized control (Appendix 4, Fig. 1; Appendix 4, Table 14). While introduced species were roughly three to four times more abundant than seeded species averaged across sites, we detected no direct treatment effects on introduced species density compared to control pasteurized plots (Appendix 4, Fig. 2; Appendix 4, Table 15).

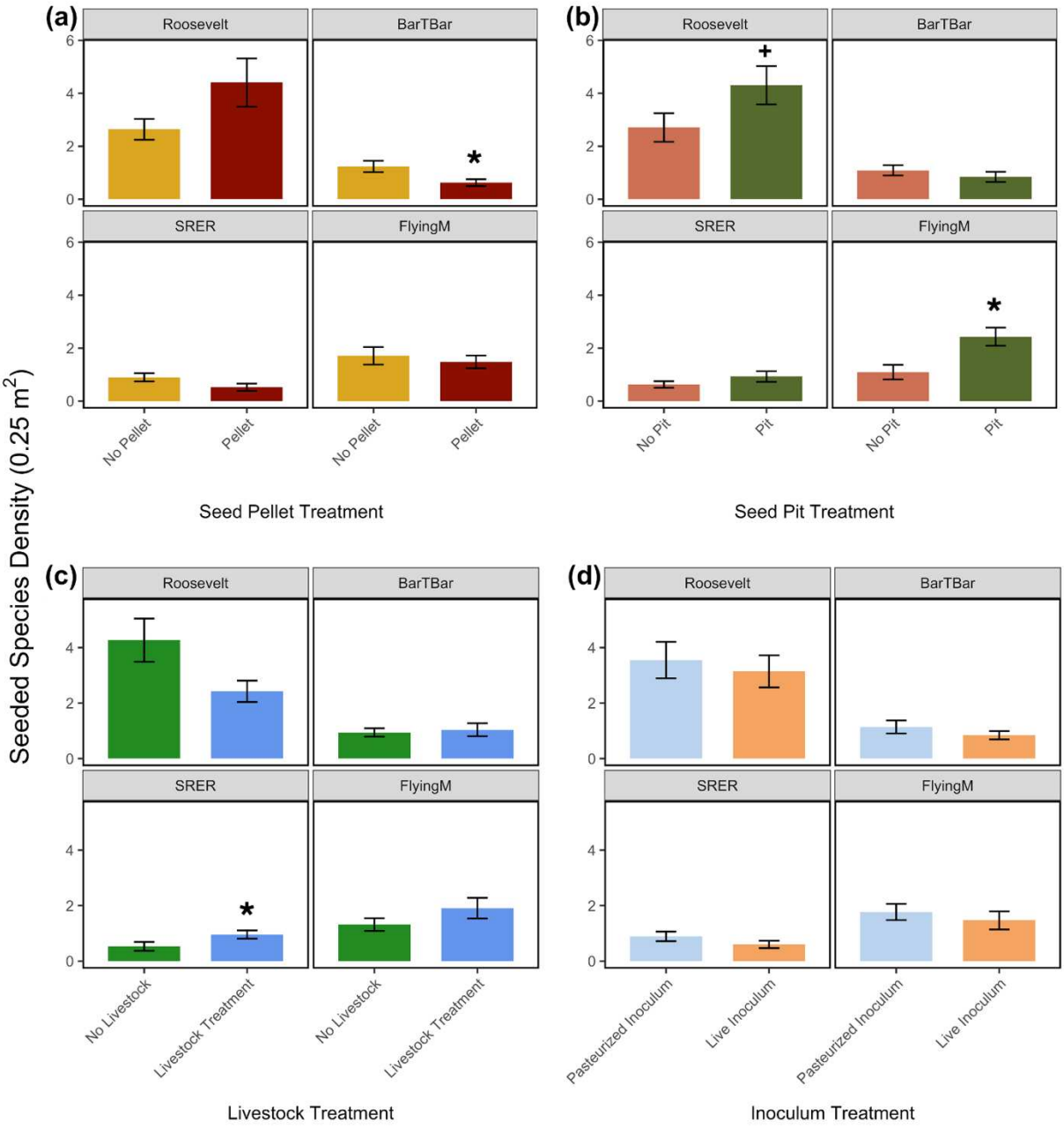

Figure 4.6: Mean observed seeded species density (± standard error) by site for pooled treatment components: **(a)** seed pellets versus broadcast seeding, **(b)** pits versus no pits, **(c)** no livestock treatment versus targeted livestock treatment, and **(d)** live versus pasteurized inoculum averaged across monitoring events. Asterisks (*) indicate significant ($p<0.05$) within site differences while plus signs (+) indicate marginal differences ($p<0.1$) between pooled groups based on FDR adjusted pairwise contrasts (Appendix 4, Tables 12, 13, 16); inoculum effects were not significant at any site (Appendix 4, Table 18).

Targeted livestock treatment had limited and variable effects

Our targeted livestock treatment was designed as a facilitative disturbance intended to increase soil surface heterogeneity and improve soil seed contact through hoof action from cattle. Although we did not detect a strong overall positive effect of livestock treatment on seeded species density (Fig 4.6c; Appendix 4, Table 16), we observed several treatment specific differences between no livestock, and targeted livestock treatment averaged across site and monitoring event (Fig. 4.7; Appendix 4, Table 17). Within the unseeded controls, targeted livestock treatment significantly reduced seeded species density under both pasteurized (~73% reduction; p=0.031) and live inoculum conditions (~86% reduction; p=0.001; Fig. 4.7; Appendix 4, Table 17). However, seeded species density increased with livestock in our broadcast seeding into pit treatments, with a marginal 2.1-fold increase under pasteurized inoculum (p=0.054) and a significant 2.7-fold increase under live inoculum (p=0.013; Fig. 4.7; Appendix 4, Table 17). Seed pellet

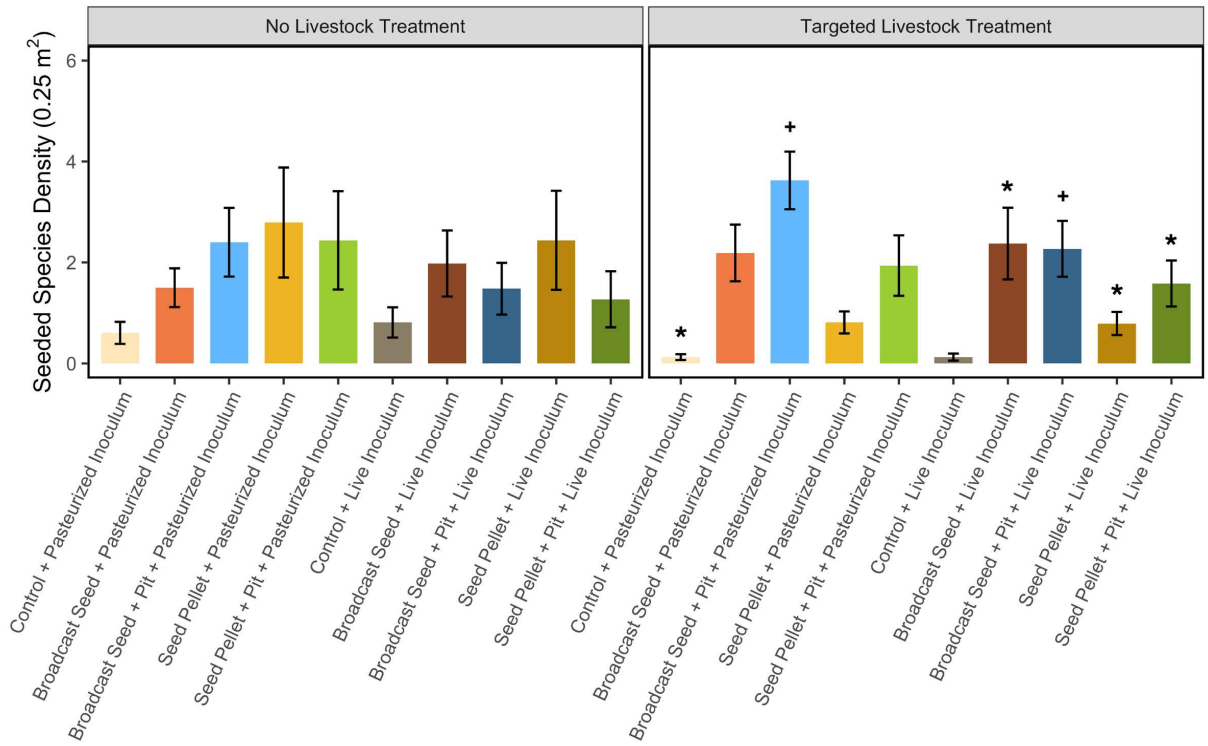

Figure 4.7: Mean observed seeded species density (± standard error) by experimental treatment and targeted livestock treatment averaged across site and monitoring event. Asterisks (*) indicate significant differences ($p<0.05$) while plus signs (+) show marginal differences ($p<0.1$) between no livestock treatment and targeted livestock treatment within experimental treatment using FDR adjusted contrasts (Appendix 4, Table 17).

treatments showed no consistent response to targeted livestock treatment, including seed pellets in pits. No detectable effects were observed for most pellet treatments, however, seeded species density was roughly 60% lower under targeted livestock treatment in the live inoculum seed pellet treatment (p=0.025; Fig. 4.7; Appendix 4, Table 17).

Soil inoculum had neutral effects across all plants

Seeded species density largely was unchanged by soil inoculum

Seeded species density was largely unchanged by the addition of live inoculum across treatments and sites. Using a pooled model comparing pasteurized and live inoculum at each site, no significant differences were detected in seeded species density at any site (Fig. 4.6d; Appendix 4, Table 18). Comparing individual treatments, rather than pooling treatments by inoculum, averaged across sites, we also detected no significant differences in seeded density comparing between pasteurized and live inoculum within most equivalent treatments (Fig. 4.4; Appendix 4, Table 19). However, live inoculum resulted in a marginal 2-fold lower seeded species density compared to pasteurized inoculum in the broadcast seeding into pit treatment (p=0.076; Appendix 4, Table 19). Consistent with the pooled results, site-specific models indicated that live inoculum did not significantly impact seeded species density within most treatments at most sites (Appendix 4, Table 20-23). One exception occurred at the Flying M site, where seeded species density was significantly lower under live inoculum in the broadcast seeded pit treatment compared to the equivalent treatment with pasteurized inoculum (~87% lower; p= 0.028; Fig. 4.5; Appendix 4, Table 23).

Soil inoculum resulted in no differences within treatment on unseeded native species

We anticipated that adding live inoculum would benefit both seeded and unseeded native species through improved soil health and positive plant-soil feedback, particularly for later successional species. However, like the results for seeded species, we did not detect increases in native species density between pasteurized and live inoculum plots within equivalent treatments (Appendix 4, Fig. 1; Appendix 4, Table 24).

Soil inoculum did not reduce introduced species reestablishment

We hypothesized that the addition of live soil inoculum would reduce the reestablishment of introduced plant species. Contrary to this expectation, live soil inoculum resulted in no effect on introduced species density within equivalent treatments averaged across site, livestock treatment and monitoring event (Appendix 4, Fig. 2; Appendix 4, Table 25).

Increased restoration intensity did not result in clear benefits to seeded species density

Finally, we hypothesized that as restoration intensity increased through the layering of restoration interventions (Fig. 4.4), we would see higher seeded species density because of strengthened direct treatment effects, including targeted livestock treatment and live soil inoculum. This hypothesis was not supported. We did not observe consistently higher mean seeded species density under these more intensive restoration interventions relative to less intensive treatments (Fig. 4.4).

DISCUSSION

Drought conditions limited treatment effects

Drylands are characterized by low water availability and high interannual climatic variability, leading to episodic conditions favorable for germination and establishment (Copeland et al., 2021; Hulvey et al., 2017; Shriver et al., 2018). Environmental conditions during and shortly after seeding are especially important, as plants in early life stages are highly vulnerable, and the transition between germination and establishment is a major bottleneck in dryland restoration efforts (Copeland et al., 2025; James et al., 2011; Larson et al., 2015; Larson & Funk, 2016). Although the use of weather forecasting across temporal scales to time seeding during favorable weather conditions is widely recommended, practical constraints often make it difficult to implement (Copeland et al., 2025; Hardegree et al., 2018; Shriver et al., 2018; Siegmund et al., 2026).

Seeding at all four sites in this experiment occurred during, and was followed by, abnormally dry conditions (Fig. 4.3), likely limiting germination and emergence of seeded species (Farrell et al., 2023). Abnormally dry conditions dominated during 2024 and 2025, with all sites experiencing periods of

moderate drought, and the more southern sites, Roosevelt and SRER, experiencing periods of severe and extreme drought conditions (Fig. 4.3). Further, most monitoring events occurred during these dry conditions known to limit seedling survival (Farrell et al., 2023). In addition to low precipitation, temperatures were well above the 30-year average (1991-2020) at most sites during the majority of the study period (Appendix 4, Fig. 3). These climatic conditions likely represented a major abiotic barrier to recruitment and likely contributed to the low densities of seeded species observed.

Treatments had context dependent effects

Despite challenging climatic conditions and relatively low seedling densities, we observed limited but informative direct treatment effects. Our most clearly supported hypothesized direct treatment effect was that propagule addition increases desirable species density. Averaged across sites, all actively seeded plots had significantly higher seeded species density compared to control plots where no seed was added. Any emergence in the control plots, therefore, reflected the natural seed bank (Fig. 4.4). At the site level, we saw greater variation in the effect of added propagules (Fig. 4.5) which may reflect differences in climatic conditions, existing seedbanks, responses to our various seeding methods (broadcast, broadcast seeding into pits, and seed pellets) and other site-specific barriers. In this study, we used the high end of the recommended seeding rate provided by seed suppliers across all four locations, but research suggests that even higher seeding rates may improve revegetation success (Barr et al., 2017; Commander et al., 2020; Genova et al., 2025; Shackelford et al., 2021). However, the additional cost incurred with higher seeding rates is not always feasible.

Seed pellets had neutral or negative effects on seeded species density

Seed pellets have been suggested as a possible alternative seeding method to broadcast seeding, in which multiple seeds are encased in a mixture of clay, amendments, and water (Gornish et al., 2019; Madsen et al., 2012). Potential benefits of seed pellets include providing protection to encased seeds between seeding and the arrival of episodic conditions favorable for germination and emergence, as well as allowing for precise delivery of soil amendments to potential germinates to ameliorate barriers such as nutrient

deficiencies (Gornish et al., 2019; Madsen et al., 2016). Seed pellets have been shown to have positive, negative, and neutral effects on seedling emergence (Gornish et al., 2019). Using our pooled model, we found that seed pellets had a neutral effect on seeded species density at three out of four sites (Fig. 4.6a) and a negative effect at one site. One challenge in seed pelletizing is selecting appropriate composition and amendments (Gornish et al., 2019; Swartz et al., 2026, Chapter 2 of this dissertation), which may partially explain the limited effects observed in this experiment. We included live or pasteurized inoculum as the amendment in our seed pellets, which was largely comprised of sand, as a result pellets quickly disintegrated rapidly after deployment even under limited precipitation and may not have offered the encased seeds effective protection until episodic germination conditions occurred.

Pitting of the soil surface had variable effects across sites

Soil surface modification through pitting has been shown to increase seeded species recruitment likely as a result of improved microsite water availability and because pits serve as sinks for resources (e.g. nutrients) from the surrounding area (Eldridge & Ding, 2023; Johnston & Mann, 2024). However, plant recruitment responses to pitting are dependent on climatic conditions and site-specific factors (Eldridge & Ding, 2023; Farrell et al., 2023; Havrilla et al., 2020; Johnston & Mann, 2024). Using our pooled model, we did not see consistent effects of pitting across sites (Fig. 4.6b). We found marginally higher seeded species density at Roosevelt and significantly higher density at Flying M, the two sites most characterized by pulse precipitation regimes, with the greatest variability in precipitation event size. We did not see differences in seeded species density between pitting and no pitting at the other two sites.

While we saw variable effects on seeded species density, pitting was the only treatment that resulted in significantly higher non-seeded native species density when averaged across sites (Appendix 4; Fig. 1), suggesting that microsite modification and associated increases in soil moisture may improve recruitment from the seed bank (Havrilla et al., 2020; Johnston & Mann, 2024). We did not observe a similar increase in unseeded introduced species (Appendix 4, Fig. 2). Since density measurements were taken within subplots that largely encompassed the pitted area of the plot, this result indicates that the pit microsite did

not promote recruitment of undesirable species, in contrast to the findings of Johnston & Mann (2024) but consistent with Havrilla et al. (2020). Further, once seedlings are established, pits have been shown to increase survival through drought conditions (Farrell et al., 2023; Johnston & Mann, 2024), so the full impact of pitting may not yet be realized at our study sites. In contrast, Eldridge & Ding (2023) demonstrate that advantages gained by pitting may be short lived because of pits filling in with sediment over time, our qualitative observations of pit fill during monitoring suggest that many pits across sites are quickly filling under two years post-pitting, indicating that benefits may not persist long term.

Live soil inoculum had neutral effects

Contrary to our hypothesis that live soil inoculation would improve soil health and support increased densities of desirable species and inhibit the reestablishment of introduced species (Duell et al., 2023), we saw almost no effect, either positive or negative, on seeded, unseeded native, or introduced species. One potential reason for this lack of effect is that our experimental sites are exposed and experience frequent windy conditions (Appendix 4, Table 5). As a result, we suspect that much of the inoculum added may have moved off site from both the broadcast inoculum and the disintegrated seed pellets, as indicated by limited inoculum visible during monitoring events, limiting the potential for new plant soil feedbacks and mycorrhizal symbiosis. A key goal of soil inoculum is to introduce a microbial community from a more intact area to enhance plant-microbial symbiosis, which can improve plant performance and resilience under harsh environmental conditions (Koziol et al., 2022; Madouh & Quoreshi, 2023; Remke et al., 2021). Soil inoculation, especially with native inoculum, has been shown to improve mycorrhizal colonization and improve restoration outcomes particularly for desirable late successional perennial species (Duell et al., 2023; Kimmell et al., 2023; Koziol et al., 2022; Marasco et al., 2023). However, these effects are likely highly context dependent, and inoculation does not always result in positive effects on the plant community (Chaudhary et al., 2020; Hoeksema et al., 2010; Peddle et al., 2025; van der Putten et al., 2016). Chaudhary et al (2020) used a whole rhizosphere soil transfer from less disturbed sites, reflecting a similar methodology to ours but without the conditioning step, and similarly showed no influence of soil microbiome transfer on

any metric of restoration success in a dryland system. The lack of detectable soil inoculum effects on species density in this study may be due to other limiting factors, including drought conditions, that constrained emergence to a degree that may have masked any influence of inoculation. With improved abiotic conditions and additional time since inoculation, the effects of our inoculum efforts may become more pronounced (Chaudhary et al., 2020). Further, biocrust inoculation studies have demonstrated the importance of soil surface stabilization through strategies such as jute cloth, on improving inoculation outcomes (e.g. Bowker et al., 2020; Gufwan et al., 2025). Other biocrust studies have demonstrated that abiotic conditions can also limit inoculation success and steps such as shading may be a strategy to overcome harsh environmental conditions (Antoninka et al., 2020; Young et al., 2019). Future studies using soil inoculation may want to consider testing these soil stabilization and shading strategies.

Targeted livestock treatment did not consistently improve or reduce seeded species density

Like our soil inoculation results, targeted livestock treatment had a largely neutral effect (Fig. 4.6c). Averaged across sites, we see both positive and negative effects of livestock treatment on seeded species density when comparing equivalent treatments (Fig. 4.7). Our targeted livestock treatment was brief and occurred only once directly following treatment installation and seeding, this amount of hoof action may not have been sufficient to create microsites and improve soil-seed contact, for example another study used slightly longer duration treatments on similarly sized areas (Driessen et al., 2011). Finally, much like our soil inoculum findings, the abiotic conditions and limited recruitment may have masked secondary treatment effects from targeted livestock treatments. Further research on the incorporation of livestock in dryland restoration efforts is needed.

Intensifying restoration interventions provided limited benefits under drought conditions

Ultimately, the persistent drought and high wind conditions across all our experimental sites likely constrained possible treatment effects. Seed-based restoration success has been clearly linked to episodic recruitment events with sufficient moisture and limited evaporation (Farrell et al., 2023; Siegmund et al., 2026). While some of our treatments were designed to ameliorate the impacts of dry conditions, the degree

of drought was likely more than these treatments could overcome. We found that combining multiple treatments, reflecting high restoration intensity, did not provide consistent benefits, and the increased cost and effort did not lead to commensurate improvements under such challenging climatic conditions. Continued monitoring of this experiment is needed since with improved moisture and more time for community assembly processes to occur treatment effects may become more fully realized. (Gornish & dos Santos, 2016). Additionally, reseeding efforts should be considered as many studies have shown that repeated seedings as a bet hedging strategy improves the likelihood of seeding during favorable conditions for increased germination and establishment (Copeland et al., 2025; Shackelford et al., 2021; Svejcar et al., 2023). Overall, our results suggest that dryland restoration strategies should prioritize aligning restoration efforts with favorable climatic windows (Farrell et al., 2023; Siegmund et al., 2026), as the effectiveness of even well-designed interventions aimed at overcoming specific barriers is strongly mediated by environmental conditions. While the treatments demonstrated here have the potential to improve dryland restoration outcomes, particularly under favorable moisture conditions, their added cost and complexity may not be justified during periods of drought.

CONCLUSION

Improving dryland restoration outcomes is inherently challenging, as demonstrated throughout this dissertation. Limited recruitment of seeded species is a common outcome in dryland seed-based restoration (Shackelford et al., 2021). However, even small gains in desirable plant emergence and establishment can have meaningful ecological consequences (Davies et al., 2024; Madsen et al., 2016). Across the chapters of this dissertation, we identified several approaches that may help achieve these incremental gains and improve dryland restoration outcomes. Specifically, we show that increasing desirable propagule availability, modifying soil microsites to buffer extreme climatic conditions, and integrating invasive species management might be effective strategies. Chapters 1 and 4 add to the growing evidence that modifying the soil surface microsite to retain moisture and reduce temperatures can improve desirable species emergence (Farrell et al., 2023; Havrilla et al., 2020; Neilly et al., 2025). Chapter 2 demonstrates that incorporating activated carbon into seed pellets may allow for a single-entry restoration intervention, where weed management and reseeding happen simultaneously, enabling seedlings to emerge and establish under reduced competitive pressure from introduced species offered by preemergent herbicides using technologically simple approaches (Davies et al., 2024; Swartz et al., 2026, Chapter 2 of this disseration). In Chapters 1 and 3, we show that invasive species management using herbicide can be an effective tool, but must be used with careful consideration of potential non-target impacts, awareness of site characteristics and potential unintended consequences such as secondary invasion (Pearson et al., 2016). Our results emphasize the need for integrated and iterative approaches to invasive species management (Brandt et al., 2023).

A central theme throughout this research is the key role of climatic conditions in constraining restoration success (Shackelford et al., 2021; Shriver et al., 2018; Stapleton et al., 2024; Svejcar et al., 2023; Svejcar & Kildisheva, 2017). Our findings add to the growing body of literature calling for the use of short to long range weather forecasting to increase the likelihood of seeding during episodic conditions favorable

for recruitment (Farrell et al., 2023; Siegmund et al., 2026). They also support the need for continued research into trait-based approaches to design seed mixes more resilient to climate extremes (Copeland et al., 2025; Dalziell et al., 2022), with an emphasis on drought conditions in drylands, and the use of bet hedging approaches such as repeated seeding efforts over time (Svejcar et al., 2023). Although in both of our seed-based restoration (SBR) field studies (Chapters 1 and 4), seeded species emergence and establishment were constrained by climatic conditions, we demonstrated treatments that may have greater efficacy if applied during years with favorable weather conditions. Pairing restoration treatments targeted to overcome specific biotic and abiotic barriers (Copeland et al., 2021; Hulvey & Aigner, 2014) with better forecasting to improve SBR outcomes will be essential as drylands expand, degradation continues, and aridity intensifies. It is imperative to prevent ecosystems from crossing thresholds into nearly irreversible highly degraded states (Berdugo et al., 2020; Suding & Hobbs, 2009).

A highlight of the research presented in this dissertation was the opportunity to collaborate with multi-disciplinary teams spanning local, federal to Tribal governments, non-profits, restoration practitioners and ecologists across the discipline. While our findings did not produce universal or consistent treatment effects, they contributed meaningful insights gained through both successes and failures. Perhaps more importantly, this work strengthened collaborative teams ready to continue advancing adaptive, community-engaged, and climate-adapted restoration strategies in dryland ecosystems (Martin, 2017; Simonson et al., 2021; Winkler et al., 2020).

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APPENDIX 1

Tables

Table 1: Seed mix used in our field restoration experiment. Included species represent a range of plant functional groups and are all commonly used in restoration efforts on the Colorado Plateau. Pure live seed (PLS) was calculated as the product of laboratory germination and purity provided by the seed supplier and is reported here as a percentage. The recommended seeding rate reflects the highest rate recommended by the seed supplier. This rate was divided by PLS (expressed as a proportion) to calculate the PLS-adjusted seeding rates used in the experiment. Asterisks (*) indicate that at least one individual emerged during the experiment.

Scientific Name	Common Name	Plant Functional Group	Germination (%)	Purity (%)	Pure Live Seed (% PLS)	Seeding Rate (g/m^2)	PLS Adjusted Seeding Rate (g/m^2)	PLS Adjusted Seeding Rate ($seeds/m^2$)
*Achillea millefolium**	Common Yarrow	Perennial Forb	97	98	95	0.112	0.118	738
Asclepias tuberosa	Butterfly Weed	Perennial Forb	66	96	63	0.785	1.238	279
*Hedysarum boreale**	Utah Sweet Vetch	Perennial Forb	82	98	81	2.802	3.478	613
Heterotheca villosa	Hairy False Goldenaster	Perennial Forb	90	59	53	0.112	0.211	157
*Linum lewisii**	Flax	Perennial Forb	69	100	69	0.673	0.976	516
Nicotiana attenuata	Cayote Tobacco	Perennial Forb	91	96	87	0.112	0.128	1116
*Penstemon palmeri**	Palmer's penstemon	Perennial Forb	95	97	92	0.336	0.364	490
*Krascheninnikovia lanata**	Winterfat	Perennial Subshrub	79	94	74	0.673	0.906	224
Achnatherum hymenoides	Indian Ricegrass	Perennial Grass (C3)	97	100	97	1.345	1.392	433
Elymus elymoides	Bottlebrush Squirreltail	Perennial Grass (C3)	85	97	82	0.673	0.816	345
*Hesperostipa comata**	Needle and Thread Grass	Perennial Grass (C3)	55	99	54	0.673	1.235	313
*Sporobolus cryptandrus**	Sand Dropseed	Perennial Grass (C3)	93	99	92	0.224	0.243	2839
*Aristida purpurea**	Purple Three-Awn	Perennial Grass (C4)	98	73	72	0.673	0.940	518
*Bouteloua gracilis**	Blue Grama	Perennial Grass (C4)	72	84	60	0.336	0.556	919
*Pleuraphis jamesii**	Galletta	Perennial Grass (C4)	94	81	76	1.345	1.767	619
Sporabolus airoides	Alkali Sacaton	Perennial Grass (C4)	50	98	49	0.336	0.686	2647
Artemisia tridentata	Big Sagebrush	Perennial Shrub	85	29	25	0.056	0.227	1251
Atriplex canescens	Four-wing Saltbush	Perennial Shrub	54	99	53	0.112	0.211	24
Ericameria nauseosa	Rubber Rabbit Brush	Perennial Shrub	85	41	35	0.056	0.161	213

Table 2: Number of zero observations of seeded species per experimental treatment and monitoring event group. *Italics* indicate groups where all observations are equal to zero.

Experimental Treatment	Season/Year Monitored	Total Observations (n)	Number of zero observations (n=0)	Percentage of zero observations
Control (Unseeded)	*Spring 2023*	*8*	*8*	*100%*
	Fall 2023	*8*	*8*	*100%*
	Spring 2024	*8*	*8*	*100%*
	Fall 2024	*8*	*8*	*100%*
Broadcast	*Spring 2023*	*8*	*8*	*100%*
	Fall 2023	8	4	50%
	Spring 2024	*8*	*8*	*100%*
	Fall 2024	8	4	50%
Seed Pellets	Spring 2023	8	7	88%
	Fall 2023	*8*	*8*	*100%*
	Spring 2024	8	6	75%
	Fall 2024	8	7	88%
Media Luna	Spring 2023	8	5	63%
	Fall 2023	8	6	75%
	Spring 2024	8	5	63%
	Fall 2024	8	3	38%
Coarse Woody Debris	*Spring 2023*	*8*	*8*	*100%*
	Fall 2023	*8*	*8*	*100%*
	Spring 2024	8	6	75%
	Fall 2024	8	6	75%

Table 3: Results of a mixed effects negative binomial regression model with a log link evaluating the effect of herbicide application (yes/no), treatment (control (unseeded), broadcast, seed pellets, media luna, coarse woody debris), and monitoring event (May 2023, September 2023, May 2024, September 2024), and all two-way interactions on A. repens density. Estimates are presented as incidence rate ratios (IRRs) obtained by exponentiating model coefficients. The model includes random effect to account for repeat measures.

Term	Estimate (β)	Standard Error	Statistic	p-value
(Intercept)	11.100	5.110	5.229	<0.001
Herbicide	0.073	0.044	-4.352	<0.001
Broadcast	1.517	0.904	0.699	0.485
Seed Pellets	0.563	0.357	-0.906	0.365
Media Luna	0.835	0.517	-0.292	0.770
Coarse Woody Debris	0.940	0.590	-0.098	0.922
Fall 2023	0.968	0.484	-0.065	0.948
Spring 2024	1.310	0.674	0.525	0.600
Fall 2024	1.073	0.518	0.147	0.883
Herbicide : Broadcast	0.616	0.400	-0.746	0.455
Herbicide : Seed Pellets	0.364	0.248	-1.484	0.138
Herbicide : Media Luna	0.355	0.241	-1.527	0.127
Herbicide : Coarse Woody Debris	0.130	0.095	-2.785	0.005
Herbicide : September 2023	23.890	12.364	6.132	<0.001
Herbicide : May 2024	1.805	0.975	1.093	0.274
Herbicide : September 2024	6.073	3.211	3.412	0.001
Broadcast : September 2023	0.733	0.463	-0.491	0.623
Seed Pellets : September 2023	2.191	1.527	1.125	0.261
Media Luna : September 2023	0.982	0.668	-0.027	0.978
Coarse Woody Debris : September 2023	0.753	0.520	-0.411	0.681
Broadcast : May 2024	0.782	0.495	-0.388	0.698
Seed Pellets : May 2024	1.076	0.759	0.104	0.918
Media Luna : May 2024	0.957	0.653	-0.064	0.949
Coarse Woody Debris : May 2024	0.746	0.528	-0.415	0.678
Broadcast : September 2024	0.438	0.274	-1.320	0.187
Seed Pellets : September 2024	1.805	1.237	0.861	0.389
Media Luna : September 2024	1.329	0.901	0.419	0.675
Coarse Woody Debris : September 2024	0.890	0.627	-0.165	0.869

Table 4: Pairwise contrasts comparing *A. repens* density by herbicide application (no/yes), experimental treatment (control (unseeded), broadcast, seed pellets, media luna, coarse woody debris) and monitoring event (May 2023, September 2023, May 2024, September 2024). Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction.

Herbicide Contrast	Treatment	Monitoring Event	Ratio	Standard Error	z Ratio	p-value
No / Yes	Control (Unseeded)	May 2023	13.640	8.189	4.352	<0.001
No / Yes	Broadcast	May 2023	22.149	13.360	5.136	<0.001
No / Yes	Seed Pellets	May 2023	37.445	24.825	5.465	<0.001
No / Yes	Media Luna	May 2023	38.472	25.127	5.588	<0.001
No / Yes	Coarse Woody Debris	May 2023	104.633	75.569	6.439	<0.001
No / Yes	Control (Unseeded)	September 2023	0.571	0.292	-1.097	0.273
No / Yes	Broadcast	September 2023	0.927	0.474	-0.148	0.882
No / Yes	Seed Pellets	September 2023	1.567	0.832	0.847	0.397
No / Yes	Media Luna	September 2023	1.610	0.862	0.890	0.373
No / Yes	Coarse Woody Debris	September 2023	4.380	2.603	2.485	0.013
No / Yes	Control (Unseeded)	May 2024	7.556	4.267	3.581	<0.001
No / Yes	Broadcast	May 2024	12.270	6.903	4.456	<0.001
No / Yes	Seed Pellets	May 2024	20.743	12.807	4.911	<0.001
No / Yes	Media Luna	May 2024	21.311	12.969	5.027	<0.001
No / Yes	Coarse Woody Debris	May 2024	57.961	39.676	5.931	<0.001
No / Yes	Control (Unseeded)	September 2024	2.246	1.196	1.519	0.129
No / Yes	Broadcast	September 2024	3.647	1.957	2.411	0.016
No / Yes	Seed Pellets	September 2024	6.165	3.378	3.320	0.001
No / Yes	Media Luna	September 2024	6.334	3.460	3.380	0.001
No / Yes	Coarse Woody Debris	September 2024	17.228	10.631	4.613	<0.001

Table 5: Pairwise contrasts comparing introduced species density (including *A. repens*) by herbicide application (no/yes), experimental treatment (control (unseeded), broadcast, seed pellets, media luna, coarse woody debris) and monitoring event (May 2023, September 2023, May 2024, September 2024). Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction.

Herbicide Contrast	Treatment	Monitoring Event	Ratio	Standard Error	z Ratio	p-value
No / Yes	Control (Unseeded)	May 2023	1.315	0.486	0.741	0.459
No / Yes	Broadcast	May 2023	1.290	0.476	0.690	0.490
No / Yes	Seed Pellets	May 2023	1.561	0.575	1.209	0.227
No / Yes	Media Luna	May 2023	1.136	0.424	0.342	0.732
No / Yes	Coarse Woody Debris	May 2023	2.159	0.811	2.048	0.041
No / Yes	Control (Unseeded)	September 2023	1.040	0.390	0.104	0.917
No / Yes	Broadcast	September 2023	1.020	0.380	0.053	0.958
No / Yes	Seed Pellets	September 2023	1.234	0.460	0.565	0.572
No / Yes	Media Luna	September 2023	0.899	0.342	-0.281	0.779
No / Yes	Coarse Woody Debris	September 2023	1.707	0.659	1.385	0.166
No / Yes	Control (Unseeded)	May 2024	0.795	0.292	-0.624	0.533
No / Yes	Broadcast	May 2024	0.780	0.286	-0.678	0.498
No / Yes	Seed Pellets	May 2024	0.944	0.346	-0.156	0.876
No / Yes	Media Luna	May 2024	0.687	0.255	-1.010	0.313
No / Yes	Coarse Woody Debris	May 2024	1.306	0.486	0.717	0.473
No / Yes	Control (Unseeded)	September 2024	2.246	1.196	1.519	0.129
No / Yes	Broadcast	September 2024	0.605	0.225	-1.350	0.177
No / Yes	Seed Pellets	September 2024	0.594	0.220	-1.405	0.160
No / Yes	Media Luna	September 2024	0.719	0.266	-0.894	0.372
No / Yes	Coarse Woody Debris	September 2024	0.523	0.195	-1.735	0.083

Table 6: Results of a mixed effects negative binomial regression model with a log link function evaluating the effect of herbicide application (yes/no), treatment (control (unseeded), broadcast, seed pellets, media luna, coarse woody debris), and monitoring event (May 2023, September 2023, May 2024, September 2024), and all two-way interactions on introduced species (including *A. repens*) density. Estimates are presented as incidence rate ratios (IRRs) obtained by exponentiating model coefficients. The model includes random effect to account for repeat measures.

Term	Estimate (IRR)	Standard Error	Statistic	p-value
(Intercept)	48.068	15.432	12.063	<0.001
Herbicide	0.761	0.281	-0.741	0.459
Broadcast	1.112	0.475	0.248	0.804
Seed Pellets	1.128	0.483	0.282	0.778
Media Luna	0.745	0.318	-0.688	0.491
Coarse Woody Debris	0.769	0.336	-0.600	0.549
September 2023	0.782	0.279	-0.690	0.490
May 2024	1.587	0.554	1.324	0.186
September 2024	1.288	0.458	0.711	0.477
Herbicide : Broadcast	1.019	0.467	0.042	0.967
Herbicide : Seed Pellets	0.842	0.386	-0.374	0.708
Herbicide : Media Luna	1.157	0.535	0.315	0.753
Herbicide : Coarse Woody Debris	0.609	0.283	-1.068	0.286
Herbicide : September 2023	1.265	0.377	0.787	0.432
Herbicide : May 2024	1.653	0.469	1.772	0.076
Herbicide : September 2024	2.172	0.635	2.651	0.008
Broadcast : September 2023	0.737	0.339	-0.665	0.506
Seed Pellets : September 2023	0.900	0.413	-0.230	0.818
Media Luna : September 2023	1.171	0.553	0.334	0.738
Coarse Woody Debris : September 2023	0.272	0.131	-2.712	0.007
Broadcast : May 2024	0.847	0.377	-0.374	0.709
Seed Pellets : May 2024	1.122	0.499	0.259	0.796
Media Luna : May 2024	1.119	0.501	0.250	0.802
Coarse Woody Debris : May 2024	0.854	0.383	-0.352	0.725
Broadcast : September 2024	0.946	0.433	-0.121	0.904
Seed Pellets : September 2024	1.449	0.664	0.809	0.419
Media Luna : September 2024	1.691	0.774	1.147	0.251
Coarse Woody Debris : September 2024	0.747	0.344	-0.633	0.526

Table 7: Pairwise contrasts comparing introduced species density (including A. repens) among experimental treatments (control (unseeded), broadcast, seed pellets, media luna, coarse woody debris) relative to the unseeded control within each monitoring event (May 2023, September 2023, May 2024, September 2024), averaged across herbicide application. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction.

Treatment Contrast	Monitoring Event	Ratio	Standard Error	z Ratio	p-value
Broadcast / Control (Unseeded)	May 2023	1.123	0.403	0.322	0.922
Seed Pellets / Control (Unseeded)	May 2023	1.036	0.372	0.097	0.922
Media Luna / Control (Unseeded)	May 2023	0.802	0.290	-0.610	0.922
Coarse Woody Debris / Control (Unseeded)	May 2023	0.600	0.218	-1.407	0.637
Broadcast / Control (Unseeded)	September 2023	0.827	0.301	-0.522	0.866
Seed Pellets / Control (Unseeded)	September 2023	0.932	0.339	-0.194	0.866
Media Luna / Control (Unseeded)	September 2023	0.939	0.351	-0.169	0.866
Coarse Woody Debris / Control (Unseeded)	September 2023	0.163	0.063	-4.694	<0.001
Broadcast / Control (Unseeded)	May 2024	0.951	0.335	-0.144	0.886
Seed Pellets / Control (Unseeded)	May 2024	1.162	0.409	0.426	0.886
Media Luna / Control (Unseeded)	May 2024	0.897	0.318	-0.308	0.886
Coarse Woody Debris / Control (Unseeded)	May 2024	0.513	0.182	-1.882	0.239
Broadcast / Control (Unseeded)	September 2024	1.062	0.384	0.167	0.868
Seed Pellets / Control (Unseeded)	September 2024	1.500	0.543	1.120	0.525
Media Luna / Control (Unseeded)	September 2024	1.356	0.485	0.849	0.528
Coarse Woody Debris / Control (Unseeded)	September 2024	0.448	0.162	-2.219	0.106

Table 8: Pairwise PERMANOVA contrasts among experimental treatments. Values are false discovery rate adjusted p-values; no contrasts are significant.

	Control	Broadcast	Seed Pellets	Media Luna
Broadcast	0.895	-	-	-
Seed Pellets	0.895	0.895	-	-
Media Luna	0.895	0.895	0.895	-
Coarse Woody Debris	0.413	0.885	0.413	0.413

Table 9: Results from a linear mixed-effects model evaluating the effects of treatment, year and their interaction on mean soil temperature (°C) during the spring growing season (March 21-May15). Estimates are presented on the response scale and represent differences relative to the reference categories (broadcast seeding treatment and 2023). The model includes random effects for plot and sampling date to account for repeated measures and shared temporal variation.

Term	Estimate	Standard Error	Statistic	p-value
(Intercept)	11.200	0.485	23.108	<0.001
Seed Pellets	-0.352	0.265	-1.328	0.184
Media Luna	0.783	0.265	2.953	0.003
Coarse Woody Debris	-1.564	0.285	-5.487	<0.001
2024	-0.538	0.630	-0.855	0.393
Seed Pellets : 2024	0.343	0.056	6.100	<0.001
Media Luna : 2024	0.306	0.056	5.449	<0.001
Coarse Woody Debris : 2024	0.835	0.060	13.895	<0.001

Table 10: Results from a linear mixed-effects model evaluating the effects of treatment, year and their interaction on mean soil moisture (%) during the spring growing season (March 21-May15). Estimates are presented on the response scale and represent differences relative to the reference categories (broadcast seeding treatment and 2023). The model includes random effects for plot and sampling date to account for repeated measures and shared temporal variation.

Term	Estimate	Standard Error	Statistic	p-value
(Intercept)	45.496	2.372	19.179	<0.001
Seed Pellets	3.056	2.867	1.066	0.287
Media Luna	5.488	2.867	1.914	0.056
Coarse Woody Debris	-5.682	2.968	-1.915	0.056
2024	16.621	1.795	9.257	<0.001
Seed Pellets : 2024	-7.312	0.637	-11.476	<0.001
Media Luna : 2024	-0.876	0.637	-1.375	0.169
Coarse Woody Debris : 2024	1.836	0.658	2.791	0.005

Table 11: Pairwise contrasts comparing soil temperature (°C) among experimental treatment within each year during the spring growing season (March 21-May15) relative to the Broadcast treatment, averaged across herbicide treatment. Estimates represent differences in mean soil moisture on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction.

Contrast	Year	Estimate	Standard Error	z Ratio	p-value
Seed Pellets - Broadcast	2023	-0.352	0.265	-1.328	0.184
Media Luna - Broadcast	2023	0.783	0.265	2.953	0.005
Coarse Woody Debris - Broadcast	2023	-1.564	0.285	-5.487	<0.001
Seed Pellets - Broadcast	2024	-0.010	0.265	-0.036	0.971
Media Luna - Broadcast	2024	1.090	0.265	4.114	<0.001
Coarse Woody Debris - Broadcast	2024	-0.729	0.285	-2.560	0.016

Table 12: Pairwise contrasts comparing soil moisture (%) among experimental treatment within each year during the spring growing season (March 21-May15) relative to the Broadcast treatment, averaged across herbicide treatment. Estimates represent differences in mean soil moisture on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction.

Contrast	Year	Estimate	Standard Error	z Ratio	p-value
Seed Pellets - Broadcast	2023	3.056	2.867	1.066	0.287
Media Luna - Broadcast	2023	5.488	2.867	1.914	0.083
Coarse Woody Debris - Broadcast	2023	-5.682	2.968	-1.915	0.083
Seed Pellets - Broadcast	2024	-4.256	2.863	-1.487	0.194
Media Luna - Broadcast	2024	4.612	2.863	1.611	0.194
Coarse Woody Debris - Broadcast	2024	-3.845	2.963	-1.298	0.194

Figures

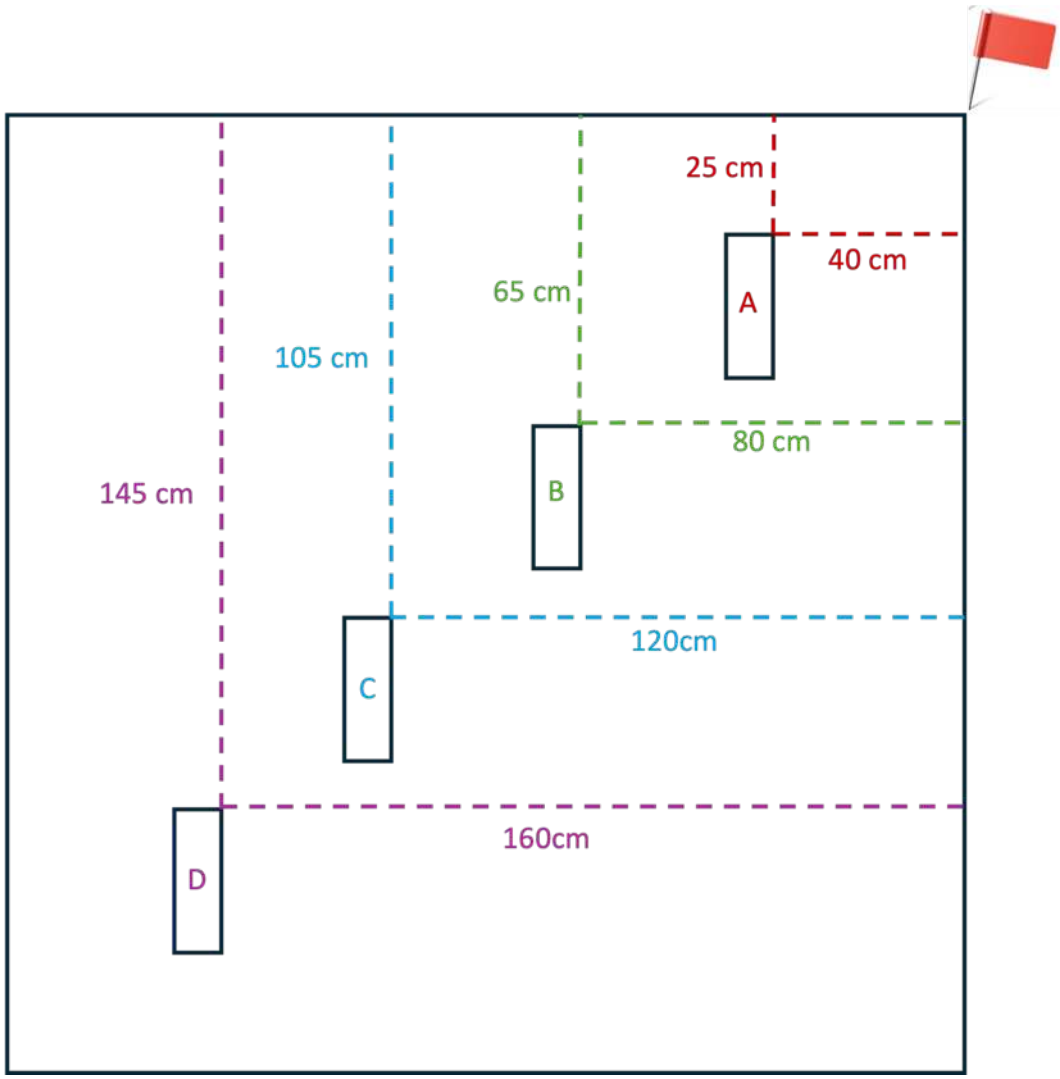

Figure 1: Schematic showing subplots used to collect vegetation density and height across the plot to capture potential spatial variability.

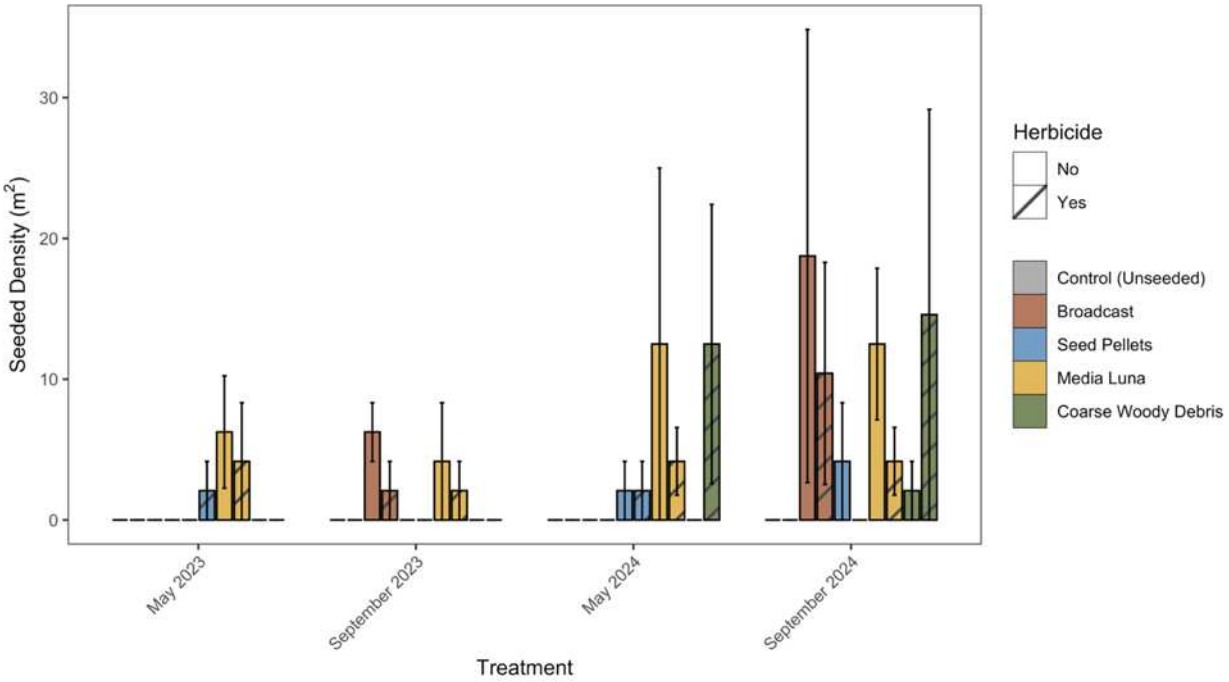

Figure 2: Mean observed (± standard error) seeded seedling density scaled to per square meter across treatments and monitoring events. Herbicide application is indicated by patterned bars. Herbicide appears to have variable impacts on seeded density with substantial variation.

APPENDIX 2

Tables

Table 1: Seed mix used in the Activated Carbon x Herbicide Study.

Activated Carbon x Herbicide Study				
Scientific Name	**Common Name**	**Plant Functional Group**	**Germination**	**Purity**
Achillea millefolium	Western Yarrow	Perennial Forb	97%	98%
Asclepias tuberosa	Butterfly Weed	Perennial Forb	66%	96%
Hedysarum boreale	Utah Sweet Vetch	Perennial Forb	82%	98%
Heterotheca villosa	Hairy False Goldenaster	Perennial Forb	90%	59%
Linum lewisii	Blue Flax	Perennial Forb	69%	100%
Nicotiana attenuata	Cayote Tobacco	Perennial Forb	91%	96%
Penstemon palmeri	Palmer's Penstemon	Perennial Forb	95%	97%
Krascheninnikovia lanata	Winterfat	Perennial Forb/Subshrub	79%	94%
Achnatherum hymenoides	Indian Ricegrass	Perennial Grass (C3)	97%	100%
Elymus elymoides	Bottlebrush Squirreltail	Perennial Grass (C3)	85%	97%
Hesperostipa comata	Needle and Thread Grass	Perennial Grass (C3)	55%	99%
Sporobolus cryptandrus	Sand Dropseed	Perennial Grass (C3)	93%	99%
Aristida purpurea	Purple Three-Awn	Perennial Grass (C4)	98%	73%
Bouteloua gracilis	Blue Grama	Perennial Grass (C4)	72%	84%
Hilaria (Pleuraphis) jamesii	Galletta	Perennial Grass (C4)	94%	81%
Sporabolus airoides	Alkali Sacaton	Perennial Grass (C4)	50%	98%
Artemisia tridentata	Big Sagebrush	Perennial Shrub	85%	29%
Atriplex canescens	Four-wing Saltbush	Perennial Shrub	54%	99%
Ericameria nauseosa	Rabbit Brush	Perennial Shrub	85%	41%

Table 2: Seed mix used in the Composition Study.

Composition Study				
Scientific Name	**Common Name**	**Functional Group**	**Germination**	**Purity**
Achillea millefolium	Western Yarrow	Perennial Forb	97%	98%
Hedysarum boreale	Utah Sweet Vetch	Perennial Forb	82%	98%
Linum lewisii	Blue Flax	Perennial Forb	69%	100%
Penstemon palmeri	Palmer's Penstemon	Perennial Forb	95%	97%
Krascheninnikovia lanata	Winterfat	Perennial Forb/Subshrub	79%	94%
Achnatherum hymenoides	Indian Ricegrass	Perennial Grass (C3)	97%	100%
Elymus elymoides	Bottlebrush Squirreltail	Perennial Grass (C3)	85%	97%
Hesperostipa comata	Needle and Thread Grass	Perennial Grass (C3)	55%	99%
Sporobolus cryptandrus	Sand Dropseed	Perennial Grass (C3)	93%	99%
Bouteloua curtipendula	Sideoats grama	Perennial Grass (C4)	15%	49%
Bouteloua gracilis	Blue Grama	Perennial Grass (C4)	72%	84%
Hilaria (Pleuraphis) jamesii	Galletta	Perennial Grass (C4)	94%	81%

Table 3: Recipes used in Activated Carbon x Herbicide and Composition studies.

Seed Pellet Recipes				
Study and Treatment	**Component**	**Ratio**	**Ingredient**	**Quantity (Volume)**
Activated Carbon x Herbicide Study: Recipe	Seed	2	Seed	0.5 tsp
	Tackifier	4	Straw	1 tsp
	Clay	4	Red Art Clay	1 tsp
Composition Study: High Clay Recipe	Seed	1	Seed	0.25 tsp
	Amendment	4	Straw or Powdered Activated Carbon or Granular Activated Carbon	1 tsp
	Clay	4	Red Art Clay	1 tsp
Composition Study: Medium Clay Recipe	Seed	1	Seed	0.25 tsp
	Amendment	8	Straw or Powdered Activated Carbon or Granular Activated Carbon	2 tsp
	Clay	4	Red Art Clay	1 tsp
Composition Study: Low Clay Recipe	Seed	1	Seed	0.25 tsp
	Amendment	12	Straw or Powdered Activated Carbon or Granular Activated Carbon	3 tsp
	Clay	4	Red Art Clay	1 tsp

Experiment 1 (Activated Carbon x Herbicide)

Table 4: Pairwise contrasts of emergence by herbicide treatment and plant functional group.

Contrast	**Odds Ratio**	**Standard Error**	**z Ratio**	**p-value**
no herbicide grass / herbicide grass	4.1755	0.4073	14.6517	<0.0001
no herbicide grass / no herbicide forb_shrub	1.9460	0.1000	12.9613	<0.0001
no herbicide grass / herbicide forb_shrub	8.6974	0.8753	21.4935	<0.0001
herbicide grass / no herbicide forb_shrub	0.4660	0.0461	-7.7212	<0.0001
herbicide grass / herbicide forb_shrub	2.0830	0.1371	11.1484	<0.0001
no herbicide forb_shrub / herbicide forb_shrub	4.4694	0.4532	14.7667	<0.0001

Table 5: Pairwise contrasts of emergence by herbicide treatment and seeding method.

Contrast	Odds Ratio	Standard Error	z Ratio	p-value
no herbicide broadcast / herbicide broadcast	3.7851	0.4832	10.4260	<0.0001
no herbicide broadcast / no herbicide seed pellet	0.6357	0.0785	-3.6695	0.0003
no herbicide broadcast / herbicide seed pellet	3.1342	0.3983	8.9892	<0.0001
herbicide broadcast / no herbicide seed pellet	0.1679	0.0214	-14.0304	<0.0001
herbicide broadcast / herbicide seed pellet	0.8280	0.1068	-1.4625	0.1436
no herbicide seed pellet / herbicide seed pellet	4.9304	0.6238	12.6106	<0.0001

Table 6: Pairwise contrasts of emergence by seeding method, herbicide treatment and carbon additions.

Contrast	Odds Ratio	Standard Error	z Ratio	p-value
broadcast no carbon no herbicide / seed pellet no carbon no herbicide	0.5140	0.0897	-3.8141	0.0002
broadcast no carbon no herbicide / broadcast carbon no herbicide	0.8452	0.1487	-0.9560	0.3516
broadcast no carbon no herbicide / seed pellet carbon no herbicide	0.6645	0.1165	-2.3323	0.0240
broadcast no carbon no herbicide / broadcast no carbon herbicide	2.8588	0.5137	5.8456	<0.0001
broadcast no carbon no herbicide / seed pellet no carbon herbicide	4.6002	0.8327	8.4304	<0.0001
broadcast no carbon no herbicide / broadcast carbon herbicide	4.2358	0.7659	7.9836	<0.0001
broadcast no carbon no herbicide / seed pellet carbon herbicide	1.8048	0.3216	3.3131	0.0014
seed pellet no carbon no herbicide / broadcast carbon no herbicide	1.6444	0.2859	2.8603	0.0059
seed pellet no carbon no herbicide / seed pellet carbon no herbicide	1.2928	0.2238	1.4833	0.1546
seed pellet no carbon no herbicide / broadcast no carbon herbicide	5.5620	0.9905	9.6356	<0.0001
seed pellet no carbon no herbicide / seed pellet no carbon herbicide	8.9501	1.6072	12.2048	<0.0001
seed pellet no carbon no herbicide / broadcast carbon herbicide	8.2411	1.4780	11.7602	<0.0001
seed pellet no carbon no herbicide / seed pellet carbon herbicide	3.5113	0.6196	7.1183	<0.0001
broadcast carbon no herbicide / seed pellet carbon no herbicide	0.7862	0.1373	-1.3773	0.1814
broadcast carbon no herbicide / broadcast no carbon herbicide	3.3824	0.6063	6.7987	<0.0001
broadcast carbon no herbicide / seed pellet no carbon herbicide	5.4427	0.9830	9.3808	<0.0001

broadcast carbon no herbicide / broadcast carbon herbicide	5.0116	0.9041	8.9343	<0.0001
broadcast carbon no herbicide / seed pellet carbon herbicide	2.1353	0.3795	4.2688	<0.0001
seed pellet carbon no herbicide / broadcast no carbon herbicide	4.3023	0.7687	8.1661	<0.0001
seed pellet carbon no herbicide / seed pellet no carbon herbicide	6.9229	1.2469	10.7427	<0.0001
seed pellet carbon no herbicide / broadcast carbon herbicide	6.3745	1.1467	10.2971	<0.0001
seed pellet carbon no herbicide / seed pellet carbon herbicide	2.7160	0.4810	5.6417	<0.0001
broadcast no carbon herbicide / seed pellet no carbon herbicide	1.6091	0.2948	2.5964	0.0126
broadcast no carbon herbicide / broadcast carbon herbicide	1.4817	0.2712	2.1479	0.0370
broadcast no carbon herbicide / seed pellet carbon herbicide	0.6313	0.1143	-2.5413	0.0141
seed pellet no carbon herbicide / broadcast carbon herbicide	0.9208	0.1694	-0.4486	0.6537
seed pellet no carbon herbicide / seed pellet carbon herbicide	0.3923	0.0715	-5.1365	<0.0001
broadcast carbon herbicide / seed pellet carbon herbicide	0.4261	0.0775	-4.6882	<0.0001

Experiment 2 (Composition)

Table 7: Pairwise contrast of emergence by seeding method.

Contrast	Odds Ratio	Standard Error	z Ratio	p-value
Broadcast / Seed Pellet	0.6410	0.1586	-1.7970	0.0723

Table 8: Pairwise contrasts of emergence by clay to amendment ratio and activated carbon additions in seed pellets.

Contrast	Odds Ratio	Standard Error	z Ratio	p-value
No Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (Low Clay)	-0.7019	0.2871	-2.4446	0.1305
No Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (Low Clay)	-0.0175	0.2931	-0.0598	0.9770
No Carbon Seed Pellet (Low Clay) - No Carbon Seed Pellet (Medium Clay)	-0.2713	0.2899	-0.9358	0.4854
No Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (Medium Clay)	-0.2794	0.2894	-0.9653	0.4854
No Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (Medium Clay)	-0.8726	0.2809	-3.1067	0.0341
No Carbon Seed Pellet (Low Clay) - No Carbon Seed Pellet (High Clay)	-0.2934	0.2884	-1.0173	0.4854
No Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (High Clay)	-0.5845	0.2870	-2.0365	0.1368
No Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (High Clay)	-0.6649	0.3024	-2.1984	0.1314
Powder Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (Low Clay)	0.6844	0.2766	2.4741	0.1305
Powder Carbon Seed Pellet (Low Clay) - No Carbon Seed Pellet (Medium Clay)	0.4307	0.2753	1.5644	0.3440
Powder Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (Medium Clay)	0.4226	0.2749	1.5373	0.3440
Powder Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (Medium Clay)	-0.1707	0.2683	-0.6360	0.6515
Powder Carbon Seed Pellet (Low Clay) - No Carbon Seed Pellet (High Clay)	0.4086	0.2749	1.4861	0.3529
Powder Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (High Clay)	0.1174	0.2725	0.4310	0.7998
Powder Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (High Clay)	0.0371	0.2757	0.1344	0.9770
Granular Carbon Seed Pellet (Low Clay) - No Carbon Seed Pellet (Medium Clay)	-0.2538	0.2801	-0.9060	0.4866
Granular Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (Medium Clay)	-0.2618	0.2805	-0.9336	0.4854
Granular Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (Medium Clay)	-0.8551	0.2712	-3.1525	0.0341
Granular Carbon Seed Pellet (Low Clay) - No Carbon Seed Pellet (High Clay)	-0.2758	0.2802	-0.9846	0.4854
Granular Carbon Seed Pellet (Low Clay) - Powder Carbon Seed Pellet (High Clay)	-0.5670	0.2785	-2.0355	0.1368
Granular Carbon Seed Pellet (Low Clay) - Granular Carbon Seed Pellet (High Clay)	-0.6474	0.2805	-2.3075	0.1314
No Carbon Seed Pellet (Medium Clay) - Powder Carbon Seed Pellet (Medium Clay)	-0.0081	0.2794	-0.0289	0.9770
No Carbon Seed Pellet (Medium Clay) - Granular Carbon Seed Pellet (Medium Clay)	-0.6013	0.2724	-2.2078	0.1314

No Carbon Seed Pellet (Medium Clay) - No Carbon Seed Pellet (High Clay)	-0.0221	0.2787	-0.0792	0.9770
No Carbon Seed Pellet (Medium Clay) - Powder Carbon Seed Pellet (High Clay)	-0.3132	0.2772	-1.1298	0.4854
No Carbon Seed Pellet (Medium Clay) - Granular Carbon Seed Pellet (High Clay)	-0.3936	0.2798	-1.4066	0.3795
Powder Carbon Seed Pellet (Medium Clay) - Granular Carbon Seed Pellet (Medium Clay)	-0.5932	0.2720	-2.1807	0.1314
Powder Carbon Seed Pellet (Medium Clay) - No Carbon Seed Pellet (High Clay)	-0.0140	0.2783	-0.0503	0.9770
Powder Carbon Seed Pellet (Medium Clay) - Powder Carbon Seed Pellet (High Clay)	-0.3052	0.2757	-1.1067	0.4854
Powder Carbon Seed Pellet (Medium Clay) - Granular Carbon Seed Pellet (High Clay)	-0.3855	0.2801	-1.3765	0.3795
Granular Carbon Seed Pellet (Medium Clay) - No Carbon Seed Pellet (High Clay)	0.5792	0.2715	2.1331	0.1317
Granular Carbon Seed Pellet (Medium Clay) - Powder Carbon Seed Pellet (High Clay)	0.2881	0.2694	1.0695	0.4854
Granular Carbon Seed Pellet (Medium Clay) - Granular Carbon Seed Pellet (High Clay)	0.2077	0.2745	0.7566	0.5777
No Carbon Seed Pellet (High Clay) - Powder Carbon Seed Pellet (High Clay)	-0.2911	0.2761	-1.0544	0.4854
No Carbon Seed Pellet (High Clay) - Granular Carbon Seed Pellet (High Clay)	-0.3715	0.2804	-1.3251	0.3921
Powder Carbon Seed Pellet (High Clay) - Granular Carbon Seed Pellet (High Clay)	-0.0804	0.2781	-0.2891	0.8971

Figures

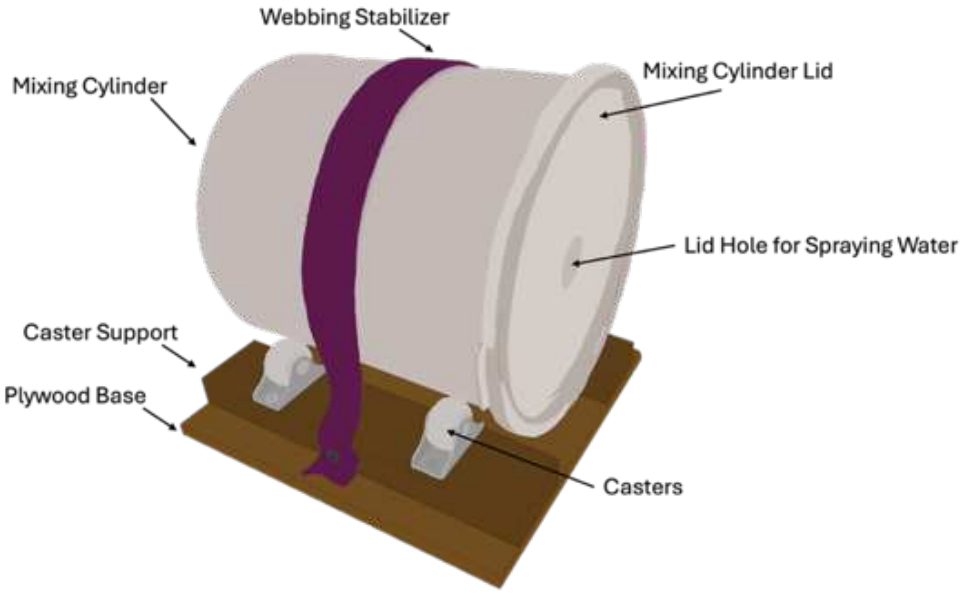

Figure 1: Tabletop seed pelletizer hand crank diagram.

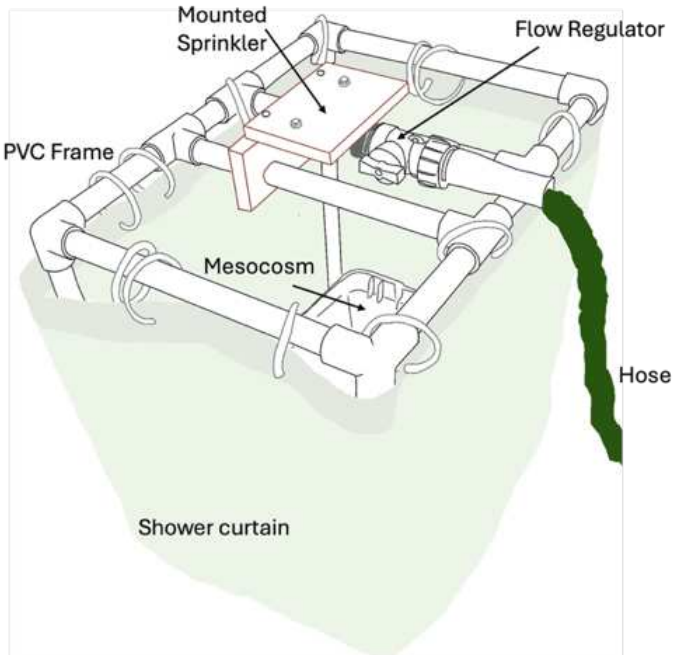

Figure 2: Custom watering device diagram with a sprinkler mounted upside down on a PVC frame that fits over each mesocosm.

APPENDIX 3

Tables

Table 1: Fixed effects including interactions and random effects used in beta regression models for each response variable modeled.

Response Variable	Fixed Effects	Interactions	Random Effects
A. elatius Canopy Cover (proportion)	Indaziflam Treatment (+/-), Site (Foothills/Post-Ag), Year (2023, 2024, 2025)	All	Unique Plot Identifier, Observer
Introduced Species Canopy Cover (proportion)	Indaziflam Treatment (+/-), Site (Foothills/Post-Ag), Year (2023, 2024, 2025)	Treatment x Site, Treatment x Year, Site x Year	Unique Plot Identifier, Observer
Native Species Canopy Cover (proportion)- Foothills only model	Indaziflam Treatment (+/-), Year (2023, 2024, 2025)	All	Unique Plot Identifier, Observer

Table 2: Results of a mixed-effects beta regression model evaluating the effects indaziflam treatment (+/-), site (Post-Ag and Foothills), and year (2023, 2024, 2025) and their interactions on *A. elatius* canopy cover as a proportion. The model includes random effects to account for repeat measures and variability by observer. Estimates are on the odds scale.

	Response Variable: *A. elatius* Canopy Cover			
Predictor	**Estimate (b)**	**Standard Error**	**Statistic**	**p-value**
Intercept – Post Ag, Control, 2023	1.088	0.341	0.246	0.805
Indaziflam Treatment	0.273	0.506	-2.565	0.010
Site - Shanahan	0.245	0.510	-2.753	0.006
Year - 2024	3.128	0.322	3.545	< 0.001
Year - 2025	7.130	0.360	5.464	< 0.001
Indaziflam Treatment: Site - Shanahan	2.932	0.736	1.461	0.1440
Indaziflam Treatment: Year - 2024	0.169	0.493	-3.604	< 0.001
Indaziflam Treatment: Year - 2025	0.177	0.488	-3.555	< 0.001
Site - Shanahan: Year - 2024	0.200	0.495	-3.254	0.001
Site - Shanahan: Year - 2025	0.081	0.522	-4.818	< 0.001
Indaziflam Treatment: Site - Shanahan: Year - 2024	4.835	0.735	2.143	0.032
Indaziflam Treatment: Site - Shanahan: Year - 2025	7.021	0.725	2.689	0.007

Table 3: Results of a mixed-effects beta regression model evaluating the effects indaziflam treatment (+/-), site (Post-Ag and Foothills), and year (2023, 2024, 2025) and their two-way interactions on introduced species canopy cover as a proportion. The model includes random effects to account for repeat measures and variability by observer. Estimates are on the odds scale.

	Response Variable: Introduced Species Canopy Cover			
Predictor	**Estimate (b)**	**Standard Error**	**Statistic**	**p-value**
Intercept – Post Ag, Control, 2023	2.334	0.812	2.437	0.015
Indaziflam Treatment	0.333	0.156	-2.344	0.019
Site - Shanahan	0.199	0.094	-3.404	< 0.001
Year - 2024	2.053	0.678	2.178	0.0294
Year - 2025	13.139	4.717	7.173	< 0.001
Indaziflam Treatment: Site - Shanahan	3.475	2.114	2.048	0.041
Indaziflam Treatment: Year - 2024	0.367	0.136	-2.707	0.007
Indaziflam Treatment: Year - 2025	0.314	0.121	-3.012	0.003
Site - Shanahan: Year - 2024	0.336	0.124	-2.958	0.003
Site - Shanahan: Year - 2025	0.081	0.031	-6.490	< 0.001

Table 4: Results of a mixed-effects beta regression model evaluating the effects indaziflam treatment (+/-) and year (2023, 2024, 2025) and their interactions on native species canopy cover as a proportion using only the Foothills site. The model includes random effects to account for repeat measures and variability by observer. Estimates are on the odds scale.

	Response Variable: Native Species Canopy Cover (Foothills Only Model)			
Predictor	**Estimate (b)**	**Standard Error**	**Statistic**	**p-value**
Intercept – Control, 2023	0.771	0.242	-0.829	0.407
Indaziflam Treatment	1.196	0.530	0.404	0.686
Year - 2024	0.688	0.146	-1.758	0.079
Year - 2025	2.202	0.464	3.742	< 0.001
Indaziflam Treatment: Year - 2024	1.628	0.481	1.650	0.099
Indaziflam Treatment: Year - 2025	1.546	0.473	1.425	0.154

APPENDIX 4

Tables

Table 1: Seed mix used in our field restoration experiment. Included species represent a range of plant functional groups and are all commonly used in restoration efforts on the Colorado Plateau. The recommended seeding rate reflects the highest rate recommended by the seed supplier.

Scientific Name	Common Name	Functional Group	PLS Seeding Rate (g PLS/m^2)	PLS Seeding Rate (PLS/m^2)
Aristida purpurea	Purple three-awn	Perennial Grass (C4)	0.614	338
Atriplex canescens	Fourwing saltbush	Shrub	0.313	36
Baileya multiradiata	Desert marigold	Perennial Forb	0.218	505
Bouteloua gracilis	Blue grama	Perennial Grass (C4)	0.279	508
Bouteloua rothrockii	Rothrock's grama	Perennial Grass (C4)	0.204	1061
Dalea candida	White prairie clover	Perennial Forb	1.252	828
Elymus elymoides	Squireltail	Perennial Grass (C3)	0.514	218
Krascheninnikovia lanata	Winterfat	Perennial Forb/Sub Shrub	0.502	136
Linum lewisii	Blue flax	Perennial Forb	0.562	210
Machaeranthera tanacetifolia	Tanseyleaf Tansyaster	Annual Forb	0.536	482
Pascopyrum smithii	Western wheatgrass	Perennial Grass (C3)	1.698	584
Penstemon palmeri	Palmer's penstemon	Perennial Forb	0.311	418
Plantago ovata	Desert Indianwheat	Annual Forb	0.215	154
Poa secunda	Sandberg bluegrass	Perennial Grass (C3)	0.412	950
Senna covesii	Coues' cassia	Perennial Forb/Sub Shrub	1.069	259
Sphaeralcea ambigua	Desert globemallow	Annual Forb	0.381	420
Vulpia octoflora	Sixweeks fescue	Annual Grass (C3)	0.283	602

Table 2: Additional species included in live soil inoculum conditioning process.

Scientific Name	Common Name	Source
Tagetes erecta	Marigold “Sparky” Variety	Back to the Roots
Allium ampeloprasum var. porrum	King Richard Leeks	Botanical Interests

Table 3: Model specification information for cross site, site-specific, and pooled models used.

Model	Response Variable	Model Family (Link Function)	Fixed Effects	Random Effects	Number of Observations
Cross-Site Seeded Model	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment × Livestock Treatment + Site + Monitoring Event	1|Unique ID	957
Roosevelt Seeded Model	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment + Livestock Treatment + Monitoring Event	1|Unique ID	240
BarTBar Seeded Model	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment + Livestock Treatment + Monitoring Event	1|Unique ID	240
SRER Seeded Model	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment + Livestock Treatment + Monitoring Event	1|Unique ID	240
FlyingM Seeded Model	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment + Livestock Treatment + Monitoring Event	1|Unique ID	237
Cross-Site Seeded Model (Pooled Seed Pellet)	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Seed Pellet Treatment × Targeted Livestock Treatment × Site + Monitoring Event	1|Unique ID	957
Cross-Site Seeded Model (Pooled Ground Modification - Pit)	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Pit Treatment × Targeted Livestock Treatment × Site + Monitoring Event	1|Unique ID	957
Cross-Site Seeded Model (Pooled Livestock Treatment)	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Targeted Livestock Treatment × Site + Monitoring Event	1|Unique ID	957
Cross-Site Seeded Model (Pooled Soil Inoculum)	Seeded Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Inoculum Treatment × Targeted Livestock Treatment × Site + Monitoring Event	1|Unique ID	957
Cross-Site Naturally Occurring Native Species Model	Naturally Occurring Native Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment × Livestock Treatment + Site + Monitoring Event	1|Unique ID	957
Cross-Site Introduced Species Model	Introduced Species Density ($0.5m^2$)	Negative Binomial (Log Link)	Experimental Treatment × Livestock Treatment + Site + Monitoring Event	1|Unique ID	957

Table 4: Precipitation event characteristics for each study (2024-2025) derived from PRISM daily data. Events were defined as one or more days with precipitation > 0 mm. Values represent mean annual metrics across both years.

Site	Mean Precipitation Events per Year	Mean Event Size (mm)	90th Percentile Event Size (mm)	Coefficient of Variation (CV) of Event Size	Mean Dry Spell (days)	Max Dry Spell (days)	Mean Annual Precipitation
Roosevelt	27	11.4	32.9	1.53	11.7	86	318.7
BarTBar	29	10.4	23.1	1.05	10.4	64	313.2
SRER	28	11.8	25.0	0.95	11.0	86	339.9
FlyingM	31	11.3	24.9	1.14	9.6	64	363.1

Table 5: Mean daily maximum and absolute maximum 10-meter wind gust (m s^{-1}) for each study site during 2024–2025 derived from ERA5 hourly reanalysis data provided by the Copernicus Climate Change Service Climate Data Store.

Site	Mean Daily Maximum Wind Gust (m s^{-1})	Maximum Daily Wind Gust (m s^{-1})
Roosevelt	10.95	23.3
BarTBar	12	26.2
SRER	11.4	23.9
FlyingM	12.2	26.5

Table 6: Pairwise contrasts comparing seeded species density for each experimental treatment relative to the Control Pasteurized Inoculum treatment, averaged across site, targeted livestock treatment and monitoring event. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$.

Contrast	Ratio	Standard Error	z Ratio	p-value	Significance
Broadcast Seed Pasteurized Inoculum / Control Pasteurized Inoculum	9.027	3.237	6.135	<0.001	*
Broadcast Seed Pit Pasteurized Inoculum / Control Pasteurized Inoculum	12.719	4.544	7.118	<0.001	*
Seed Pellet Pasteurized Inoculum / Control Pasteurized Inoculum	5.161	1.868	4.533	<0.001	*
Seed Pellet Pit Pasteurized Inoculum / Control Pasteurized Inoculum	6.823	2.433	5.384	<0.001	*
Control Live Inoculum / Control Pasteurized Inoculum	1.267	0.530	0.565	0.572	
Broadcast Seed Live Inoculum / Control Pasteurized Inoculum	8.832	3.157	6.095	<0.001	*
Broadcast Seed Pit Live Inoculum / Control Pasteurized Inoculum	6.521	2.332	5.243	<0.001	*
Seed Pellet Live Inoculum / Control Pasteurized Inoculum	5.455	1.981	4.673	<0.001	*
Seed Pellet Pit Live Inoculum / Control Pasteurized Inoculum	4.333	1.566	4.058	<0.001	*

Table 7: Results from a mixed effects negative binomial regression model with a log link evaluating the effect of experimental treatment, targeted livestock treatment, site, monitoring event and the interaction between experimental treatment and targeted livestock treatment on seeded species density. Estimates are presented as incidence rate ratios (IRRs) obtained by exponentiating model coefficients. The model includes random effect to account for repeat measures. Significance is indicated by an asterisk (*) at $\alpha = 0.05$.

Term	Estimate (IRR)	Standard Error	Statistic	p-value	Significance
(Intercept)	0.874	0.327	-0.359	0.719	
Broadcast Seed Pasteurized Inoculum	3.811	1.651	3.088	0.002	*
Broadcast Seed Pit Pasteurized Inoculum	4.632	2.009	3.535	<0.001	*
Seed Pellet Pasteurized Inoculum	3.633	1.555	3.013	0.003	*
Seed Pellet Pit Pasteurized Inoculum	3.801	1.635	3.104	0.002	*
Control Live Inoculum	1.755	0.799	1.236	0.216	
Broadcast Seed Live Inoculum	3.335	1.449	2.773	0.006	*
Broadcast Seed Pit Live Inoculum	2.094	0.919	1.683	0.092	
Seed Pellet Live Inoculum	4.519	1.934	3.524	<0.001	*
Seed Pellet Pit Live Inoculum	1.910	0.863	1.433	0.152	
Targeted Livestock Treatment	0.275	0.165	-2.158	0.031	*
BarTBar	0.307	0.063	-5.798	<0.001	*
SRER	0.202	0.040	-8.031	<0.001	*
FlyingM	0.465	0.097	-3.675	<0.001	*
Spring 2025	1.836	0.317	3.516	<0.001	*
Fall 2025	0.592	0.103	-3.008	0.003	*
Broadcast Seed Pasteurized Inoculum : Targeted Livestock Treatment	5.611	3.985	2.429	0.015	*
Broadcast Seed Pit Pasteurized Inoculum : Targeted Livestock Treatment	7.539	5.328	2.858	0.004	*
Seed Pellet Pasteurized Inoculum : Targeted Livestock Treatment	2.018	1.456	0.973	0.331	
Seed Pellet Pit Pasteurized Inoculum : Targeted Livestock Treatment	3.222	2.296	1.643	0.100	
Control Live Inoculum : Targeted Livestock Treatment	0.521	0.435	-0.781	0.435	
Broadcast Seed Live Inoculum : Targeted Livestock Treatment	7.012	4.953	2.757	0.006	*
Broadcast Seed Pit Live : Targeted Livestock Treatment	9.700	6.938	3.177	0.001	*
Seed Pellet Live Inoculum : Targeted Livestock Treatment	1.458	1.053	0.522	0.602	
Seed Pellet Pit Live Inoculum : Targeted Livestock Treatment	5.145	3.782	2.229	0.026	*

Table 8: Pairwise contrasts comparing seeded species density at the Roosevelt site for each experimental treatment relative to the Control Pasteurized Inoculum treatment, averaged across targeted livestock treatment and monitoring event. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$.

Roosevelt					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Broadcast Seed Pasteurized Inoculum / Control Pasteurized Inoculum	2.951	1.331	2.400	0.018	*
Broadcast Seed Pit Pasteurized Inoculum / Control Pasteurized Inoculum	3.993	1.762	3.138	0.003	*
Seed Pellet Pasteurized Inoculum / Control Pasteurized Inoculum	6.206	2.677	4.231	<0.001	*
Seed Pellet Pit Pasteurized Inoculum / Control Pasteurized Inoculum	4.909	2.130	3.666	0.001	*
Control Live Inoculum / Control Pasteurized Inoculum	0.910	0.446	-0.192	0.847	
Broadcast Seed Live Inoculum / Control Pasteurized Inoculum	4.914	2.166	3.612	0.001	*
Broadcast Seed Pit Live Inoculum / Control Pasteurized Inoculum	5.588	2.476	3.884	<0.001	*
Seed Pellet Live Inoculum / Control Pasteurized Inoculum	3.522	1.554	2.854	0.006	*
Seed Pellet Pit Live Inoculum / Control Pasteurized Inoculum	3.496	1.532	2.857	0.006	*

Table 9: Pairwise contrasts comparing seeded species density at the BarTBar site for each experimental treatment relative to the Control Pasteurized Inoculum treatment, averaged across targeted livestock treatment and monitoring event. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$ and marginal significance is indicated by a period (.) at $\alpha = 0.1$.

BarTBar					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Broadcast Seed Pasteurized Inoculum / Control Pasteurized Inoculum	8.045	5.407	3.102	0.017	*
Broadcast Seed Pit Pasteurized Inoculum / Control Pasteurized Inoculum	6.863	4.627	2.857	0.019	*
Seed Pellet Pasteurized Inoculum / Control Pasteurized Inoculum	2.502	1.778	1.290	0.296	
Seed Pellet Pit Pasteurized Inoculum / Control Pasteurized Inoculum	2.358	1.688	1.199	0.297	
Control Live Inoculum / Control Pasteurized Inoculum	1.916	1.413	0.881	0.425	
Broadcast Seed Live Inoculum / Control Pasteurized Inoculum	6.241	4.286	2.666	0.023	*
Broadcast Seed Pit Live Inoculum / Control Pasteurized Inoculum	3.184	2.230	1.654	0.177	
Seed Pellet Live Inoculum / Control Pasteurized Inoculum	4.005	2.759	2.014	0.099	.
Seed Pellet Pit Live Inoculum / Control Pasteurized Inoculum	0.862	0.693	-0.185	0.853	

Table 10: Pairwise contrasts comparing seeded species density at the SRER site for each experimental treatment relative to the Control Pasteurized Inoculum treatment, averaged across targeted livestock treatment and monitoring event. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Marginal significance is indicated by a period (.) at $\alpha = 0.1$.

SRER					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Broadcast Seed Pasteurized Inoculum / Control Pasteurized Inoculum	6.705	5.244	2.433	0.067	.
Broadcast Seed Pit Pasteurized Inoculum / Control Pasteurized Inoculum	7.652	5.978	2.604	0.067	.
Seed Pellet Pasteurized Inoculum / Control Pasteurized Inoculum	2.548	2.098	1.136	0.329	
Seed Pellet Pit Pasteurized Inoculum / Control Pasteurized Inoculum	2.803	2.289	1.263	0.329	
Control Live Inoculum / Control Pasteurized Inoculum	1.385	1.195	0.378	0.706	
Broadcast Seed Live Inoculum / Control Pasteurized Inoculum	4.370	3.498	1.842	0.196	
Broadcast Seed Pit Live Inoculum / Control Pasteurized Inoculum	3.511	2.854	1.545	0.275	
Seed Pellet Live Inoculum / Control Pasteurized Inoculum	1.430	1.245	0.411	0.706	
Seed Pellet Pit Live Inoculum / Control Pasteurized Inoculum	2.669	2.178	1.203	0.329	

Table 11: Pairwise contrasts comparing seeded species density at the FlyingM site for each experimental treatment relative to the Control Live Inoculum treatment, averaged across targeted livestock treatment and monitoring event. The Control Live Inoculum treatment was used as the reference level due to no emergence in the Control Pasteurized Inoculum plots. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$ and marginal significance is indicated by a period (.) at $\alpha = 0.1$.

FlyingM					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Broadcast Seed Pasteurized Inoculum / Control Live Inoculum	3.256	2.892	1.329	0.210	
Broadcast Seed Pit Pasteurized Inoculum / Control Live Inoculum	35.531	30.490	4.161	<0.001	*
Seed Pellet Pasteurized Inoculum / Control Live Inoculum	2.250	2.050	0.890	0.373	
Seed Pellet Pit Pasteurized Inoculum / Control Live Inoculum	11.834	10.058	2.907	0.015	*
Broadcast Seed Live Inoculum / Control Live Inoculum	10.545	8.970	2.769	0.015	*
Broadcast Seed Pit Live Inoculum / Control Live Inoculum	4.708	4.151	1.757	0.105	
Seed Pellet Live Inoculum / Control Live Inoculum	7.915	6.798	2.409	0.032	*
Seed Pellet Pit Live Inoculum / Control Live Inoculum	6.230	5.393	2.113	0.055	.

Table 12: Pairwise contrasts comparing seeded species density among seed pellet and broadcast seeded pooled treatments and site, averaged across monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$.

Seed Pellet						
Site	**Contrast**	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Roosevelt	Pellet/No Pellet	1.454	0.385	1.415	0.157	
BarTBar	Pellet/No Pellet	0.460	0.140	-2.547	0.011	*
SRER	Pellet/No Pellet	0.646	0.206	-1.371	0.170	
FlyingM	Pellet/No Pellet	0.987	0.305	-0.044	0.965	

Table 13: Pairwise contrasts comparing seeded species density among pooled ground modification (pits) and site, averaged across monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at α = 0.05 and marginal significance is indicated by a period (.) at α = 0.1.

Ground Modification (Pit) Treatment						
Site	**Contrast**	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Roosevelt	Pit/No Pit	1.614	0.466	1.659	0.097	.
BarTBar	Pit/No Pit	0.785	0.251	-0.757	0.449	
SRER	Pit/No Pit	1.425	0.474	1.065	0.287	
FlyingM	Pit/No Pit	2.947	0.933	3.413	0.001	*

Table 14: Pairwise contrasts comparing naturally occurring native species density for each experimental treatment relative to the Control Pasteurized Inoculum treatment, averaged across site, targeted livestock treatment and monitoring event. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at α = 0.05 and marginal significance is indicated by a period (.) at α = 0.1.

Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Broadcast Seed Pasteurized Inoculum / Control Pasteurized Inoculum	1.164	0.233	0.758	0.504	
Broadcast Seed Pit Pasteurized Inoculum / Control Pasteurized Inoculum	1.579	0.317	2.274	0.052	.
Seed Pellet Pasteurized Inoculum / Control Pasteurized Inoculum	1.263	0.252	1.168	0.312	
Seed Pellet Pit Pasteurized Inoculum / Control Pasteurized Inoculum	1.578	0.314	2.293	0.052	*
Control Live Inoculum / Control Pasteurized Inoculum	1.376	0.276	1.592	0.167	
Broadcast Seed Live Inoculum / Control Pasteurized Inoculum	1.425	0.284	1.775	0.137	
Broadcast Seed Pit Live Inoculum / Control Pasteurized Inoculum	1.988	0.403	3.392	0.003	*
Seed Pellet Live Inoculum / Control Pasteurized Inoculum	1.052	0.212	0.249	0.803	
Seed Pellet Pit Live Inoculum / Control Pasteurized Inoculum	2.048	0.420	3.493	0.003	*

Table 15: Pairwise contrasts comparing introduced species density for each experimental treatment relative to the Control Pasteurized Inoculum treatment, averaged across site, targeted livestock treatment and monitoring event. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. No contrasts are significant at $\alpha = 0.05$.

Contrast	Ratio	Standard Error	z Ratio	p-value	Significance
Broadcast Seed Pasteurized Inoculum / Control Pasteurized Inoculum	0.803	0.185	-0.950	0.814	
Broadcast Seed Pit Pasteurized Inoculum / Control Pasteurized Inoculum	0.832	0.193	-0.793	0.814	
Seed Pellet Pasteurized Inoculum / Control Pasteurized Inoculum	1.082	0.249	0.342	0.825	
Seed Pellet Pit Pasteurized Inoculum / Control Pasteurized Inoculum	0.840	0.195	-0.751	0.814	
Control Live Inoculum / Control Pasteurized Inoculum	0.646	0.151	-1.876	0.546	
Broadcast Seed Live Inoculum / Control Pasteurized Inoculum	0.777	0.179	-1.095	0.814	
Broadcast Seed Pit Live Inoculum / Control Pasteurized Inoculum	1.052	0.241	0.221	0.825	
Seed Pellet Live Inoculum / Control Pasteurized Inoculum	0.883	0.203	-0.541	0.825	
Seed Pellet Pit Live Inoculum / Control Pasteurized Inoculum	0.943	0.217	-0.257	0.825	

Table 16: Pairwise contrasts comparing seeded species density among pooled livestock treatment and site, averaged across monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$.

Targeted Livestock Treatment						
Site	**Contrast**	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Roosevelt	Targeted Livestock Treatment/ No Livestock	0.748	0.214	-1.013	0.311	
BarTBar	Targeted Livestock Treatment/ No Livestock	1.031	0.324	0.097	0.923	
SRER	Targeted Livestock Treatment/ No Livestock	2.062	0.686	2.175	0.030	*
FlyingM	Targeted Livestock Treatment/ No Livestock	1.402	0.435	1.088	0.277	

Table 17: Pairwise contrasts comparing seeded species density between targeted livestock treatment and no livestock treatment within experimental treatment, averaged across site and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at α = 0.05 and marginal significance is indicated by a period (+) at α = 0.1.

Treatment	Contrast	Ratio	Standard Error	z Ratio	p-value	Significance
Control Pasteurized Inoculum	Targeted Livestock Treatment/No Livestock	0.275	0.165	-2.158	0.031	*
Broadcast Seed Pasteurized Inoculum	Targeted Livestock Treatment/No Livestock	1.545	0.592	1.135	0.257	
Broadcast Seed Pit Pasteurized Inoculum	Targeted Livestock Treatment/No Livestock	2.076	0.785	1.930	0.054	.
Seed Pellet Pasteurized Inoculum	Targeted Livestock Treatment/No Livestock	0.556	0.225	-1.451	0.147	
Seed Pellet Pit Pasteurized Inoculum	Targeted Livestock Treatment/No Livestock	0.887	0.344	-0.309	0.757	
Control Live Inoculum	Targeted Livestock Treatment/No Livestock	0.143	0.084	-3.323	0.001	*
Broadcast Seed Live Inoculum	Targeted Livestock Treatment/No Livestock	1.930	0.730	1.740	0.082	.
Broadcast Seed Pit Live Inoculum	Targeted Livestock Treatment/No Livestock	2.671	1.052	2.493	0.013	*
Seed Pellet Live Inoculum	Targeted Livestock Treatment/No Livestock	0.401	0.163	-2.248	0.025	*
Seed Pellet Pit Live Inoculum	Targeted Livestock Treatment/No Livestock	1.417	0.606	0.814	0.416	

Table 18: Pairwise contrasts comparing seeded species density among pooled inoculum type (live versus pasteurized) and site, averaged across livestock treatment and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. No contrasts are significant at $\alpha = 0.05$.

Soil Inoculum Treatment						
Site	**Contrast**	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Roosevelt	Live Inoculum/Pasteurized Inoculum	0.947	0.265	-0.194	0.846	
BarTBar	Live Inoculum/Pasteurized Inoculum	0.767	0.237	-0.860	0.390	
SRER	Live Inoculum/Pasteurized Inoculum	0.650	0.214	-1.308	0.191	
FlyingM	Live Inoculum/Pasteurized Inoculum	0.862	0.266	-0.482	0.629	

Table 19: Pairwise contrasts comparing seeded species density under live versus pasteurized inoculum within each experimental treatment averaged across site, targeted livestock treatment and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Marginal significance is indicated by a period (.) at $\alpha = 0.1$.

Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Control Live Inoculum/Control Pasteurized Inoculum	1.267	0.530	0.565	0.938	
Broadcast Seed Live Inoculum/ Broadcast Seed Pasteurized Inoculum	0.978	0.272	-0.078	0.938	
Broadcast Seed Pit Live Inoculum/ Broadcast Seed Pit Pasteurized Inoculum	0.513	0.141	-2.427	0.076	.
Seed Pellet Live Inoculum/ Seed Pellet Pasteurized Inoculum	1.057	0.303	0.193	0.938	
Seed Pellet Pit Live Inoculum/ Seed Pellet Pit Pasteurized Inoculum	0.635	0.178	-1.620	0.263	

Table 21: Pairwise contrasts comparing seeded species density under live versus pasteurized inoculum within each experimental treatment at the BarTBar site, averaged across targeted livestock treatment and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. No contrasts were significant at $\alpha = 0.05$.

BarTBar					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Control Live Inoculum/Control Pasteurized Inoculum	1.916	1.413	0.881	0.549	
Broadcast Seed Live Inoculum/ Broadcast Seed Pasteurized Inoculum	0.776	0.405	-0.487	0.626	
Broadcast Seed Pit Live Inoculum/ Broadcast Seed Pit Pasteurized Inoculum	0.464	0.267	-1.336	0.454	
Seed Pellet Live Inoculum/ Seed Pellet Pasteurized Inoculum	1.601	0.974	0.773	0.549	
Seed Pellet Pit Live Inoculum/ Seed Pellet Pit Pasteurized Inoculum	0.365	0.270	-1.362	0.454	

Table 22: Pairwise contrasts comparing seeded species density under live versus pasteurized inoculum within each experimental treatment at the SRER site, averaged across targeted livestock treatment and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. No contrasts were significant at $\alpha = 0.05$.

SRER					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Control Live Inoculum/Control Pasteurized Inoculum	1.385	1.195	0.378	0.882	
Broadcast Seed Live Inoculum/ Broadcast Seed Pasteurized Inoculum	0.652	0.404	-0.691	0.816	
Broadcast Seed Pit Live Inoculum/ Broadcast Seed Pit Pasteurized Inoculum	0.459	0.303	-1.178	0.816	
Seed Pellet Live Inoculum/ Seed Pellet Pasteurized Inoculum	0.561	0.431	-0.752	0.816	
Seed Pellet Pit Live Inoculum/ Seed Pellet Pit Pasteurized Inoculum	0.952	0.662	-0.070	0.944	

Table 23: Pairwise contrasts comparing seeded species density under live versus pasteurized inoculum within each experimental treatment at the FlyingM site, averaged across targeted livestock treatment and monitoring events. The contrast between Control Pasteurized Inoculum and Control Live Inoculum could not be estimated due to no emergence in the Control Pasteurized Inoculum treatment. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. Significance is indicated by an asterisk (*) at $\alpha = 0.05$.

FlyingM					
Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Broadcast Seed Live Inoculum/ Broadcast Seed Pasteurized Inoculum	3.238	2.427	1.568	0.156	
Broadcast Seed Pit Live Inoculum/ Broadcast Seed Pit Pasteurized Inoculum	0.133	0.099	-2.697	0.028	*
Seed Pellet Live Inoculum/ Seed Pellet Pasteurized Inoculum	3.518	2.770	1.597	0.156	
Seed Pellet Pit Live Inoculum/ Seed Pellet Pit Pasteurized Inoculum	0.526	0.377	-0.896	0.370	

Table 24: Pairwise contrasts comparing naturally occurring native species density under live versus pasteurized inoculum within each experimental treatment, averaged across site, targeted livestock treatment and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. No contrasts were significant at $\alpha = 0.05$.

Contrast	**Ratio**	**Standard Error**	**z Ratio**	**p-value**	**Significance**
Control Pasteurized Inoculum/Control Live Inoculum	1.376	0.276	1.592	0.360	
Broadcast Seed Pasteurized Inoculum/ Broadcast Seed Live Inoculum	1.225	0.243	1.023	0.360	
Broadcast Seed Pit Pasteurized Inoculum/ Broadcast Seed Pit Live Inoculum	1.259	0.254	1.141	0.360	
Seed Pellet Pasteurized Inoculum/ Seed Pellet Pasteurized Inoculum	0.833	0.167	-0.915	0.360	
Seed Pellet Pit Pasteurized Inoculum/ Seed Pellet Pit Live Inoculum	1.297	0.263	1.284	0.360	

Table 25: Pairwise contrasts comparing introduced species density under live versus pasteurized inoculum within each experimental treatment, averaged across site, targeted livestock treatment and monitoring events. Ratios are on the response scale. P-values were adjusted for multiple comparisons using a false discovery rate (FDR) correction. No contrasts were significant at $\alpha = 0.05$.

Contrast	Ratio	Standard Error	z Ratio	p-value	Significance
Control Pasteurized Inoculum/Control Live Inoculum	0.646	0.151	-1.876	0.303	
Broadcast Seed Pasteurized Inoculum/ Broadcast Seed Live Inoculum	0.967	0.222	-0.144	0.885	
Broadcast Seed Pit Pasteurized Inoculum/ Broadcast Seed Pit Live Inoculum	1.265	0.287	1.035	0.614	
Seed Pellet Pasteurized Inoculum/ Seed Pellet Pasteurized Inoculum	0.816	0.184	-0.899	0.614	
Seed Pellet Pit Pasteurized Inoculum/ Seed Pellet Pit Live Inoculum	1.123	0.256	0.508	0.765	

Figures

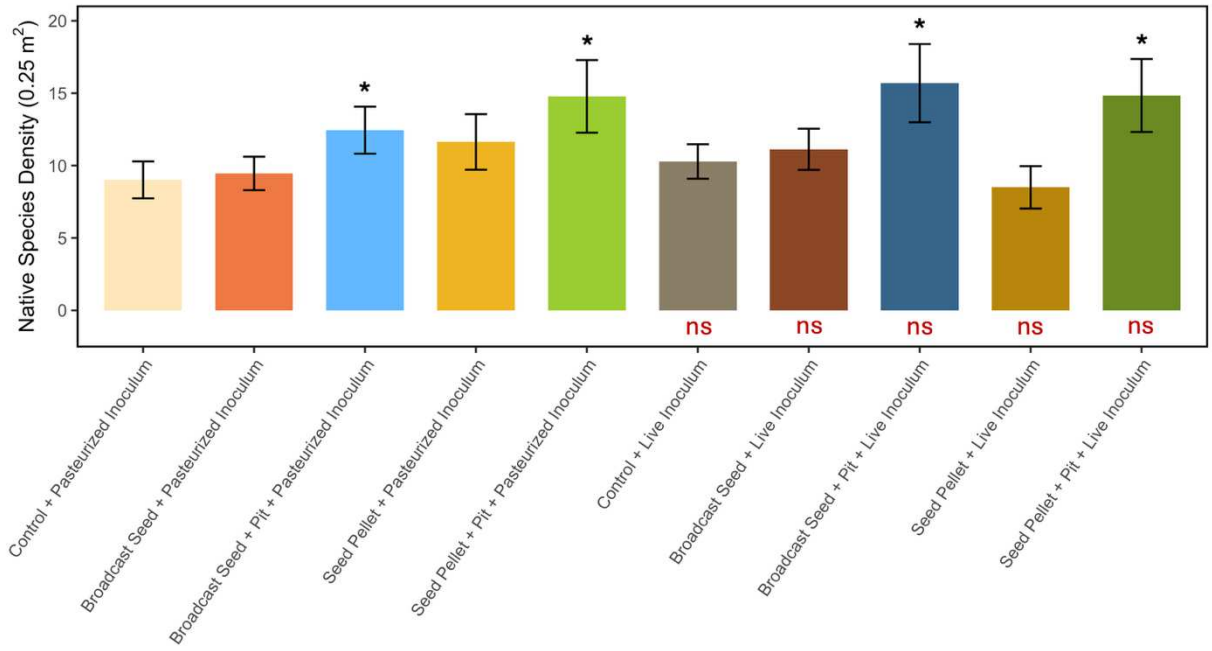

Figure 1: Mean observed naturally occurring species density (± standard error) by experimental treatment averaged across site, targeted livestock treatment and monitoring event. Black asterisks (*) above bars indicate significant differences ($p<0.05$) from the Control Pasteurized Inoculum treatment using FDR adjusted comparisons (Appendix 4, Table 14). Red symbols beneath live inoculum treatments indicate contrasts comparing live and pasteurized inoculum within treatment using FDR-adjusted comparisons (Appendix 4, Table 24), treatments share a common color with darker shades indicating live inoculum. ns denotes non-significant differences; no significant differences were observed within treatment pasteurized-live comparisons.

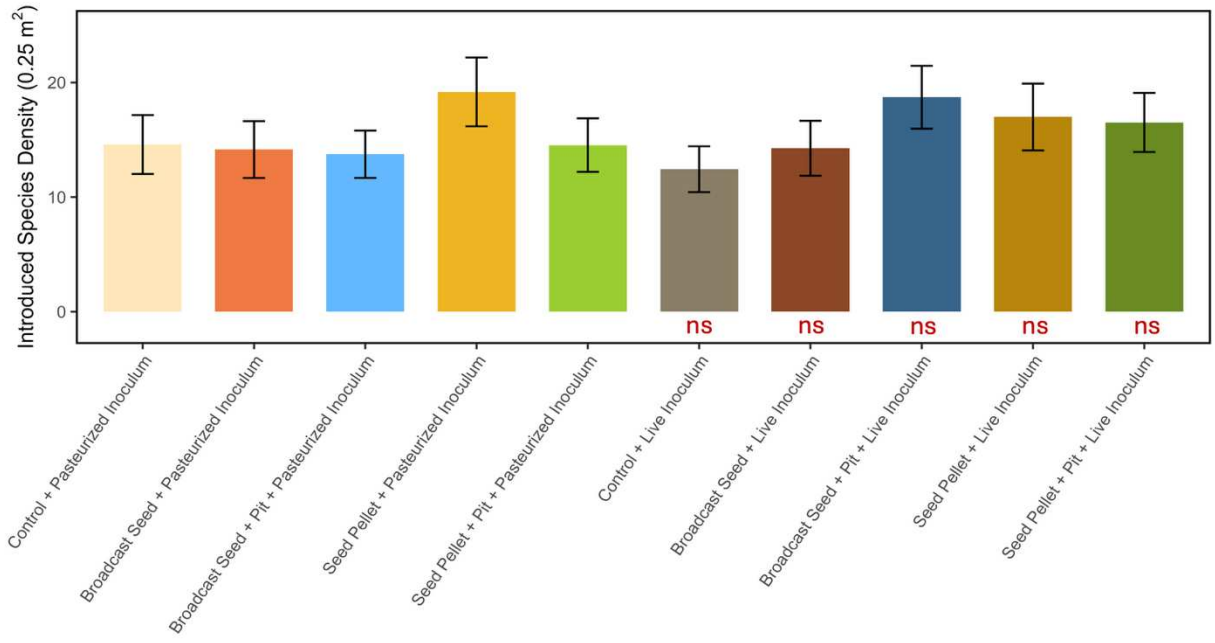

Figure 2: Mean observed introduced species density (± standard error) by experimental treatment averaged across site, targeted livestock treatment and monitoring event. No experimental treatments are significantly different from the Control Pasteurized Inoculum treatment using FDR adjusted contrasts (Appendix 4, Table 15). Similarly, no significant differences were observed within treatment pasteurized-live comparisons using FDR adjusted contrasts (Appendix 4, Table 25).

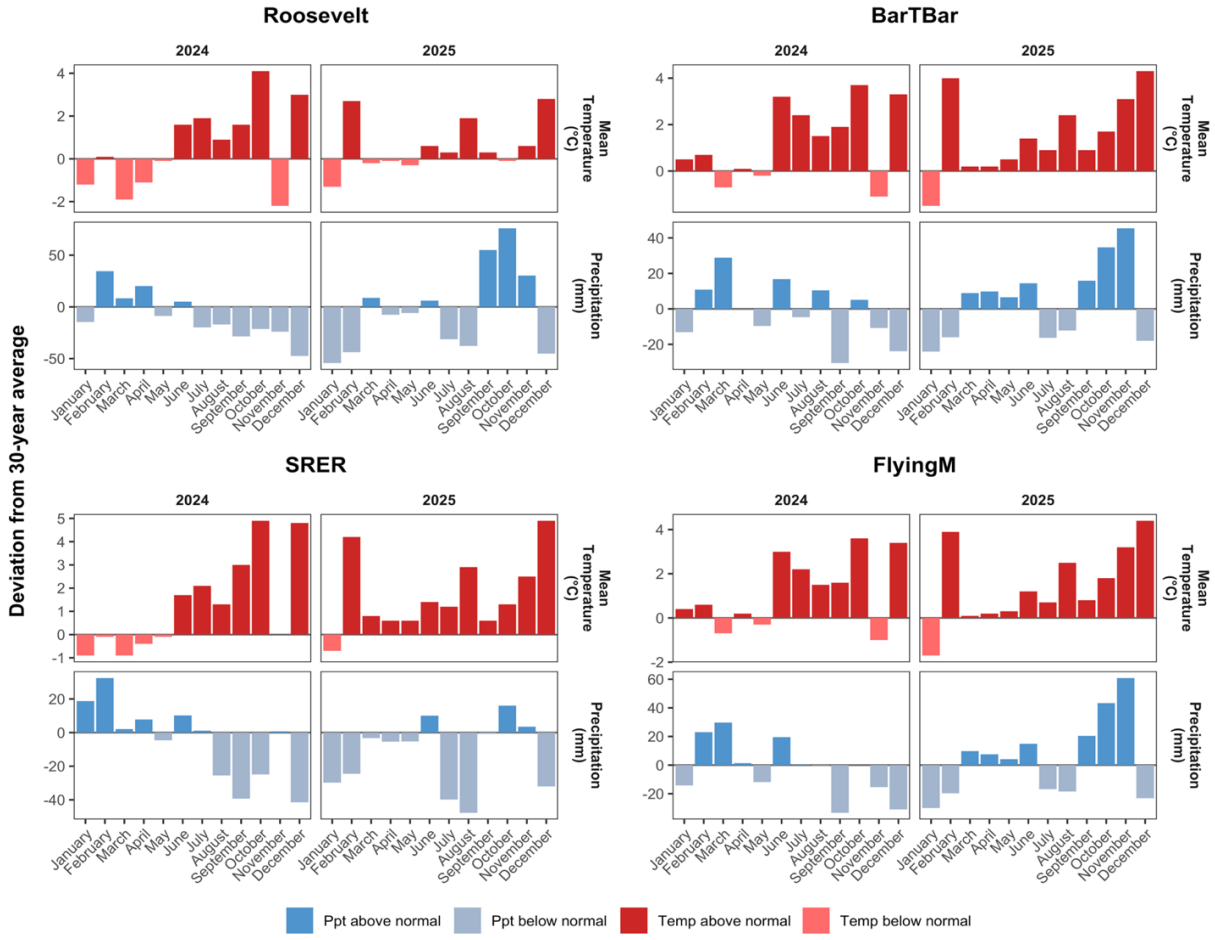

Figure 3: Monthly deviations in mean temperature and precipitation from 30-year climate normals (1991-2020) at each site in 2024 and 2025. Positive values, represented by darker colors, show higher than average observed precipitation and temperature. Negative values, shown in lighter colors indicate below average temperature and precipitation. Climate data were obtained from PRISM.