

RESEARCH ARTICLE



Restoring closed trails in the Sonoran Desert: interactions of seed timing, seed source, and ripping

Helen I. Rowe^{1,2,3} , Tiffany A. Sprague¹, Becky Ball⁴, Debbie Langenfeld⁵, Lisa Rivera⁵

Ecological restoration is a promising way to improve ecological function, habitat connectivity, and esthetic values for recreation. However, effective restoration practices for arid environments remain elusive. To help fill this knowledge gap, we tested ripping soils, seed mixtures, including adding native seed bank topsoils, and seeding timing on permanently closed trails at sites in the Sonoran Desert, Arizona, U.S.A. Ripping had the desired effect of decreasing soil bulk density and increasing infiltration and water-holding capacity of closed trails. However, ripping increased non-native plant cover by 14.1% and decreased native plant cover by 2.2% by the fourth year of the study. Seed mixtures performed best when planted before the winter rains compared to before the summer monsoon, but only 3 of the 10 seeded species persisted across years. The seed bank topsoil application was most effective at increasing native species richness in the first year and yielded an average of two more plant species than unseeded plots over the 4-year experiment, but only in unripped plots. By the fourth year of the study, plots on the ripped and unripped closed trails had similar levels of plant cover and richness as the nearby native plant community, even in unseeded plots, suggesting that in small disturbed areas, the plant community has the potential to regenerate without inputs if disturbance is removed.

Key words: desert restoration, seed bank, seed timing, seeding, soil ripping, trails

Implications for Practice

- Closed trails recovered to similar levels of native species richness and coverage compared to the nearby reference plant community in the Sonoran Desert within 4 years.
- Although the practice of ripping soils had measurable increases in water-holding capacity and infiltration, decreased bulk density, and increased seed establishment, it also increased non-native plant cover.
- The use of local seed bank soils as a seed treatment had early effectiveness that may hasten the establishment of native plants at a site using local ecotype materials with relatively low cost.

Introduction

Developing best practices in arid land restoration presents many challenges. A key component of restoration is the establishment and growth of native plant communities, which can be hindered by unpredictable environmental factors created by drought, climatic change, and variability (Muñoz-Rojas et al. 2016). Specific challenges associated with recreation include soil compaction, the reduction of natural vegetation and its associated seed bank, and the loss of soil components such as biocrust and soil microbial communities. Carefully matching site conditions with appropriate techniques and materials can help improve restoration outcomes (Defalco et al. 2012; Grman et al. 2015). However, complete recovery from large disturbances rarely occurs, and developing tools with high success rates should be an important priority (Jones et al. 2018).

One area of concern to land managers is restoration of permanently closed trails. Foot and vehicle traffic on trails not only removes vegetation and causes soil compaction, but causes loss of biocrusts and soil biotic communities important for revegetation (Belnap 2002; Lei 2004; Pickering et al. 2010; Antoninka et al. 2020). Compaction increases the bulk density of the soil, resulting in a decrease in moisture retention and root aeration, preventing seedling establishment and growth (Lei 2004; Bassett et al. 2005). One way to increase moisture retention and negate the effects of compaction is by manually breaking up the soil. Modifications such as ripping or tilling can increase water availability and plant root system establishment (Bainbridge 2007; Kinyua et al. 2010; Wilcox et al. 2012; Ruthrof et al. 2013). These practices

Author contributions: HR conceived and designed the research; HR, TS, DL, LR, BB performed the experiments; HR, BB analyzed the data; BB contributed soil analysis; HR, DL, LR, BB, TS wrote and edited the manuscript.

¹Parsons Field Institute, McDowell Sonoran Conservancy, 7729 East Greenway Road, Suite 100, Scottsdale, AZ 85260, U.S.A.

²School of Earth and Sustainability, Northern Arizona University, Flagstaff, AZ 86011, U.S.A.

³Address correspondence to H. I. Rowe, email helen@mcdowellsonoran.org

⁴School of Mathematical and Natural Sciences, Arizona State University at the West Campus, 4701 West Thunderbird Road, Glendale, AZ 85306, U.S.A.

⁵Citizen Science Program, McDowell Sonoran Conservancy, 7729 East Greenway Road, Suite 100, Scottsdale, AZ 85260, U.S.A.

© 2021 The Authors. Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

doi: 10.1111/rec.13532

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.13532/supinfo>

break up the soil surface, enhancing water infiltration and plant rooting (Montalvo et al. 2002; Snyman 2003; Osunbitan et al. 2005; Kinyua et al. 2010; Ruthrof et al. 2013). However, soil disturbance can alter microbial communities, reducing important functions in the soil such as nitrogen fixation (Smith et al. 2016) and reducing arbuscular mycorrhizal fungi (Jasper et al. 1991) important for plant germination, establishment, and growth (Smith & Read 2008). Ripping is also expensive, requiring labor and heavy machinery.

Seeding is a common technique to overcome seed limitation and aid plant establishment (Grman et al. 2015). Choosing the correct genetic source of seeds can influence short- and long-term success of a revegetation project (Lesica & Allendorf 1999; Herget 2014). Commercially produced seeds might not incorporate locally sourced seeds, whose use can help maintain genetic diversity and local adaptations (McKay et al. 2005; Herget et al. 2015). However, using diverse seed sources can help accommodate changing environmental conditions (Broadhurst et al. 2008). As an alternative to collecting or purchasing seed, the seed banks found in the upper few centimeters of nearby soil provide a repository of local genetic material (Putwain & Gillham 1990; Miller et al. 2017). That soil also contains beneficial mycorrhizal symbionts that increase plant nutrient and water uptake from soil (Al-Karaki 2013). Using this local soil to inoculate plant seedlings has been shown to increase plant growth more effectively than commercial products (Rowe et al. 2007; Emam 2016).

Low availability of soil moisture is a major obstacle to successful revegetation using seed (Bainbridge 2007; James et al. 2019). Thus, timing is an essential consideration when implementing restoration strategies. Planting early rather than later in the rainy season generally yields more germination (Turner et al. 2006; Ruthrof et al. 2013; James et al. 2019). However, Sonoran Desert plants exhibit strong among-year and among-season dormancy patterns (Gremer et al. 2016), and although most species germinate after winter rains (Venable et al. 1993; Venable & Pake 1999), it is unclear whether planting before the summer monsoon or the winter rains will maximize establishment. The best season for seeding could be informed by when plant species produce seed in the wild because exposure to natural field conditions may help induce germination (Adondakis & Venable 2004; Frischie & Rowe 2012). However, seeding too early puts seeds at more risk of seed loss through predation or wind (Defalco et al. 2012; Lai et al. 2016).

Our objective was to assess the efficacy of restoration treatments in reestablishing native vegetation on permanently closed trails. Specifically, we sought to compare the following: (1) the

common practice of ripping to unripped, compacted soil on native plant cover and richness and seedling establishment; (2) the timing of seeding commercial mixes on seedling establishment; (3) the application of native soil from beneath nearby shrubs (seed bank soils) with commercial seed mixtures on native plant richness; and (4) the practice of ripping with and without debris to improve plant establishment. These comparisons allowed us to ask the following research questions: (1) Does seeding with commercial seeds or seed bank soils accelerate introduction of native annual and perennial plants and mimic species richness of reference plant communities? (2) Do different seeding times or ripping affect plant establishment over time? (3) Does the addition of debris on ripped soils improve plant establishment compared with ripping alone?

Methods

Study Site

The McDowell Sonoran Preserve (henceforth Preserve) encompasses 12,375 ha of Sonoran Desert Upland habitat (Brown et al. 1979) at the northeastern edge of the Phoenix metropolitan area in Scottsdale, Arizona, U.S.A. Our study sites were in the northern region of the Preserve (between 33°48'26"N, 111°48'47"W and 33°47'46"N, 111°49'41"W) at elevations between 875 and 905 m and underlain predominantly by decomposed granite (Skotnicki 2016). Soils are Aridisols, with a roughly equal mix of Typic Haplargids and Typic Haplocambids. The plant community was *Ericameria laricifolia*—*Parkinsonia microphylla*—mixed scrub association (Jones & Hull 2014).

During this study, July 2016–March 2020, January mean temperature was 13.2°C (range of 2.9–22.8°C), and July mean temperature was 32.5°C (range of 22.1–41.5°C; Station 21001, Flood Control District of Maricopa County 2020). Rainfall varied over the course of the study with significantly below-average rainfall in the summer of 2018 and above-average rainfall in 2019 and the winter of 2020 (Table 1). The Sonoran Desert's rainy seasons occur in the winter (October–March) and in the summer (June–September) with winter rains typically delivering more overall precipitation (but see 2018, Table 1).

Ripping and Seeding Treatments

Preserve managers use ripping and debris application to keep visitors off closed trails and to allow for natural recovery of

Table 1. Precipitation over the study period taken at the nearest Flood Control District of Maricopa County rain gauge, Fraesfield Mountain (#76200). The deviation column indicates the annual minus the long-term (1990–2019) mean of annual precipitation recorded at the gauge. The October–March time period includes precipitation from months in the prior year.

| Year | Total annual rainfall (cm) | Deviation | Winter rains, October–March (cm) | Monsoon rains, June–September (cm) |
|------|----------------------------|-----------|----------------------------------|------------------------------------|
| 2016 | 22.5 | −7.5 | 12.7 | 8.6 |
| 2017 | 28.9 | −1.1 | 24.5 | 4.2 |
| 2018 | 17.2 | −12.8 | 4.5 | 11.9 |
| 2019 | 41.5 | 11.5 | 32.4 | 1.6 |
| 2020 | — | — | 30.4 | — |

these areas. In early 2016, we chose 10 closed trail segments that were scheduled to be ripped. Segments were at least 30 m long, relatively uniform (no more than 10% slope, not gullied or severely eroded), and without large rocks. Half of each segment was ripped using a Kubota KX41 (Grapevine, TX, U.S.A.) with a 38-cm bucket with 20-cm teeth. Rip depth was at least 17 cm. The other half of each segment was left unripped as the control. To provide a more uniform surface between the ripped and unripped sides, we raked and removed large soil clumps from the ripped side. In the 10 trail segments, we established four 1×1.5 -m plots on each ripped and unripped segment (80 plots total), ensuring a buffer of at least 1 m between plots. In 2016, we randomly assigned four experimental seed treatments in both ripped and unripped plots in a split plot design as follows: (1) a 10-species seed mix applied before the first of the monsoon rains (summer treatment); (2) a 10-species seed mix applied before the first winter rains (winter treatment); (3) soils collected from beneath nearby shrubs applied before the first winter rains (seed bank treatment); (4) control (unseeded, Fig. 1).

For the summer and winter seeding treatments, we chose a native seed mix that reflected species found within the study area containing the following functional groups: annual forbs, perennial forbs/subshrubs, and perennial grasses (Table 2). Although the functional group of annual grasses is not represented in the seed mix, *Elymus elymoides* (Squirreltail) is a shorter-lived, early successional grass. The winter and summer seed was purchased from local producers in a single batch, but it was not necessarily local ecotype seed (Table 2). Following the recommendations of Roundy and Call (1988) and Munshower (1994) for broadcast seeding in semiarid sites, we seeded at a rate of 1,000 seeds per 1.5-m^2 plot (667 seeds/m^2) based on seed count estimated by mass. We estimated an average seed weight based on three grab samples of weighed seed per plant species (Table 2). We weighed the summer and winter seeds at the same time, and seeds were applied to summer treatment plots on 22–25 July 2016. Winter seeds were refrigerated at 5°C in

paper bags until applied to winter treatment plots on 14 November 2016. Before applying seeds, we loosened the top 1–2 cm of soil on all unripped plots (including the unseeded plots) by rolling a circular rake (Garden Weasel, Secaucus, NJ, U.S.A.) 8–10 times over the surface. Seeds were hand broadcast close to the ground evenly across the 1×1.5 -m plot boundary. After spreading seed, all plots (ripped and unripped) were rolled with the Garden Weasel three times in each direction without exerting pressure to incorporate the seed with the soil. Unseeded plots (controls) received raking treatments on the same day as the winter seed applications.

For the soil bank treatment, on 16 November 2016, we collected 0.5 L of topsoil, including the litter on top, to a depth of 6 cm from each of 10 individual shrubs or trees in a parallel band 5 and 20 m from the segments. Soils under shrubs and trees, and the litter, foster high seed bank densities in arid environments (Guo et al. 1998; Filazzola et al. 2019). Seeds in arid environments are denser in the top 0–1 cm but can be unevenly distributed throughout a 10-cm profile with smallest and largest seeds on the surface and medium to large seeds settling lower in the profile (Guo et al. 1998). We coarsely sieved the soils in the field to remove debris greater than 1-cm diameter (Rowe et al. 2009). Any removed seeds and roots (cut into pieces less than 2 cm in length for better mixing) were added back (Rowe et al. 2009). We thoroughly mixed the soils among all segments and removed six subsamples for nutrient analysis in the Soil Biogeochemistry Lab at Arizona State University (ASU, see below). The remaining soils were applied to plots on 17 November 2016 at a rate of 1.5 L per 1.5-m^2 plot using the same approach as the purchased seed mixtures. This amount of soil may hold roughly 30–270 seeds (Guo et al. 1998), but because we did not quantify the number of seeds applied, the commercial and the seed bank seeding rates were likely different, which was considered when comparing results. Two *Cylindropuntia bigelovii* (Teddy-bear cholla) balls were added to each seed bank treatment plot.

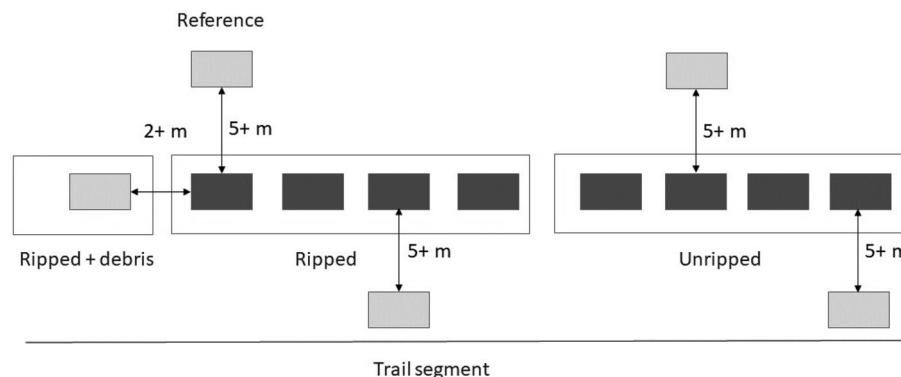


Figure 1. Conceptual diagram of experimental design. In 2017, eight plots (dark gray rectangles) were placed in a split plot design in which half of each trail segment was ripped and a half was left unripped. The four seeding treatments (winter seed, summer seed, seed bank soil, and unseeded control) were randomly assigned to the four ripped and four unripped plots. Summer seed was broadcast July 2016; winter seed and seed bank were broadcast November 2016. Prior to sampling in 2020, two additional treatments were added to compare the original plots to the reference community and to ripping and debris (pale gray rectangles). Reference community plots were placed at least 5 m away from original plots, and ripped + debris plots were placed at least 2 m away from the end plot on the ripped side. These segments were replicated 10 times across the northern area in the McDowell Sonoran Preserve, Scottsdale, Arizona, U.S.A.

Table 2. Seeding rates and mix for winter and summer seed treatments. Plots are 1.5 × 1.0 m.

| Seed company | Latin name | Common name | Growth form | Successional status | Seeds per plot | Weight (g) per 100 seeds |
|--------------|------------------------------------------|--------------------|--------------------------|---------------------|----------------|--------------------------|
| Granite Seed | <i>Eschscholzia californica mexicana</i> | California poppy | Annual forb | Early | 100 | 0.169 |
| Granite Seed | <i>Senna covesii</i> | Desert senna | Annual forb | Early | 100 | 0.445 |
| Granite Seed | <i>Salvia columbariae</i> | Chia | Annual forb | Early | 100 | 0.070 |
| Granite Seed | <i>Elymus elymoides</i> | Squirreltail | Perennial grass | Early | 100 | 0.669 |
| Granite Seed | <i>Calliandra eriophylla</i> | Fairy duster | Shrub/sub-shrub | Late | 100 | 2.516 |
| Granite Seed | <i>Heteropogon contortus</i> | Tanglehead | Perennial grass | Late | 100 | 0.761 |
| Granite Seed | <i>Sphaeralcea ambigua</i> | Desert globemallow | Perennial forb/sub-shrub | Mid-late | 100 | 0.195 |
| Granite Seed | <i>Psilostrophe cooperi</i> | Paperflower | Perennial forb/sub-shrub | Mid-late | 100 | 4.299 |
| Granite Seed | <i>Aristida purpurea</i> | Purple threeawn | Perennial grass | Mid | 100 | 0.165 |
| Armenta Seed | <i>Baileya multiradiata</i> | Desert marigold | Annual forb | Early | 100 | 0.070 |

We performed a greenhouse soil seed bank assay on the composited seed bank soils not applied to plots to identify species present in the seed bank. Soils were stored in dark and dry conditions at 4°C in open 18.93 L buckets for 10 weeks prior to the assay. On 26 January 2017, 40 sterilized trays (17 × 12 × 5.5 cm) were filled 4 cm deep with 0.816 L 2:1 Perlite:sterilized (autoclaved) soil mixture. Thirty trays received a top 1-cm (0.20 L) layer of seed bank soil, leaving 10 trays as blanks. The lack of plant emergence in the blank trays confirmed that the sterilized soil did not contain seeds and that the trays were not contaminated throughout the assay. Trays were watered twice daily for 3 minutes on an automated sprinkler system. Weekly, trays were rearranged to randomized bench locations to assure even growing conditions, and the workbench was sprayed with fungicide. We visually inspected the trays three times per week and identified any seedlings to species. By 22 May 2017, no more seedling emergence had been detected for 2 weeks, and we ended the seed bank assay.

Soil Sampling

To characterize the soils in the study area, we collected 90 soil samples between 28 April 2016 and 3 May 2016, after ripping but prior to seed application. Using a 5.08-cm-diameter corer, we collected one soil sample from each plot (outside of the 1.0 × 0.5 m inner plot to avoid disturbing the sampling area) per trail segment (10 segments × 8 plots) and one reference sample taken 1–5 m from each segment in an undisturbed area representative of the native vegetation in the area. No precipitation occurred during this period; therefore, soil water content (SWC) should not have differed between sampling dates. Cores were taken up to 15 cm deep, depending on compaction and underlying rocks. Due to the sandy soil texture, the core did not hold its shape as it was removed from the ground, so we estimated bulk density calculations based on the natural settling of the soil after removal. Soil cores were taken to the Soil Biogeochemistry Lab at ASU the same morning and stored at 4°C.

To analyze the soils, the samples were removed from the cores, weighed, then sieved to 2 mm. The soil fraction smaller than 2 mm was weighed and used for all remaining analyses.

We dried a 25 ± 0.5-g subsample at 105°C for 24 hours for calculation of gravimetric SWC. This value was then used to estimate the total dry weight of soil in the core, and bulk density was calculated as the grams of dry soil and rocks per cubic centimeter of soil volume. We then incinerated the subsample at 550°C for 3 hours to calculate the loss on ignition (LOI), an estimate of organic matter content (Dean 1974; Hoogsteen et al. 2015). We measured soil texture using the hydrometer method (Sheldrick & Wang 1993). Remaining soil from the four treatment plots was bulked within ripping treatment per segment and, along with six random samples from the seed bank soils, were ground to a homogenous powder in a Spex ball mill and analyzed for carbon and nitrogen content using a PE2400 CHN Elemental Analyzer.

Water Infiltration

To understand how ripping affected water infiltration after 3 years, we used a random stratified approach to measure water infiltration on six segments in October 2018. We tested infiltration at nine locations on each segment: three between ripped plots, three between unripped plots, and three reference community locations in between shrubs and not under perennial canopy at least 5 m from each segment. We used a modified single chamber infiltration set-up following Herrick et al. (2009, Chapter 8), which provides a relative indication of infiltration capacity under saturated conditions. To facilitate a more constant release of water, we modified the water delivery into the infiltration ring. We fitted a 2.54-cm hole drilled into the bottom of a round plastic food container (12-cm diameter × 4.5-cm tall) onto the mouth of a 1 L smooth, plastic water bottle. The container was secured in place by screwing on the bottle's lid. We drilled a 1.6-cm hole into the bottle's lid to allow water to flow from the bottle into the food container when inverted. To ensure even distribution of water across the soil, we punctured 25 evenly spaced 3-mm diameter holes into the food container lid. Three evenly spaced pinholes were pricked in the bottom of the food container mid-radius to allow air to escape when inverted.

The 12-cm diameter food container fits snugly into the metal infiltration ring. The water maintained a height of 3 cm in the food container and kept a constant head of pressure as intended in Herrick et al. (2009). To conduct the infiltration test, we laid a moistened towel over the sample area, poured 740 mL of water slowly over the towel, and inserted the infiltration ring to a depth of 3 cm. We then inverted the infiltrometer and, once the water in the food container equilibrated, settled the infiltrometer into the ring. As soon as the infiltrometer equilibrated again, we started a timer. Once the water level in the bottle had lowered at least 2 cm, we stopped the timer immediately following an equilibration in the food container. We recorded the time and volume of water released during that span.

Plant Cover and Richness Surveys

To reduce edge effects, we conducted plant sampling in a nested 0.5×1 -m area centered within each plot. On 18 March 2016, we visually estimated the percentage plant cover of individual plant species in each unripped plot as baseline data prior to seeding treatments. Baseline estimates were conducted only on unripped plots because there was no plant growth on the recently ripped plots. In March 2017, 2018, 2019, and 2020, we estimated plant cover by species and ground cover using the following cover classes: 0%, 0–0.1%, 0.1–1%, 1–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, greater than 95% (Peet et al. 1998). Because we could not be sure that the species in the plots came from the seed mix and not from the surrounding community or existing seed bank, we counted all individuals of each species in the commercial seed mix in each plot. Because Sonoran Desert annuals tend to germinate from October through January and grow through early May (Venable & Pake 1999), this timing should have captured seeded species germination and establishment, but we cannot rule out that we may have missed species that germinated in the fall and did not persist.

In the final year of the experiment (2020), to enable further comparison of the plant community established by each treatment, we added two new treatments (Fig. 1). The first was placed in areas adjacent to the trail segments to compare the original plots to the reference plant community (reference community plots) and the second in ripped areas of the trail segments that were not seeded but had debris (ripped + debris plots) to assess the additive effect of debris compared with the unseeded ripped plots. The four reference community plots per segment (40 new 0.5×1 -m plots total) were placed at least 5 m from the treatment plots, with two plots on the ripped side and two on the unripped side (Fig. 1), following the same parameters used in placing the original plots. In order to compare similar vegetation types (grass and forb), areas that were dominated by a single individual plant (>50% cover) were eliminated and new locations 1 m farther away were selected. The ripped + debris plots were placed in portions of the ripped trail segments adjacent to our treatment plots (Fig. 1). These areas had been ripped at the same time as our treatment plots but were not raked smooth, leaving uneven swales and contours. Debris had been added to these segments after ripping. We installed one plot per segment (10 new 0.5×1 -m plots) at least 2 m from

the most distant ripped treatment plot (Fig. 1). We followed the same rules as used in placing the original plots with the addition that debris must not cover greater than 25% of the plot. If the area 2 m from the treatment plot did not meet these parameters, the plot was moved 0.5 m farther away until no rules were violated. The new plots were sampled together with original plots in March 2020 as described previously.

Statistical Analyses

Soil parameters (LOI, bulk density, SWC, and infiltration) were analyzed using a mixed model with ripping (three factors: ripped, unripped, and reference community) as the fixed effect, and plots were blocked by segment, included as the random effect (JMP Pro 16, SAS). Residuals were checked for assumptions of normality. SWC was log-transformed and infiltration rate was natural log-transformed to meet assumptions. Soil nutrient parameters (C, N) were analyzed using a mixed model with ripping and seed bank soils (four factors: ripped, unripped, reference community, and seed bank soils treatment) as the fixed effect and segment as the random effect. In this analysis, percentage carbon and nitrogen were log-transformed. The same soil nutrient parameters were analyzed again with the topsoil treatment removed to compare the field treatments.

To determine if there were any pre-treatment differences in vegetation on the unripped plots, we used a mixed model with seeding as the fixed factor (four levels: unseeded, winter, summer, and seed bank) and segment as the random effect. Response variables included native plant richness, native cover, and non-native cover.

Based on our split plot design, we analyzed the data using a standard least squares model with a restricted maximum likelihood (REML) variance component estimate in a full factorial with three fixed factors: the whole plot factor (ripped, unripped), nested effect of seeding (unseeded, winter, summer, and seed bank), and year (2017, 2018, 2019, and 2020, see Table 3). Random effects were added to the model to account for the split plot design: segment, segment \times rip, and segment \times year. Response variables were native plant cover (all, annual, and perennial), native plant richness (all, annual, and perennial), and non-native cover and richness (JMP Pro 16, SAS). In addition, to compare the cumulative effects without averaging over year, we analyzed the final year data alone in a two-way standard least squares model with REML in a full factorial with ripping and seed treatment as fixed factors and segment and segment \times rip as random effects (final year two-way, see Table 3). To include the additional reference community treatments added in 2020, we analyzed the data in a one-way standard least squares model with REML with one combined factor of seeding and ripping treatments (10 levels: ripped unseeded, unripped unseeded, ripped summer seed, unripped summer seed, ripped winter seed, unripped winter seed, ripped seed bank, unripped seed bank, reference community, and ripped + debris) as the fixed factor and segment and segment \times rip as random effects (final year one-way, see Table 3).

Tukey's *F* test was used for all multiple comparisons (JMP Pro 16, SAS). Residuals were checked for homoscedasticity

Table 3. Objectives of the three different statistical models and the included effects used for comparing plant cover and richness. Yes or no indicates whether the effect was included in the model. RC/RD indicates the reference community (RC) and ripped + debris (RD) treatments added in the last year of the study.

| Purpose | Statistical model | | | Fixed effects | | | | Random effects | | |
|---------------------------------------------------------------|-----------------------|-----------------------|----------------|---------------|---------------|----------------|-------|----------------|--|--|
| | Seed treatment | Rip treatment | Year | Segment | Segment × rip | Segment × year | RC/RD | | | |
| Check for pre-treatment differences | Yes | No, unripped only | No, 2016 only | Yes | No | No | No | | | |
| Assess success of the treatments over time | Yes | Yes | Yes, 2017–2020 | Yes | Yes | Yes | No | | | |
| Assess success in the final year without averaging over time | Yes | Yes | No, 2020 only | Yes | Yes | No | No | | | |
| Compare the combined seed and rip treatments to the new RC/RD | Combined seed and rip | Combined seed and rip | No, 2020 only | Yes | Yes | No | Yes | | | |

and we log-transformed native plant cover (all, annual, and perennial) and non-native cover. Upon examination of the residual normal quantile plots, native richness and non-native richness were within normal bounds and did not require transformation. The count data of seeded species (number of individuals of each seeded species from the commercial seed mixes) were zero-inflated and overdispersed, so we used a general linearized model (GLM) with a quasi-Poisson distribution (given that the variance was greater than the mean) and compared via analysis of deviance using an *F* test in R (version 4.0.2, Crawley 2007; Ver Hoef & Boveng 2007; Ball & Virginia 2012). We used the same factors described above in the full factorial with three fixed factors and three random effects, with the exception that the seeding treatment included only three levels (winter, summer, and unseeded). We did not include the seed bank soil treatment because we did not know the composition of the seed bank a priori and therefore did not count seeded species individuals.

Results

Soil Physical and Chemical Properties

Ripping reduced bulk density and raised LOI to levels comparable to the reference community soils, and SWC was significantly higher in ripped plots than the unripped or natural desert areas (Table 4). Three years after ripping, water infiltration rates were greater in the ripped treatments than the unripped and reference community soils (Table 4). Neither the ripped nor unripped treatments differed in soil texture from the reference community soils, but the unripped plots had a higher proportion of silt and less sand than the ripped plots.

Soils collected for the seed bank treatment had significantly higher percentage carbon and nitrogen than the ripped and unripped soils and neighboring reference community soils (Table 4), although carbon to nitrogen (C:N) ratios were constant across all treatments. When the seed bank treatment data were not included in the model, the reference community soils contained significantly greater percentage carbon than the unripped soils and were marginally equivalent to the ripped soils (Table 4), but no differences in percentage nitrogen were found among treatments (Table 4). The percentage carbon mirrors the difference in LOI between native soils and unripped soils, suggesting a difference in organic carbon content, but ripped and unripped soils did not significantly differ in their percentage carbon content despite the difference in LOI.

Plant Cover

Prior to adding treatments, native plant cover on unripped plots ranged from 1.7 to 2.9% cover, and non-native plant cover ranged from 3.45 to 7.45%. There were no pre-existing treatment differences (native: $F_{[3,21.6]} = 0.25, p = 0.857$; non-native: $F_{[3,26.1]} = 0.39, p = 0.763$). After treatment application, native plant cover (total, perennial, and annual) was greater in ripped segments until the final year (Fig. 2A, year × rip interaction,

Table 4. Soil properties of ripped and unripped segments, compared to nearby undisturbed reference community soils and seed bank soils (nutrient analysis only). LOI, loss on ignition; SWC, soil water content. Soil samples were taken prior to the application of seeding and seed bank treatments in 2016, except for the seed bank soils, collected in November 2016. Infiltration was measured in October 2018. Values are mean \pm standard error ($n = 40$ for ripped and unripped, $n = 10$ for reference community, $n = 6$ for seed bank soils). Lowercase letters indicate significant differences ($p < 0.05$) among treatments from a mixed model with treatment (three factors: ripped, unripped, and reference community) as the fixed effect and segment as the random effect. For the nutrient analysis results, the first letter indicates results from analysis described above, and the second letter indicates significant differences among treatments with the same model, with seed bank soils included as a treatment effect in the model.

| | <i>Ripped</i> | <i>Unripped</i> | <i>Reference community</i> | <i>Seed bank soils</i> |
|-----------------------------------------|------------------------|------------------------|----------------------------|------------------------|
| Bulk density (g/cm^3) | 1.36 ± 0.02^a | 1.44 ± 0.02^b | 1.31 ± 0.03^a | — |
| SWC (% g/g) | 3.34 ± 0.20^a | 2.11 ± 0.24^b | 2.04 ± 0.25^b | — |
| LOI (%) | 2.77 ± 0.15^a | 2.08 ± 0.11^b | 2.67 ± 0.25^{ab} | — |
| Sand (%) | 88.61 ± 0.81^a | 84.89 ± 0.95^b | 86.18 ± 2^{ab} | — |
| Silt (%) | 9.96 ± 0.83^a | 13.36 ± 0.91^b | 12.63 ± 2.01^{ab} | — |
| Clay (%) | 1.43 ± 0.19 | 1.73 ± 0.21 | 1.18 ± 0.36 | — |
| Carbon (%) | $0.33 \pm 0.05^{ab/b}$ | $0.31 \pm 0.04^{b/b}$ | $0.51 \pm 0.11^{a/b}$ | 3.20 ± 0.21^a |
| Nitrogen (%) | $0.036 \pm 0.01^{a/b}$ | $0.037 \pm 0.01^{a/b}$ | $0.051 \pm 0.010^{a/b}$ | 0.30 ± 0.02^a |
| C:N | 9.12 ± 0.53 | 9.67 ± 1.28 | 10.62 ± 1.99 | 10.74 ± 0.31 |
| Infiltration (mm/minute) | 9.68 ± 2.47^a | 3.19 ± 1.21^b | 5.92 ± 1.55^a | — |

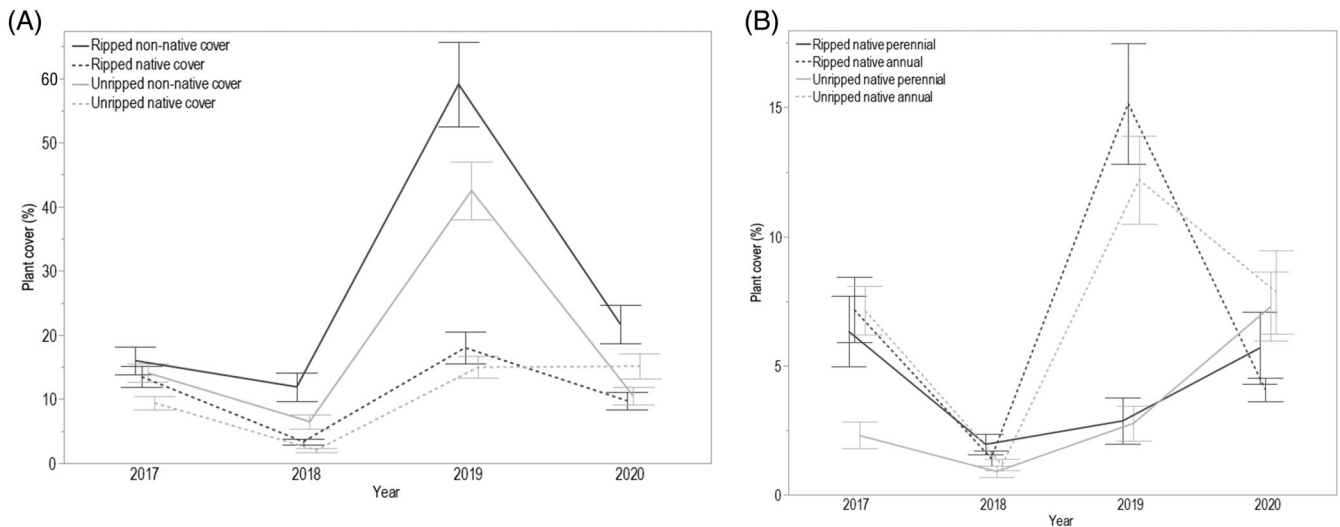


Figure 2. Mean (A) native and non-native plant cover and (B) native annual and perennial plant cover in ripped and unripped plots from 2017 to 2020. Error bars represent ± 1 SE.

Table S1). This result was also reflected using the two-way analysis in which total and annual native plant cover was lower in ripped plots than unripped plots in the final year (Fig. 2A & 2B; Table S2).

The response of annual plant cover to seeding depended on ripping, but perennial and total plant cover were not affected by seeding treatments in the full model (rip \times seed interaction, Table S1). Annual plant cover, when averaged over the years, was greater in the ripped winter seeded treatment ($\bar{x} = 10.97 \pm 2.31\%$ SE) than ripped seed bank ($5.13 \pm 1.02\%$), ripped summer seeded ($5.95 \pm 1.26\%$), unripped summer seeded ($5.27 \pm 0.88\%$), and ripped unseeded ($5.78 \pm 1.25\%$). In the final year, no seeding treatment differences in plant cover were found using the two-way analysis (Table S2). However, in the final year one-way analysis, the reference community had the highest annual plant cover compared

with the ripped + debris and ripped seed bank treatments (Fig. 3A; Table S3).

Overall, non-native plant cover was greater in the ripped than unripped plots, with the largest separation occurring in 2019 (Fig. 2A; Table S1, rip \times year interaction and rip treatment). The seeding treatment main effect was also significant for non-native plant cover in the three-way analysis (Table S1); unseeded control plots tended to have more non-native plant cover than the other treatments averaged over ripping and year, but the treatment means were not significantly separated using Tukey's HSD test, likely due to the marginally significant main effect. In the final year, non-native cover in the ripped plots was higher than unripped plots using the two-way analysis (Fig. 2; Table S2). When comparing the treatments to reference community and ripped + debris plots in the one-way analysis, the reference community plots had more non-native cover than unripped

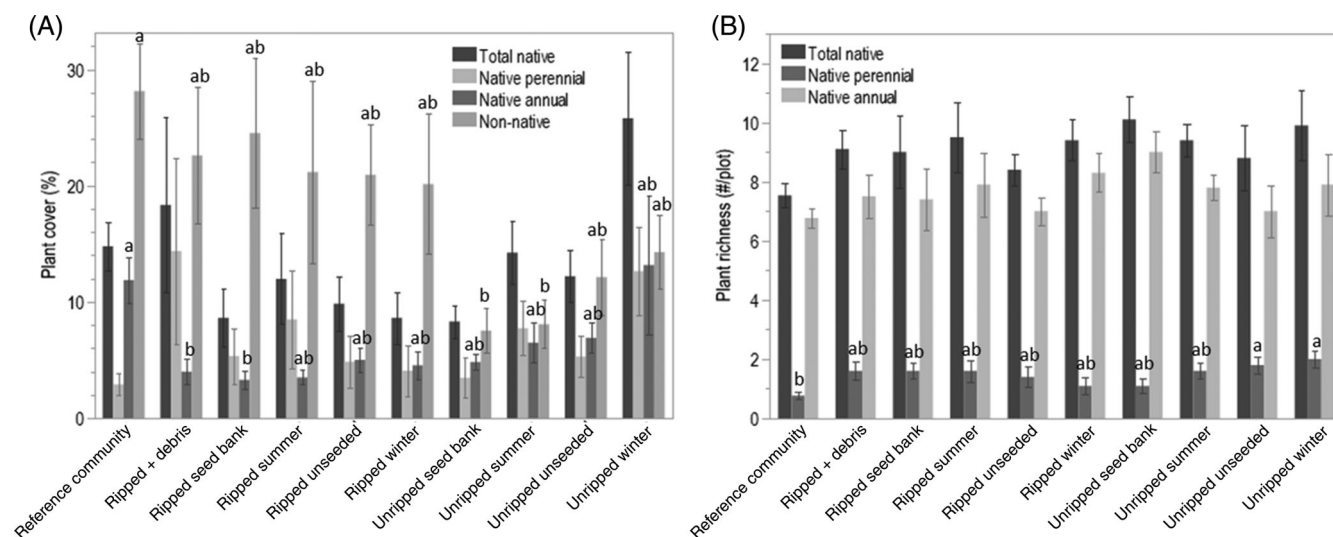


Figure 3. (A) Native (total, perennial, annual) and non-native cover and (B) native richness (total, perennial, and annual) among treatments and reference community plots in the last year of the study (2020). Treatments included four levels of seeding (winter commercial seed, summer commercial seed, seed bank soil, and unseeded control) applied to each of two levels of ripping treatment (ripped or unripped) and ripped + debris in a one-way ANOVA (10 levels). Lowercase letters represent differences in treatments within functional group using Tukey's multiple comparisons analysis. Error bars represent ± 1 SE. Plots are 1.5×1.0 m.

seed bank and unripped summer treatments (Fig. 3A; Table S3) but were not different from the other treatments.

Plant Richness

Native plant richness had no a priori treatment differences ($F_{[3,22,7]} = 1.68$, $p = 0.199$). Averaged over year, native plant richness (total and annual) differed between ripped and unripped treatments, depending on the seed treatment (seed \times rip interaction, Table S1). In this interaction, native plant richness (total and annual) was highest in the unripped seed bank treatment, but not different among the ripped seed bank and other treatments (Fig. 4A). The difference in native plant richness between ripped and unripped treatments also depended on year (rip \times year interaction, Table S1). In the interaction, unripped plots had higher species richness than ripped plots in the first year (2017), but that difference leveled off in subsequent years (Fig. 4B). In the final year, there were no differences at the $\alpha = 0.05$ level in native plant richness in either the ripped whole plot and nested seed treatments or their interaction using the two-way analysis (Table S2). However, using the one-way analysis, the reference community had lower perennial plant richness than the unripped winter and unripped unseeded treatments but no differences compared with the other treatments (Fig. 3B; Table S3). It is possible that the lower perennial plant richness in reference community plots might have been a relic of placing reference plots such that they were not dominated by one individual plant, which would have been perennial. There was an outlier in the one-way model comparing annual richness. We ran the model both ways (included and excluded); excluding it from the model increased the significant difference in total richness from marginal to significant at the $\alpha = 0.05$ level. However, likely due to the marginal significance, there

were not post hoc differences either way, so we reported results with the outlier included in the model.

Six species of non-native annuals were found in the plots: *Bromus rubens* (Red brome), *Schismus barbatus* (Common Mediterranean grass), *Erodium cicutarium* (Redstem stork's bill), *Herniaria hirsute* (Hairy rupturewort), *Oncosiphon piluliferum* (Globe chamomile), and *Sonchus oleraceus* (Common sowthistle). The main seeding treatment effect was significant (Table S1), and the unseeded treatment ($\bar{x} = 2.44 \pm 0.09$ SE) had more non-native species than the summer seeded treatment (2.16 ± 0.9), but was not different from the other treatments. Although unripped plots had significantly more non-native species detected compared to ripped plots (Table S1), the difference was less than one species ($\bar{x} = 2.41 \pm 0.07$ SE; 2.24 ± 0.6 , respectively).

Seeded Species

Individual seeded species counts overall (total) and for *Salvia columbariae* (Chia) among the commercial seed mixes and unseeded controls were highest in the winter treatments compared to the summer and the unseeded controls and in the ripped compared to the unripped plots (Fig. 5; Table S4). All six species that established had significant seed timing treatment effects; four species had higher counts in the winter seeded treatments, and two species had higher counts in the summer seeded treatments (Fig. 5). Individual counts of five of the six species that established varied by year or had a year interaction effect (Fig. 5). Only *S. columbariae* (Chia), *Sphaeralcea ambigua* (Desert globemallow), and *Senna covesii* (Desert senna) persisted across the 4 years sampled (Table 5) and also showed up in the unseeded plots (Fig. 5). There were no significant interaction effects, except for *S. covesii*, which had significant seed \times rip and year \times rip interaction effects (Table S4;

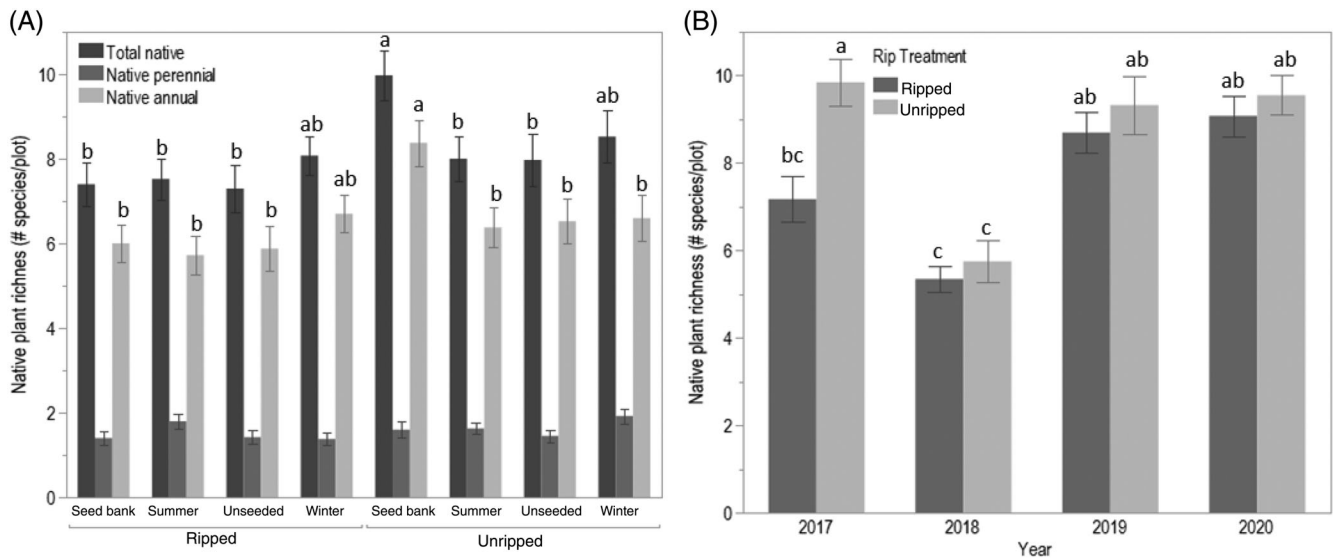


Figure 4. Significant (A) native richness rip \times seed and (B) rip \times year interactions based on the full model with three factors (year, seeding, and ripping treatments). Treatments included four levels of seeding (winter commercial seed, summer commercial seed, seed bank soil, and unseeded control) applied to each of two levels of ripping (ripped or unripped) treatment, with four levels of year (2017, 2018, 2019, 2020). Bars represent ± 1 SE. Lowercase letters represent differences in means using Tukey's multiple comparisons analysis. Plots are 1.5×1.0 m.

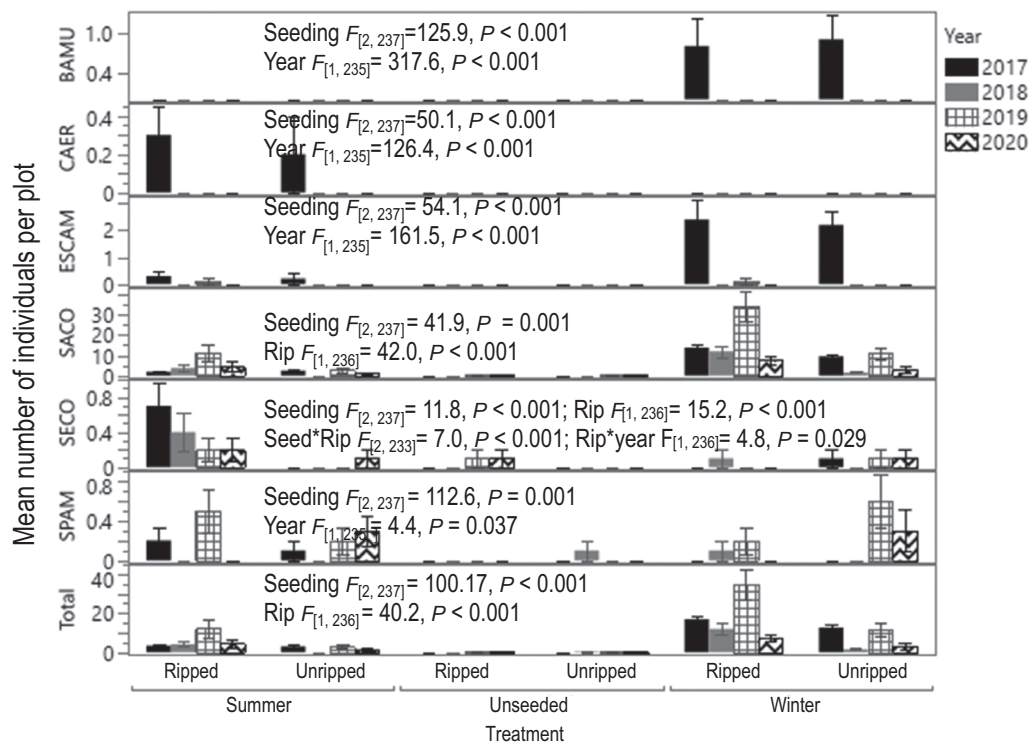


Figure 5. Mean number of seeded individuals by ripping, seed treatment, and year. Figure includes only the six species that established in the 10-species commercial seed mixture. Analysis was performed using GLM with a quasi-Poisson distribution in a full factorial with three factors: ripping, seeding, and year. Treatments included three levels of seeding (winter commercial seed, summer commercial seed, and unseeded control) applied to each of two levels of ripping treatment (ripped or unripped, six levels). Species codes are as follows: BAMU, *Baileya multiradiata*; CAER, *Calliandra eriophylla*; ESCA, *Eschscholzia californica mexicana*; SACO, *Salvia columbariae*; SECO, *Senna covesii*; SPAM, *Sphaeralcea ambigua*. All significant tests ($p < 0.05$) are shown. Bars represent ± 1 SE. Plots are 1.5×1.0 m.

Table 5. Seeded species and total seedling counts by year. All species listed were included in the summer and winter treatment seeding mixes, except for *Cylindropuntia bigelovii*, which was added as small stem pieces (a.k.a. “cholla balls”) to the seed bank treatment. These are shown as “number of live cholla balls/number added” totaled across all plots. PLS is the % pure live seed provided by the supplier.

| Scientific name | Plant form | Total # seedlings | | | | PLS |
|------------------------------------------|---------------------|-------------------|------|------|------|--------|
| | | 2017 | 2018 | 2019 | 2020 | |
| <i>Salvia columbariae</i> | Forb | 278 | 172 | 601 | 176 | 99.83% |
| <i>Eschscholzia californica mexicana</i> | Annual forb | 51 | 1 | 2 | 0 | 99.93% |
| <i>Sphaeralcea ambigua</i> | Perennial sub-shrub | 3 | 2 | 16 | 6 | 87.68% |
| <i>Senna covesii</i> | Perennial sub-shrub | 8 | 5 | 4 | 5 | 98.90% |
| <i>Baileya multiradiata</i> | Biennial | 17 | 0 | 0 | 0 | N/A |
| <i>Calliandra eriophylla</i> | Perennial sub-shrub | 5 | 0 | 0 | 1 | 99.26% |
| <i>Aristida purpurea</i> | Perennial grass | 0 | 0 | 0 | 0 | 80.27% |
| <i>Elymus elymoides</i> | Perennial grass | 0 | 0 | 0 | 0 | 91.10% |
| <i>Heteropogon contortus</i> | Perennial grass | 0 | 0 | 0 | 0 | 42.79% |
| <i>Psilostrophe cooperi</i> | Perennial sub-shrub | 0 | 0 | 0 | 0 | 69.48% |
| <i>Cylindropuntia bigelovii</i> | Perennial succulent | 10/40 | 5/40 | 2/40 | 1/40 | N/A |

Fig. 5). The three species of seeded grasses and one of the subshrubs did not appear at all (Table 5). The pure live seed (PLS) associated with the species that germinated were all greater than 87%, but the species that did not appear ranged from 42 to 99% (Table 5; Fig. 5).

Seed Bank Results

The remainder of the seed bank soils collected, but not applied to the plots, were used in a greenhouse seed bank seed assay. A total of 18 plant species emerged in this assay; 16 of these species were also detected in plots that received seed bank soils as a seeding treatment (Tables S5 & S6). The two plant species that grew in the greenhouse but not in the field seed bank plots were *Lycium exsertum* (Arizona desert-thorn), a perennial shrub, and *Gilia flavocincta* (Lesser yellowthroat gilia), an annual forb. Both species are native to the study area, and *G. flavocincta* emerged in the other seeded and unseeded treatments (Table S6). The field soil bank plots had 27 unique additional species that did not establish in the greenhouse (Table S6). Eight species (not including the cholla balls) occurred in the seed bank plots that did not occur in the unseeded plots (Table S6). However, six species occurred in the unseeded plots but not the seed bank plots (Table S6). In the first year, 25% of the cholla balls were still alive in the plots; by 2020, only one survived (Table 5).

Discussion

Given the current challenges we face in arid lands restoration of uncertain rainfall, low plant establishment, and disturbed soils, we need to continue to improve our ability to match materials and approaches to disturbed site conditions. In this study, we explored solutions to these challenges to effectively establish native plants by testing commercial seed and local seed bank soils, timing of seeding treatments, and the practices of ripping soils and adding debris. We found that the seed bank treatment had promising early results that persisted in unripped plots, whereas few species established from the commercial seed

mix. By the final year, most seeded and unseeded plots had similar levels of plant cover and richness as the reference community. Ripping increased non-native plant cover across all years and native plant cover until the final year. Both winter seeding and ripping increased commercial seed establishment and resulted in increased annual native plant cover. We did not detect differences in plant cover or richness with the addition of debris to ripped areas compared to ripped only treatments, but ripped + debris plots had fewer plant species than reference plots. Overall, ripping can promote plant cover but should be used with caution, given the increase in non-native cover. Commercial seeding can promote native species establishment, especially when broadcast in the winter, but the use of seed bank soils may be more effective for increasing native plant richness.

Ripping treatments conferred advantages of decreased bulk density and increased SWC and organic matter, the latter of which was likely due to mixing plant residue into the soils. Increased water infiltration rates 3 years after ripping indicated a sustained benefit from this practice. Others have also documented increased infiltration rates, reduced surface run-off, and reduced soil bulk density with ripping (Wilcox et al. 2012; Ruthrof et al. 2013). These properties were likely the mechanism by which plant cover increased in ripped treatments more than in unripped plots during the first 2 years of the study. In the final year of the study, native plant cover remained stable in the unripped plots but decreased in the ripped plots, likely due to low monsoonal precipitation coupled with fairly late winter rainfall in 2020. These dry conditions could have caused greater evaporation from larger pore spaces than in the compacted soils or competition for water with non-native species, particularly the non-native annual *Bromus rubens*.

Other studies have shown greater benefits from ripping than we observed. For example, Kinyua et al. (2010) found that tilling the top 5 cm of topsoil resulted in a threefold increase in biomass, and significant treatment differences remained after 7 years even though vegetation had declined. Others have seen favorable results with ripping and seeding; ripping to 40 cm was associated with deeper root architecture and higher survival

and growth in two tree species, even in the sandy soils of their Australian site (Ruthrof et al. 2013), and ripping to 30 cm with adult tree removal resulted in increased understory and seedling growth (Yates et al. 2000). In contrast, Montalvo et al. (2002) found that ripping did not affect the establishment of six seeded species. This raises the question of whether soils in our study were compacted severely enough to affect plant establishment and growth. Soils with a bulk density of greater than 1.6 g/cm^3 tend to restrict root growth (McKenzie et al. 2002). Our soils were slightly less dense than this metric, so it is possible they were not impacted enough to restrict root growth, although ripping did increase native plant establishment for the seeded species (two seeded species and total seeded species) and growth early in the study. Species can respond differently to soil compaction. For example, one study found that even low soil strength (0.6 MPa) likely creates a barrier for an agave species, whereas other species improved establishment with an intermediate level of compaction (Bassett et al. 2005).

Non-native cover was consistently higher in the ripped plots compared to the unripped plots across years. This was most noticeable in 2019, the wettest year of the study. Treatments that support native plant recovery also often support the establishment of non-native plants (Banerjee et al. 2006; Woods et al. 2012; Fick et al. 2016; Abella & Chiquoine 2019). By contrast, in an experiment performed on recently graded land, non-native plant emergence was lower in ripped compared to unripped treatments, which the authors attribute to a depleted seed bank (Montalvo et al. 2002). At our site, the nearby reference community and seed bank was likely a seed source for non-native annuals, as evidenced by the seed bank assay and the higher level of non-native cover in the reference community.

The commercial seed mixes in general did not perform well, despite relatively high PLS rates, and no grasses established from the mixture. Many other studies have described difficulties in arid land seeding. Abella and Newton (2009) reviewed 8 seeding studies and only 12 of the 28 species, including one of the species seeded in our study (*Baileya multiradiata*), had successful establishment in at least one of the studies. Their review found that seedling establishment was not well predicted by rainfall or improved by irrigation, and ripping was inconclusive (Abella & Newton 2009). A review of direct seeding found an 18% rate of seed germination or survival averaged across the experiments and ecosystems examined (Palma & Laurance 2015). Drought and irregular rainfall patterns are major obstacles to the successful revegetation of arid lands (Al-Karaki 2013) but are not the only limiting factors (Grman et al. 2015; Commander et al. 2017). Different establishment and dispersal filters can limit seeding success, such as mismatched environmental conditions to the seeded species, low seeding rates (Grman et al. 2015), seed predation, seed movement (Defalco et al. 2012), and seed dormancy (Palma & Laurance 2015). In fact, many Sonoran Desert annuals naturally exhibit a bet hedging approach in which germination is spread over multiple seasons or years even if presented with ideal germination conditions, which helps spread the risk of unfavorable conditions (Venable & Pake 1999; Adondakis & Venable 2004; Gremer et al. 2016). Bet hedging may be in conjunction with predictive germination (timing

germination with favorable conditions) and causes germination to correlate imperfectly to favorable conditions (Adondakis & Venable 2004).

At our site, seeding in the winter in ripped plots was most successful and translated into increased native annual cover in ripped winter plots. During the time between the summer and winter seeding application (July to November 2016) the winter seeds were refrigerated while the summer seeds were exposed to ambient conditions (summer heat and monsoons) as well as possible seed predation. Success of winter seeding could be due to refrigeration of winter seeds breaking dormancy better than field conditions and/or a loss of summer seeded seeds from the site (Defalco et al. 2012). However, for some species, such as *Calliandra eriophylla* and *Senna covesii*, summer seeding improved establishment. Our study site received fairly normal rainfall in the seasons following seeding, which likely helped initial seedling establishment. However, drought conditions during the monsoon and winter seasons preceding 2018 sampling may explain the lack of persistence of three seeded species that had established the previous year (*B. multiradiata*, *C. eriophylla*, and *Eschscholzia californica mexicana*). Only three seeded species persisted at our site (*S. columbariae*, *S. covesii*, and *Sphaeralcea ambigua*); for these species, bet hedging might have played a role such that germination was spread across years.

At a global scale, we face shortfalls in producing and storing adequate amounts of native seed to aid restoration efforts (Merritt & Dixon 2011). Seed bank soils can be one way to fill that gap, provided there are relatively undisturbed areas nearby from which to gather material. A recent investigation in fescue-dominated areas supports using the local seed bank to help reestablish the native plant community in conjunction with herbicide (GeFellers et al. 2020). Topsoils are commonly salvaged prior to large disturbances such as mining or road construction, where they are stored, then reapplied (e.g. Putwain & Gillham 1990; Abella et al. 2015). However, it is not common practice to salvage soils from beneath plants in reference communities for use as a seed source in other restoration efforts, except for use as mycorrhizal inoculants (Rowe et al. 2007; Emam 2016). Yet in our study, seeding with seed bank soils onto unripped plots increased plant diversity, as indicated by greater native plant richness than other seeded and unseeded treatments. This occurred even though the estimated seeding rate of the seed bank soils was lower than that applied to the commercial seed plots. Seed bank plots received an estimated 30–270 seeds (as suggested by Guo et al. 1998) of approximately 18 species, as estimated by the greenhouse assay. By comparison, we added approximately 1,000 seeds of 10 species to each commercial seed plot, based on seed count estimated by mass. Thus, the seed bank treatment likely received more species but fewer seeds than the commercially seeded plots.

In contrast to the unripped seed bank plots, seed bank plots that were ripped had significantly lower species richness, which may be explained by pre-existing conditions and interactions with the seed bank additions. All unripped plots had a small amount of pre-existing plant cover and an undisturbed seed

bank, and the soil microbial community had less recent disturbance compared to the ripped plots, although both had previously been disturbed by trampling on the trail. The seed bank soils had elevated carbon and nitrogen (but similar C:N ratio) compared with the soils in the plots. Thus, the increased species richness in the unripped seed bank plots might be explained by an additive benefit of the biotic (microorganisms and seeds) and/or abiotic (nutrients) components of the seed bank soils to the less disturbed plants and soils of the unripped plots (Rowe et al. 2007), not seen in the more disturbed ripped plots. Topsoil seed banks have many beneficial components, including seed with locally adapted genotypes, mycorrhizal fungi, and nutrients (Putwain & Gillham 1990; Miller et al. 2017), and may be the most appropriate genetic source of seed for areas with low disturbance (Lesica & Allendorf 1999), which can help maintain genetic diversity and local adaptations (McKay et al. 2005; Herget et al. 2015). Genetically diverse plant materials can improve establishment success under a range of conditions, increase pest and pathogen resistance, and support recovery after disturbances or climate extremes (summarized by Basey et al. 2015). Due to the disturbance caused in collecting local soils, there may be limitations of this approach at large scales, but this might be ameliorated by applying seed bank soils in restoration islands (Hulvey et al. 2017).

The interventions studied here may not always be necessary. In our case, given the favorable comparisons of native vegetation between unripped, unseeded plots and reference community plots, recovery of native cover and richness without intervention appears possible. The area of trail disturbance was small, relative to the surrounding reference community, and the soil was still able to support plant growth, despite compaction. However, in cases where intervention is needed, such as with heavy invasion, depleted seed bank, or no neighboring native plant community that can act as a seed source, our results provide evidence of three plant species as well as the seed bank soils that establish well in these conditions.

Our study contributes to the growing knowledge of which arid species establish well from seed and which treatments promote establishment (Abella et al. 2009; Abella & Newton 2009). Additional options for promoting germination are also being explored, including ways of protecting seeds through coatings, different planting techniques, agglomeration, and pellets (Madsen et al. 2016). Other techniques that may increase success include barrier structures to capture seeds and litter (Fick et al. 2016) and restoration islands to help propagate native materials across large disturbed areas (Hulvey et al. 2017). Administering multiple applications of the seed mix throughout the year can help match species-specific needs with appropriate temperature and other environmental conditions (Defalco et al. 2012). Matching site-specific conditions with appropriate restoration interventions continues to be our challenge, but the lessons learned here regarding seeding timing, seed bank soil application, and ripping improve our understanding of when and how to apply these techniques. Ultimately, although purchased seed may be more readily available and convenient, it might not be well adapted to site conditions. The extra effort of appropriately collecting seed bank soils or seeds and planting

within seed transfer zones can potentially increase seeding success and drive more adapted, and therefore more resilient, restoration outcomes (Miller et al. 2017).

Acknowledgments

We thank S. Jones, D. Setaro, and J. P. Solves for contributing their excellent botany skills. For their logistical support, we acknowledge S. Hamilton and J. Loleit, City of Scottsdale, and D. Hansen, YRU contracting. We appreciate all of the McDowell Sonoran Conservancy citizen scientists and M. Tluczek who helped implement treatments, build field supplies, and collect data, including B. Sowle, who created the infiltration device, Dr. J. Weser at Scottsdale Community College for his help and use of the greenhouse, and Dr. St. Laurent and the NAU Statistical Lab for their guidance on statistical analysis. We acknowledge the City of Scottsdale for funding this project. We are grateful to two anonymous reviewers and the coordinating editor, Dr. A. Faist, for their comments that helped improve this manuscript.

LITERATURE CITED

- Abella SR, Chiquoine LP (2019) The good with the bad: when ecological restoration facilitates native and non-native species. *Restoration Ecology* 27:343–351
- Abella SR, Chiquoine LP, Newton AC, Vanier CH (2015) Restoring a desert ecosystem using soil salvage, revegetation, and irrigation. *Journal of Arid Environments* 115:44–52
- Abella SR, Gunn JL, Daniels ML, Springer JD, Nyoka SE (2009) Using a diverse seed mix to establish native plants on a Sonoran Desert burn. *Native Plants Journal* 10:21–31
- Abella SR, Newton AC (2009) A systematic review of species performance and treatment effectiveness for revegetation in the Mojave Desert, U.S.A. Pages 45–74. In: Fernandez-Bernal A, De La Rosa MA (eds) *Arid environments and wind erosion*. Nova Science Publishers, Inc., Hauppauge, New York
- Adondakis S, Venable DL (2004) Dormancy and germination in a guild of Sonoran Desert annuals. *Ecology* 85:2582–2590
- Al-Karaki GN (2013) The role of mycorrhiza in the reclamation of degraded lands in arid environments. Pages 823–836. In: Shahid SA, Taha FK, Abdelfattah MA (eds) *Developments in soil classification, land use planning and policy implications: innovative thinking of soil inventory for land use planning and management of land resources*. Springer Science + Business Media, Berlin, Germany
- Antoninka A, Faist A, Rodriguez-Caballero E, Young KE, Chaudhary VB, Condon LA, Pyke DA (2020) Biological soil crusts in ecological restoration: emerging research and perspectives. *Restoration Ecology* 28:1–6
- Bainbridge DA (2007) *A guide for desert and dryland restoration*. Island Press, Washington D.C.
- Ball BA, Virginia RA (2012) Meltwater seep patches increase heterogeneity of soil geochemistry and therefore habitat suitability. *Geoderma* 189–190: 652–660
- Banerjee MJ, Gerhart VJ, Glenn EP (2006) Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. *Restoration Ecology* 14:339–348
- Basey AC, Fant JB, Kramer AT (2015) Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal* 16:37–52
- Bassett IE, Simcock RC, Mitchell ND (2005) Consequences of soil compaction for seedling establishment: implications for natural regeneration and restoration. *Austral Ecology* 30:827–833

- Belnap J (2002) Impacts of off-road vehicles on nitrogen cycles in biological soil crusts: resistance in different U.S. deserts. *Journal of Arid Environments* 52:155–165
- Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1:587–597
- Brown D, Love C, Pase C (1979) A digitized classification system for the biotic communities of North America, with community (series) and association examples for the Southwest. *Journal of the Arizona-Nevada Academy of Science* 14:1–16
- Commander LE, Golos PJ, Miller BP, Merritt DJ (2017) Seed germination traits of desert perennials. *Plant Ecology* 218:1077–1091
- Crawley MJ (2007) *The R book*. John Wiley & Sons, Ltd., Chichester, United Kingdom
- Dean WE (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. *Journal of Sedimentary Research* 44:242–248
- Defalco LA, Esque TC, Nicklas MB, Kane JM (2012) Supplementing seed banks to rehabilitate disturbed Mojave Desert shrublands: where do all the seeds go? *Restoration Ecology* 20:85–94
- Emam T (2016) Local soil, but not commercial AMF inoculum, increases native and non-native grass growth at a mine restoration site. *Restoration Ecology* 24:35–44
- Fick SE, Decker C, Duniway MC, Miller ME (2016) Small-scale barriers mitigate desertification processes and enhance plant recruitment in a degraded semi-arid grassland. *Ecosphere* 7:1–16
- Filazolza A, Liczner AR, Westphal M, Lortie CJ (2019) Shrubs indirectly increase desert seed banks through facilitation of the plant community. *PLoS One* 14:1–15
- Flood Control District of Maricopa County (2020) Weather information. <https://www.fcd.maricopa.gov/3833/Get-Weather-Information> (accessed 18 Dec 2020)
- Frischie SL, Rowe HI (2012) Replicating life cycle of early-maturing species in the timing of restoration seeding improves establishment and community diversity. *Restoration Ecology* 20:188–193
- GeFellers JW, Buehler DA, Moorman CE, Zobel JM, Harper CA (2020) Seeding is not always necessary to restore native early successional plant communities. *Restoration Ecology* 28:1485–1494
- Gremer JR, Kimball S, Venable DL (2016) Within-and among-year germination in Sonoran Desert winter annuals: bet hedging and predictive germination in a variable environment. *Ecology Letters* 19:1209–1218
- Grman E, Bassett T, Zirbel CR, Brudvig LA (2015) Dispersal and establishment filters influence the assembly of restored prairie plant communities. *Restoration Ecology* 23:892–899
- Guo QF, Rundel PW, Goodall DW (1998) Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. *Journal of Arid Environments* 38:465–478
- Herget ME (2014) An investigation of the impacts of seed origin on grassland restoration success. Master's Thesis. University of Wyoming, Laramie
- Herget ME, Hufford KM, Mummey DL, Shreading LN (2015) Consequences of seed origin and biological invasion for early establishment in restoration of a North American grass species. *PLoS One* 10:e0119889
- Herrick JE, Van Zee WJ, Havstad MK, Burkett ML, Whitford GW (2009) *Monitoring manual for grassland, shrubland and savanna ecosystems*. Volume II: design, supplementary methods and interpretation. USDA-ARS Jornada Experimental Range, Las Cruces, New Mexico
- Hoogsteen MJJ, Lantinga EA, Bakker EJ, Groot JCJ, Tittone PA (2015) Estimating soil organic carbon through loss on ignition: effects of ignition conditions and structural water loss. *European Journal of Soil Science* 66:320–328
- Hulvey KB, Leger EA, Porensky LM, Roche LM, Veblen KE, Fund A, Shaw J, Gornish ES (2017) Restoration islands: a tool for efficiently restoring dry-land ecosystems? *Restoration Ecology* 25:S124–S134
- James JJ, Sheley RL, Leger EA, Adler PB, Hardegree SP, Gornish ES, Rinella MJ (2019) Increased soil temperature and decreased precipitation during early life stages constrain grass seedling recruitment in cold desert restoration. *Journal of Applied Ecology* 56:2609–2619
- Jasper DA, Abbott LK, Robson AD (1991) The effect of soil disturbance on vesicular-arbuscular mycorrhizal fungi in soils from different vegetation types. *New Phytologist* 118:471–476
- Jones HP, Jones PC, Barbier EP, Blackburn RC, Rey Benayas JM, Holl KD, McCrackin M, Meli P, Montoya D, Mateos DM (2018) Restoration and repair of Earth's damaged ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 285:20172577
- Jones S, Hull C (2014) Vegetation and flora of the McDowell Sonoran Preserve, Maricopa County, Arizona. *Canotia* 10:1–34
- Kinyua D, McGeoch LE, Georgiadis N, Young TP (2010) Short-term and long-term effects of soil ripping, seeding, and fertilization on the restoration of a tropical rangeland. *Restoration Ecology* 18:226–233
- Lai L, Chen L, Lianhe J, Zhou J, Zheng Y, Shimizu H (2016) Seed germination of seven desert plants and implications for vegetation restoration. *Annals of Botany Plants* 8:plw031
- Lei SA (2004) Soil compaction from human trampling, biking, and off-road motor vehicle activity in a blackbrush (*Coleogyne ramosissima*) shrubland. *Western North American Naturalist* 64:125–130
- Lesica P, Allendorf FW (1999) Ecological genetics and the restoration of plant communities: mix or match? *Restoration Ecology* 7:42–50
- Madsen MD, Davies KW, Boyd CS, Kerby JD, Svejcar TJ (2016) Emerging seed enhancement technologies for overcoming barriers to restoration. *Restoration Ecology* 24:S77–S84
- McKay JK, Christian CE, Harrison S, Rice KJ (2005) 'How local is local?' – a review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432–440
- McKenzie N, Coughlan K, Cresswell H (2002) Soil physical measurement and interpretation for land evaluation. CSIRO Publishing, Collingwood, Victoria
- Merritt DJ, Dixon KW (2011) Restoration seed banks – a matter of scale. *Science* 332:21–22
- Miller BP, Sinclair EA, Menz MH, Elliott CP, Bunn E, Commander LE, et al. (2017) A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. *Restoration Ecology* 25:605–617
- Montalvo AM, McMillan PA, Allen EB (2002) The relative importance of seeding method, soil ripping, and soil variables on seeding success. *Restoration Ecology* 10:52–67
- Muñoz-Rojas M, Erickson TE, Martini DC, Dixon KW, Merritt DJ (2016) Climate and soil factors influencing seedling recruitment of plant species used for dryland restoration. *Soil* 2:287–298
- Munshower FF (1994) *Practical handbook of disturbed land revegetation*. Lewis Publishers, CRC Press, Boca Raton, Florida
- Osunbitan JA, Oyedele DJ, Adekolu KO (2005) Tillage effects on bulk density, hydraulic conductivity and strength of a loamy sand soil in southwestern Nigeria. *Soil and Tillage Research* 82:57–64
- Palma AC, Laurance SGW (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? *Applied Vegetation Science* 18:561–568
- Peet RK, Wentworth TR, White PS (1998) A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63:262–274
- Pickering CM, Hill W, Newsome D, Leung YF (2010) Comparing hiking, mountain biking and horse riding impacts on vegetation and soils in Australia and the United States of America. *Journal of Environmental Management* 91:551–562
- Putwain PD, Gillham DA (1990) The significance of the dormant viable seed bank in the restoration of heathlands. *Biological Conservation* 52:1–16
- Roundy BA, Call CA (1988) Revegetation of arid and semiarid rangelands. Pages 607–635. In: Tueller PT (ed) *Vegetation science applications for rangeland analysis and management*. Kluwer Academic Publishers, Dordrecht, Boston, London
- Rowe HI, Brown CS, Claassen VP (2007) Comparisons of mycorrhizal responsiveness with field soil and commercial inoculum for six native montane species and *Bromus tectorum*. *Restoration Ecology* 15:44–52
- Rowe HI, Brown CS, Paschke MW (2009) The influence of soil inoculum and nitrogen availability on restoration of high-elevation steppe communities invaded by *Bromus tectorum*. *Restoration Ecology* 17:686–694

- Ruthrof KX, Fontaine JB, Buizer M, Matusick G, McHenry MP, Hardy GEJ (2013) Linking restoration outcomes with mechanism: the role of site preparation, fertilisation and revegetation timing relative to soil density and water content. *Plant Ecology* 214:987–998
- Sheldrick BH, Wang C (1993) Particle size distribution. Pages 499–511. In: Carter MR (ed) *Soil sampling and methods of analysis*. Canadian Society of Soil Science, Lewis Publishers, Ann Arbor, Michigan
- Skotnicki SJ (2016) Geology of the McDowell Mountains. Arizona Geological Survey contributed map CM-16-A, 1 map plate
- Smith CR, Blair PL, Boyd C, Cody B, Hazel A, Hedrick A, et al. (2016) Microbial community responses to soil tillage and crop rotation in a corn/soybean agroecosystem. *Ecology and Evolution* 6:8075–8084
- Smith S, Read D (2008) *Mycorrhizal symbiosis*. 3rd edition. Academic Press, New York
- Snyman HA (2003) Revegetation of bare patches in a semi-arid rangeland of South Africa: an evaluation of various techniques. *Journal of Arid Environments* 55:417–432
- Turner SR, Pearce B, Rokich DP, Dunn RR, Merritt DJ, Majer JD, Dixon KW (2006) Influence of polymer seed coatings, soil raking, and time of sowing on seedling performance in post-mining restoration. *Restoration Ecology* 14:267–277
- Venable DL, Pake C, Caprio A (1993) Diversity and coexistence of Sonoran Desert winter annuals. *Plant Species Biology* 8:207–216
- Venable DL, Pake CE (1999) Population ecology of Sonoran Desert annual plants. Pages 115–142. In: Robichaux R (ed) *The ecology of Sonoran Desert plants and plant communities*. University of Arizona Press, Tucson
- Ver Hoef JM, Boveng PL (2007) Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology* 88:2766–2772
- Wilcox BP, Fox WE, Prcin LJ, McAlister J, Wolfe J, Thomas DM, Knight RW, Hoffman DW, Smeins FE (2012) Contour ripping is more beneficial than composted manure for restoring degraded rangelands in Central Texas. *Journal of Environmental Management* 111:87–95
- Woods SR, Fehmi JS, Backer DM (2012) An assessment of revegetation treatments following removal of invasive *Pennisetum ciliare* (buffelgrass). *Journal of Arid Environments* 87:168–175
- Yates CJ, Hobbs RJ, Atkins L (2000) Establishment of perennial shrub and tree species in degraded *Eucalyptus salmonophloia* (salmon gum) remnant woodlands: effects of restoration treatments. *Restoration Ecology* 8:135–143

Supporting Information

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

Table S1. Results of standard least squares model analysis with a REML variance component estimate for percent cover and total species richness by functional type.

Table S2. Results of standard least squares model analysis with a REML variance component estimate for percent cover and total species richness by functional type for the final year of the study (2020).

Table S3. Results of one-way standard least squares model analysis with a REML variance component estimate for percent cover and total species richness by functional type for the final year, with one combined fixed factor of ripping and seed treatment.

Table S4. Results of a general linearized model (GLM) with a quasi-Poisson distribution compared with analysis of deviance using an *F* test.

Table S5. Plant species established in the seed bank treatment in the field experiment and greenhouse assay (1 = presence; 0 = absence).

Table S6. Occurrence frequency of plant species identified in study by treatment.

Coordinating Editor: Akasha Faist

Received: 3 March, 2021; First decision: 24 May, 2021; Revised: 19 August, 2021; Accepted: 19 August, 2021