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RESEARCH ARTICLE

Effectiveness of seed sowing techniques for sloped restoration sites

Nicole Tamura[1], Megan E. Lulow[2], Chris A. Halsch[1], Matthew R. Major[2], Kathleen R. Balazs[1], Paige Austin[1], Travis E. Huxman[1], Sarah Kimball[1,3]

Practitioners are challenged with choosing among many potentially effective methods for sowing seed in ecological restoration projects to achieve sufficient native plant establishment. We tested the effectiveness of seed sowing techniques on moderate and steep slopes in a Mediterranean climate by measuring native seedling density immediately following germination, as well as plant density, recruitment success, and soil movement through the second growing season. We calculated cost effectiveness of different methods as the native plant density per dollar spent sowing seed. While all sowing techniques resulted in significant native establishment compared with unseeded controls, hydro seeding on moderate slopes was the most cost effective (native seedlings established per dollar spent). Although all steep-sloped seeding techniques resulted in high densities of native species, all methods also resulted in significant soil loss. Shrubs preferred hand seeding followed by jute netting on steep slopes, while forbs reached greatest densities with hydro seeding on moderate slopes. Seedlings of species with heavy seeds were present in greater densities than species with lighter seeds in imprint sowing treatments. The "best" seed sowing technique varied depending on slope and metric of success (native density, species richness, shrub density, or forb density). Different combinations of slope, technique, and success metric resulted in significantly different project costs, which implies opportunities for savings given careful decision-making relative to mitigation needs on heterogeneous landscapes. Evaluations of techniques for restoring slopes are limited, yet critical for expanding the area capable of being restored and the application of limited conservation funding.

Key words: coastal sage scrub, cost-effective restoration, erosion control, restoration of steep slopes, seeding methods, seed weight, native establishment

Implications for Practice

- Seeding native shrubs on steep slopes can result in equal or greater establishment when compared with seeding on moderate slopes. Germination on steep slopes was increased by adding jute netting, but mortality made the extra cost not worth the effort when comparing second-year density to hand-seeded areas without jute netting.
- Hydro seeding may be especially successful for native forbs. Imprint seeding seems to work best for species with larger, heavier seeds, at least in areas that have a tendency to experience strong wind speed events.
- Decisions regarding seeding methods are improved with information on slope characteristics of the site, carefully chosen success metrics, germination biology of the species, and costs of seed sowing methods.

Introduction

Ecological restoration of highly degraded landscapes, especially those dominated by non-native plant species, frequently involves sowing native seed after reducing non-native cover (Cox & Allen 2008). Adding native plants as seeds, rather than as container plants, may be a cost-effective restoration method, especially in remote areas or across large regions (Lengyel et al. 2012; Kimball et al. 2015). Successful establishment of native plants reduces non-native establishment and can also reduce soil erosion (Kimball et al. 2014*b*; Knutson et al. 2014). This may be especially critical on slopes, where non-native invasive species may not be as deeply rooted as native species or where removal of non-native plants must be paired with seeding native plants to prevent erosion (Bochet et al. 2009). When faced with large areas that require seeding of native plants, it is important to use the seeding method that yields the highest native establishment for the lowest cost (Kulpa et al. 2012).

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[1]Center for Environmental Biology, BioSci—CEB, University of California, Irvine, CA 92697-1450, U.S.A.
[2]Irvine Ranch Conservancy, 4727 Portola Parkway, Irvine, CA 92620, U.S.A.
[3]Address correspondence to S. Kimball, email skimball@uci.edu

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There are many different methods for sowing seed, and options vary depending on the slope grade or accessibility of the site (Montalvo et al. 2002; Brennan & Leap 2014). Seed sowing methods that were initially developed for agricultural practices can be adopted for restoration because they provide a logical approach to large-scale efforts. Methods include drill seeding, which utilizes a tractor attachment that drops seeds through rotating disks at fairly uniform depth and distance, varying with terrain and driving speed (Yurkonis et al. 2010). Hydro seeding uses a slurry mixture of seeds, mulch, and water that is sprayed through a hose extension, or dropped via helicopter, making it useful for steeper slopes or areas otherwise inaccessible to mechanized equipment (Stott et al. 2010). Imprinting utilizes an attachment with angled teeth that forms an impression when rolled across soil. Seed may be either broadcast or placed in a hopper that drops seed ahead of the roller, and then pushed into the soil (Dixon 1990; CalTrans 2004; Monsen et al. 2004). Traditional drill and imprint seeders were designed to be pulled behind wheeled tractors, limiting access to moderate slopes (0–20°). Customized designs for steeper terrain have recently been marketed for tracked machinery, increasing range, but still inaccessible to very steep slopes (>30°). Hand broadcast seeding involves spreading seed by hand, often followed by raking or tamping seed into the ground with hand-held tools (DeSimone 2013). On steep slopes, sowing is sometimes followed by an application of straw, mulch, or jute netting to help protect soil from erosion and provide a buffer against evaporation, wind, and solar radiation (Shao et al. 2014). Comparing multiple sowing techniques in terms of applicability to the slope of the site, effectiveness according to chosen success metrics, and cost is important to making wise management decisions (Beyers 2004).

Each seed sowing technique deposits seeds in a different way, influencing germination. When sowing native plants in restoration, it is useful to consider the germination rates and dormancy-breaking requirements of the species being seeded to make decisions regarding seeding rate, species mix, and timing of seeding in addition to sowing technique (Doll et al. 2011). Sowing techniques are most effective when they result in a soil surface that provides favorable conditions for seedling establishment, such as one that traps and retains seeds or that provides larger holes for greater infiltration of water into the soil (Chambers 2000). Seed mass could be used as a predictor of seed germination and seedling emergence relative to burial depth, and a sowing method such as hydro seeding that allows for thinner layers of topsoil has resulted in greater germination for species with smaller seed (Montalvo et al. 2002; Limon & Peco 2016).

Despite the importance of understanding effectiveness of different seeding techniques, there are surprisingly few published studies comparing multiple seeding methods for the same seed mix in the same location (Yurkonis et al. 2008). Existing studies tend to compare only two to three seed sowing methods (Montalvo et al. 2002; Yurkonis et al. 2010), and practitioners generally do not have the opportunity or resources to conduct rigorously replicated experiments to determine which method to use (DeSimone 2013). In a previous study at our project site, native shrub and forb species germinated at greater density in hand than in drill-seeded plots (Kimball et al. 2014*b*), while native grass species germinated more in drill than in hand-seeded plots (Kimball et al. 2015). In another study comparing drill, hydro, and imprint seeding for native grasses, drill seeding resulted in the highest germination across the study area, but hydro seeding was best for sloped areas (CalTrans 2004). Comparisons between sowing methods demonstrate varying results depending on year in which seeding occurred, season within a year, slope of the site, and seed biology of the species, demonstrating the importance of interacting factors and replication of tests under different environmental conditions (different years, different sites) to develop conclusions regarding best practices for restoration (Montalvo et al. 2002; Wilson et al. 2004; Larson et al. 2011).

As different seed sowing techniques may result in differences in the proportion of seeds of each species that germinate, they also likely result in varying communities of seedlings that compete with one another during initial establishment (Fowler 1988; Ambrose & Wilson 2003). Collecting data on seedling density as well as end-of-season persistence can help clarify which species are favored with which seed sowing technique. It may also be important to collect data in more than 1 year due to possible variation in second-year recruitment patterns that are likely influenced by first-year establishment (Zeiter et al. 2006). More than one season of data collection may be especially critical in environments characterized by interannual variation in precipitation because seeds sown in a relatively dry year may not germinate until the following growing season (Finch-Savage & Leubner-Metzger 2006).

In this experiment, we focused on five different sowing methods used in the restoration of a Mediterranean-climate shrub community on typical landscapes that can be categorized as either moderate or steeply sloped. Southern California's coastal sage scrub plant community is a semi-arid shrub community that hosts a diversity of drought-deciduous shrubs and subshrubs, as well as a number of herbaceous annuals and biennials (Rundel 2007). Similar to other Mediterranean-climate plant communities, coastal sage scrub has been negatively impacted by stressors including agriculture, urbanization, nitrogen deposition, drought, reduced fire intervals, and invasion of non-native species (Talluto & Suding 2008; Kimball et al. 2014*a*). The purpose of this study is to determine the most effective seeding method across variable terrain, which is characteristic of open space and rangelands in southern California. Here, we compare drill, hydro, imprint, and hand seeding, both with and without jute netting, with respect to sowing cost and resulting native plant density and diversity. We also measured soil movement to assess the influence of sowing methods on soil stability. We included a test of hydro mulch (nonseeded) areas to measure the effect of the slurry mixture used in hydro seeding on soil stability. Based on results from previous studies, we hypothesized that application of hydro mulch and jute netting would decrease soil movement by serving as a protective ground cover (Mitchell et al. 2003; Prats et al. 2013) and that species with smaller seeds would be most abundant when hydro seeded, while species with larger seeds would be most abundant when

Table 1. Species used in the seed mix, their functional group and average seed mass (per seed) used in analyses, and the seeding rate in pure live seed pounds per acre. For each sowing treatment, we listed the method that resulted in the greatest number of emergent seedlings recorded in 2015 after germination-triggering rains, as well as the method that was most cost effective in terms of the number of seedlings per dollar spent on sowing. Bold treatments indicate the slope that resulted in the greatest number of seedlings and the most cost-effective method. Missing cases indicate species that did not germinate in the first growing season. Note that these last four columns are simple maximum values. In some cases, the treatment that resulted in the second or third highest value may not be very different.

Species	*Functional Group*	*Seed Mass (mg)*	*PLS lbs/acre*	*Moderate Slope Sowing Treatment with Maximum Emergence*	*Steep Slope Sowing Treatment with Maximum Emergence*	*Moderate Slope Most Cost-Effective Method*	*Steep Slope Most Cost-Effective Method*
Acmispon glaber	Shrub	0.895	3.0	Hydro	**Jute**	Hydro	**Jute**
Artemisia californica	Shrub	0.092	1.5	Hydro	**Jute**	Hydro	**Jute**
Castilleja exserta	Forb (annual)	0.100	0.5	**Hydro**	Hand	**Hydro**	Hand
Chaenactis artemisiifolia	Forb (annual)	0.420	0.5	—	—	—	—
Chaenactis glabriuscula	Forb (annual)	0.420	0.5	—	—	—	—
Cryptantha intermedia	Forb (annual)	1.260	0.5	Imprint	**Jute**	**Hydro**	Jute
Deinandra fasciculata	Forb (annual)	0.686	0.75	Hydro	**Jute**	**Hydro**	Hydro
Encelia californica	Shrub	1.485	0.6	**Hydro**	Jute	**Hydro**	Jute
Eriogonum fasciculatum	Shrub	0.370	2.5	Drill	**Jute**	**Drill**	Jute
Eschscholzia californica	Forb (annual or perennial)	1.145	0.75	**Hydro**	Hydro	**Hydro**	Hydro
Eucrypta chrysanthemifolia	Forb (annual)	0.410	0.25	—	—	—	—
Isocoma menziesii	Shrub	0.356	0.75	Drill	**Jute**	**Drill**	Jute
Lupinus bicolor	Forb (annual or perennial)	4.680	1.0	—	—	—	—
Lupinus succulentus	Forb (annual)	26.230	2.0	**Hydro**	Jute	**Hydro**	Hydro
Malacothrix saxatilis	Forb (perennial)	0.209	0.15	Drill/Hydro/Imprint	**Jute**	Drill	**Jute**
Mirabilis laevis var. crassifolia	Forb (perennial)	26.610	2.0	**Hydro**	Jute	**Hydro**	Hand
Phacelia cicutaria	Forb (annual)	0.820	0.5	—	—	—	—
Phacelia parryi	Forb (annual)	0.250	0.5	**Hydro**	Hydro	**Hydro**	Hydro
Plantago erecta	Forb (annual)	1.665	1.75	Hydro	**Jute**	Hydro	**Hand**
Salvia apiana	Shrub	2.785	1.6	Hydro	**Jute**	Hydro	**Jute**
Salvia columbariae	Forb (annual)	0.897	0.75	Hydro	**Jute**	**Hydro**	Jute
Salvia mellifera	Shrub	0.961	2.5	Hydro	**Jute**	Drill	**Jute**

drill seeded (Montalvo et al. 2002). Based on observations from previous restoration seed sowings adjacent to the current study area (Kimball et al. 2015), we anticipated decreased germination and survivorship of native plants on steeper slopes.

Methods

Experimental Design

The study site is located in the West Loma Ecological Restoration Experiment, which is within the Irvine Ranch National Landmark in the Santa Ana Mountains in Orange County, CA, U.S.A. (33.765571, −117.739561). The climate is Mediterranean, with a mean annual precipitation of 327 mm (Kimball et al. 2014*b*). Rainfall was well below average during the study, with 175 mm of precipitation during the October–May 2014–2015 growing season, and 154 mm during the 2015–2016 growing season (http://ocpublicworks.com/howdoi/obtain/rainfall_data). The slope of the site was moderate near the top of the ridge and increased in steepness as it dropped into the canyon bottom. Slopes of approximately 5–17° are common throughout the landscape of this open-space reserve, typical of many restoration project sites. Here we define such slopes as "moderate" and contrast them with areas that land managers have seen as potentially more difficult, between 18° and 30°, which we call "steep." Our study included a test of five seed sowing methods and two unseeded controls, with each treatment applied to the slope (moderate or steep) on which it was feasible, resulting in a total of nine slope-treatment combinations (hereafter "sowing treatments") in a randomized block design (Fig. S1, Supporting Information). Jute netting was only tested on steep slopes, because this method is thought to decrease erosion and increase seedling establishment (Mitchell et al. 2006). The imprint area was seeded by hand prior to imprinting with a custom-made imprinter mounted on the front end of a bulldozer (Natures Image, Lake Forest, CA, U.S.A.). Hand seeding was followed by tamping to ensure seed–soil contact. The drill seeder was a FLEXII-88-grass drill mounted on a tractor (Truax Company, Inc., New Hope, MN, U.S.A.). It was calibrated to put out ~130 lb/acre of seed at the highest output (5th gear). We used the main seed box (also known as the "fluffy seed box") for all of our premixed seed. Hydro mulch and hydro seeding was conducted with an Imperial 3000 mounted on a roll-off (Bowie Industries, Inc., Bowie, TX, U.S.A.). Each method was applied in three replicate 3 × 40-m strips perpendicular to the slope, and seeded areas received the same mix of shrub and forb species, selected from the nearby native-dominated coastal sage scrub "reference" community (Table 1). Seed sowing treatments were randomly assigned within each of the three sets of seeding strips. The moderate and steep slope seeding strips were each split into three blocks (upper, mid, and lower), for a total of nine replicate plots per sowing treatment. Unseeded hydro mulch and control treatments were both located on steep slopes, because the moderate-sloped area was part of a mitigation project that required complete seeding. For each of the different seed sowing methods, all associated costs were recorded for evaluation of cost effectiveness.

All seeding occurred in areas that had been treated for non-native weeds from 2009 to 2015. During this period, seeds of non-native annual grasses were depleted from the seedbank substantially, but seeds of non-native forbs such as *Brassica nigra* remained viable. *B. nigra* grew substantially faster than native perennials. Crews used a hand held Red Weeder (Smucker Manufacturing, Inc., Harrisburg, OR, U.S.A.) to swipe glyphosate across the top of *B. nigra* individuals with the wick applicator when the non-native was approximately 5 cm higher than the natives. Three subsequent weeding events used a combination of hand weeding and wicking, depending on weed height. Seeding was completed between 17–21 November, 2014, before the December arrival of germination-triggering rains for the 2014–2015 growing season. Jute netting (SiteOne Landscape Supply, Roswell, GA, U.S.A.) was added to the hand-seeded plots on 18 November. Immediately after seeding was completed, we installed sets of rebar in order to measure erosion (Levin et al. 2006; Chaplot 2013). In each block treatment, three rebar pairs were hammered 1.25 m in the ground so that approximately 0.25 m remained above the surface. The two rebars in each pair were set 1 m apart from each other, leveled with the ground surface. In each seeding strip, one rebar pair was placed 1.5 m from the top of the block, and each of three seeding strips were divided into three blocks located at 3, 18, and 33.5 m (10, 60, and 110 ft) downslope.

Data Collection

The first survey, conducted 7 and 9 January, 2015, was taken approximately 2 weeks after the first germination-triggering rains of the season. We counted seedlings within 0.5×0.5-m quadrats located 3 m downslope from the top of each experimental block (or 6 m, 21 m, and 36.5 m from the top of each seeding strip). In each quadrat, native and non-native seedlings were identified and counted. Some species not included in the seed mix also germinated in our plots (non-native, invasive species), and they were also tallied.

To measure seedling survival beyond initial germination, we counted individuals in 1×1-m quadrats at the peak of the spring growing season, mid-April, 2015. In mid-March, 2016, we again counted all species within those same 1×1-m quadrats. During the second year of sampling we conducted separate counts for perennial seedlings (individuals that germinated during the 2015–2016 growing season) and 1-year-olds (surviving individuals from the 2014–2015 growing season). Taller, non-native, invasive species were reduced via manual weeding according to restoration practices in the larger area in March 2015, November 2015, and February 2016. Despite these removal efforts, non-native species continued to be present in our second year of monitoring, and we recorded their density along with that of native plants.

Soil movement was measured by balancing a level across each rebar pair in a consistent, fixed position, and measuring the distance from the level to the ground, at 10-cm interval along each meter length transect. Data collection occurred on five dates throughout the experiment, 14 January, 11 February, and 4 March of 2015, and 20 January and 2 May, 2016. These dates were selected to provide information on soil movement across each rainy season. Soil movement was calculated by measuring the change in average distance for a paired rebar station between each time point (e.g. first change = average distance on 14 January – average distance on 11 February), so that positive numbers indicate deposition and negative numbers indicate erosion. Microtopography was investigated by measuring the change in variance at each erosion transect. An increase in variance along the transect would indicate an increase in topographic relief at a location.

Data Analysis

We conducted mixed-model ANOVAs to determine whether the density of seedlings in January 2015 varied depending on the sowing treatment, with block (seeding strip and sampling position) included as a random factor in the model. Tukey post hoc tests were used to determine significant differences among groups. Separate analyses were conducted for number of native plants, number of native shrubs, number of native forbs, number of non-native plants, and native species richness. All data were $\ln + 1$ transformed prior to analysis so that the residuals were approximately normally distributed. All statistical tests were conducted with SAS version 9.4 (SAS Institute Inc. 2012).

The density data collected in spring of 2015 and 2016 were from larger permanently marked plots, while the January 2015 seedling data were from smaller unmarked quadrats, so we analyzed spring density in separate analyses, using repeated measures mixed model ANOVAs. We analyzed whether the density of plants varied depending on sowing treatment, year, or the interaction between the two fixed factors. Block was again included as a random factor in the analysis. For density data collected in April 2016, we also wanted to understand how many of the plants were survivors from the first year compared with how many were newly established seedlings. For this reason, we ran separate mixed model ANOVAs to determine whether the density of all native plants (including annuals as well as perennials), native perennial seedlings, and native perennial adults varied depending on sowing treatment, with block as a random factor.

We used regression analyses to determine whether seed mass was related to the species' responses to sowing treatment. We calculated response ratios for each species in each seed sowing treatment to estimate how each species responded to that particular seed sowing method as compared with an estimate of the establishment potential of the species across all sowing treatments. Response ratios were calculated as ln(average seedling density in treatment/average seedling density in all

Table 2. The cost of each seed sowing method per hectare and cost effectiveness (native plants per dollar spent on seeding per m^2), calculated as the density of native shrub seedlings immediately following germination-triggering rains and as the density of native plants in spring of the second growing season (2016). Mean and SE values used in the numerators are graphed in Figures 1 and 2.

Slope	*Treatment*	*Total Cost ($/ha)*	*2015 Native Shrub Seedlings/$*	*2015 Native Forb Seedlings/$*	*2015 Native Seedlings/$*	*2016 Native Shrubs/$*	*2016 Native Forbs/$*	*2016 Native Plants/$*
Moderate	Drill	9,510	128	99	209	17	68	85
Moderate	Hand	10,683	18	44	62	14	72	85
Moderate	Hydro	12,721	137	271	408	8	81	89
Moderate	Imprint	10,621	69	99	168	11	65	76
Steep	Hand	10,868	96	139	96	14	86	100
Steep	Hydro	13,215	107	188	107	11	45	56
Steep	Hydro mulch	12,227	29	34	29	4	24	28
Steep	Jute	19,720	203	159	203	14	43	57

seeded areas). Seed mass (measured as the average weight of 100 seeds per species) was ln-transformed prior to analyses so that residuals were approximately normally distributed.

To determine whether soil movement varied depending on sowing treatment, time, or the interaction between the two factors, we used repeated measures, mixed-model ANOVAs with block as a random factor. We used the same model with change in variance as the dependent variable to investigate whether changes in microtopography were influenced by seed sowing treatment. Total soil movement over the course of the study was analyzed by ANOVA with sowing method as a fixed factor.

We determined the cost effectiveness of each seeding method by first estimating the number of native plants per acre based on the average number of native plants per sampling area. We then divided the density of native plants per acre by the cost per acre of each seed sowing method to determine the plants/$/acre. Seed sowing techniques influence germination and combine with postgermination conditions to influence establishment, recruitment, and persistence (Yurkonis et al. 2008), so we calculated cost effectiveness for both the number of seedlings in 2015 and for the resulting plants in 2016. We compared cost effectiveness per species (Table 1) as well as for all native plants and for each functional group separately (Table 2).

Results

Initial Establishment

All seed sowing treatments resulted in significantly more native seedlings than unseeded hydro mulch and control areas (Fig. 1A, Tables S1A & S2). The treatment with the most native seedlings was hydro seeding on moderate slopes, followed by hand seeding with jute netting on steep slopes, which both demonstrated nearly an order of magnitude greater density than the least-effective methods on the same slopes (Fig. 1A, Table S2). Other seeded treatments had fewer native seedlings in January, yet the unseeded control area contained essentially no native plants (Fig. 1A). Interestingly, both high and low densities were achieved on both the moderate and steep slopes, suggesting that the potential for significant introduction of native plant cover is possible in many landscape locations.

Native species richness was significantly greater in all the seeded treatments than the unseeded controls, except for hand seeding on moderate slopes, which resulted in significantly fewer native species than other seeded treatments (Fig. 1B, Table S2). Among native shrubs, hand seeding with the addition of jute netting on steep slopes resulted in significantly more seedlings than imprint or hand seeding on moderate slopes (Fig. 1C). For native forb seedlings, hydro seeding on moderate slopes had the best results, followed by hand seeding with jute netting and hydro seeding on steep slopes (Fig. 1D). Hand and imprint seeding on moderate slopes resulted in the fewest native forbs out of the seeded treatments (Table S2). An unanticipated pattern was that the hydro mulch treated plots had consistently more native plants than the control plots. This could be due to treatment-induced microclimate effects promoting native germination, either from the existing seed bank or from surrounding seeded areas. Another possibility is that this pattern was due to contamination associated with the hydro seeding infrastructure, but this is unlikely because the hydro mulch plots were treated prior to the hydro seeding plots (which included mulch and seeds), and the equipment was cleaned and flushed prior to use. There was no significant effect of seed sowing treatment on the density of non-native seedlings (Fig. 1E, Table S2).

Abundance and Diversity Through Time

Results from repeated measures, mixed-model ANOVAs testing the effect of seed sowing treatment through time showed that there was a significant effect of sowing treatment on all variables (native density, native species richness, native shrub density, native forb density, and non-native density) (Fig. 2, Table S1B). These variables also changed from year to year, with new seedlings germinating in the second year of the study, resulting in a significantly greater density of native plants overall by 2016 than in the first growing season of the experiment (Fig. 2A, Table S3A). Hand seeding with jute netting on steep slopes had the greatest density of native plants in 2015, followed by hydro seeding on moderate slopes in 2016, hand seeding with jute netting on steep slopes in 2016, and hydro seeding on steep slopes in 2015 and 2016 (Fig. 2A, Table S3A). As expected, the unseeded treatments (steep hydro mulch and steep control) had the lowest density of native plants (Fig. 2A, Table S3A).

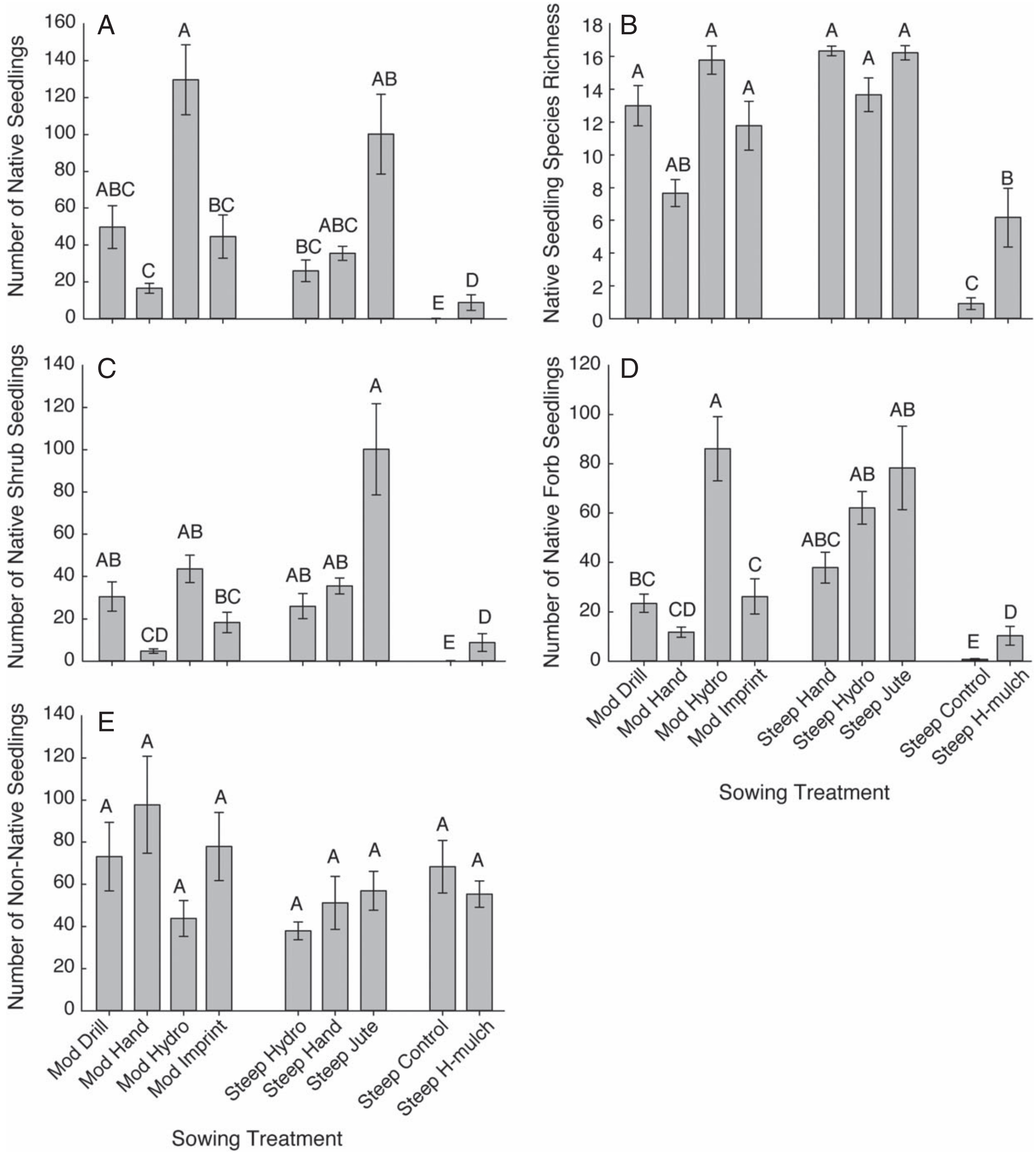

Figure 1. The abundance of native and non-native seedlings in the different seed sowing treatments, collected following emergence in January of 2015. Seed sowing treatments are abbreviated on the *x*-axis: Mod, moderate slope; steep, steep slope; hydro, hydro-seeded; jute, hand-seeded and covered with jute netting; control, no seeding; h-mulch, hydro-seeder mulch without seeds. Values are means ± 1 SE per 0.25-m^2 quadrats. Letters above each bar indicate results from Tukey post hoc tests where shared letters indicate no significant differences among treatments ($p > 0.05$).

Similar results were found when examining the effect of both year and sowing treatment on native species richness (Fig. 2B, Table S3B). All seeded treatments had significantly more native species than unseeded controls (Fig. 2B). Species richness of native plants did not change significantly from year to year in the seeded treatments and did not vary depending on the specific seeding method that was used. However, there was a significant year-by-treatment interaction, driven by an increase in native species in unseeded control plots in the second year of the study (Tables 2B & S3B).

While the density of native plants increased overall from 2015 to 2016, plant functional groups varied in their direction of change. The density of native shrubs decreased significantly from 2015 to 2016, indicating some degree of shrub

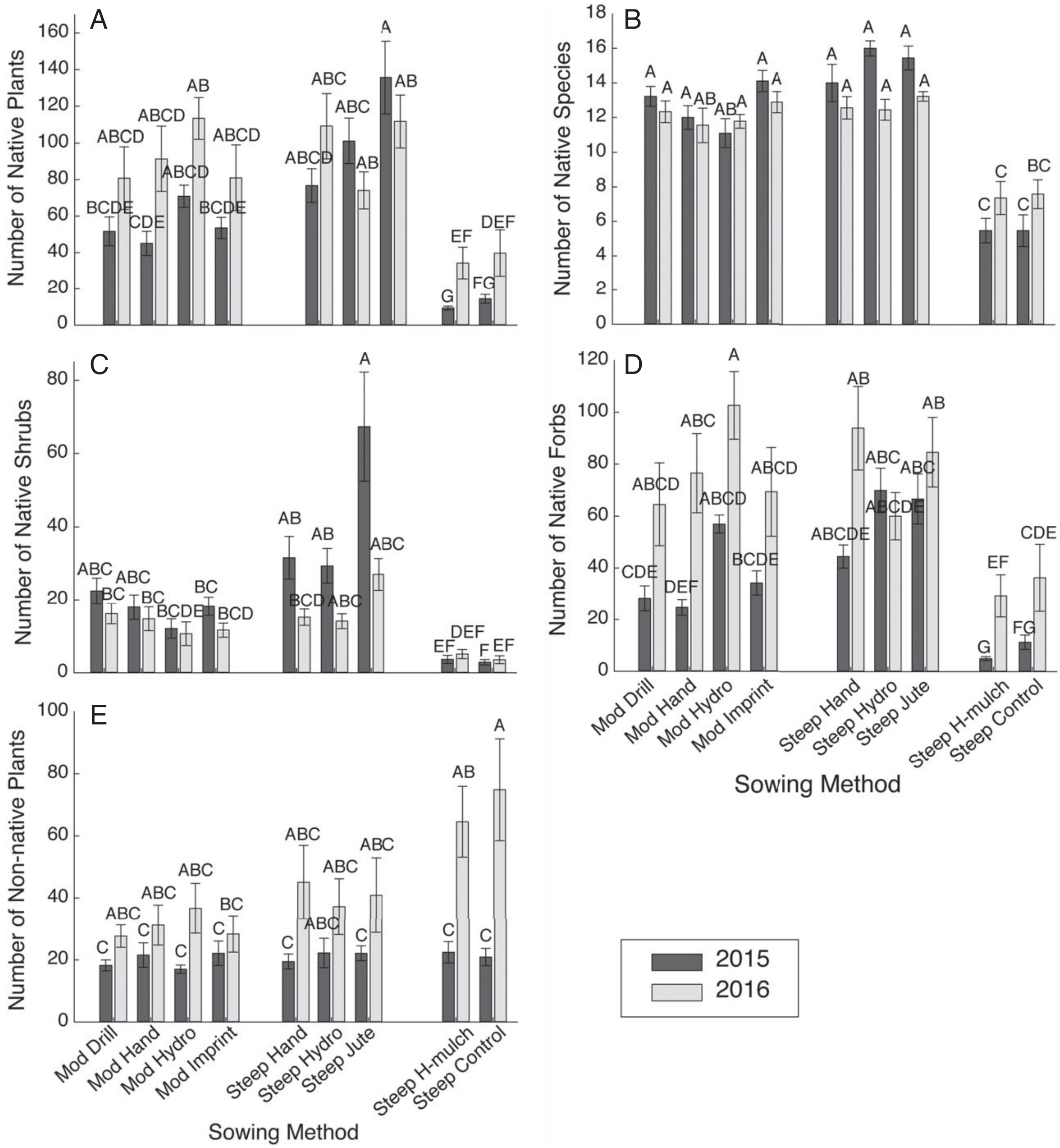

Figure 2. Density collected in spring of 2015 and 2016 in the different seed sowing treatments. Mod, moderate slope; steep, steep slope; hydro, hydro-seeded; jute, hand seeded and covered with jute netting; control, no seeding; h-mulch, hydro-seeder mulch without seeds. Values are means ± 1 SE per 1 m^2 quadrats. Results from repeated measures ANOVAs testing the influence of seed sowing method on each of these variables are provided in Table 2B. Letters above each bar indicate results from Tukey post hoc tests where shared letters indicate no significant differences among treatments ($p > 0.05$).

mortality between growing seasons, mixed with the emergence of new shrub seedlings in 2016 (Fig. 2C, Tables S1B & S3C). Shrub density also varied significantly depending on the sowing treatment (Table S1B). The three steep sloped sowing treatments had the greatest number of shrubs overall in both years, while hydro seeding on moderate slopes had the lowest shrub density of all seeded areas (Fig. 2C, Table S3C). This result is contrasted by native forb density, which was significantly greater in 2016 than in 2015 (Fig. 2D). For forbs, hydro seeding on moderate slopes along with hand seeding with jute netting resulted in the greatest density (Table S3D). Unseeded areas consistently had fewer forbs than seeded areas (Table S3), but their presence suggests that forb reproduction in the first year may be an important source of seed for the second year increase in density (as compared to any native seeds retained in the seed bank). In 2016, there were significantly more non-native species in unseeded (control and hydro mulch) plots than in plots that had been seeded with native plants in 2015 (Fig. 2E, Tables S1B & S3E).

Recruitment in the Second Growing Season

Native seedlings germinated in all seed sowing treatments during the second year of the study, such that the effect of sowing treatment on the density of native perennial seedlings in 2016 was just barely significant (Table S1C). Hand-seeded areas on moderate slopes had more perennial seedlings than jute netting on steep slopes (Table S4), possibly because there was more space and light available to seedlings on the hand-seeded moderate slope, which had a slightly lower density of native seedlings than the other seeded plots in the previous growing season (Fig. 1). There was a much stronger effect of seed sowing treatment on the number of adult native perennials (those that germinated during the first year of the study and survived through the second growing season). Hand seeding with jute netting on steep slopes resulted in the greatest density of adult perennials, followed by hand seeding on steep slopes, hydro seeding on moderate and steep slopes, imprinting on moderate slopes, and drill seeding on moderate slopes (Table S4). Hand seeding on moderate slopes had the fewest native perennial adults out of the seeded treatments and the most perennial seedlings in 2016. The steep slope control treatment, followed by the steep slope hydro mulch treatment, had significantly fewer native perennial adults than the seeded plots (Table S4).

Most of the perennials that germinated in the second year of the study were the native forb, *Malacothrix saxatilis* (Table S5). Drill seeding on moderate slopes, followed by hand seeding on moderate and steep slopes had the greatest number of *M. saxatilis* seedlings, and the seedlings also germinated well in unseeded treatments plots (Table S5). The moderate slope hand-seeded plots also seemed to produce a considerably large number of *Acmispon glaber* seedlings in 2016 as well, relative to the other treatments. Of the perennial species that germinated in 2016, most were *A. glaber*, followed by *Erigonum fasciculatum*, then *Artemisia californica* (Table S5).

Seed Mass

Heavier seeds tended to have higher cover in the imprint sowing treatment than in other seed sowing treatments, while lighter seeds had lower cover in the imprint sowing treatment ($R^2 = 0.247$, $p = 0.025$). There was no significant relationship between response to other seed sowing treatments and seed mass (Table S6).

Soil Stability

Measurements of soil movement indicated erosion in all sowing treatments (Fig. 3, Table S7). The amount of soil movement varied through time such that deposition was measured between the first and the second date of measurement, as well

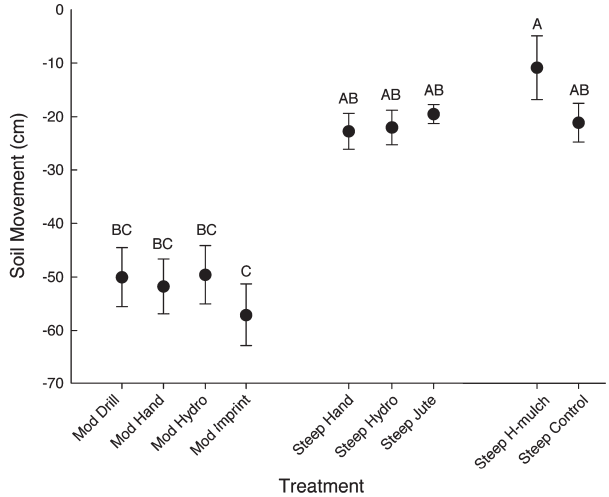

Figure 3. The change in soil height over the course of the study in each sowing treatment. Values are means ± 1 SE. Letters above each bar indicate results from Tukey post hoc tests where shared letters indicate no significant differences among treatments ($p > 0.05$).

as between the second and the third date of measurement (Table S7). After that, all areas experienced erosion, with the most erosion occurring on the moderate slopes. Differences among sowing treatments did not vary significantly within moderate- and steep-sloped areas (Fig. 3). Changes in variance indicated slight changes in microtopography between measurements, with no significant effect of time or sowing treatment. The significant treatment-by-time interaction was due to a decrease in microtopography in the steep hydro-seeded treatment between the third and fourth date of measurement, followed by an increase in microtopography in the same treatment between the fourth and fifth date of measurement (Table S7).

Cost Effectiveness

Hand seeding followed by jute netting on steep slopes was the most expensive seed sowing treatment, due to the high cost of materials and labor (Table 2). However, this method was quite successful, resulting in the highest number of native shrubs per unit area (Table 1), and the second highest average number of all native seedlings per unit area, following hydro seeding on moderate slopes. Hydro seeding on moderate slopes resulted in the greatest average native seedlings per dollar expended, due to the large numbers of native forbs that germinated in this treatment. By 2016, mortality of some 2015 plants along with new seedling establishment resulted in less of a difference among sowing treatments in terms of overall native density, which impacted the cost analysis. The steep slope hand-seeded area (without jute netting) resulted in the highest overall native density/$ in 2016, followed by hydro seeding on moderate slopes and other moderate-slope seeding methods (Table 2).

Discussion

In this study, we evaluated several approaches for the seeding and establishment phase of ecological restoration projects associated with moderate- and steep-sloped sites. Our goal was to understand native species performance—overall, as species, or as different functional types—in the context of estimating cost effectiveness and providing conservation practitioners with approaches to maximize their limited funding for enhancing landscapes. Despite the sloped nature of our study site and the known challenges of conducting restoration on slopes (Bochet et al. 2009), all of our seed sowing techniques resulted in successful native establishment. The "best" sowing method varied depending on the metric of success. For example, hydro seeding on moderate slopes resulted in the most native seedlings, especially forbs, immediately following germination. However, by mid-growing season of that first year, native density was highest in the steep jute netting treatment, which occurred due to the high native shrub survival in those plots. By mid-May the following year, the steep jute netting treatment still had significantly more native shrubs than other sowing treatments, but several other sowing treatments had equally high native density and diversity as a result of increased densities of other functional types. Drill seeding was the least expensive sowing method, followed by hand seeding. Both methods eventually resulted in a high density of native plants (>40/m^2 in 2015 and >70/m^2 in 2016), making these methods generally the most cost effective.

Seed sowing methods influenced the resulting native community partially because the methods deposit seeds at different depths, differentially altering germination of each species, and partially due to patterns of competition among establishing plants (Montalvo et al. 2002; Yurkonis et al. 2010). Germination rates of some coastal sage scrub species, such as *Eriogonum fasciculatum* and *Artemisia calfornica*, are improved with light exposure (Keeley 1987; Barton et al. 2016), so they may be expected to establish more with methods that place seeds close to the surface, such as hand and hydro seeding (Limon & Peco 2016). In our study, the two shrub species germinated most in jute-seeded areas. Surface seed deposition can also have negative effects, such as exposure to high winds and animals, along with increased potential for movement downhill with gravity. In this study, hydro seeding on moderate slopes resulted in the most native forbs, perhaps due to increased sunlight, while slightly lower emergence in drill-seeded plots on moderate slopes may have been caused by decreased sunlight exposure. Previous studies suggest hand seeding leads to greater germination rates because seed is scattered evenly and at natural distances from other seed (Yurkonis et al. 2010; Kimball et al. 2014*b*). In this study, broadcasted seed alone did not result in as many native seedlings as the other seeded treatments, although it was very cost effective.

Seed sowing technique can also influence the amount of moisture that is retained in the soil and erosion of the soil surface. With hydro seeding, the protective layer of mulch allows for less negative soil water potentials to develop in soils and plants between rainfall events as a result of reduced soil water evaporation (Chambers 2000). Placing jute netting over broadcasted seeds supposedly prevents erosion which may aid in native germination (Mitchell et al. 2003). Furthermore, greater germination of native shrubs in this treatment may have further helped to prevent soil erosion. Steep slopes are typically more challenging for establishing native plants from seed than less sloped areas due to erosion (Bochet et al. 2009). Our result that steep-sloped hand seeding with jute netting resulted in greater shrub density is consistent with another study, which suggested protective vegetative covers such as jute netting aided in survivorship of native woody species (Ziegler et al. 2000). However, only approximately 30% of native shrubs survived to the second year in our steep jute netting plots, and the high mortality may be representative of the challenges of conducting restoration on steep slopes.

Seed sowing techniques influenced germination, favoring some species over others, and this must have influenced patterns of establishment, persistence, and second-year recruitment (Fowler 1988; DeSimone & Zedler 1999). For example, native shrubs and forbs may compete with each other for resources (Kimball et al. 2014*b*; Kimball et al. in press), and this was evident in the result that forbs had the greatest density in hydro-seeded treatments on moderate slopes, while shrubs had the lowest density in those plots. In this study, we included both forbs and shrubs in the same seeding mix because we wanted to include a diversity of species in the test of seed sowing techniques. However, it may be that, postgermination, the faster-growing forbs were favored over the slower-growing shrubs, consistent with our previous conclusion that forbs and shrubs establish best when planted separately (Kimball et al. 2014*b*; Kimball et al. 2015).

Germination in the second year of the study could be from seeds that were seeded with the different sowing treatments in the previous year or from seeds that were produced at the end of the first growing season. Surprisingly, even the unseeded control plots exhibited second-year native establishment, suggesting that seeds dispersed from the surrounding seeded plots and germinated in the second year despite low rainfall in both years of the study. *Malacothrix saxatilis* had the greatest number of seedlings of all the perennial seedlings in the second year of the experiment. There were more second-year seedlings of this species than any other native in all treatments, and it may be a good option for practitioners that need a species that produces many seedlings annually and disperses into surrounding areas. For *Acmipson glaber* and *Artemesia californica*, second year seedlings were primarily in the hand seeding treatment on moderate slopes, while *Eriogonum fasciculatum* had the most second year seedlings in the hydro-seeded treatment on moderate slopes. This pattern was surprising because this sowing treatment had the fewest shrubs in 2016. It may be that *E. fascisulatum* had less competition from other shrubs in areas with this sowing treatment.

It was surprising that moderate-sloped plots experienced more soil erosion than steep-sloped plots. The hydro mulch treatment (without seeds) had the least erosion, but this treatment was not significantly different from other steep-sloped areas. Our results do not indicate that hydro mulch would be a worthwhile erosion-prevention technique, although hydro mulch has been shown elsewhere to reduce sediment loss (Prats et al. 2013). Similarly, jute netting on steep slopes did not significantly reduce erosion relative to other steep-sloped sowing methods, but jute netting has elsewhere been shown to reduce erosion (Mitchell et al. 2003). However, perennial species establishment and growth can influence ecohydrological processes so as to enhance fine soil particle retention (Ravi et al. 2017). Thus, the development of biomass on the steep-versus-moderate slopes is likely an important component of the soil movement patterns we documented. Another surprising result was that density in the different seed sowing treatments was mostly not significantly related to seed weight. Heavier seeded species were found in higher densities in the imprinted area, somewhat consistent with a previous study, in which large seeded species were found at higher densities in imprint-seeded and drill-seeded areas than hydro-seeded areas (Montalvo et al. 2002). Our study site regularly experienced strong winds, and lighter seeds may have been blown out of the imprinting depressions immediately after seeding.

The most cost-effective method (greatest density of native plants per dollar spent sowing seed per acre) varied depending on the metric of native density used in the formula. When calculated with the number of seedlings immediately following germination in 2015, hydro seeding on moderate slopes was the most cost effective. By contrast, drill seeding was the least costly and had the next best seedling establishment in 2015, but was half as cost effective as hydro seeding on moderate slopes. Similar to other cost effective findings by our group, we determined that different sowing methods can succeed in reaching equivalent native density with different costs (Kimball et al. 2015). The most cost effective treatment (using the number of native plants in the second growing season in the formula) was hand seeding on steep slopes, followed by hydro seeding on moderate slopes. Treatments such as jute netting had a similar native density per acre as hand seeding on steep slopes, but were about half as cost effective. Therefore, the better cost-effective option for practitioners would be to implement hand seeding on steep slopes.

In conclusion, this study identified possible sowing techniques that may provide the optimum native establishment and native cover for steep and moderate slopes, as well as the associated cost effectiveness and erosion control of each treatment. We found that restoration on steep slopes could be very successful, despite notions that erosion and seed implementation are challenges on steeper slopes (Bochet et al. 2009). Hydro seeding, which is more commonly used on steep-sloped sites, was also found to be very successful on moderate-sloped sites. The best sowing method for a restoration project will ultimately depend on the project's site and its goals. For example, if a land manager were looking for high shrub cover on a steep slope, the best sowing method, based on our results, would be hand seeding with jute netting. By contrast, if cost efficiency were the top priority, hand seeding on the steep slope would provide for the greatest native density per dollar spent. In conclusion, the goals, risk comfort, and timelines of each restoration project need to be evaluated before deciding which seed sowing technique is best for different measures of success. More research is needed on the valuation of ecological community traits, what the relationships or ecological trade-offs are among these traits, and how they relate to native community resilience over time in order to determine how to utilize metrics of success most appropriately and conduct cost–benefit analyses.

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Supporting Information

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

Table S1. Results from analyses on plant density.
Table S2. Density of seedlings in January of 2015.
Table S3. Results from Tukey post hoc tests on the influence of year and seed sowing treatment on density of plants in April 2015 and March 2016.
Table S4. Results from ANOVAs comparing numbers of native and non-native plants in March of 2016 with sowing method as a fixed factor.
Table S5. Average perennial seedlings and perennial adults per treatment in March 2016.
Table S6. Results from linear regressions on the relationship between seed weight (ln-transformed) and response ratios calculated for each seed sowing treatment.
Table S7. Results of repeated measures, mixed model ANOVAs on soil movement through time.
Figure S1. Schematic diagram demonstrating seed sowing treatments and sampling areas.

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