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Influence of fire and mechanical sagebrush reduction treatments on restoration seedings in Utah, United States

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RESEARCH ARTICLE

Influence of fire and mechanical sagebrush reduction treatments on restoration seedlings in Utah, United States

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Overabundance of woody plants in semiarid ecosystems can degrade understory herbaceous vegetation and often requires shrub reduction and seeding to recover ecosystem services. We used meta-analysis techniques to assess the effects of fire and mechanical shrub reduction over two post-treatment timeframes (1–4 and 5–10 years) on changes in cover and frequency of 15 seeded species at 63 restoration sites with high potential for recovery. Compared to mechanical treatments, fire resulted in greater increases in seeded species. Native shrubs did not increase, and forbs generally declined over time; however, large increases in perennial grasses were observed, suggesting that seeding efforts contributed to enhanced understory herbaceous conditions. We found greater increases in a few non-native species than native species across all treatments, suggesting the possibility that interference among seeded species may have influenced results of this regional assessment. Differences among treatments and species were likely driven by seedbed conditions, which should be carefully considered in restoration planning. Site characteristics also dictated seeded species responses: while forbs showed greater increases in cover over the long term at higher elevation sites considered to be more resilient to disturbance, surprisingly, shrubs and grasses had greater increases in cover and frequency at lower elevation sites where resilience is typically much lower. Further research is needed to understand the causes of forb mortality over time, and to decipher how greater increases of non-native relative to native seeded species will influence species diversity and successional trajectories of restoration sites.

Key words: *Artemisia tridentata*, dryland restoration, herbaceous understory, mechanical treatment, restoration seeding, seedling establishment, shrub encroachment

Implications for Practice

- Practitioners must consider seedbed conditions and species requirements when planning restoration seedings to accommodate differences in disturbance intensity and sowing depth created by treatments.
- A priori knowledge of the resilience potential of restoration sites, species nativity, and species performance should be used to formulate seeding mixes that minimize rapid increases in one species from interfering with other species in the mixture when species diversity is a management goal.
- Variation in restoration outcomes among plant community types indicates that lower elevation, warm/dry temperature/moisture sites stand to gain the most from shrub treatment and seeding efforts.
- While increases in seeded grasses were observed for all treatment types, relatively low performance of forbs exposes a fundamental shortfall for restoration practitioners in this ecosystem.

ecosystems in the last century (Eldridge et al. 2011; Archer et al. 2017). When woody plants become overabundant in semiarid ecosystems, as manifested by shrub densities exceeding historical ranges of variation, numerous ecosystem services, such as provisioning of food and habitat for wildlife, forage for livestock, and soil stabilization, are compromised (Archer & Predick 2014; Wilcox et al. 2017). In addition, soil erosion can increase as a result of degraded understory herbaceous vegetation, often resulting in lower restoration potential (Pierson et al. 2011). Consequently, remediating herbaceous understory vegetation and achieving a desired shrub density is a common land management goal (Archer et al. 2017), and often requires

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Introduction

Increased woody plant dominance is one of the most pronounced and widespread vegetation shifts within semiarid

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land managers to simultaneously reduce shrub abundance and seed restoration sites with a mix of suitable plant species (Knutson et al. 2014; Hardegree et al. 2016). However, this strategy relies on the pivotal assumption that restoration sites will exhibit resilience to disturbance (i.e. Chambers et al. 2014a) and that shrub reduction treatments will increase resource availability for seeded species as well as support understory species growth. Accordingly, recovery of ecosystem services may become contingent on the resilience of the remaining understory herbaceous vegetation (Chambers et al. 2017) and the success of seedings (Monsen 2004), yet a clear understanding of the manifold interactions between shrub reduction treatments and seeded species responses on such sites does not currently exist (Miller et al. 2014; Pyke et al. 2015).

The fact that shrub reduction has not consistently enhanced understory herbaceous vegetation in many semiarid ecosystems beckons a careful examination of how various treatments influence the factors known to control success of restoration seedings (Archer & Predick 2014). Shrub reduction treatments may differ in their capacity to create suitable conditions for establishment and persistence of certain species due to contrasting effects on soil surface conditions as well as resource availability (Young et al. 1990; Montalvo et al. 2002; Condon et al. 2011; Chambers et al. 2014a). While mechanical treatments are effective at creating furrows and pits that modify hydrology (i.e. water capture and infiltration) and improve establishment of seeded species (Hardegree et al. 2016), they also run the risk of proliferating invasive annual species in the short term or intensifying soil erosion and sediment entrainment (Miller et al. 2014; Monaco et al. 2017). Mechanical treatments also can cause excessive loosening of seedbed firmness and soil friability, thereby compromising the success of seedings by altering the depth of seed placement (Monsen & Stevens 2004). In contrast, the application of fire treatments to burn woody species is typically effective and low cost. Yet depending on burn intensity, litter and seeds on the soil surface can be entirely consumed, reducing native seed banks and increasing erosion potential of treated sites (Pierson et al. 2013). Fire treatments can also produce resins and waxes that, when deposited on soil surfaces, can create water repellent soil layers that limit soil water infiltration, increase soil erosion and run-off (Debano 2000), and inhibit emergence of seeded species (Miller et al. 2013).

Mechanical and fire treatments also can vary widely in how they impact resource pools available to residual species in the plant community which, in turn, influences seeded species (Lefler & Ryel 2012; Roundy et al. 2014). Soil water and nutrient availabilities for herbaceous vegetation typically increase following shrub reduction in semiarid shrub and woodland ecosystems (Rau et al. 2014; Roundy et al. 2014). However, changes in herbaceous production vary with time since treatment (Archer & Predick 2014), and competition for these resources remain intense, creating a strong biotic filter that mediates abundance of seeded species as well as the assembly of post-treatment plant communities (Pyke & Archer 1991; Hulvey & Aigner 2014).

Diverse seed mixtures are deemed necessary to increase species diversity, rapidly stabilize soils, and prevent the spread of invasive species (Burton et al. 2006; Davies et al. 2014),

yet few studies simultaneously consider treatment and species interactions among functional groups (i.e. shrubs, forbs, grasses) across broad ecological regions. While establishment success and subsequent increases in species abundance over time depend on species traits, site suitability for individual species (Monsen 2004; Calvino-Cancela 2011), biophysical indicators of site resilience (Chambers et al. 2017), and complex interactions among species in the mix, we still know very little about these interactions despite years of site-specific evaluations. There is need to evaluate appropriate species mixtures that work best with specific shrub reduction treatments (e.g. Knutson et al. 2014) and identify general patterns among functional groups and plant community types known to differ in resilience potential (Chambers et al. 2014a). In addition, the relative merits and ecological implications of seeding mixes composed of native and non-native species are equally complex (Asay et al. 2003; Knutson et al. 2014). For example, non-native species may establish more rapidly and interfere with the establishment and growth of native species that exhibit less vigorous seedling growth and development (Waldron et al. 2005; Thompson et al. 2006; Nafus et al. 2016). In order to refine management options and produce the broadest array of conservation benefits and ecosystem services, research is needed to understand interactions among species within seed mixes (James et al. 2013; Leger & Baughman 2015).

Although combined application of shrub reduction treatment and seeding is a major component of ecosystem management to enhance herbaceous vegetation in the western United States, generalizations regarding the relative success of treatments and species combinations are still lacking. Numerous shrub reduction and seeding treatments have been explored for semiarid shrublands and shrubsteppe ecosystems, yet much of what we know stems from specific treatment, or set of treatments, applied to a limited number of sites (Hardegree et al. 2016; Summers & Roundy 2018). To address this need, we examined 63 big sagebrush (*Artemisia tridentata* Nutt.)-dominated restoration sites where shrubs were reduced with fire or mechanical treatments with the goal of identifying patterns in short- and long-term changes in the cover and frequency of species and functional groups (e.g. shrubs, forbs, grasses). We asked the following questions: (1) Do mechanical (aerator and pipe harrow) and fire treatments differentially influence the relative cover and frequency of seeded species? (2) Do native and non-native species differ in relative cover and frequency following shrub reduction? (3) Do plant communities with varying resilience potential experience differences in seeded species cover and frequency?

Methods

To assess the relative performance of seeded species following the application of shrub reduction treatments, we used data collected from Utah Watershed Restoration Initiative (UWRI) projects. The UWRI is a collaborative effort among landowners, private organizations, and state and federal agencies to enhance wildlife and biological diversity and water quality and yield through management approaches such as mechanical vegetation manipulations (UWRI 2018).

Table 1. Functional group classification, name, code, and origin (i.e. nativity) of 15 species evaluated for changes in the cover and frequency on shrub reduction restoration sites in Utah, United States.

Functional Group	Species	Common Name	Species Code	Origin
Shrub	<i>Artemisia tridentata</i> spp. Nutt.	Sagebrush	ARTR	Native
Shrub	<i>Atriplex canescens</i> (Pursh) Nutt.	Fourwing saltbrush	ATCA	Native
Shrub	<i>Bassia prostrata</i> (L.) A.J. Scott	Forage kochia	BAPR	Non-native
Forb	<i>Linum perenne</i> L.	Blue flax	LIPE	Non-native
Forb	<i>Melilotus officinalis</i> (L.) Lam.	Yellow sweetclover	MEOF	Non-native
Forb	<i>Medicago sativa</i> L.	Alfalfa	MESA	Non-native
Forb	<i>Onobrychis viciifolia</i> Scop.	Sainfoin	ONVI	Non-native
Forb	<i>Sanguisorba minor</i> Scop.	Small burnet	SAMI	Non-native
Grass	<i>Agropyron cristatum</i> (L.) Gaertn.	Crested wheatgrass	AGCR	Non-native
Grass	<i>Psathyrostachys juncea</i> (Fisch.) Nevski	Russian wildrye	PSJU	Non-native
Grass	<i>Achnatherum hymenoides</i> (Roem. & Schult.) Barkworth	Indian ricegrass	ACHY	Native
Grass	<i>Elymus lanceolatus</i> (Scribn. & J.G. Sm.) Gould	Thickspike wheatgrass	ELLA	Native
Grass	<i>Leymus cinereus</i> (Scribn. & Merr.) Á. Löve	Great Basin wildrye	LECI	Native
Grass	<i>Pascopyrum smithii</i> (Rydb.) Á. Löve	Western wheatgrass	PASM	Native
Grass	<i>Pseudoroegneria spicata</i> (Pursh) Á. Löve	Bluebunch wheatgrass	PSSP	Native

After reviewing metadata from 1,438 completed restoration project sites associated with the UWRI (as of 2013), we selected projects conducted on big sagebrush (*Artemisia tridentata* Nutt.)-dominated lands that met the following criteria: (1) both shrub reduction and seeding treatments were applied and (2) both pre- and post-treatment data were available for analysis, with post-treatment data comprised of either short term (1–4 years), long term (5–10 years), or both timeframes. A total of 63 project sites met these criteria (Table S1). Sites were classified by plant community type (determined from dominant sagebrush subspecies: basin big sagebrush, *A. t. ssp. tridentata*; Wyoming big sagebrush; *A. t. ssp. wyomingensis*; and mountain big sagebrush, *A. t. ssp. vaseyana*). These community types are known to vary in biophysical indicators of ecosystem resilience to disturbance and resistance to invasion by exotic annual grasses (Chambers et al. 2014a, 2014b, 2017). For example, *A. t. ssp. wyomingensis* communities at lower elevations are exposed to warm-dry temperature/precipitation regimes and typically have lower herbaceous vegetation productivity, resistance to annual grass invasion, and resilience to disturbance compared to *A. t. ssp. vaseyana* sites at higher elevation montane sites that experience cold/moist conditions, greater herbaceous vegetation productivity, and higher resilience to disturbance (Chambers et al. 2014a, 2014b). In contrast, *A. t. ssp. tridentata* sites typically occur in deep, well-drained soils on lower montane slopes and are characteristically warmer than *A. t. ssp. vaseyana* sites and are wetter and have deeper soils than *A. t. ssp. wyomingensis* sites (Shultz 2009; West et al. 1978). All sites were considered critical winter habitat areas for wild ungulates. In addition, cattle grazed all sites before treatments were applied; however, use by cattle was typically deferred for at least 2 years to temporarily minimize damage to sensitive seeded areas, and resumed after this rest period.

Treatment types and seeded species lists were compiled from project site records maintained by the Utah Big Game Range Trend Studies Project (Utah Division of Wildlife Resources [DWR]; <https://wildlife.utah.gov/range-trend.html>).

Treatments were categorized as one of two mechanical treatments (aerator or pipe harrow), or fire (including both natural and prescribed fire). Each site was seeded with a custom mix of species deemed most suitable for the environmental, soil, and vegetation conditions. Of the many species seeded in these mixes, we identified a group of 15 perennial species (i.e. seven grasses, five forbs, and seven grasses) that were commonly seeded across many sites (Table 1).

Mechanical treatments were applied with implements pulled by a bulldozer or tractor. The aerator consisted of a double drum roller with affixed blades that penetrated the soil and created shallow depressions for water catchment while simultaneously crushing and chopping woody vegetation (RanchWorx, Palm Harbor, FL, U.S.A.; Summers & Roundy 2018). Thus, the aerator has low surface disturbance, promotes water infiltration, and creates furrows to trap water and seeds. In contrast, the pipe harrow (regionally known as Dixie harrow) consists of a series of 2-m × 10-cm diameter pipes with spikes arranged at alternating angles to rip shrubs and cause considerable scarification and disturbance to the soil surface as debris is dragged (Dahlgren et al. 2006). Finally, unlike the two mechanical shrub reduction treatments, fire intensity and the continuity of burned area across sites depended on available fuel and subsequent fire intensity yet fires typically burn through the vegetation and may also consume seeds and litter on the soil surface. As most fires typically do not greatly disturb soils other than influencing litter and duff on the soil surface, a chain was commonly dragged across sites to help incorporate seeds (e.g. Cain 1971; Table S1).

Most project sites (i.e. 46/63) were seeded using a broadcast method by sowing larger seeded species (e.g. most grasses and forbs) before applying mechanical treatments, then sowing the smaller seeded species (e.g. *A. tridentata* spp. and *Bassia prostrata*) after applying mechanical treatments. This method dispersed the seed mix from a box mounted in front of the rear drum (aerator) or directly from the tractor (pipe harrow). In contrast, for seven sites, a rangeland drill was used for seeding species when sites contained fewer standing shrubs (e.g.

after fire) and rock obstacles (Table S1). For the remaining 10 sites, aerial seeding was applied over rough terrain inaccessible to large ground equipment, or when project sites were seeded as part of large-scale rehabilitation efforts for which ground equipment was impractical. Although different seeding methods were used to account for site conditions and equipment availability, seeding rates for a given species (i.e. the weight of seed applied per hectare) were consistent across sites.

Canopy cover (grasses and forbs) and frequency (shrubs) of seeded species were monitored with a standard protocol used by the Utah Division of Wildlife Resources (UDWR) Range Trend Studies Project (UDWR 2018). Each site was sampled by randomly establishing one 152.4-m baseline transect in the treatment area. Along this baseline transect, five 30.5-m belts were placed perpendicularly at predetermined positions (3.4, 40.8, 78.9, 113.0, and 150.9 m). A steel stake was placed at the beginning of each belt to ensure consistent placement of future sampling. Vegetation was monitored along each of the five belts using 20 nested frequency quadrats of 25-cm $\times$ 25-cm placed at 1.5-m intervals. Quadrats were customized with clear markings indicating five nested areas of increasing space: (1) 1, (2) 5, (3) 25, (4) 50, and (5) 100%. Using these markings, percentage canopy cover of grass and forb species was estimated visually by assigning species to one of seven possible cover classes modified from Daubenmire (1959): (1) 0.01–1%, (2) 1.1–5%, (3) 5.1–25%, (4) 25.1–50%, (5) 50.1–75%, (6) 75.1–95%, and (7) 95.1–100%. For shrubs, frequency was estimated by searching nested areas 1–5 and recording the first area that contained a rooted plant; smaller areas were scored higher, such that nested areas 1–5 were scored from 5 to 1, respectively. Nested frequency was deemed a better source of data to assess seeded shrubs because canopy cover data included mature shrubs that had not been seeded, but whose canopies overtopped smaller seedlings. For each herbaceous species, we calculated average percentage cover (based on midpoint cover class values) and for each shrub species we calculated nested frequency (based on summed scores for each belt) and accompanying standard deviations for each site ($n = 5$). Although we anticipated that many of focal species existed on these project sites prior to seeding and treatment, we could not account for changes in cover and frequency directly resulting from the establishment of new plants from the seeding versus changes associated with growth and colonization of preexisting plants because nonseeded control areas were not monitored. Consequently, our study is limited to detecting relative changes in cover and frequency among treatment and species as opposed to directly assessing establishment of seeded species.

Statistical Analyses

Given the limitations of our study design (i.e. variable seeding years, monitoring years, customized species mixes for project sites, and unequal number of sites monitored in each timeframe), we chose to calculate a standardized metric of effect size to quantify changes in species cover and frequency and analyze this dataset using meta-analysis techniques. Meta-analysis is ideal for situations when results across multisite long-term

experiments are used to assess and synthesize outcomes of different management strategies (Koricheva & Gurevitch 2014). To do this, we first calculated mean and variance using data from each belt for seeded species cover and/or frequency for each project site ($n = 5$), which were used to calculate effect sizes as the natural log of the ratio between post- and pre-treatment ($\ln[\text{post/pre}] = \ln\text{RR}$) that were weighted by the inverse of study site variance (Hedges & Vevea 1998; Gurevitch & Hedges 1999). Effect size estimates were calculated for both short- and long-term timeframes. Despite the differences in sample sizes and the limitations outlined above, meta-analysis enabled us to make comparisons among treatments, species, and plant community types because mean effect sizes with high precision (lower variance) are weighted more heavily than studies with higher variance.

Effect size estimates were computed and analyzed with the metafor package for R (www.r-project.org) using the RStudio console (www.rstudio.com). Multiple comparison tests were not conducted, but effect size estimates were graphed with 95% confidence intervals (CIs) to visually compare effects, which were considered significantly different from zero or a contrasting effect size estimate if 95% CIs did not overlap zero or each other, respectively (Nakagawa & Cuthill 2007). Analyses were performed with the R meta-analysis (RMA) function and fixed-effect models (Viechtbauer 2010) to independently evaluate the influence of six moderator factors on seeded species abundance: functional group, species origin, sagebrush community type, shrub reduction treatment, seeded species identity, and treatment $\times$ species interaction. These models make conditional inferences (i.e. only to the set of project sites included in the analysis; Hedges & Vevea 1998) and tested the null hypotheses that moderator levels are different (Q_M -test; $H_0: \beta_1 = \beta_2 \dots \beta_i = 0$; $\alpha = 0.05$). Due to all forbs being non-native species, the effect of origin was analyzed for grasses and shrubs only. Actual pre- and post-treatment cover and nested frequency values (i.e. mean $\pm$ SE) were also summarized by species for each timeframe.

Results

Actual Frequency and Cover Values

Frequency of native shrubs changed little between pre- and post-treatment, yet the non-native species *Bassia prostrata* increased during post-treatment for both timeframes (Figs. 1A & 2A)). In contrast, all forbs increased in cover during post-treatment in the short term, but over the long term, the magnitude of these increases was notably lower except for *Medicago sativa* (Figs. 1B & 2B). Grass cover was highly variable among species; however, even the species with relatively smaller increases after 1–4 years showed marked increases after 5–10 years (Figs. 1C & 2C). Actual pre-treatment values also indicate that numerous species were already present on these sites due to prior restoration efforts or nativity to sites (i.e. *Artemisia tridentata* spp., *B. prostrata*, *Linum perenne*, *M. sativa*, *Agropyron cristatum*, *Achnatherum hymenoides*, *Pascopyrum smithii*, and *Pseudoroegneria spicata*). By

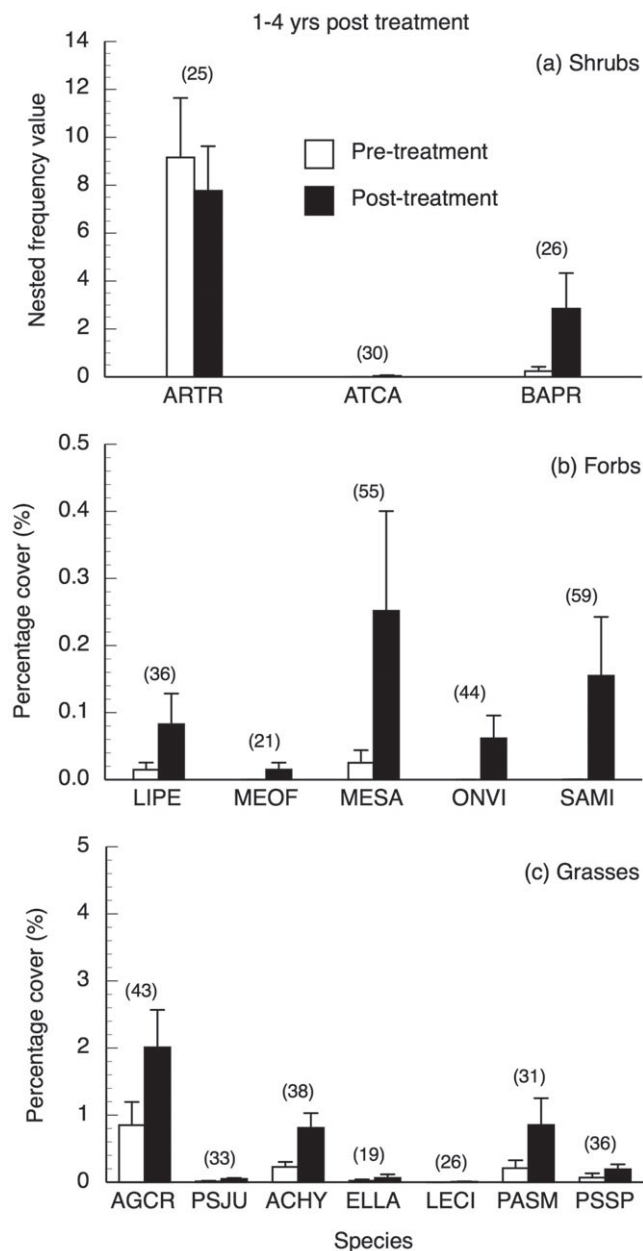


Figure 1. Mean (+ SE) nested frequency and cover of 15 seeded species evaluated prior (pre) and 1–4 years after applying shrub removal and seeding treatments (post). Values in parentheses, directly above bars, indicate the number of sites included in the analysis for each species.

Seeded species included three shrubs (A: ARTR, *Artemisia tridentata*; ATCA, *Atriplex canescens*; BAPR, *Bassia prostrata*), five forbs (B: LIPE, *Linum perenne*; MEOF, *Melilotus officinalis*; MESA, *Medicago sativa*; ONVI, *Onobrychis viciifolia*; SAMI, *Sanguisorba minor*), and seven grasses (C: AGCR, *Agropyron cristatum*; PSJU, *Psathyrostachys juncea*; ACHY, *Achnatherum hymenoides*; ELLA, *Elymus lanceolatus*; LECI, *Leymus cinereus*; PASM, *Pascopyrum smithii*; PSSP, *Pseudoroegneria spicata*). Note: different scale on y-axis for forbs and grasses.

comparison, five of the seeded species were first introduced to sites by seedings conducted during our assessment period (i.e. *Atriplex canescens*, *Melilotus officinalis*, *Onobrychis viciifolia*,

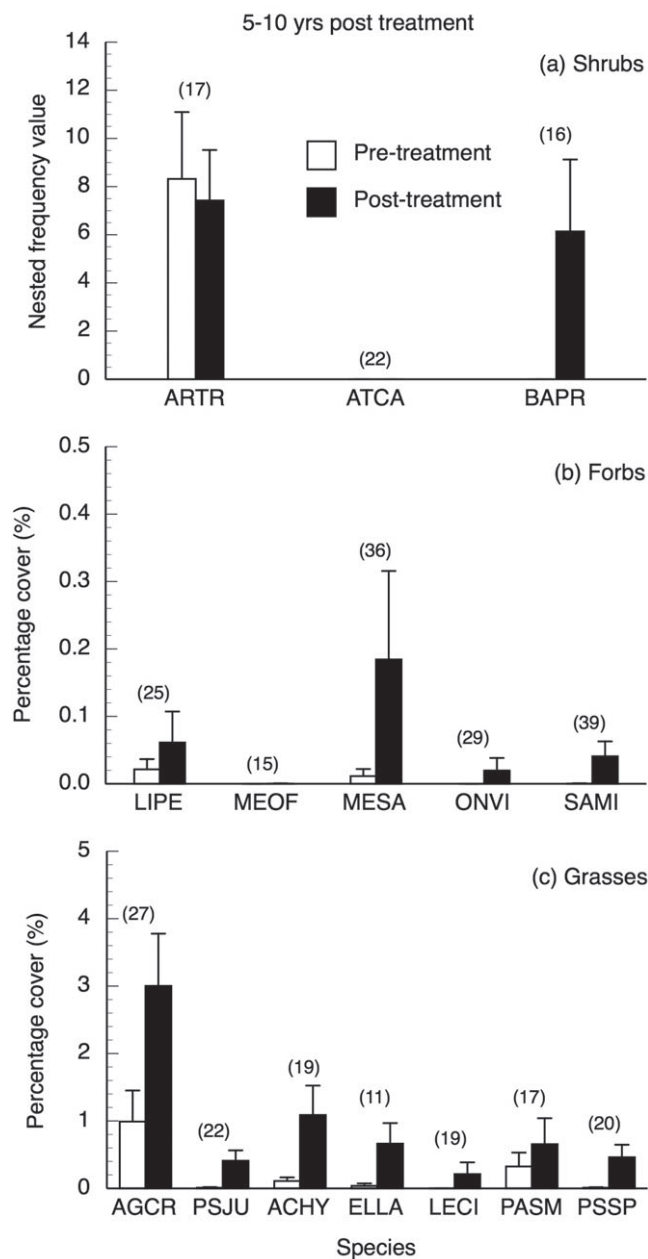


Figure 2. Mean (+ SE) nested frequency and cover of 15 seeded species evaluated prior (pre) and 5–10 years after applying shrub removal and seeding treatments (post). Details are provided in Figure 1.

Sanguisorba minor, and *Leymus cinereus*), and all increases in abundance can be attributed to plant establishment from seeding.

Contrasts of Functional Group and Species Origin

All three functional groups demonstrated significant increases in cover or frequency during both timeframes (Table S2; Fig. 3). Increases for grasses and shrubs exceeded those for forbs. Grasses and shrubs increased between the two timeframes, while forbs slightly declined. Cover and frequency of non-native

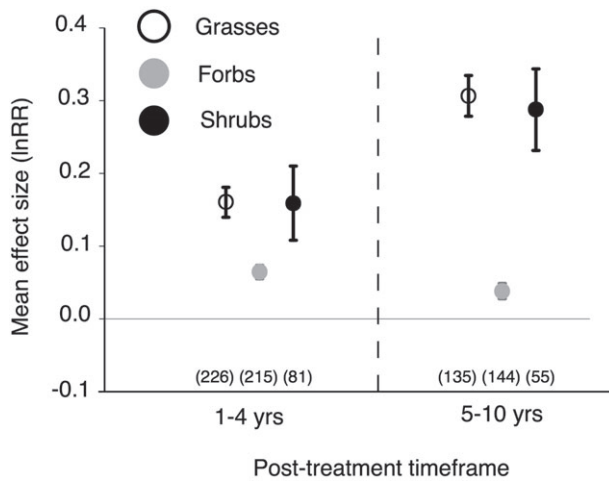


Figure 3. Mean ($\pm$ 95% CI) effect size estimates for shrubs, forbs, and grasses (pooled for seeded species and shrub reduction treatments) evaluated during two post-treatment timeframes. Values in parentheses, directly below symbols, indicate the number of project site $\times$ species combinations included in meta-analysis of functional groups (Table S2). Effect size estimates are considered significantly different than zero or a contrasting effect size estimate if 95% CIs did not overlap zero or each other, respectively.

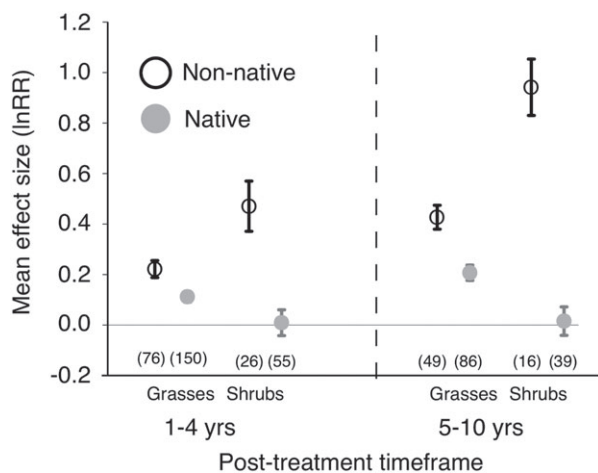


Figure 4. Mean ($\pm$ 95% CI) effect size estimates for non-native and native species (pooled for seeded species and shrub reduction treatments) evaluated during two post-treatment timeframes (Table S2). Details are provided in Figure 3.

species exceeded native species in both timeframes, especially for shrubs, whose native counterpart showed no net change in either timeframe (Fig. 4). Differences between non-native and native species were most pronounced in the long term.

Species and Treatment Effects

Tests of species, treatment, and the species by treatment interaction were highly significant for all functional groups in both timeframes with the exception of the borderline significant effect of treatment on grasses in the short term (Table S3).

Bassia prostrata frequency increased much more than the native shrubs and its frequency was more than 2-fold greater in the fire treatment compared to mechanical shrub removal treatments (Figs. 5A & 6A). Forb cover was also generally higher in the fire treatment, especially for *M. sativa* in both timeframes and *S. minor* after 5–10 years. All forbs except *M. officinalis* also increased in the pipe harrow treatment in the short term, but this effect disappeared in the long term for *M. sativa* and *S. minor*. In contrast, cover for three forb species (i.e. *L. perenne*, *O. vicifolia*, and *S. minor*) increased in the aerator treatment, but only in the short term. For grasses, although the main effect of treatment was not significant in the short term, treatments influenced grass species differently (significant species by treatment interaction; Table S3). For example, *L. cinereus* was not affected by any of the treatments; yet cover of *P. smithii* increased in the mechanical treatments but not in the fire treatment. The most dramatic variation in grass species responses among treatments appeared in the long term when increases in *A. cristatum*, *Elymus lanceolatus*, *L. cinereus*, and *Pseudoroegneria spicata* within the fire treatment exceeded both mechanical treatments. Cover for *A. cristatum* and *Psathyrostachys juncea* were also higher in the pipe harrow treatment compared to the aerator treatment. Although grass cover was generally lower in the aerator treatment compared to the other treatments in the long term, the aerator treatment increased the overall cover of four grasses, especially the native grass *A. hymenoides*.

Contrasts of Plant Community Types

Seeded shrub frequency and grass cover were notably higher in both timeframes at *A. t. ssp. wyomingensis* sites compared to sites dominated by the other two sagebrush subspecies (Table S2; Fig. 7A). Increases in seeded grasses and shrubs between short- and long-term timeframes were also more pronounced at lower elevation, *A. t. ssp. wyomingensis* sites. Sagebrush plant communities also strongly differed in seeded forb cover, which, when compared to the other communities, was greatest in *A. t. ssp. tridentata* communities in the short term, but greatest in *A. t. ssp. vaseyana* communities over the long term.

Discussion

A consensus is developing that the restoration of degraded sagebrush steppe and semiarid shrublands through fire and mechanized approaches, followed by seeding native species, has had limited success (Pyke et al. 2013; Knutson et al. 2014; Svejcar et al. 2017). This is particularly true for sites considered to have low resilience to disturbance (i.e. Chambers et al. 2014b) that have suffered extensive alterations to vegetation, soils, and hydrology and where current land use may also be perpetuating degraded understory conditions (Morris & Rowe 2014; Bestelmeyer et al. 2015). Although similar degraded conditions are common throughout the regions evaluated in this study, it is important to emphasize that the particular sites we evaluated encompassed a collection of restoration locations that were not similarly degraded. In addition, qualitative attributes

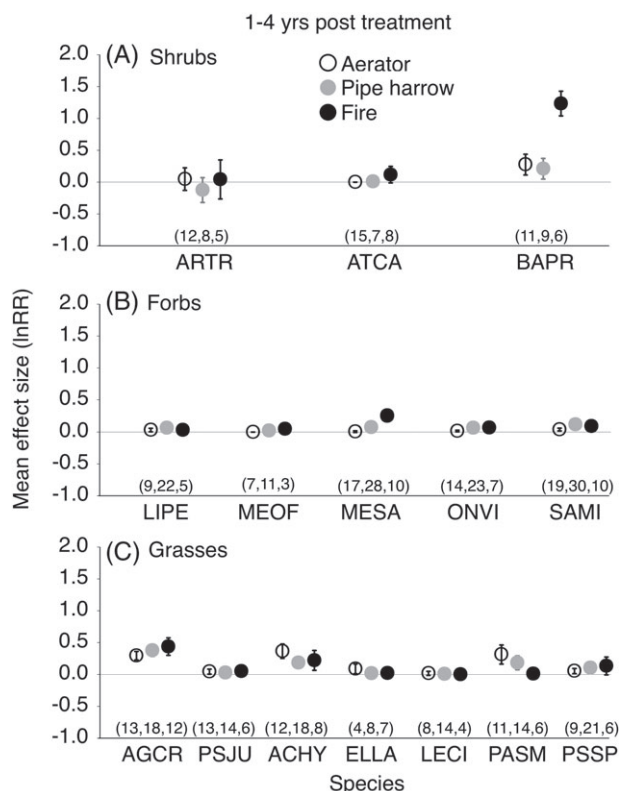


Figure 5. Mean ($\pm$ 95% CI) effect size estimates for 15 seeded species evaluated 1–4 years after applying shrub removal and seeding treatments (Table S3). Species codes are defined in Figure 1 and details are provided in Figure 3.

of rangeland health (Pyke et al. 2002), as well as site resilience to disturbance and resistance to invasion by exotic annual grasses (Miller et al. 2014; Chambers et al. 2017), were generally understood, and a rigorous panel of experts evaluated the likelihood of success and matched treatments to site conditions (UWRI 2018). Thus, our study provides a clear picture—for sites where many of the typical constraints to restoration success were avoided—of how fire and two mechanical shrub reduction treatments, aerator, and harrow, differentially influenced the responses of 10 preexisting herbaceous species and 5 seeded species that had not previously existed on the study sites.

Seeded species identity and shrub reduction treatments strongly interacted, which offers new insight into treatment and species combinations that enhance understory vegetation conditions. First, it is clear that fire promoted both short- and long-term increases in seeded species that exceeded the mechanical treatments for three non-native species (*Bassia prostrata*, *Medicago sativa*, and *Agropyron cristatum*) as well as long-term increases in the forb *S. minor* and three other perennial grasses. The effectiveness of fire may be related to its greater overall reduction in shrub cover relative to the mechanical treatments at these restoration sites (C. Riginos 2018, The Nature Conservancy, personal communication). Accordingly, competition for soil resources between seeded species and surviving shrub plants (i.e. primarily *Artemisia tridentata*

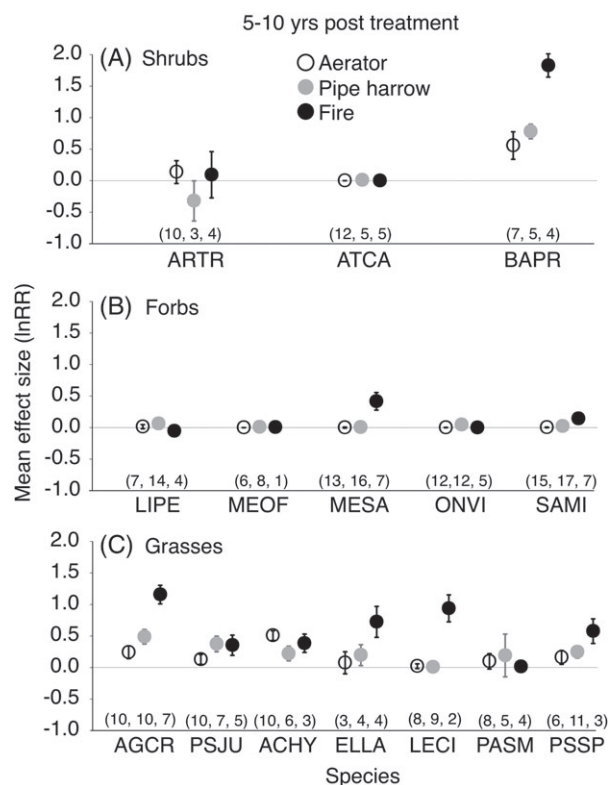


Figure 6. Mean ($\pm$ 95% CI) establishment effect size for 15 seeded species evaluated 5–10 years after applying shrub removal and seeding treatments (Table S3). Species codes are defined in Figure 1 and details are provided in Figure 3.

ssp.) may have been lower in the fire treatment, offering more favorable conditions for a broad range of species to experience successful growth. Greater increases for seeded species within the fire treatment may also be a consequence of heterogeneous soil surface conditions produced by fire, which often creates mosaics of burned and unburned patches and a greater number of regeneration niches for seeded species (Pyke et al. 2013). Fire, through the combustion of plant biomass and organic matter on the soil surface, has also been linked to enriching soils with limiting mineral nutrients that are known to promote seedling growth (Rau et al. 2007; Miller et al. 2013). Fire also creates bare soil surfaces where seeds may have occurred in more favorable safe sites. For example, the most successful seeded species, *B. prostrata*, is known to establish best on bare soils following wildfires, and establishment becomes poor when seeding into thick vegetation or litter (Monaco et al. 2003; Sullivan et al. 2013).

In contrast, compared to the fire treatment sites, which were commonly chained to incorporate seeds into the soil to improve plant establishment (Table S1; Madsen et al. 2015), the mechanical treatments may have buried aerial- and broadcast-dispersed seeds deeper, thus compromising seedling establishment and growth. Accordingly, by creating deep divots, the aerator treatment showed consistently lower species abundances compared to the other treatments. In addition,

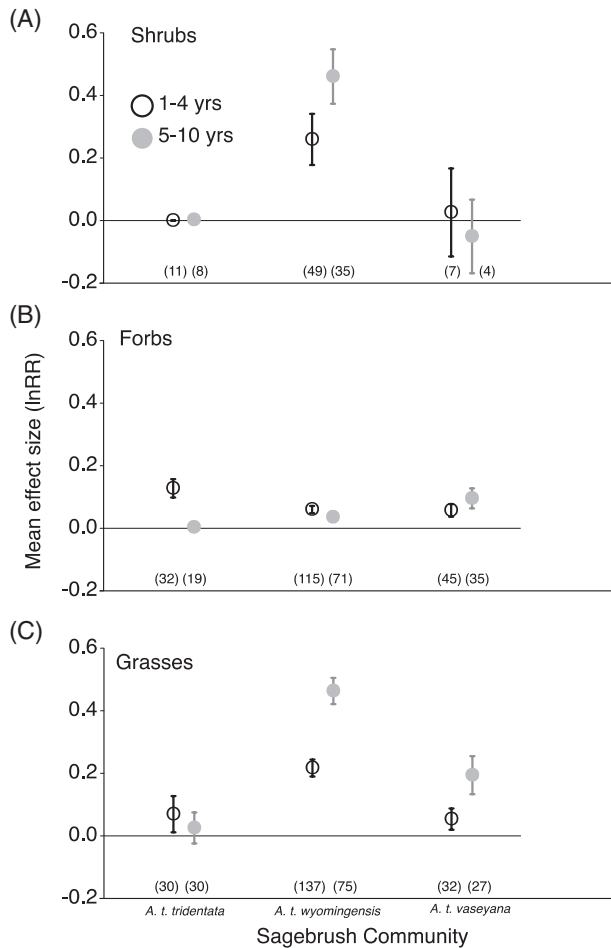


Figure 7. Mean ($\pm$ 95% CI) effect size estimates for sagebrush plant community type (pooled for seeded species and shrub reduction treatments) evaluated during two post-treatment timeframes (Table S2). Details are provided in Figure 3.

compared to the aerator, *A. cristatum* increased more in the long term in the pipe harrow treatment that created small furrows. The furrows also may have been advantageous for forbs; our assessment showed that cover for many of the seeded forbs was higher in the pipe harrow treatment, similar to Dahlgren et al. (2006), who found that pipe harrow treatments increased forb cover more than 3% relative to an aerator treatment.

Recent analyses purport that basing the performance of species on geographic origin (i.e. non-native vs. native) is a false dichotomy since all plant species appear to follow the same “rules” for establishment and growth (Leffler et al. 2014; Lemoine et al. 2016). However, greater performance of non-native species relative to native species is clearly portrayed from our assessment, suggesting that relative differences between these species identified nearly 50 years ago still stand (Hull 1971). It is not clear from our results whether non-native species show greater adaptation to the conditions at restoration sites, but traits exhibited by these species, including high seedling vigor, drought tolerance, rapid growth, and recovery from defoliation are often sought in breeding programs (Asay

et al. 2003), and likely contributed to the better performance of non-native species. In contrast, seed enhancement programs for native species have focused less on these traits, but instead typically emphasize selection for seed and seedling traits to overcome seed production bottlenecks and development of plant materials for distinct geographic locations. The tradeoff is a shorter history of selection for adaptations such as stress tolerance (Jones et al. 2015; Leger & Baughman 2015; Staub et al. 2016). However, despite the lesser performance of native species in our study, four of the five native grass species showed significant levels of persistence over the long term, suggesting that these currently available and widely utilized native seed sources effectively assisted in the recovery of degraded understory conditions.

An ongoing challenge for restoration practitioners will be to better understand how to manipulate seedbed conditions such that poorer performing native species can achieve higher establishment and greater increases following disturbance. For example, attaining ideal sowing depths is challenging for mixed species broadcast seedings, especially when they are conducted prior to applying mechanical shrub reduction treatments, which was the most common method used across our study sites. In our study, we speculate that some of the differences among treatments and species were inevitably due to seedbed conditions and species preferences for these conditions. For example, if seeds are buried too deep, few grasses can produce seedlings that will successfully establish, while some species that are known to emerge well from greater depths will experience favorable establishment conditions due to exceptional coleoptile growth from deep depths (i.e. *A. cristatum* and *Achnatherum hymenoides*; Asay & Johnson 1983; Young et al. 1994). The timing of sowing seeds should also be considered to account for differences in microenvironmental requirements for germination and life stage transitions from seedlings to established plants among seeded species (i.e. James et al. 2011); some species may perform better when seeded earlier in the autumn and prior to snow accumulation (i.e. *A. tridentata* spp.; Meyer & Monsen 1992; Lambert 2005), while others perform best when seeded on top of snow (i.e. *B. prostrata*; Page et al. 1994; Tilley et al. 2006). Consequently, our observation of greater increases in *B. prostrata* relative to *A. tridentata* spp. may have stemmed from the former experiencing more ideal conditions since shrubs were seeded after snow accumulation across the restoration sites evaluated here (K. Gunnell, 2018 Utah Division of Wildlife Resources, personal communication).

Lower abundance of seeded forbs compared to shrubs and grasses echoes the concern that establishment of this critical understory component is a major concern to plant community diversity and provisioning of ecosystem services for wild ungulates and imperiled wildlife species (Scotter 1980; Wirth & Pyke 2003; Dumroese et al. 2015; Pennington et al. 2016). The mechanisms responsible for lower persistence of forbs are not entirely clear, but we speculate there could be a host of possible factors at play across these restoration sites. First, because our restoration sites are within critical habitat for wild ungulate species, the decline in forb abundance may be due to spring and summer utilization. For example, mule deer (*Odocoileus hemionus*),

especially females, are known to utilize recently treated and seeded areas more than untreated areas (King & Smith 1980; Skousen et al. 1989) and greatly reduce palatable forb species, such as the seeded species we assessed (Austin & Urness 1983; Kay & Bartos 2000). Nonetheless, even under heavy utilization from wild ungulates, our results indicated significant increases in forbs relative to pre-treatment conditions over the long term, particularly in higher elevation *A. t. ssp. vaseyana* plant communities and from the introduction and establishment of three new species to the understory. These results are promising because seeding forbs is a primary reason for restoring understory vegetation in this region because they contribute to the diets of both wild ungulates and greater sage-grouse (*Centrocercus urophasianus*) (Kufeld 1973; Lyons et al. 1996; Dahlgren et al. 2015). Second, relative to grasses and shrubs, the forbs we evaluated were shorter lived and have been shown to accrue mortality over time on seeded sagebrush sites in Utah, and their persistence varies by species and intensity of utilization by rodents, livestock, and wild ungulates (Hewitt et al. 1982; Rumbaugh 1983; Rosenstock & Stevens 1989). However, we stress that decreases in forbs over time were evident only at the *A. t. ssp. tridentata* and *ssp. wyomingensis* sites; whereas forb cover was highest and increased over time at higher elevation *A. t. ssp. vaseyana* sites that are known to have cooler/moister temperature/precipitation regimes as well as higher resilience to disturbance (Chambers et al. 2014b, 2017). Third, most of our study sites experienced cattle grazing with variable spring and fall use, which undoubtedly can influence the productivity and persistence of herbaceous vegetation and recent seedings (Rice & Westoby 1978; Brotherson & Brotherson 1981; Beck & Mitchell 2000). It is also important to note that our assessment focused on species that were considered to be broadly adapted across a diversity of project sites and that other forb species matched to specific site conditions may have responded differently. For example, while the majority of the commercial seed comes from genetic sources from outside of Utah, future research to explore the benefits of using site-matched genotypes for native species is critically needed to enhance genetic diversity of restoration sites and improve the recovery of native plant communities (Bower et al. 2014; Leger & Baughman 2015).

A cautionary result of our assessment is the possibility that the increases of non-native seeded species may have interfered with either the establishment or growth of native species within the same seed mix (i.e. Pyke et al. 2013; Knutson et al. 2014). This speculation is based on the observation of more rapid increases in abundance for the most successful species in each functional group (i.e. *B. prostrata*, *M. sativa*, and *A. cristatum*), while native counterparts were slower to increase, possibly due to competitive exclusion. Rapid development of these three species has been linked to their capacity to diminish species richness and suppress later developing species (Monaco et al. 2003; Sheley & Carpinelli 2005; Gunnell et al. 2010). Furthermore, *B. prostrata* and *A. cristatum* were specifically developed for use into warm/dry temperature/precipitation regimes typical of the lower elevation *A. t. ssp. wyomingensis* plant communities (Asay et al. 2003; Tilley et al. 2006) where we found notably greater increases in seeded shrubs and grasses compared to the

cooler, higher elevation sagebrush communities (i.e. *A. t. ssp. vaseyana*). The relative abundance of *B. prostrata* may be of particular concern on these restoration sites, especially given its ability to spread within sagebrush ecosystems following disturbances (Gray & Muir 2013). Subsequent monitoring is needed to determine if vigorous species that rapidly establish diminish over time as native sagebrush plants recover or whether they spread outside of the seeded area into native shrublands (Frischknecht & Plummer 1955; Sullivan et al. 2013). Similarly, disentangling potential interference among seeded species is challenging in this context because seed mixes varied across sites and we did not simultaneously analyze species abundances in the same response years.

We conclude that all three functional groups experienced notable increases, but just a few species were actually responsible for these increases. In addition, the greatest increases were in non-native seeded species that tended to do better within certain shrub reduction treatments. The interaction between species and treatment was most dramatic over the long term due to fire having a greater influence than mechanical treatments on species abundance. Based on these results, the influence of potential shrub reduction treatments on restoration seedings should be considered on a species-by-species basis. More broadly, because the sites we evaluated had high potential for success, our study offers an unbiased comparison of species, treatment, and plant community types. Comparisons among *Artemisia* plant community types further emphasized that lower elevation *A. t. ssp. wyomingensis* sites, which are typically the most degraded and express the lowest resilience to environmental stresses and resistance to invasion than the other plant community types, stood to gain the most from seeding and experienced greater increases in seeded grasses and shrubs. In contrast, the higher elevation *A. t. ssp. vaseyana* sites, which have characteristically cold/moist temperature/precipitation regimes compared to the other two community types, experienced much higher forb persistence over the long term. Greater increases for non-native seeded species also signal the need to better understand the long-term implications and potential pitfalls of shifting understory composition from native to introduced exotic species (e.g. Rottler et al. 2015). Future research is also needed to determine how post-treatment wildlife management influences forb persistence. In addition, greater seeded species increases within the fire treatment beckons the need to develop management strategies to utilize the period following wildfires to opportunistically seed sites (Eiswerth et al. 2009; Davies et al. 2013; Pyke et al. 2013). Lastly, further research is needed to clarify how mechanical treatments influence seedbed conditions, especially for native species that have not been specifically developed for the prevailing anthropogenic disturbances that currently exist within sagebrush ecosystems.

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Supporting Information

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

Table S1. Summary of project sites showing treatment type, sagebrush community, seeding method, year of monitoring, and general site characteristics.

Table S2. Meta-analysis test of moderators (Q_m) for studies of functional group (shrub, forb, and grass), species origin (non-native and native), and plant community type.

Table S3. Meta-analysis test of moderators (Q_m) for studies of species, treatment, and the interaction of species and treatment for three functional groups.

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