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Disturbance Type and Sagebrush Community Type Affect Plant Community Structure After Shrub Reduction☆

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ABSTRACT

Treatments to reduce shrub cover are commonly implemented with the objective of shifting community structure away from shrub dominance and toward shrub and perennial grass codominance. In sagebrush (*Artemisia* L.) ecosystems, shrub reduction treatments have had variable effects on target shrubs, herbaceous perennials, and non-native annual plants. The factors mediating this variability are not well understood. We used long-term data from Utah's Watershed Restoration Initiative project to assess short-term (1 − 4 yr post-treatment) and long-term (5 − 12 yr post-treatment) responses of sagebrush plant communities to five shrub reduction treatments at 94 sites that span a range of abiotic conditions and sagebrush community types. Treatments were pipe harrow with one or two passes, aerator, and fire with and without postfire seeding. We analyzed effect sizes (log of response ratio) to assess responses of sagebrush, perennial and annual grasses and forbs, and ground cover to treatments. Most treatments successfully reduced sagebrush cover over the short and long term. All treatments increased long-term perennial grass cover in Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities, but in mountain big sagebrush (ssp. *vaseyana* [Rydb.] Beetle) communities, perennial grasses increased only when seeded after fire. In both sagebrush communities, treatments generally resulted in short-term, but not long-term, increases in perennial forb cover. Annual grasses (largely invasive cheatgrass, *Bromus tectorum* L.) increased in all treatments on sites dominated by mountain big sagebrush but stayed constant or decreased on sites dominated by Wyoming big sagebrush. This result was unexpected because sites dominated by Wyoming big sagebrush are typically thought to be less resilient to disturbance and less resistant to invasion than sites dominated by mountain big sagebrush. Together, these results indicate some of the benefits, risks, and contingent outcomes of sagebrush reduction treatments that should be considered carefully in any future decisions about applying such treatments.

Introduction

Woody and herbaceous plants are widely known to compete for limited shared resources in dryland systems (Blaisdell, 1949; Scholes and Archer, 1997; Riginos, 2009; Eldridge et al., 2011; Ratajczak et al., 2012). In many ecosystems, increases in woody vegetation due to changing fire, grazing, and/or climate regimes have led to declines in perennial grass cover and productivity, which can reduce the availability of forage for livestock and wildlife (Scholes and Archer, 1997; Tobler et al., 2003; Van Auken, 2009; Eldridge et al., 2011). A common management objective is to reduce woody cover and increase perennial grass cover and production without creating undesired consequences for the community, such as increasing cover of invasive species (Archer and Predick, 2014).

The big sagebrush (*Artemisia tridentata* Nutt.) ecosystems of the western United States are undergoing widespread and rapid change due to a variety of factors, including non-native species invasions, livestock grazing, and changes in fire regimes (Wisdom and Chambers, 2009; Davies et al., 2011b). In some areas, fire has become more frequent, leading to declines in shrub cover and increases in invasive annuals, whereas in other areas fire has been suppressed, leading to increases in woody cover (Crawford et al., 2004; Baker, 2006; Davies

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et al., 2011b). In places with high sagebrush cover, managers have long used a variety of methods to reduce shrub cover, including prescribed fire, heavy equipment and implements, and herbicides to increase abundance and productivity of herbaceous species (Hull and Vaughn, 1951; Vallentine, 1989; McDaniel et al., 1991; Beck et al., 2012).

The conceptual basis for sagebrush reduction is that the ecological influence of sagebrush will remain suppressed for a significant period after treatments are applied, releasing perennial grasses and forbs from competition and increasing their productivity and abundance. Such shifts in the relative cover of different major plant guilds or structural elements, if they occur, can increase the forage available to livestock and ungulate wildlife and improve habitat cover for some other wildlife species (Beck et al., 2012; Fulbright et al., 2018). Increased herbaceous perennial plant production may also help increase ecosystem resistance to exotic annual species such as cheatgrass or downy brome (*Bromus tectorum* L.) (Chambers et al., 2014; Rau et al., 2014). On the other hand, fire and soil surface disturbances associated with mechanical treatments can also promote the spread of invasive species (D'Antonio and Vitousek, 1992; Reisner et al., 2013). Avoiding the spread or increase in abundance of cheatgrass is a high priority because it has the capacity to dramatically shorten fire return intervals and has already caused significant rangeland degradation over millions of hectares of the Intermountain West (Bradley and Mustard, 2007; Balch et al., 2013). Understanding these diverse outcomes of vegetation change has risen in priority as managers are tasked with maintaining habitat for the sensitive greater sage-grouse *(Centrocercus urophasianus)*.

Numerous studies have been conducted to evaluate the effectiveness of sagebrush reduction treatments, but most have focused on single sites and/or short-term responses (Wambolt and Payne, 1986; Watts and Wambolt, 1996; Dahlgren et al., 2006; Beck et al., 2009; Davies et al., 2011a). The handful of studies that have spanned a larger geographic area have been limited to Wyoming big sagebrush communities (*A. tridentata* ssp. *wyomingensis* Beetle & Young) (Hess and Beck, 2012; Pyke et al., 2014), which occur in more arid, lower-elevation regions relative to mountain big sagebrush (*A. tridentata* ssp. *vaseyana* [Rydb.] Beetle). Results among these studies, as well as among treatments within studies, have been variable. Although some results have shown increases in perennial grass and forb production or cover after sagebrush reduction (Crawford et al., 2004; Dahlgren et al., 2006; Monaco et al., 2017), others have not (Wambolt et al., 2001; Davies et al., 2011a; Davies and Bates, 2014; Pyke et al., 2014); and while some have shown increases in cheatgrass after sagebrush reduction (Davies et al., 2011a; Davies and Bates, 2014; Monaco et al., 2017), others have not (Pyke et al., 2014). The factors mediating these forms of variability are not well understood, underscoring the need for cross-site and cross-treatment comparisons over both short- and long-term response times.

Here, we compare responses of major plant guilds and ground cover on 94 sites subject to fire or mechanical (pipe harrow and aerator) sagebrush reduction methods. Sites span much of the state of Utah, with a range of abiotic conditions and dominant sagebrush communities (largely mountain and Wyoming big sagebrush). Plant community responses were monitored in short-term (1 − 4 yr post-treatment) and longer-term (5 − 12 yr post-treatment) time frames. Specifically, we ask 1) Across all sites, how do treatments compare in their effects on major plant guilds and ground cover attributes, in short-term and long-term time frames? 2) Do the effects of treatments differ between sagebrush communities? and 3) Do the effects of treatments differ depending on abiotic site conditions?

Methods

Data Source

All data were collected on projects conducted through Utah's Watershed Restoration Initiative (WRI) (https://wri.utah.gov/wri/). The WRI is a public-private partnership program aimed at improving watersheds and wildlife habitat through restoration and postfire rehabilitation in Utah. Each project is planned, reviewed, ranked, and executed at the local level. Project plans take many factors into consideration, including vegetation trends, site suitability for different shrub reduction treatments, and appropriate revegetation species for post-treatment seeding.

We reviewed WRI project areas to identify suitable sites for addressing our research questions. We identified 94 sagebrush-dominated WRI sites that were subject to fire ($n = 35$) or mechanical shrub reduction using an aerator ($n = 20$) or a pipe harrow passed over the vegetation once ("one-way"; $n = 18$) or twice ("two-way"; $n = 21$) (Fig. 1). The aerator is a double drum roller that is pulled by a bulldozer or tractor (Lawson Series Tandem Aerator, RanchWorx, Clifton, TX). Its blades crush and chop vegetation and penetrate the soil to create small depressions. The pipe harrow, or Dixie harrow, is made up of several 2 m − long pipes with spikes at alternating angles that rip up shrubs and break up the soil surface as they are pulled by a tractor or bulldozer. The pipe harrow, especially when passed over the vegetation twice, results in a more intense disturbance to both shrubs and the soil surface than the aerator. Fire included both prescribed ($n = 6$) and wild ($n = 29$) fires. Although the latter are not deliberate "treatments" to reduce shrub cover and generally occur under more extreme burning conditions, we included them in this study in order to compare the effects of fire with the effects of other treatments. This is important given the prevalence and intensity of fire as a disturbance in sagebrush ecosystems.

All aerator and pipe harrow sites and 23 of the fire sites were seeded with a custom, site-specific mix of perennial forbs, perennial grasses, and sagebrush (see Wilder et al., 2018 for more details). Seed was broadcast either aerially or from a seed box on the aerator or harrow after treatments. This yielded five general site types (hereafter "treatments"; Table 1): fire-seeded, fire-unseeded, aerator, harrow-one-way, and harrow-two-way. All seeded sites were rested from livestock grazing for at least 2 yr post seeding. Because certain treatments are more appropriate for certain site characteristics, pretreatment conditions were not equivalent across all treatments. For example, the two-way harrow treatment was generally applied at sites with higher sagebrush cover than sites with the one-way harrow treatment, and mechanical treatments were not applied to sites with steep slopes inaccessible to large machinery. These differences are detailed further in the "Results" section.

The 94 project sites span a range of elevation (1 400 − 3 000 m) and annual average precipitation (200 − 700 mm) and occur within a variety of sagebrush communities, mostly in the Wasatch and Uinta Mountains, Colorado Plateaus, and Central Basin and Range Level III Ecoregions of Utah (Omernik and Griffith, 2014). We used pretreatment cover data (see later) to classify each site according to the dominant sagebrush species or subspecies at the site: Wyoming big sagebrush, mountain big sagebrush, basin big sagebrush (*A. tridentata* ssp. *tridentata*), or "other" (black sagebrush, *Artemisia nova* A. Nelson, or mixed *A. nova* and *A. tridentata*).

We compiled a database of vegetation and ground cover characteristics at each site before and after fire or mechanical shrub reduction. Sites were monitored between 1999 and 2013 by the Division of Wildlife Resources (DWR) Range Trend Studies program (https://wildlife.utah.gov/range-trend.html) every 3 − 5 yr on a rotating monitoring schedule, regardless of the date the treatment was applied. To accommodate this variable schedule, we classified each monitoring event as pretreatment, short-term post-treatment (1 − 4 yr), or long-term post-treatment (5 − 12 yr). Long-term data were available for 56 out of 94 sites.

Because species composition varied from site to site, we analyzed cover of major plant functional groups (i.e., guilds)—broad elements of community structure—and ground cover attributes for cross-site comparison. We categorized plant cover as sagebrush, perennial grasses, annual grasses, perennial forbs, and annual forbs and ground attributes as biological crust cover, litter cover, and bare ground (mineral soil). Cover was measured within treatment areas at each site along five parallel 30-m long transects spaced 30 m apart. Grass, forb, sagebrush, biological crust, litter, and bare ground were measured using a modified Daubenmire

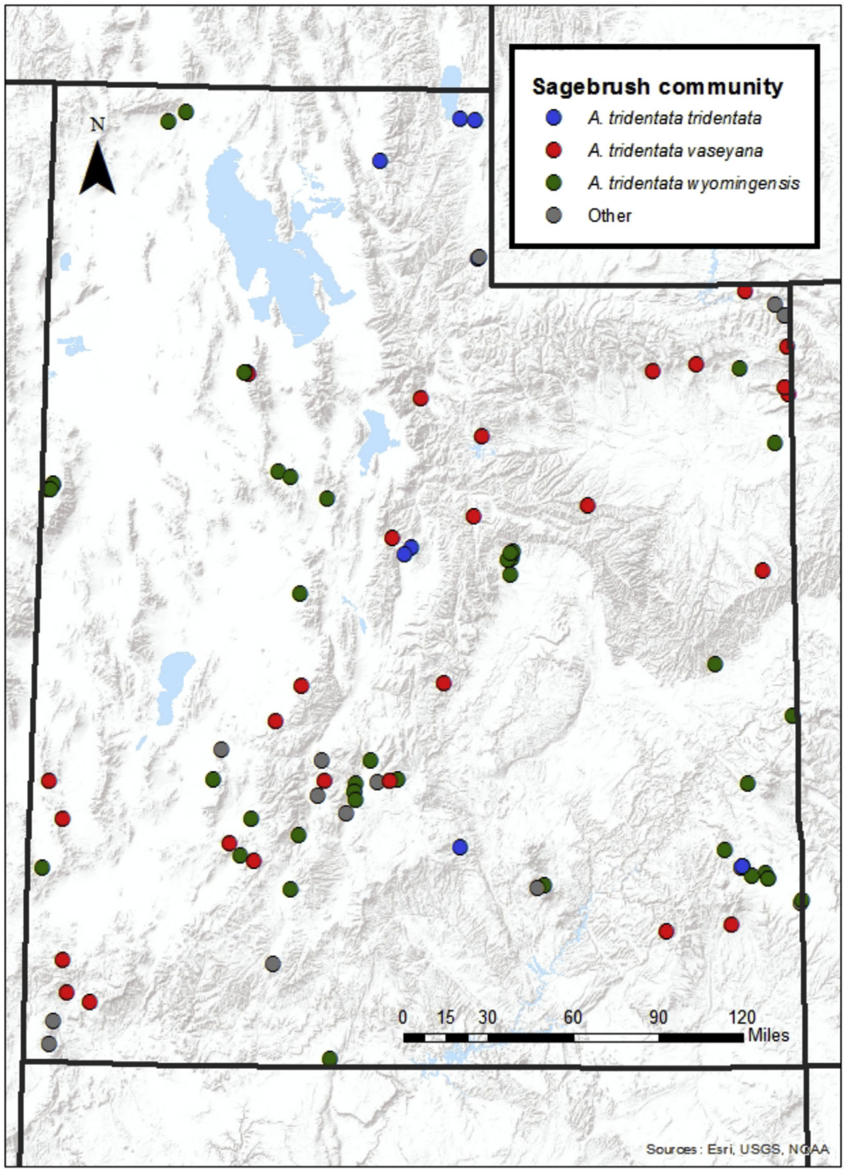

Figure 1. Map of Watershed Restoration Initiative study sites in Utah used in this analysis.

(1959) method; 0.25 m × 0.25 m quadrats were placed every 1.5 m along each 30-m transect ($n = 20$ per transect), and cover was determined using an ocular estimation in seven classes: 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 analysis, cover for each quadrat was treated as the midpoint of the observed cover class value; these values were averaged for each transect. Slope and elevation were measured at or near the start of the first transect. Because different transects often represented different aspects, we did not explicitly test effects of aspect, although we acknowledge it to be a potentially important explanatory variable. Precipitation was taken as the 30-yr average precipitation (1981 − 2010) for each site using PRISM (Parameter-elevation Relationships on Independent Slopes Model) climate data (http://www.prism.oregonstate.edu).

Analyses

We assessed the magnitude of change in cover of major plant guilds and ground cover attributes for the five treatments (fire-seeded, fire-unseeded, aerator, harrow-one-way, and harrow-two-way) using effect

Table 1
Distribution of sites across treatments and sagebrush *(Artemisia tridentata)* communities, for both short-term and long-term (in parentheses) time frames. Sites are Watershed Restoration Initiative sites in Utah.

	Aerator	Fire-seeded	Fire-unseeded	Harrow one-way	Harrow two-way	Total
A. t. tridentata	5 (5)	2 (0)	0 (0)	2 (0)	0 (0)	9 (5)
A. t. vaseyana	1 (1)	6 (3)	10 (6)	4 (2)	6 (4)	27 (16)
A. t. wyomingensis	9 (6)	11 (6)	2 (0)	9 (6)	13 (6)	44 (24)
Other shrubs	5 (4)	4 (4)	0 (0)	3 (1)	2 (2)	14 (11)
Total	20 (16)	23 (13)	12 (6)	18 (9)	21 (12)	94 (57)

size analysis (Hedges et al., 1999). For each treatment site, we calculated effect sizes for each cover category as the natural log of the response ratio of post-treatment and pretreatment (lnRR = ln[post/pre]) using the *escalc* function within the *metafor* package for R (Viechtbauer, 2010). We did this for both short-term and long-term post-treatment time frames. Significance levels of mean effect size estimates were determined using the RMA function and fixed-effects models (z-test; H_0: mean effect size = 0). Further, we analyzed differences among treatments for all sites combined, as well as separately within each of the two most common sagebrush community types, mountain and Wyoming big sagebrush, using the *mod* function within *metafor*. The *mod* function allows the user to test models of effect size as a function of "moderators," or predictor variables, and is analogous to the *lm* function in linear modeling (Viechtbauer, 2010). The test statistic is a Q_M-test, with H_0: $b_1 = b_2 = 0$ (beta coefficient estimates all equal zero). Because the Q_M-test reports overall significant differences among treatments, we also specified linear contrasts within *metafor* for multiple comparisons among pairwise treatment combinations. To supplement effect size analyses, we examined patterns of actual pretreatment and post-treatment cover measurements (rather than change in cover) in response to treatments, both across all sagebrush communities together and within mountain and Wyoming sagebrush communities separately, using 1-way ANOVAs and post-hoc Tukey's tests in the *multcomp* package in R. We also used 1-way ANOVAs to test whether site variables (precipitation, elevation, and slope) differed among treatments and sagebrush communities. We then used multiple linear regression to analyze the effects of these continuous site variables on effect sizes for each major plant guild and ground cover response, first for all sites (regardless of treatment) and then separately for each treatment type.

Results

Vegetation Responses

All treatments reduced sagebrush cover in the short term (1 − 4 yr). However, fire reduced sagebrush cover significantly more than the aerator and one-way harrow treatment (but not the two-way harrow treatment) over the short-term time frame. This was true for all communities considered together and for the two main sagebrush communities (Fig. 2A; Tables S1 − S3). This pattern generally weakened in the long term (5 − 12 yr) (Fig. 2B). When all communities were considered together, long-term fire effects on sagebrush cover were similar to the effects of the other treatments. However, within the mountain big sagebrush − dominated sites, the fire-seeded treatment had a much greater negative effect on sagebrush cover than other treatments.

Despite these differences among treatments on sagebrush cover, the net effect in the long term was to maintain the pretreatment relative rank of sagebrush cover across the different treatments. Before the treatments were applied, sagebrush cover for all sagebrush communities combined was significantly greater for the two-way harrow sites than for the aerator and fire sites ($F = 4.41$, df = 4, $P = 0.003$; Fig. 2C). Five to 12 yr after treatments, sagebrush cover was reduced across all treatments and rank order of cover was the same as pretreatment such that there were still significant treatment-level differences ($F = 3.75$, df = 4, $P = 0.01$) with the greatest sagebrush cover in the sites treated with a two-way harrow and least sagebrush cover in the burned and aerator sites (see Fig. 2C).

Across all sagebrush communities combined, perennial grass cover increased in the short term in all but the fire-unseeded treatment—the only treatment that did not receive seed addition (Fig. 3A). This increase was greatest in the aerator treatment (significantly greater than all other treatments; linear contrasts in Table S1, available online at https://doi.org/10.1016/j.rama.2019.01.007). In the long term and across all sites, the fire-seeded treatment showed the greatest increase in perennial grass cover (significantly more than any other treatment; see Table S1), while the fire-unseeded sites continued to show no increase in grass cover (Fig. 3B). The large positive effect of the fire-seeded treatment on perennial grasses was consistent for both major sagebrush communities across time. In both the short and long term, the rank order of treatment effects was the same in mountain and Wyoming big sagebrush communities, but in general perennial grass cover increased much more in Wyoming than mountain or basin big sagebrush communities (Fig. 3B; Tables S2, S3, available online at https://doi.org/10.1016/j.rama.2019.01.007). It is important to note that perennial grass cover, considered across all sagebrush communities, was initially highest in the fire-unseeded treatment (which is likely why these sites were not seeded) and lowest in the fire-seeded and one-way harrow treatments (Fig. 3C; $F = 2.04$, df = 4, $P = 0.09$). After 5 − 12 yr, perennial grass cover across all sagebrush communities did not differ significantly by treatment; the net effect of the treatments was to increase perennial grass cover so that all five treatments became more similar ($F = 0.76$, df = 4, $P = 0.55$). However, results were somewhat different when the data were broken down by sagebrush community: the net effect within mountain big sagebrush − dominated communities was no change in perennial grass cover, whereas in Wyoming big sagebrush communities it was an increase in perennial grass cover for all treatments (Fig. 3C).

Across all sagebrush communities and within both mountain and Wyoming big sagebrush communities, perennial forb cover increased in the short term in all treatments except the aerator treatment (Fig. 4A). Perennial forb cover increased significantly more in the two fire and two harrow treatments than the aerator treatment when all sagebrush communities were considered together; forb cover also increased more in the fire-unseeded treatment than the fire-seeded and the two harrow treatments (see Table S1). In the long term, however, most treatments did not result in a significant or substantial increase in perennial forb cover (Fig. 4B and C). When all sagebrush communities were considered together, the fire-seeded treatment showed the greatest positive effect and the aerator treatment showed a negative effect (see Fig. 4B; Table S1). Long-term results differed somewhat between mountain and Wyoming big sagebrush communities; within mountain communities, one-way harrow treatment reduced forb cover substantially, whereas it increased forb cover in Wyoming communities (see Tables S2, S3). In contrast, aerator treatment substantially reduced forb cover in Wyoming big sagebrush communities. Despite these treatment effects, initially greater forb cover at fire-unseeded sites persisted from pretreatment to 5 − 12 yr post treatment. Pretreatment forb cover (considering all communities together) did not differ significantly by treatment, but substantially greater forb cover occurred in the fire-unseeded treatment than other treatments (Fig. 4C). After 5 − 12 yr, forb cover was still relatively low across all treatments and still substantially (but not significantly; $F = 1.45$, df = 4, $P = 0.23$) greater in the fire-unseeded treatment relative to other treatments.

Annual grass cover was largely made up of invasive cheatgrass. In the short term, considering all sagebrush communities together, only the fire-seeded treatment reduced annual grass cover (significantly different from all other treatments). The effect was neutral in the aerator and one-way harrow treatments, whereas annual grass cover increased in the fire-unseeded and two-way harrow treatments (significantly different from the other three treatments) (see Fig. 5A; Table S1). In the long term, across all communities, both the fire-seeded and aerator treatments reduced annual grass cover (both significantly different from the other three treatments), both harrow treatments had neutral effects, and the fire-unseeded treatment increased annual grass cover (significantly different from the other four treatments; see Table S1). These patterns, however, differed to some extent depending on sagebrush community. Most notably, in the long term, annual cover in the fire-seeded treatment decreased in Wyoming big sagebrush communities but increased in mountain communities (Fig. 5B; see Tables S2, S3). Some of these differences in response across treatments and communities may be related to underlying differences among sites in terms of their vulnerability to invasion, potentially indicated by pretreatment

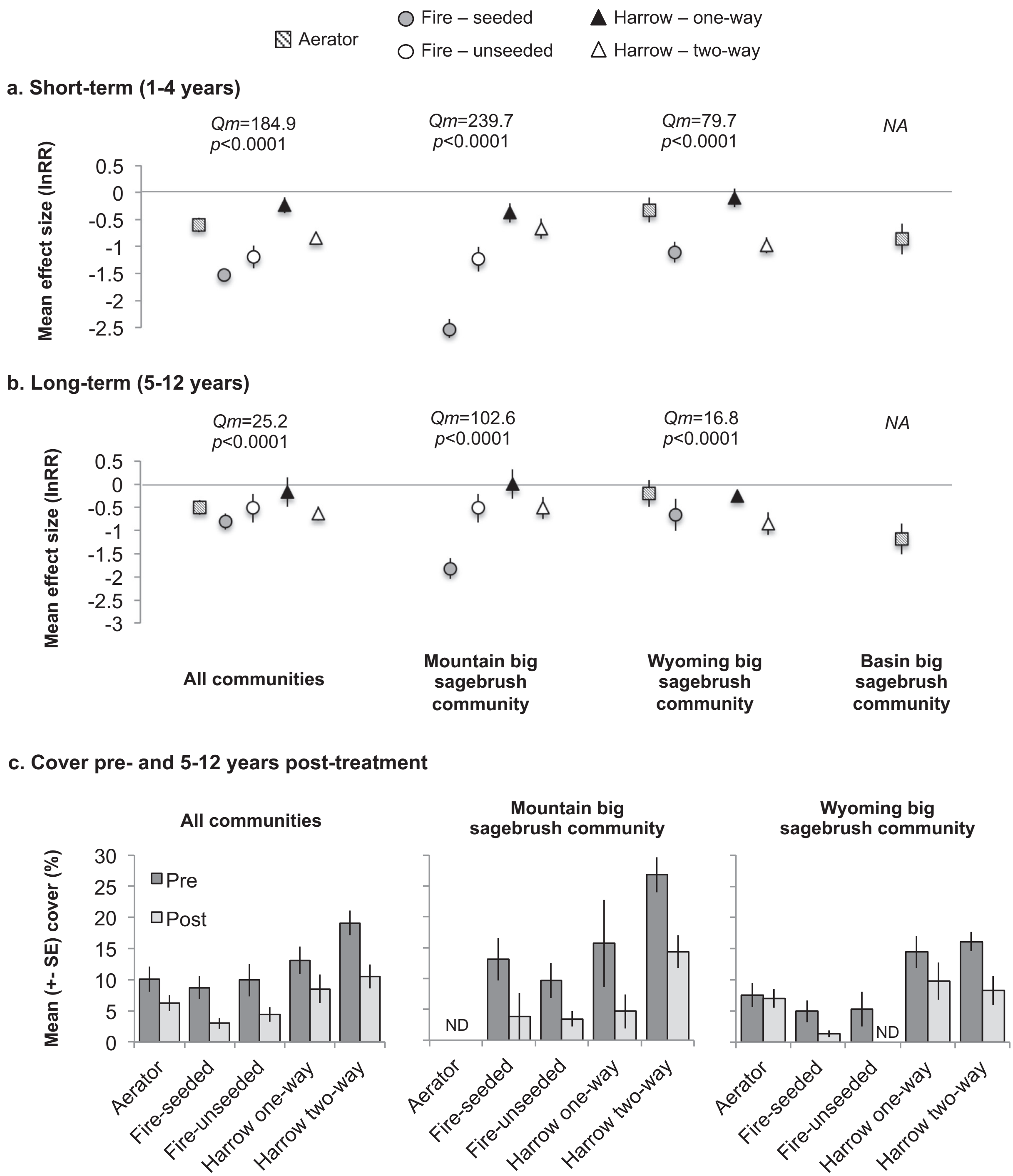

Figure 2. Change in sagebrush cover in response to five treatments on Watershed Restoration Initiative sites in Utah: **a,** mean effect sizes (± 95% confidence interval [CI]) of change in cover in the short term, 1 − 4 yr post treatment, **b,** mean effect sizes (± 95% CI) of change in cover in the long term, 5 − 12 yr post treatment, and **c,** mean (± SE) sagebrush cover pretreatment and 5 − 12 yr post treatment.

differences in annual grass cover ($F = 3.65$, df = 4, $P = 0.008$). Sites treated with the pipe harrow had much lower pretreatment annual cover than other treatments, and annual cover remained low at these sites (Fig. 5C). Fire sites had the highest pretreatment annual grass cover, and although annual grass cover decreased in these treatments at some sites, in general post-treatment annual grass cover was still greater in the fire treatments than in other treatments (Fig. 5C; $F = 4.11$, df = 4, $P = 0.006$).

Annual forb cover across all sites had significant short-term increases in three treatments (both fire treatments and two-way harrow) and did not change significantly in the aerator and one-way harrow treatments (Fig. 6A; see Table S1). The same general pattern of treatment effects was present in each of the sagebrush communities considered, but short-term annual forb response was more positive in mountain than in Wyoming big sagebrush communities. In the long term, the effects of treatment for annual forb cover depended even more on sagebrush community; in mountain big sagebrush communities, treatments had neutral to positive effects on annual forb cover, whereas in Wyoming big sagebrush communities treatments had neutral to negative effects (Fig. 6B; Tables S2, S3). In mountain big sagebrush communities, forb cover generally increased slightly from pretreatment to post-treatment, whereas in Wyoming big sagebrush

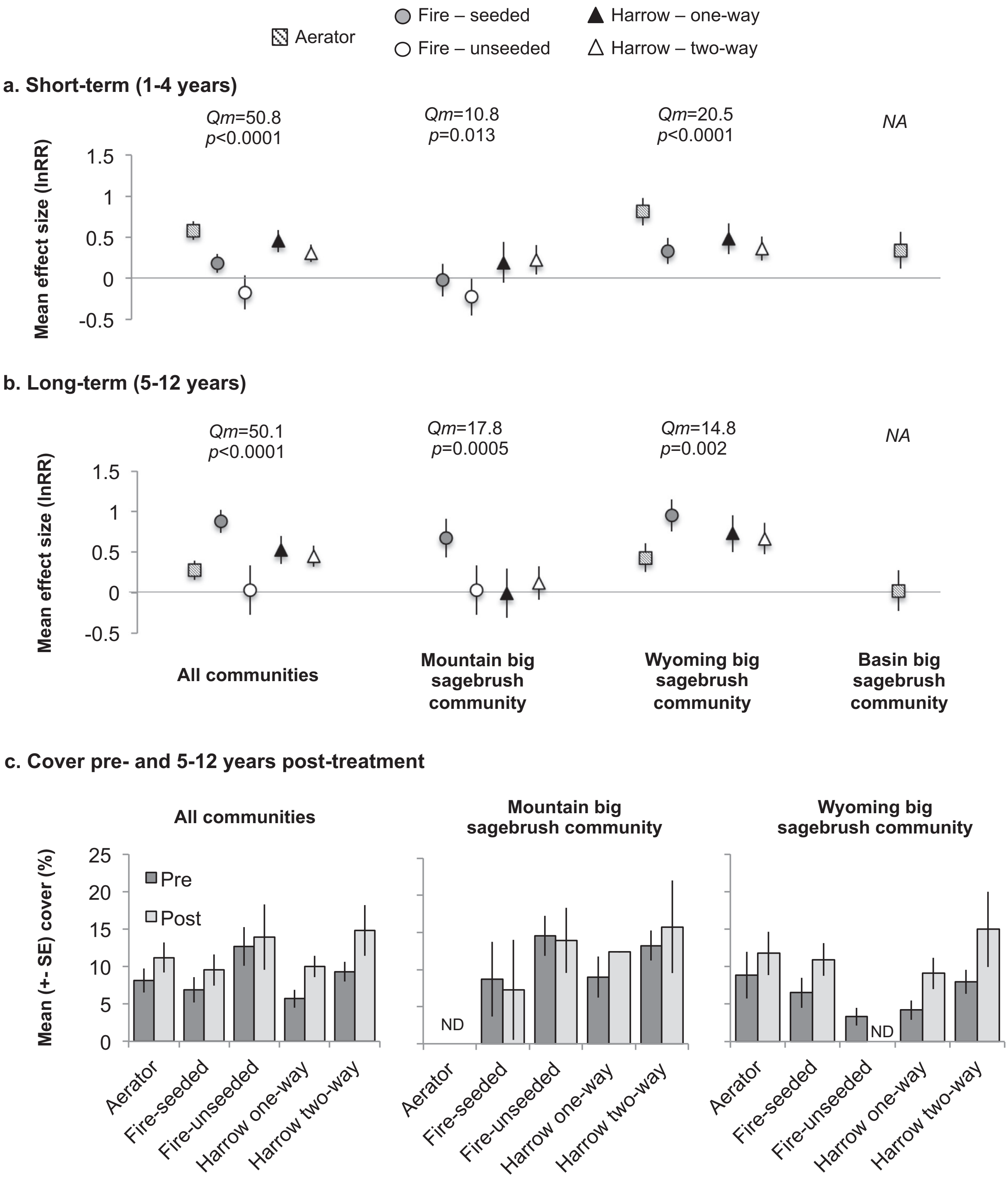

Figure 3. Change in perennial grass cover in response to five treatments on Watershed Restoration Initiative sites in Utah: **a,** mean effect sizes (± 95% confidence interval [CI]) of change in cover in the short term, 1 — 4 yr post treatment, **b,** mean effect sizes (± 95% CI) of change in cover in the long term, 5 — 12 yr post treatment, and **c,** mean (± SE) perennial grass cover pretreatment and 5 — 12 yr post treatment.

communities, annual forb cover decreased substantially in most treatments (Fig. 6C). When all sagebrush communities were considered together, there was no statistical difference among treatments before or after treatments were applied.

Ground Cover Responses

In the long term, and considering all sagebrush communities, the effects of shrub-reduction treatments on the percent of ground covered by litter were neutral to positive (Fig. 7A). The two-way harrow treatment increased litter the most, significantly more than the fire-unseeded and aerator treatments (see Table S1). However, these results differed somewhat by sagebrush community. In sites dominated by Wyoming big sagebrush, all treatments resulted in increased litter, whereas the effects were more neutral to negative in sites dominated by mountain and basin big sagebrush. Results were similar in the long-term and short-term (results not shown) time frames.

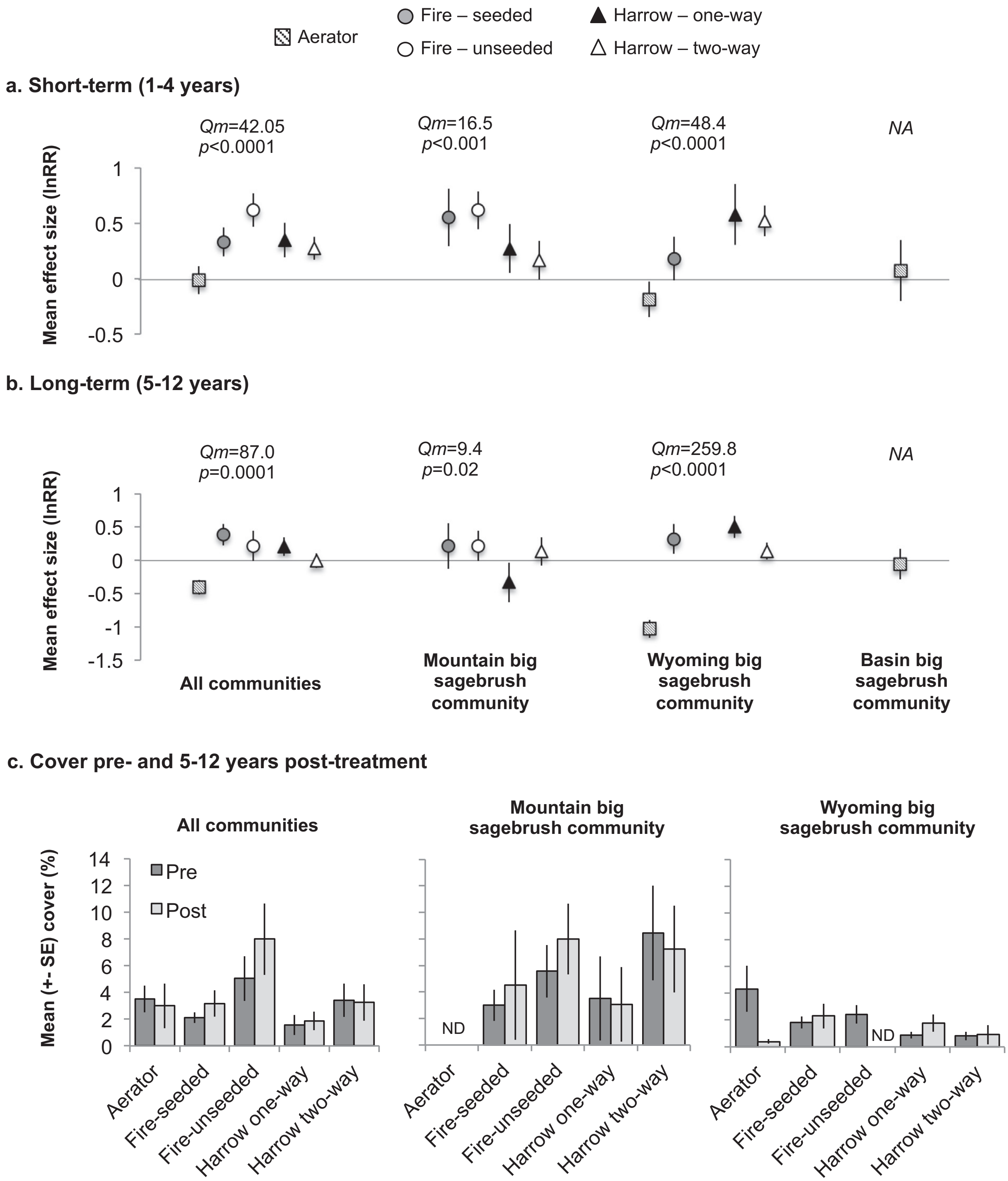

Figure 4. Change in perennial forb cover in response to five treatments on Watershed Restoration Initiative sites in Utah: **a,** mean effect sizes (± 95% confidence intervals [CI]) of change in cover in the short term, 1 – 4 yr post treatment, **b,** mean effect sizes (± 95% CI) of change in cover in the long term, 5 – 12 yr post treatment, and **c,** mean (± SE) perennial forb cover pretreatment and 5 – 12 yr post treatment.

Almost all treatment-community combinations resulted in a long-term decrease in biological crust cover (Fig. 7B). When considering all communities together, aerator, fire-seeded, and one-way harrow showed significant decreases, with nonsignificant negative responses in the fire-unseeded and two-way harrow treatments (see Table S1). In general, sites dominated by mountain big sagebrush experienced less of a decrease in biological crusts than sites dominated by Wyoming big sagebrush. The magnitudes of these decreases, however, were relatively small; for example, aerator (the biggest effect) decreased from 3.16% to 1.74% biological crust cover.

The long-term effects of treatments on bare ground also varied by treatment and sagebrush community. Across all sites, bare ground increased significantly in aerator and fire-seeded treatments and decreased significantly in the two-way harrow treatment (Fig. 7C; see Table S1). These patterns were more pronounced in sites dominated by Wyoming than mountain big sagebrush. Across all sites, the magnitude of change ranged from an increase of 6.4% (fire-seeded: 14.3% pretreatment to 20.7% post-treatment) to a decrease of 8.5% (harrow two-way: 29.3% pretreatment to 20.8% post-treatment).

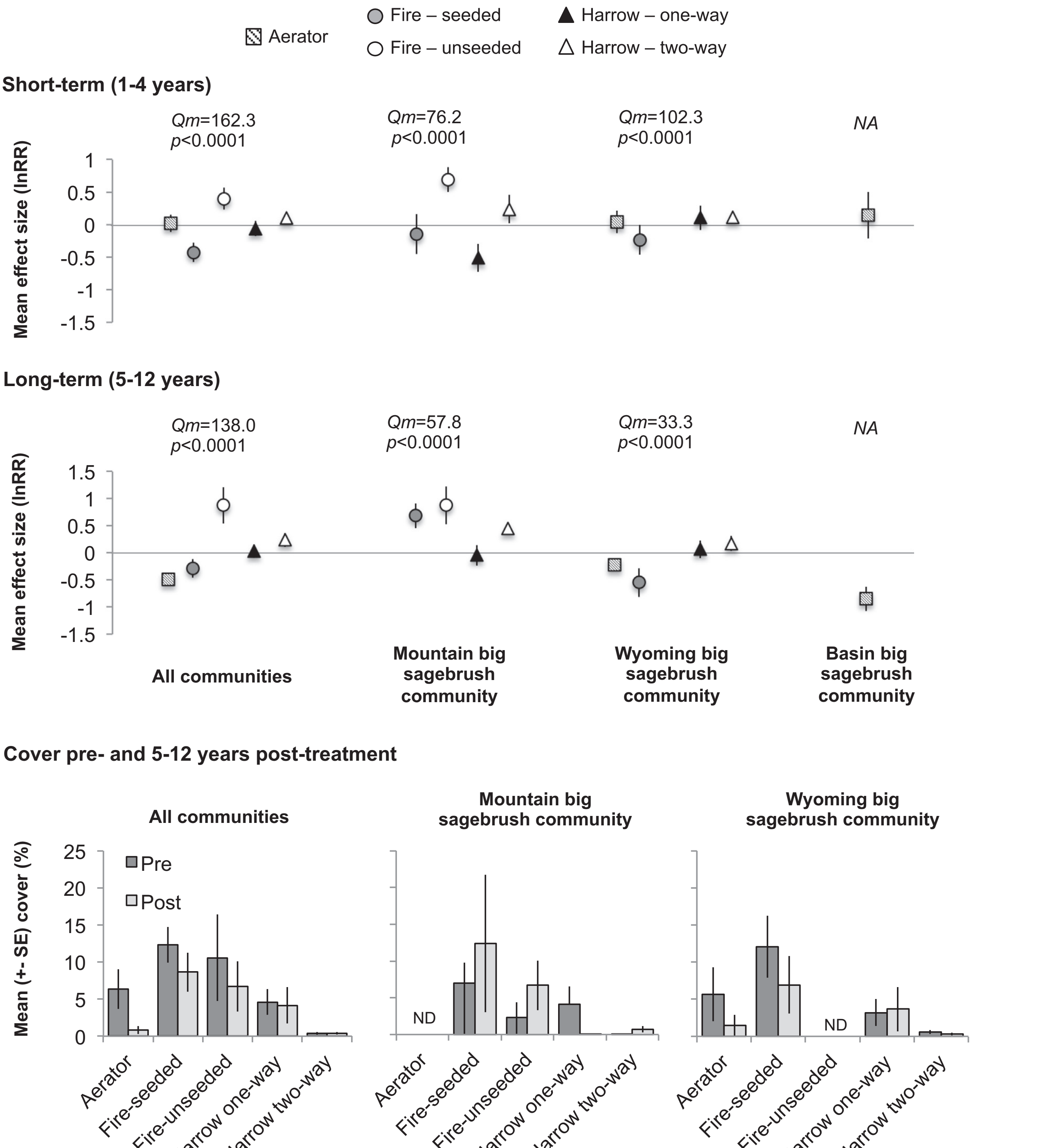

Figure 5. Change in annual grass cover in response to five treatments on Watershed Restoration Initiative sites in Utah: **a,** mean effect sizes (± 95% confidence intervals [CI]) of change in cover in the short term, 1 − 4 yr post treatment, **b,** mean effect sizes (± 95% CI) of change in cover in the long term, 5 − 12 yr post treatment, and **c,** mean (± SE) annual grass cover pretreatment and 5 − 12 yr post treatment.

Site Characteristics

Elevation, precipitation, and, to a lesser extent, percent slope all varied by sagebrush community (elevation: $F = 5.2$, df = 3, $P = 0.003$; precipitation: $F = 18.6$, df = 3, $P < 0.0001$; slope degree: $F = 2.2$, df = 3, $P = 0.094$). Sites dominated by mountain big sagebrush had the highest elevation (mean = 2 176 ± 62 m), greatest precipitation (mean = 447 ± 16 mm), and steepest slope (mean = 2.0 ± 0.11%). Sites dominated by Wyoming big sagebrush and "other shrubs" had the lowest elevations (mean Wyoming = 1 923 ± 37 m; mean "other" = 1 907 ± 92 m), with sites dominated by basin big sagebrush in between (mean = 1 946 ± 72 m). Precipitation was least for sites dominated by Wyoming big sagebrush (mean = 309 ± 8 mm) and intermediate for sites dominated by basin big sagebrush (mean = 395 ± 33 mm) and other shrubs (mean = 332 ± 28 mm). Slope values were similar for all but sites dominated by mountain big sagebrush (1.6 − 1.7% for Wyoming, basin, and other shrub).

These site characteristics also varied among treatments (elevation: $F = 3.8$, df = 4, $P = 0.007$; slope: $F = 5.2$, df = 4, $P = 0.0008$; precipitation: $F = 5.7$, df = 4, $P = 0.0004$), at least in part because

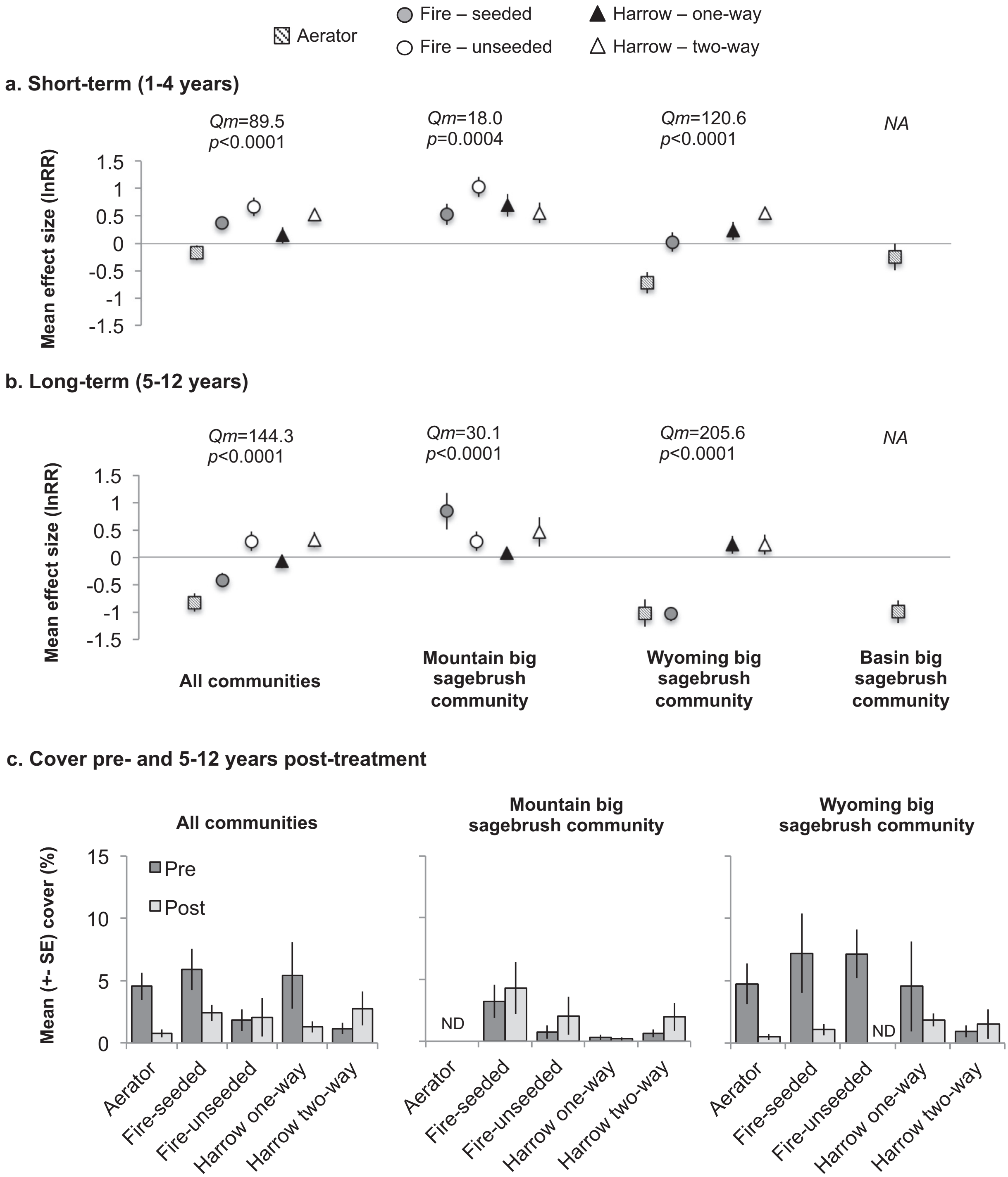

Figure 6. Change in annual forb cover in response to five treatments on Watershed Restoration Initiative sites in Utah: **a,** mean effect sizes (± 95% confidence interval [CI]) of change in cover in the short term, 1 – 4 yr post treatment, **b,** mean effect sizes (± 95% CI) of change in cover in the long term, 5 – 12 yr post treatment, and **c,** mean (± SE) annual forb cover pretreatment and 5 – 12 yr post treatment.

treatments were not equally distributed across community types (see Table 1). Elevation was significantly higher at the fire-unseeded and two-way harrow sites than the fire-seeded sites, with aerator and one-way harrow in between (aerator: 1 932 ± 64 m; fire-seeded: 1 845 ± 59 m; fire-unseeded: 2 158 ± 82 m; one-way harrow: 2 023 ± 69 m; two-way harrow: 2 117 ± 62 m). Slope was steeper at the fire sites, especially fire-seeded, and shallowest at the aerator sites (aerator: 3.6 ± 0.5%; fire-seeded: 10.8 ± 2.3%; fire-unseeded: 9.3 ± 2.3%; one-way harrow: 4.2 ± 0.5%; two-way harrow: 4.6 ± 0.7%). Precipitation was also greatest for the two fire treatments, especially fire-unseeded, and least at the aerator sites (aerator: 326 ± 18 mm; fire-seeded: 381 ± 15 mm; fire-unseeded: 461 ± 35 mm; one-way harrow: 323 ± 18.7 mm; two-way harrow: 343 ± 21 mm).

Although elevation, slope, and precipitation differed among sagebrush communities and treatments, they had few detectable effects on the cover of the major plant guilds. Precipitation had a negative effect on sagebrush cover's short-term response to treatments (Table S4, available online at https://doi.org/10.1016/j.rama.2019.01.007), but only at aerator and fire-seeded sites, and this negative effect did not

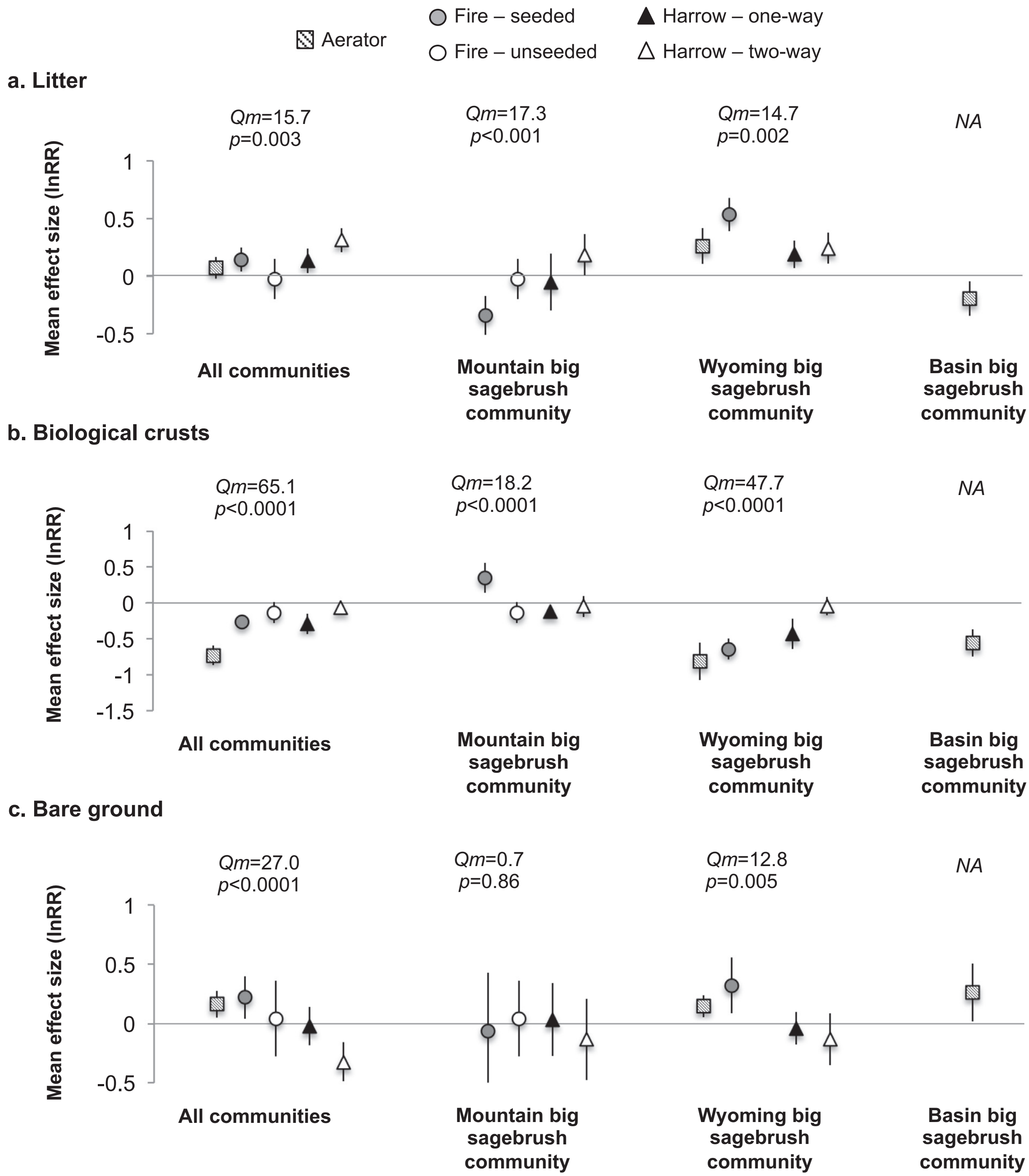

Figure 7. Change in ground cover in response to five treatments on Watershed Restoration Initiative sites in Utah. Mean effect sizes (± 95% confidence interval [CI]) of change in cover in the long term, 5−12 yr post treatment, for **a,** litter, **b,** biological crusts (mostly mosses), and **c,** bare ground.

persist in the long term. Percent slope had a negative effect on perennial grass cover's short-term response (see Table S4), but only at the fire-seeded sites, and again, this effect did not persist in the long term. There was a marginally significant positive effect of precipitation on long-term perennial forb cover response for all sites pooled together; within each of the five treatments, this relationship was positive but not statistically significant. Within aerator sites, there was also a significant negative effect of slope on perennial forb response ($\beta = -1.17$, $P = 0.021$). For annual grasses, in the short term, none of these site variables had an overall effect, but slope had a significant positive effect within the aerator treatment ($\beta = 0.89$, $P = 0.019$). In the long term, both slope and elevation had significant overall positive effects on annual grass cover's response to treatments for all sites pooled together; within each of the five treatments, these patterns were consistent but not statistically significant. There were no significant effects of elevation, slope, or precipitation on annual forb responses.

Discussion

Managers typically plan woody vegetation reduction treatments with the goal of altering the relative composition of major plant guilds, specifically 1) reducing excess or decadent woody vegetation and 2) stimulating an increase in perennial grass and forb cover while 3) not increasing, and ideally decreasing, annual grass and forb cover and 4) maintaining or improving soil stability. We found that the effects of mechanical sagebrush removal and wildfire varied considerably depending on the treatment (type of disturbance), subspecies of sagebrush treated, and pretreatment conditions. Site attributes (e.g., elevation and precipitation) were of minor importance in influencing cover responses and in general were of limited value in explaining vegetation responses among treatments.

Most treatments were successful in reducing sagebrush cover over the short- and long-term time frames. The two fire treatments and the two-way harrow treatment resulted in the largest short-term reduction in sagebrush cover; however, this was not the case in the long term. Across most treatment and community combinations, sagebrush cover appeared to be rebounding proportional to pretreatment cover by 5 − 12 yr post-treatment. Only the fire-seeded treatment within mountain big sagebrush communities maintained a distinctly negative long-term effect on sagebrush cover. This may have been linked to the marked increase in perennial grass cover in this treatment, which could have suppressed sagebrush establishment post fire (Porensky et al., 2014; Davies et al., 2017).

The initially greater decrease in sagebrush cover in the fire and two-way harrow treatments are not surprising; fire and two-way harrow are more intensive treatments characterized by greater mortality of sagebrush (Davies et al., 2009), in contrast to one-way mechanical treatments that can leave some sagebrush plants alive (Dahlgren et al., 2006). Perhaps more surprising is that the effect of fire on sagebrush cover 5 − 12 yr post fire was, in many cases, similar to the effects of mechanical treatments. This is especially surprising for the Wyoming big sagebrush community type, which has generally been found to take longer than the mountain big sagebrush community to recover from fire (Baker, 2006; Lesica et al., 2007). Numerous studies have found that Wyoming big sagebrush cover remains low for many years post fire compared with reference sites or mechanical treatments (Watts and Wambolt, 1996; Nelle et al., 2000; Hess and Beck, 2012); however, at least one (Pyke et al., 2014) found that fire and mowing reduced Wyoming big sagebrush cover to the same degree. Some of the variation among these different studies may be related to prefire grass cover, fire intensity, or the effects of seeding versus not seeding post fire.

Perennial grass cover often increased in response to shrub reduction treatments, but the magnitude of the response depended on both treatment type and sagebrush community. In the long term, the fire-seeded treatment showed the greatest relative increase in perennial grass cover, whereas the fire-unseeded treatment—the only treatment without any seed addition—showed the smallest relative increase. This indicates that both seeding and reducing shrub cover were important for increasing perennial grasses post treatment. Across all sites, the fire-unseeded treatment had the highest initial perennial grass cover, which supports the decision not to seed them. There was no net change in perennial grass cover in this treatment in the long term, perhaps indicating that these sites were producing perennial grasses at or near their potential. In the other four treatments, shrub reduction and seeding enabled perennial grass cover to “catch up” to the fire-unseeded treatment. However, the increases in perennial grass cover were almost all observed in Wyoming big sagebrush communities, while little long-term net change occurred in the mountain big sagebrush communities. Possibly this difference is due to the fact that Wyoming big sagebrush communities had lower initial perennial grass cover than mountain big sagebrush communities and were not producing perennial grasses at their site potential. The fire-seeded treatment showed a more delayed response than other treatments, with a more positive response in the long term than short term. In absolute terms, the changes in perennial grass cover were not dramatic; the greatest increases in absolute cover occurred in the two harrow treatments within Wyoming big sagebrush communities (Fig. 3C), which averaged 5% and 7%, respectively (e.g., sites went from 20% to 25% grass cover), but most treatment-community combinations saw average changes of 0 − 3%.

Results of other studies on the effects of sagebrush reduction by fire or mechanical treatments on perennial grasses have been variable. While some have shown no evidence of an increase in perennial grass cover (Wambolt et al., 2001; Dahlgren et al., 2006; Davies et al., 2011a; Davies and Bates, 2014; Chambers et al., 2014; Pyke et al., 2014), other studies found modest to substantially increased perennial grass cover as a result of fire and mechanical treatments (Wambolt and Payne, 1986; Hess and Beck, 2012; Swanson et al., 2016, 2018). A meta-analysis of 134 different responses from studies that used a variety of treatments to reduce woody cover in sagebrush systems showed no lasting (> 2 yr post treatment) positive effects of these treatments on perennial grass cover (Monaco et al., 2017). Another multisite analysis also showed increased perennial cover post mowing but attenuation of this effect over time (Swanson et al., 2016). Similarly, a global analysis showed positive effects of brush reduction on herbaceous biomass in drylands, particularly in drier rather than wetter sites; the effect peaked 5 yr post brush reduction and then attenuated to near-zero positive effect, which was interpreted as the consequence of woody vegetation growing back and suppressing herbaceous plants (Archer and Predick, 2014). Our results indicate that, in the sagebrush ecosystem, some of the variability in observed responses may be due to differences in time since shrub reduction, shrub community, and pretreatment grass cover (i.e., some sites had more scope to increase than others).

Surprisingly, perennial grass response was not related to precipitation in our data. It is possible that grazing intensity was positively correlated with precipitation, thereby removing any effect of precipitation on grass cover. Lack of good data on pretreatment and post-treatment grazing by domestic livestock and wildlife is one limitation to our study, as well as most others like it. Variation in post-treatment grazing intensity has likely contributed to the overall variation in perennial grass responses seen here and across shrub reduction studies since grazing can affect post-treatment recovery trajectories (Bates and Davies, 2014). Additionally or alternatively, the effects of aspect and microtopography, which we were unable to account for, may have outweighed the effects of precipitation.

Perennial forb cover at our study sites increased in most treatments in the short term (1 − 4 yr post treatment), but those effects rarely persisted into the long term (5 − 12 yr post treatment). We found slight long-term increases in forb cover within the fire-seeded and two harrow treatments in Wyoming big sagebrush communities, but these amounted to < 1% increase in absolute perennial forb cover. Several reasons may explain why forb cover did not increase greatly in the long term. First, some of these sites may naturally support only very low forb cover (e.g., 1 − 3%). Second, the seeded forb species tended to be short-lived (Wilder et al., 2018). Third, grazing, especially by ungulates, could have kept forb cover low. And fourth, as sagebrush recovered and became more abundant again post treatment, it may have competitively suppressed forbs (Avirmed et al., 2015). Regardless of the mechanism, the pattern we observed is consistent with numerous other studies that have found no lasting increase in perennial forb cover after shrub reduction (Fischer et al., 1996; Nelle et al., 2000; Dahlgren et al., 2006; Davies et al., 2011a; Davies and Bates, 2014; Pyke et al., 2014). Notably, in our study, perennial forb cover decreased substantially in the aerator treatment within Wyoming big sagebrush communities—possibly because sagebrush cover was not reduced over the long term under these conditions.

One of the prevailing concerns about shrub reduction treatments and wildfires in sagebrush ecosystems is that they risk promoting the spread of annual grasses and forbs, especially cheatgrass. For example, Davies and colleagues (Davies et al., 2011a, 2012; Davies and Bates, 2014) found dramatic increases in annual cover after mowing and mowing + seeding relative to control sites, even at sites that had few annuals present before the experiment began; Monaco et al. (2017) found that woody reduction led to significant long-term increases in cheatgrass cover in 134 woody plant-reduction studies; and Swanson et al. (2018) found increased cheatgrass cover post fire in a 51-site study. In our study, treatments had a wide variety of effects on annual grass cover (primarily cheatgrass) and annual forb cover. Sites that experienced fires started out with greater cover of annuals than other treatments, which likely made them more prone to burning due to ample fine fuels (Diamond et al., 2009). Within mountain big sagebrush communities, fire (with and without seeding) and the two-way harrow treatments resulted in significant increases in annual grass cover in the long term, but the absolute increase was very small in the two-way harrow treatment (0.7% more annual grass cover), whereas it was larger and more variable in the two fire treatments (averaging 4.4% and 5.4% more cover post fire in fire-unseeded and fire-seeded, respectively). Patterns were similar for annual forbs, but with smaller increases (~1% for all three treatments). Within Wyoming big sagebrush communities, no treatments experienced significant increases in annual grass or forb cover, and both annual grass and forb cover decreased significantly in the aerator and fire-seeded treatments (averaging 4.1% and 5.1% less annual grass cover and 4.2% and 6.1% less annual forb cover post treatment, respectively). There was no consistent relationship between patterns of change in perennial grass and annual grass and forb cover, suggesting that competitive suppression by perennial grasses did not strongly influence annuals' responses to treatments. Monaco et al. (2017) similarly found no clear negative relationship between perennial and annual grasses' responses to a variety of treatments.

Another concern about mechanical shrub reduction treatments and fires is that they may negatively impact biological crusts and result in a net increase in bare ground. Biological crusts are important for stabilizing soil surfaces, preventing erosion, and helping to prevent invasive annual grass establishment (Belnap and Gillette, 1998; Deines et al., 2007; Peterson, 2013). At our study sites, biological crusts consisted largely of mosses. Here, we saw significant decreases in biological crust cover in multiple treatments within Wyoming big sagebrush communities, but not in mountain big sagebrush communities. Decreases in biological crusts in Wyoming big sagebrush communities may have been caused by the physical effects of the treatments themselves, as well as the reduction in shrub cover; shrubs provide a cooler, moister refuge for mosses that cannot grow in the interspaces at these relatively drier sites (Davies et al., 2007). Bare ground also increased in both the aerator and fire-seeded treatments in the Wyoming communities, but not in mountain big sagebrush communities. Together, these findings indicate that shrub reduction treatments can have substantial negative long-term effects on the amount of ground protected from wind and water erosion, especially in Wyoming big sagebrush communities. This is generally consistent with other studies. For example, Davies and Bates (2014) found a threefold to fourfold decrease in biological crust cover in mowed treatments relative to reference sites, and Pyke et al. (2014) also found significant decreases in biological crust cover in fire and mowed treatments, with associated increases in bare ground.

In general, the study sites dominated by Wyoming big sagebrush showed more negative effects of treatments than sites dominated by mountain big sagebrush for ground cover parameters, but more positive effects of treatments in terms of increased perennial grass cover and decreased annual cover. The latter is somewhat surprising, given that Wyoming big sagebrush tends to occur at lower-elevation, lower-precipitation sites that are generally considered less resilient to disturbances and less resistant to cheatgrass invasion (Wisdom and Chambers, 2009; Chambers et al., 2014). One potential consideration is that many of our sites dominated by Wyoming big sagebrush were at relatively high elevation (1 400 − 2 200 m), experienced relatively high precipitation (230 − 406 mm), and had low initial cover of annual grasses and forbs compared with the conditions in Wyoming big sagebrush communities evaluated in previous studies (mostly < 1 500 m elevation and 150 − 350 mm rainfall) (Davies et al., 2011a; Chambers et al., 2014; Davies and Bates, 2014; Pyke et al., 2014). We found that mountain big sagebrush communities showed little change in perennial cover and increased in annual cover. This is surprising given the higher precipitation and presumed greater resilience to disturbance and resistance to invasions at these sites. It is possible that the high pretreatment shrub cover at some of these sites (particularly higher biomass mountain big sagebrush sites) meant that treatments had a large impact in reducing both shrub and perennial herbaceous cover, enabling annuals to establish (Bates et al., 2013). The vulnerability of mountain big sagebrush communities to increases in annuals after disturbances has received little attention and indicates that sagebrush reduction treatments should be applied cautiously, even at higher-elevation, higher-productivity sites, to limit increases in invasive species like cheatgrass (Balch et al., 2013; Bradley et al., 2016).

Management Implications

Understanding the positive and negative effects of different disturbances in the sagebrush ecosystems of the Intermountain West has become a high priority as practitioners work to manage these systems for sage-grouse habitat and fire risk. Sagebrush reduction treatments are typically implemented with the goal of altering community structure and the cover of major plant guilds, to benefit livestock and grazing ungulates or to reduce the risk of intense fire followed by cheatgrass invasion where shrub cover is high (Swanson et al., 2016). We found that shrub reduction treatments—whether deliberate (mechanical treatments, prescribed fire) or unplanned wildfires followed by deliberate seeding or no seeding—generally had some positive effects on the understory community through increasing perennial grasses and forbs that may benefit livestock and large wild ungulates and may be important to maintaining longer-term herbaceous production and diversity. However, these came at some risk of increasing annual grasses and forbs and increasing soil exposed to erosion. Here, treatments were matched to site conditions as much as possible. For example, sites with lower perennial grass cover prefire were seeded post fire, while sites with higher perennial grass cover prefire were not. Sites treated with the heaviest mechanical disturbance, the two-way harrow, tended to be higher-elevation, higher-precipitation sites with high pretreatment sagebrush cover compared with sites treated with a one-way harrow or aerator. These decisions were effective at reducing sagebrush cover where it was highest and promoting perennial grasses where they had the lowest cover. However, these decisions were not necessarily effective at limiting the spread or expansion of annual grass cover at treated sites. As might be expected, annual grass cover showed the greatest positive responses in sites with higher disturbance intensities (fire and two-way harrow treatments) and on steeper slopes. Surprisingly, annual grasses showed some of the largest relative increases at higher-elevation, higher-precipitation sites dominated by mountain big sagebrush—sites that are typically thought to have higher resilience to disturbance and resistance to annual grass invasion. Possibly, less intense interventions at these sites or different timing relative to the age and size distribution of shrubs could have been more effective at promoting perennial herbaceous cover and limiting the spread of annuals (Swanson et al., 2016, 2018). Together, these results indicate some of the benefits and risks of well-planned sagebrush reduction treatments on sites with relatively low initial annual grass cover.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2019.01.007.

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