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Original Research

Understory Responses to Tree Thinning and Seeding Indicate Stability of Degraded Pinyon-Juniper Woodlands[☆]David W. Huffman^{*}, Michael T. Stoddard, Judith D. Springer, Joseph E. Crouse

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ABSTRACT

Depauperate understory plant communities resulting from intensive livestock grazing in pinyon-juniper woodlands of the western United States may represent degraded stable states, resistant to ecological restoration treatments. In this study, we analyzed 10-yr understory plant community responses to restoration treatments that included tree thinning to approximate historical densities of pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*), scattering of thinning slash to improve soil conditions, and seeding at two woodland sites (Craig Ranch and Goose Pond) in northwestern Arizona. Results showed that thinning resulted in significant reductions in tree density at both sites, as well as reductions in tree basal area at the Goose Pond site. Boles, branches, and tops of the thinned trees scattered across the study sites resulted in few changes to woody surface fuel loading. Thinning and addition of woody material, along with seeding, resulted in only minor changes in understory cover and species richness at both sites. However, plant cover and species richness were both negatively correlated with tree density. Degraded conditions at the sites appeared to be stable, and we suggest that treatments implemented in our studies may have not been intensive enough to produce significant understory responses and meet restoration objectives. Managers aiming to restore understory diversity at similar sites may be required to use heavier thinning prescriptions and repeated seeding. More work is needed to test new restoration approaches that are designed to drive degraded pinyon-juniper woodlands over resilience thresholds toward more diverse understory communities.

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Introduction

Pinyon-juniper ecosystems are highly variable in composition and structure and are distributed broadly on semiarid sites across western North America (Romme et al., 2009). Degraded ecological conditions stemming from intensive land use are common in pinyon-juniper woodlands and historical savannas. For example, intensive fuelwood harvesting in the mid- to late 1800s left previously wooded landscapes of the Great Basin and Southwest denuded of tree cover (Young and Budy, 1979; Bahre and Hutchinson, 1985; Creque et al., 1999). Similarly, extensive areas of woodland were converted to grassland for livestock production by chaining, cabling, burning, and other methods in the mid-1900s (Young and Budy, 1979; Romme et al., 2009). In contrast, degradation in the form of increases in tree density, loss of understory plant community abundance, and accelerated soil erosion have been widely reported in woodlands and savannas across the range of the pinyon-juniper type (Campbell, 1999; Jacobs and Gatewood, 1999;

Brockway et al., 2002; Romme et al., 2009). Increased tree cover in these systems is thought to be due to a combination of natural and anthropogenic factors including intensive livestock grazing, climatic variability, increases in atmospheric CO₂, and interruption of natural fire regimes (Altschul and Fairley, 1989; Shinneman et al., 2008; Poulos et al., 2009; Romme et al., 2009; Margolis, 2014). Even in persistent woodlands where tree cover may have been minimally affected by fire exclusion, intensive livestock grazing has resulted in decreases in understory diversity and increased soil erosion (Beymer and Klopatek, 1992; Shinneman et al., 2008). On severely degraded sites, ecological conditions may represent alternative stable states that are resistant to restoration treatments.

Since Holling's (1973) seminal discourse on the topic of ecosystem dynamics, the term "resilience" has received much attention in scientific literature and fields of natural resource management. Holling (1973) defined ecological resilience as "a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables." A central aspect of ecological resiliency is "resistance," which is defined as the "ease or difficulty of changing the system" (Walker et al., 2004). Although recently resilience has been viewed normatively as a desirable property (Brand and Jax, 2007), in Holling's (1973) original definition, resilience is interpreted as neither desirable nor undesirable (Seidl

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et al., 2015). Ecological systems functioning within natural ranges of variability, as well as those that have been simplified or degraded, may exhibit stable state conditions that are resistant to management actions. For example, Carpenter and Cottingham (1997) described processes leading to degradation and the development of new resilience mechanisms that must be overcome to restore lake ecosystems. Suding et al. (2004) explained that ecological resilience to restoration may indicate a shift of a plant community to an alternative degraded state. Similarly, Briske et al. (2008) explain that strong negative feedbacks may increase resilience of alternative stable states and challenge restoration of degraded rangelands.

In cases of ecosystem degradation, a goal of ecological restoration is to drive systems from stable, degraded states, across resilience thresholds, toward more desirable basins of attraction (Walker et al., 2004). To facilitate such transition, degraded woodland systems may require active restoration treatments that include manipulation of vegetation structure, alteration of microclimate and soil conditions, and addition of seeds or propagules (Rey Benayas et al., 2009). Restoration treatments developed for degraded pinyon-juniper ecosystems commonly include tree thinning, amending soil conditions by adding organic matter and thinning slash, and seeding with native understory plant species (Jacobs and Gatewood, 1999; Huffman et al., 2008a; Jacobs, 2015). Tree thinning can reduce interference and competitive effects and provide more light and soil resources for understory plants. Some restoration thinning prescriptions call for close adherence to site-specific, historical reference conditions. This approach centers on retaining all pre-Euro-American settlement trees (i.e., those that predate onset of industrial land uses), plus keeping some number of postsettlement trees to account for recent mortality and removing the remainder (e.g., Huffman et al., 2008a). In some persistent woodlands, thinning intensity following this approach may be minor due to relatively high numbers of presettlement-aged trees (Romme et al., 2009). Addition of organic matter, commonly done by scattering woody material or “slash” remaining from thinning activities, can ameliorate microclimatic conditions, provide safe sites for seedling establishment, and increase microbial activity in soils (Tongway and Ludwig, 1996; Breshears and Barnes, 1999; Stoddard et al., 2008). Although thinning, slash additions, and seeding have been shown to be generally effective for increasing understory production and abundance, some studies have failed to find important effects of these treatments (Lavin et al., 1981; Brockway et al., 2002; Huffman et al., 2013). Seeding with native species can increase understory cover (Redmond et al., 2014), and appropriate seed mixes can be developed using information from local observations, as well as reports describing species composition and relative abundance at minimally impacted reference sites.

In this study, we examined understory plant community responses to ecological restoration treatments at two pinyon-juniper woodland sites in northwestern Arizona. Both sites were described by local land managers as showing undesirable conditions in terms of high tree density, low understory cover, and low plant species richness. These conditions were considered to be due primarily to livestock grazing history and changes to the natural fire regimes. At these sites we established two small, identical studies to experimentally address the following research questions: 1) Do restoration treatments including tree-thinning prescriptions guided by reference conditions, scattering thinning slash, and seeding lead to increases in plant cover and species richness? 2) How do understory responses differ across sites with contrasting soils characteristics; and 3) Can such treatments move understory conditions to more diverse, stable states?

Methods

Study Sites

We initiated repeated studies in 2002 at two sites (“Craig Ranch” [CR] and “Goose Pond” [GP]) on Grand Canyon—Parashant National

Monument near Mount Trumbull, Arizona (Fig. 1). The two sites were within 5 km of one another and were generally similar in terms of vegetation and woodland structure; however, the sites differed in soil characteristics. Soils at the CR site (lat. 36°26′1″N, long. 113°9′40″W) are shallow to deep gravelly sandy loams to very cobbly clays, derived from limestone, basalt, and sandstone alluvium and colluvium. Soils at the GP site (lat. 36°24′46″N, long. 113°12′15″W) are shallow to very deep, very cindery loams derived from alluvial and colluvial, scoriaceous basalt, and pyroclastics (USDA Soil Conservation Service, unpublished). Although the sites differed in terms of soil texture and parent material, in 2002 soils at both sites were characterized by erosion pavement, presumably due to livestock grazing. Elevation of the sites ranges approximately 1900–1950 m. Average annual precipitation in the area near the sites is ≈50 cm and is distributed in a bimodal seasonal pattern with notable peaks during the months of July–August and December–January (WRCC, 2015).

Vegetation at the sites is classified as Great Basin Cold Temperature Woodland (Brown, 1994). Overstories were composed exclusively of pinyon pine (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* Torr.). Trees were generally arranged in all-aged groups with pronounced interstitial openings (“interspaces”). Understory vegetation composition was typical of pinyon-juniper woodlands in northwestern Arizona. Understory vegetation was generally sparse in spatial distribution and depauperate in species (Stoddard et al., 2008). Livestock grazing was halted at both sites in the early 2000s, just before initiation of this study. No livestock grazing was permitted at either site during the course of our research.

Study Design and Field Sampling

At each of the two sites, we delineated 9 ha for study. Each 9-ha area was divided into two 4.5-ha units, and one of each pair was randomly selected for treatment while the other remained as an untreated control. Thus, at each site, separate but identical studies were designed. Sample plots to characterize pretreatment conditions and post-treatment responses of overstory structure, forest floor, and understory vegetation were arrayed on a 60-m systematic grid, established 60 m from the treatment boundaries within the units (i.e., 60-m treatment buffer). Six sample plots per unit were established ($N = 12$ per site) (see Fig. 1).

Sample plots established in the study units were circular and 0.04 ha in size. For long-term monitoring purposes, we used steel rebar driven into the soil to mark plot centers, and these points were georeferenced. In 2002, before treatments were implemented, we measured tree density, size, and species composition; woody surface fuel loading; and understory community characteristics on each plot. All live and dead trees on plots were numbered using aluminum tags nailed to tree bases. Species and diameter at root collar (drc) of each tree (live and dead) were recorded. To determine tree ages, we collected increment cores from all live trees ≥ 20 cm drc and from a 20% random subsample of smaller trees (< 20 cm drc). Fuel loading was estimated using methods described in Brown (1974). One 15-m planar fuels transect was established on each plot with the proximal end anchored at plot center, and the transect direction was determined randomly. A piece of steel rebar was driven into the soil at the distal end of each fuels transect for subsequent relocation and remeasurement. On each transect, forest floor depth was measured at points every 1.5 m, and layers were classified as “litter” layer (recent, undecomposed) and “duff” (lower, decomposing). Woody surface fuels intersecting transects were measured for diameter and tallied by moisture timelag classes according to Brown (1974). Timelag classes represent the length of time required for wetting or drying of fuels of different sizes, relative to the equilibrium moisture content. Timelag classes were “1-hr” (< 0.63 cm), “10-hr” (0.63–2.5 cm), “100-hr” (2.5–7.6 cm), and “1 000-hr” (> 7.6 cm). The largest timelag class (1 000-hr) was further subdivided into sound (“1 000-hr-s”) and rotten (“1000-hr-r”) categories. To sample understory

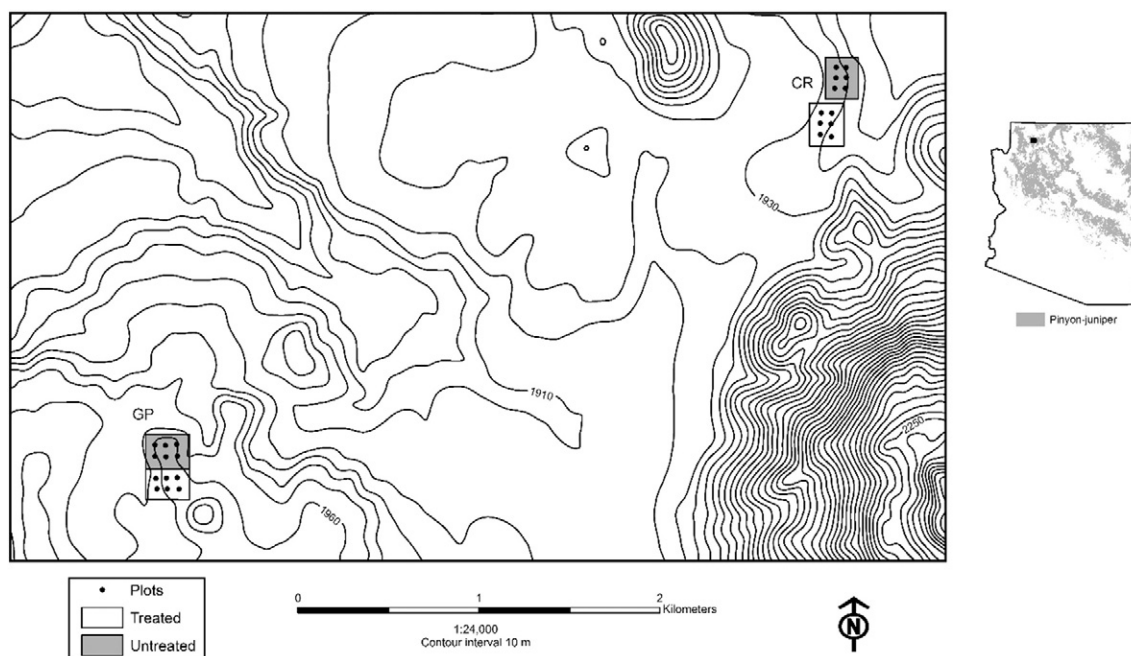


Figure 1. Two study sites, Craig Ranch (CR) and Goose Pond (GP), selected for restoration studies on Grand Canyon – Parashant National Monument in northwestern Arizona. Map shows untreated (shaded) units and units receiving experimental restoration treatments (unshaded). Dots within units represent sample plots.

community characteristics, we established one 50×10 m belt transect centered on each plot. Belts were oriented parallel with plot aspect, and end points were monumented for subsequent remeasurement using rebar. Ten 1-m^2 (50×200 cm) quadrats were systematically arrayed at 5-m intervals along the centerline of each belt. Within each quadrat, we ocularly estimated cover of substrate, classified as litter, bare soil, rock, and wood (pieces ≥ 7.5 cm in diameter), and plant basal cover. We also estimated plant aerial cover by species. Within the entire area of each belt, we catalogued all plant species observed. Tree canopy cover was estimated using a densitometer at 16 points equally spaced along belt centerlines. Measurements were conducted in 2002 (pretreatment) and 2014 (10-yr post treatment). Huffman et al. (2008a) reported on immediate post-treatment (2004) effects on overstory structure, woody surface fuels, and understory cover.

Prescription Development and Treatment Implementation

At each site, we tested efficacy of forest restoration approaches that have been described elsewhere (see Jacobs and Gatewood, 1999; Fulé et al., 2001; Stoddard et al., 2008). The overall goal of the prescription developed was to increase understory cover and species richness. The prescription included thinning trees to lower densities and approximate overstory structure presumed to occur at the sites near the time of Euro-American settlement (ca 1880). We also prescribed that thinning material (tree boles, branches, and tops) would be lopped and scattered across nearby interspaces. This technique in concert with seeding has been shown to slow soil movement, improve soil function, and increase understory abundance (Jacobs and Gatewood, 1999; Stoddard et al., 2008; Jacobs, 2015).

To determine trees to be thinned and those to be retained, increment cores collected in the field were analyzed in the laboratory following standard techniques of dendrochronology (Stokes and Smiley, 1996). Linear regression of tree establishment date and drc data suggested that pinyon pine trees > 25 cm drc were likely to be > 130 yr of age ($R^2 = 0.57$; $P < 0.001$). Age-diameter relationships for juniper were poor ($R^2 < 0.15$). On the basis of our findings for pinyon pine, we presumed all pinyon and juniper trees > 25 cm drc predated Euro-

American settlement of the region and live trees of this size and larger were retained at both sites. Most trees < 25 cm drc were thinned. However, to account for trees that may have died since Euro-American settlement, approximately two trees < 25 cm drc were retained for each dead pinyon or juniper tree (snag, log, or cut stump) > 25 cm drc found, and effort was made to retain these smaller trees near the dead presettlement tree structures in order to approximate arrangement and spatial variability of historical stands. Retaining a greater number of smaller trees than indicated by dead tree evidence was precautionary to safeguard against unanticipated, additional disturbance (Waltz et al., 2003). Indeed, in 2002–2003 during treatment implementation, the Southwest experienced a severe drought, which, along with an associated outbreak in pinyon ips (*Ips confusus*), resulted in regional-scale dieback of pinyon pine (Breshears et al., 2005; Floyd et al., 2009). Slash from thinned trees was lopped to ≤ 1 m in length and scattered. Thinning was completed in November 2003. Thinning and mortality reduced tree densities 55–69% at the two sites.

Following completion of thinning, sites were seeded using a native species mix. We selected five grasses, one forb, and four shrub species (Fig. 2). Selection of species for seeding was based on observations of local occurrence, baseline data from belt transects (see Appendix A), and community data reported in published literature concerning relict areas in the vicinity of our study sites (Mason et al., 1967; Thatcher and Hart, 1974; Rowlands and Brian, 2001). We assumed a seed mix that included species and functional groups (i.e., C_3 and C_4 grasses, perennial forb, and shrubs) adapted to a variety of microhabitats would be effective for increasing understory diversity. We used hand seeders to broadcast at a rate of 18 kg ha^{-1} . This rate met common standards for range rehabilitation (Clary, 1988). We chose to seed half the amount in late fall and half in early summer in order accommodate germination and establishment requirements for both cool and warm season species (see Fig. 2). Using site-preparation methods such as plowing or disking before seeding was not feasible. Similarly, we did not harrow or rake the restoration units after the seed was broadcast but instead used thinning slash to provide cover and mulch for the seeds. Seeding was done at each site in November 2003 and March 2004.

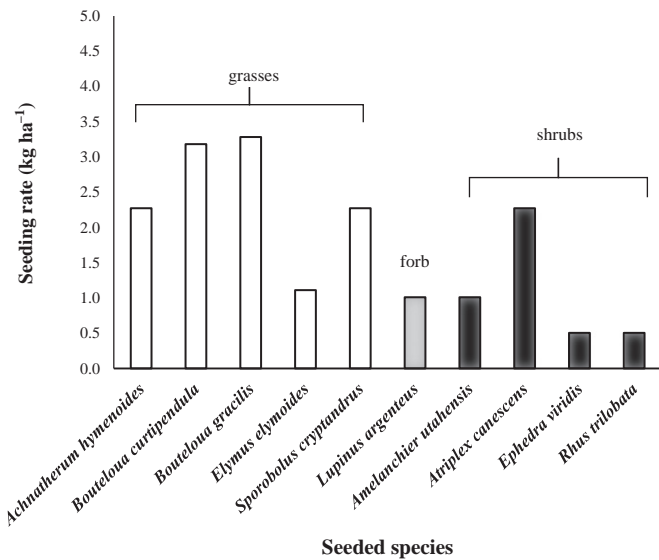


Figure 2. Seed mix used in restoration treatments at both study sites (Craig Ranch and Goose Pond) in Grand Canyon – Parashant National Monument, Arizona. Figure shows rates (kg ha⁻¹) applied at each site by species and functional group; white bars indicate seeded grass species, gray bar shows the seeded forb, and black bars show shrubs.

Analysis

Our main interest in this study was on effects of the restoration treatment on understory cover and species richness at the two study sites. We used student’s *t*-tests ($\alpha = 0.10$) to compare untreated and treated units at both sites before treatment (2002) and 10 yr post treatment. We tested for differences between units in the following overstory structural characteristics: tree density (no. ha⁻¹), basal area (m² ha⁻¹), relative importance of pinyon and juniper trees, and canopy cover (%). Relative importance was calculated as the percentage of the tree density added to the percentage of the stand basal area composed by each species (Husch et al., 2003). Thus, an importance value of 200 for a species would indicate its complete dominance of a sample plot. We also used *t*-tests to compare understory community characteristics between untreated and treated units before treatment implementation and 10 yr post treatment at both sites ($\alpha = 0.10$). Characteristics tested were total plant cover (%), as well as cover of the following functional groups: annual forbs, cacti, shrubs, C₃ graminoids, C₄ grasses, perennial forbs, shrubs, tree seedlings, and non-native plant species. We also compared total species richness (no. 500 m⁻²) and richness of

species within the functional groups described earlier. Although not statistically tested, we calculated quadrat-level frequency (%) for each species observed at pretreatment (2002) and post-treatment (2014) measurements. This was determined as the number of quadrats on which a species was observed, divided by the total number of quadrats sampled within the experimental unit (i.e., 60), multiplied by 100. To test for relationships between plant cover and species richness, as well as microsite variables, we used Spearman’s rank correlation test ($\alpha = 0.05$). Variables tested were cover (%) of litter, wood, and rock; density of all trees and density of juniper and pinyon trees separately; basal area of all trees and basal area of juniper and pinyon trees separately; and canopy cover observed in 2014.

Results

CR Site

We found no differences in pretreatment (2002) means for overstory structural characteristics (Table 1), forest floor, woody surface fuels (Table 2), or understory community characteristics (Table 3) between the untreated and treated units at the CR site. Thinning small (< 25 cm drc) overstory trees shifted the diameter distribution at the CR site, from positively skewed to closer to normal (Fig. 3B). Thinning resulted in significant differences in tree density, and 10 yr after treatment implementation (2014), < 50% of the pretreatment number remained (see Table 1). Although thinning resulted in only a 7% decrease, stand basal area was significantly different between the untreated and treated units in 2014 (see Table 1). Thinning did not result in differences in tree species composition, and relative importance values of pinyon and juniper remained similar between the untreated and treated units (see Table 1). Similarly, there were no effects of treatment on tree canopy cover at the CR site and mean values were > 23%. Litter depth was similar between the untreated and treated units in 2014; however, duff depth was significantly lower in the treated unit at this time (see Table 2). We found significantly lower surface fuel loading in the treated unit for the 1-hr timelag class compared with the untreated unit. In addition, we found significantly higher loading for the 1 000-hr sound class in the treated unit versus the untreated unit (see Table 2). Loading was similar between units for all other wood surface fuel classes 10 yr after treatment at the CR site.

Total understory cover (all functional groups) in 2014 was significantly higher in the treated unit (7.0% ± 4.8 SD) compared with the untreated (3.7% ± 2.9 SD) unit at the CR site in 2014. This result appeared to be driven by small differences in both C₃ graminoids and C₄ grasses, shrubs, and tree seedling cover; however, no statistically significant differences in cover within individual functional groups were detected between the untreated and treated units (see Table 3). Plant cover showed

Table 1 Means of overstory structural characteristics in untreated and treated units at Craig Ranch (CR) and Goose Pond (GP) study sites (standard deviations shown in parentheses) in Grand Canyon – Parashant National Monument, Arizona. Shown are conditions before treatment implementation (2002) and 10 yr post treatment (2014). Bold values followed by different lowercase letters indicate statistically different means ($P < 0.10$) within years.

Site	Variable	2002		2014	
		Untreated	Treated	Untreated	Treated
CR	Tree density (no. ha ⁻¹)	904.2 (238.4)	645.8 (142.7)	891.7 (236.5) a	291.7 (84.7) b
	Tree basal area (m ² ha ⁻¹)	41.1 (16.3)	31.1 (9.6)	42.6 (16.0) a	28.6 (8.8) b
	Pinyon importance ⁺	53.4 (17.4)	56.2 (9.4)	52.3 (18.7)	39.3 (20.3)
	Juniper importance ⁺	146.6 (17.3)	143.7 (9.4)	147.1 (18.7)	160.7 (20.3)
	Tree canopy cover (%)	37.5 (10.4)	29.2 (7.6)	31.2 (15.3)	23.9 (7.3)
GP	Tree density (no. ha ⁻¹)	650.0 (144.0)	845.8 (629.2)	458.3 (199.2) a	262.5 (112.6) b
	Tree basal area (m ² ha ⁻¹)	22.8 (7.9)	27.0 (18.8)	19.4 (10.1)	21.6 (19.4)
	Pinyon importance ⁺	118.8 (21.8)	105.6 (21.9)	80.1 (27.9) a	44.2 (33.8) b
	Juniper importance ⁺	81.2 (21.8)	94.3 (21.8)	120.0 (27.9) b	155.8 (33.8) a
	Tree canopy cover (%)	31.2 (11.7)	27.5 (13.0)	21.9 (11.0)	28.1 (15.7)

⁺ Relative importance index. See Methods for calculation.

Table 2

Mean forest floor depths and surface fuel loadings by timelag class for Craig Ranch (CR) and Goose Pond (GP) study sites (standard deviations shown in parentheses) in Grand Canyon—Parashant National Monument, Arizona. Shown are conditions before treatment implementation (2002) and 10 yr post-treatment (2014). Bold values followed by different lowercase letters indicate statistically different means ($P < 0.10$) within years.

Site	Variable	2002		2014	
		Untreated	Treated	Untreated	Treated
CR	Litter (cm)	0.4 (0.3)	0.3 (0.2)	0.3 (0.4)	0.2 (0.1)
	Duff (cm)	0.4 (0.3)	0.4 (0.4)	0.9 (0.7) a	0.2 (0.4) b
	1-hr (Mg ha ⁻¹)	0.6 (0.7)	0.4 (0.2)	0.7 (0.6) a	0.3 (0.2) b
	10-hr (Mg ha ⁻¹)	1.5 (1.7)	0.8 (1.0)	0.5 (1.1)	0.6 (0.8)
	100-hr (Mg ha ⁻¹)	2.9 (7.0)	0.0 (0.0)	1.4 (3.5)	1.9 (3.5)
	1000-hr-s (Mg ha ⁻¹)	0.0 (0.0)	1.1 (2.8)	0.0 (0.0) b	2.4 (2.7) a
	1000-hr-r (Mg ha ⁻¹)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
GP	Litter (cm)	0.2 (0.1)	0.2 (0.1)	0.4 (0.3)	0.2 (0.2)
	Duff (cm)	0.8 (0.2)	1.0 (0.7)	0.6 (0.6)	0.5 (0.7)
	1-hr (Mg ha ⁻¹)	0.7 (0.5)	0.4 (0.4)	0.6 (0.8)	0.4 (0.3)
	10-hr (Mg ha ⁻¹)	1.6 (1.2)	1.3 (1.9)	1.4 (1.1)	0.8 (1.1)
	100-hr (Mg ha ⁻¹)	1.4 (2.4)	0.0 (0.0)	1.9 (2.4)	8.1 (10.9)
	1000-hr-s (Mg ha ⁻¹)	1.8 (3.2)	7.0 (15.1)	6.5 (8.9)	5.3 (6.5)
	1000-hr-r (Mg ha ⁻¹)	3.0 (5.2)	1.6 (3.8)	1.1 (2.8)	0.0 (0.0)

significant, negative correlations with juniper density and tree basal area (Table 4). We found no significant difference in total species richness between the untreated and treated units at the CR site; however, the treated unit had significantly more C₄ grass and shrub species than the untreated unit (see Table 3). Similar to our findings for understory cover, species richness showed significant, negative correlations with tree basal area, juniper basal area, and canopy cover (see Table 4).

GP Site

Similar to the CR site, we found no differences in pretreatment (2002) means for overstory structural characteristics (see Table 1), forest floor, woody surface fuels (see Table 2), or understory community characteristics (Table 5) between the untreated and treated units at the GP site. Tree thinning resulted in significantly lower tree density in the treated unit compared with the untreated unit (see Table 1) and led to a more even distribution of size classes 10 yr post treatment as compared with pretreatment conditions (Fig. 3D). However, we found no significant difference in tree basal area between units. Thinning resulted in significant differences in relative importance of tree species, with pinyon pine showing relatively lower dominance and juniper gaining dominance in the treated unit compared with the untreated unit (see Table 1). We found no significant difference between units in

canopy cover, and means were > 21%. Forest floor depths and woody surface fuel loading were variable. No significant differences for any of these variables were detected between the untreated and treated units at the GP site (see Table 2).

Total understory plant cover ranged 4.6–4.9%, and we found no significant difference between the untreated and treated units at the GP site in 2014. Similarly, few differences in cover were detected within plant functional groups; however, we found significantly greater cover of C₃ graminoids and C₄ grasses in the treated compared with the untreated unit (see Table 5). Total understory plant cover showed significant negative correlations with pinyon pine tree density and pinyon basal area (see Table 4). Significantly more species were found in the treated unit than the untreated unit, and this difference appeared to be driven by richness of native species including C₃ graminoids and C₄ grasses (see Table 5). Richness showed significant negative correlations with total tree density and pinyon pine density (see Table 4).

Discussion

Tree thinning prescriptions that aimed to approximate presettlement stand structure and species composition resulted in significant reductions in tree density at both the CR and GP sites, as well as reductions in tree basal area at the GP site (see also Huffman et al., 2008a). Tree density changes were mainly driven by thinning of smaller trees because these were presumed to be relatively young (i.e., not presettlement). Boles, branches, and tops of the thinned trees were scattered across the study sites; however, this material resulted in few changes to woody surface fuel loading. Thinning and addition of woody material, along with seeding, resulted in only minor changes in understory cover and species richness at both sites. Understory responses appeared related to microsite conditions as evidenced by significant negative correlations with tree density at both sites. In addition, Spearman's rho values were relatively high and suggested positive correlations between understory response and wood cover at both sites, although these relationships were not statistically significant (see Table 3). Thus, although the two sites contrasted in terms of soil characteristics, understory responses to restoration treatments at both sites appeared to be similar.

Minor changes in cover and species richness at CR and GP contrast with results of other studies that have reported significant increases in herbaceous cover following similar pinyon-juniper restoration treatments (e.g., Jacobs and Gatewood, 1999; Stoddard et al., 2008; Jacobs, 2015). For example, Jacobs and Gatewood (1999) studied restoration responses on two pinyon-juniper savanna sites in New Mexico and found total herbaceous cover on untreated controls ranged about 15–38%, whereas herbaceous cover on plots where all trees were removed ranged about 71–75%. At these sites, notable herbaceous responses may be

Table 3

Understory cover (%) and species richness (500 m⁻²) measured pretreatment (2002) and 10 yr post-treatment (2014) at the Craig Ranch site (standard deviations [SDs] shown in parentheses) in Grand Canyon—Parashant National Monument, Arizona. Bold values followed by different lowercase letters indicate statistically different means ($P < 0.10$) within yrs. Total understory cover (all functional groups) was significantly higher in the treated unit (7.0% ± 4.8 SD) compared with the untreated (3.7% ± 2.9 SD) unit in 2014.

Functional group	Cover (%)				Species richness (no. 500 m ⁻²)			
	2002		2014		2002		2014	
	Untreated	Treated	Untreated	Treated	Untreated	Treated	Untreated	Treated
Native species	7.1 (3.3)	5.0 (2.1)	3.7 (2.9)	7.0 (4.8)	17.1 (1.2)	17.8 (1.8)	21.7 (2.6)	24.3 (3.6)
Annual forbs	1.2 (0.9)	1.5 (1.1)	< 0.01 (0.01)	0.01 (0.02)	2.5 (1.0)	2.8 (1.0)	0.8 (0.8)	0.7 (0.8)
Cacti	0.0 (0.0)	0.1 (0.1)	< 0.01 (0.01)	0.0 (0.0)	1.5 (0.8)	1.3 (0.5)	1.3 (0.8)	1.8 (0.8)
C ₃ graminoids	0.4 (0.6)	0.1 (0.1)	0.3 (0.4)	0.4 (0.3)	2.8 (1.0)	1.8 (0.8)	3.2 (0.8)	2.5 (0.5)
C ₄ grasses	0.6 (0.5)	0.4 (0.5)	0.3 (0.4)	0.9 (0.9)	2.3 (0.5)	2.3 (0.5)	1.8 (0.4) a	2.7 (0.5) b
Perennial forbs	1.1 (1.5)	0.7 (0.5)	0.5 (0.3)	0.9 (0.5)	2.8 (0.4)	3.5 (1.0)	8.2 (1.8)	8.8 (3.7)
Shrubs	3.5 (4.3)	2.1 (2.7)	2.5 (3.1)	4.5 (4.0)	3.0 (1.3)	4.0 (1.1)	4.2 (1.2) a	5.8 (0.8) b
Trees	0.2 (0.3)	0.1 (0.1)	0.03 (0.02)	0.2 (0.3)	2.2 (0.4)	2.0 (0.0)	2.2 (0.4)	2.0 (0.0)
Non-native species	0.0 (0.0)	0.0 (0.0)	< 0.01 (0.01)	< 0.01 (0.01)	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	0.8 (1.2)

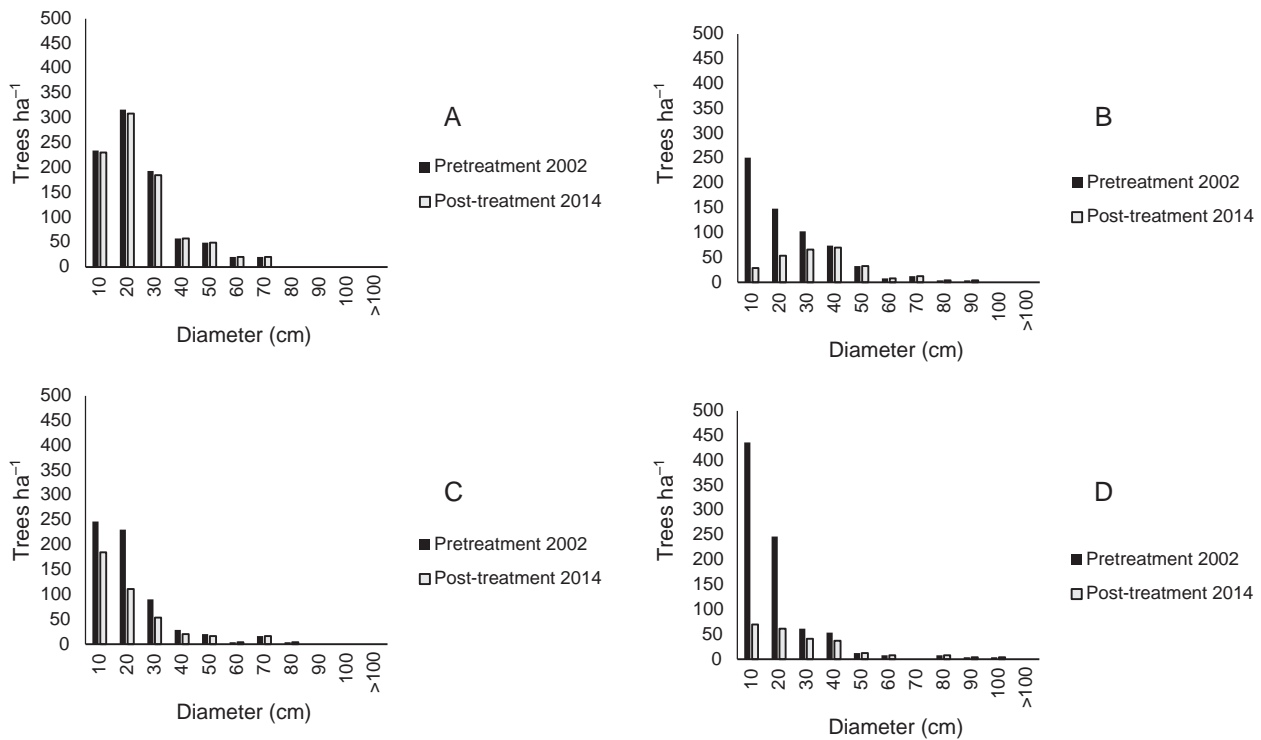


Figure 3. Diameter distributions before treatment (Pretreatment 2002) and 10 yr after treatment implementation (Post-treatment 2014). Figure shows the untreated and treated units at the Craig Ranch site (A and B, respectively) and the untreated and treated units at the Goose Pond site (C and D, respectively) in Grand Canyon – Parashant National Monument, Arizona.

expected due to soil conditions and a relatively high monsoon index (i.e., proportion of annual precipitation occurring during the summer) (Romme et al., 2009). In contrast, at woodland sites where summer

Table 4

Spearman's ρ and P values for rank correlation tests between plant cover and species and characteristics in 2014 at Craig Ranch and Goose Pond study sites in Grand Canyon – Parashant National Monument, Arizona. Bold values indicate significant correlations ($n = 12$) at $P < 0.05$.

Variable	Plant cover (%)		Species richness (no. 500 m ⁻²)	
	Spearman's ρ	P value	Spearman's ρ	P value
CR site				
Litter cover (%)	-0.0629	0.8459	0.1652	0.6079
Soil cover (%)	0.0281	0.9310	0.4321	0.1607
Wood cover (%)	0.3765	0.2278	0.1207	0.7086
Rock cover (%)	0.1049	0.7456	-0.5624	0.0570
Tree density (no. ha ⁻¹)	-0.4659	0.1269	-0.4789	0.1152
Juniper density (no. ha ⁻¹)	-0.6760	0.0158	-0.4085	0.1874
Pinyon density (no. ha ⁻¹)	-0.2474	0.4383	-0.3623	0.2471
Tree basal area (m ² ha ⁻¹)	-0.6154	0.0332	-0.5800	0.0481
Juniper basal area (m ² ha ⁻¹)	-0.5734	0.0513	-0.6468	0.0230
Pinyon basal area (m ² ha ⁻¹)	-0.2028	0.5273	-0.2250	0.4821
Canopy cover (%)	-0.2064	0.5198	-0.5832	0.0465
GP site				
Litter cover (%)	-0.3217	0.3079	-0.2081	0.5163
Soil cover (%)	0.3077	0.3306	0.4268	0.1664
Wood cover (%)	0.3993	0.1985	0.3351	0.2870
Rock cover (%)	0.2817	0.3751	-0.1776	0.5808
Tree density (no. ha ⁻¹)	-0.5106	0.0899	-0.7282	0.0072
Juniper density (no. ha ⁻¹)	0.2120	0.5083	-0.4563	0.1359
Pinyon density (no. ha ⁻¹)	-0.7183	0.0085	-0.6146	0.0335
Tree basal area (m ² ha ⁻¹)	-0.1259	0.6967	-0.2751	0.3867
Juniper basal area (m ² ha ⁻¹)	-0.0140	0.9656	-0.0529	0.8703
Pinyon basal area (m ² ha ⁻¹)	-0.7203	0.0082	-0.4974	0.0999
Canopy cover (%)	-0.2838	0.3714	0.0326	0.9199

precipitation is less important, herbaceous understory productivity may be expected to be low. However, Stoddard et al. (2008) reported understory cover to increase from 1.6% to 16.3%, and from 0.4% to 12.4%, 2 yr following slash addition and seeding on small plots at two woodland sites immediately adjacent to CR and GP, respectively. It should be noted that experimental plots used by Stoddard et al. (2008) were located in open interspaces, and community responses on microsites under tree canopy were not examined. Furthermore, experimental seeding rates tested by Stoddard et al. (2008) were more than fourfold higher than those applied in our study. Jameson (1967) described a negative exponential relationship between herbaceous production and tree canopy cover for pinyon-juniper woodlands in northern Arizona. In this relationship, the inflection point of the curve was near 25%, and herbage production changed relatively little across higher values (> 25%) of canopy cover (Jameson, 1967). Thus, although we did not investigate biomass, understory cover responses in our studies may have been limited in part by negligible differences in tree canopy cover between treated and untreated units. In fact, due to drought-related mortality taking place during treatment implementation, canopy cover at the GP sites was higher in the treated unit than in the untreated unit (see Table 1). More intensive thinning may be needed to reverse severe degradation of understory communities in these woodland sites.

Minor increases in plant cover at the two sites may also have been related to the quantities of slash added to the soil surfaces in treatment implementation. Slash and residue from tree thinning serve a number of beneficial functions for improving environmental conditions for understory plant communities and restoring semiarid woodlands (Lavin et al., 1981; Breshears and Barnes, 1999; Jacobs, 2015). For example, Tongway and Ludwig (1996) showed that placement of *Acacia ancurra* branches on degraded soil patches increased water infiltration and soil respiration, decreased erosion rates, moderated surface temperatures, and increased nitrogen availability in the woodlands of Australia. Similarly, Hastings et al. (2003) reported reduced erosion after harvesting slash was added to microsites on pinyon-juniper watersheds of New

Table 5

Understory cover (%) and species richness (500 m^{-2}) measured pretreatment (2002) and 10 yr post treatment (2014) at the Goose Pond site (standard deviations shown in parentheses) in Grand Canyon – Parashant National Monument, Arizona. Bold values followed by different lowercase letters indicate statistically different means ($P < 0.10$) within yrs. Total understory cover (4.6–4.9%, all functional groups) was not significantly different between the treated and untreated units in 2014.

Functional group	Cover (%)				Species richness (no. 500 m^{-2})			
	2002		2014		2002		2014	
	Untreated	Treated	Untreated	Treated	Untreated	Treated	Untreated	Treated
Native species	3.4 (4.1)	1.2 (1.2)	4.8 (4.0)	4.4 (1.6)	7.5 (1.6)	8.2 (1.0)	17.8 (3.4) a	21.8 (3.1) b
Annual forbs	< 0.01 (0.01)	< 0.01 (0.01)	0.02 (0.02)	0.02 (0.02)	0.5 (0.5)	0.8 (0.4)	1.7 (1.9)	1.8 (1.5)
Cacti	0.0 (0.0)	0.0 (0.0)	< 0.01 (0.01)	< 0.01 (0.01)	0.8 (0.4)	0.8 (0.4)	1.0 (0)	0.8 (0.4)
C ₃ graminoids	0.0 (0.0)	0.0 (0.0)	0.5 (0.5) a	1.3 (0.7) b	0.3 (0.5)	0.3 (0.5)	1.0 (0) a	1.5 (0.5) b
C ₄ grasses	0.0 (0.0)	0.01 (0.01)	0.0 (0.0) a	0.4 (0.3) b	0.0 (0.0)	0.2 (0.4)	0.0 (0.0) a	2.5 (0.5) b
Perennial forbs	0.1 (0.1)	0.2 (0.2)	0.4 (0.3)	0.4 (0.2)	2.2 (0.8)	1.5 (0.8)	9.2 (1.5)	9.2 (1.8)
Shrubs	2.8 (3.4)	0.8 (1.2)	3.7 (3.3)	1.5 (1.4)	1.5 (0.5)	2.5 (0.5)	3.0 (1.4)	3.8 (1.2)
Trees	0.6 (0.8)	0.3 (0.4)	0.2 (0.2)	0.7 (1.0)	0.2 (0.4)	2.0 (0)	2.0 (0.0)	2.2 (0.4)
Non-native species	0.0 (0.0)	0.0 (0.0)	0.05 (0.03)	0.2 (0.2)	0.0 (0.0)	0.2 (0.4)	3.5 (1.0)	2.8 (2.1)

Mexico. Stoddard et al. (2008) showed that slash additions decreased soil movement, increased potential for arbuscular mycorrhizae, and increased soil microbial biomass. However, Stoddard et al. (2008) experimentally applied slash at rates 6–17 \times and 6–8 \times higher than mean post-treatment slash totals we observed, respectively, at the CR and GP sites (see Table 2). Because of the documented benefits of slash addition for restoration of semiarid woodlands, we did not test for effects of slash removal activities, such as broadcast burning or mastication, on understory responses. Other studies have indicated that burning slash may increase nutrient availability in soils, shift understory species composition, and increase cover of non-native species (Haskins and Gehring, 2004; Bates et al., 2011; Huffman et al., 2013; Redmond et al., 2014). Results from our studies suggest that treatments (i.e., tree thinning, addition of slash, and seeding) may have not been intensive enough at either site to produce substantial understory responses and achieve successful restoration within a 10- to 15-yr timeframe.

Resilience of degraded ecosystems and the importance of recognizing alternative stable states and positive feedbacks have been previously discussed in literature related to conservation and restoration ecology (Westoby et al., 1989; Friedel, 1991; Laycock, 1991; Suding et al., 2004; Savage and Mast, 2005). For example, Friedel (1991) described environmental thresholds that, once crossed, would allow arid rangelands to rapidly transition to new stable states that were not easily reversed. Similarly, Laycock (1991) reviewed cases of ecological degradation reported in various rangeland systems that showed little response to passive restoration that removed or reduced numbers of grazers at the study sites. Jameson (1987) theorized a cusp-catastrophe model for pinyon-juniper ecosystem dynamics, controlled primarily by relative moisture, grazing, and fire. In this model, transition between grassland and woodland states could be abrupt and woodlands, once established, could be persistent under various climatic conditions (Jameson, 1987). Allen (2002) described changes in pinyon-juniper woodlands of Bandelier National Monument wherein intensive livestock grazing and reduced fire frequency following Euro-American settlement in the late 1800s led to increases in tree establishment and contributed to accelerated erosion and soil degradation. We suggest that similar processes occurred at the CR and GP study sites. For example, Altschul and Fairley (1989) described early reports of range depletion on the Arizona Strip, including on the landscape now within the Grand Canyon – Parashant National Monument, beginning with settlement of the region around 1870. Overgrazing during this time resulted from expanding herds of horses and cattle, seasonally large numbers of sheep, and successive severe droughts (Altschul and Fairley, 1989). Mid – 20th century range reports on file with the Bureau of Land Management (BLM) (Arizona Strip District Office, BLM, St. George, Utah, unpublished) indicate that

grass cover in our study area had been depleted by unregulated grazing before 1900, and intensive livestock use continued through 1969. Examination of repeat aerial photographs and historical maps indicated that water sources for livestock were improved (catchments, pipelines, etc.) after 1940 at both sites (Huffman et al., 2008a). Fire history of the site is not known, but other studies of woodlands in the region have indicated fire regimes characterized by infrequent, high-severity fires (Rowlands and Brian, 2001; Huffman et al., 2008b; Bauer and Weisberg, 2009). Thus, intensive and persistent livestock grazing, periodic droughts, and possibly reduced fire disturbance, in concert, may have led to deterioration of understory communities and transition of the woodlands at our two study sites to new degraded stable states. Conditions at the sites presently appear to be resistant to the treatments tested, which were intended to produce notable increases in understory cover and species richness.

Implications

Resilient degraded conditions, resistant to restoration prescriptions that are based on approximating site-specific historical conditions, present land managers with a conundrum. Managers are faced with choosing between strict adherence to prescriptions that use historical conditions as targets and those that may be more intensive and rely on successional processes to return woodland structure to within natural ranges of variation over longer periods of time. For example, in our study, heavier thinning that significantly reduced canopy cover would require cutting presettlement trees. Heavier thinning may encourage greater understory increases (Jameson, 1967) and also would be expected to produce more woody material for improving soil conditions and microclimate in open interspaces (Stoddard et al., 2008). Further, successful restoration of understory diversity may require seeding at heavier rates than tested in our studies. More work is needed to test new restoration approaches that are designed to drive degraded pinyon-juniper woodlands over resilience thresholds toward more diverse understory communities.

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Appendix A.

Quadrat-level frequency (%) of occurrence for understory plant species observed in untreated and treated units at Craig Ranch (CR) and Goose Pond (GP) sites in Grand Canyon–Parashant National Monument, Arizona. Brackets indicate pretreatment (2002) frequencies, and unbracketed values are post-treatment (2014) frequencies. Bold font indicates non-native species. Asterisks indicate species seeded as part of the restoration treatments

Functional group	Species	CR		GP		
		Untreated	Treated	Untreated	Treated	
Annual/Biennial forb	<i>Arabis</i> sp.	[10.0] 0	x	x	x	
	<i>Chamaesyce revoluta</i>	x	[3.3] 0	x	x	
	<i>Cordylanthus parviflorus</i>	[66.7] 0	[55.0] 0	x	x	
	<i>Descurainia incana</i>	[0] 3.3	x	[1.7] 0	x	
	<i>Descurainia pinnata</i>	[1.7] 3.3	x	x	x	
	<i>Descurainia sophia</i>	[0] 3.3	x	[0] 16.7	15.0	
	<i>Draba</i> sp.	[3.3] 0	[1.7] 0	x	[0] 1.7	
	<i>Epilobium brachycarpum</i>	x	x	x	[0] 1.7	
	<i>Eriogonum cernuum</i>	x	x	x	[0] 3.3	
	<i>Gilia ophthalmoides</i>	x	x	[0] 1.7	x	
	<i>Lactuca serriola</i>	x	[0] 1.7	[0] 1.7	[0] 5.0	
	<i>Lappula occidentalis</i>	x	x	[0] 1.7	x	
	<i>Lepidium</i> sp.	x	x	[0] 10.0	x	
	<i>Linum neomexicaum</i>	x	[0] 5.0	x	x	
	<i>Lupinus kingii</i>	x	[0] 1.7	x	[0] 3.3	
	<i>Phlox gracilis</i>	x	x	[0] 3.3	x	
	Cactus	<i>Polygonum douglasii</i>	x	[8.3] 0	x	1.7
		<i>Verbascum thapsus</i>	x	x	[0] 3.3	[0] 1.7
		<i>Cylindropuntia whipplei</i>	[0] 1.7	x	x	x
		<i>Opuntia erinacea</i>	x	[1.7] 0	x	x
<i>Opuntia macrorhiza</i>		x	x	x	[0] 1.7	
<i>Opuntia</i> sp.		x	x	[0] 1.7	x	
<i>Achnatherum hymenoides*</i>		x	x	x	[0] 1.7	
<i>Aristida purpurea</i>		[5.0] 3.3	21.7	x	x	
<i>Aristida adscensionis</i>		x	[1.7] 0	x	x	
<i>Bouteloua curtispindula*</i>		[6.7] 11.7	[0] 16.7	x	[0] 6.7	
Graminoid	<i>Bouteloua gracilis*</i>	[28.3] 30.0	[15.0] 25.0	x	[3.3] 20.0	
	<i>Bromus tectorum</i>	x	[0] 1.7	[0] 16.7	30.0	
	<i>Carex</i> sp.	[20] 0	x	x	x	
	<i>Carex geophila</i>	[0] 21.7	1.7	x	x	
	<i>Elymus elymoides*</i>	[3.3] 13.3	33.3	[0] 55.0	[0] 80.0	
	<i>Koeleria macrantha</i>	[1.7] 1.7	x	x	x	
	<i>Poa fendleriana</i>	33.3	35.0	[0] 1.7	[0] 6.7	
	<i>Sporobolus cryptandrus*</i>	[0] 1.7	x	x	[0] 8.3	
	<i>Asclepias asperula</i> ssp. <i>asperula</i>	[0] 1.7	x	x	x	
	<i>Astragalus argophyllus</i>	x	x	x	[0] 1.7	
Perennial forb	<i>Boechera fendleri</i>	[0] 33.3	[0] 23.3	[0] 18.3	[0] 31.7	
	<i>Chaenactis douglasii</i>	x	x	[0] 15.0	[0] 10.0	
	<i>Chamaesyce fendleri</i>	x	[0] 3.3	x	[0] 1.7	
	<i>Cirsium neomexicanum</i>	x	x	x	[0] 1.7	
	<i>Convolvulus arvensis</i>	x	x	x	[0] 3.3	
	<i>Cymopterus</i>	[0] 1.7	x	x	x	

(continued)

Functional group	Species	CR		GP	
		Untreated	Treated	Untreated	Treated
Shrub	<i>purpureus Eriogonum corymbosum</i>	[0] 28.3	[0] 58.3	[0] 1.7	[0] 21.7
	<i>Eriogonum racemosum</i>	[0] 3.3	x	x	x
	<i>Erigeron divergens</i>	x	x	[0] 1.7	[0] 1.7
	<i>Eriogonum umbellatum</i>	[35.0] 0	[65.0] 0	[5] 0	[20.0] 0
	<i>Hymenoxys cooperi</i>	31.7	40.0	x	[0] 1.7
	<i>Hymenopappus filifolius</i>	[6.7] 26.7	25.0	[3.3] 0	[3.3] 0
	<i>Lesquerella intermedia</i>	[1.7] 13.3	[0] 16.7	x	x
	<i>Lomatium nevadense</i>	[0] 6.7	[0] 10.0	x	x
	<i>Lotus wrightii</i>	[0] 3.3	[0] 1.7	x	[0] 3.3
	<i>Lupinus argenteus*</i>	x	x	x	x
	<i>Marrubium vulgare</i>	x	x	[0] 6.7	x
	<i>Packera multilobata</i>	[0] 3.3	[0] 1.7	[0] 16.7	[0] 8.3
	<i>Penstemon barbatus</i>	[0] 5	x	x	x
	<i>Penstemon linarioides</i>	[3.3] 0	[5.0] 0	x	1.7
	<i>Penstemon palmeri</i>	x	x	[1.7] 3.3	[0] 1.7
	<i>Penstemon thompsoniae</i>	[0] 11.7	[0] 18.3	x	x
	<i>Phaseolus angustissimus</i>	x	x	[3.3] 26.7	18.3
	<i>Phlox amabilis</i>	x	[0] 6.7	[0] 5.0	[0] 5
	<i>Physalis hederifolia</i>	x	x	x	[0] 1.7
	Tree	<i>Psoralidium tenuiflorum</i>	[0] 6.7	[0] 28.3	x
<i>Sphaeralcea</i> sp.		x	[0] 1.7	[0] 50.0	[0] 35.0
<i>Amelanchier utahensis*</i>		x	x	x	x
<i>Artemisia tridentata</i>		[1.7] 1.7	6.7	[5.0] 23.3	6.7
<i>Atriplex canescens*</i>		x	x	x	x
<i>Ephedra viridis*</i>		x	[0] 3.3	x	x
<i>Ericameria nauseosa</i>		x	[3.3] 0	x	x
<i>Gutierrezia sarothrae</i>		[6.7] 11.7	13.3	x	[0] 1.7
<i>Purshia stansburiana</i>		[18.3] 16.7	[6.7] 13.3	[20.0] 21.7	[16.7] 16.7
<i>Quercus turbinella</i>		[3.3] 6.7	8.3	x	x
Tree	<i>Rhus trilobata*</i>	x	x	x	x
	<i>Yucca baccata</i>	[0] 1.7	1.7	[0] 1.7	x
	<i>Juniperus osteosperma</i>	[1.7] 5	3.3	[3.3] 3.3	6.7
	<i>Pinus edulis</i>	[11.7] 8.3	10.0	18.3	11.7

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