



## Grass Mortality and Turnover Following Core Rangeland Restoration Practices<sup>☆</sup>



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### ABSTRACT

In rangelands, management interventions have sought to minimize disturbances that decrease survival of perennial grasses to avoid compositional shifts toward less desirable species. However, the effects of rangeland management techniques on perennial grass survival and turnover are not known for individual species because the discipline has largely focused on structural metrics, measuring cover or biomass rather than tracking individual plants. In this study, we quantified perennial grass survival and recruitment in response to core rangeland restoration practices across multiple soil types to determine the potential for different interventions to cause shifts to undesirable grass community assemblages. We mapped individual grass tufts and recorded basal area annually. We used these maps to track survival and recruitment of grasses in response to mechanical brush removal, chemical woody plant control, and low-intensity prescribed burning. Additionally, we performed ordinations of the grass community to explore compositional shifts resulting from management interventions. We found perennial grass mortality to be higher for mechanically treated plots on all soil types than it was in chemically treated plots, burned plots, or untreated controls. Levels of mortality from fire were similar to baseline mortality in control plots for all soil types. However, relative species turnover was variable among soils and treatments. Brush removal only resulted in compositional shifts on sandy soils, where annual grasses and species capable of rapid expansion following disturbance became dominant. Differential responses are related to differences in species turnover, which is a function of individual grass species mortality and recruitment mediated by interactions between management approach and abiotic conditions. Given this response variability, understanding effects of management actions on perennial grass turnover and the potential for those actions to result in a community shift toward less desirable species is necessary for managers to achieve restoration goals on encroached rangelands.

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### Introduction

Survival, life expectancy, and life span are key demographic parameters that determine individual plant responses to disturbance and management in rangelands (Lauenroth and Adler, 2008). Species that are dominant in many ecosystems are more likely to have longer life spans and higher life expectancies (Lorimer et al., 2001; Grime, 2007a, b; Lauenroth and Adler, 2008). This relationship between longevity and dominance is hypothesized to occur because species with longer life spans exhibit fewer fluctuations in population growth rates, which

results in those populations maintaining persistence in systems while other species fluctuate in relative abundance and experience local extinctions (Schoener, 1983; Ehrlén and Lehtilä, 2002). Persistence allows for exploitation of optimal conditions for population growth by maintaining a constant presence in the system, and it provides a mechanism for continued growth under conditions of environmental stress and disturbance (Ozinga et al., 2007; Lauenroth and Adler, 2008). Therefore, differential longevity among species has a potentially long-term influence on plant community composition and structure (Harcombe, 1987; Pacala et al., 1996). However, the relationship between longevity and dominance is mediated by disturbance. There is often a trade-off among life history strategies with long-lived plant species lacking traits necessary for rapid recolonization following disturbance (Crawley and Ross, 1990; Grime, 2007a, b). Therefore, low survival of long-lived species in response to intense disturbance can lead to community compositional shifts as long-lived, slow-growing species are replaced by rapidly colonizing, fast-growing species (Tilman, 1990; Louault et al., 2005). Interactions between species are mediated by species-specific interactions with the abiotic environment because of differential

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resource availability associated with differing abiotic conditions (Grime, 1977; Fynn et al., 2005). This leads to additional variability in species compositional response to disturbance beyond that resulting from the interactions among the biotic components of the ecosystem.

In rangelands, management interventions have often centered on a solitary utilitarian objective and, as a result, have sought to minimize disturbances that decrease survival of long-lived perennial grasses and provide opportunities for shorter-lived species that respond to increases in bare ground (Herrick et al., 2006; Fuhlendorf et al., 2012; Twidwell et al., 2013). Such turnover is presumed to set the stage for undesirable regime shifts in grassland community composition, increasing the dominance of less desirable annuals and weedy perennial species. Concern for such regime shifts is evident in the state and transition models within the Ecological Site Description database, which is the dominant management framework for rangelands in the United States (RIESM, 2010). Shifts in dominance among native herbaceous functional groups is the third most dominant ecosystem change depicted in state and transition models, occurring on 57% of the land area described in the Ecological Site Description database (Twidwell et al., 2013). The potential for rangeland management actions to cause grass mortality has therefore been at the forefront of rangeland decision making historically (Wright and Klemmedson, 1965; Wright, 1970, 1982; Johnson and Strang, 1983). Rangeland managers are therefore making decisions in the absence of empirical data and have used grass mortality concerns as one of the leading reasons to avoid using fire and to use mechanical or chemical options for controlling woody invaders instead (Taylor et al., 2011). Similar concerns have not been raised regarding the potential for grass mortality to result from chemical and mechanical brush control. While multiple long-term studies have shown that prescribed fire has not caused major compositional shifts in grassland communities (Ansley et al., 2004; Towne and Kemp, 2008; Howe, 2011; Taylor et al., 2011), no study has directly compared relative differences in mortality and compositional change to commonly used management techniques. Moreover, the relative contributions of different rangeland management techniques to grass survival and turnover are not known for individual species because the discipline of range science has largely focused on structural metrics of cover or biomass instead of tracking the mortality and recruitment of individual plant tufts (Lauenroth and Adler, 2008; Zimmermann et al., 2008, 2010; Thapa et al., 2011). This important knowledge gap needs to be addressed to provide objective information on the relative effect of various interventions on grass mortality and turnover.

In this study, we quantified survival and recruitment of perennial grass species in response to core rangeland restoration practices replicated across a soil texture gradient. To do this, we mapped individual perennial grass tufts and recorded basal area in permanently established plots on an annual basis (Weaver and Clements, 1938; Lauenroth and Adler, 2008; Silvertown and Charlesworth, 2001). We used these maps to track survival, recruitment, and relative turnover of grass species in response to mechanical brush removal, chemical control of woody species, low-intensity prescribed burning, and in untreated controls. Additionally we performed ordinations of the entire grass community, both annuals and perennials, to explore species compositional shifts resulting from management interventions across a soil gradient ranging from fine clays to coarse sands. Soil texture has been found to be an important driver of species responses to disturbance in this system, with more rapid recovery of grasses occurring on fine-textured soils (Powell and Box, 1967). In addition, different types of restoration practices create differing levels of disturbance to the soil, and this has also been shown to vary with soil texture (Pinard et al., 2000). We therefore expect that herbaceous response to intervention will vary on the basis of soil texture and the type of intervention strategy employed. Specifically, we hypothesized that 1) mechanical treatments would result in the highest mortality rates because they cause the highest levels of soil disturbance; 2) coarse-textured soils would have higher turnover than fine-textured soils because they facilitate species

that respond readily to rapid increases in resource availability; and 3) high levels of disturbance would result in community compositional shifts as long-lived plant species are replaced by species capable of rapid recolonization following disturbance. Findings from our study provide an objective source of information that separates perceptions from the ecological realities of the potential for different management interventions to cause perennial grass mortality and community compositional shifts.

## Methods

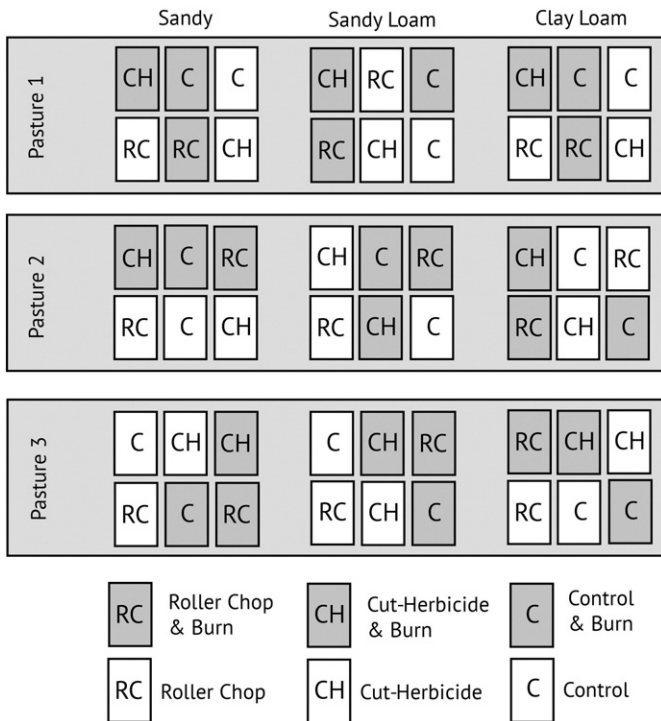
### Study Site

This research was conducted at the Chaparrosa Ranch in Zavala County in southwest Texas (lat 28.9°N, long 100.0°W). The Chaparrosa Ranch is a privately owned hunting and cattle enterprise spanning 36 360 ha. Individual pastoral units vary in size, ranging from 500 to 5 000 ha. Soils vary within the larger pastures, ranging from fine clayey to coarse sandy textures. Vegetation community composition is consistent across the site. Many of the sites are best characterized as a heavily encroached *Prosopis-Acacia* shrubland dominated by *Acacia rigidula* Benth, *Prosopis glandulosa* Torr, and *Acacia schaffneri* (S. Watson) F. J. Herm. The dominant grasses at the study site include *Hilaria belangeri* (Steud.) Nash, *Bouteloua hirsuta* Lag., *Aristida purpurea* Nutt., and *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult. The site has a subtropical climate with average annual rainfall of 560 mm that is bimodally distributed, with a majority of precipitation events occurring in spring and fall (Jacoby et al., 1981).

### Experimental Design

We established a full factorial experiment to test for differences in grass mortality and recruitment among three core rangeland restoration treatments: chemical (cut-herbicide), mechanical (roller-chop), and fire. Three pastures were selected to implement shrubland restoration treatments within a randomized complete block design (Fig. 1). The three pastures located on the ~24 000-ha Chaparrosa Ranch differed in land-use history. Pastures were located within 15 km of one another and varied in size from ~1 300 ha to ~9 700 ha. One pasture was grazed with high-intensity, low-duration grazing during the recent past. Another pasture underwent extensive herbicide testing in the 1960s across much of the pasture and was periodically grazed since. No shrub management was reported for the third pasture, and it also was periodically grazed (Mattox, 2013). All pastures are currently moderately grazed with rotation into pastures depending on site conditions.

Within each pasture, three soil types were selected to represent the range of soil textures observed on the study site. Soil types were Antosa-Bobillo sand association (sand), Webb fine sandy loam soils (sandy loam), and Chacon clay loam soils (clay loam) (Soil Survey Staff, 2013). These soil types occurred in each of the three pastures selected. At the beginning of the study, in early spring 2010, 54 plots, each approximately 40 × 25 m, were established. We used a full factorial design with three pastures × three soil types × three treatments (one mechanical, one chemical, one control) with two repetitions for a total of 54 plots (see Fig. 1). Plots were blocked by soil types and soil blocks were replicated across the three pastures, such that each unique soil-pasture combination contained six plots, each separated by a vegetated buffer of ~10 m. One of three treatments, chemical (cut-herbicide), mechanical (roller-chop), and control (untreated), was randomly assigned to two plots within each soil block in each pasture. Roller-chopping uses a cylindrical drum (Pasture Aerator, Lawson Mfg. Inc., now RanchWorx, Palm Harbor, FL) equipped with blades towed behind a tractor to cut and crush woody vegetation at the soil surface (Fulbright et al., 1991; Blanco et al., 2005). We used roller-chopping as a mechanical method for this study because it provided a gradient of soil disturbance with high disturbance from roller-chopping, low soil disturbance from cut-



**Figure 1.** Diagram of experimental design. At the beginning of the study, in early spring 2010, 54 plots, each approximately  $40 \times 25$  m, were established. We used a full factorial design with three pastures  $\times$  three soil types  $\times$  three treatments (one mechanical, one chemical, one control) with two repetitions for a total of 54 plots. Plots were blocked by soil types and soil blocks were replicated across the three pastures, such that each unique soil-pasture combination contained six plots, each separated by a vegetated buffer of  $\sim 10$  m. One of three treatments, chemical (cut-herbicide), mechanical (roller-chop), and control (untreated), was randomly assigned to two plots within each soil block in each pasture. In February 2013, a prescribed fire treatment was randomly assigned to one of each of the treatment replicates within the blocks on each pasture for a total of 27 burned plots. The resulting treatments in 2013, replicated and balanced across pastures and soil blocks, were 1) control (no brush removal and unburned), 2) burned (no brush removal), 3) cut-herbicide (unburned), 4) cut-herbicide and burned, 5) roller-chop (unburned), and 6) roller-chop and burned. (Adapted from Wonkka, C. L., D. Twidwell, J. B. West, and W. E. Rogers. 2016. Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration. *Ecological Applications* 26:128–145).

herbicide treatment, and no soil disturbance in control plots. In cut-herbicide treatments, we cut all shrubs and trees in the plot at the base and sprayed a 15% Remedy herbicide (Dow AgroSciences LLC, Indianapolis, IN) and diesel mixture on the cut stumps. Two yr following mechanical and chemical treatments, in February 2013, a prescribed fire treatment was randomly assigned to one of each of the treatment replicates within the soil blocks across all three pastures for a total of 27 burned plots. The resulting treatments in 2013, replicated and balanced across pastures and soil blocks, were 1) control (no brush removal and unburned), 2) burned (no brush removal), 3) cut-herbicide (unburned), 4) cut-herbicide and burned, 5) roller-chop (unburned), and 6) roller-chop and burned (see Fig. 1). Burned plots were separated by disked fire-breaks and ignited separately with ring fires. We established five ( $1\text{-m}^2$ ) subplots in random locations within each plot for sampling perennial grass demography, marking the corners with rebar for relocation.

Each growing season (late summer/early fall), from 2010 (pretreatment) until 2013, we mapped the basal area of each perennial grass tuft in the subplot each year during peak perennial grass production, by drawing it to the nearest  $\text{cm}^2$  on gridded paper with one square representing  $1\text{ cm}^2$ , providing a mapped location for each individual perennial grass in 2010 (before treatment), 2011, 2012, and 2013. We measured the distance from the subplot corner posts to the center of the grass tuft to map its location within the subplot and identified each tuft to species.

Fire temperatures at each subplot were recorded during the prescribed burn using ceramic tile pyrometers painted with 10 temperature-indicating lacquers (OMEGALAQ Liquid Temperature Lacquers; Omega, Inc.) that melted from  $79^\circ\text{C}$  to  $640^\circ\text{C}$ . Percent scorch was visually estimated immediately following the burns for each subplot.

#### Data Analysis

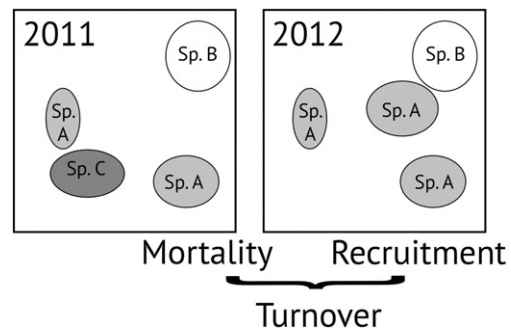
Using the mapped basal areas, we were able to determine mortality, recruitment, and relative species turnover of grasses within subplots (Fig. 2). We defined individuals as individual perennial grass tufts for purposes of quantifying survival and recruitment. This assumption is reasonable given that the majority of the grass species at the study site are perennial warm season tufted bunch grasses (see Appendix). We did not include annual species in the analysis because by definition they undergo 100% mortality at the end of each growing season. Moreover, they accounted for  $< 10\%$  of the annual average herbaceous cover on all soil types. Perennial grass mortality in burned plots was calculated from subplots that actually burned during the prescribed fire. Mortality was considered to have occurred when an individual was not present in the location it was mapped in the previous year, because it was now bare ground or occupied by an individual of a different species. Recruitment was considered to have occurred when an individual was present in a location it was not previously mapped in because that spot was bare ground or previously occupied by another species. Relative species turnover quantifies the proportion of the total species pool that turns over each year. We calculated relative species turnover for each subplot for each year using the following equation (Diamond, 1969).

$$\text{Turnover@time } t + 1 = (U_t + U_{t+1}) / (S_t + S_{t+1}) \quad (1)$$

where  $U_t$  is the number of species present in the subplot during year  $t$  that were not present in year  $t + 1$ ;  $U_{t+1}$  is the number of species present in the subplot during year  $t + 1$  that were not present in year  $t$ ;  $S_t$  is the total number of species present in the subplot during year  $t$ ; and  $S_{t+1}$  is the total number of species present in the subplot during year  $t + 1$ .

We tested for differences in mortality, recruitment, relative species turnover, and percent cover of bare ground among brush removal treatments and soil types using analysis of variance (ANOVA) for the randomized complete block design or repeated measures ANOVA for the randomized complete block design where appropriate, with pasture included as a random effect account for blocking in both types of analysis and pasture and year included as random effects when multiple years were included in the analysis.

We tested for differences in mortality among treatments for the first year following the respective treatment using data on plant mortality from 2010 to 2011 for chemical and mechanical treatments and from



**Figure 2.** Conceptual diagram of mortality, recruitment, and species turnover. Mortality occurs when an individual was not present in the location it was mapped in the previous year. Recruitment occurs when an individual was present in a location it was not previously mapped in. Relative species turnover quantifies the proportion of the total species pool that turns over each year.

2012 to 2013 for the fire treatment. Thus, we only compared mortality for the first year following treatment because fires were set in the dormant season just before the end of the study (February 2013). As a result, we only had 1 yr (2013) of postfire mortality data. Mortality resulting from fire was determined for the entire plot by averaging the mortality of subplots that had actually burned in each plot. At the time the fires were conducted, fuels were lower than the recommended 2 240 to 3 360 kg/ha needed for effective prescribed burning in this region (Lyons et al., 1998) because of a long-term drought. Therefore, the fire temperatures were low and the resulting low intensity burns did not carry well across the discontinuous fuels. We therefore included only those plots that had actually burned in the fire in the analysis. We included only controls that had been burned as the fire treatment, unburned controls as the control treatment, unburned roller-chopped plots as the mechanical treatment, and unburned cut-herbicide plots as the chemical treatment to maintain a balanced design for the analysis. Additionally, we tested for significant differences in mortality between 2011 control plots and 2013 control plots to determine that it would be appropriate to compare mortality in the sampling period following cut-herbicide and roller-chopping (2011) to mortality in the sampling period following prescribed burning (2013). We also tested for differences in mortality, recruitment, and relative species turnover among control, chemical, and mechanical treatments during all years of the study. Additionally, we tested for differences in bare ground among treatments on different soils in the sampling period following treatment to determine relative levels of soil disturbance caused by the treatments. We performed multiple comparisons to compare the mean response of each soil type and treatment at each year using Tukey's honest significant difference (HSD) test. We set  $\alpha = 0.05$  to determine significance in all analyses.

We used multivariate analyses to test for differences in the trajectory of grass community composition following treatments. Permutational multivariate ANOVA (PERMANOVA) was used to test for differences in community composition resulting from different brush removal treatments on different soil types. PERMANOVA is commonly used in ecological community analyses where data often do not conform to the assumptions of MANOVA (Anderson et al., 2005). The PERMANOVA was parameterized using soil, treatment, year, and their interaction as main effects and pasture as a random effect. A Bonferroni correction was applied to  $P$  values for multiple comparisons to adjust the familywise error rate for the large number of comparisons. Nonmetric multidimensional scaling with Bray-Curtis distances (Beals, 1984) was used to visualize differences in the grass community composition among soils and brush removal treatments. All analyses were performed using the R statistical computing package (R Development Core Team, 2010). We tested for changes in percent cover of species thought to be driving ordination patterns across brush removal treatments and soil types using repeated measures ANOVA or MANOVA (for groups of species) for the randomized complete block design.

## Results

### Mortality and Recruitment

Perennial grass mortality differed among core rangeland restoration treatments in the year following treatment initiation (Table 1). Since

**Table 1**  
Analysis of variance results of tests for differences in mortality 1 yr following treatment (2011 for chemical and mechanical, 2013 for fire) on different soil types

	Sum sq	Mean sq	NumDF	DenDF	F value	P
Treatment	3.41	1.14	3	22	77.37	< 0.001
Soil	0.07	0.03	2	22	2.30	0.124
Treatment:Soil	0.08	0.01	6	22	0.88	0.525

Abbreviations: Sum sq, sum of squares; Mean sq, mean square value; NumDF, numerator degrees of freedom; DenDF, denominator degrees of freedom.

neither brush removal treatment had an effect on mortality of burned versus unburned plots on any soils ( $F = 1.15$ ,  $P = 0.32$ ) and mortality in control plots did not differ in the sampling period following cut-herbicide and roller-chopping treatments and the sampling period following prescribed burns ( $F = 1.72$ ,  $P = 0.19$ ), it was possible to directly compare the amount of perennial grass mortality resulting from prescribed fire with the amount of perennial grass mortality resulting from the brush removal treatments and untreated controls. Mean mortality of perennial grasses was higher in mechanically treated plots than burned plots, cut-herbicide treated plots, and controls ( $F = 77.37$ ;  $P < 0.001$ ). There were similar mortality rates in burned plots, cut-herbicide plots, and untreated controls on all soil types (see Table 1, Fig. 3). Recruitment did not differ significantly among brush removal treatments overall ( $F = 0.94$ ;  $P = 0.396$ ).

### Relative Species Turnover

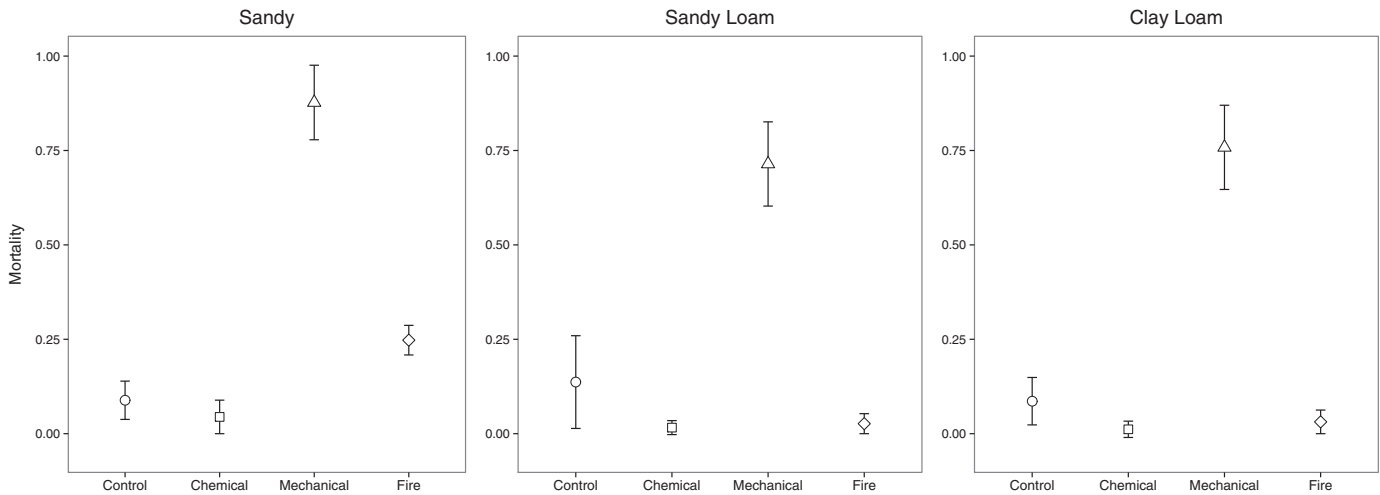
We found significant treatment-by-year and treatment-by-soil interactions in relative species turnover (Table 2, Fig. 4). On sandy soils and clay loam soils, turnover was higher for mechanically treated plots than control plots or chemically treated plots (Tukey's HSD: sandy soils, control vs. mechanical,  $P < 0.001$ ; mechanical vs. chemical,  $P < 0.001$ ; clay loam soils, control vs. mechanical,  $P < 0.001$ ; mechanical vs. chemical,  $P < 0.001$ ); control plots were not different from chemically treated plots on those soils (Tukey's HSD: sandy soils, control vs. chemical,  $P = 0.11$ ; clay loam soils, control vs. chemical,  $P = 0.58$ ). On sandy loam soils, mechanical plots had higher relative species turnover than control plots (Tukey's HSD  $P < 0.001$ ). Chemically treated plots on sandy loam soils did not differ from control plots or mechanically treated plots (Tukey's HSD: control vs. chemical,  $P = 0.05$ ; chemical vs. mechanical,  $P = 0.12$ ). Mechanically treated plots had higher relative species turnover than both control and chemically treated plots in 2011 and 2012, but all treatments had similar levels of turnover in 2013 (Tukey's HSD: 2011, control vs. mechanical,  $P < 0.001$ ; mechanical vs. chemical,  $P < 0.001$ ; control vs. chemical,  $P = 0.05$ ; 2012, control vs. mechanical,  $P < 0.001$ ; mechanical vs. chemical,  $P < 0.001$ ; control vs. chemical,  $P = 0.83$ ; 2013, control vs. mechanical,  $P = 0.18$ ; mechanical vs. chemical,  $P = 0.56$ ; control vs. chemical,  $P = 0.45$ ).

### Change in Percent Bare Ground Resulting from Treatments

Change in percent bare ground from pretreatment sampling to the sampling period following initiation of treatment differed among treatments and across soils. Differences were similar among treatments on sandy loam and clay loam soils (Tukey HSD: sandy loam vs. clay loam,  $P = 0.97$ ). However, roller-chopping increased bare ground more on sandy plots than on clay plots and sandy loam plots (Tukey HSD: sandy vs. sandy loam,  $P = 0.03$ ; sandy vs. clay loam,  $P = 0.001$ ). In fact, mean percent bare ground was almost 60% greater on sandy soils in the sampling period following treatment than during pretreatment sampling, while it was only 6% and 19% greater after treatment on clay and sandy loam soils, respectively.

### Community Composition

PERMANOVA revealed a significant year main effect and a significant treatment by soil interaction (Table 3). Multiple comparison procedures revealed that year 2013 differed from pretreatment (2010) composition (Table 4). In sandy soils (Fig. 5A), mechanically treated plots separated from control plots in ordination space. Chemically treated plots differed from control plots also, although to a lesser extent. This shift was driven by an increased abundance of *Heteropogon contortus*, *Eragrostis barrelieri*, and *Cenchrus spinifex*, as evidenced by these species' occupation of the same ordination space as mechanically treated plots on sandy soils (Fig. 5B). This finding was corroborated by ANOVA results for each of these species. The ANOVA for *H. contortus* showed a



**Figure 3.** Mortality (mean  $\pm$  SE) measured 1 yr following treatment (2011) for brush removal treatments (control, cut herbicide, and mechanical) and 1 yr following fire (2013) on three different soil types: sandy, sandy loam, and clay loam.

significant soil  $\cdot$  treatment interaction ( $F = 5.54$ ,  $P = 0.005$ ). Multiple comparisons revealed differences between sandy soils and sandy loam soils and sandy soils and clay loam soils for mechanical treatments (Tukey HSD sandy vs. sandy loam,  $P = 0.008$ ; sandy vs. clay loam,  $P = 0.003$ ). The MANOVA for *H. contortus*, *E. barrelieri*, and *C. spinifex* showed a significant soil  $\cdot$  treatment interaction ( $F = 5.54$ ,  $P = 0.005$ ). Multiple comparisons revealed differences between treatments on sandy soils versus sandy loam soils and sandy soils versus clay loam soils for mechanical treatments (Tukey HSD: sandy vs. sandy loam,  $P = 0.008$ ; sandy vs. clay loam,  $P = 0.003$ ). There were not differences among other soil-treatment combinations. On sandy loam soils, there was no strong, observable directional shift in community composition as a result of brush control treatments. While the multiple comparisons within PERMANOVA showed a difference between control plots and chemically treated plots, this was not a strong effect, as is evidenced by the location of the treatments in ordination space. All three treatments were

highly overlapping and occupied the same ordination space on sandy loam soils (Fig. 5B). Similarly, there was no strong observable compositional shift relative to treatments on clay loam soils, with all three treatments overlapping in ordination space. However, there was greater variation in community composition on clay soils, especially those that were mechanically treated (Fig. 5C) with a few plots separating toward *Nassella leucotricha* in ordination space (Fig. 5D). ANOVA showed no treatment  $\cdot$  soil effect for *N. leucotricha* ( $F = 0.119$ ,  $P = 1.86$ ).

## Discussion

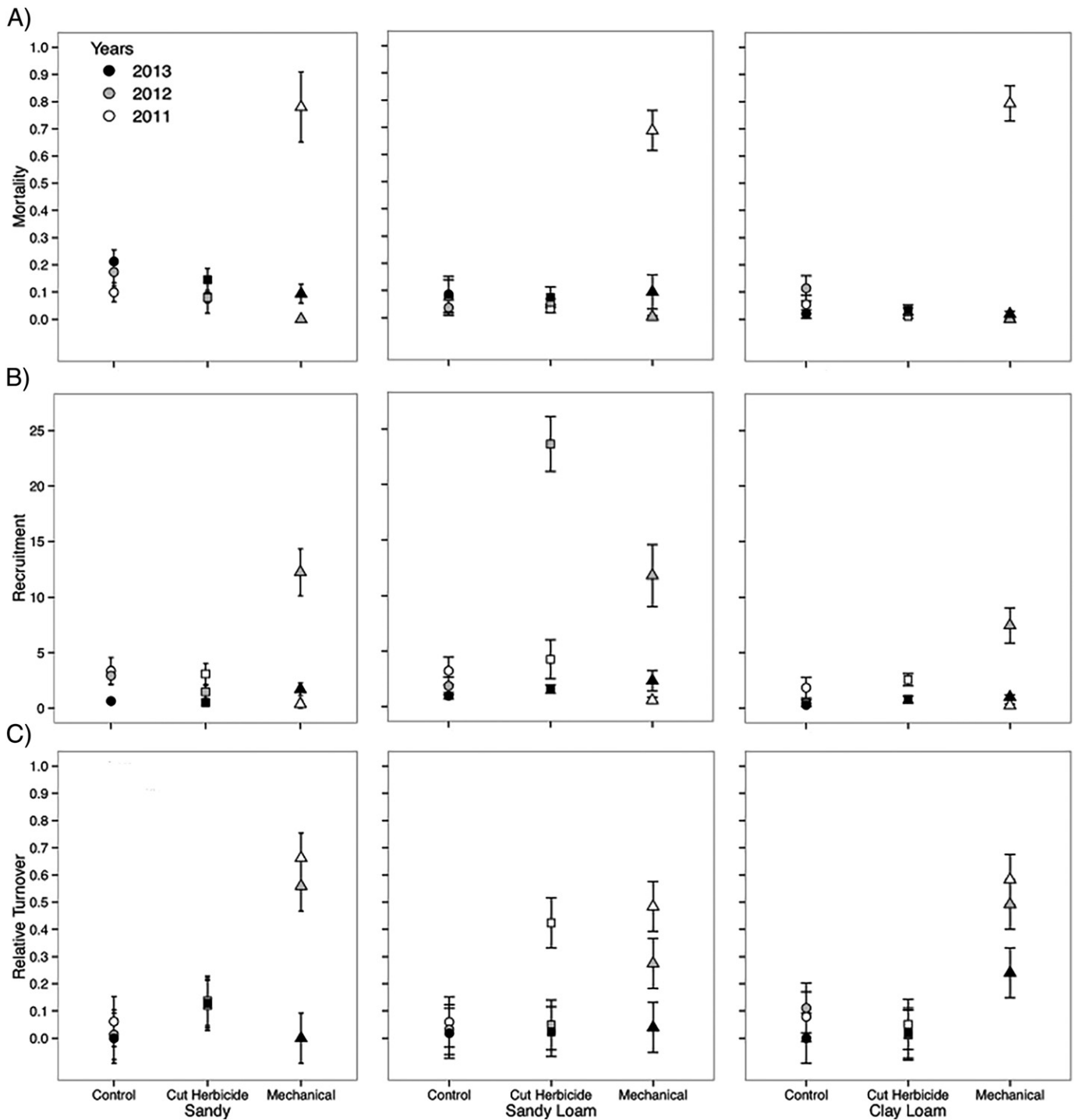
The results of this study showed differential perennial grass mortality, species turnover, and grass community composition shifts among core rangeland restoration treatments and across soils. Woody plants compete with the herbaceous understory in mixed woody-herbaceous systems for essential resources such as light, nutrients, and water (Smit and Rethman, 2000). As a result, grass abundance is frequently increased by removing brush in previously encroached rangelands (Ansley et al., 2004; Throop and Archer, 2007). However, as our study shows, grass community response to release from competition with shrubs is not static but rather varies depending on brush removal method employed, postremoval conditions, and underlying biotic and abiotic characteristics of the system (Morton and Melgoza, 1991; Scholes and Archer, 1997; McClaran and Angell, 2006). The effects of increased soil resource availability on the herbaceous community following brush removal are mediated by the physiology of the individual species present as they interact with one another and with the abiotic environment (Scholes and Archer, 1997; Bestelmeyer et al., 2006; McClaran and Angell, 2006). This study shows high grass mortality in mechanically treated plots where intense soil disturbance, evidenced by high cover of bare ground immediately following disturbance, caused direct damage to perennial grasses. High perennial grass mortality following woody brush removal has been shown in other studies to be the result of fast growth of tuft grasses increasing tuft mortality rates due to an increase in density, which increases grass competition (Zimmermann et al., 2015). This is not likely the case in our study, however, given that chemical treatment did not increase grass mortality and only the direct disturbance effect of mechanical clearing led to high mortality rates.

Fire resulted in levels of mortality similar to baseline mortality in control plots for all soil types. The low-intensity fires conducted in this study are typical of the majority of prescribed fires used in rangelands (Twidwell et al., 2016), so the results of this study provide evidence that counters fire-related grass mortality concerns and the subsequent preference for mechanical or chemical options in rangeland restoration.

**Table 2**

Repeated measures analysis of variance results of tests for differences in mortality, recruitment, and turnover in response to different brush removal treatments on different soil types for all 4 yr of the study (2010–2013)

	Sum Sq	Mean Sq	NumDF	DenDF	F value	P
<b>Mortality</b>						
Treatment	1.43	0.72	2	133	56.43	< 0.001
Soil	0.06	0.03	2	133	2.24	0.110
Yr	1.78	0.89	2	133	70.26	< 0.001
Treatment:Soil	0.04	0.01	4	133	0.70	0.591
Treatment:Yr	4.49	1.12	4	133	88.51	< 0.001
Soil:Yr	0.06	0.01	4	133	1.16	0.330
Treatment:Soil:Yr	0.07	0.01	8	133	0.66	0.729
<b>Recruitment</b>						
Treatment	225	112.5	2	133	0.94	0.396
Soil	432	215.9	2	133	1.81	0.167
Yr	1054	527.1	2	133	4.42	0.014
Treatment:Soil	480	120.1	4	133	1.01	0.406
Treatment:Yr	634	158.4	4	133	1.33	0.262
Soil:Yr	469	117.3	4	133	0.98	0.419
Treatment:Soil:Yr	798	99.7	8	133	0.84	0.572
<b>Turnover</b>						
Treatment	3.30	1.65	2	133	43.19	< 0.001
Soil	0.02	0.01	2	133	0.23	0.793
Yr	1.42	0.71	2	133	18.63	< 0.001
Treatment:Soil	0.47	0.12	4	133	3.06	0.019
Treatment:Yr	1.08	0.27	4	133	7.06	< 0.001
Soil:Yr	0.21	0.05	4	133	1.36	0.253
Treatment:Soil:Yr	0.45	0.05	8	133	1.49	0.168



**Figure 4.** Mortality, recruitment, and relative species turnover (measured as the sum of the number of species unique to time  $t$  plus the number of species unique to time  $t + 1$  divided by total number of species in time  $t$  + total number of species in time  $t + 1$ ) (mean  $\pm$  SE) in response to different methods of brush removal (control, cut herbicide, and mechanical) on three different soil types: sandy, sandy loam, and clay loam 1 (white), 2 (gray), and 3 (black) yr following treatment (2011, 2012, and 2013, respectively).

One study conducted in Namibia has shown higher mortality of perennial grasses immediately following fire, but fire ultimately lowered overall mortality in the long term by reducing self-shading and competition among grasses (Zimmermann et al., 2010). Experimental studies that explore the range of responses possible in more extreme conditions are generally lacking (Twidwell et al., 2016). While low-intensity fires were not effective at reducing resprouting shrub cover (Wonkka et al., 2016), extreme fire during drought has been shown to be effective at causing mortality of resprouting shrubs (Twidwell et al., 2016). Similar experimental manipulations are needed in more extreme conditions

that quantify survival, life expectancy, and life span of grass species while accounting for complex responses relevant to rangeland managers, such as the adaptive capacity of rangeland communities and their resilience to extreme events.

While high levels of mortality occurred following mechanical treatment in all soil textures, responses in recruitment, relative species turnover, and community composition varied among soil textures. This is likely the result of an interaction between the magnitude of soil disturbance, which often varies with soil texture (Pinard et al., 2000) and individual tolerances of the species present on the different soils to

**Table 3**

Permutational multivariate analysis of variance results of tests for differences in grass communities resulting from different brush removal treatments (chemical, mechanical, and control) on different soils (sandy, sandy loam, and clay loam) in 2010 (representing pretreatment conditions) through 2013

	Df	Sums Sq	Mean Sq	F-value	R <sup>2</sup>	P
Treatment	2	1.68	0.84	3.63	0.02	< 0.001
Soil	2	16.30	8.15	35.21	0.24	< 0.001
Yr	1	0.97	0.97	4.17	0.01	0.002
Treatment:Soil	4	2.96	0.74	3.20	0.04	< 0.001
Treatment:Yr	2	0.47	0.24	1.02	0.01	0.410
Soil:Yr	2	0.51	0.25	1.10	0.01	0.316
Treatment:Soil:Yr	4	0.57	0.14	0.62	0.01	0.963
Residuals	198	45.83	0.23		0.66	
Total	215	69.28			1.00	

disturbance (Scholes, 1990; Buonopane et al., 2005). Recruitment was high in sandy soils following mechanical treatment, but not chemical. However, relative species turnover was also high for this treatment on sandy soils, suggesting previously abundant grasses were being replaced on these soils following treatment. This finding was corroborated by the ordination which showed community trajectories following disturbance on sandy soils diverged, with new species replacing the individuals killed by the mechanical treatment more often than on the other soils. The shift in species composition on mechanically treated sandy soils was driven by increases in *Heteropogon Contortus*, *Cenchrus spinifex*, and *Eragrostis barrelieri*. This shift in dominance was pronounced on sandy soils because soil disturbance from mechanical treatments was more intense on these soils. This is evidenced by an increase in bare ground of almost 60% on average following mechanical treatment on sandy soils, while bare ground on sandy loam and clay soils increased by only 19% and 6%, respectively. We also observed a distinct dune pattern suggesting the rolling drum employed in the mechanical treatment resulted in soil churning. We also observed many uprooted grasses following mechanical treatment on sandy soils, which was not evident in other soils, suggesting that the loose soil formation of sandy soils resulted in greater disturbance on these soils, while the soil aggregates in clay loam and sandy loam soils provided more stability to soil structure during treatment with heavy mechanical equipment (Bronick and Lal, 2005). This is consistent with other studies that

**Table 4**

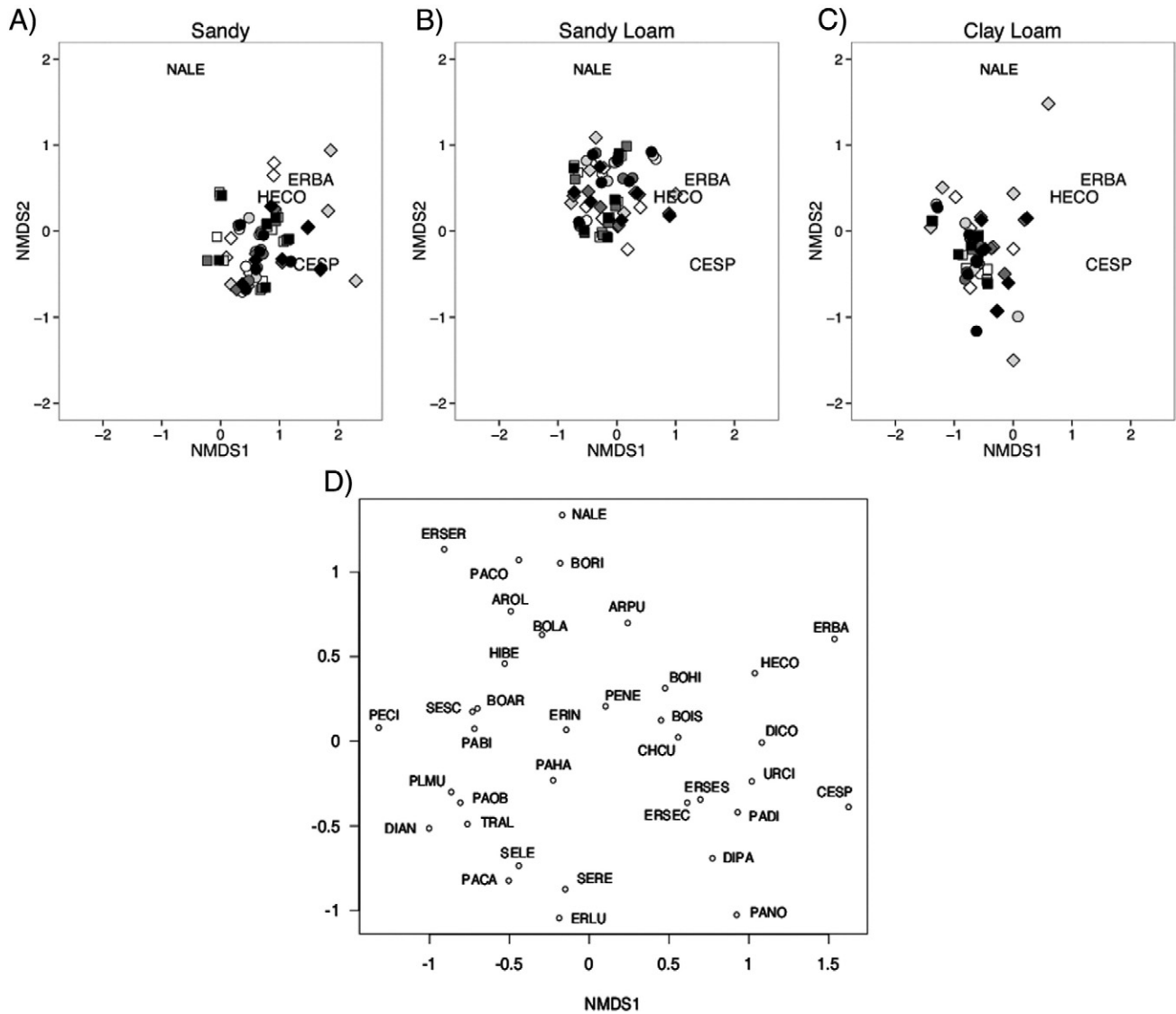
Multiple comparisons for significant main effects and interactions resulting from a permutational multivariate analysis of variance results of tests for differences in grass communities resulting from different brush removal treatments (chemical, mechanical, and control) on different soils (sandy, sandy loam, and clay loam) in 2010 (representing pretreatment conditions) through 2013. *P* values are corrected with a Bonferroni method to control the familywise error rate given the large number of multiple comparisons explored

Comparison	Df	Sums sq	Mean sq	F value	R <sup>2</sup>	P
<b>Yr</b>						
2010 vs. 2011	1	0.55	0.55	1.73	0.02	1.000
2010 vs. 2012	1	0.33	0.33	1.12	0.01	1.000
2010 vs. 2013	1	0.90	0.90	3.01	0.03	0.030
2011 vs. 2012	1	0.38	0.38	1.14	0.01	1.000
2011 vs. 2013	1	0.88	0.88	2.60	0.02	0.165
2012 vs. 2013	1	0.26	0.26	0.82	0.01	1.000
<b>Treatment:Soil</b>						
<b>Sandy:</b>						
Control vs. Chemical	1	0.79	0.79	3.85	0.08	0.030
Control vs. Mechanical	1	1.12	1.12	4.80	0.09	0.015
Mechanical vs. Chemical	1	0.75	0.75	2.77	0.06	0.165
<b>Sandy Loam:</b>						
Control vs. Chemical	1	0.58	0.58	2.94	0.06	0.030
Control vs. Mechanical	1	0.46	0.46	1.90	0.04	0.899
Mechanical vs. Chemical	1	0.61	0.61	2.67	0.05	0.135
<b>Clay Loam:</b>						
Control vs. Chemical	1	0.78	0.78	3.63	0.07	0.075
Control vs. Mechanical	1	0.69	0.69	2.64	0.05	0.225
Mechanical vs. Chemical	1	1.13	1.13	4.74	0.09	0.015

showed the extent of soil disturbance from mechanical equipment to be greater on coarser soils (Jusoff and Majid, 1992; Pinard et al., 2000). While competitive environments are altered by all levels of disturbance (Grime, 1977; Huston, 1979), patches of disturbed soil interspersed among patches of established individuals create a more favorable environment for perennial species, as they can spread vegetatively or through seed from the established patches into adjacent disturbed sites where there is little competition for the new individual (Paine and Levin, 1981). In the mechanically treated sandy soils of this study, however, high levels of bare ground with few established individuals remaining to spread into the newly available habitat tended to favor “weedy” species such as *Heteropogon Contortus*, *Cenchrus spinifex*, and *Eragrostis barrelieri* because they readily establish in disturbed areas where there is little competition from established individuals.

The competitive advantage of *Heteropogon Contortus*, *Cenchrus spinifex*, and *Eragrostis barrelieri* over longer-lived perennial species is also likely related to the lower water-holding capacity of coarse sandy soils, which favors plants that can react quickly to biologically available water (Hamerlynck et al., 2002; Huxman et al., 2005). These species were able to replace previously dominant long-lived perennial grasses because of a trade-off among life history strategies with long-lived plant species lacking traits necessary for rapid recolonization following disturbance (Crawley and Ross, 1990; Grime, 2007a, b). Annual species, such as *Eragrostis barrelieri*, have high reproductive output and high allocation of resources to rapid growth, allowing them to respond quickly and efficiently to resource availability and reduced competition following high levels of disturbance (Grime, 1977). Similarly, while *Heteropogon contortus* and *Cenchrus spinifex* are both perennial species, *Heteropogon* has been found to readily establish in disturbed areas by taking advantage of episodically favorable precipitation conditions and diminished competition (Dye and Walker, 1987). *Cenchrus* is a short-lived perennial that is self-compatible and therefore capable of high reproductive output (Liebman et al., 2001). It is considered a “weedy” species that colonizes quickly in disturbed areas, especially on sandy soils (Matocha et al., 2010). Increases in these species comport with findings in other brush removal studies of shifts to dominance of “increaser” species, or species adapted to take advantage of conditions created by brush removal (Bedunah and Sosebee, 1984; Angassa, 2002; Angassa and Oba, 2009; DeMaso et al., 2013). Community shifts can be transient, however. It is difficult to know whether the shift to annual and “weedy” perennial species will persist, and it can be highly dependent on soils and postdisturbance conditions such as rainfall patterns or grazing pressure. For instance, in a long-term mesquite removal study at the Santa Rita Experimental Range, a shift in dominance to *Aristida* spp. following mesquite removal persisted long after mesquite regained preremoval cover, but only in areas with sufficient precipitation (McClaran and Angell, 2006), while in more arid areas of the study, compositional shifts were short-lived (Browning et al., 2008).

Recruitment was also high on intermediate-textured soils in this study, but relative species turnover was lower, suggesting that despite high mortality following mechanical brush removal, the grass community on this soil type recovered quickly following the release from competition with woody brush and was not replaced with new species following mechanical disturbance. In fact, intermediate sandy loam soils also had the highest levels of recruitment on chemically treated plots and high levels of recruitment on mechanically treated plots as well, suggesting the species present on this soil type were able to exploit increased resource availability following brush removal. *Hilaria belangeri* and *Urochloa ciliatissima* were both abundant on sandy loam soils before and after brush removal, driving recruitment on sandy loam soils. These grasses exhibit a rhizomatous growth form that can more quickly colonize disturbed areas through vegetative spread than cespitose species that rely on sexual reproduction and establishment via seed (Mack et al., 1989; Skarpe, 2001). These species likely replaced some of the nonrhizomatous grasses present in these plots before treatment. However, the ordination shows little shift in community



**Figure 5.** Nonmetric multidimensional scaling of the grass community for yr 2010 (pretreatment) through 2013. Treatment and years are coded as follows: Shapes represent brush removal treatments of control (circles), cut herbicide (squares), and mechanical (diamonds); Colors represent yr 2013 (black), 2012 (dark gray), 2011 (light gray), and pretreatment 2010 (white). **A–C,** Site scores for sandy, sandy loam, and clay loam, respectively. **D,** Species scores.

composition for any treatment on sandy loam soils, suggesting that these grasses were abundant before treatment was initiated. A shift in relative abundance for one of the treatments would have manifested as a shift in ordination space for that treatment relative to control and pretreatment plots.

Mechanically treated plots on clay loam soils had the lowest levels of recruitment and, as a result, high relative species turnover. The ordination shows a slight shift in some of the mechanically treated plots on clay loam soils, but not nearly as pronounced as that observed for sandy soils, suggesting that the relative species turnover is driven by a lack of replacement of species present before treatment rather than replacement by different species. The slight shift in ordination in the first year following mechanical treatment is driven by *Nassella leucotricha*, which has been shown to increase in this area following mechanical brush removal (Powell and Box, 1967; Rollins and Bryant, 1986) and likely increased in dominance relative to other species, explaining the shift in ordination space with no accompanying large increase in relative species turnover for 2011.

Previous studies have shown that species turnover differs with scale of inquiry. Turnover is found to be higher at smaller scales, with response to disturbance more stable at broader scales (van der Maarel

and Sykes, 1993; Plotkin et al., 2000; Ulrich and Buszko, 2003; Bossuyt and Hermy, 2004). The results of this study suggest that variation in species turnover on soils of differing textures likely contributes to these differences in turnover with respect to scale. This is consistent with findings that plant species turnover is highly dependent on local biotic and abiotic conditions (van der Maarel and Sykes, 1993; Holt et al., 1995). Thus as heterogeneity of conditions increases with scale, localized high rates of turnover are offset by lower rates elsewhere in the landscape.

### Management Implications

Understanding the potential effects of management actions on mortality and turnover of perennial grass species and the potential for those actions to lead to a community shift toward less desirable species is necessary for managers to achieve restoration goals in woody brush—encroached semiarid rangelands. Interventions that lead to high levels of soil disturbance can cause high levels of perennial grass mortality and lead to higher likelihood of community compositional shifts depending on the specific propagules available for colonization and post-treatment climatic conditions (Pacala et al., 1996; Laurance

et al., 2006). Managers should therefore be cautious in applying mechanical treatments, especially on sandy soils that experience more intense disturbance from heavy machinery than fine-textured soils. Historically, managers debated the use of fire as a rangeland management tool due to concerns regarding excessive perennial grass mortality following prescribed fire (Wright and Klemmedson, 1965; Wright, 1982; Johnson and Strang, 1983). The same concerns have not been expressed regarding the use of chemical and mechanical brush control methods in encroached rangelands (Kreuter et al., 2001; McGinty and Ueckert, 2001; Hamilton, 2004). The findings of this study show that perennial grass mortality is higher following mechanical brush control than fire. In fact, levels of mortality from fire were similar to baseline mortality in control plots. This finding is supported by a long-term study in a similar system, which found that even high-intensity fire conducted during drought when perennial grasses were already experiencing stress did not result in the loss of desirable forage species from the system (Taylor et al., 2011).

A more complete understanding of the effects of core rangeland restoration techniques might provide incentive for managers to use the most effective and efficient methods for brush management and removal rather than basing management on inaccurate perceptions of the potential for different management interventions to cause perennial grass mortality and community compositional shifts. Fire should also be weighed against other brush management tools on the basis of its

importance to the maintenance of the grass layer itself. Fire removes senescent standing grass litter, reducing potential negative effects of accumulated dead plant biomass on grass productivity. This positive effect can outweigh immediate negative effects of direct grass mortality from fire (Moloney, 1990; Snyman, 2004; Zimmermann et al., 2015). In addition, studies such as this one that elucidate the potential for different trajectories of change following brush removal in communities with different baseline biotic and abiotic conditions provide valuable information for the development of frameworks that can be applied on the landscape to effectively manage brush encroached rangelands.

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## Appendix. Mortality (individuals/year/treatment) for each perennial grass species present in subplots averaged across replicates for each treatment

Code	Species	Functional group <sup>1</sup>	Scientific name	Mortality										
				Sandy			Sandy loam			Clay loam				
				Control	Chem.	Mech.	Control	Chem.	Mech.	Control	Chem.	Mech.		
AROL	Oldfield threeawn	A	<i>Aristida oligantha</i>											
ARPU	Purple threeawn	P	<i>Aristida purpurea</i>	0.03	0.07	0.20	0	0	0.23	0.00	0.00	0.00		
BOAR	Needle grama	A	<i>Bouteloua aristidoides</i>											
BOHI	Hairy grama	P	<i>Bouteloua hirsuta</i>	0.03	0.10	0.10	0.07	0.07	0.23	0.04	0.03	0.07		
BOIS	King Ranch bluestem	PI	<i>Bothriochloa ischaemum</i> var. <i>songarica</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
BOLA	Silver bluestem	P	<i>Bothriochloa laguroides</i>	0.00	0.00	0.00	0.03	0	0	0.00	0.00	0.00		
BORI	Texas grama	P	<i>Bouteloua rigidiseta</i> var. <i>rigidiseta</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
CESP	Sandbur	P	<i>Cenchrus spinifex</i>	0.00	0.10	0.13	0	0	0.07	0.00	0.00	0.00		
CHCU	Hooded windmill	P	<i>Chloris cucullata</i>	0.03	0.07	0.30	0	0.04	0.17	0.00	0.03	0.07		
DIAN	Kleburgs bluestem	PI	<i>Dichanthium annulatum</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
DICO	Fall witchgrass	P	<i>Digitaria cognata</i>	0.00	0.00	0.30	0	0	0	0.00	0.00	0.00		
DIPA	Texas cottontop	P	<i>Digitaria patens</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
ERBA	Mediterranean lovegrass	AI	<i>Eragrostis barrelieri</i>											
ERIN	Plains lovegrass	P	<i>Eragrostis intermedia</i>	0.00	0.00	0.00	0	0	0.07	0.00	0.00	0.00		
ERLU	Mourning lovegrass	P	<i>Eragrostis lugens</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
ERSEC	Red lovegrass	P	<i>Eragrostis secundiflora</i>	0.00	0.00	0.03	0	0	0	0.00	0.00	0.00		
ERSER	Texas cupgrass	P	<i>Eriochloa sericea</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
ERSES	Tumble lovegrass	P	<i>Eragrostis sessilispa</i>	0.07	0.00	0.20	0	0.04	0.07	0.00	0.00	0.00		
HECO	Tanglehead	P	<i>Heteropogon contortus</i>	0.07	0.03	0.03	0	0	0.07	0.00	0.00	0.00		
HIBE	Curly mesquite	PR	<i>Hilaria belangeri</i>	0.03	0.03	0.00	0.03	0.11	0.33	0.00	0.00	0.40		
NALE	Texas wintergrass	P	<i>Nassella leucotricha</i>	0.00	0.00	0.00	0.03	0	0	0.00	0.00	0.00		
PABI	Pink papasgrass	P	<i>Pappophorum bicolor</i>	0.00	0.07	0.20	0	0.07	0.67	0.04	0.00	0.47		
PACA	Canary grass	AC	<i>Phalaris caroliniana</i>											
PACO	Kleingrass	P	<i>Panicum coloratum</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
PADI	Dallis grass	PI	<i>Paspalum dilatatum</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
PAHA	Halls panic	P	<i>Panicum hallii</i> var. <i>hallii</i>	0.00	0.03	0.17	0.07	0	0.07	0.00	0.00	0.00		
PANO	Bahia grass	PR	<i>Paspalum notatum</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
PAOB	Vine mesquite	PR	<i>Panicum obtusum</i>	0.00	0.00	0.03	0	0	0	0.00	0.00	0.00		
PECI	Buffel grass	PI	<i>Pennisetum ciliare</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
PENE	Bentspike bristlegrass	PI	<i>Pennisetum nervosum</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
PLMU	Tobosa	PR	<i>Pleuraphis mutica</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
SELE	Plains bristlegrass	P	<i>Setaria leucopila</i>	0.03	0.10	0.43	0	0.07	0.17	0.08	0.00	0.43		
SERE	Reverchon bristlegrass	P	<i>Setaria reverchonii</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
SESC	Southwestern bristlegrass	P	<i>Setaria scheelei</i>	0.00	0.00	0.00	0	0	0.03	0.00	0.00	0.07		
TRAL	White tridens	P	<i>Tridens albescens</i>	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00		
URCI	Fringed signalgrass	PR	<i>Urochloa ciliatissima</i>	0.13	0.03	0.27	0.03	0	0.27	0.00	0.00	0.03		

<sup>1</sup> Functional group indicates perennial warm season tufted native bunchgrass; A, annual; P, perennial; PI, perennial warm season tufted introduced bunchgrass; AI, annual introduced; PR, perennial warm season native rhizomatous; AC, annual cool season.

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