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RESEARCH ARTICLE

# Long-term plant community trajectories suggest divergent responses of native and non-native perennials and annuals to vegetation removal and seeding treatments

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**Land managers frequently apply vegetation removal and seeding treatments to restore ecosystem function following woody plant encroachment, invasive species spread, and wildfire. However, the long-term outcome of these treatments is unclear due to a lack of widespread monitoring. We quantified how vegetation removal (via wildfire or management) with or without seeding and environmental conditions related to plant community composition change over time in 491 sites across the intermountain western United States. Most community metrics took over 10 years to reach baseline conditions posttreatment, with the slowest recovery observed for native perennial cover. Total cover was initially higher in sites with seeding after vegetation removal than sites with vegetation removal alone, but increased faster in sites with vegetation removal only. Seeding after vegetation removal was associated with rapidly increasing non-native perennial cover and decreasing non-native annual cover. Native perennial cover increased in vegetation removal sites irrespective of seeding and was suppressed by increasing non-native perennial cover. Seeding was associated with higher non-native richness across the monitoring period as well as initially higher, then declining, total and native species richness. Several cover and richness recovery metrics were positively associated with mean annual precipitation and negatively associated with mean annual temperature, whereas relationships with weather extremes depended on the lag time and season. Our results suggest that key plant groups, such as native perennials and non-native annuals, respond to restoration treatments at divergent timescales and with different sensitivities to climate and weather variation.**

**Key words:** climate variability, Intermountain West, rehabilitation, restoration, vegetation management, wildfire

### Implications for Practice

- Short-term monitoring (<10 years) following vegetation removal and seeding can underestimate the potential for long-term recovery of native perennial cover and the suppressive effect of seeding on non-native annual cover.
- Seeding non-native perennial grasses after vegetation removal can accelerate the recovery of total vegetation cover but may also lead to lower native perennial cover.
- Decisions about when and where to conduct vegetation removal and seeding treatments, and expectations for recovery rate, could be informed by including the effects of climate and weather variability on the treatment responses of key plant groups, such as native and non-native perennials and non-native annuals.

## Introduction

Vegetation removal and seeding treatments are broadly applied across the intermountain western United States (Redmond et al. 2014; Pilliod et al. 2017; Copeland et al. 2018); however, their effects on plant communities remain unclear due to relatively scarce monitoring efforts (U.S. General Accounting Office 2003), particularly over long timescales. Long-term assessments of the impact of vegetation management actions on plant communities are needed to understand their effects on ecosystem function, diversity, and resilience. Characterizing

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the impacts of treatments is particularly important given predictions for increasing wildfire (Abatzoglou & Kolden 2011) and drought associated with climate change (Cook et al. 2015) in the western United States, which are likely to amplify the need for restoration.

The need to understand the potential for enduring impacts of common management practices on plant community characteristics is underscored by the extensive areas treated for multiple resource management objectives across major woodland and shrubland types in the western United States. Since 1940, at least 3.76 million hectares have been treated across the Great Basin (Pilliod et al. 2017) and 1.97 million hectares in the warm deserts and Colorado Plateau (Copeland et al. 2018) on Bureau of Land Management lands alone. Vegetation management actions in the intermountain western United States frequently target multiple objectives including increasing the abundance of forage plant species for livestock or wildlife, decreasing wildfire risk and invasive species abundance, and reducing soil erosion (Peppin et al. 2014; Copeland et al. 2018). Common overstory woody species (i.e. juniper subsp., *Juniperus* spp., and big sagebrush, *Artemisia tridentata subsp.*) are frequently removed with prescribed fire or various mechanical treatments to reduce competition for light, soil moisture, and nutrients and thereby encourage the growth of herbaceous species. Seeding treatments are often applied to increase forage cover and reduce erosion following wildfire (Beyers 2004), or woody species removal (Pilliod et al. 2017). Managers commonly choose to seed non-native perennial species in tandem with perennial natives (Pilliod et al. 2017; Copeland et al. 2018) due to the relatively high cost of native species and the effectiveness of seeded non-native perennial species in outcompeting non-native annuals, providing forage, and decreasing erosion (Gornish et al. 2016).

Restoration practices such as overstory vegetation removal or seeding can have divergent impacts on major groups (native vs. non-native, annual vs. perennial) of species within the plant community. Seeding non-native perennial grasses may reduce the abundance of annual invasive species by increasing competition for space (Ott et al. 2003; Davies et al. 2010). However, successful seeding of non-native perennial grasses can lead to their persistence in high abundance (Ambrose & Wilson 2003), which tends to depress cover and diversity of perennial native species (Heidinga & Wilson 2002; Munson & Lauenroth 2012; Nafus et al. 2015). Seeded non-native perennial grasses can also be difficult to remove and may create barriers to establishment of native grasses in subsequent seeding efforts (Hulet et al. 2010). If either vegetation removal or seeding treatments cause a decrease in species or functional group richness, the resulting plant communities may become less resilient to disturbance or climate variation (Johnson et al. 1996). In addition, mechanical disturbance of the soil surface that often accompanies seeding or vegetation removal can lead to soil erosion due to reduced plant cover and loss of soil stabilization, particularly in arid regions (Duniway et al. 2015).

While overstory woody vegetation (tree and shrub) removal and seeding are expected to generally increase the cover and richness of understory species, the magnitude and direction of these changes may vary due to site climate and extreme weather (Fig. 1). Time since vegetation treatment is also an important factor, especially because slow-growing perennial species in the western United States may have a lag in their response to both climate trends or weather extremes and vegetation management actions (Anderson & Inouye 2001; Brookshire & Weaver 2015). This suggests that short-term changes following treatments may not parallel long-term outcomes. Characterizing the effects of vegetation management actions on plant community composition requires recognizing the influence of both weather extremes around the time of treatment or monitoring and site factors such as average climatic conditions. Weather variation is likely to alter vegetation recovery by affecting germination and seedling establishment from natural seed banks or seeding treatments (Bakker et al. 2003; Shriver et al. 2018). Drought stress resulting from combinations of high temperatures and low precipitation surrounding the management treatment or wildfire recovery period may temporarily reduce vegetative recovery or lead to more lasting effects (Nafus et al. 2016; Groves & Brudvig 2019). Short-term weather following treatments can also significantly affect successional trajectories by influencing competitive dynamics and relative success of seeded species (Bakker et al. 2003; Munson & Lauenroth 2014).

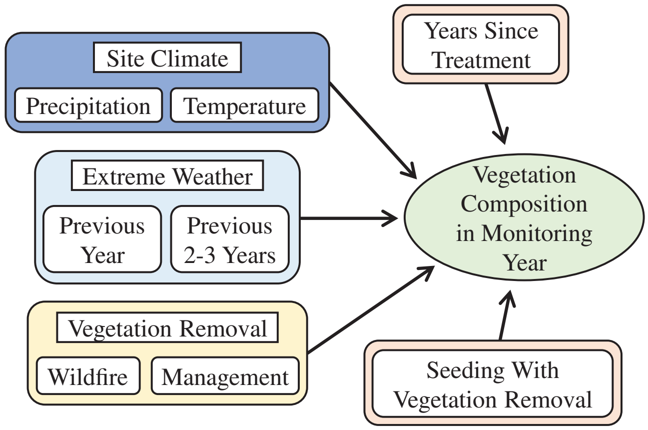

Figure 1. Conceptual diagram indicating how vegetation composition in each monitoring year can be related to site climate, extreme weather relative to the monitoring year, vegetation removal and/or seeding, and time since treatment.

Here, our goal was to determine how vegetation removal associated with management or wildfire with or without seeding affected differential patterns in long-term (20–year) recovery of major components of shrubland and woodland understory plant community composition in the intermountain western United States. We considered how plant community change was associated with temporal variation in weather extremes as well as site average climate conditions. We tested for trends in plant community metrics related to management goals: total plant cover and richness, cover of native and non-native perennials and non-native annuals, richness of non-native species and native perennials, and community turnover. We expected overstory vegetation removal to initially decrease plant cover and species richness and elevate community turnover compared to sites without removal. These expectations were based on wildfire and mechanical overstory vegetation removal generally decreasing vegetative cover across most species groups initially, leading to lower species richness and altering the relative abundance of some species or groups. As plant communities recovered over time, we expected that vegetation cover and species richness would increase, and turnover decrease, in sites with vegetation removal compared to sites without vegetation removal (Ott et al. 2003; Redmond et al. 2013). Recognizing the potential for seeding to accelerate vegetation recovery, we expected that seeding in conjunction with vegetation removal would lead to a smaller initial drop and faster increase in diversity and cover of perennials and lower cover of non-native annuals (due to competition) than in sites with vegetative removal alone. Finally, we predicted that change in plant community composition over time would be associated with extreme weather and/or site climate variables, such as temperature and precipitation, associated with plant establishment and growth rates in this relatively dry region.

## Methods

### Vegetation Monitoring Data

We compiled vegetation cover data from 491 sites (2,058 visits) monitored between 1992 and 2017 with and without vegetation management actions from the Utah Big Game Range Trends Studies database, hereafter “range trends” (Fig. 2, Utah Division of Wildlife Resources 2017). Range trends sites are primarily located in woodlands and shrublands identified as important big game habitat across all of the major ecoregions in Utah (Fig. 2) and include sites established to monitor vegetation management treatments partially funded by the state of Utah (Watershed Restoration Initiative 2018). Treatment types include a range of methods for vegetation removal through management actions, as well as vegetation removal via wildfire, which may or may not be accompanied by seeding treatments. Major objectives of vegetation management treatments (either removal or seeding) include increasing forage for wildlife and livestock and reducing cover of non-native annuals. Site mean annual temperatures range from 3.2 to 16.2°C (mean 7.9°C), mean annual precipitation from 229 to 710 mm (mean 403 mm, October 1986–September 2017, PRISM Climate Group 2017), and elevations range from 1,301 to 3,048 m (mean 2,058 m). At each site, five 30.5 m lines were set perpendicular at pre-determined random distances to a 152.4 m transect. Along each line, understory vegetative cover by species was measured within each of 20 equally spaced 25 × 25–cm plots, for a total of 100 plots per site once during the growing season (May–September, variable by site).

We narrowed the pool of potential sites to those with similar environmental conditions by removing sites from the non-vegetation removal category that fell outside of the climate space (defined by mean annual temperature and precipitation) occupied by sites in the vegetation removal category (Figs. S1–S3, Supporting Information). The resulting selected sites were classified into one of three categories: vegetation removal via management actions or wildfire alone (42 sites),

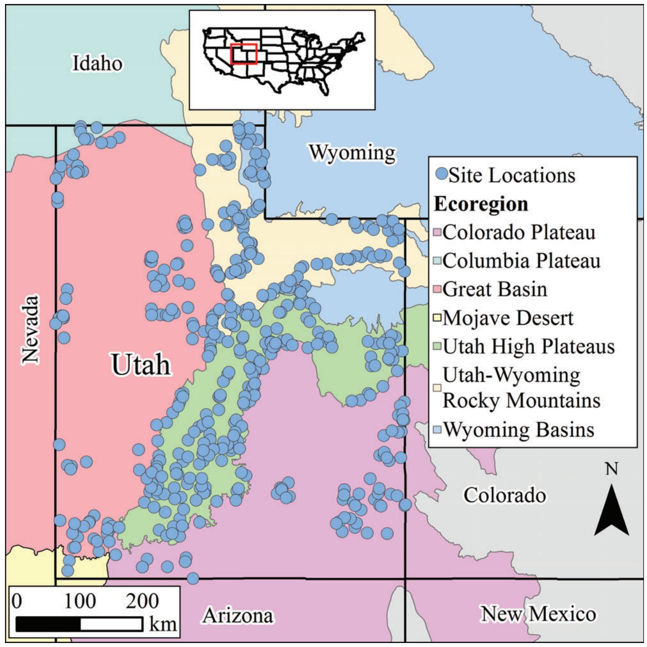


Figure 2. Study site locations in Utah by ecoregion (Omernik & Griffith 2014).

vegetation removal with seeding (75 sites), and sites without recent vegetation removal or seeding (374 sites, details on treatments in Appendix S1; baseline vegetation characteristics, Figs. S4 & S5). Only sites where vegetation removal and seeding occurred within 5 years of the first monitoring date were included in those respective categories.

Among the final group of sites chosen for this study, most occur in pinyon-juniper woodland (264 sites), deciduous shrubland (47 sites), or big sagebrush shrubland and steppe (45 sites) according to their potential vegetation type (LANDFIRE 2012). The most common overstory tree species (>5% of the total nonseedling density) for the selected range trends sites at the beginning of the monitoring period (or prevegetation removal) were Utah juniper (*Juniperus osteosperma*, 136 sites) and two-needle pinyon (*Pinus edulis*, 59 sites). The most common shrub species (>10% of the total non-seedling density) were big sagebrush (mountain, *Artemisia tridentata* ssp. *vaseyana*, 217 sites or Wyoming, ssp. *wyomingensis*, 112 sites), snakeweed (*Gutierrezia sarothrae*, 176 sites), and yellow rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus*, 109 sites, see Appendix S2). Median cover within the selected sites at the beginning of monitoring was dominated by native shrubs (16.0%), followed by native perennial grasses (5.7%), native trees (2.6%), and native perennial forbs (2.0%, see Table S1 for the most common species within each group).

### Compiling Plant Community Variables

The baseline monitoring date for change calculations was selected for each site either up to 5 years prior to vegetation removal and seeding or the first monitoring date for sites without recent vegetation removal or seeding. All analyses were restricted to sites with a minimum of three monitoring visits and at least 10 years of postbaseline monitoring measurements. Monitoring data were also restricted to a 20-year period per site due to the limited number of measurements beyond 20 years.

We aggregated mean cover values and species richness (species number) into site total and group values based on species lifespan (annual, perennial) and origin (native, non-native, for the continental United States) according to the PLANTS database (USDA NRCS 2016). For cover and richness variables we calculated change as the difference from the baseline sampling date. Our variables were change in total cover, annual non-native cover, perennial non-native cover, perennial native cover, total richness, non-native richness, and perennial native richness. We did not include native annual cover or richness nor did we separate out non-native perennial from non-native annual richness as these community components were relatively minor at most sites. We estimated community turnover with Bray–Curtis dissimilarity (R vegan package, Oksanen et al. 2017), a metric which includes both abundance and species identity, as well as the proportion of species that appeared and disappeared between time intervals (R codyn package, Hallett et al. 2016).

### Climate and Weather Variables

For potential covariates in statistical models, we extracted mean annual precipitation and temperature for each monitoring site (October 1986–September 2017, 4 km resolution, PRISM Climate Group 2017). We calculated standardized anomalies for precipitation and temperature, a measure of extremes uncorrelated with climate means, and defined as the difference between short-term (variable, defined below) and long-term (1986–2017) climate divided by the long-term standard deviation for each climate variable (equation in Appendix S3, Wilks 2011). Since the influence of climate extremes could vary by time interval prior to sampling and season, we calculated standardized anomalies for two time intervals and two seasons. We calculated cool season (October–March) anomalies for the year prior to sampling and the mean of anomalies for 2–3 years prior to sampling. We calculated warm season (April–September) anomalies just prior to sampling with growing season period based on the sampling date for that site and year (see Appendix S3 for details) as well as for the 2- to 3-year period prior to sampling.

### Statistical Analysis

We followed a sequence of steps to arrive at a set of predictor variables and model structure for each response variable. First, we considered climate and weather variables that were significantly correlated with each response variable using nonparametric Kendall's rank correlation tests (Murray & Conner 2009) and adjusted $p$ values for multiple correlation tests (false discovery rate procedure, Benjamini & Hochberg 1995).

Second, we narrowed each set of predictor variables further by using hierarchical partitioning, a method to evaluate the importance of environmental variables in the presence of multicollinearity (R hier.part package, simulation $n = 500$, Chevan & Sutherland 1991). We also included three nonenvironmental variables as candidate predictor variables in model selection for all response variables: category of vegetation removal or seeding, years since the baseline year used to calculate cover change, and region of Utah (important component of sampling protocol because all sites in each of the five regions were typically measured in the same year). We included an interaction between the category of vegetation removal or seeding and year since baseline in candidate models to address the question of whether vegetation removal with or without seeding affected change in the community response variable over time. To determine if the trend in plant community change was nonlinear, we also tested if inclusion of a quadratic term led to a better model fit. We included change in non-native cover relative to the baseline year as a candidate predictor in models for native perennial cover and richness to test for potential competitive interactions between the two groups (e.g. Nafus et al. 2015).

Third, we constructed linear-mixed effects models with the selected predictor variables to account for repeated measures at the same sites over time (R lme4 package, Bates et al. 2015). For each response variable we selected a random effects model structure by comparing a model with a random term adjusting the intercept by monitoring site and a model with an additional term adjusting for the slope for change over time by monitoring site with the Akaike information criterion (AIC, Zuur et al. 2009). We removed predictor variables with $p > 0.05$ significance one at a time and compared models fit with maximum likelihood with likelihood ratio tests (Zuur et al. 2009) with Kenward–Roger degrees of freedom for fixed effects in mixed models (R pbkrtest package, Kenward & Roger 1997; Halekoh & Højsgaard 2014). We also tested for significant differences between the three vegetation removal/seeding categories with a Tukey test (R multcomp package, Hothorn et al. 2008) and combined terms when nonsignificant differences between two categories were detected along with similar significant contrasts with the third category. Final mixed models were refit with restricted maximum likelihood. Standardized coefficient values for predictors were estimated with fixed effects only. The significance of individual terms was calculated with an $F$ test (Kenward–Roger df, SS Type III, Anova function, R car package, Fox & Weisberg 2011). All analyses were conducted in R version 3.5.2 (R Core Team 2018).

## Results

### Vegetation Cover

Total cover in vegetation removal sites with or without seeding dropped below baseline (0–5 years prior to vegetation removal) initially, with less of a drop in seeded sites (Fig. 3A). Total cover in both of these removal categories increased, and sites without seeding increased at a faster rate than those with seeding (interaction between treatment category and year post-baseline, $F = 14.5$, $p < 0.001$, Fig. 3A, Tables S2 & S3). Cover in sites with vegetation removal and seeding increased

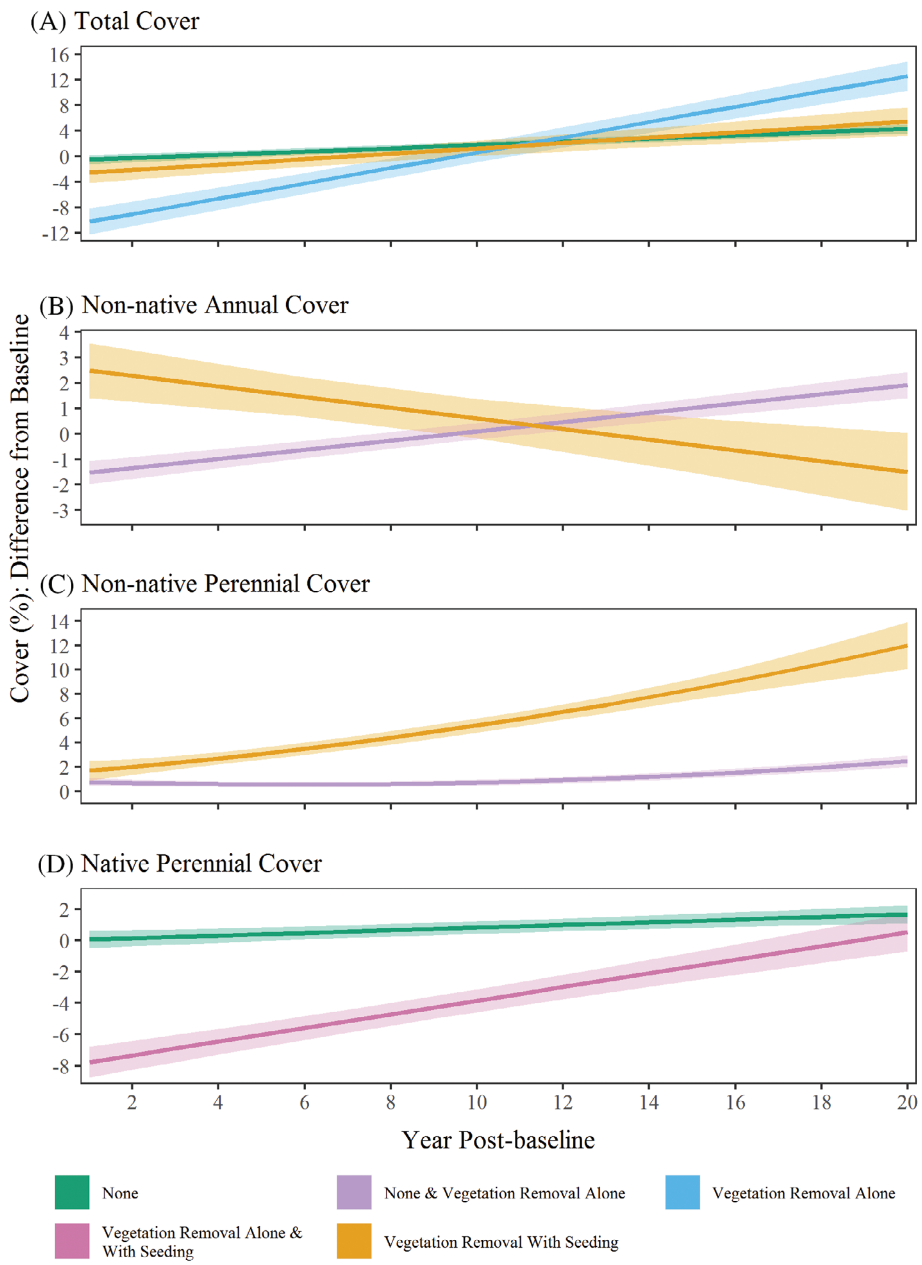


Figure 3. Fitted values (±Kenward–Roger SE) for change in (A) total, (B) non-native annual, (C) non-native perennial, (D) native perennial cover relative to baseline by vegetation removal and seeding category over years post-baseline.

to reach baseline levels (zero change values) after $7.0 \pm 1.2$ (SE) years post-baseline whereas sites with vegetation removal alone reached baseline levels after $9.5 \pm 1.5$ years (Fig. 3A). Annual non-native cover was initially higher in seeded sites, but declined to baseline values after approximately $12.9 \pm 0.9$ years (interaction term, $F = 10.0$, $p = 0.002$, Fig. 3B, Tables S4 & S5). No difference in non-native annual cover was observed between sites with vegetation removal alone and those without vegetation removal (all unseeded sites) and non-native annual cover tended to increase in these unseeded sites (Fig. 3B, Tables S4 & S5). Non-native perennial cover increased in sites with seeding after vegetation removal, with an average of $12.0 \pm 1.9\%$ higher cover compared to baseline values after 20 years (interaction term, $F = 17.8$, $p < 0.001$, Fig. 3C, Tables S6 & S7). There was no significant difference in non-native perennial cover between sites with vegetation removal alone and sites without recent vegetation removal (all unseeded sites) and relatively little change in cover over time in these sites (Fig. 3C, Tables S6 & S7). Cover of perennial native species, on the other hand, was initially much lower than baseline for sites with vegetation removal (with and without seeding) compared to sites without recent vegetation removal (interaction term, $F = 10.7$, $p = 0.001$, Fig. 3D, Tables

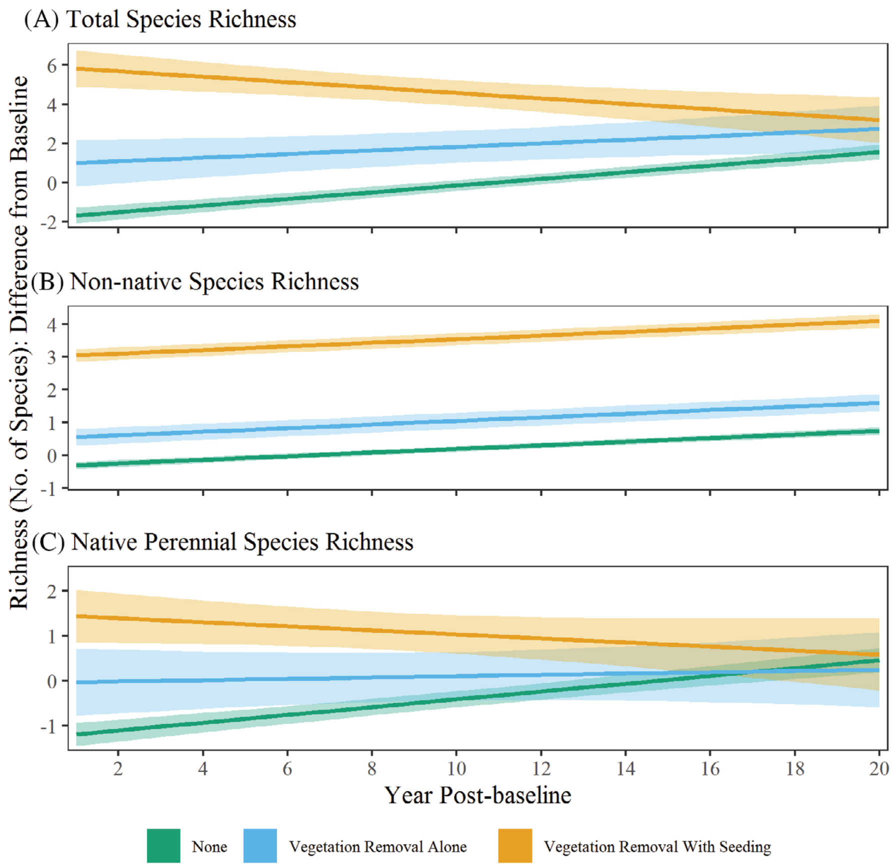


Figure 4. Fitted values (± Kenward–Roger SE) for change in (A) total, (B) non-native, and (C) native perennial richness relative to baseline by vegetation removal and seeding category over years post-baseline.

S8 & S9). Perennial native cover in vegetation removal sites (with and without seeding) reached baseline after approximately 18.8 ± 1.1 years (Fig. 3D). Change in non-native cover was negatively associated with change in perennial native cover, leading to an approximately −1.5% drop in native cover with each 10% increase in non-native cover ($F = 41.8$, $p < 0.001$, Fig. S6, Tables S8 & S9). Total cover and perennial native cover also slightly increased from baseline values in sites without vegetation removal or seeding (Fig. 3A & D). Only non-native perennial cover change followed a nonlinear trajectory over time, with a slightly accelerating trend with number of years post-baseline (convex form, Fig. 3C, Table S6 & S7).

### Species Richness

Species richness in sites with vegetation removal and seeding was initially much higher than baseline with 5.8 ± 0.9 species estimated at year 1, but richness subsequently declined slightly over the 20-year monitoring period post-baseline in those sites (interaction term, $F = 6.2$, $p = 0.002$, Fig. 4A, Tables S10 & S11). By contrast, the initially lower species richness relative to baseline levels in unseeded vegetation removal sites (1.0 ± 1.2 species, year 1) and sites without vegetation removal (−1.7 ± 0.4 species, year 1) slightly increased over time (Fig. 4A). Non-native species richness compared to baseline was highest in sites with seeding (3.0 ± 0.2 species, year 1) compared to sites where no seeding occurred (vegetation removal alone, 0.6 ± 0.3 species, no vegetation removal, −0.3 ± 0.1 species, year 1, Fig. 4B). Non-native species richness increased at a rate of approximately 0.12 ± 0.02 species per year (sp/year) across all categories of vegetation removal and seeding without a significant effect of category on trend over time (no significant interaction, Fig. 4B, Tables S12 & S13). Similar to the trends for total species richness, native perennial richness was initially higher than baseline in seeded sites; however, richness then declined over the monitoring period in these sites (interaction term, $F = 3.2$, $p = 0.042$, Fig. 4C, Tables S14 & S15). Little change in native perennial richness compared to baseline was observed in sites with vegetation removal alone (Fig. 4C, Tables S14 & S15). Non-native cover was not significantly related to change in native species richness and therefore was not retained in the final model (Tables S14 & 15). Slight increases in species richness for all categories were observed for sites without any recent vegetation removal (Tables S10–S15).

### Community Turnover

Bray–Curtis dissimilarity between monitoring periods was highest in the sites with vegetation removal with or without seeding initially (interaction between treatment category

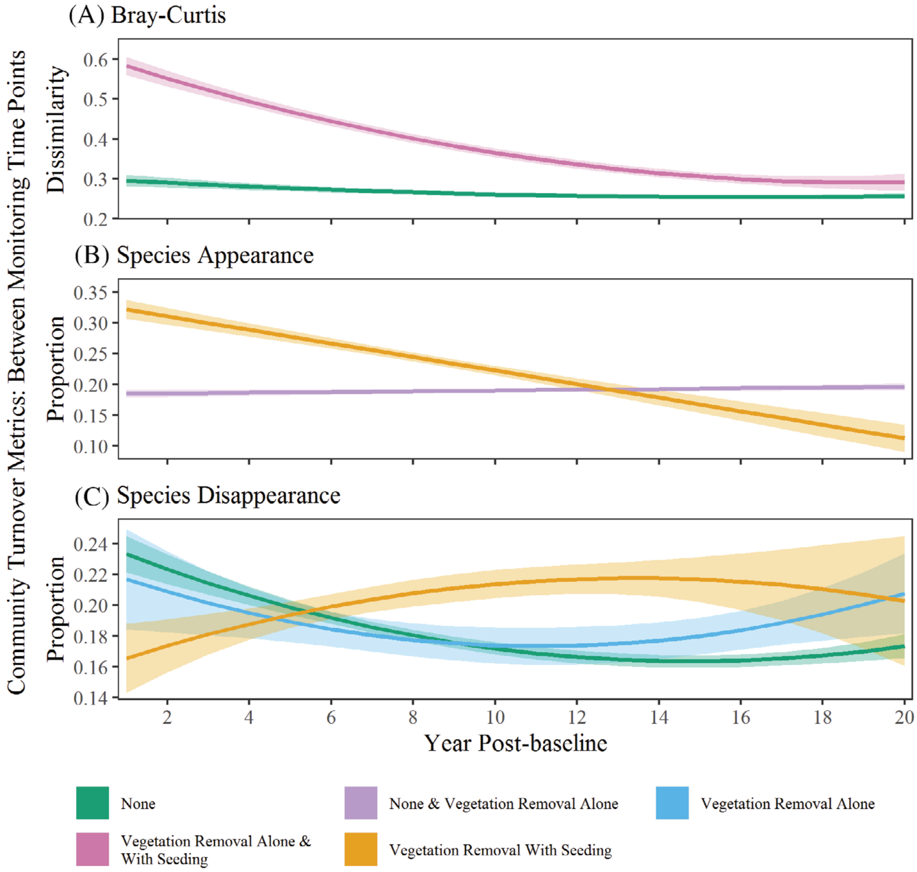


Figure 5. Fitted values (±Kenward-Roger SE) for (A) Bray–Curtis dissimilarity, (B) species appearance, (C) species disappearance community turnover metrics between monitoring time points by vegetation removal and seeding category over years post-baseline.

and year post-baseline, $F = 41.7$, $p < 0.001$, Fig. 5A, Tables S16 & S17). Community dissimilarity between monitoring periods decreased over time in the vegetation removal sites, reaching levels close to those of sites without vegetation removal by the end of the 20 year monitoring period (Fig. 5A). The proportion of new species appearing between time periods was initially higher in the seeded sites ($32 \pm 2\%$ in year 1) than unseeded sites with or without vegetation removal ($18 \pm 1\%$ in year 1, interaction term, $F = 36.7$, $p < 0.001$, Fig. 5B, Tables S18 & S19). However, by the end of the 20-year monitoring period the estimated proportion of new species appearing between time periods was lower in the seeded sites ($11 \pm 2\%$, year 20) than in unseeded sites with or without vegetation removal ($20 \pm 1\%$, year 20, Fig. 5B). The proportion of species disappearing between monitoring periods increased in sites where seeding occurred after vegetation removal, but this effect plateaued over time (interaction term, $F = 4.3$, $p = 0.002$; Fig. 5C; Tables S20 & S21). In contrast, species disappearance for both categories of sites without seeding followed a nonlinear convex form, with an initial decline and then increase by the end of the 20-year monitoring period (Fig. 5C). Sites without vegetation removal or seeding were less dynamic based on community turnover metrics, with lower values for Bray–Curtis dissimilarity and the proportion of species disappearing than the other categories (Fig. 5A & C).

#### Influence of Site Climate and Weather Extremes

Climate variables, both mean conditions and weather extremes (anomalies), were strongly associated with most plant community composition metrics. The direction of temperature and precipitation relationships with plant community variables varied between mean climate and short-term extremes, as well as across seasons and time period prior to the monitoring year for weather extremes (Tables S3–S21, odd numbers, Fig. 6). Higher mean annual temperatures were associated with lower total cover and native perennial cover, lower total richness and native perennial richness, and increased community turnover as indicated by higher dissimilarity and rate of species disappearance (Fig. 6A–C). Higher site mean annual precipitation was associated with higher total cover and non-native perennial cover, higher total richness and native perennial richness, and decreased community turnover indicated by lower rates of species disappearance and appearance between monitoring visits (Fig. 6D–F). Higher temperature anomalies in the cool season were associated with increases in total, non-native annual, and native perennial cover, whereas higher temperature

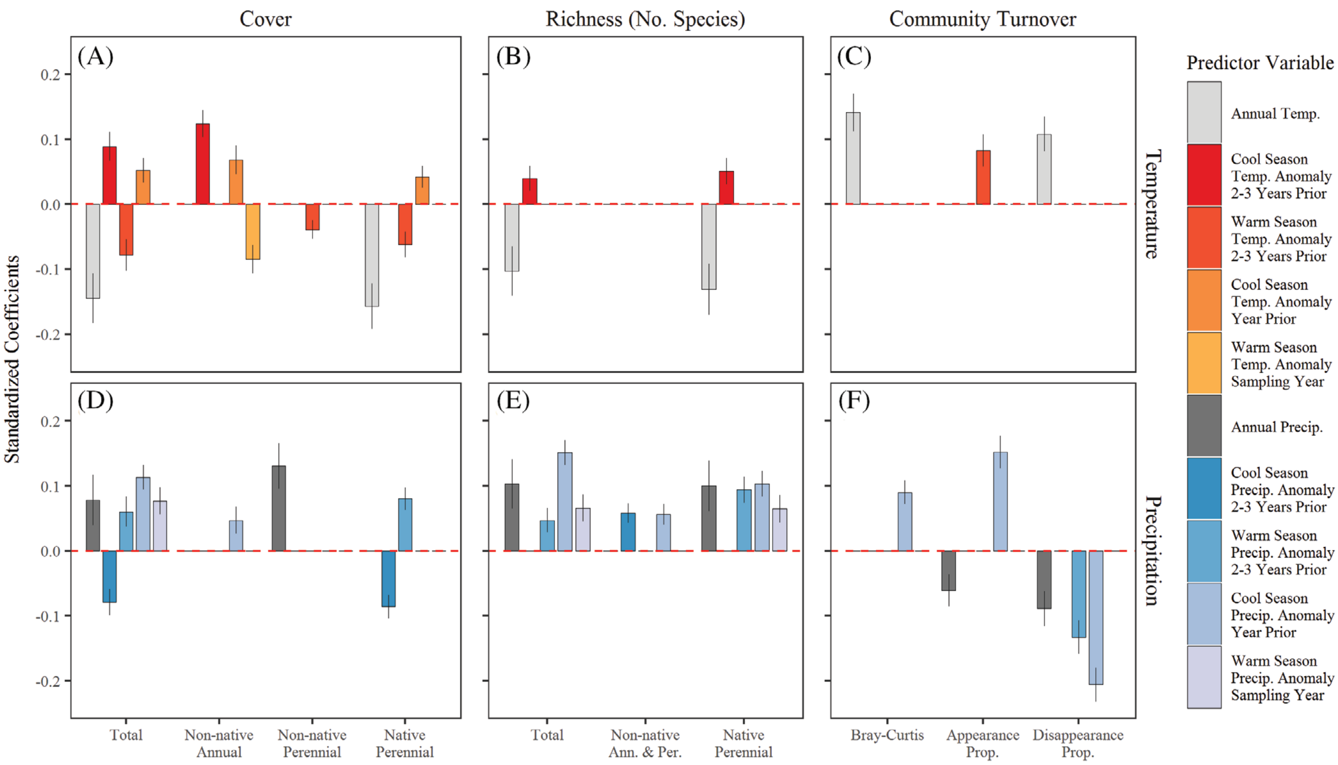


Figure 6. Standardized coefficients that indicate the direction (positive or negative) and strength of the relationship between predictor variables: mean climate and weather extremes for temperature (top row) and precipitation (bottom row) and response variables: cover (first column, A, D) species richness (second column, B, E), and community turnover metrics (third column, C, F).

anomalies in the warm season were associated with decreases in total, non-native annual, non-native perennial, and native perennial cover (Fig. 6A). Higher cool season temperature anomalies 2–3 years prior to the monitoring year were positively associated with total and native perennial species richness, whereas higher warm season anomalies 2–3 years prior to the monitoring year were associated with a higher proportion of species appearance (Fig. 6B & C). Higher precipitation anomalies were typically positively related to cover, richness, community dissimilarity, and species appearance, and negatively related to species disappearance (Fig. 6D–F). However, cool season precipitation anomalies 2–3 years prior to the monitoring year were negatively related to total cover and native perennial cover (Fig. 6D).

## Discussion

Our results suggest that vegetation removal and seeding treatments strongly affect initial plant community composition posttreatment as well as the rate of change over time. Elements of community structure that vegetation management actions seek to promote were slow to recover to baseline levels; both total cover and cover of native perennials did not reach baseline levels for 7–10 and 19 years, respectively. Among richness and cover variables, there were few indications of stabilizing trends (plateau relationships). On the other hand, stabilizing trends were indicated for some community turnover metrics (dissimilarity and proportion of species disappearance), with values for vegetation removal sites approaching those in sites without recent vegetation removal by the end of the 20-year monitoring period.

Our results indicate that monitoring for long-term periods (>10 years) is needed to fully capture the effects of management actions on plant community properties, especially with the slow-growing perennial species dominant in this study region (Anderson & Inouye 2001; Duniway et al. 2018). In particular, our results suggest that only considering short-term outcomes in vegetation management decisions fails to recognize important shifts in species composition that can affect long-term community resilience. For example, our results show that monitoring 5 years posttreatment underestimates the potential for recovery of perennial species, particularly natives, and the suppressive effect of seeding on non-native annual cover. Slow recovery and variability in vegetation response is also likely affected by the low and variable precipitation of this study region and much of the western United States where the same management treatments are conducted in similar vegetation types (juniper woodlands and sagebrush shrublands).

The increase in higher non-native perennial cover we observed with seeding is probably due to introduced perennial grasses which are commonly included in seed mixes in these study sites (analysis of a subset of range trends sites, Wilder et al. 2019) and generally across the western United States (Redmond et al. 2013; Copeland et al. 2018). Non-native perennial grasses are used in restoration in this region due to their high rates of establishment, productivity, and capacity to stabilize soils and suppress non-native annual species (Ott et al. 2003; Svejcar et al. 2017). However, high abundance of non-native perennial grasses can also lead to dense stands which competitively exclude native shrubs, forbs, and perennial grasses (Bakker et al. 2003; Nafus et al. 2015; Williams et al. 2017). In our study, we found lower cover of non-native annual species with seeding, which is a goal common among similar restoration treatments (Pilliod et al. 2017; Copeland et al. 2018). On the other hand, increases in non-native perennial cover were associated with decreases in perennial native cover. The exponential increase in non-native perennial cover also contrasted with the slow rate of increase in native perennial cover after vegetation removal (approximately 19 years to reach baseline cover values). In addition, our final models suggested that cover of both non-native and native perennial groups was still increasing, rather than stabilizing, 20 years posttreatment. As a whole, these results indicate that managers seeding combinations of perennial non-natives and natives should consider species' relative growth rates and interspecific competition over longer time periods that reflect population responses to treatments.

Species-specific factors outside of non-native or native status are also likely important in determining performance in response to treatments. In a short-term study (0–10 years) with a portion of the same core range trend dataset as this analysis, non-native grasses generally increased more than natives with seeding, but both non-native and native species varied widely in their cover response (Wilder et al. 2019). Additional research is warranted by the increasing species richness of seed mixes applied on public lands in this region (Copeland et al. 2018) and the higher costs and effort associated with seeding a diverse suite of native species (Peppin et al. 2011).

Our results show that the effects of vegetation removal and seeding treatments on plant community attributes, particularly cover and richness, are highly dependent on site climate and extreme weather, including lagged relationships with extremes at least up to 2–3 years prior to monitoring. The generally positive relationships between cover and richness and higher mean precipitation, and negative relationships with higher mean temperatures, highlight the importance of water limitation on plant growth in the study area. Cool and warm season weather extremes differentially related to cover, perhaps due to temperature limitations to growth in the cool season compared to water limitation in the warm season. Our results underscore the need to incorporate spatial and temporal environmental variation in understanding recovery dynamics (e.g. West & Yorks 2006; Bernstein et al. 2014), particularly given the potential for long-term impacts of climate extremes on vegetation recovery in water-limited regions (Anderson & Inouye 2001). In addition to direct impacts of weather extremes on plant growth and survival following restoration treatments, weather may alter the competitive relationships in the early establishment phase, leading to lasting effects on community composition (Young et al. 2015). Though beyond the scope of our study, we observed that relationships with climate means and extremes varied among species groups (such as annuals vs. perennials), suggesting that climate variation could indirectly affect treatment outcomes via altering the abundances of competing species.

Treatment outcomes could also be affected by specific management techniques beyond the broad categories used in this study, such as the mastication of remaining woody material (Provencher & Thompson 2014), the sequence of treatments, and the density and composition of the seed mix (Grman et al. 2013). Although wildfire and mechanical vegetation removal both tend to at least temporarily reduce perennial plant cover, the former is less selective and may have distinct effects on the physical properties of a site leading to differences in response to seeding (Wilder et al. 2019). Experimental trials that test different vegetation treatments at multiple sites across environmental gradients (e.g. SageSTEP, McIver et al. 2010; southwestern U.S. restoration field trail network, U.S. Geological Survey 2018) could provide insight regarding the interaction between specific treatment techniques, climate, and soil conditions (Gellie et al. 2018).

Relatively few studies have addressed the effects of vegetation removal and seeding on plant communities over decadal timescales (but see: Bates et al. 2005; Hanna & Fulgham 2015), particularly over large spatial scales. Yet monitoring over broad spatiotemporal scales is necessary to address the slow recovery rates of perennial vegetation (Anderson & Inouye 2001) and the outcomes of the widespread application of similar management treatments over the last 70 years across the intermountain United States (Pilliod et al. 2017; Copeland et al. 2018). Our results suggest that treatments to restore degraded dryland systems could benefit from weighing the rates of recovery of key plant community characteristics against desired outcomes with respect to plant community composition. Furthermore, we observed that climate variation across space and at different temporal scales had significant impacts on recovery patterns. Such variation must be included when evaluating restoration success and may be a major source of divergent responses to similar management treatments across sites and years.

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## Supporting Information

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

**Figure S1.** Convex hull of original dataset for sites vegetation removal category for mean annual temperature and precipitation.
**Figure S2.** Convex hull of final dataset for sites vegetation removal category for mean annual temperature and precipitation.
**Figure S3.** Density plots for final dataset for sites vegetation removal category for mean annual temperature and precipitation.
**Figure S4.** Baseline total, annual non-native, perennial non-native, and perennial native cover by treatment category.
**Figure S5.** Baseline total, non-native, and native perennial richness by treatment category.
**Figure S6.** Association between change in non-native cover and change in perennial native cover compared to the baseline monitoring period.
**Table S1.** Common species within the range trends cover transects at the beginning of the monitoring period by native and lifespan group.
**Table S2.** Predictors for final linear mixed model for total cover.
**Table S3.** Standardized coefficients and standard error for final linear mixed model for total cover.
**Table S4.** Predictors for final linear mixed model for non-native annual cover.
**Table S5.** Standardized coefficients and standard error for final linear mixed model for non-native annual cover.
**Table S6.** Predictors for final linear mixed model for non-native perennial cover.
**Table S7.** Standardized coefficients and standard error for final linear mixed model for non-native perennial cover.
**Table S8.** Predictors for final linear-mixed model for native perennial cover.
**Table S9.** Standardized coefficients and standard error for final linear-mixed model for native perennial cover.
**Table S10.** Predictors for final linear mixed model for total species richness.
**Table S11.** Standardized coefficients and standard error for final linear-mixed model for total species richness.
**Table S12.** Predictors for final linear mixed model for non-native species richness.
**Table S13.** Standardized coefficients and standard error for final linear mixed model for non-native species richness.
**Table S14.** Predictors for final linear mixed model for native perennial species richness.
**Table S15.** Standardized coefficients and standard error for final linear mixed model for native perennial species richness.
**Table S16.** Predictors for final linear mixed model for Bray–Curtis dissimilarity.
**Table S17.** Standardized coefficients and standard error for final linear mixed model for Bray–Curtis dissimilarity.
**Table S18.** Predictors for final linear mixed model for species appearance.
**Table S19.** Standardized coefficients and standard error for final linear-mixed model for species appearance.
**Table S20.** Predictors for final linear model for species disappearance.
**Table S21.** Standardized coefficients and standard error for final linear-mixed model for species disappearance.
**Appendix S1:** Treatment types included within treatment categories.
**Appendix S2:** Dataset details for common woody species calculation.
**Appendix S3:** Calculation details for weather extremes (standardized anomalies).

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**Supplementary Information:** Long-term plant community trajectories suggest divergent responses of native and non-native perennials and annuals to vegetation removal and seeding treatments

**Appendix S1:** Treatment types included within treatment categories

The vegetation removal category included 22 sites with prescribed fire or wildfire, 8 sites with lop and scatter treatments, 7 sites with other types of mechanical removal involving soil disturbance (undefined or roller chopper, bull hog mulcher, and chaining), and 5 sites split between logging and hand-thinning treatments. The seeded site category included both sites where seeding followed wildfire or management vegetation removal or sites where the seeding involved soil and vegetation disturbance due to the use of heavy equipment for seeding (e.g. drills). Seeded sites included 40 sites with mechanical removal of overstory vegetation with soil disturbance (harrow, chaining, bull hog mulcher, discing, undefined), 19 sites with prescribed fire or wildfire (including 6 with chaining), and 16 sites with vegetation disturbance associated with seedbed preparation or seeding (aerator, seed drill).

**Appendix S2:** Dataset details for common woody species calculation

Common overstory woody species identity and occurrence were determined with non-seedling density measurements from belt transects associated with the cover transect data used in the core analyses measured at the baseline period, which was pre-vegetation removal for wildfire and management sites

**Appendix S3:** Calculation details for weather extremes (standardized anomalies)

Definition of growing season anomaly: Apr.-month prior to sampling month if sampled in days 1-15 of the month, or month of sampling if sampled days 16-30/31. For example, if the site was sampled on June 14$^{th}$, the included months would be April and May. If the site was sampled on June 22$^{nd}$, the included months would be April, May, and June.

Example equation for a weather extreme variable (standardized anomaly) calculated for cool season (Oct.-Mar.) temperatures in the year prior to treatment:

$$\text{Cool Season Temperature Prior Year Anomaly} = \frac{\text{Site Oct.-Mar. Temperature Prior to Year of Sampling - Site Mean Oct.-Mar. Temperatures 1986-2017}}{\text{Standard Deviation of Site Oct.-Mar. Temperatures 1986-2017}}$$

## Supplementary Tables

**Table S1.** Common species (top 3 species based on number of sites) within the range trends cover transects at the beginning of the monitoring period (baseline period, pre-vegetation removal for wildfire and management sites) by native and lifespan group (native to the lower 48 sites, and perennial/biennial or annual status from the PLANTS USDA database) and lifeform (tree, shrub, grass, or forb). Only one native annual grass species was identified within the selected sites (*Vulpia octoflora*).

| Native Status & Lifeform | Group | Species | Number of Sites |
|---|---|---|---:|
| Non-native Annual | Grass | *Bromus tectorum* | 319 |
| | | *Bromus arvensis* | 48 |
| | | *Vulpia myuros* | 14 |
| | Forb | *Tragopogon dubius* | 164 |
| | | *Alyssum desertorum* | 135 |
| | | *Ceratocephala testiculata* | 121 |
| Native Annual | Grass | *Vulpia octoflora* | 81 |
| | Forb | *Descurainia pinnata* | 172 |
| | | *Polygonum douglasii* | 161 |
| | | *Collinsia parviflora* | 160 |
| Non-native Perennial | Grass | *Agropyron cristatum* | 153 |
| | | *Poa pratensis* | 110 |
| | | *Thinopyrum intermedium* | 80 |
| | Forb | *Medicago sativa* | 32 |
| | | *Melilotus officinalis* | 9 |
| | | *Convolvulus arvensis* | 8 |
| Native Perennial | Tree | *Juniperus osteosperma* | 168 |
| | | *Pinus edulis* | 106 |
| | | *Pinus ponderosa* | 13 |
| | Shrub | *Artemisia tridentata* | 411 |
| | | *A. t. vaseyana* | 271 |
| | | *A. t. wyomingensis* | 125 |
| | | *A. t. tridentata* | 21 |
| | | *Gutierrezia sarothrae* | 284 |
| | | *Chrysothamnus viscidiflorus* | 258 |
| | Grass | *Elymus elymoides* | 336 |
| | | *Poa secunda* | 286 |
| | | *Achnatherum hymenoides* | 251 |
| | Forb | *Phlox longifolia* | 282 |
| | | *Astragalus convallarius* | 148 |
| | | *Sphaeralcea coccinea* | 148 |

**Supplementary Tables for Model Predictors and Standardized Coefficients**

Cool Season: Oct.-Mar.; Warm Season: Apr.-Sep.; Growing Season: Apr.-month prior to sampling; Mean Annual values are from 1986-2017. Raw polynomial values are reported to aid in interpretation, although the models were fitted with orthogonal polynomials. No Seeding = Vegetation removal alone (no seeding). Seeding = Vegetation removal with seeding. None = No vegetation removal. All Veg. Removal = Combined category for all sites with vegetation removal, with or without seeding. No Seeding/None = Combined category for all unseeded sites, vegetation removal alone & no vegetation removal categories. Pseudo-$R^2$ values are calculated with the rsquared function in the R piecewiseSEM package (Lefcheck 2015) which separates the variability associated with fixed and random components in linear mixed models (Nakagawa & Schielzeth 2013; Johnson 2014). Marginal $R^2$ values include the fixed effects only whereas conditional $R^2$ values include both fixed and random effects.

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**Table S2.** Predictors for final linear mixed model for total cover (random effects for site on intercept and slope over time, marginal $R^2$ = 0.17, conditional $R^2$ = 0.67) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 2.4 | 1 | 560 | 0.122 |
| Two-Three Year Prior Cool Season Mean Temperature Anomalies | 16.6 | 1 | 1234 | <0.001 |
| Two-Three Year Prior Warm Season Mean Temperature Anomalies | 10.6 | 1 | 1255 | 0.001 |
| Two-Three Year Prior Cool Season Precipitation Anomalies | 15.4 | 1 | 1166 | <0.001 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 7.0 | 1 | 1213 | 0.008 |
| Year Prior Cool Season Mean Temperature Anomalies | 7.3 | 1 | 1235 | 0.007 |
| Year Prior Cool Season Precipitation Anomalies | 34.6 | 1 | 1229 | <0.001 |
| Growing Season Prior to Sampling Date Precipitation Anomalies | 13.8 | 1 | 1272 | <0.001 |
| Mean Annual Temperature | 14.7 | 1 | 529 | <0.001 |
| Mean Annual Precipitation | 4.1 | 1 | 521 | 0.044 |
| Sampling Region | 4.0 | 4 | 597 | 0.004 |
| Treatment Category | 11.4 | 2 | 559 | <0.001 |
| Year Post-baseline | 27.1 | 1 | 465 | <0.001 |
| Treatment Category * Year Post-baseline | 14.5 | 2 | 600 | <0.001 |

**Table S3.** Standardized coefficients and standard error for final linear mixed model for total cover (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Cool Season Mean Temperature Anomalies | 0.089 | 0.022 |
| Two-Three Year Prior Warm Season Mean Temperature Anomalies | -0.078 | 0.024 |
| Two-Three Year Prior Cool Season Precipitation Anomalies | -0.079 | 0.020 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 0.060 | 0.023 |
| Year Prior Cool Season Mean Temperature Anomalies | 0.052 | 0.019 |
| Year Prior Cool Season Precipitation Anomalies | 0.113 | 0.019 |
| Growing Season Prior to Sampling Date Precipitation Anomalies | 0.077 | 0.021 |
| Mean Annual Temperature | -0.145 | 0.038 |
| Mean Annual Precipitation | 0.078 | 0.039 |
| Sampling Region-Northeastern | -0.100 | 0.046 |
| Sampling Region-Northern | -0.134 | 0.047 |
| Sampling Region-Southeastern | -0.084 | 0.046 |
| Sampling Region-Southern | -0.164 | 0.044 |
| No Seeding | -0.230 | 0.048 |
| Seeding | -0.047 | 0.050 |
| Year Post-baseline | 0.111 | 0.021 |
| No Seeding * Year Post-baseline | 0.227 | 0.042 |
| Seeding * Year Post-baseline | 0.034 | 0.041 |

**Table S4.** Predictors for final linear mixed model for non-native annual cover (random effects for site on intercept and slope over time, marginal $R^2 = 0.06$, conditional $R^2 = 0.61$) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 0.1 | 1 | 875 | 0.735 |
| Two-Three Year Prior Cool Season Mean Temperature Anomalies | 35.7 | 1 | 1104 | <0.001 |
| Year Prior Cool Season Mean Temperature Anomalies | 9.7 | 1 | 1285 | 0.002 |
| Year Prior Cool Season Precipitation Anomalies | 5.1 | 1 | 1242 | 0.025 |
| Growing Season Prior to Sampling Date Mean Temperature Anomalies | 15.3 | 1 | 1275 | <0.001 |
| Sampling Region | 6.6 | 4 | 573 | <0.001 |
| Treatment Category: Seeding & None/No Seeding | 11.2 | 1 | 560 | 0.001 |
| Year Post-baseline | 19.5 | 1 | 462 | <0.001 |
| Treatment Category * Year Post-baseline | 10.0 | 1 | 821 | 0.002 |

**Table S5.** Standardized coefficients and standard error for final linear mixed model for non-native annual cover (contrast: central sampling region, No seeding/None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Cool Season Mean Temperature Anomalies | 0.124 | 0.021 |
| Year Prior Cool Season Mean Temperature Anomalies | 0.068 | 0.022 |
| Year Prior Cool Season Precipitation Anomalies | 0.047 | 0.021 |
| Growing Season Prior to Sampling Date Mean Temperature Anomalies | -0.085 | 0.022 |
| Sampling Region-Northeastern | -0.107 | 0.044 |
| Sampling Region-Northern | -0.233 | 0.046 |
| Sampling Region-Southeastern | -0.106 | 0.047 |
| Sampling Region-Southern | -0.077 | 0.046 |
| Seeding | 0.172 | 0.051 |
| Year Post-baseline | 0.102 | 0.023 |
| Seeding * Year Post-baseline | -0.142 | 0.045 |

**Table S6.** Predictors for final linear mixed model for non-native perennial cover (random effects for site on intercept and slope over time, marginal $R^2$ = 0.09, conditional $R^2$ = 0.81) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 0.8 | 1 | 549 | 0.372 |
| Two-Three Year Prior Warm Season Mean Temperature Anomalies | 7.3 | 1 | 1069 | 0.007 |
| Mean Annual Precipitation | 13.9 | 1 | 540 | <0.001 |
| Sampling Region | 1.5 | 4 | 530 | 0.199 |
| Treatment Category: Seeding & None/No Seeding | 55 | 1 | 702 | <0.001 |
| Year Post-baseline$^2$ | 9.8 | 2 | 374 | <0.001 |
| Treatment Category * Year Post-baseline$^2$ | 17.8 | 2 | 525 | <0.001 |

**Table S7.** Standardized coefficients and standard error for final linear mixed model for non-native perennial cover (contrast: central sampling region, No seeding/None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Warm Season Mean Temperature Anomalies | -0.039 | 0.014 |
| Mean Annual Precipitation | 0.131 | 0.035 |
| Sampling Region-Northeastern | -0.034 | 0.041 |
| Sampling Region-Northern | -0.033 | 0.043 |
| Sampling Region-Southeastern | -0.034 | 0.043 |
| Sampling Region-Southern | -0.099 | 0.042 |
| Seeding | 0.022 | 0.061 |
| Year Post-baseline | -0.123 | 0.065 |
| Year Post-baseline$^2$ | 0.216 | 0.068 |
| Seeding * Year Post-baseline | 0.226 | 0.135 |
| Seeding * Year Post-baseline$^2$ | 0.010 | 0.095 |

**Table S8.** Predictors for final linear mixed model for native perennial cover (random effects for site on intercept and slope over time, marginal $R^2 = 0.19$, conditional $R^2 = 0.74$) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 14.6 | 1 | 586 | <0.001 |
| Two-Three Year Prior Warm Season Mean Temperature Anomalies | 9.5 | 1 | 1282 | 0.002 |
| Two-Three Year Prior Cool Season Precipitation Anomalies | 23.3 | 1 | 1127 | <0.001 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 21.2 | 1 | 1100 | <0.001 |
| Year Prior Cool Season Mean Temperature Anomalies | 5.8 | 1 | 1214 | 0.016 |
| Mean Annual Temperature | 20.0 | 1 | 528 | <0.001 |
| Non-native cover | 41.8 | 1 | 1638 | <0.001 |
| Sampling Region | 4.2 | 4 | 556 | 0.002 |
| Treatment Category: All Veg. Removal & None | 48.1 | 1 | 560 | <0.001 |
| Year Post-baseline | 8.9 | 1 | 472 | 0.003 |
| Treatment Category * Year Post-baseline | 10.7 | 1 | 624 | 0.001 |

**Table S9** Standardized coefficients and standard error for final linear mixed model for native perennial cover (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Warm Season Mean Temperature Anomalies | -0.062 | 0.020 |
| Two-Three Year Prior Cool Season Precipitation Anomalies | -0.086 | 0.018 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 0.080 | 0.017 |
| Year Prior Cool Season Mean Temperature Anomalies | 0.042 | 0.017 |
| Mean Annual Temperature | -0.157 | 0.035 |
| Non-native cover | -0.139 | 0.021 |
| Sampling Region-Northeastern | 0.009 | 0.044 |
| Sampling Region-Northern | 0.058 | 0.046 |
| Sampling Region-Southeastern | 0.002 | 0.045 |
| Sampling Region-Southern | -0.115 | 0.043 |
| All Veg. Removal | -0.331 | 0.048 |
| Year Post-baseline | 0.062 | 0.021 |
| All Veg. Removal * Year Post-baseline | 0.133 | 0.041 |

**Table S10.** Predictors for final linear mixed model for total species richness (random effects for site on intercept and slope over time, marginal $R^2 = 0.16$, conditional $R^2 = 0.67$) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 1.8 | 1 | 567 | 0.184 |
| Two-Three Year Prior Cool Season Mean Temperature Anomalies | 4.3 | 1 | 1100 | 0.038 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 6.1 | 1 | 1205 | 0.014 |
| Year Prior Cool Season Precipitation Anomalies | 60.8 | 1 | 1257 | 0.000 |
| Growing Season Prior to Sampling Date Precipitation Anomalies | 10.3 | 1 | 1290 | 0.001 |
| Mean Annual Temperature | 7.4 | 1 | 533 | 0.007 |
| Mean Annual Precipitation | 7.1 | 1 | 513 | 0.008 |
| Sampling Region | 5.2 | 4 | 552 | 0.000 |
| Treatment Category | 27.5 | 2 | 543 | 0.000 |
| Year Post-baseline | 32.5 | 1 | 453 | 0.000 |
| Treatment Category * Year Post-baseline | 6.2 | 2 | 605 | 0.002 |

**Table S11.** Standardized coefficients and standard error for final linear mixed model for total species richness (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Cool Season Mean Temperature Anomalies | 0.040 | 0.019 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 0.047 | 0.019 |
| Year Prior Cool Season Precipitation Anomalies | 0.151 | 0.019 |
| Growing Season Prior to Sampling Date Precipitation Anomalies | 0.066 | 0.021 |
| Mean Annual Temperature | -0.103 | 0.038 |
| Mean Annual Precipitation | 0.103 | 0.038 |
| Sampling Region-Northeastern | -0.019 | 0.045 |
| Sampling Region-Northern | 0.155 | 0.046 |
| Sampling Region-Southeastern | 0.028 | 0.045 |
| Sampling Region-Southern | 0.094 | 0.044 |
| No Seeding | 0.108 | 0.052 |
| Seeding | 0.385 | 0.053 |
| Year Post-baseline | 0.126 | 0.022 |
| No Seeding * Year Post-baseline | -0.035 | 0.044 |
| Seeding * Year Post-baseline | -0.145 | 0.041 |

**Table S12.** Predictors for final linear mixed model for non-native species richness (random effects for site on intercept and slope over time, marginal $R^2 = 0.29$, conditional $R^2 = 0.72$) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 2.5 | 1 | 721 | 0.117 |
| Two-Three Year Prior Cool Season Precipitation Anomalies | 14.4 | 1 | 1118 | <0.001 |
| Year Prior Cool Season Precipitation Anomalies | 12.6 | 1 | 1191 | <0.001 |
| Sampling Region | 4.4 | 4 | 529 | 0.002 |
| Treatment Category | 138.9 | 2 | 520 | <0.001 |
| Year Post-baseline | 51.9 | 1 | 441 | <0.001 |

**Table S13.** Standardized coefficients and standard error for final linear mixed model for non-native species richness (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Cool Season Precipitation Anomalies | 0.058 | 0.015 |
| Year Prior Cool Season Precipitation Anomalies | 0.056 | 0.016 |
| Sampling Region-Northeastern | 0.021 | 0.038 |
| Sampling Region-Northern | 0.091 | 0.041 |
| Sampling Region-Southeastern | -0.062 | 0.040 |
| Sampling Region-Southern | -0.040 | 0.040 |
| No Seeding | 0.101 | 0.031 |
| Seeding | 0.507 | 0.030 |
| Year Post-baseline | 0.122 | 0.017 |

**Table S14.** Predictors for final linear mixed model for native perennial species richness (random effects for site on intercept and slope over time, marginal $R^2$ = 0.11, conditional $R^2$ = 0.64) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 1.7 | 1 | 563 | 0.198 |
| Two-Three Year Prior Cool Season Temperature Anomalies | 6.8 | 1 | 1106 | 0.009 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 22.9 | 1 | 1213 | <0.001 |
| Year Prior Cool Season Precipitation Anomalies | 26.9 | 1 | 1258 | <0.001 |
| Growing Season Prior to Sampling Date Precipitation Anomalies | 9.5 | 1 | 1291 | 0.002 |
| Mean Annual Temperature | 11.6 | 1 | 529 | 0.001 |
| Mean Annual Precipitation | 6.4 | 1 | 520 | 0.012 |
| Sampling Region | 3.8 | 4 | 553 | 0.005 |
| Treatment Category | 8.8 | 2 | 542 | <0.001 |
| Year Post-baseline | 22.5 | 1 | 446 | <0.001 |
| Treatment Category * Year Post-baseline | 3.2 | 2 | 600 | 0.042 |

**Table S15.** Standardized coefficients and standard error for final linear mixed model for native perennial species richness (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Cool Season Temperature Anomalies | 0.051 | 0.020 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 0.094 | 0.020 |
| Year Prior Cool Season Precipitation Anomalies | 0.103 | 0.020 |
| Growing Season Prior to Sampling Date Precipitation Anomalies | 0.065 | 0.021 |
| Mean Annual Temperature | -0.131 | 0.039 |
| Mean Annual Precipitation | 0.100 | 0.039 |
| Sampling Region-Northeastern | 0.041 | 0.046 |
| Sampling Region-Northern | 0.147 | 0.047 |
| Sampling Region-Southeastern | 0.070 | 0.046 |
| Sampling Region-Southern | 0.136 | 0.045 |
| No Seeding | 0.075 | 0.051 |
| Seeding | 0.211 | 0.052 |
| Year Post-baseline | 0.107 | 0.023 |
| No Seeding * Year Post-baseline | -0.055 | 0.045 |
| Seeding * Year Post-baseline | -0.099 | 0.042 |

**Table S16.** Predictors for final linear mixed model for Bray-Curtis dissimilarity (random effects for site on intercept and slope over time, marginal $R^2$ = 0.23, conditional $R^2$ = 0.66) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| Predictors | F-statistic | df | KR df | P-value |
|---|---|---|---|---|
| Intercept | 135.6 | 1 | 513 | <0.001 |
| Year Prior Cool Season Precipitation Anomalies | 24.9 | 1 | 1129 | <0.001 |
| Mean Annual Temperature | 24.1 | 1 | 508 | <0.001 |
| Treatment Category: All Veg. Removal & None | 105.9 | 1 | 574 | <0.001 |
| Year Post-baseline$^2$ | 5.3 | 2 | 399 | 0.0053 |
| Treatment Category * Year Post-baseline$^2$ | 41.7 | 2 | 446 | <0.001 |

**Table S17.** Standardized coefficients and standard error for final linear mixed model for Bray-Curtis dissimilarity (contrast: None treatment category).

| Predictors | Coefficients | SE |
|---|---|---|
| Year Prior Cool Season Precipitation Anomalies | 0.090 | 0.018 |
| Mean Annual Temperature | 0.141 | 0.029 |
| All Veg. Removal | 0.873 | 0.090 |
| Year Post-baseline | -0.240 | 0.099 |
| Year Post-baseline$^2$ | 0.182 | 0.094 |
| All Veg. Removal * Year Post-baseline | -0.799 | 0.171 |
| All Veg. Removal * Year Post-baseline$^2$ | 0.276 | 0.108 |

**Table S18.** Predictors for final linear mixed model species appearance (proportion new species between sampling dates, random effects for site on intercept, identical marginal and conditional $R^2 = 0.11$) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 248.9 | 1 | 731 | <0.001 |
| Two-Three Year Prior Warm Season Temperature Anomalies | 11.3 | 1 | 1519 | 0.001 |
| Year Prior Cool Season Precipitation Anomalies | 36.6 | 1 | 1561 | <0.001 |
| Mean Annual Precipitation | 6.0 | 1 | 494 | 0.015 |
| Sampling Region | 5.5 | 4 | 531 | <0.001 |
| Treatment Category: Seeded & No Seeding/None | 68.4 | 1 | 1676 | <0.001 |
| Year Post-baseline | 0.3 | 1 | 1428 | 0.574 |
| Treatment Category * Year Post-baseline | 36.7 | 1 | 1531 | <0.001 |

**Table S19.** Standardized coefficients and standard error for final linear mixed model for species appearance (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Warm Season Temperature Anomalies | 0.083 | 0.025 |
| Year Prior Cool Season Precipitation Anomalies | 0.152 | 0.025 |
| Mean Annual Precipitation | -0.061 | 0.025 |
| Sampling Region-Northeastern | -0.077 | 0.03 |
| Sampling Region-Northern | -0.062 | 0.032 |
| Sampling Region-Southeastern | -0.009 | 0.031 |
| Sampling Region-Southern | 0.053 | 0.031 |
| No Seeding/None | 0.452 | 0.055 |
| Year Post-baseline | 0.014 | 0.025 |
| No Seeding/None * Year Post-baseline | -0.324 | 0.053 |

**Table S20.** Predictors for final linear model for species disappearance (proportion species lost between sampling dates, random effects for site on intercept, identical marginal and conditional $R^2 = 0.13$) with F-statistics (sum of squares type III), degrees of freedom, Kenward-Roger degrees of freedom, and p-values.

| **Predictors** | **F-statistic** | **df** | **KR df** | **P-value** |
|---|---|---|---|---|
| Intercept (Sampling Region-Central) | 77.5 | 1 | 519 | <0.001 |
| Two-Three Year Prior Warm Season Precipitation Anomalies | 25.8 | 1 | 1515 | <0.001 |
| Year Prior Cool Season Precipitation Anomalies | 60.5 | 1 | 1543 | <0.001 |
| Mean Annual Temperature | 16.4 | 1 | 545 | <0.001 |
| Mean Annual Precipitation | 11.3 | 1 | 481 | 0.001 |
| Sampling Region | 2.6 | 4 | 530 | 0.033 |
| Treatment Category | 4.7 | 2 | 673 | 0.009 |
| Year Post-baseline$^2$ | 12.5 | 2 | 1384 | <0.001 |
| Treatment Category * Year Post-baseline$^2$ | 4.3 | 4 | 1452 | 0.002 |

**Table S21.** Standardized coefficients and standard error for final linear mixed model for disappearance (contrast: central sampling region, None treatment category).

| **Predictors** | **Coefficients** | **SE** |
|---|---|---|
| Two-Three Year Prior Warm Season Precipitation Anomalies | -0.133 | 0.026 |
| Year Prior Cool Season Precipitation Anomalies | -0.206 | 0.026 |
| Mean Annual Temperature | 0.108 | 0.027 |
| Mean Annual Precipitation | -0.089 | 0.027 |
| Sampling Region-Northeastern | -0.01 | 0.031 |
| Sampling Region-Northern | -0.017 | 0.032 |
| Sampling Region-Southeastern | 0.061 | 0.031 |
| Sampling Region-Southern | 0.051 | 0.031 |
| No Seeding | -0.042 | 0.111 |
| Seeding | -0.273 | 0.104 |
| Year Post-baseline | -0.544 | 0.133 |
| Year Post-baseline$^2$ | 0.448 | 0.131 |
| No Seeding * Year Post-baseline | 0.039 | 0.257 |
| Seeding * Year Post-baseline | 0.617 | 0.225 |
| No Seeding * Year Post-baseline$^2$ | 0.024 | 0.171 |
| Seeding * Year Post-baseline$^2$ | -0.281 | 0.145 |

## Supplementary Figures

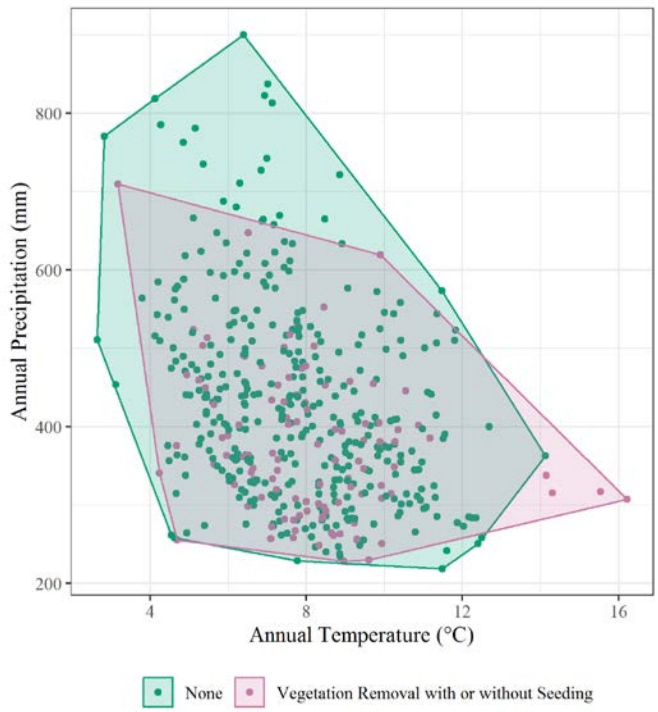


**Figure S1.** Convex hull of original dataset for sites without vegetation removal and with vegetation removal, with or without seeding, for mean annual temperature and precipitation.

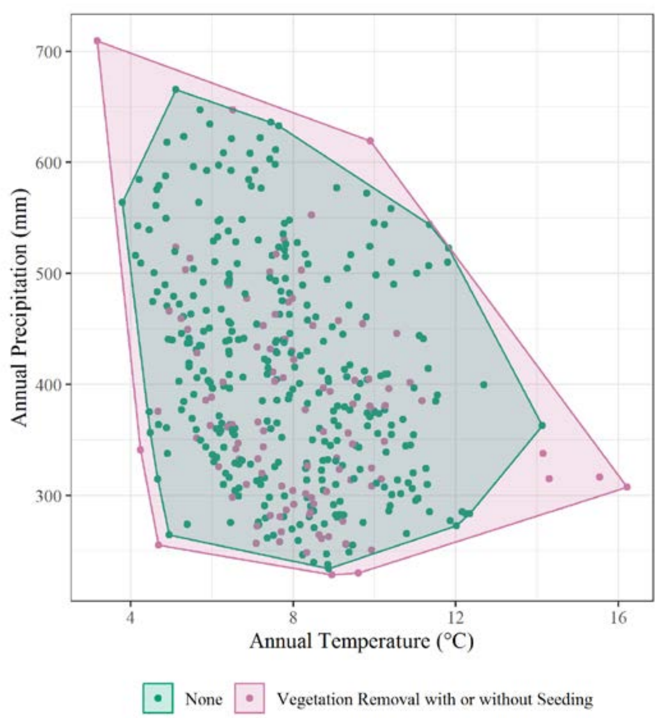


**Figure S2.** Convex hull of final dataset for sites without vegetation removal and with vegetation vegetation removal, with or without seeding, for mean annual temperature and precipitation.

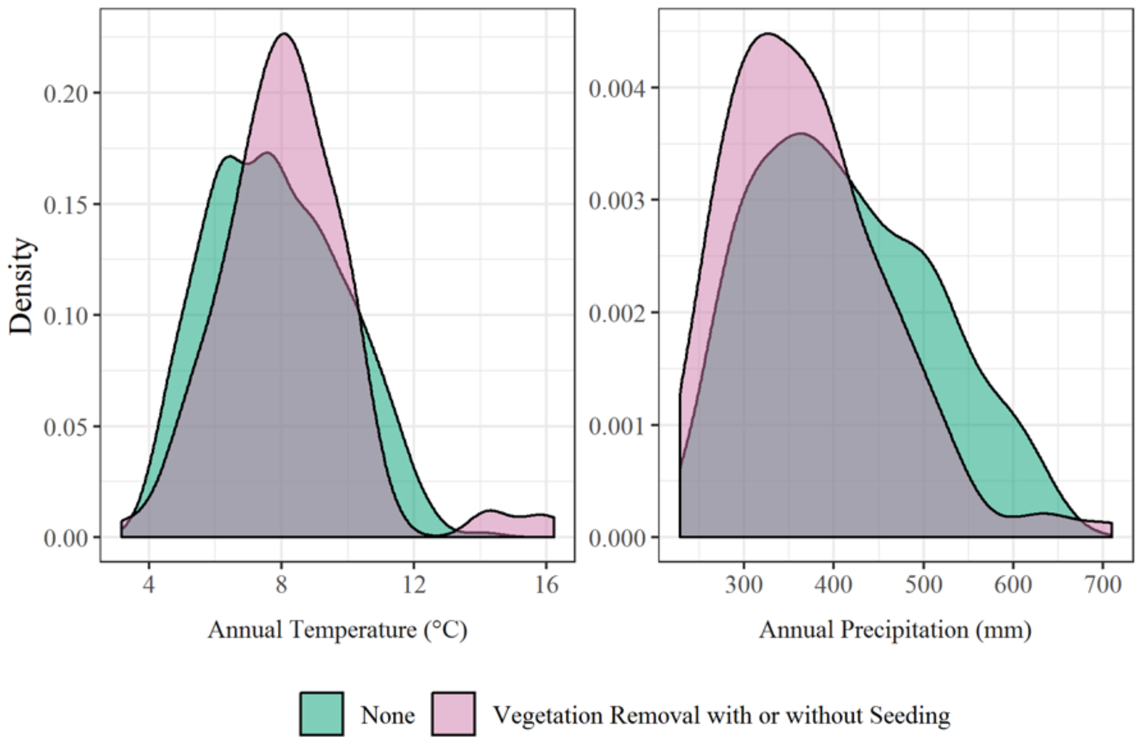


**Figure S3.** Density plots for final dataset for sites without vegetation removal and with vegetation vegetation removal, with or without seeding, for mean annual temperature and precipitation.

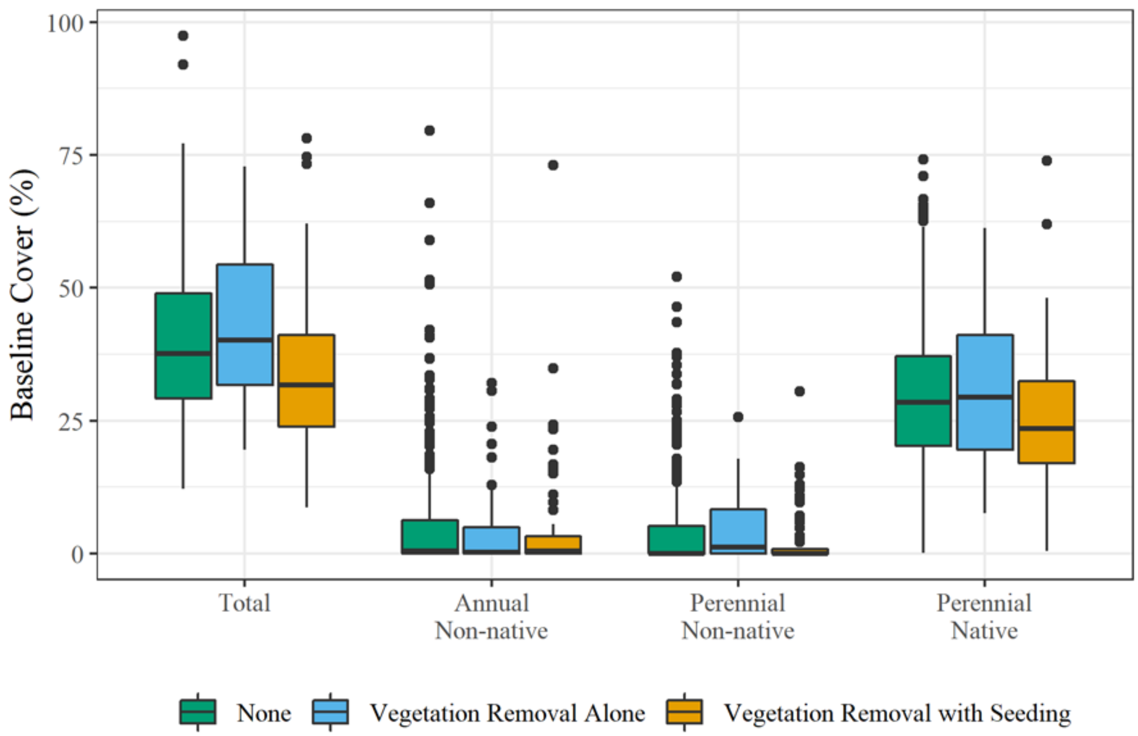


**Figure S4.** Baseline total, annual non-native, perennial non-native, and perennial native cover (percent) by treatment category.

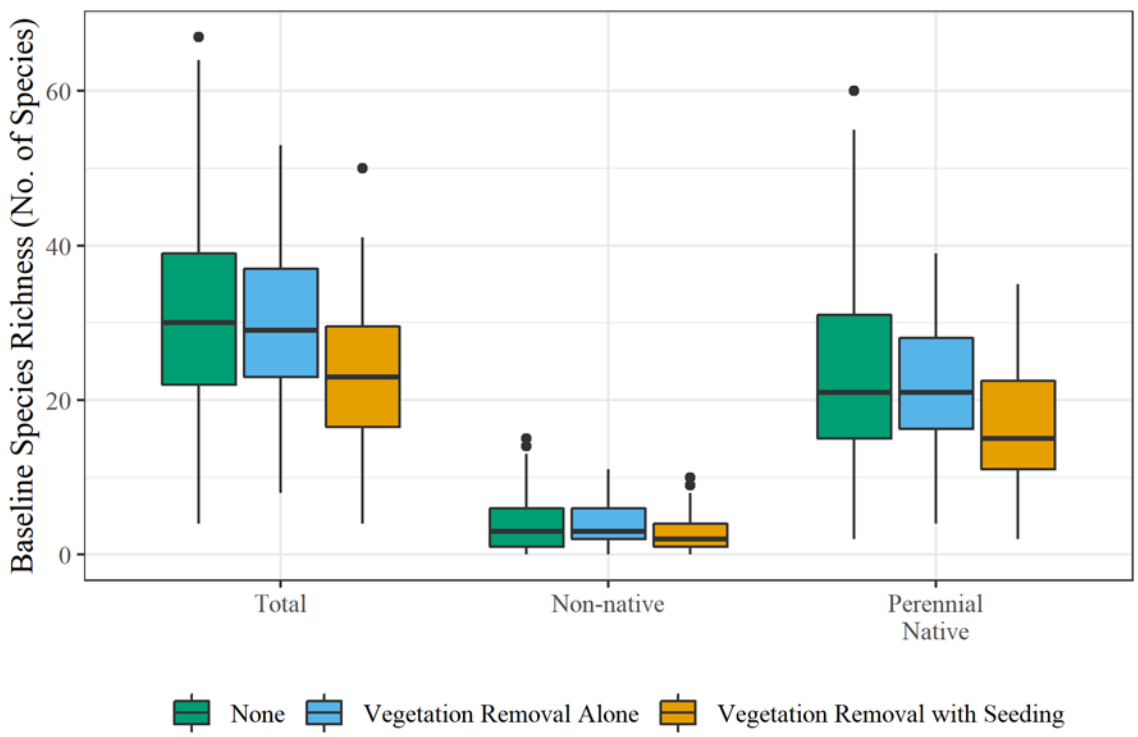


**Figure S5.** Baseline total, non-native, and native perennial richness (number of species) by treatment category.

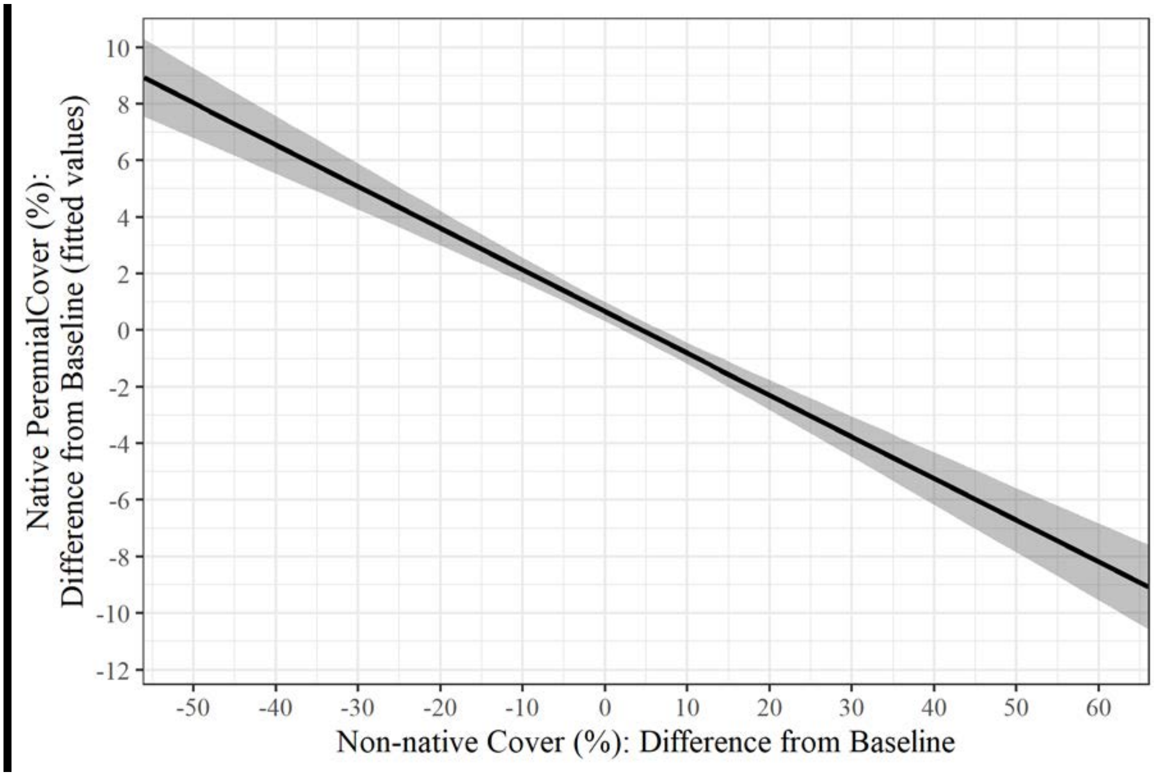


**Figure S6**. Association between change in non-native cover and change in perennial native cover compared to the baseline monitoring period.