THESIS

RESTORATION IMPACTS ON UNDERSTORY PLANT SPECIES IN A COLORADO FRONT RANGE PONDEROSA PINE AND DOUGLAS-FIR FOREST

Submitted by

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ABSTRACT

RESTORATION IMPACTS ON UNDERSTORY PLANT SPECIES IN A COLORADO FRONT RANGE PONDEROSA PINE AND DOUGLAS-FIR FOREST

Land managers working in Colorado's ponderosa pine – dominated forests are faced with many challenges concerning forest health and resiliency, such as higher tree densities, greater risk of high severity wildfire, and depauperate understory plant communities. Restoration treatments designed to move forests toward less degraded conditions that are more in line with those found prior to the settlement era are being increasingly implemented, and have been shown to decrease stand density, minimize ladder fuels, and decrease severe fire risk. However the impacts of such treatments on understory plants are less clear, especially over the long-term. To address this knowledge gap, I quantified changes in the richness, cover, and composition of understory grass, forb, and shrub species, and in the density and composition of trees regenerating in the understory, following restoration treatments at a 383-ha site located near Trumbull, Colorado. The site, which was treated in 2002, was chosen by the Upper South Platte Watershed Protection and Restoration Project (USPWPRP) as a priority area for restoration and was the first area on the Pike National Forest to receive such treatments. In 2004, 15 randomly located 1000-m^2 plots were established in treated stands, with five north-, five south-, and five east- or west-facing plots. Twenty randomly located plots were also established in nearby untreated stands, with slopes, aspects, and elevations comparable to treated plots. Data were collected in 2004, 2005, 2006 and 2014 (two, three, four, and 12 years post-treatment).

Overstory stand structure post-treatment indicated that the goals of the restoration treatment were met, with basal areas reduced from 20.3 to 8.1 m^2 ha^{-1} on north aspects, from 14.8 to 10.9 m^2 ha^{-1} on east and west aspects, and from 12.7 to 5.1 m^2 ha^{-1} on south aspects. Site factors such as treatment and aspect influenced tree seedling (<1.37 m tall) recruitment twelve years post-treatment. Tree regeneration in treated plots consisted of mostly ponderosa pine less than 45 cm tall, suggesting that they largely established post-treatment, while regeneration in untreated plots consisted of mostly Douglas-fir of varying sizes. Understory richness, cover, and composition also changed significantly during the 10-year period of observation. The most dramatic changes occurred on north-facing aspects, perhaps because these relatively mesic aspects are generally considered to be the most favorable for plant growth, and because the considerable reduction in basal area that they experienced ensured that ample resources were available for understory vegetation. Treated plots on north aspects saw increases in total, forb, graminoid, and native species richness in one or more years. Exotic species richness also increased on north aspects following treatment, although values were low. Plant communities further revealed changes in composition between treated and untreated plots on north and east/west aspects post-treatment. This study shows that restoration treatments can stimulate understory vegetation in the long-term, having few negative effects, which would be the increase in exotics and overly abundant tree regeneration on north aspects. Site factors can further influence understory response, with the most dramatic responses occurring on more mesic sites and/or where treatments are most aggressive.

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1. INTRODUCTION

Currently many land managers in dry coniferous forests of the western United Stated are faced with challenges concerning forest health and resiliency, such as elevated stand densities and increased area burned annually by high severity wildfires (Schoennagel et al., 2004). A primary factor that has contributed to these challenges is fire suppression since the settlement era (Baker et al., 2007; Chiono et al., 2012; Donnegan et al., 2001; Knapp et al., 2013; Metlen & Fiedler, 2006). By excluding wildfire from these fire-dependent forests, forest ecosystem dynamics have been changed. We are seeing high densities of ponderosa pine and an increase in small shade-intolerant trees, such as Douglas-fir that contribute ladder fuels, as well as a decrease in understory plant cover and diversity (Fajardo et al., 2007; Moore et al., 2006). Logging and livestock grazing have also contributed to these challenges by removing large diameter trees and disrupting natural fire regimes (Moore et al., 2006). As a result, large amounts of ponderosa pine regeneration established in the early 1900s (Moore et al., 2006) creating dense stands that have allowed for more shade intolerant species to move in; this has affected wildfire size, frequency, and severity by creating vast forest landscapes with heavy ladder and canopy fuels that carry stand replacing crown fires.

Forest restoration treatments aimed at addressing these challenges have become increasingly popular in recent decades (Chiono et al., 2012; Stephens et al., 2012; Youngblood, Metlen, & Coe, 2006). These treatments are intended to create stand structures more resilient to wildfire, such as those that occurred historically (Kaufmann et al., 2001; Kaufmann et al., 2006). Historical reference conditions of stands are typically consulted when deciding on proper restoration goals (Metlen & Fiedler, 2006). These conditions have been obtained through historical accounts and dendrochronological reconstructions of stand structure and disturbance regimes (Kaufmann et al., 2001; Kaufmann et al., 2006). Traditionally, dry coniferous forests have been thought to be adapted to low and moderate severity wildfires with generally lower tree densities than we are currently seeing (Brown et al., 1999; Brown et al., 2004; Dodson, Metlen, & Fiedler, 2006; Kaufmann et al., 2001; 2006; Odion et al., 2014). This disturbance regime creates large-tree dominated stand structures with openings and vigorous understory communities (Metlen & Fiedler, 2006), putting some of the current dry coniferous forests in the west out of their historical range of variability.

Prescribed fire is an attractive restoration treatment option because it can best mimic the natural disturbance process it is designed to replace (Stephens et al., 2012). Yet forest managers in the western United States are constrained by the social stigma of prescribed fires getting out of control, as well as economic and administrative issues that come along with prescribed fire use. Alternatives to prescribed fire, such as mechanical or hand thinning treatments, can also be used to accomplish stand structure goals by reducing tree basal areas, stand density, and ladder fuels (Chiono et al., 2012; Stephens et al., 2012). Common thinning treatments include removing horizontal and vertical fuel loadings to alleviate adverse affects from wildfires by reducing continuity in live and dead forest fuels (Agee & Skinner, 2005; Collins et al., 2007).

Although restoration treatments in dry coniferous forests of the Western United States are often intended primarily to manage potential fire behavior and stand structure, they can also impact understory vegetation diversity, composition, and cover (Dodson et al., 2008). Understory vegetation communities are an important component of these forests, where they provide important ecosystem functions and contain a large portion of forest species diversity (Fajardo et al., 2007, Metlen & Fiedler, 2006). Understory vegetation can be either positively or negatively impacted by treatments (Abella & Springer, 2014; Dodson et al., 2008), with the direction and magnitude of the impact tied to a multitude of factors. Treatments can modify understory vegetation by damaging or killing plants, increasing light, water, and nutrient availability for plant growth, and exposing the mineral soil typically needed for seed germination (Dodson et al., 2008; Hart & Kaye, 1998). Ideally, restoration treatments should maintain or increase total native plant cover and diversity. They can also promote the invasion of undesirable exotic species, particularly if exotics were common within or surrounding the area prior to the treatment and if the treatment heavily disturbs the forest floor (Collins et al., 2007; McGlone et al., 2009). Understory vegetation may experience temporary reductions in cover immediately following treatment, but longer-term increases often subsequently occur (Abella & Springer, 2014). Understory communities also tend to be most stimulated in areas where pre-treatment forests were closed-canopied, where understories were depauperate, and where treatments reduced canopy cover to 50% or less (Stephens et al., 2012; Abella & Springer, 2014), such as on north facing aspects.

In the Colorado Front Range, the first uncharacteristically large and severe wildfire to occur was the Buffalo Creek Fire, which burned in 1996. The Buffalo Creek Fire burned about 4,900 hectares in the Upper South Platte watershed, 37% of which burned as a high severity fire with complete or nearly complete overstory mortality (www.mtbs.gov). Severe storm events immediately following the fire caused considerable runoff and erosion that resulted in two fatalities and adversely affected downstream reservoirs that were critical to Denver's water supply (Culver et al., 2004). The Upper South Platte Watershed Protection and Restoration Project (USPWPRP), a collaborative partnership among Denver Water, the USDA Forest Service, the Colorado State Forest Service, Colorado State University, and the Environmental Protection Agency, was borne in 1998 out of the Buffalo Creek Fire and its aftermath. The project's objectives were to reduce the potential for adverse effects due to wildfire on water quality, human life, and property by creating more sustainable forest conditions that existed prior to human settlement in the early 1800s; sustainable forest conditions were to be created by thinning stands, maintaining snags and downed logs, and establishing openings to promote native vegetation for soil stability (Culver et al., 2004).

In this study, I assessed the short-term (two to four years post-treatment) and long-term (12 years post-treatment) impacts of a 2002 USPWPRP restoration treatment on understory vegetation. This treatment was among the first to be implemented in the Colorado Front Range, and thus it provides a unique opportunity to explore such impacts. Specifically, my objectives were to:

1. Quantify treatment impacts on total understory species richness and cover, and on species richness and cover within groups based on life form, life span, and nativity, across gradients of time since treatment and aspect;
2. Explore treatment-related compositional changes in understory plant communities with respect to aspect and time since treatment; and
3. Examine restoration treatment impacts on the density and composition of tree regeneration across an aspect gradient 12 years post-treatment.

2. METHODS

2.1 Study Area

The study area is located on Pike National Forest lands within the Upper South Platte watershed of the Colorado Front Range, USA, approximately 60 km southwest of Denver (Figure 1). Elevations range from 2000 to 2400m. The climate is warm and dry with average January and July temperatures of -3° C and 18.6°C respectively (www.wrcc.dri.edu). Precipitation averages 40 cm annually, most of which occurs during the summer (www.wrcc.dri.edu). There is no persistent snowpack in most winters. The study area is generally underlain by poorly developed, highly erodible, and excessively drained gravely soils weathered from Pikes Peak granite (Moore, 1992).

Vegetation in the study area is characteristic of montane forests of the Colorado Front Range (Kaufmann et al., 2006; Peet, 1981). Mature ponderosa pine (*Pinus ponderosa*) generally dominates overstories on south and west facing slopes. Ponderosa pine also intermixes with mature Douglas-fir (*Pseudotsuga menziesii*) on northern and eastern slopes. Douglas-fir is commonly present as an understory tree on all aspects. Diverse graminoids (e.g., *Carex rossii*, *Koeleria macrantha*, *Muhlenbergia montana*), forbs (e.g., *Achillea millefolium*, *Allium cernuum*, and *Heterotheca villosa*) and shrubs (e.g., *Ribes cereum*, *Arctostaphylos uva-ursi*) characterize the understory vegetation (Johnston, 2005; Peet, 1981).

Wildfire and management histories are also characteristic of montane forests of the Colorado Front Range (Brown et al., 1999; Donnegan et al., 2001; Kaufmann et al., 2006). Forests historically burned with a mixed-severity fire regime that included surface fires with inclusions of crown fires (Brown et al., 1999). Relic stump observations and historical records suggest several periods of heavy harvesting in the area in the late 1800s and early 1900s, prior to the establishment of the Pike National Forest (DeLay, 1989; Johnston, 2005); grazing was also widespread during this time. A policy of fire suppression has been in place since the early 1900s. The study area has not experienced wildfire, logging, grazing, or other management activities in the last 50 years (Pike National Forest, unpublished data).

2.2 Study Sites

Field sampling was conducted in one treated and two untreated sites. The 383 ha treatment site adjacent to the small town of Trumbull was chosen by the USPWPRP as a priority area for restoration (Johnston, 2005), and was the first area to receive such treatments on the Pike National Forest. Mechanical treatments were implemented from September to November 2002. Trees up to approximately 35 cm in diameter at breast height (DBH; 1.37 m) were sheared near ground level using a boom-mounted hot saw on a tracked vehicle that could maneuver on slopes up to 60%. Cut trees were crushed and broken apart by driving over them with the vehicle. In early 2003, hand crews used chain saws to further reduce stand densities. Hand crews also sectioned, piled and burned some residual slash material. Untreated sites at Hatch Gulch (279 ha) and Sugar Creek (268 ha) were selected to match the physical-environmental conditions, land use history, and stand structure of the Trumbull site prior to treatment. Both untreated sites were positioned as close as possible to the treated site, and are within four kilometers

2.3 Field Sampling

Plot establishment occurred during the summer of 2004, two years following the treatment at Trumbull (Figure 1). All plots were 20-m × 50-m (1000-m^2) in size and were randomly located. At the treated site, 15 plots were established. They were stratified by aspect, with five each on north-, south-, and east- or west-facing slopes (± 20° of the cardinal direction). Thirteen untreated plots were established in the Sugar Creek site and seven untreated plots were establishedin the Hatch Gulch site. Untreated sites combined, five north-, seven south-, and eight east- or west-facing plots were estabished. Plots were separated by at least 100 m. Plots were installed with the long side placed perpendicular to the contour of the slope. Slope, aspect, elevation, and UTM coordinates were subsequently measured in the field for each plot.

2.4 Overstory Tree and Tree Regeneration Measurements

To assess overstory stand structure in each 1000-m^2plot, all trees over breast height (1.37 m) tall were permanently tagged and measured for DBH, species, and live or dead status. To reconstruct pre-treatment structure in the treated plots, all recently cut trees (i.e., stumps) were also tagged and measured for species and diameter at stump height (DSH), and their pre-treatment DBH was estimated from a linear regression based on DBH and DSH measurements of trees in two untreated plots (*DBH = -2.8617 + 0.9025 x DSH*, n=139, r^2=0.99). Cut trees whose reconstructed DBH values were negative were assumed to have been less than breast height tall at the time of treatment and were dropped. Measurements occurred in 2004 or 2005, two to three years following treatment.

Tree regeneration was recorded during the summer of 2014, 12 years post-treatment. In each plot, the height and species of all live trees less than breast height tall were measured in 12 5-m^2 plots, located at the 0-m, 7.5-m, and 15-m marks of four 15-m transects. The 15-m transects ran parallel to the short side of the plot and were equally spaced along the long side of the plot.

2.5 Understory Vegetation Measurements

Understory vegetation (less than breast height tall) data were collected using the modified-Whittaker nested vegetation sampling method (Stohlgren, Falkner, & Schell, 1995). Surveying occurred during the summers of 2004, 2005, 2006, and 2014, two, three, four, and 12 years post-treatment. Plots were surveyed in a random order every year to avoid biases due to changes in plant phenology across the survey period. Percent cover of each understory plant species and of forest floor components such as soil, litter, rock, and wood was estimated in 10 1-m^2 subplots that were arranged systematically inside the perimeter of the 1000-m^2 plot. The presence of all additional species was also documented for the plot. Most plants were identified to species but some species that were difficult to distinguish outside of peak morphological development were identified to genus (i.e. *Carex, Chenopodium, Solidago*); hereafter, plants identified only to genus are also referred to as species.

Species were subsequently classified in three ways. First, species were classified by their life form as forbs, graminoids, shrubs, or trees. Second, species were classified by their life span as either short-lived or long-lived species. Short-lived species are those species that are annual or biennial and long-lived species are those that are perennial. Lastly, species were classified as either native or exotic to the continental United States. Classifications were made using the USDA Plants Database (www.plants.usda.gov).

2.6 Statistical Analysis

I evaluated the representativeness of the untreated plots by comparing their topographic characteristics, such as slope and elevation, to topographic characteristics of the treated plots. I also compared stand structure characteristics such as basal area (BA), trees per hectare (TPH), quadratic mean diameter (QMD), percent ponderosa pine BA, percent ponderosa pine TPH, and ponderosa pine QMD of untreated plots to the pre-treatment reconstructions of the treated plots. These analyses were performed using an analysis of variance (ANOVA) in SAS OnDemand (GLIMMIX procedure; SAS Institute Inc., Cary, NC, US), modeling the characteristics against aspect, treatment, and their interaction. Distributions used were negative binomial for slope, elevation, TPH, and QMD, and lognormal for BA. Percent ponderosa pine BA and TPH were modeled with a beta distribution and were rescaled prior to analysis to accommodate zero values in the dataset (Smithson & Verkuilen, 2006). Site was included in the models as a random effect. Post-hoc least squares means tests were calculated for aspect × treatment, “slicing” on aspect to isolate treatment effects for each aspect. Significance was determined using a $P < 0.05$.

To evaluate restoration effects on overstory trees and tree regeneration, I compared BA, TPH, QMD, percent ponderosa pine BA, percent ponderosa pine TPH, and ponderosa pine QMD for untreated and treated plots two years post-treatment, and I compared tree regeneration per hectare for untreated and treated plots 12 years post-treatment. Analyses were performed in SAS ONDemand (GLIMMIX procedure) as above. A negative binomial distribution was used in the model for tree regeneration.

Restoration impacts on a variety of understory species richness and cover characteristics two, three, four, and 12 years post-treatment were examined using repeated measures ANOVA in SAS OnDemand (GLIMMIX procedure). Graminoids, forbs and shrubs were included in analyses, but trees were not. Analyses were conducted by modeling each richness and cover characteristic against aspect, treatment, year, and all interactions. Richness was modeled with a Poisson distribution and cover was modeled with a beta distribution; cover of exotic species, shrubs, and short-lived species were rescaled prior to analysis to accommodate zero values in the dataset (Smithson & Verkuilen, 2006). The spatial power covariance structure was used in all models to account for a higher level of correlation between two repeated observations closer in time than between two observations further apart in time. Site was included in the models as a random effect. Post-hoc least squares means tests were performed for aspect × treatment × year, "slicing" on aspect × year to isolate treatment effects for each aspect × year combination. Significance was determined using a $P < 0.05$ and marginal significance was determined using a $P < 0.10$.

Differences in understory plant composition among plots were investigated using Non-Metric Multidimensional Scaling (NMDS) and Multi-Response Permutation Procedures (MRPP) in PC-ORD 6.0 (McCune & Grace, 2002). These analyses utilized species-level absolute cover data, with species that were present in the 1000-m^2 plot but not in any cover subplots given a nominal value of 0.01%. As with richness and cover analyses, tree species were excluded. Two separate NMDS ordinations were created, for two and 12 years post-treatment, to visualize compositional differences with respect to aspect and treatment for those years. Dimensionality of the data sets was assessed by running 250 preliminary ordinations using a step-down in dimensionality procedure (i.e. one- through three-dimensional solutions were calculated for each of the 250 runs) and a random starting configuration. Each run used the Sørenson distance measure to calculate the distance matrix, a stability criterion of 0.000001, and a maximum of 500 iterations. The best preliminary ordinations were the ones whose configurations minimized the number of dimensions while minimizing stress, and where the Monte Carlo P-value from 250 runs with randomized data was less than 0.05. Final ordination runs were conducted with the optimal preliminary ordination configurations used as the starting configurations. The final ordinations were rotated to align aspect with axis 1. I used Multi-Response Permutation Procedures (MRPP) in PC-ORD to test for differences in composition between treatments. Analyses were conducted separately for each aspect × year combination (six analyses). A Sørenson distance measure was used again to calculate the distance matrix and enhance correspondence between the NMDS and MRPP results. The data were rank-transformed to help correct the loss of sensitivity of distance measures as community heterogeneity increased (McCune & Grace, 2002). Significance was assessed with a Bonferoni adjusted p-value ($P < 0.008$ (0.05/6)) to account for multiple comparisons.

An Indicator Species Analysis (ISA) was done in PC-ORD on absolute cover data collected two and 12 years post-treatment. This method was used to contrast performance of individual species between treated and untreated plots. In contrast to other analyses, we analyzed all plots together rather than by aspect to identify those species that were universally representative of the treated and untreated conditions for that year. An indicator value (IV) of zero means no indication and one means perfect indication, where perfect indication means that the presence of a species points to a particular group without error. Species were then assigned as an indicator to the group for which it achieved the highest IV and a Monte Carlo p-value of less than 0.05.

3. RESULTS

3.1 Representativeness of Untreated Plots

The topographic and stand structure characteristics of the untreated plots generally reflect those of the treated plots prior to treatment (Table 1). Treated and untreated plots did not differ in elevation for any of the three aspect categories, and they did not differ in slope except on east/west aspects; slopes of untreated east/west plots were 12% greater than those treated east/west plots. Furthermore, stand reconstructions of the treated plots revealed that prior to treatment TPH, QMD, as well as percent ponderosa pine BA, percent ponderosa pine TPH, and ponderosa pine QMD were comparable among treated and untreated plots for all aspects. Basal area between untreated and treated plots prior to treatment was also similar on north and east/west aspects, but on south aspects BA was 30% lower in treated than untreated plots.

3.2 Treatment Effects on Overstory Tree Structure

The restoration treatment had a large impact on overstory structure (Table 2). Two to three years following the treatment, plots that were treated had BA reduced by 60% on north aspects, 27% on east/west aspects, and 59% on south aspects relative to those that were untreated. Similarly, TPH in treated plots, when compared to untreated plots, was reduced by 92% on north aspects, 75% on east/west aspects, and 77% on south aspects. Small overstory trees were targeted for removal during the treatment, which increased the QMD of the treated plots relative to the untreated plots for north and east/west aspects, with QMDs of treated plots 17 cm and 14 cm greater on north and east/west aspects, respectively, than those of untreated plots. Although not significant, percent ponderosa pine BA increased from 87% to 93% and percent ponderosa pine TPH increased from 81% to 96% averaged across all aspects following treatment. Ponderosa pine QMD increased on north aspects from 18 cm to 31 cm.

3.3 Treatment Effects on Tree Regeneration

Tree regeneration densities (trees < 1.37 m tall) were highly variable across the plots 12 years post-treatment. Total tree regeneration density varied with aspect ($P < 0.001$) and with the interaction of treatment and aspect ($P = 0.007$), but not with treatment per se ($P = 0.714$) (Figure 2). Regeneration values in treated and untreated plots were comparable on north and east/west facing aspects. Meanwhile on south facing aspects, regeneration was 85% greater in untreated than in treated plots. Most of the tree regeneration was occurring on north aspects in both treated and untreated plots. For all aspects, treated plots were dominated by ponderosa pine regeneration, which comprised 93% of all regenerating trees (Figure 2a). Furthermore, regeneration in treated plots tended to be small, with nearly all seedlings under 45cm in height (97% of all regeneration, Figure 2b). However, in untreated plots, regenerating trees were largely Douglas-fir (90% of all regeneration), and regenerating trees over 45 cm tall were more commonly encountered (26% of all regeneration).

3.4 Treatment Effects on Understory Vegetation

A total of 173 understory plant species were found across all 35 plots and all 4 years of observation. Of these species 127 were forbs, 27 were graminoids, and 19 were shrubs; 41 were short-lived species and 132 were long-lived species; 152 were native species and 21 were exotic species. Of the exotic species, six are Colorado List B and two are Colorado List C noxious weeds (Table 4).

When I examined total understory plant species richness and cover, treatment effects were most pronounced on north slopes (Table 3, Figure 3). On north aspects, total richness was greater in treated plots than in untreated plots for all years of observation, with 1.5 times more species found in treated plots across all years. On east/west aspects, total richness was also greater in treated than in untreated plots three years post-treatment. Total cover was marginally greater on north-facing treated plots compared to their untreated counterparts four years post-treatment, and were significantly greater 12 years post-treatment; values in north-facing treated plots were 2.1 times greater than in untreated plots four years post-treatment, and 2.3 times greater 12 years post-treatment.

When I analyzed the understory vegetation data by life form, treatment effects were found for forb richness, graminoid richness, and shrub cover (Table 3, Figure 4), and differences were seen on north and east/west aspects. On north aspects, both forb and graminoid richness were greater in treated than untreated plots two, three, and four years post-treatment; forb richness was also marginally greater 12 years post-treatment. Averaged across all years with significant or marginally significant differences, forb richness in north-facing plots was 1.6 times greater in treated than untreated areas, while graminoid richness was 1.5 times greater. Also on north aspects, shrub cover was significantly greater 12 years post treatment, with 2.9 times greater cover in treated than untreated plots in this year. Meanwhile, east/west facing plots were also somewhat responsive to the treatment, with 1.4 times and 1.3 times more forb species found in treated than untreated plots three and four years post-treatment. Shrub cover was also significantly higher on east/west aspects three, four, and 12 years post-treatment, averaging 8 times greater cover in treated than untreated plots for those three years of observation. Shrub species that were most prevalent were *Arctostaphylos uva-ursi* (kinnikinnik), *Ribes cereum* (wax currant), and *Cercocarpus montanus* (mountain mahogany).

When I examined the understory vegetation richness and cover data based on life span classifications, treatment effects were also found, but again they were primarily restricted to north aspects (Table 3, Figure 5). On north aspects, short-lived species richness was dramatically higher in treated than untreated plots for all four years of observation; 13 short-lived species were found on treated plots and three were found on untreated plots averaged across all years, a 4.4-fold increase due to treatment. Also on north aspects, short-lived species cover showed a significant increase (7.5-fold) in treated plots two years post-treatment, and a marginal increase in treated plots 12 years post-treatment. Similarly, long-lived species richness was significantly greater in north-facing treated plots three and four years post-treatment and marginally greater two and 12 years post-treatment; averaged across all years, 46 long-lived species were found on treated plots and 37 were found on untreated plots, an increase due to treatment of 1.2 times. Long-lived species cover was significantly greater four and 12 years post-treatment, with long-lived species cover 2.1 and 2.3 times greater in treated plots in these years.

Lastly, when I parsed the understory vegetation richness and cover data by nativity, treatment effects were found for both native and exotic richness as well as for native cover, but only on north aspects (Table 3, Figure 6). Native richness in treated plots was marginally or significantly greater two, three, and four years post-treatment, while exotic richness was marginally or significantly greater in treated plots for all years of observation. Averaged across all years, native richness was 1.3 times greater in treated than untreated plots. Seven exotic species were found on treated plots and less than one (0.2) was found on untreated plots averaged across all years, an increase due to treatment of 34 times. Native cover also showed a significant increase on north aspects in treated plots 12 years post-treatment, with native cover 2.2 times greater in treated than untreated plots in this year. Exotic cover showed a marginal increase in treated plots on north aspects four years post-treatment. Exotic species driving the increases in exotic richness in treated plots included those on the Colorado noxious weed list such as the long-lived forb *Linaria vulgaris* (butter and eggs) and the short-lived forb *Verbascum thapsus* (common mullein), as well as those not on the list such as the short-lived forbs *Lactuca serriola* (prickly lettuce) and *Tragopogon dubius* (yellow salsify) (Table 4). Nonetheless, plant communities in treated plots remained native-dominated, with exotics averaged across all years accounting for 11% of total richness on north aspects, and 7% to 8% on east/west and south aspects, and 6% of total cover on north aspects, and 1% to 2% on east/west and south aspects. Exotics were virtually absent from untreated plots, accounting for only 2% of total richness and <1% of total cover across all aspects and years.

The NMDS ordination for plots two years post-treatment (2004) yielded a three-dimensional solution that explained 78% of the total variation in the understory plant community data set (Figure 7a, stress = 10.8, P = 0.004), and the NMDS ordination for plots 12 years post-treatment (2014) yielded a three-dimensional solution that explained 74% of the total variation (Figure 7b, stress = 11.9, P = 0.004). Axis 1 explained 65% of the variation in the data set in 2004 and 53% of the variation in 2014; furthermore, axis 1 strongly separated plots by aspect for both years, indicating that plant communities on north, east/west, and south plots differed markedly in their composition. Meanwhile, axis 2 explained 12% of the variation in 2004 and 20% of the variation in 2014, and separated the plots somewhat by treatment, indicating modest compositional differences due to treatment. The MRPP results further support this interpretation, and show that two years post-treatment, treated and untreated plots were compositionally different only on east/west facing aspects, while 12 years post-treatment, treated and untreated plots were compositionally different on north and east/west facing aspects (Table 5).

ISA yielded six potential indicator species for the untreated plots and 17 species for the treated plots in 2004. The top indicator species in 2004, two years post-treatment, were *Ribes cereum*, a native long-lived shrub, in the untreated plots and *Chenopodium spp.*, a native short-lived forb, in the treated plots (Table 6). In 2014, 12 years post-treatment, there were 16 potential indicator species for the treated plots and only one indicator species for the untreated plots (Table 5). The top indicator species in 2014 were the native perennial forb *Chamaesyce fendleri* in the untreated plots and the exotic short-lived forb *Verbascum thapsus* in the treated plots (Table 5).

4. DISCUSSION

4.1 Representativeness of Untreated Plots

The restoration treatment at Trumbull was the first of its kind to be implemented on the Pike National Forest and one of the first to be implemented in the Colorado Front Range, limiting the availability of replicate treatments sites and creating challenges related to pseudoreplication (Hurlbert, 1984, van Mantgem et al., 2001). Pseudoreplication is defined as "the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent" (Hurlbert, 1984). I attempted to minimize these challenges using a variety of tactics so that much-needed information on the short- and long-term effects of restoration treatments could be obtained. First, untreated sites were carefully selected to represent the pre-treatment condition of the treated site. This was verified by comparing topographic and pre-treatment stand structural characteristics between untreated and treated plots; with the exception of slope on east/west aspects and BA on south aspects, all characteristics were found to be similar between the two plot types. Second, plots were located at least 100 m apart (and were usually at least 200 m apart) to minimize the likelihood that plots within sites were correlated. Third, site was included in the ANOVA models as a random effect, thereby accounting for the fact that plots were clustered within sites in the analyses. Together, these tactics give me confidence that the significant differences found here represent a treatment effect, and are not an artifact of a pseudoreplicated study design.

4.2 Treatment Effects on Overstory Tree Structure

Restoration treatments are becoming increasingly utilized to make overly dense Colorado Front Range and other western dry coniferous forests more resistant to uncharacteristically severe wildfires (Miller & Urban, 2000; Youngblood et al., 2006). This can be done by restoring forest stands toward a more historical condition that retains large old growth trees and decreases the density of trees to create large canopy openings. Post-treatment stand characteristics indicate that this objective was likely met at the treated site I studied. Increases in QMD following treatment suggest that most of the trees removed were of smaller diameter and the larger old growth trees were retained. This reduced the treated sites basal area by 50% across all aspects, creating a forest stand structure with large canopy openings. Furthermore, ponderosa pine trees were favored over Douglas-fir, as percent of BA and TPH comprised by ponderosa pine increased post-treatment.

Changes like these to the stand structure can reduce the risk of severe wildfire by decreasing ladder fuels that could carry a surface fire into the forest canopy and by breaking up the forest canopy (Knapp et al., 2013). Mechanical thinning is designed to develop and protect the vertical and horizontal forest structure from disturbance (Youngblood et al., 2006). Removing small trees from below the forest canopy reduces ladder fuels that could potentially carry a surface fire into the crown of the forest as well as the continuity of canopy vegetation (Stephens et al., 2012; Youngblood et al., 2006). For example, research modeling fire hazard and fuel treatment longevity of a mechanically thinned coniferous forest site found that fire hazard noticeably decreased seven years post-treatment, and fire hazard was considered low (Stephens et al., 2012); this same study also found that fire hazard significantly increased seven year post-treated in control units that experienced no fuel treatments, and this indicates that continued passive management of coniferous forests has further increased the already high fire hazards (Stephens et al., 2012).

4.3 Treatment effects on Tree Regeneration

Tree seedling establishment in dry coniferous forests is known to be impacted by factors such as weather and site conditions (Kaufmann et al., 2000; Knapp et al., 2013). My findings illustrate the effects that site factors, such as aspect and overstory stand structure, have on the density and composition of regenerating trees. I found seedlings were considerably more abundant on north aspects in both treated and untreated plots where microclimates are most suitable for germination and survival (Knapp et al., 2013). Coarse woody debris resulting from the treatment may have also created “safe sites” for seedling establishment and survival in treated plots, as woody debris provides dead shade, reduces temperatures near the soil surface, and may increase humidity levels (Fajardo et al., 2007). Interestingly, total regeneration densities did not differ between treated and untreated plots on north aspects, but composition did. Despite the presence of some large overstory ponderosa pine trees in untreated north-facing plots, the majority of regeneration there consisted of Douglas-fir. This could suggest that there may be a lack of suitable sites for pine regeneration, which has also been noted by others (Knapp et al., 2013). Douglas-fir, however, is a shade tolerant species that regenerates well under dense canopies without disturbance to create bare mineral soil (Knapp et al., 2013). On north-facing treated aspects, the lack of a comparable amount of Douglas-fir regeneration suggests that much of the pre-existing regeneration was likely killed in these plots during treatment activities. Instead, on north-facing treated plots, most of the regeneration was comprised of ponderosa pine. These regenerating trees were primarily less than 45 cm tall, suggesting that they established post-treatment in response to the increased availability of bare mineral soil (Knapp et al., 2013). Significant recruitment has been found to occur for up to 10 years after the stand is treated (Fajardo et al., 2007; Thomas & Waring, 2014).

Overly abundant regeneration, in both untreated and treated plots, should be monitored and possibly managed for. The presence of Douglas-fir regeneration of multiple size classes in untreated areas poses a risk to fire hazard. These trees contribute to ladder fuels and reduce crown base height making it easier for a surface fire to become a crown fire (Youngblood et al., 2006). In treated plots, ponderosa pine has been regenerating in dense cohorts, especially on north aspects, which if left unmanaged could revert back to stand conditions similar to those that were found pre-treatment.

4.4 Treatment Effects on Understory Vegetation

Restoration treatments can have both positive and negative effects understory vegetation. The initial effects on vegetation after treatment can cause damage and kill some plants from heavy equipment, as well as allow for invasion of exotic species into newly disturbed areas. However, reducing overstory trees creates less competition and increases the availability of light, water, and other resources; these factors ultimately produce vigorous and diverse understory communities (Knapp et al., 2013; Moore et al., 2006). Creating productive and diverse understory vegetation communities can create forage for wildlife and protect soil from erosion (Moore et al., 2006). In this study, restoration treatments aimed at creating more appropriate overstory stand structure conditions also maintained or increased understory species richness and cover and modestly altered species composition; increases in richness and cover in treated plots were most apparent on north aspects, very variable on east/west aspects (i.e. forb and graminoid cover was higher in untreated plots), and no differences were found on south aspects. The changes in richness, cover, and composition that I observed were driven by the establishment of long-lived and short-lived graminoids and forbs, which by and large were native. While changes were observed for all four periods of observation, increases in vegetation cover largely depended on time since treatment with significant increases occurring four or more years post-treatment. My findings are consistent with those of other studies (Abella & Springer, 2014; Collins et al., 2007; Dodson et al., 2008; Knapp et al., 2013; Metlen & Fiedler, 2006; Moore et al., 2006; Wayman & North, 2007), and taken as a whole, they suggest such treatments may also be effective at moving understory plant communities toward conditions believed to prevalent historically (Metlen & Fiedler, 2006).

While the restoration treatments can increase understory species richness and cover, in my study these significant findings were constrained mostly to plots on northern aspects (Figure 8). Aspect is a major environmental gradient that determines where and how readily vegetation can become established. In the northern hemisphere, air temperature, soil temperature, and vapor pressure deficit all tend to be lower on north aspects, making the environment more conducive to plant growth (Cantlon, 1953). I found that north facing treated plots contained 45% more understory species and averaged 10% more cover compared to south facing plots, suggesting that understory plants were able to benefit from these conditions once much of the forest overstory was removed. Similar findings were also shown by Olivero and Hix (1998), who found that species richness was significantly higher on north aspects compared to south aspects. North aspects in the treated unit contained the highest BA and tree density pre-treatment and experienced the largest reduction in those measurements due to thinning. This could also contribute to strong increases in richness and cover, because effects on understory vegetation have been found to be most pronounced where these measurements are initially low under closed canopies (Abella & Springer, 2014; Dodson et al., 2007).

Understory responses to the restoration treatment varied across species life form and longevity groupings, similar to findings supported by other research (Collins et al., 2007; Dodson et al., 2007; 2008; Metlen & Fiedler, 2006; Moore et al., 2006; Thomas & Waring, 2014). Forbs and graminoids had the most positive response in terms of increasing species richness in response to thinning. Similarly, short-lived species (annual/biennial forbs and graminoids) also responded positively to the treatment. Site disturbances that expose bare mineral soil and increase light availability must occur in order for short-lived species to become established (Dodson et al., 2007). Fire-excluded pine forests are experiencing an absence of short-lived species that are occurring in forests that have burned recently; this indicates that they might need disturbance to remain part of the vegetation community (Dodson et al., 2007). Shrub cover also responded positively to the treatment, with the greatest increases on east/west aspects, but this large increase was due to the fact that shrub cover was very low in east/west untreated plots.

Although restoration treatments aim to promote native understory species, the disturbance created can also allow for the establishment of exotic species (McGlone et al., 2009). Consequently, when there is a disturbance created from a thinning, this gives some exotic species an advantage to compete more effectively in higher resource areas (Metlen & Fiedler, 2006). Exotics were also favored particularly on north aspects, comprising 11% of total richness and 6% of total cover. The treatment site had eight Colorado noxious weeds invade the area and these noxious weeds were found more around areas of heavy disturbance, such as old burn pile scars. However, exotic richness and cover remained relatively low and plant communities are still dominated by native vegetation. Invasion of exotic species is dependent on characteristics of the invading species, the susceptibility of the system, and climate (Dodson et al., 2008; Abella & Fornwalt, 2014). Considering studies that have looked at exotic cover response post-wildfire (Abella & Fornwalt, 2014; Fornwalt et al., 2010), this study found comparable exotic coverage percentages to areas that had experienced low to moderate burn severity. Although an increase in exotic species may be unavoidable, these short-term consequences may be better to deal with than the risk of catastrophic wildfire burning through the ecosystem, potentially creating an even more suitable environment for exotics in severely burned areas (Abella & Fornwalt, 2014; Dodson et al., 2008; Metlen & Fiedler, 2006). The presence of exotic species (especially noxious) can be important to note because they can potentially change plant community composition resulting in effects on water/nutrient availability and fuel/fire dynamics (Collins et al., 2007) and should be monitored.

Community composition of treated areas can also shift and create varying species composition across a landscape. The variance in compositional difference among plots was mostly explained by aspect, regardless of treatment, and this is due to preferred growing environments for individual plants (Olivero & Hix, 1998). Untreated plots two years post-treatment were indicated by *Ribes cereum*, which is a native long-lived shrub species. Treated plots two years post-treatment were indicated by *Chenopodium spp.,* which can be a native short-lived (annual) species that prefers full sunlight. Treated and untreated plots had different species compositions on east/west aspects two years post-treatment, which changes could have occurred in the two growing seasons post-treatment and before the area was first monitored in 2004. Untreated plots 12 years post-treatment were indicated by *Chamaesyce fendleri*, which is a native long-lived plant that grows from a large woody taproot in either sun or shade. Treated plots 12 years post-treatment were indicated by *Verbascum thapsus*, which is an exotic short-lived species that prefers full sunlight and site disturbance. Potential factors influencing changes in species composition could be the change in site conditions and the interaction between the existing plant community and the treatment (Wayman & North, 2007).

Species cover was comparable to untreated plots initially after treatment but total species and some species groups experienced increased cover four or more years post-treatment. Responses of understory vegetation have been found to vary depending on the percentage of the canopy that is opened up and the accumulation of course woody debris (Abella & Springer, 2014; Collins et al., 2007). A commonality among several studies that found long-term increases in vegetation cover occurred from a substantial reduction in overstory tree basal area that persisted through time (Abella & Springer, 2014). An initial resource pulse after the treatment could have contributed to increased exotic richness, but exotic species may end up being relatively short-lived once resources start to become more limiting over time, which in turn favors more resource efficient natives (Metlen & Fiedler, 2006). Low levels of vegetation cover initially after treatment were likely due to heavy equipment use and leftover slash from the restoration treatment obstructing immediate growth (Metlen & Fiedler, 2006). It has been suggested though that thinning alone is not sufficient enough to remove small trees and promote nutrient cycling (Metlen & Fiedler, 2006), and that thinning treatments followed by prescribed burning can promote fire-dependent flora while stimulating nutrient cycling and decomposition resulting in greater belowground resource availability (Dodson et al., 2007; Grady & Hart, 2006; Metlen & Fiedler, 2006; Wayman & North, 2007).

5. CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Restoration is meant to be a process by which management actions return the function and structure of an area to conditions that are compatible with its historical range of variability (Covington et al., 2006; Metlen & Fiedler, 2006). Monitoring of these management actions allows managers to better assess how well a treatment satisfied this goal. This and other studies conducted in dry coniferous forests of the western United States have shown that restoration treatments aimed at reducing the risk of uncharacteristically severe fire by modifying overstory structure may have few unfavorable effects on understory vegetation (Abella & Springer, 2014; Collins et al., 2007; Dodson et al., 2008; Knapp et al., 2013; Metlen & Fiedler, 2006; Moore et al., 2006; Wayman & North, 2007). These treatments can potentially enhance understory plant richness and cover, especially in areas where pre-treatment forests were dense and treatments were aggressive enough to substantially change the stand structure (such as on north aspects), and especially over the long-term (such as 10 or more years post-treatment). Although post-treatment exotic invasions generally occur, in many cases the level of increase is minor as I found, and not likely to inhibit native plants or cause other ecological damage. Nonetheless, exotic species in restored areas should be carefully monitored and potentially controlled if this falls in line with management goals. Perhaps the most noteworthy unfavorable effect may be a considerable amount of post-treatment tree regeneration on north aspects. Some new regeneration is desirable in treated areas, and the dominant species I found (ponderosa pine) regenerating in these areas is more desirable than the dominant species I found regenerating in untreated areas (Douglas-fir). Nonetheless, the level of regeneration is excessive and may likely cause management challenges in the future (Thomas & Waring, 2014). Regeneration should probably be effectively controlled in order to not repeat the same cycle of overly dense forest growth. If treatments are revisited and maintained in the future, efforts could potentially be focused toward north aspects where most of the tree regeneration is occurring.

This and other studies can also provide managers and other interested parties with insight into approaches for monitoring understory vegetation. Understanding of the responses seen after a forest stand is restored can create even better decision-making when it comes to future treatments. Gathering measurements before and after treatments, in both treated and untreated areas, would provide a more complete picture of the changes in understory vegetation caused by treatments (Underwood, 1992). Early monitoring is important to capture any initial changes in disturbance based species, both native and exotic (Abella & Springer, 2014). Delayed increases in understory vegetation cover indicate that monitoring should also take place at least 4 years post-treatment to accurately assess the long-term trajectory of these plant communities. Monitoring both total understory species and specific groups of species (i.e. exotic, short-lived, etc.) can show competitive advantages of certain species groups (Abella & Springer, 2014). Also if available, more than one treated area should be monitored along with untreated areas to avoid a pseudoreplicated study design. Considering factors like these in a monitoring program will enhance study designs and statistical analyses used to detect impacts of restoration treatments.

6. TABLES AND FIGURES

Table 1. Pre-treatment means (standard error) of slope, elevation, basal area (BA), trees per hectare (TPH), and quadratic mean diameter (QMD) for all live trees greater than 1.37 m tall, and for ponderosa pine (PIPO), in treated plots (n=15) and untreated plots (n=20) in the Colorado Front Range. Bolded *P* values are < 0.05. Pairwise differences between treated and untreated plots within each aspect category are indicated with letters next to the means.

Aspect And Treatment	**Slope (%)**	**Elevation (m)**	**BA (m^2 ha^{-1})**	**TPH (trees ha^{-1})**	**QMD (cm)**	**PIPO BA (%)**	**PIPO TPH (%)**	**PIPO QMD (cm)**
NORTH								
Treated	29.0	2056	19.3	1928	11	72	55	13
	(4.3)	(25.3)	(1.3)	(102.5)	(0.5)	(11.1)	(12.4)	(1.1)
Untreated	35.6	2125	20.3	1194	15	56	39	18
	(2.6)	(46.5)	(1.2)	(148.3)	(0.7)	(10.4)	(7.6)	(1.3)
EAST/WEST								
Treated	24.0 ^{a}	2052	17.7	732	18	94	94	18
	(2.9)	(13.9)	(2.1)	(98.9)	(0.9)	(5.8)	(5.5)	(1.0)
Untreated	35.4 ^{b}	2152	14.8	480	20	67	57	23
	(1.7)	(28.1)	(1.3)	(47.5)	(1.5)	(10.1)	(11.4)	(1.4)
SOUTH								
Treated	32.8	2104	8.8 ^{a}	296 b	21	97	94	21
	(1.8)	(21.8)	(1.5)	(84.1)	(2.0)	(2.8)	(3.1)	(2.0)
Untreated	33.4	2142	12.7 ^{b}	272 b	27	96	94	27
	(2.7)	(44.3)	(1.5)	(78.5)	(2.3)	(1.7)	(2.7)	(2.5)
***ANOVA* Results**	***p***	***p***	***p***	***p***	***p***	***p***	***p***	***p***
Aspect	0.306	0.297	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Treatment	**0.007**	0.596	0.359	0.436	0.436	0.611	0.564	0.223
Aspect × Treatment	0.108	0.586	0.055	0.555	0.725	0.311	0.108	0.956

Table 2. Post-treatment means (standard error) of basal area (BA), trees per hectare (TPH), and quadratic mean diameter (QMD) for all live trees greater than 1.37 m tall, and for ponderosa pine (PIPO), in treated plots (n=15) and untreated plots (n=20) in the Colorado Front Range. Bolded *P* values are < 0.05. Pairwise differences between treated and untreated plots within each aspect category are indicated with letters next to the means.

Aspect and Treatment	**BA (m^{2}ha^{-1})**	**TPH (trees ha^{-1})**	**QMD (cm)**	**PIPO BA (%)**	**PIPO TPH (%)**	**PIPO QMD (cm)**
NORTH						
Treated	8.1^{a}	98^{a}	32^{a}	86	95	31^{a}
	(1.16)	(11.58)	(1.20)	(9.4)	(7.4)	(1.1)
Untreated	20.3^{b}	1194^{b}	15^{b}	56	39	18^{b}
	(1.18)	(148.3)	(0.74)	(10.4)	(7.6)	(1.3)
EAST/WEST						
Treated	10.9^{a}	120^{a}	34^{a}	94	94	34
	(2.46)	(26.83)	(1.21)	(6.4)	(5.7)	(1.3)
Untreated	14.8^{b}	480^{b}	20^{b}	67	57	23
	(1.28)	(47.47)	(1.50)	(10.1)	(11.4)	(1.4)
SOUTH						
Treated	5.1^{a}	62^{a}	33	100	100	33
	(0.88)	(8.60)	(2.63)	(0)	(0)	(2.6)
Untreated	12.7^{b}	272^{b}	27	96	94	27
	(1.51)	(78.54)	(2.32)	(1.7)	(2.7)	(2.5)
ANOVA Results	***p***	***P***	***p***	***p***	***p***	***p***
Aspect	**0.004**	**<0.001**	**0.008**	**<0.001**	**<0.001**	**0.025**
Treatment	**<0.001**	0.091	0.189	0.612	0.562	0.146
Aspect × Treatment	0.096	**0.011**	**0.008**	0.309	0.069	0.105

Table 3. Summary of repeated measures ANOVA results (*P*-values) for richness and cover of natives, exotics, graminoids, forbs, shrubs, short-lived, long-lived, and total species in the Colorado Front Range. Bolded *P*-values are <0.05.

Attribute	**Aspect**	**Treatment**	**Year**	**Aspect x Treatment**	**Aspect x Year**	**Treatment x Year**	**Aspect x Treatment x Year**
Total Species							
Richness	**<0.001**	0.204	**<0.001**	**0.006**	0.481	0.148	0.407
Cover	0.424	0.788	**0.036**	0.101	**0.002**	**0.035**	**0.013**
Forbs							
Richness	**0.001**	**<0.001**	**<0.001**	0.070	0.456	0.137	0.244
Cover	0.642	0.824	0.347	**0.016**	**0.290**	0.739	0.378
Graminoids							
Richness	**0.029**	0.116	0.119	**0.012**	**0.016**	0.493	0.845
Cover	**<0.001**	0.951	**0.001**	**0.006**	**<0.001**	**0.004**	**0.035**
Shrubs							
Richness	**0.008**	0.252	0.325	0.948	0.326	**0.003**	0.717
Cover	0.136	0.357	0.188	0.109	0.614	0.054	0.175
Short-Lived							
Richness	**0.024**	0.222	**<0.001**	**<0.001**	0.296	0.789	0.881
Cover	0.650	0.423	**<0.001**	**0.010**	0.332	0.556	0.944
Long-Lived							
Richness	**<0.001**	0.390	**0.009**	0.056	0.372	0.084	0.293
Cover	0.464	0.498	**0.048**	0.198	**<0.001**	**0.006**	**0.011**
Natives							
Richness	**0.006**	0.061	**<0.001**	0.272	0.548	0.078	0.139
Cover	0.332	0.845	**0.029**	0.201	**<0.001**	**0.021**	**0.006**
Exotics							
Richness	**<0.001**	0.354	0.296	**<0.001**	0.627	0.552	0.721
Cover	0.622	**<0.001**	0.845	0.249	0.999	0.921	0.965

Table 4. Percent of plots with exotic species presence for all treated (T) and untreated (U) plots in years 2004, 2005, 2006, and 2014 in the Colorado Front Range. Colorado noxious weeds have been labeled with an asterisk.

Species	T 2004	T 2005	T 2006	T 2014	U 2004	U 2005	U 2006	U 2014
Graminoids								
Agropyron cristatum	20	0	0	0	0	0	0	0
Bromus inermis	0	0	0	13	0	0	0	0
**Bromus tectorum*	13	13	13	13	0	0	0	0
Hordeum vulgare	7	0	0	0	0	0	0	0
Poa pratensis	0	7	0	7	5	0	0	0
Triticosecale rimpaui	27	33	20	27	0	0	0	0
Forbs								
**Carduus nutans*	27	33	40	13	10	15	5	0
**Centaurea diffusa*	0	7	0	0	0	0	0	0
**Cirsium arvense*	33	60	53	53	10	10	5	0
Lactuca seriola	67	80	53	40	15	10	0	0
**Linaria dalmatica*	13	7	13	13	0	0	0	0
**Linaria vulgaris*	40	40	33	47	0	0	5	5
Melilotus officinalis	27	13	0	0	0	0	0	0
Nepeta cataria	7	7	0	0	0	0	0	0
Plantago major	0	0	0	0	0	5	0	0
Salsola tragus	0	7	0	0	0	0	0	0
**Tanacetum vulgare*	7	0	0	0	0	0	0	0
Taraxacum officinale	33	40	47	27	5	5	5	5
Tragopogon dubius	27	40	20	53	5	20	0	20
**Verbascum thapsus*	100	100	100	100	50	50	35	35

Table 5. Summary statistics for MRPP pairwise comparisons for ranked Sorensen distances between treated and untreated plots by aspect (six groups) for years 2004 (2 years post-treatment) and 2014 (12 years post-treatment) with significant *P*-values bolded.

Year	**Aspect**	**A**	***P*-value**
2004	North	0.096	0.066
2014	North	0.2454	**0.002**
2004	East/West	0.204	**0.002**
2014	East/West	0.206	**0.002**
2004	South	-0.002	0.474
2014	South	0.021	0.282

Table 6. Indicator Species Analysis table showing all significant ($p < 0.05$) indicator species for treated and untreated sites in years 2004 (2 years post-treatment) and 2014 (12 years post-treatment).

ISA 2004			**ISA 2014**		
Species	**Indicator Value**	**P-value (<0.05)**	**Species**	**Indicator Value**	**P-value (<0.05)**
Untreated			**Untreated**		
Artemisia frigida	79.9	0.006	*Chamaesyce fendleri*	49.4	0.013
Chamaesyce fendleri	45.0	0.009			
Heterotheca villosa	72.5	0.029			
Pseudoroegnaria spicata	61.9	0.043			
Rhus trilobata	50.0	0.002			
Ribes cereum	88.4	0.009			
Treated			**Treated**		
Apocynum androsaemifolium	33.3	0.008	*Apocynum androsaemifolium*	33.3	0.008
Artemisia campestris	58.4	<0.001	*Artemisia campestris*	71.6	<0.001
Arctostaphylos uva-ursi	64.0	0.024	*Arctostaphylos uva-ursi*	74.5	0.002
Chenopodium spp.	82.8	0.013	*Carex spp.*	73.5	0.002
Cirsium arvense	32.8	0.035	*Cirsium arvense*	49.4	0.006
Cryptantha virgata	66.8	0.017	*Cryptantha virgata*	60.6	0.041
Eriogonum alatum	53.3	<0.001	*Eriogonum alatum*	60.0	<0.001
Erysimum capitatum	61.8	0.032	*Erigeron compositus*	73.7	<0.001
Erigeron compositus	62.4	0.005	*Lactuca seriola*	39.5	0.013
Lactuca seriola	64.1	0.001	*Linaria vulgaris*	46.1	0.006
Linaria vulgaris	40.0	0.004	*Penstemon glaber*	37.6	0.031
Melilotus officinalis	26.7	0.025	*Ribes leptanthum*	26.7	0.027
Pulsatilla patens	55.5	0.039	*Rubus idaeus*	26.7	0.026
Ribes leptanthum	26.7	0.025	*Tetraneuris acaulis*	26.7	0.028
Taraxacum officinale	35.6	0.013	*Tragopogon dubius*	67.4	<0.001
Tetraneuris acaulis	26.7	0.027	*Verbascum thapsus*	84.9	<0.001
Tragopogon dubius	48.8	0.002			

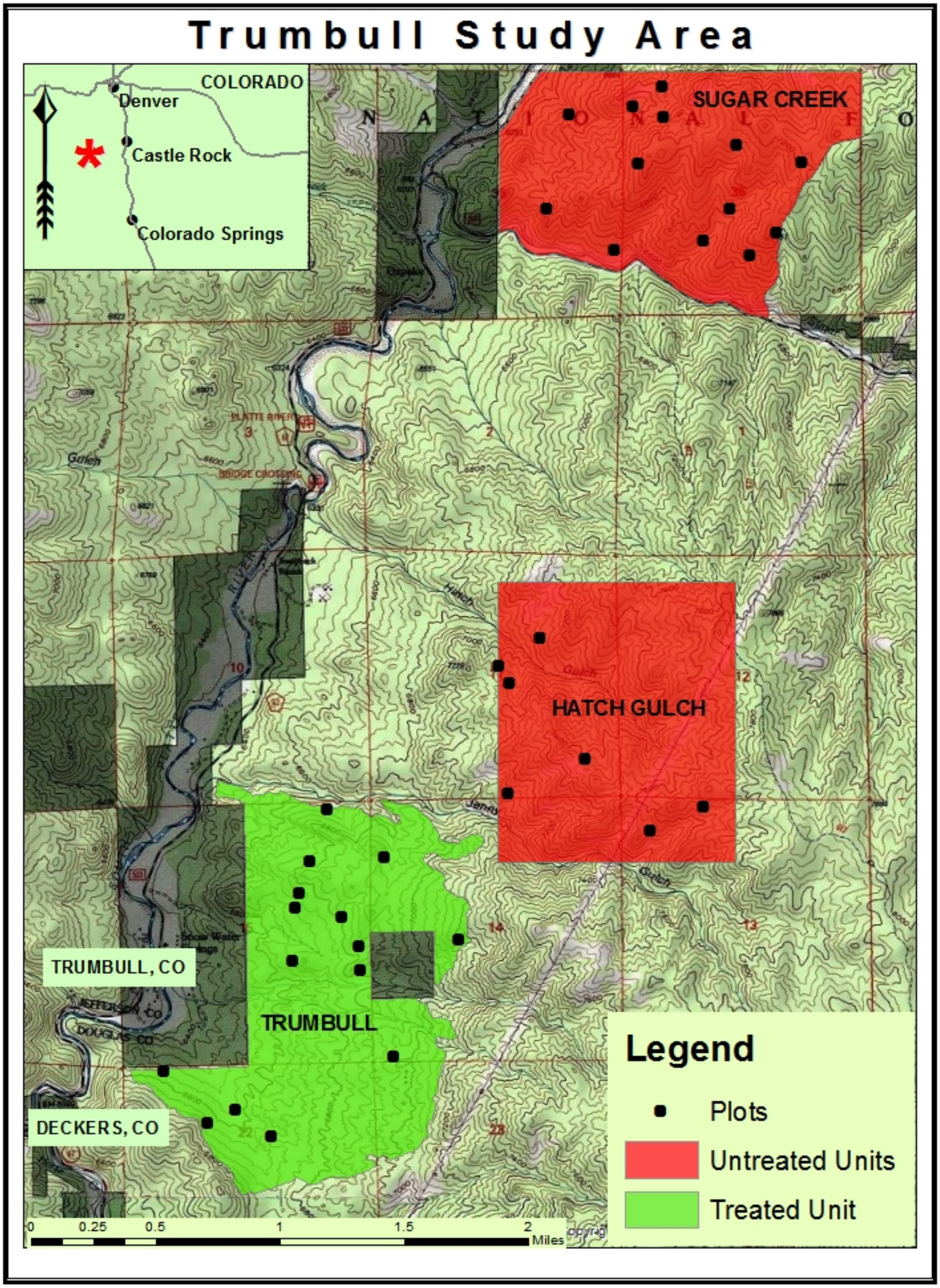

Figure 1. Map of the study area located in the Colorado Front Range, 60 km southwest of Denver, Colorado, USA. Greyed out areas are privately owned land.

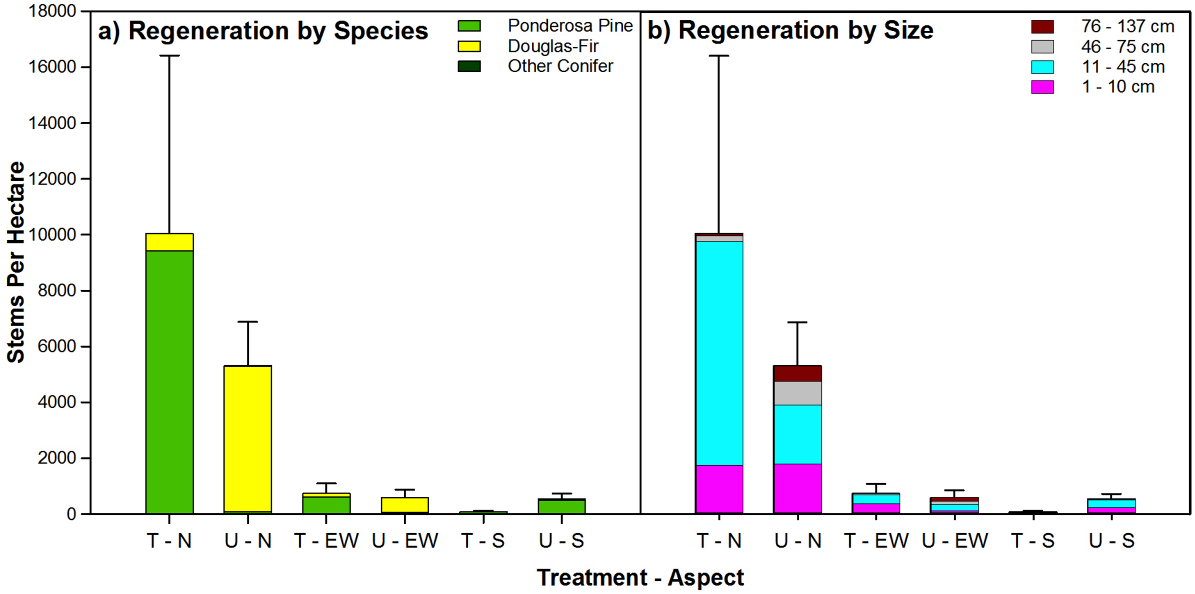

Figure 2. Coniferous tree seedling (<1.36 m tall) densities (mean ± 1 standard error) across treatment and aspect in a Colorado Front Range forest. Graph A shows regeneration density by species and graph B shows regeneration density by size. Treatments are expressed at either 'U' or 'T' (i.e. untreated or treated) and aspects are displayed as 'N', 'EW', or 'S' (i.e. north, east/west, or south).

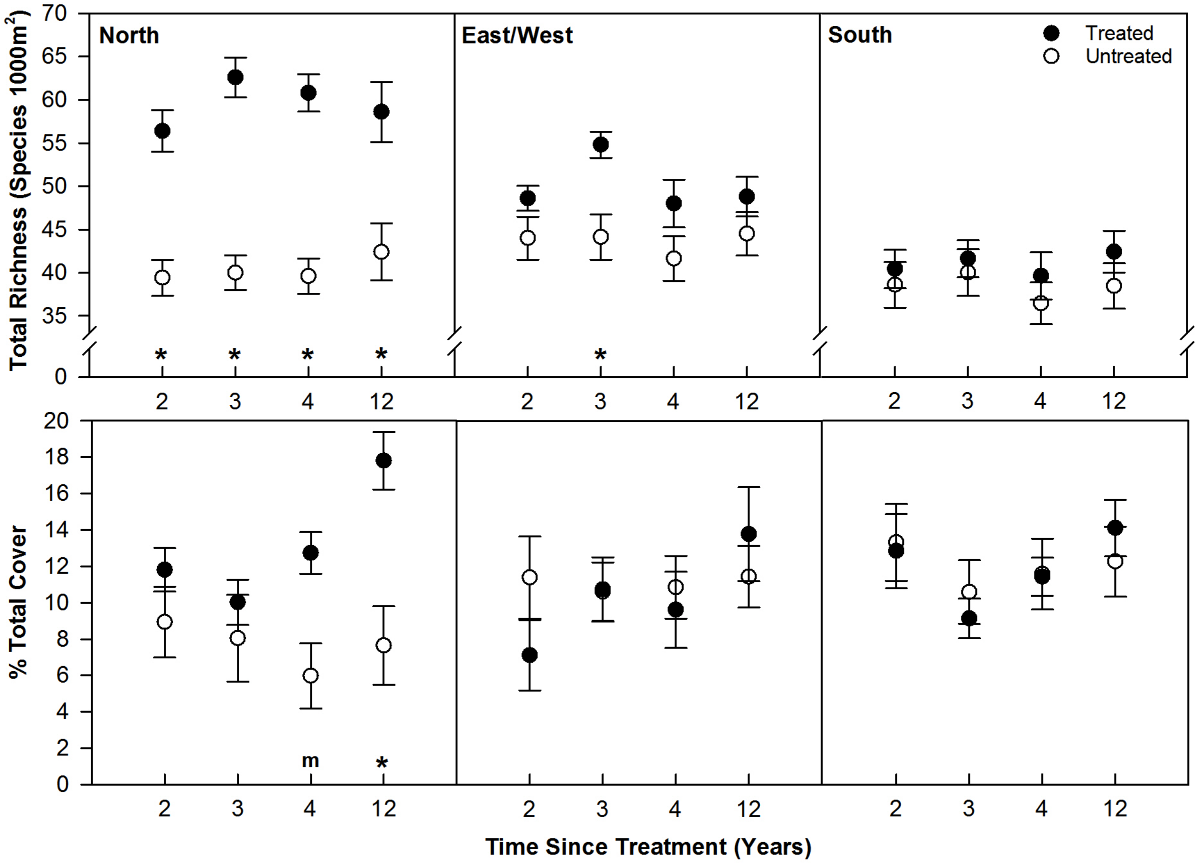

Figure 3. Mean (± standard error) total understory plant species richness and cover for treated and untreated plots in the Colorado Front Range. Data are presented by aspect (north, east/west, and south) and by time since treatment (2, 3, 4, and 12 years following the forest restoration treatment). Years with significant differences (*P*<0.05) between treated and untreated plots, by aspect, are labeled with ‘*’, and marginal differences (*P*<0.10) are labeled with ‘m’.

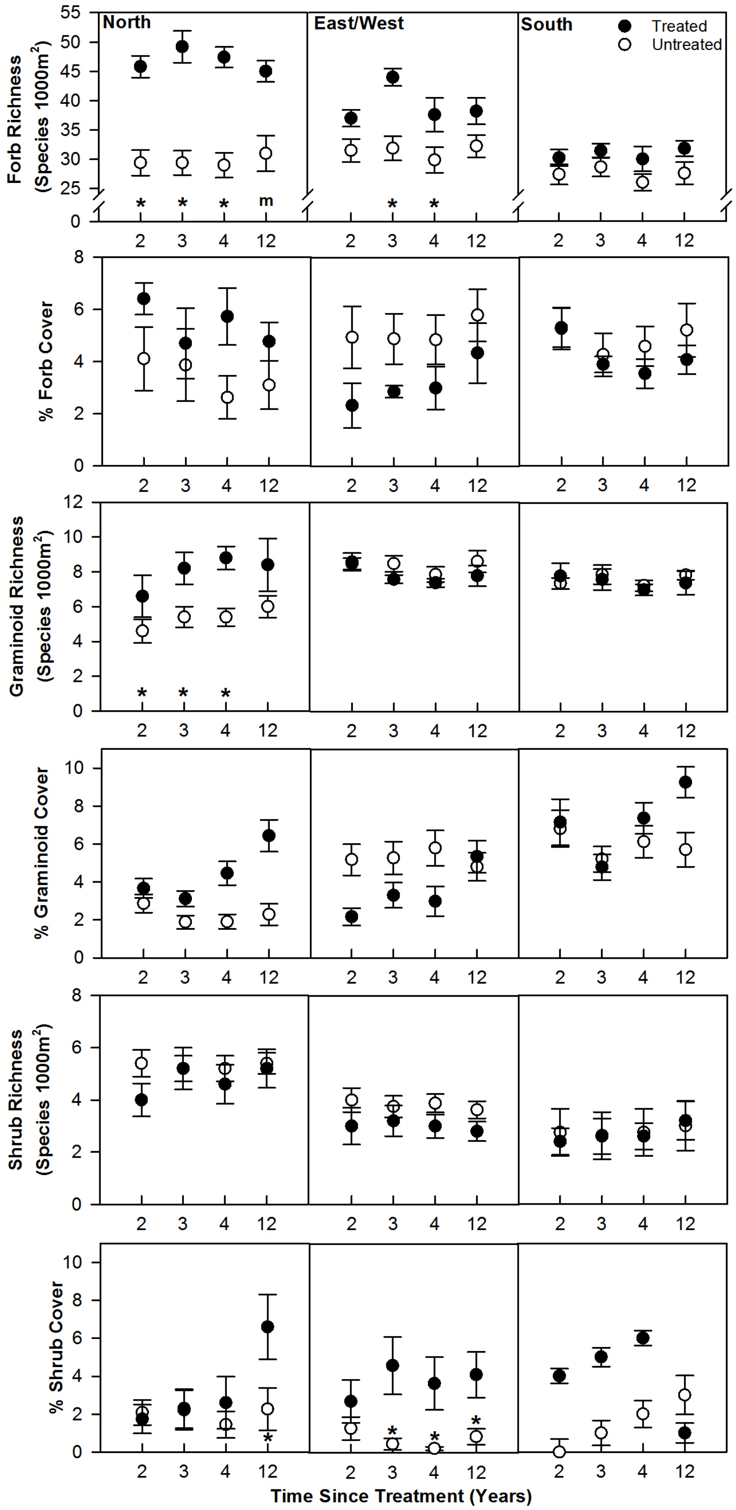

Figure 4. Mean (± standard error) forb, graminoid, and shrub richness and cover for treated and untreated plots in the Colorado Front Range. Data are presented by aspect (north, east/west, and south) and by time since treatment (2, 3, 4, and 12 years following the forest restoration treatment). Years with significant differences (*P*<0.05) between treated and untreated plots, by aspect, are labeled with '*', and marginal differences (*P*<0.10) are labeled with 'm'.

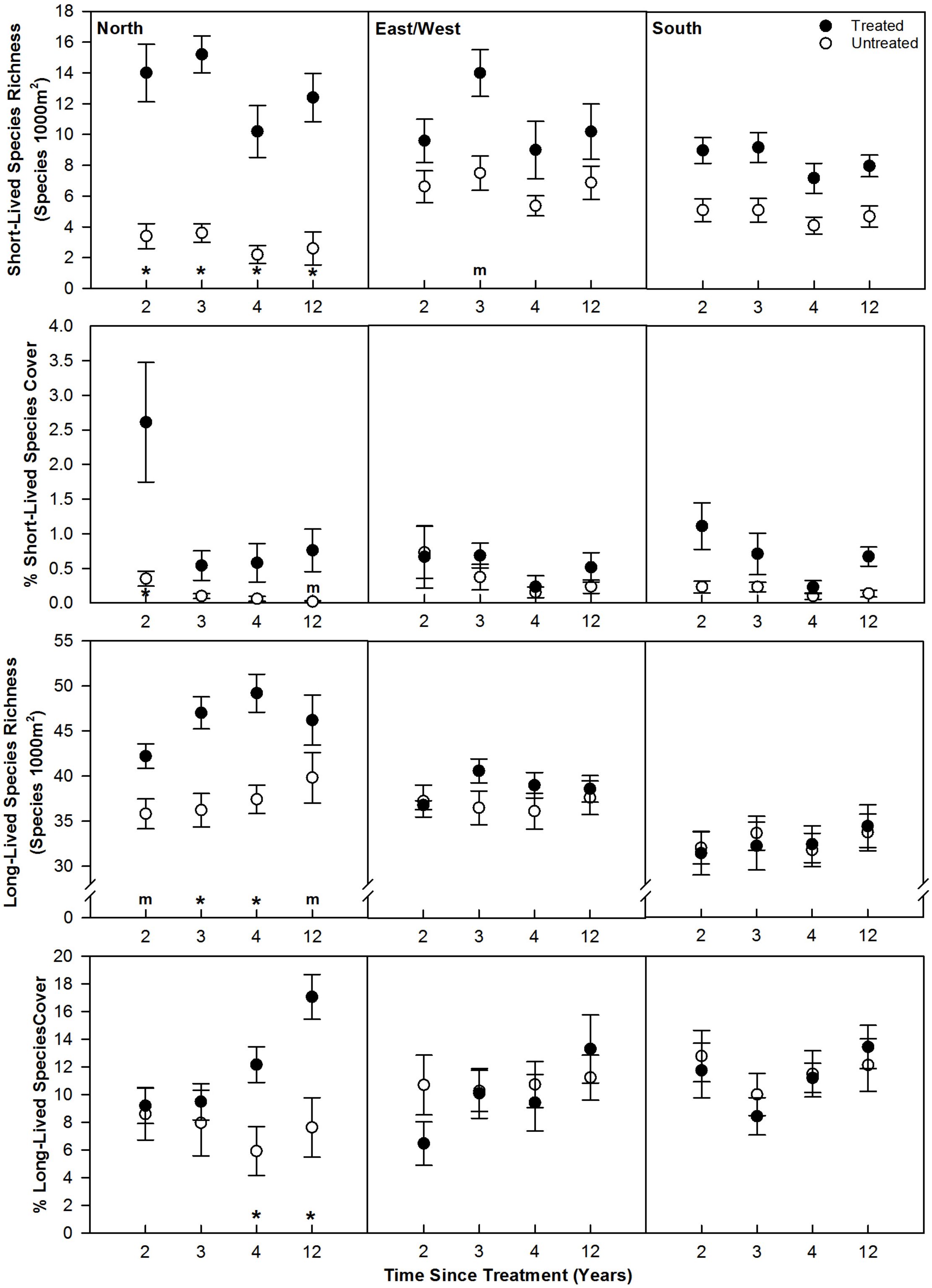

Figure 5. Mean (± standard error) short-lived and long-lived species richness and cover for treated and untreated plots in the Colorado Front Range. Data are presented by aspect (north, east/west, and south) and by time since treatment (2, 3, 4, and 12 years following the forest restoration treatment). Years with significant differences (*P*<0.05) between treated and untreated plots, by aspect, are labeled with '*', and marginal differences (*P*<0.10) are labeled with 'm'.

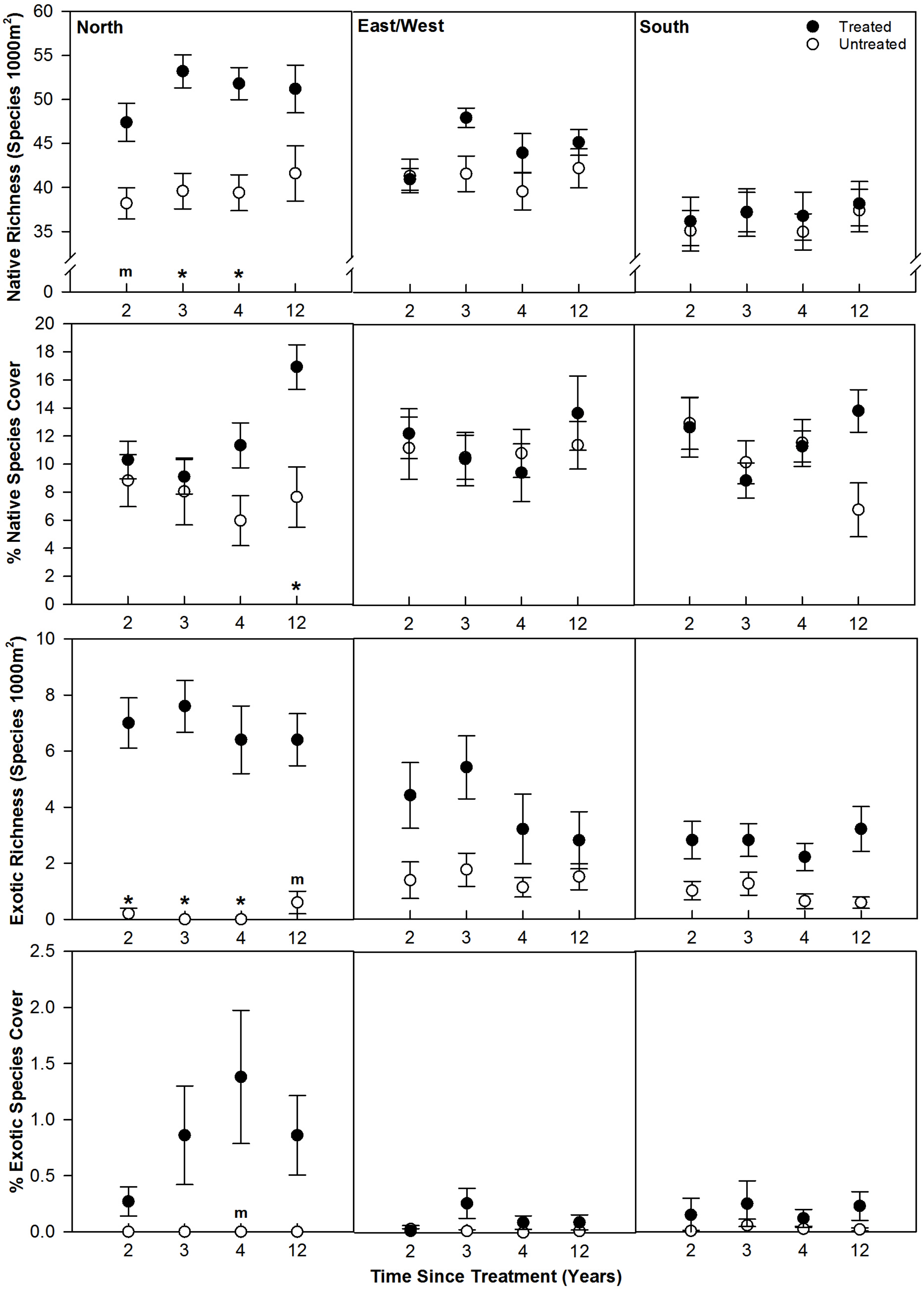

Figure 6. Mean (± standard error) native and exotic species richness and cover for treated and untreated plots in the Colorado Front Range. Data are presented by aspect (north, east/west, and south) and by time since treatment (2, 3, 4, and 12 years following the forest restoration treatment). Years with significant differences (*P*<0.05) between treated and untreated plots, by aspect, are labeled with '*', and marginal differences (*P*<0.10) are labeled with 'm'.

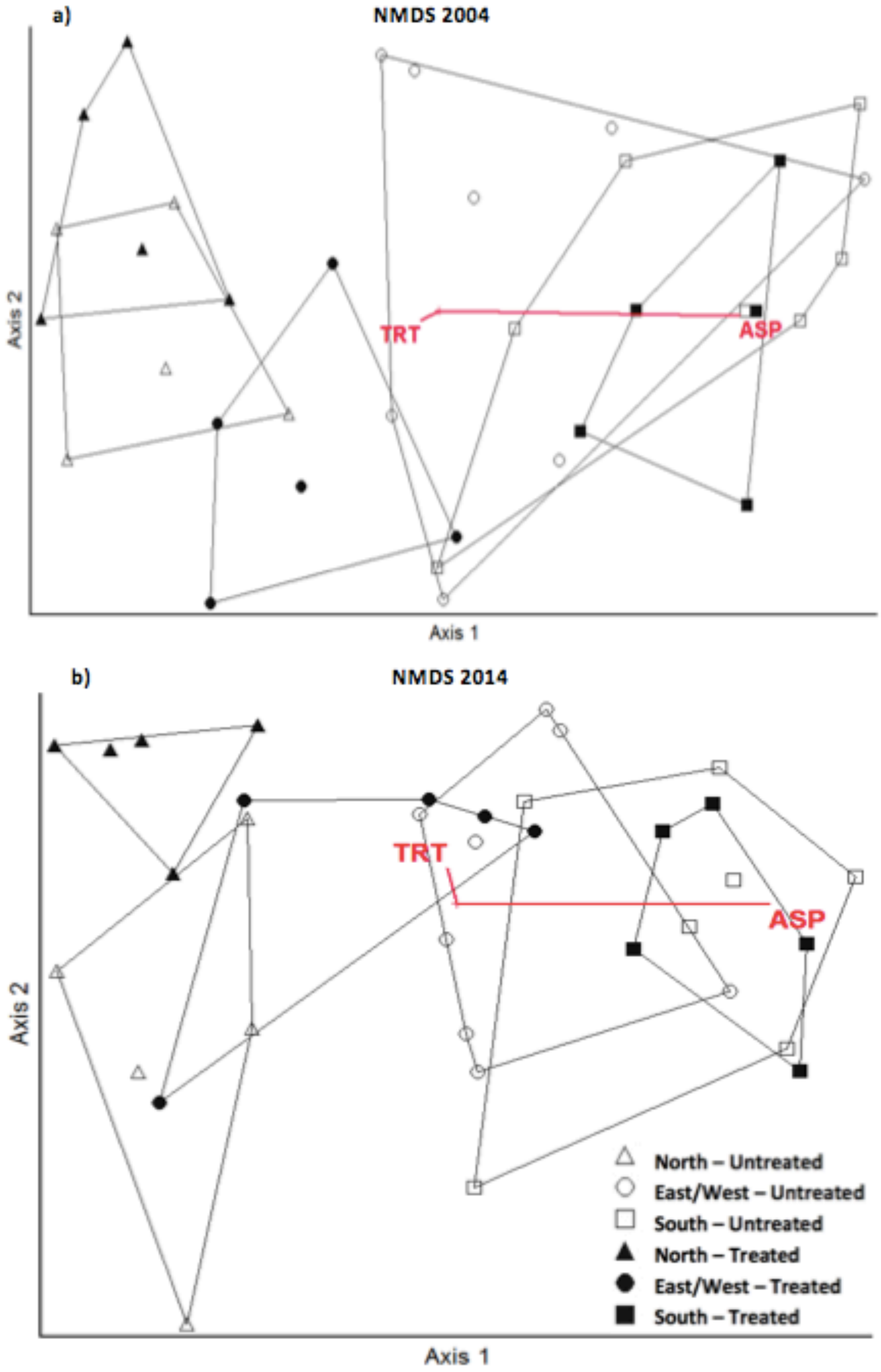

Figure 7. Non-Metric Multidimensional Scaling (NMDS) graphs for plots in years 2004 (graph a – 2 years post-treatment) and 2014 (graph b – 12 years post-treatment). Treated plots are solid, untreated plots are hollow, and different shapes represent aspect categories. Convex hulls are drawn around each treatment × aspect group.

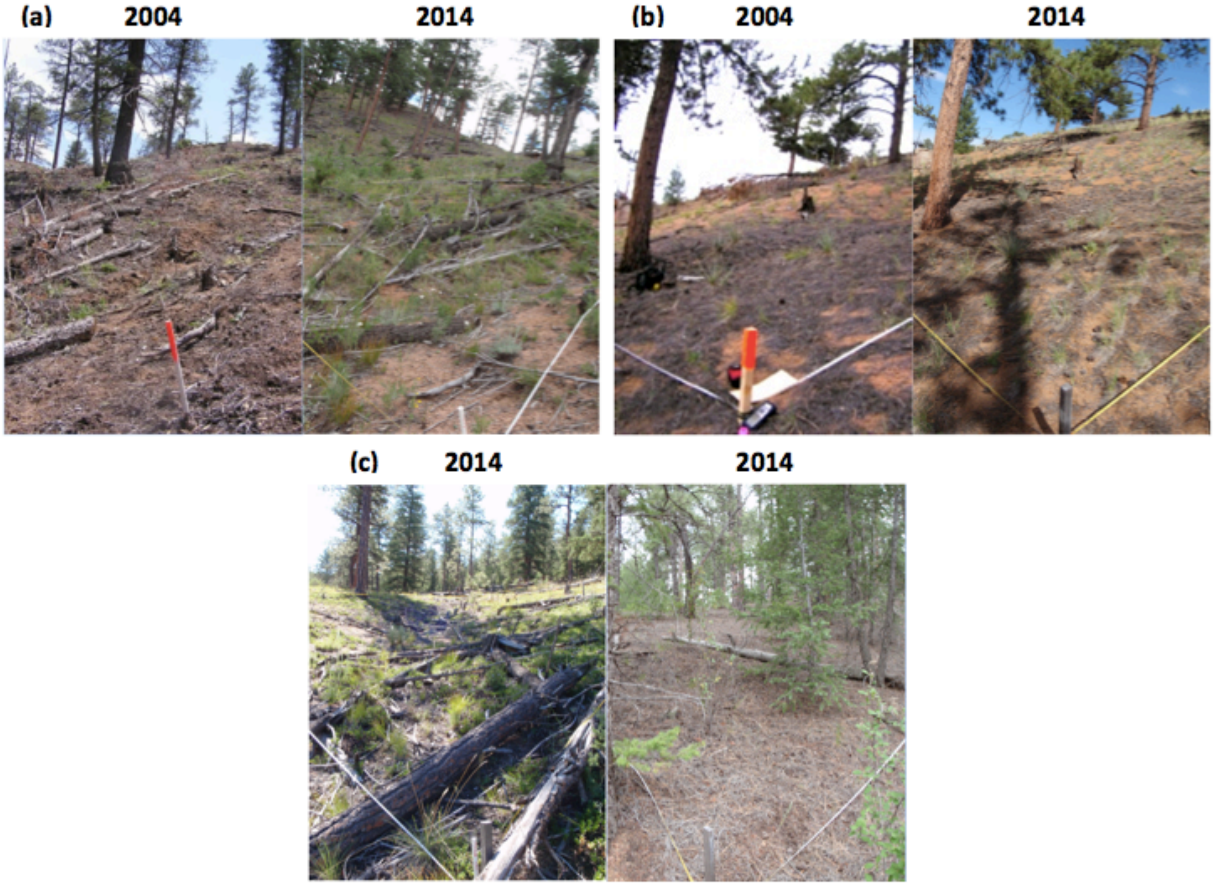

Figure 8. These photos are representative examples of changes in the forest understory following the 2002 restoration treatment in the Colorado Front Range. Photo set A shows changes in understory vegetation in the treated unit on a north facing aspect 2 (2004) and 12 (2014) years post-treatment. Photo set B shows changes in understory vegetation in the treated unit on a south facing aspect 2 (2004) and 12 (2014) years post-treatment. Photo set C shows differences in understory vegetation on north aspects in the treated unit (left) and untreated unit (right) 12 (2014) years post-treatment.

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