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Mulching fuels treatments promote understory plant communities in three Colorado, USA, coniferous forest types ☆

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A B S T R A C T

Mulching fuels treatments have been increasingly implemented by forest managers in the western USA to reduce crown fire hazard. These treatments use heavy machinery to masticate or chip unwanted shrubs and small-diameter trees and broadcast the mulched material on the ground. Because mulching treatments are relatively novel and have no natural analog, their ecological impacts are poorly understood. We initiated a study in 2007 to examine the effects of mulching on vascular understory plant communities and other ecological properties and processes. We established 15 study areas in Colorado, USA, distributed across three broadly-defined coniferous forest types: pinyon pine – juniper (*Pinus edulis – Juniperus* spp.); ponderosa pine (*P. ponderosa*) and ponderosa pine – Douglas-fir (*Pseudotsuga menziesii*); and lodgepole pine (*P. contorta*) and mixed conifer (lodgepole pine, limber pine (*P. flexilis*), and other conifers). Measurements were conducted along 50-m transects 2–4 years post-treatment (2007 or 2008), and again 6–9 years post-treatment (2012), in three mulched and three untreated stands per study area. Mulching dramatically reduced overstory basal area (i.e., basal area of trees >1.4 m tall) and increased forest floor biomass (i.e., the biomass of litter, duff, and woody material <2.5 cm in diameter) for all three forest types, as evidenced by previous measurements conducted in our mulched and untreated stands 2–4 years post-treatment. The total richness and cover of understory plant species in mulched stands 2–4 years post-treatment were either similar to, or greater than, the richness and cover in untreated stands for the three forest types; however, by 6–9 years post-treatment, total understory plant richness and cover in mulched stands were always greater. The stimulatory effect of mulching on understory plants was largely driven by the response of graminoids and forbs; mulching had little effect on shrub richness or cover. The increases in total understory plant richness and cover in mulched stands 6–9 years post-treatment occurred despite the fact that understory plants tended to be heavily suppressed in localized areas where the forest floor layer was deep, because such areas were rare. Exotic plant richness and cover were commonly higher in mulched than untreated stands in both sampling periods, but nonetheless understory plant communities remained highly native-dominated. Taken as a whole, our findings suggest that mulching treatments promoted denser and more diverse native understory plant communities in these three Colorado coniferous forest types, particularly over the longer-term.

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1. Introduction

Fuels treatments are routinely implemented in forests of the western USA to mitigate crown fire hazard by reducing ladder fuels and overstory density and continuity. Western forest managers must weigh many factors when deciding how best to treat fuels for a particular stand or group of stands. Prescribed fire and managed wildfire are often viewed as ideal fuels treatments because most western forests were historically regulated by fire, but weather, air quality, liability, and other issues commonly render them impractical (Cleaves et al., 2000; Williamson, 2007; Quinn-Davidson and Varner, 2012). Commercial timber harvesting practices are generally less constrained by such issues and can be used to treat fuels while generating revenue; however, their use requires well-stocked stands of merchantably-sized trees and a viable timber industry, both of which are lacking throughout much of the west (Keegan et al., 2006).

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Mulching is a mechanical fuels treatment that has been increasingly utilized by western forest managers when and where fire, timber harvesting, and other fuels treatments are not viable options (Hood and Wu, 2006; Kane et al., 2009; Battaglia et al., 2010; Kreye et al., 2014 and references therein; Roundy et al., 2014). Mulching treatments use heavy machinery to masticate or chip unwanted shrubs and small-diameter trees and broadcast the mulched material on the ground. Mulching therefore reduces ladder fuels and opens up the overstory like other fuels treatments, but it does not reduce the total amount of fuels in a stand; it only alters the fuels' size and spatial arrangement. The resulting mulched material is typically dominated by irregularly-shaped, small- to medium-sized (<7.6 cm in diameter) woody particles (Kane et al., 2009; Battaglia et al., 2010; Kreye et al., 2014 and references therein; Young et al., 2015). The mulched material and the pre-existing organic forest floor layer commonly become integrated and compacted during mulching operations (Hood and Wu, 2006; Kane et al., 2009; Battaglia et al., 2010; Kreye et al., 2014 and references therein; Young et al., 2015). While the mulch is often heterogeneously distributed within and across stands, it nonetheless can add considerable depth and mass to the forest floor (Hood and Wu, 2006; Kane et al., 2009; Reiner et al., 2009; Battaglia et al., 2010; Young et al., 2015).

Because mulching is a relatively novel treatment with no natural analog, its ecological consequences are poorly understood. For example, only a handful of studies have detailed how vascular understory plant (i.e., graminoid, forb, and shrub) communities respond following mulching in western forests (Collins et al., 2007; Owen et al., 2009; Wolk and Rocca, 2009; Kane et al., 2010; Redmond et al., 2014). The various aspects of mulching treatments may each impact understory plant communities in unique ways, making it difficult to predict net treatment effects and how such effects vary through time. The heavy machinery used to implement mulching treatments may crush, uproot, or even target understory plants, resulting in immediate declines in understory plant properties such as richness, cover, and productivity (Collins et al., 2007). Yet as with other disturbances that open up the overstory, mulching may ultimately promote understory plants – both native and exotic – as plants become equilibrated to the reduction in competition with overstory trees (Brockway et al., 2002; Lindgren et al., 2006; Metlen and Fiedler, 2006; Fornwalt and Kaufmann, 2014; Abella and Springer, 2015 and references therein). Adding mulched material to the forest floor may further benefit understory plants by moderating soil temperature and increasing soil moisture and nutrient availability (Owen et al., 2009; Fornwalt and Rhoades, 2011; Rhoades et al., 2012, 2015). On the other hand, the mulched material may suppress understory plants by acting as a physical barrier to their establishment and/or growth (Xiong and Nilsson, 1999 and references therein; Wolk and Rocca, 2009; Kane et al., 2010; Rhoades et al., 2015); the suppressive effects of mulch may be especially apparent if it is deep (Xiong and Nilsson, 1999 and references therein; Wolk and Rocca, 2009).

The increasingly frequent implementation of mulching treatments in western forests necessitates a more thorough understanding of how they impact understory plant communities and other ecological properties and processes across a range of time frames and forest types. To help address this need, in 2007 we initiated a study to investigate the ecological effects of mulching (Battaglia et al., 2010; Rhoades et al., 2012; Faist et al., 2015). We established 15 study areas in Colorado, distributed across three broadly-defined coniferous forest types: pinyon pine – juniper (*Pinus edulis* – *Juniperus* spp.); ponderosa pine (*P. ponderosa*) and ponderosa pine – Douglas-fir (*Pseudotsuga menziesii*); and lodgepole pine (*P. contorta*) and mixed conifer (lodgepole pine, limber pine (*P. flexilis*), and other conifers). Here, we report on the shorter-term (i.e., 2–4 years post-treatment) and longer-term (i.e., 6–9 years post-treatment) stand-scale effects of mulching on a variety of understory plant richness and cover variables for each of these forest types. Furthermore, because the mulched material is often heterogeneously distributed within as well as across stands, we also report on how the depth of the integrated forest floor layer (i.e., the mulch and the pre-existing organic forest floor) impacts understory plant richness and cover in these forest types at a localized scale.

2. Methods

2.1. Study areas and study design

In 2007 and 2008, we established 15 landscape-scale study areas in Colorado, USA, on lands managed by federal (USDA Forest Service or USDI Bureau of Land Management), state (Colorado State Parks), or private entities (Table 1; Battaglia et al., 2010; Rhoades et al., 2012; Faist et al., 2015). The study areas each encompassed operational-scale mulched stands and untreated stands, and were distributed across three broadly-defined forest types. Four study areas were located in pinyon pine – juniper (hereafter "PJ") forests of southwestern Colorado. These study areas tended to be the lowest in elevation, the driest, and the warmest, with elevations averaging ca. 2180 m, annual precipitation averaging ca. 400 mm, and annual temperature averaging ca. 8 °C (PRISM, 2015). Four study areas were located on the eastern slope of the Front Range, in ponderosa pine and ponderosa pine – Douglas-fir forests (hereafter "PP"). Elevations averaged ca. 2220 m, annual precipitation averaged ca. 530 mm, and annual temperature averaged ca. 7 °C (PRISM, 2015). The remaining seven study areas were located in lodgepole pine and mixed conifer forests (hereafter "LP/MC"). Mixed conifer forests were co-dominated by three or more conifer species, with either lodgepole pine or limber pine being the most abundant. LP/MC study areas were located on both the eastern and the western slope of the Front Range, and were the highest in elevation, the wettest, and the coolest. Average elevations were ca. 2760 m, average annual precipitation was ca. 570 mm, and average annual temperature was ca. 4 °C (PRISM, 2015).

We installed a 50-m transect in three mulched and three untreated stands within each of the 15 study areas (Fig. 1), yielding a total of 90 transects. Untreated stands were located within 1 km of mulched stands, in areas with similar aspect, slope, elevation, soils, and pre-treatment overstory composition and structure. All transects were randomly located and permanently marked.

Mulching treatments at all of the study areas were accomplished by either chipping trees and shrubs with a Morbark© chipper (LP/MC study areas SLL and WNC), or by masticating trees and shrubs with a vertical shaft or rotary ax mower on a Hydroax© (the remaining 13 study areas). Although all mulching treatments were conducted to reduce crown fire hazard, the prescriptions implemented were necessarily variable due to differences in specific management objectives, the equipment utilized, and pre-treatment stand conditions. All treatments occurred between 2003 and 2006. Mulching treatments dramatically reduced overstory (i.e., trees >1.4 m tall) basal area, as evidenced by previous research conducted along our mulched and untreated transects in 2007 and 2008 (Table 1; Battaglia et al., 2010). In PJ stands, overstory basal area was reduced by 60%, averaging 17 m^2 ha^{-1} in untreated stands and 7 m^2 ha^{-1} in mulched stands. In PP stands, average overstory basal area dropped by 58% following mulching (from 26 to 11 m^2 ha^{-1}), and in LP/MC stands, it dropped by 78% (from 33 to 7 m^2 ha^{-1}). Mulching also dramatically increased the biomass of the organic forest floor in mulched stands, primarily through the deposition of small woody particles (<2.5 cm in diam-

Table 1
Attributes of the 15 study areas, Colorado, USA. Sampling within each study area occurred in three untreated and three mulched stands. Precipitation and temperature values are 30-year normals (PRISM, 2015). Overstory (trees >1.4 m tall) composition reflects the dominant species prior to the implementation of mulching treatments, with species listed in order of abundance. Overstory basal area and forest floor biomass reflect conditions 2–4 years post-treatment. Forest floor biomass is the cumulative biomass of litter, duff, and woody material <2.5 cm in diameter. See Battaglia et al. (2010) for more information on the study areas and how treatments impacted the overstory and forest floor.

Study area, nearest city/town	Elevation (m)	Total annual precip (mm)	Mean annual temp (°C)	Overstory composition	Overstory basal area (m^2 ha^{-1})		Forest floor biomass (Mg ha^{-1})	
					Untreated	Mulched	Untreated	Mulched
Pinyon pine – juniper								
CH, Salida	2386	293	7	Pinyon pine, juniper spp.	29	5	20	42
IC, Cortez	1916	362	10	Juniper spp., pinyon pine	10	2	11	40
MAM, Dolores	2243	482	8	Juniper spp., pinyon pine	9	4	15	39
SUM, Cortez	2176	475	8	Juniper spp., pinyon pine	18	15	10	26
Ponderosa pine and ponderosa pine – Douglas-fir								
BK, Buffalo Creek	2288	519	7	Ponderosa pine, Douglas-fir	27	13	19	54
LSP, Fort Collins	2087	532	9	Ponderosa pine, Douglas-fir	35	17	41	69
NF, Foxton	2128	481	8	Ponderosa pine, Douglas-fir	26	6	12	43
WS, Woodland Park	2364	576	6	Ponderosa pine	16	7	11	34
Lodgepole pine and mixed conifer								
COL, Central City	2839	612	4	Lodgepole pine	33	7	21	47
COS, Cascade	2909	581	4	Limber pine, ponderosa pine, Douglas-fir	30	15	23	67
GGP, Golden	2818	619	4	Lodgepole pine	32	9	20	49
SLL, Ward	2780	628	4	Lodgepole pine, ponderosa pine, Douglas-fir	32	14	35	106
SLP, Ward	2700	550	5	Lodgepole pine, ponderosa pine, Douglas-fir	44	0	26	110
SM, Granby	2641	472	3	Lodgepole pine	34	3	38	61
WNC, Nederland	2623	540	5	Lodgepole pine	21	7	35	87

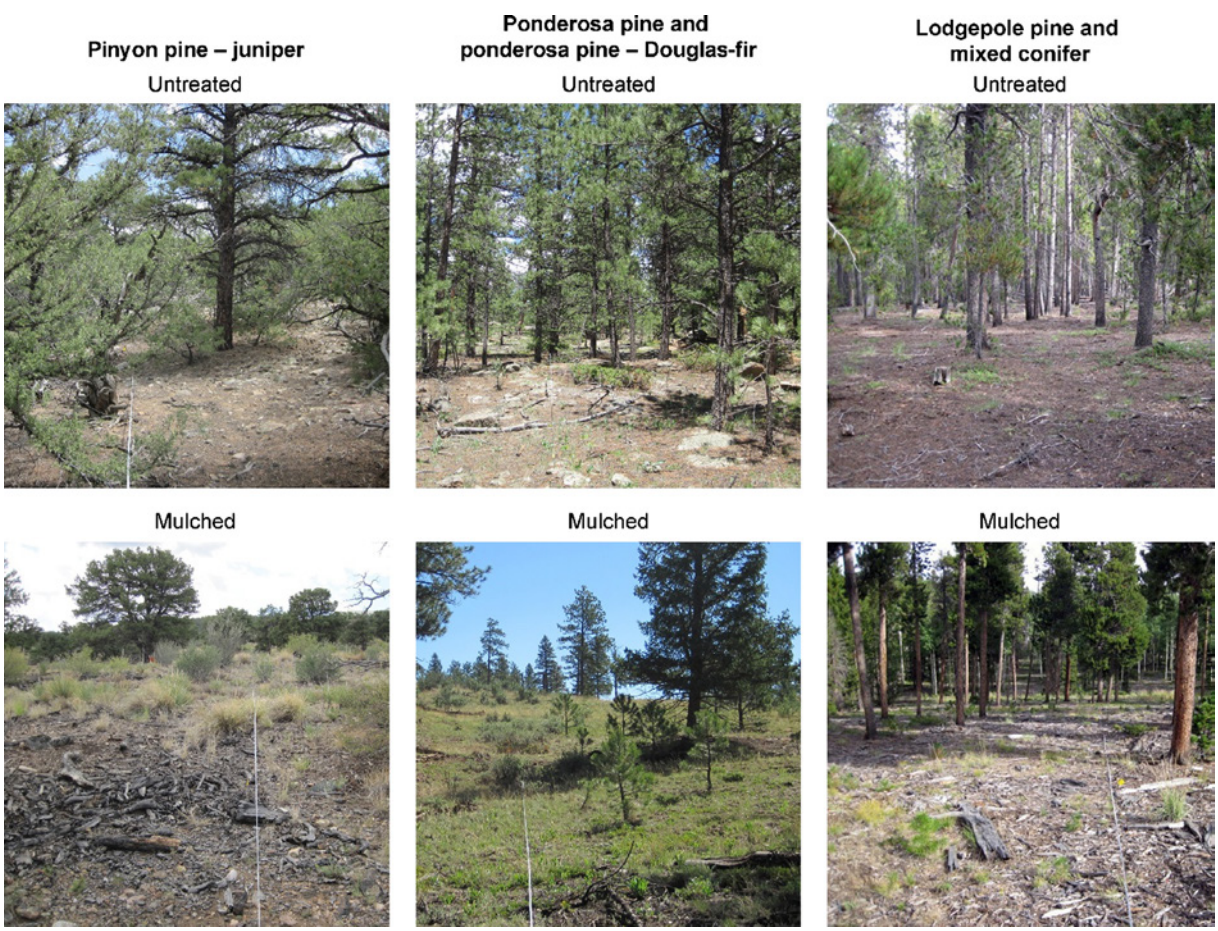

Fig. 1. Representative untreated and mulched stands (i.e., transects), by forest type. The photos were taken 6–9 years post-treatment. The stands depicted are from the CH (pinyon pine – juniper), WS (ponderosa pine and ponderosa pine – Douglas-fir), and GGP (lodgepole pine and mixed conifer) study areas.

eter; Table 1; Battaglia et al., 2010). Our definition of the forest floor includes litter, duff, and small wood because mulching operations often caused them to become integrated into a single compact layer. Forest floor biomass increased from 14 Mg ha^{-1} in untreated stands to 37 Mg ha^{-1} in mulched stands in PJ forests, from 20 to 50 Mg ha^{-1} in PP forests, and from 28 to 75 Mg ha^{-1} in LP/MC forests.

2.2. Field data collection

We established 1-m^2 (1-m × 1-m) quadrats along each 50-m transect, and within these, we measured vascular understory plants. Measurements were conducted twice, first 2–4 years post-treatment (summers 2007 or 2008), and again 6–9 years post-treatment (summer 2012). We visually estimated the aerial percent cover of graminoids, forbs, and shrubs in 25 quadrats per transect, placed at two meter increments. In 13 quadrats per transect, we further recorded the presence of all species and estimated cover of those species that were exotic to the continental USA. If we were uncertain about the identity of a plant, we collected and pressed a sample from outside the quadrat for later identification, and estimated its cover as a precaution. While most plants were ultimately identified to the species level (78% of observations; varieties and subspecies were not distinguished), in some instances plants were only identified to the genus level (19% of observations) or were not identified at all (3% of observations) because hybridization was common or because key morphological characteristics were not sufficiently developed. We determined the life span (i.e., annual, biennial, or perennial), growth form (i.e., graminoid, forb, or shrub), and nativity (i.e., native or exotic to the continental USA) of each plant using The PLANTS Database and local botanical keys (Harrington, 1964; Weber and Wittmann, 2001; Ackerfield, 2015; USDA NRCS, 2015). Nomenclature follows The PLANTS Database (USDA NRCS, 2015).

Additionally, 2–4 and 6–9 years post-treatment, we quantified the depth of the forest floor layer in all 25 quadrats per transect. Forest floor depth was calculated as the average of values measured at the quadrat center and at each corner.

2.3. Data analyses

Some data were omitted from the dataset prior to analyses. First, data from several stands were omitted because of disturbances during the course of the study. Two untreated stands in one PP study area (WS) were damaged by a tornado in summer 2008 after sampling was completed, and two untreated and two mulched stands in another PP study area (NF) were burned in the 2012 Lower North Fork Fire just prior to sampling. All data from these stands were dropped. Second, understory plant observations not identified to either the genus or species level were dropped. Hereafter both genus- and species-level identifications are referred to as species.

We used repeated-measures generalized linear mixed models to examine the stand-scale (i.e., transect-scale) effects of mulching on understory plant communities for each of the six forest type × time since treatment combinations. Analyses were conducted in SAS 9.4 (GLIMMIX procedure; SAS Institute Inc., Cary, North Carolina, USA) for a variety of understory plant richness and cover variables (i.e., graminoid, forb, shrub, total plant, and exotic plant richness and cover). Richness variables were scaled up to the stand by tallying the cumulative number of species recorded across the 13 quadrats per transect, while cover variables were scaled up by averaging the 25 quadrat values. We modeled each richness/cover variable against the predictor variables treatment, forest type, time since treatment, and all interactions. Richness variables were modeled using a negative binomial distribution. Cover variables, converted to a proportion and rescaled per Smithson and Verkuilen (2006) as necessary to accommodate 0 and 1 values, were modeled using a beta distribution. Treatment and forest type were included in the models as fixed effects, and study area was included as a random effect. Time since treatment was included as a random effect with transect as the repeated-measures subject and with the two sampling periods for each transect correlated by a first-order autoregressive covariance structure. We then compared treatments for each of the six forest type × time since treatment combinations using least squares means with a Tukey adjustment. Significance in these and all other analyses was assessed with an $\alpha = 0.050$, while marginal significance was assessed with an $\alpha = 0.100$.

Quantile regressions that model upper – or near-maximum – quantiles of a response variable in relation to a predictor variable have been increasingly viewed as useful analytical tools when other unmeasured predictor variables may be further constraining the response (Koenker and Bassett, 1978; Cade and Noon, 2003). Thus, we explored how near-maximum total understory plant richness and cover in mulched areas are influenced by the depth of the forest floor at a localized (i.e., quadrat) scale by fitting 0.9 quantile regressions, as we recognized that understory plants in mulched areas may be limited by factors other than forest floor depth (e.g., overstory canopy cover). Analyses, which were run using the QUANTREG procedure in SAS, used data collected in mulched stands 6–9 years post-treatment and were conducted separately for each forest type. Other studies (Xiong and Nilsson, 1999) suggested that the relationship between forest floor depth and understory plant variables can be linear or quadratic. Therefore, we modeled total understory plant richness and cover as a function of both forest floor depth and forest floor depth squared, removing the squared term if it was not significant. We used the Wald test statistic to assess the significance of the final models. Unfortunately, the QUANTREG procedure currently cannot accommodate random effects, and so we were unable to account for the potential correlation among quadrats within the same transect, or for the potential correlation among transects within the same study area. Because of this, we view these analyses as best used to gain general insight into the relationship between near-maximum understory plant richness and cover and forest floor depth, rather than to make precise richness or cover predictions for specific depths.

3. Results

3.1. Graminoid, forb, shrub and total richness and cover

Mulching treatments stimulated the stand-scale richness of graminoid and forb species for several forest types and sampling periods (Table 2; Fig. 2). In PJ forests, graminoid and forb richness in mulched stands always exceeded that of untreated stands, with mulched stands in both sampling periods containing an average of 4 graminoid species (a 37–39% increase over values in untreated stands) and 8 forb species (a 55–75% increase) across the 13 1-m^2 quadrats. Graminoid and forb richness in mulched PP and LP/MC stands were less consistently elevated. Mulched PP stands had marginally greater or greater graminoid richness than untreated stands during both sampling periods, and marginally greater forb richness 2–4 years post-treatment; in these instances, values in mulched stands were 38–46% higher than values in untreated stands. Meanwhile, mulched LP/MC stands had greater graminoid richness than untreated stands 6–9 years post-treatment (a 36% increase), and marginally greater or greater forb richness during both sampling periods (a 30–113% increase).

Mulching more consistently stimulated stand-scale graminoid and forb cover (Table 2; Fig. 3). Graminoid and forb cover were

Table 2
Generalized linear mixed model p-values for the effects of treatment, forest type, time since treatment, and all interactions on stand-scale (i.e., transect-scale) understory plant richness and cover variables. Richness was calculated as the cumulative number of species recorded across 13 1-m^2 quadrats.

Understory plant variable	Treatment	Forest type	Time since treatment	Treatment × forest type	Forest type × time since treatment	Treatment × time since treatment	Treatment × forest type × time since treatment
Richness (species 13 m^{-2})							
Graminoid	<0.001	0.056	0.481	0.929	0.004	0.834	0.738
Forb	<0.001	0.057	0.045	0.538	0.447	0.099	<0.001
Shrub	0.082	0.700	0.223	0.508	0.276	0.107	0.529
Total plant	<0.001	0.196	0.130	0.906	0.046	0.076	0.016
Exotic plant	<0.001	0.202	0.948	<0.001	0.104	0.833	0.225
Cover (%)							
Graminoid	<0.001	0.504	<0.001	0.312	0.943	0.113	0.913
Forb	<0.001	0.305	<0.001	0.230	0.027	0.030	0.443
Shrub	0.806	0.858	<0.001	0.581	<0.001	<0.001	0.462
Total plant	0.001	0.329	<0.001	0.265	0.002	<0.001	0.906
Exotic plant	<0.001	0.562	0.158	0.026	0.010	0.440	0.273

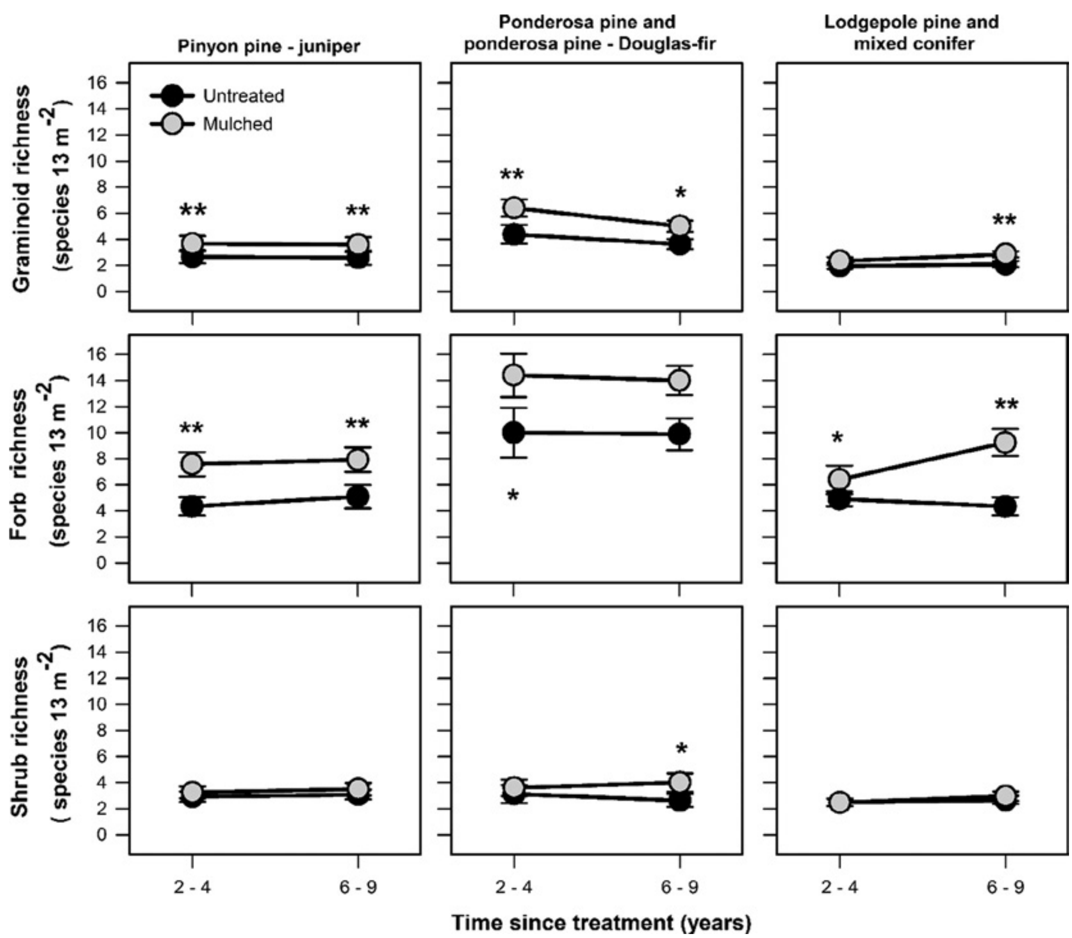

Fig. 2. Mean (±1 standard error) graminoid, forb, and shrub richness in untreated and mulched stands (i.e., transects), by forest type and time since treatment. Richness was calculated as the cumulative number of species recorded across 13 1-m^2 quadrats. An "**" indicates significant differences (α = 0.050) and an "*" indicates marginally significant differences (α = 0.100) between treatments for that forest type and sampling period.

higher in mulched compared to untreated stands during our initial post-treatment survey in PP and LP/MC forests, and were higher in all three forest types during our subsequent survey. The increases in cover during the last sampling period were particularly marked; graminoid and forb cover in mulched stands relative to untreated stands were 110–158% higher in PJ forests, 187–269% higher in PP forests, and 223–510% higher in LP/MC forests.

In contrast to graminoid and forb richness and cover, mulching had little effect on the richness and cover of shrub species at the stand scale (Table 2; Figs. 2 and 3). Shrub richness was only marginally elevated in mulched PP stands, and shrub cover was only elevated in mulched LP/MC stands. Furthermore, these increases were only observed in the last sampling period.

Differences in total understory plant richness and cover between mulched and untreated stands reveal the overall stimulatory effect of mulching treatments on understory plant communities (Table 2; Fig. 4). Total understory plant richness was greater in mulched than untreated stands in PJ and PP forests 2–4 years post-treatment and in all forest types 6–9 years post-treatment, while total understory plant cover was greater in mulched than

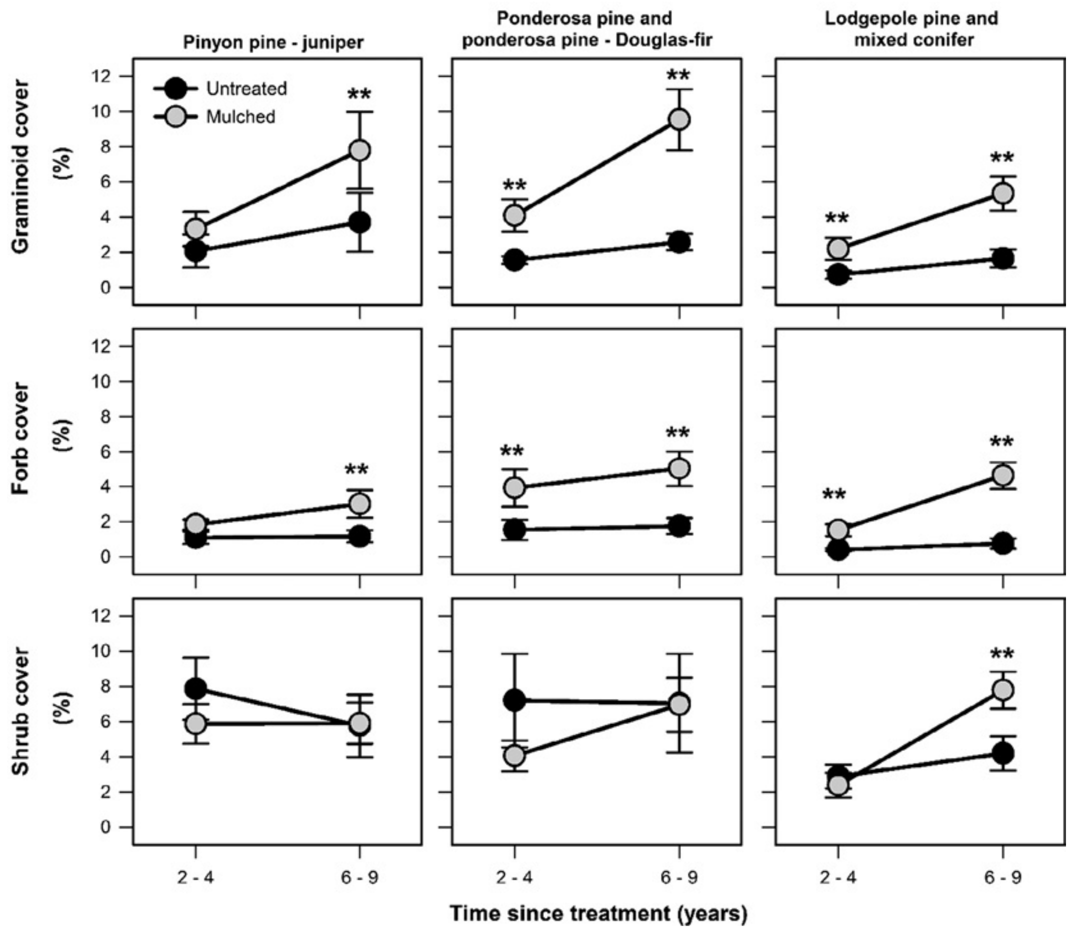

Fig. 3. Mean (±1 standard error) graminoid, forb, and shrub cover in untreated and mulched stands (i.e., transects), by forest type and time since treatment. An "**" indicates significant differences (α = 0.050) between treatments for that forest type and sampling period.

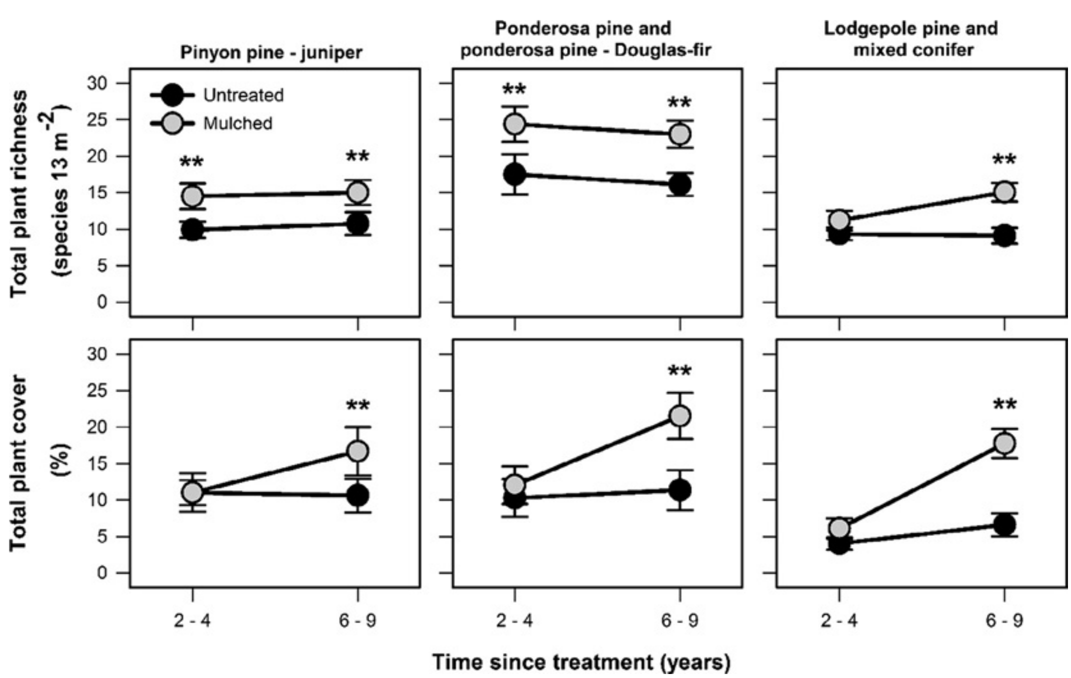

Fig. 4. Mean (±1 standard error) total understory plant richness and cover in untreated and mulched stands (i.e., transects), by forest type and time since treatment. Richness was calculated as the cumulative number of species recorded across 13 1-m^2 quadrats. An "**" indicates significant differences (α = 0.050) between treatments for that forest type and sampling period.

untreated stands in all forest types 6–9 years post-treatment. By the time mulching treatments were 6–9 years old, average total understory plant richness in mulched stands ranged from 15 to 23 species 13 m^{-2} across the three forest types (a 40–65% increase over values in untreated stands), and average total understory plant cover ranged from 17 to 22% (a 57–169% increase).

Greater total understory plant richness and cover in mulched stands 6–9 years post-treatment occurred despite the fact that increasing the depth of the forest floor layer tended to negatively impact them at the localized scale (Fig. 5). In mulched PJ stands, near-maximum total understory plant richness decreased non-significantly with increasing forest floor depth, while near-maximum total understory plant cover increased with increasing forest floor depth when depths were less than about 3 cm, but then declined with increasing depth when depths were greater than this. Meanwhile, near-maximum total understory plant richness and cover in mulched PP and LP/MC stands exhibited a negative relationship with forest floor depth across the entire range of depths. Forest floor depths in excess of 8 cm were necessary to essentially eliminate understory plants in PJ stands, while depths in excess of 11 and 17 cm were necessary in PP and LP/MC stands, respectively. These depths, however, were extremely uncommon, accounting for <1% of measurements.

3.2. Exotic plant richness and cover

We encountered 19 exotic plant species along our transects, six of which are on Colorado's noxious weed list (Table 3). Of the 10 exotic plant species encountered in PJ forests, the noxious weed cheatgrass (*Bromus tectorum*) was by far the most common. The percent of PJ stands containing cheatgrass varied little with treatment or sampling period, with the species being present in about half of them. The noxious weeds Canada thistle (*Cirsium arvense*) and dandelion (*Taraxacum officinale*) were the most common of the 10 exotic species found in PP forests. Both these species were more often found in mulched than untreated stands. Canada thistle was never encountered in untreated PP stands, and it was encountered in 20% of mulched stands 2–4 years post-treatment and 50% of mulched stands 6–9 years post-treatment. Dandelion was encountered in 13% and 0% of untreated PP stands 2–4 years and 6–9 years post-treatment, respectively, and in 70% and 30% of mulched PP stands 2–4 years and 6–9 years post-treatment. Canada thistle was also by far the most common of the 11 exotic species found in LP/MC forests. Canada thistle was rarely present in untreated LP/MC stands but was present in 38% of mulched stands 2–4 years post-treatment and 71% of mulched stands 6–9 years post-treatment.

As might be anticipated given the exotic plant species patterns just described, the effects of mulching treatments on exotic richness and cover were not necessarily consistent across forest types (Table 2; Fig. 6). Exotic richness and cover were generally not stimulated by mulching treatments in PJ stands, with increased values observed only for exotic richness 2–4 years post-treatment. Across all treatments and sampling periods, exotic richness in PJ stands averaged 1 species 13 m^{-2} and comprised 11% of total understory plant richness, while exotic cover averaged 1% and comprised 6% of total understory plant cover. In contrast, exotic richness and cover were consistently stimulated by mulching treatments in PP and LP/MC stands. However, exotic richness and cover values in mulched PP and LP/MC stands were low both 2–4 and 6–9 years post-treatment; average exotic richness never exceeded 3 species 13 m^{-2} and average exotic cover never exceeded 2% for either forest type or sampling period. Furthermore, average exotic richness and cover in mulched PP and LP/MC stands always comprised 10% or less of total understory plant richness and cover.

4. Discussion

4.1. Graminoid, forb, shrub, and total richness and cover

We found that mulching treatments, as implemented in Colorado PJ, PP, and LP/MC forests to reduce crown fire hazard, tended to stimulate understory graminoid, forb, and shrub communities as a whole. Untreated stands were characterized by fairly depauperate

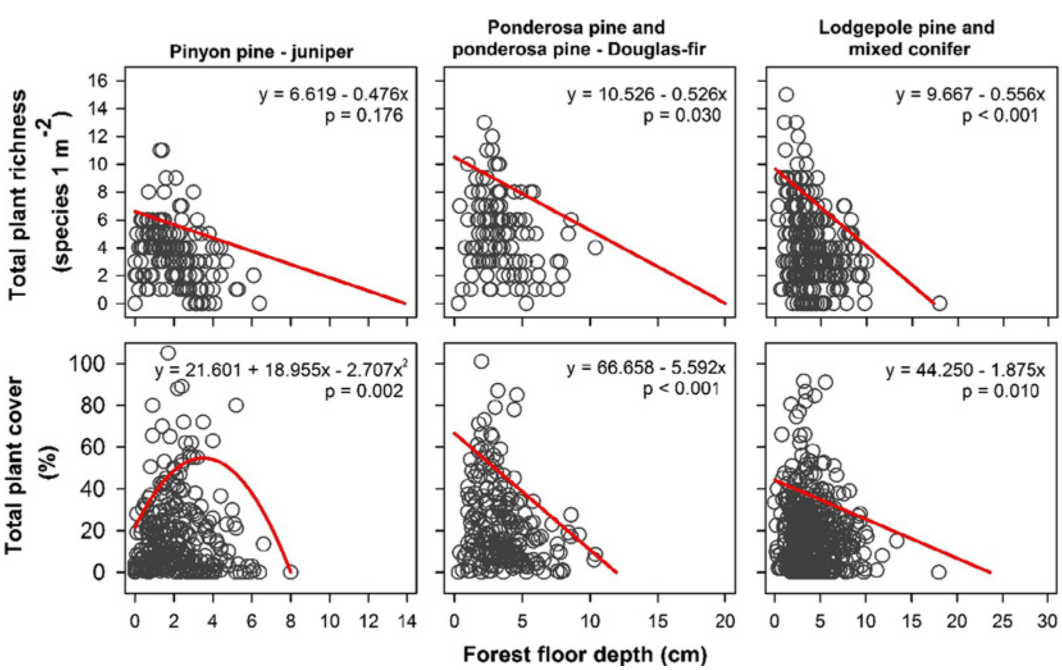

Fig. 5. Relationship between the total richness and cover of understory plant species and forest floor depth at the localized (i.e., 1-m^2 quadrat) scale, by forest type. Data are from mulched stands 6–9 years post-treatment. Forest floor depth is the cumulative depth of litter, duff, and woody material <2.5 cm in diameter. Note that the scale of forest floor depth is not consistent across forest types.

Table 3
Exotic plant species documented across study stands (i.e., transects) during the two sampling periods, by forest type, and the percent of untreated and mulched stands containing each. An "*" indicates that the species is classified as noxious by the state of Colorado.

Species	Life span and growth form	2–4 years post-treatment		6–9 years post-treatment	
		Untreated	Mulched	Untreated	Mulched
Pinyon pine – juniper					
Alyssum (*Alyssum simplex*)	Annual forb	25	0	33	8
Field brome (*Bromus arvensis*)	Annual graminoid	0	17	0	0
Smooth brome (*Bromus inermis*)	Perennial graminoid	0	0	0	8
Cheatgrass (*Bromus tectorum*)*	Annual graminoid	50	42	42	42
Musk thistle (*Carduus nutans*)*	Biennial/perennial forb	0	25	0	0
Bur buttercup (*Ceratocephala testiculata*)	Annual forb	17	8	25	17
Prickly lettuce (*Lactuca serriola*)	Annual/biennial forb	0	50	8	0
European stickseed (*Lappula squarrosa*)	Annual/biennial forb	8	8	25	25
Tumblemustard (*Sisymbrium altissimum*)	Annual/biennial forb	0	17	0	0
Yellow salsify (*Tragopogon dubius*)	Annual/biennial forb	0	25	0	33
Ponderosa pine and ponderosa pine – Douglas-fir					
Smooth brome (*Bromus inermis*)	Perennial graminoid	13	10	0	10
Musk thistle (*Carduus nutans*)*	Biennial/perennial forb	0	20	0	20
Canada thistle (*Cirsium arvense*)*	Perennial forb	0	20	0	50
Bull thistle (*Cirsium vulgare*)*	Biennial forb	0	0	0	10
Prickly lettuce (*Lactuca serriola*)	Annual/biennial forb	0	20	0	0
Yellow toadflax (*Linaria vulgaris*)*	Perennial forb	0	30	0	30
Kentucky bluegrass (*Poa pratensis*)	Perennial graminoid	0	20	0	20
Dandelion (*Taraxacum officinale*)	Perennial forb	13	70	0	30
Yellow salsify (*Tragopogon dubius*)	Annual/biennial forb	0	10	0	30
Mullein (*Verbascum thapsus*)*	Biennial forb	0	30	13	10
Lodgepole pine and mixed conifer					
Smooth brome (*Bromus inermis*)	Perennial graminoid	0	5	0	0
Canada thistle (*Cirsium arvense*)*	Perennial forb	0	38	5	71
Bull thistle (*Cirsium vulgare*)*	Biennial forb	0	5	0	5
Prickly lettuce (*Lactuca serriola*)	Annual/biennial forb	0	0	0	5
Marsh cudweed (*Gnaphalium uliginosum*)	Annual forb	5	0	0	0
Timothy (*Phleum pratense*)	Perennial graminoid	0	0	0	5
Canada bluegrass (*Poa compressa*)	Perennial graminoid	0	0	0	10
Kentucky bluegrass (*Poa pratensis*)	Perennial graminoid	0	0	0	5
Dandelion (*Taraxacum officinale*)	Perennial graminoid	5	24	10	48
Yellow salsify (*Tragopogon dubius*)	Annual/biennial forb	0	14	0	5
Mullein (*Verbascum thapsus*)*	Biennial forb	0	10	0	0

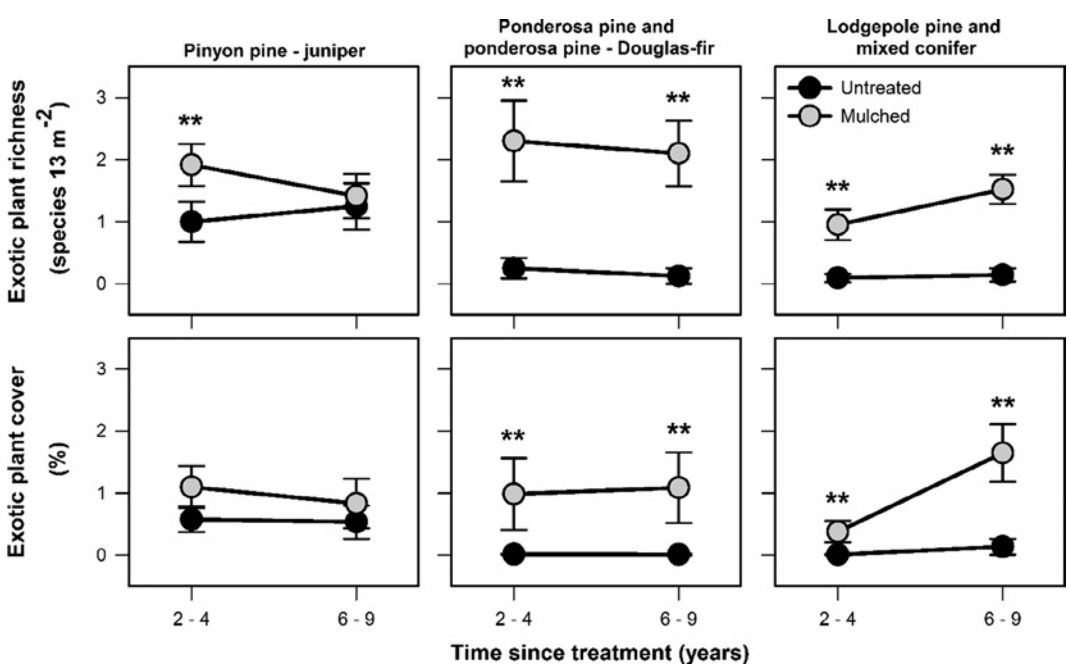

Fig. 6. Mean (±1 standard error) exotic plant richness and cover in untreated and mulched stands (i.e., transects), by forest type and time since treatment. Richness was calculated as the cumulative number of species recorded across 13 1-m^2 quadrats. An "**" indicates significant differences ($\alpha = 0.050$) between treatments for that forest type and sampling period.

understories, with average total understory plant richness values for all forest types and years ranging from only 9–18 species across the 13 1-m^{-2} quadrats per transect, and cover values ranging from only 4–11%. Mulching increased total understory plant richness and cover – primarily due to increases in graminoids and forbs – such that by the time of the 6–9 years post-treatment sampling period, average total richness increased 40–65% (to 15–23 species across the 13 1-m^{-2} quadrats) and average total cover increased 57–69% (to 17–22%). A primary explanation for these stand-scale responses is likely the increased availability of light, water, and other resources due to the dramatic reduction in the forest overstory (Palik et al., 1997; Bates et al., 2000; Prescott, 2002 and references therein). It has long been known that understory plants typically benefit from more open growing conditions in western forests. Jameson (1967), for example, showed that graminoid and forb biomass more than doubled as overstory canopy cover dropped from 50 to 10% in both PJ and PP forests of Arizona. Moreover, more recent research has documented how fuels treatments in particular can also stimulate understory plants, particularly when treatments are aggressive in removing overstory trees (Bates et al., 2000; Brockway et al., 2002; Lindgren et al., 2006; Metlen and Fiedler, 2006; Abella and Springer, 2015 and references therein).

The timing of our observations (2–4 years and 6–9 years post-treatment) likely allowed ample opportunity for understory plants to respond to the increases in resource availability brought about by overstory reductions. Many studies in western forests have found neutral or even negative impacts of fuels treatments and other disturbances on understory plants immediately after they occur (Thysell and Carey, 2001; Collins et al., 2007; Huffman et al., 2013; Fornwalt and Kaufmann, 2014; Abella and Springer, 2015 and references therein). Yet longer-term studies conducted five or more years following disturbance commonly report positive impacts (Laughlin et al., 2006; Lindgren et al., 2006; Thomas and Waring, 2014; Abella and Fornwalt, 2015; Abella and Springer, 2015 and references therein). Our study, which to our knowledge is the longest-term study of mulching treatment impacts on understory plants, revealed that trends of increased richness and cover began developing in the three forest types during the 2–4 years post-treatment sampling period, but were most pronounced during the 6–9 years post-treatment sampling period. Our results and those from related studies of a similar duration highlight the particular importance of longer-term observations for assessing the response of understory plants to disturbance.

With mulching treatments, reductions in the forest overstory are accompanied by the addition of mulched material to the pre-existing organic forest floor layer (Kane et al., 2009; Battaglia et al., 2010; Young et al., 2015). Our 0.9 quantile regression results depict the relationship between forest floor depth and near-maximum total understory plant richness and cover for localized areas within mulched stands (Koenker and Bassett, 1978; Cade and Noon, 2003), and provide insight into whether mulch addition per se hinders and/or enhances understory plants. We found that the effect of an increasingly deep forest floor layer on understory plants varied somewhat with forest type, but by and large was negative. Interestingly, in PJ forests, increasing the depth of the forest floor actually increased near-maximum total understory plant cover, so long as depths remained below about 3 cm. Working in experimental plots at these same PJ study areas, Rhoades et al. (2012) found that soils underneath a forest floor layer of about 3 cm had lower maximum summer temperatures and higher moisture than bare soils; when these findings are combined with ours, they suggest that at low depths, any suppressive effect of the forest floor on total understory plant cover due to the physical barrier it might create was outweighed by improvements in belowground growing conditions in this very warm, dry forest type. Meanwhile in PP and LP/MC forests, near-maximum total understory plant richness and cover were negatively related to forest floor depth for the entire range of depths, suggesting that the physical barrier created by mulch addition always suppressed plants more than any belowground changes stimulated them (Rhoades et al., 2012). Wolk and Rocca (2009) similarly found that increasing forest floor depth decreased near-maximum total understory plant richness and cover for a mulched PP forest in Colorado.

Thus, the stand-scale increase in understory plants that resulted from mulching treatments occurred despite the fact that augmenting the forest floor layer with mulched material could suppress understory plant establishment and growth, particularly if the mulch was deep. These seemingly contradictory patterns of understory plant response to mulching treatments can begin to be reconciled by recognizing that mulching operations do not generally distribute the mulched material evenly across the ground; rather, it is typically heterogeneously distributed, such that stands contain some areas with no mulch, and other areas with a mulch layer of various depths (Wolk and Rocca, 2009; Battaglia et al., 2010). Furthermore, the forest floor depths required to essentially eliminate understory plants in mulched stands – depths in excess of 8, 11, and 17 cm for PJ, PP, and LP/MC forests, respectively – were almost never encountered. In fact, mean forest floor depths in untreated and mulched stands 6–9 years post-treatment were largely comparable, averaging about 2 cm in PJ forests and 4–5 cm PP and LP/MC forests (data not shown), although the bulk density of the forest floor in mulched stands was probably greater (Battaglia et al., 2010). Nonetheless, it appears that the stimulatory effects of overstory tree removal on understory plants more than compensated for any suppressive effects of mulch addition, and in some instances (i.e., in PJ stands where forest floor depth was less than 3 cm), both overstory tree removal and mulch deposition seem to have contributed positively to the overall enhancement of understory plants.

Whether stand-scale increases in understory plants following mulching treatments are desirable ultimately depends on management objectives. Understory plant establishment and growth may be considered undesirable if it substantially increases the amount, height, and connectivity of surface fuels, contradicting the treatments' crown fire hazard mitigation objectives. However, for treatments aimed not only at reducing crown fire hazard but also at restoring more ecologically appropriate conditions, such as those being implemented in many PP forests following a century of fire suppression and densification of the forest overstory, increases in understory plant richness and cover may be welcome. For example, the Colorado Front Range Landscape Restoration Initiative, a ten-year initiative through which restoration treatments are being implemented on approximately 1200 ha of PP forest annually, has treatment objectives that include the reduction of crown fire hazard as well as the promotion of denser and more diverse understory plant communities (Underhill et al., 2014).

4.2. Exotic plant richness and cover

Exotic plants are well-known to be stimulated by disturbance (Hobbs and Huenneke, 1992 and references therein). Thus, we were surprised to find only subtle effects of mulching treatments on exotic plants in PJ forests, especially given the positive response we observed in this forest type for understory plants in general, and given that exotic plants were likely present in the pre-treatment plant community (as evidenced by exotic plant values in untreated stands). Moreover, other studies have reported that mulching and other fuels treatments can favor exotic plants in PJ forests. For example, Owen et al. (2009) found that mulching increased cheatgrass cover in a southwestern Colorado study area four growing seasons following treatment, from <1% in untreated

PJ stands to >4% in mulched stands. Working in southeastern Utah, Redmond et al. (2014) found that mulching increased the relative density of exotic species two growing seasons post-treatment, with this increase being driven primarily by prickly lettuce (*Lactuca serriola*), prickly Russian thistle (*Salsola tragus*), and tall tumblemustard (*Sisymbrium altissimum*). Perhaps the droughty conditions in 2012, the year of our 6–9 year post-treatment sampling period, curtailed the increase in exotic plants that was beginning to develop in mulched PJ stands during the previous sampling period. Nearly all of the exotic plant species we encountered in these stands were annuals and biennials, the germination and growth of which can be strongly influenced by precipitation patterns (Rao and Allen, 2010). We hope to conduct additional sampling to gain insight into whether the exotic plant trends we observed in PJ forests are applicable over even longer time frames.

In contrast to PJ forests, we found that exotic plants were clearly stimulated by mulching in PP and LP/MC forests. Similar exotic plant patterns have been documented following mulching in these forest types (Collins et al., 2007; Wolk and Rocca, 2009; Kane et al., 2010), and following other disturbances as well (Huisinga et al., 2005; Metlen and Fiedler, 2006; Freeman et al., 2007; Fornwalt et al., 2010; Abella and Springer, 2015 and references therein). Yet we also found that exotic plant richness and cover comprised 10% or less of total understory plant richness and cover in mulched PP and LP/MC stands, suggesting that exotic plants may not pose a major management concern at this time. Nonetheless, we feel that exotic plants – and Canada thistle in particular – in our PP and LP/MC stands warrant continued attention. Canada thistle was found in 20% and 38% of the mulched PP and LP/MC stands 2–4 years post-treatment, respectively, and 50 and 71% of stands 6–9 years post-treatment, but was largely absent from untreated stands. Wolk and Rocca (2009) also found that Canada thistle responded favorably to mulching treatments in Colorado PP forests, documenting it in 75% of thinned plots where unwanted shrubs and trees were mulched and distributed on the ground, in 31% of thinned plots where unwanted shrubs and trees were taken offsite, and in none of the untreated plots; their findings therefore suggest that Canada thistle may benefit from not only from reductions in the forest overstory, but also from the mulch itself. This disturbance-stimulated, perennial species can reproduce aggressively through both seeds and extensive belowground organs, which may be contributing to its success in mulched stands (Donald, 1994; Heimann and Cussans, 1996).

5. Conclusions

The various aspects of mulching fuels treatments – the intentional or unintentional damage to understory plants by heavy machinery, the removal of overstory trees, and the deposition of mulched material – interacted to promote denser and more diverse understory plant communities at the stand scale in three Colorado coniferous forest types. Graminoids and forbs in particular tended to increase following mulching, often substantially so. These trends began developing 2–4 years post-treatment but were most pronounced 6–9 years post-treatment, underscoring the importance of evaluating mulching impacts on understory plants over a range of time frames. The increases in understory plants in mulched stands 6–9 years post-treatment occurred despite the fact that plants tended to be heavily suppressed in localized areas where mulch contributed to a deep forest floor layer, because such areas were rare. While exotic plants also commonly responded positively to mulching at the stand scale, values were low. That these trends extended across all three coniferous forest types studied here suggests they may be generalizable to elsewhere in the western USA where similar mulching treatments occurred.

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References

Abella, S.R., Fornwalt, P.J., 2015. Ten years of vegetation assembly after a North American mega-fire. Glob. Change Biol. 21, 789–802.

Abella, S.R., Springer, J.D., 2015. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. For. Ecol. Manage. 335, 281–299.

Ackerfield, J., 2015. Flora of Colorado. Botanical Research Institute of Texas Press, Fort Worth, Texas, USA.

Bates, J.D., Miller, R.F., Svejcar, T.J., 2000. Understory dynamics in cut and uncut western juniper woodlands. J. Range Manag. 53, 119–126.

Battaglia, M.A., Rocca, M.E., Rhoades, C.C., Ryan, M.G., 2010. Surface fuel loadings and potential crown fire behavior within mulching treatments in Colorado coniferous forests. For. Ecol. Manage. 260, 1557–1566.

Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. J. Environ. Manage. 64, 179–197.

Cade, B.S., Noon, B.R., 2003. A gentle introduction to quantile regression for ecologists. Front. Ecol. Environ. 1, 412–420.

Cleaves, D.A., Martinez, J., Haines, T.K., 2000. Influences on Prescribed Burning Activity and Costs in the National Forest System. General Technical Report SRS-37. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Collins, B.M., Moghaddas, J.J., Stephens, S.L., 2007. Initial changes in forest structure and understory plant communities following fuel reduction activities in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 239, 102–111.

Donald, W.W., 1994. The biology of Canada thistle (*Cirsium arvense*). Rev. Weed Sci. 6, 77–101.

Faist, A.M., Stone, H., Tripp, E.A., 2015. Impacts of mastication: soil seed bank responses to a forest thinning treatment in three Colorado (USA) conifer forest types. Forests 6, 3060–3074.

Fornwalt, P.J., Kaufmann, M.R., 2014. Understory plant community dynamics following a large, mixed severity wildfire in a *Pinus ponderosa – Pseudotsuga menziesii* forest, Colorado, USA. J. Veg. Sci. 25, 805–818.

Fornwalt, P.J., Rhoades, C.C., 2011. Rehabilitating slash pile burn scars in upper montane forests of the Colorado Front Range. Natural Areas J. 31, 177–182.

Fornwalt, P.J., Kaufmann, M.R., Stohlgren, T.J., 2010. Impacts of mixed severity wildfire on exotic plants in a Colorado ponderosa pine – Douglas-fir forest. Biol. Invasions 12, 2683–2695.

Freeman, J.P., Stohlgren, T.J., Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., Brown, C.S., 2007. Rapid assessment of postfire plant invasions in coniferous forests of the western United States. Ecol. Appl. 17, 1656–1665.

Harrington, H.D., 1964. Manual of the Plants of Colorado. Swallow Press, Chicago, Illinois, USA.

Heimann, B., Cussans, G.W., 1996. The importance of seeds and sexual reproduction in the population biology of *Cirsium arvense* – a literature review. Weed Res. 36, 493–503.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6, 324–337.

Hood, S., Wu, R., 2006. Estimating fuel bed loadings in masticated areas. In: Andrews, P., Butler, B. (Eds.), Fuels Management – How to Measure Success. Proceedings RMRS-P-41. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA, pp. 333–340.

Huffman, D.W., Stoddard, M.T., Springer, J.D., Crouse, J.E., Chancellor, W.W., 2013. Understory plant community responses to hazardous fuels reduction treatments in pinyon-juniper woodlands of Arizona, USA. For. Ecol. Manage. 289, 478–488.

Huisinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D., McGlone, C.M., 2005. Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. J. Torrey Botanical Soc. 132, 590–601.

Jameson, D.A., 1967. The relationship of tree overstory and herbaceous understory vegetation. J. Range Manag. 20, 247–249.

Kane, J.M., Varner, J.M., Knapp, E.E., 2009. Novel fuelbed characteristics associated with mechanical mastication treatments in northern California and south-western Oregon, USA. Int. J. Wildland Fire 18, 686–697.

Kane, J.M., Varner, J.M., Knapp, E.E., Powers, R.F., 2010. Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest. Appl. Veg. Sci. 13, 207–220.

Keegan III, C.E., Morgan, T.A., Gebert, K.M., Brandt, J.P., Blatner, K.A., Spoelma, T.P., 2006. Timber-processing capacity and capabilities in the western United States. J. Forest. 104, 262–268.

Koenker, R., Bassett, G., 1978. Regression quantiles. Econometrica 46, 33–50.

Kreye, J.K., Brewer, N.W., Morgan, P., Varner, J.M., Smith, A.M.S., Hoffman, C.M., Ottmar, R.D., 2014. Fire behavior in masticated fuels: a review. For. Ecol. Manage. 314, 193–207.

Laughlin, D.C., Moore, M.M., Bakker, J.D., Casey, C.A., Springer, J.D., Fulé, P.Z., Covington, W.W., 2006. Assessing targets for the restoration of herbaceous vegetation in ponderosa pine forests. Restor. Ecol. 14, 548–560.

Lindgren, P.M.F., Ransome, D.B., Sullivan, D.S., Sullivan, T.P., 2006. Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest. Can. J. For. Res. 36, 48–61.

Metlen, K.L., Fiedler, C.E., 2006. Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA. For. Ecol. Manage. 222, 355–369.

Owen, S.M., Sieg, C.H., Gehring, C.A., Bowker, M.A., 2009. Above- and below-ground responses to tree thinning depend on the treatment of tree debris. For. Ecol. Manage. 259, 71–80.

Palik, B.J., Mitchell, R.J., Houseal, G., Pederson, N., 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Can. J. For. Res. 27, 1458–1464.

Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22, 1193–1200.

PRISM [PRISM Climate Group], 2015. PRISM Climate Data. <http://prism.oregonstate.edu>. Oregon State University, Corvallis, Oregon, USA (accessed 12 November 2015).

Quinn-Davidson, L.N., Varner, J.M., 2012. Impediments to prescribed fire across agency, landscape and manager: an example from northern California. Int. J. Wildland Fire 21, 210–218.

Rao, L.E., Allen, E.B., 2010. Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. Oecologia 162, 1035–1046.

Redmond, M.D., Zelikova, T.J., Barger, N.N., 2014. Limits to understory plant restoration following fuel-reduction treatments in a piñon – juniper woodland. Environ. Manage. 54, 1139–1152.

Reiner, A.L., Vaillant, N.M., Fites-Kaufman, J., Dailey, S.N., 2009. Mastication and prescribed fire impacts on fuels in a 25-year old ponderosa pine plantation, southern Sierra Nevada. For. Ecol. Manage. 258, 2365–2372.

Rhoades, C.C., Battaglia, M.A., Rocca, M.E., Ryan, M.G., 2012. Short- and medium-term effects of fuel reduction mulch treatments on soil nitrogen availability in Colorado conifer forests. For. Ecol. Manage. 276, 231–238.

Rhoades, C.C., Fornwalt, P.J., Paschke, M.W., Shanklin, A., Jonas, J.L., 2015. Recovery of small pile burn scars in conifer forests of the Colorado Front Range. For. Ecol. Manage. 347, 180–187.

Roundy, B.A., Miller, R.F., Tausch, R.J., Young, K., Hurlet, A., Rau, B., Jessop, B., Chambers, J.C., Eggett, D., 2014. Understory cover responses to piñon – juniper treatments across tree dominance gradients in the Great Basin. Rangeland Ecol. Manage. 67, 482–494.

Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol. Methods 11, 54–71.

Thomas, Z., Waring, K.M., 2014. Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in northern New Mexico, USA. Forest Sci. 61, 93–104.

Thysell, D.R., Carey, A.A., 2001. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation. Can. J. For. Res. 31, 1513–1525.

Underhill, J.L., Dickinson, Y., Rudney, A., Thinnes, J., 2014. Silviculture of the Colorado Front Range Landscape Restoration Initiative. J. Forest. 112, 484–493.

USDA NRCS [US Department of Agriculture, Natural Resources Conservation Service], 2015. The PLANTS Database. <http://plants.usda.gov>. National Plant Data Team, Greensboro, North Carolina, USA.

Weber, W.A., Wittmann, R.C., 2001. Colorado Flora: Western Slope. University Press of Colorado, Niwot, Colorado, USA.

Williamson, M.A., 2007. Factors in United States Forest Service district rangers' decision to manage a fire for resource benefit. Int. J. Wildland Fire 16, 755–762.

Wolk, B., Rocca, M.E., 2009. Thinning and chipping small-diameter ponderosa pine changes understory plant communities on the Colorado Front Range. For. Ecol. Manage. 257, 85–95.

Xiong, S.J., Nilsson, C., 1999. The effects of plant litter on vegetation: a meta-analysis. J. Ecol. 87, 984–994.

Young, K.R., Roundy, B.A., Bunting, S.C., Eggett, D.L., 2015. Utah juniper and two-needle piñon reduction alters fuel loads. Int. J. Wildland Fire 24, 236–248.