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Ecological niches of tree species drive variability in conifer regeneration abundance following fuels treatments

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ABSTRACT

One goal of fuels treatments is to limit potential fire behavior by reducing overstory tree density, but this may precipitate regeneration, which contributes to increasing potential fire behavior over time. To understand factors that influence tree regeneration in treated stands, we compared abundance of advance and post treatment regeneration in 5–14-year-old thinning and mastication treatments covering approximately 2600 ha within two National Forests in Colorado, U.S.A. The study sites were dominated by two species with complimentary regeneration niches. Ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) is less shade tolerant, but more fire and drought resistant than Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). We considered three critical features of the post treatment environment: species composition, forest structure (especially density), and site characteristics. Regeneration densities at the plot level varied considerably: 37% of the plots had no regeneration, while 15% had more than double the average density. High-density areas tended to occur in moist sites, mostly on north aspects that were dominated by Douglas-fir in the overstory. These areas are where wildfire mitigation benefits will likely deteriorate most rapidly. The vast majority (69%) of all regeneration was Douglas-fir. 31% of all regeneration occurred post treatment. In this group, ponderosa pine abundance was positively related to time since treatment but Douglas-fir was not, suggesting a stronger positive effect of treatment for ponderosa pine, although Douglas-fir was still more abundant. This is likely because treatments reduced the seed source for Douglas-fir more than for ponderosa pine while reducing total overstory density to create conditions that met the regeneration requirements of this shade intolerant species. Advanced regeneration was common throughout the study area, consisting of nearly 80% Douglas-fir and only 13% ponderosa pine. Although the abundance of advance regeneration decreased over time since treatment, likely due to mortality given that we encountered few sapling-sized trees, surviving trees reduce treatment longevity and have the potential for subsequent growth release and contribution to fuel hazard development. Conifer regeneration did not vary between mastication and thinning treatments. The impact of regeneration on treatment longevity was highly variable at smaller-than-stand scales. On the Colorado Front Range, moist sites with low overstory density and mature Douglas-fir to provide a seed source are where treatment effectiveness is likely to degrade most rapidly. These areas with abundant regeneration may be best left untreated, or managers should anticipate the need to re-treat them more frequently.

1. Introduction

Fuels reduction treatments aimed at reducing high severity wildfire potential are common forest management activities throughout the western U.S. (Litschert et al., 2012; North et al., 2009; Reynolds et al., 2013; Schwilk et al., 2009; Stephens et al., 2012; Westerling et al., 2006), including our study area on the Colorado Front Range (Addington et al., 2018). Hazardous fuels reduction treatments seek to reduce the quantity and connectivity of surface and crown fuels to decrease the likelihood of high severity wildfire in dry forests, and frequently seek to shift composition toward large individuals of early-seral, fire-adapted tree species (Addington et al., 2018; Agee and Skinner, 2005; Hoffman et al., 2018). Treatment types utilized in the western U.S. include mechanical methods such as thinning and/or mulching (masticating or chipping) fuels, as well as prescribed burning (Graham et al., 2004).

Abbreviations: AICc, corrected Akaike information criterion; DBH, Diameter at breast height; SDI, stand density index

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Treatment effectiveness deteriorates over time as hazardous fuels re-accumulate (Fulé et al., 2012; Hudak et al., 2011) and potential fire behavior is modified by regenerating trees growing into the canopy (Ex et al., 2019). Consequently, the length of time required for a treated stand to return to pre-treatment levels of potential fire behavior can be substantially reduced by abundant tree regeneration, especially when regeneration occurs soon after treatment (Tinkham et al., 2016). The release of large quantities of advance regeneration retained following treatment would presumably similarly shorten the effective lifespan of treatments. Low residual stand densities following treatments can be similar to those prescribed for silvicultural regeneration treatments, such as the seed cut in shelterwood regeneration systems (Addington et al., 2018; Francis et al., 2018; Shepperd and Battaglia, 2002; Shepperd et al., 2006). Therefore, while mechanical fuels treatments may reduce fire hazard in the short-term, they may also work against themselves in the long-term by increasing regeneration rates in the absence of fire or other maintenance disturbances. Treatment effects have been shown to persist for 10–20 years in western conifer forests (Battaglia et al., 2008; Chiono et al., 2012; Graham et al., 2004; Stephens et al., 2012; Vaillant et al., 2013). Several modeling studies have identified tree regeneration dynamics as a critical determinant of fuels treatment longevity (Collins et al., 2011, 2013; Ex et al., 2019; Tinkham et al., 2016).

Tree regeneration rates following treatments are likely to vary by species according to their regeneration requirements. The species composition of dry, mixed-conifer forests along the Colorado Front Range is dominated by fire-adapted ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which is a later seral species than ponderosa pine that is also less tolerant of fire (Bradley et al., 1992). Douglas-fir has become overly abundant along the Colorado Front Range relative to ponderosa pine in the absence of wildfire over the past century (Battaglia et al., 2018; Kaufmann et al., 2006; Peet, 1981) because the two species have complementary regeneration niches. Ponderosa pine is more shade intolerant, germinating readily on bare mineral soil and growing well under open canopy conditions like those created following fire (Bonnet et al., 2005; Shepperd and Battaglia, 2002; Shepperd et al., 2006). Douglas-fir, in contrast, is relatively shade tolerant and thrives under cooler and wetter conditions, as in the understory of forests where periodic surface fires are absent (Hermann and Lavender, 1990). In forests that have become overly dense largely due to the encroachment of Douglas-fir, fuels treatments may attempt to reduce the proportion of Douglas-fir in stands to promote ponderosa pine while decreasing overall forest density to approximate historic range of variability (Addington et al., 2018; Briggs et al., 2017; Battaglia et al., 2018). Juveniles of late seral, fire intolerant conifers such as Douglas-fir remain vulnerable to fire for much longer than those of early seral species such as ponderosa pine. While Douglas-fir trees generally maintain long crowns (Hermann and Lavender, 1990) that connect the surface and the canopy fuels in a stand (Keeley et al., 2004), ponderosa pine juveniles quickly develop thick basal bark that is resistant to fire damage (Battaglia et al., 2008).

Fuels reduction treatment prescriptions themselves can substantially influence the abundance and composition of tree regeneration via their effects on residual overstory density and species composition of seed-bearing trees, and the slash treatment method utilized. Reductions in subsequent Douglas-fir regeneration have been documented following wildfire (Rodman et al., 2020) and following fuels treatments that preferentially remove it as a seed source (Francis et al., 2018), despite its well-documented dispersal ability (Bonnet et al., 2005; Chambers et al., 2016; Donato et al., 2009). Reductions in overstory density can favor regeneration of shade intolerant species like ponderosa pine by increasing light availability (Boyden et al., 2005; Chen, 1997; Francis et al., 2018). Reducing overstory density may also promote the release of advance regeneration (Ruel et al., 2000), which would hasten the return to a forest structure with high torching potential. Lastly, different slash treatment activities manipulate dead woody surface fuels (Stephens and Moghaddas, 2005), which can protect seedlings from desiccation (Fajardo et al., 2007). With thinning treatments foresters have discretion to manipulate slash by removing it entirely or leaving slash on the ground in varying amounts and in pieces of different sizes. In mastication treatments, trees are shredded in place using machinery which always redistributes the fuel load to the surface in generally smaller and more tightly compact pieces (Keane et al., 2018; Kreye et al., 2014; Stephens and Moghaddas, 2005; Wolk et al., 2020).

While forest managers can exercise some control over the regeneration environment via treatment prescriptions, site characteristics such as aspect, elevation, and slope are what ultimately dictate the lower and upper bounds on local temperature and moisture conditions, which in turn strongly influence conifer germination and growth. Tree regeneration can be limited by high temperatures and low moisture in dry, mixed-conifer forests (Petrie et al., 2016). In mountainous regions of the western U.S., vegetation composition and structure often vary systematically between hotter, drier south aspects, and cooler, wetter north aspects (Francis et al., 2018; Lydersen and North, 2012). According to their regeneration niches in the dry, mixed-conifer forest type, ponderosa pine dominates at lower elevations and on south-facing slopes, while Douglas-fir becomes more abundant with increasing elevation and on north aspects. More abundant ponderosa pine regeneration has been observed after fires on cooler north-facing slopes, which receive less solar radiation and therefore have lower rates of evapotranspiration and less evaporative drying than south and west facing slopes (Rother and Veblen, 2016). Several studies have found post-fire ponderosa pine and Douglas-fir regeneration densities are positively correlated with elevation (Chambers et al., 2016; Dodson and Root, 2013; Haffey et al., 2018; Kemp et al., 2016; Rother and Veblen, 2016), reflecting decreasing average temperature and increasing moisture availability with increasing elevation (Peet, 1981). Recent research suggests that at lower elevations, climate change and high severity fire may lead Douglas-fir and ponderosa pine forests throughout the western U.S to transition to new ecosystems following fire due to their inability to regenerate adequately (Davis et al., 2019). The effects of elevation, aspect, and shading by overstory trees are typically intensified as slope increases (Marquis, 1965; Prévost and Raymond, 2012).

Our overarching objective with this work was to examine how treatment prescriptions and site conditions influence the abundance and variability of regeneration of two conifer species with contrasting regeneration requirements, Douglas-fir and ponderosa pine. Our aim is to inform effective fuels mitigation strategies by better understanding factors that predispose stands to development of structure (abundant post-treatment tree regeneration) and composition (high proportion of fire-intolerant species) associated with deterioration of fuels treatment effectiveness. We expected that lower residual overstory density would promote ponderosa pine more than Douglas-fir, and that Douglas-fir would be more inhibited by site moisture limitations, but that abundance of both species would be related to abundance of conspecific mature trees in the overstory. We explored these hypotheses using a space for time substitution approach to investigate regeneration abundance in 5–14-year-old treatments in dry, mixed conifer stands across a gradient of moisture availability by aspect, elevation, and slope. We also sampled in thinned and masticated stands to assess whether treatment type was an important predictor of regeneration abundance.

2. Materials and methods

2.1. Field methods

Our study area included 50 wildfire treatment units in the Boulder (Fig. 1A) and South Platte Ranger Districts (Fig. 1B) of the Pike-San Isabel and Arapaho-Roosevelt National Forests, Colorado. Some

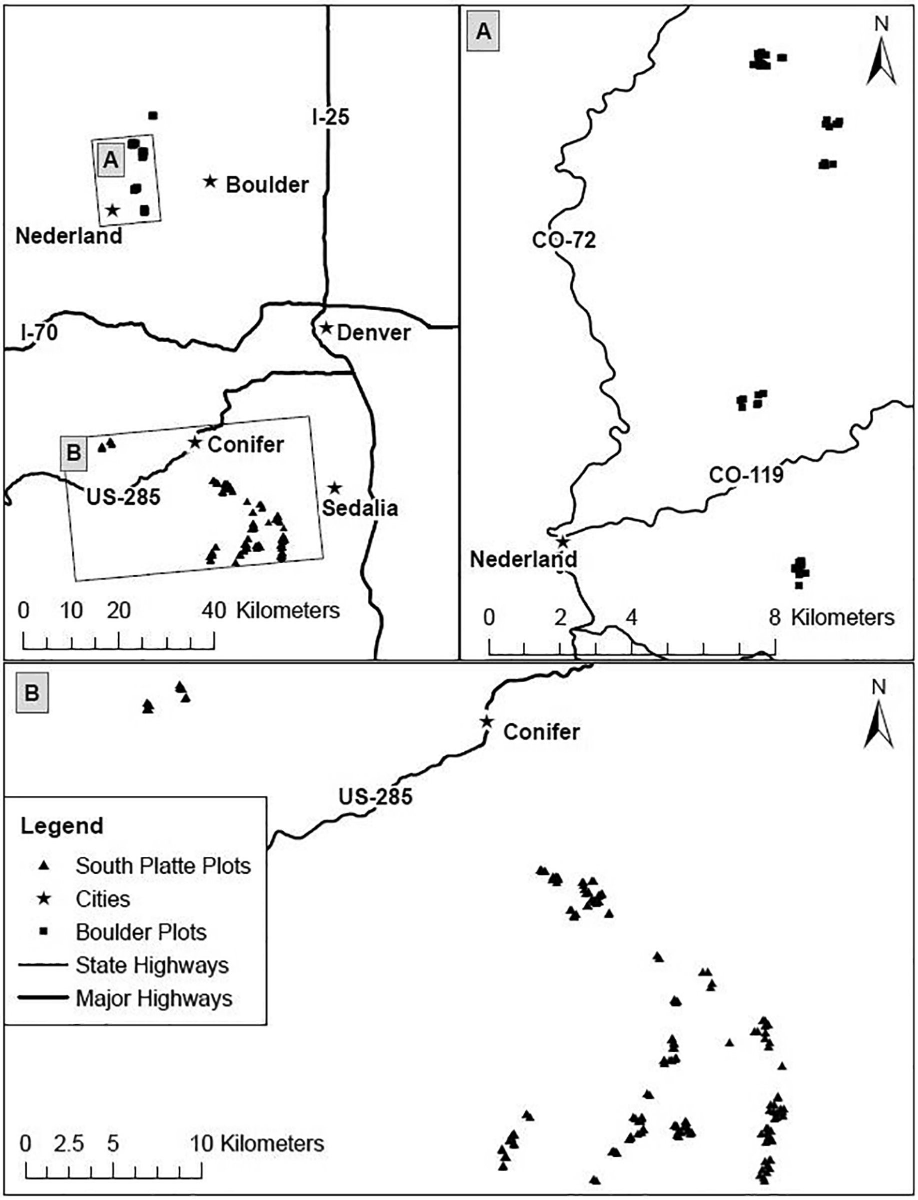

Fig. 1. Plot locations in the (A) Boulder and (B) South Platte Ranger Districts, including on Denver Water land.

additional units were sampled in the South Platte watershed on land belonging to Denver Water. Forests in the lower montane zone (from about 1600 to 2600 m in elevation, depending on latitude) in the study area are mainly dense ponderosa pine and Douglas-fir mixtures on north aspects transitioning to more open ponderosa pine-dominated forests on south aspects. Lodgepole pine (*Pinus contorta* subsp. *latifolia)* becomes a more important stand component especially on north aspects in the upper montane zone (approximately 2300–2900 m, depending on latitude). Other common tree species include Rocky Mountain juniper (*Juniperus scopulorum*), quaking aspen (*Populus tremuloides*), and limber pine (*Pinus flexilis*) (Peet, 1981). In the South Platte Ranger District, soils are derived from weathered granite of the Pikes Peak formation and are especially coarse-grained (Graham, 2003). In the Boulder Ranger District, soils are more variable but still generally rocky, coarse in texture, and shallow (Peet, 1981). Vegetation in the understory and forest openings includes bunchgrasses such as Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*) in the South Platte, as well as spike fescue (*Leucopoa kingii*) in the Boulder Ranger District. Shrub species throughout both areas include mountain mahogany (*Cercocarpus montanus*), kinnikinnick (*Arctostaphylos uva-ursi*), and common juniper (*Juniperus communis*). Total annual precipitation and mean annual temperature range from about 457 mm and 8.2 °C at lower elevations (near Twin Cedars, CO at 1890 m) to 546 mm and 4.8 °C at higher elevations (near Nederland, CO at 2500 m) (PRISM, 2017).

We sampled in a chronosequence of units treated in 2003–2012, 5–14 years before sampling. Material from the mastication treatment units was not removed. Material from the thinning treatment units was either left in place, removed as product, lopped and scattered, piled (and sometimes burned), or some combination of all these. Both mastication and thinning treatments occurred in the South Platte Ranger District, while only thinning treatments occurred in the Boulder Ranger District.

Conifer regeneration was sampled in 229 total plots, each with a 3.59-m radius (0.01 acres) (Fig. A1), which were randomly placed within the units but stratified as evenly as possible across elevation (approximately 1880–2870 m) and by north or south aspect (within 45° of each), and in the South Platte, by treatment type (Fig. 2). The species of all conifer regeneration in the plots was recorded, and then basal cross sections were collected for age determination. Regeneration was

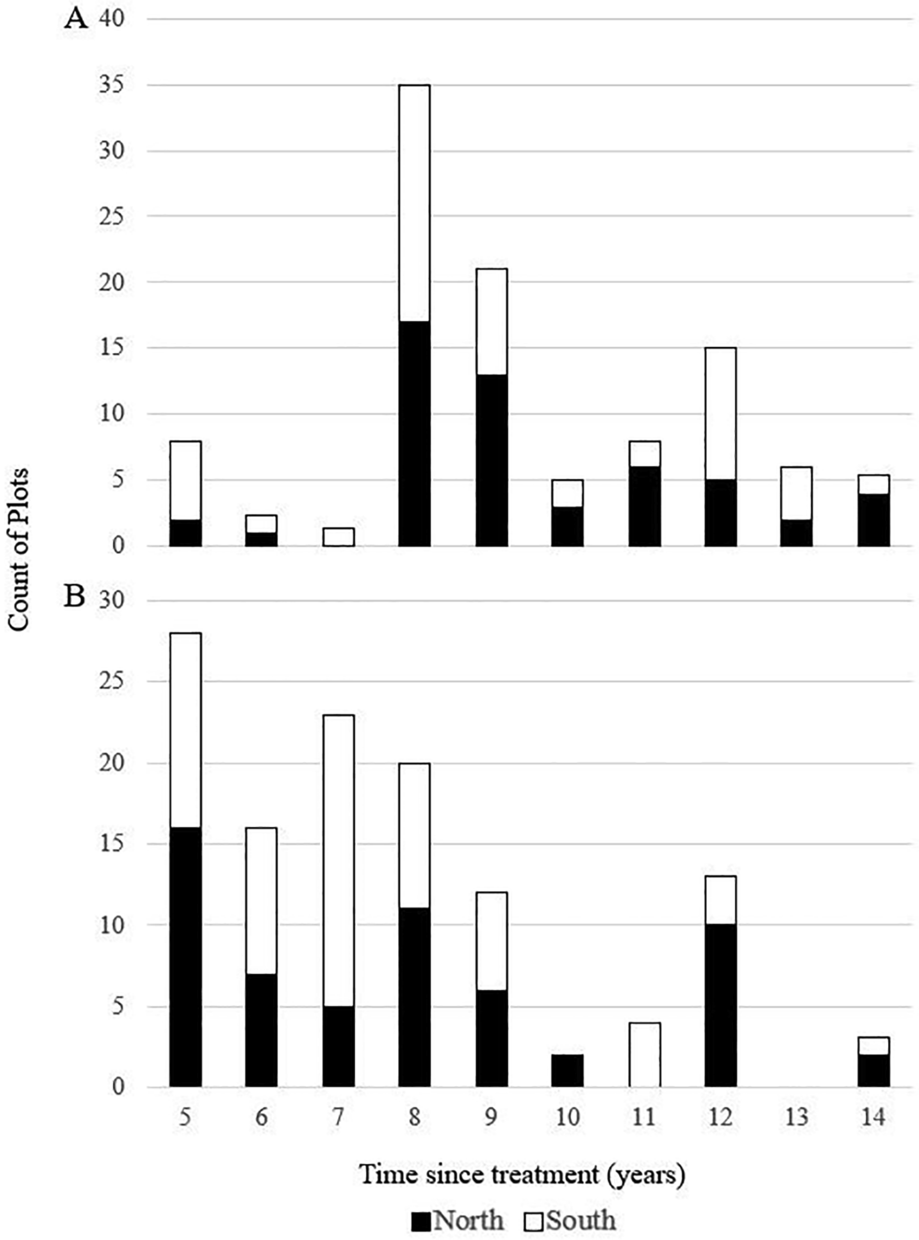

Fig. 2. Sample size of all plots by (A) mastication, and (B) thinning treatment types and by aspect (north or south), and time since treatment (TST) in years.

considered to be any understory tree less than 1.37 m (4.5 feet) tall. In plots where more than approximately 30 conifer seedlings were collected from the first half of a regeneration plot, the remaining seedlings in the plot were not collected for aging but species and heights were recorded. (This applied to only seven plots.) We did not attempt to sample first-year germinant seedlings with succulent stems because although they were very numerous, most were unlikely to survive (Shepperd et al., 2006). Basal cross-sections were sanded and polished, and then the annual rings were counted under a microscope to ascertain establishment years. These years were then compared to treatment years for each unit to categorize seedlings as advance or post-treatment regeneration. There were 136 total seedlings from 5 plots that were counted but not collected and therefore not aged (Table 1) according to our methods described above. In these plots, we applied the proportions of post treatment versus advance regeneration counts by species from the sample of seedlings that were aged to the sample of seedlings that were counted only and included them in the analysis. Additionally, data from two plots with very high regeneration density that were sampled this way were excluded from the analysis because we failed to record all the seedlings within the plot area.

Conifer saplings (trees taller than 1.37 m but less than 12.7 cm (5 in.)) in diameter at breast height (DBH)) were also recorded by species and live or dead status in the 3.59-m radius regeneration plots. Live overstory trees and snags greater than 1.37 m tall and 12.7 cm in DBH were sampled using a 2.30 m^2 ha^{-1} (10 ft^2 ac^{-1}) basal area factor prism. The species, DBH (cm), height (to the nearest 0.30 m, or 1 foot), and live or dead status of each tree was recorded. Trees ha^{-1}, basal area (m^2 ha^{-1}), and stand density index (SDI, a measure of residual overstory density) (Reineke, 1933) of each species (Douglas-fir or ponderosa pine) and as a total for each plot were calculated using this data. Site characteristics may be indirectly represented by the maximum height of trees or the cover of shrubs or herbaceous vegetation (Carmean, 1975; Daubenmire, 1976), so the height of the tallest tree in each plot was measured as a basic indicator of site quality (Clutter et al., 1983), and understory vegetation cover data were collected using ocular cover estimates from three 1 m^2 quadrats for herbaceous plants and 15.24 m

Table 1
Total observed conifer regeneration counts by species, advance vs post treatment regeneration status, treatment type, & aspect from 227 plots. Other conifer species include lodgepole pine, Rocky Mountain juniper, limber pine, and Engelmann spruce.

	Mastication	Thinning	North	South	Total
Douglas-fir	559	620	1028	151	1179
Advance Regen.	351	466	696	121	817
Post Trt Regen.	146	105	221	30	251
Not aged	62	49	111	0	111
Ponderosa pine	205	119	170	154	324
Advance Regen.	57	75	52	80	132
Post Trt Regen.	125	42	109	58	167
Not aged	23	2	9	16	25
Other conifers	21	179	188	12	200
Advance Regen.	8	83	81	10	91
Post Trt Regen.	13	96	107	2	109
Not aged	0	0	0	0	0
Totals	785	918	1386	317	1703
	Totals				
Advance Regen.	1040				
Post Trt Regen.	527				
Not aged	136				

(50-ft) line-intercept transects for shrubs. For each, the total percent cover of vegetation was used as another potential basic indicator of site quality (Clutter et al., 1983), and the percent cover of vegetation from the quadrat nearest plot center and from a 9.14 m (30-ft) portion of the shrub transect centered on the regeneration plot was used as a basic indicator of potential competitive or facilitative effects. For further description of our methods for sampling understory vegetation and a schematic of the plot layout, see Appendix A. At each plot, we recorded the elevation in meters, aspect (categorically within 45° of north or south), and percent slope.

2.2. Analytical methods

Using generalized linear mixed models with a negative binomial distribution, we first tested whether conifer regeneration varied by treatment type in preliminary analyses using plots from just the South Platte, as only this area contained both thinning and mastication treatment types. Separate models were developed for four conifer regeneration groups: advance and post-treatment regeneration of Douglas-fir, and advance and post-treatment regeneration of ponderosa pine. Because preliminary analyses revealed that conifer regeneration in the four groups did not vary by treatment type, we subsequently pooled plots across treatment types and included plots from both ranger districts to test for variation by the predictors describing site characteristics, species composition and forest structure in Table 2. We used plots as our unit of observation rather than treatment units to better characterize variation in conifer regeneration abundance at sub-unit scales. Treatment unit was included as a random intercept term in the models, but we acknowledge the potential for the spatial autocorrelation of residual error within treatment units. Analyses were performed in R (R Development Core Team, 2013) using the Glmmadmb package (Bolker et al., 2012).

The distribution of each model containing all potential predictors and interactions (Table 2) was chosen using the corrected Akaike information criterion (AICc) (Burnham and Anderson, 2003). Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial distributions were considered as options for modeling our count data, and the negative binomial distribution was deemed appropriate in every case because the data was both overdispersed and included zeros (Zuur et al., 2009). We first built a full model containing all potential predictors, and then chose a final model for each regeneration group using backwards stepwise selection to manually remove the least important term until AICc was minimized. Appendix B contains these model selection tables (Tables B1, B2, B3, and B4). Insignificant predictors were dropped only if they raised AICc by 2 points or less, as long as the final selected model was no more than 2 AICc points higher than the lowest AICc model in the selection process. The results of model selection with and without potential outliers (plots with especially high regeneration counts) were compared. For all groups with the exception of ponderosa pine advance regeneration, the models including outliers were used because the same predictors were selected with or without outliers. For ponderosa pine advance regeneration, however, parameters could not be reliably estimated during model selection when three outliers were included, so the model with outliers excluded was used. Time since treatment was included in every model regardless of its significance because it varied widely among treatment units. We checked for collinearity between the predictors in each final model using the variance inflation factor (VIF) function from the car package (Fox and Weisberg, 2019) and confirmed the VIF did not exceed 5 for each predictor (James et al., 2014). Raw parameter estimates were exponentiated for interpretation as incidence rate ratios. Emtrends from the Emmeans package (Lenth et al., 2018) was used to evaluate significant interactions, as the incident rate ratios for interactions are not interpretable by themselves. All lower-order terms in significant interactions were kept. Statistical significance was evaluated at the alpha = 0.05 level.

3. Results

In total, 227 plots were included in the analysis, 179 of which were in the South Platte and 48 of which were in the Boulder Ranger District (Fig. 1). Mean conifer regeneration was 7.5 trees per 3.59-m radius plot or 1846 trees ha^{-1}, while median conifer regeneration was 2 trees plot^{-1} or 494 trees ha^{-1}. There was wide variability in regeneration abundance at the plot-level: 37% percent of the plots had no understory conifers and another 41% had 10 or less, while 4% of the plots contained 30 or more, including one plot with 181 seedlings. Most conifer regeneration encountered was Douglas-fir and ponderosa pine, and overall, Douglas-fir was much more abundant (Table 1): 1179 total Douglas-fir seedlings were observed compared to only 324 ponderosa pine seedlings (69% Douglas-fir). Lodgepole pine, Engelmann spruce (*Picea engelmannii*), limber pine, and Rocky Mountain juniper regeneration were also observed in low abundance. Almost two-thirds of the conifers were advance regeneration, and almost half were Douglas-fir advance regeneration.

The residual treatment overstory in the plots we sampled consisted mainly of Douglas-fir and ponderosa pine, and was denser on north aspects. Lodgepole pine, limber pine, Engelmann spruce, and Rocky Mountain juniper were also observed in lesser abundance in some plots. Mean residual overstory density was 270.1 trees ha^{-1} or 16.0 m^2 ha^{-1} in basal area in treatments on north aspects, and 148.9 trees ha^{-1} or 12.3 m^2 ha^{-1} in basal area in treatments on south aspects (Table 3). Douglas-fir was more abundant in the overstory on north aspects, while ponderosa pine dominated south aspects (Table 3).

Douglas-fir advance regeneration decreased by about 30% for every year after treatment (Table 2) and increased by 10–14% for every one-unit increase in Douglas-fir SDI (Table 2). Ponderosa pine advance regeneration did not vary over time since treatment but decreased by about 6% with every 1 m^2 increase in total overstory basal area (Table 2). Post treatment Douglas-fir regeneration did not vary over

Table 2
Conifer regeneration response by species and advance or post treatment status with n = the number of observations, and the parameter estimates with 95% confidence intervals for each significant predictor included in the selected model, and their significance codes: 0.001 '***', 0.01 '**', 0.05 '*'. Parameter estimates are interpreted as incidence rate ratios, such that values greater than 1 represent a percent increase in the response for every one-unit increase in the parameter, while values less than one represent a percent decrease in the response for every one-unit increase. Time since treatment (TST) was included in each model even when it was not significant (NS). "Interaction" denotes that a term was involved in a significant interaction (Interaction*). The incidence rate ratios for significant interactions are not interpretable by themselves, so instead we report results from the Emmeans package (Lenth et al., 2018).

	Advance regeneration Douglas-fir	Advance regeneration ponderosa pine	Post treatment Douglas-fir	Post treatment ponderosa pine
Predictors	n = 225	n = 224	n = 225	n = 227
Slope	Interaction	.	0.96* (0.934–0.996)	.
Aspect (with respect to South)	Interaction	0.459* (0.231–0.910)	0.216*** (0.091–0.515)	0.273** (0.113–0.659)
Elevation	.	.	.	.
Slope:Aspect Interaction	Interaction*	.	.	.
Aspect:Elevation Interaction	.	.	.	.
Time Since Treatment (TST)	0.685*** (0.572–0.820)	NS	NS	1.405** (1.131–1.745)
Basal Area (BA)	.	0.921** (0.870–0.974)	.	.
Trees ha^{-1} (TPH)	.	.	.	0.992** (0.987–0.998)
Stand Density Index (SDI)	.		0.895*(0.807–0.993)	.
Response Species BA	.	.	.	.
Response Species TPH	.	.	.	1.007* (1.001–1.013)
Response Species SDI	1.104*** (1.041–1.171)	.	1.314*** (1.191–1.45)	.
Maximum Tree Height	.	.	.	.
% Shrub/Whole Plot	.	.	.	.
% Herbaceous/Whole Plot	.	.	.	.
% Shrub/Regeneration Plot	.	.	.	.
% Herbaceous/Regeneration Plot	.	.	.	.

time since treatment. Post treatment Douglas-fir regeneration also increased by 31% for every one-unit increase in Douglas-fir SDI (Table 2), and increased by almost 10% for every one unit decrease in total overstory SDI. Post treatment ponderosa pine increased by about 40% for every one year after treatment (Table 2). It also increased slightly ($< 1\%$) with increasing ponderosa pine trees ha^{-1} in the overstory and decreased (by 1%) with increasing trees ha^{-1} of all overstory species (Table 2).

Eighty-three percent of regeneration was found on north aspects, but there were many plots on both aspects with no regeneration (Fig. 3). Mean total conifer regeneration density ranged from 2.8 trees $plot^{-1}$ or 681.2 trees ha^{-1} on south aspects to 13.6 trees $plot^{-1}$ or 3362.4 trees ha^{-1} on north aspects. On south aspects, the majority of plots contained no juvenile trees, about a third of plots contained 1–10 trees, and only about 9% of plots contained greater than 10 trees. On north aspects, however, 16% of plots had no juvenile trees, half contained 1–10 trees, and about a third contained greater than 10 trees (Fig. 3).

For Douglas-fir advance regeneration, the simple relationship with aspect was not significant (Table 2), but there was a significant interaction between slope and aspect (Table 2). The trends for slope on each aspect were small and negative; however, neither was significantly different from zero (Emtrends slope trends = -0.012 for south and -0.001 for north, confidence level 0.95), making this interaction significant strictly in the statistical sense. Any potential ecological interpretations of this would be highly speculative without additional corroborating data. There was 49% as much ponderosa pine advance regeneration on south aspects as on north aspects (Table 2). Post treatment Douglas-fir regeneration decreased by about 4% for every 1% increase in slope (Table 2). There was 22% as much post treatment Douglas-fir and 27% as much post treatment ponderosa pine regeneration on south aspects as on north aspects (Table 2). No regeneration groups varied by maximum tree height nor by any measure of understory vegetation (Table 2).

4. Discussion

In this study, we examined the regeneration response of tree species with contrasting regeneration niches in 5–14-year-old fuels treatments across site characteristics, species composition, forest structure, and treatment types in order to better understand implications of these interactions to improve longevity of future fuels reduction efforts. Regeneration densities varied considerably at the plot level. This was more pronounced on north aspects where cooler and wetter conditions

Table 3
Mean post treatment conditions (standard deviations in parentheses) by aspect (north or south) and treatment type (mastication or thinning) where conifer regeneration abundance and composition were characterized.

	North			South			All
	Mast.	Thin	Both	Mast.	Thin	Both	
# Plots	53	59	112	53	62	115	227
Basal area (m^2 ha^{-1})	15.6 (7.2)	16.4 (6.7)	16.0 (7.0)	12.5 (7.2)	12.1 (6.8)	12.3 (6.9)	14.1 (7.2)
Trees ha^{-1}	207.1 (147.1)	326.6 (279.6)	270.1 (233.7)	139.7 (123.8)	156.7 (133.7)	148.9 (128.9)	208.7 (197.2)
Douglas-fir basal area (%)	61.4 (36.4)	38.3 (35.0)	49.2 (37.4)	23.9 (33.6)	9.7 (18.7)	16.3 (27.4)	32.5 (36.6)
Ponderosa pine basal area (%)	33.5 (33.9)	43.3 (35.2)	38.6 (34.8)	74.6 (34.9)	84.5 (24.3)	80.0 (30.0)	59.6 (38.4)
% Shrub cover/plot	17.1 (17.5)	15.8 (20.0)	16.4 (18.8)	21.7 (23.0)	11.8 (18.0)	16.3 (20.9)	16.4 (19.9)
% Shrub cover/ regeneration plot	17.1 (19.0)	15.5 (20.7)	16.3 (19.8)	23.7 (27.0)	12.2 (19.5)	17.5 (23.9)	16.9 (21.9)
% Herbaceous cover/plot	11.6 (10.4)	7.0 (5.5)	9.2 (8.5)	13.9 (9.1)	9.3 (6.5)	11.4 (8.1)	10.3 (8.3)
% Herbaceous cover/ regeneration plot	13.5 (17.2)	6.6 (6.2)	9.9 (13.0)	11.5 (10.4)	9.6 (8.1)	10.5 (9.2)	10.2 (11.2)
Maximum tree height (m)	18.4 (2.9)	16.3 (3.4)	17.3 (3.3)	18.4 (3.5)	16.0 (3.1)	17.1 (3.5)	17.2 (3.4)

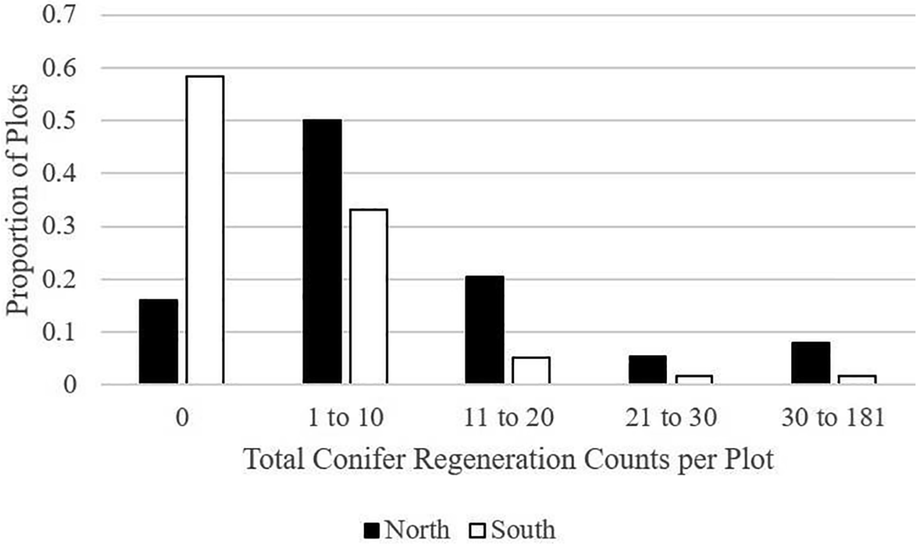

Fig. 3. Distribution of regeneration counts for plots by aspect.

resulted in occasional plots with very large numbers of Douglas-fir regeneration, which was not inconsistent with our expectations given the ecological requirements of this species. Contrary to our predictions, the negative relationship between residual overstory density and post treatment regeneration abundance was stronger for Douglas-fir than for ponderosa pine. However, only post treatment ponderosa pine regeneration significantly increased over time since treatment, and the positive relationship between seedling abundance and the density of conspecific mature trees in the overstory was much stronger for Douglas-fir than for ponderosa pine. This suggests that Douglas-fir regeneration is more limited by seed availability. Douglas-fir advance regeneration was abundant but decreased over time since treatment, which is more likely due to mortality than to growth into taller size classes of trees triggered by decreased overstory density. Aspect, residual overstory density, and species composition were better predictors of regeneration abundance than treatment type, which suggests that slash management didn't impact regeneration niches as much as reducing overstory density.

Conifer regeneration densities were extremely variable at the plot level, especially among plots on north aspects (Fig. 3). Although the mean density we observed was 1846 trees ha^{-1}, plot level regeneration density ha^{-1} ranged from 0 to 44,726 trees ha^{-1}. Fully 37% of our plots contained no regeneration, and 14.5% of plots had more than double the average density. These results indicate great variability in the rate at which treatment effectiveness is deteriorating over time as a result of tree regeneration (Tinkham et al., 2016). Our findings are consistent with prior work in the study area and contrast with findings from ponderosa pine-dominated forests in other parts of the western U.S. Observations of combined ponderosa pine and Douglas-fir regeneration by Francis et al. (2018) in Front Range treated stands averaged greater than 500 trees ha^{-1} by 10 years after treatment. Briggs et al. (2017) reported the mean density of conifer juveniles in treated and untreated stands on the Colorado Front Range as 3939 trees ha^{-1}, a value comparable to ours that also encompasses wide variability (42% of their plots contained no regeneration). Although our values also appear consistent with 10-year post treatment densities in excess of a thousand trees ha^{-1} reported for the Black Hills of South Dakota by Battaglia et al. (2008), densities from the Black Hills study were consistently higher and less variable than the values we report here. In contrast, the regeneration abundance we observed appears much higher than ten year post treatment values reported by Fajardo et al. (2007) in western Montana: 33–86 trees ha^{-1} for ponderosa pine and 8–156 trees ha^{-1} for Douglas-fir; and five year post treatment values reported in northern Arizona by Bailey and Covington (2002) and Fulé et al. (2005): only 14–75 trees ha^{-1}. We note, however, that Fajardo et al. (2007) did not include advance regeneration and Bailey and Covington (2002) only sampled regeneration greater than 20 cm in height. Our results suggest that treatment longevity will deteriorate most rapidly in areas where regeneration density is greatest, and that these sites are more likely to occur on north aspects.

More than 80% of juvenile trees sampled in this study were found on north aspects, and the maximum density observed on north aspects (44,726 trees ha^{-1}) was much higher than on south aspects (9884 trees ha^{-1}). This is presumably because the relatively cooler and wetter environment at these locations favored conifer regeneration, especially Douglas-fir. This adds to an existing body of evidence associating greater regeneration abundance with north aspects (Ertl, 2015; Francis et al., 2018; Larson and Franklin, 2005; Rother and Veblen, 2016). In general, the dominant condition on south aspects was of no regeneration or low levels of tree regeneration, with rare occurrences of dense patches of juvenile trees. In contrast, on north aspects, the dominant condition was of low-to-moderate levels of tree regeneration, with a higher frequency of dense patches of juveniles, and only occasional occurrences of treeless plots. Given Douglas-fir's affinity for cool, moist environments, it is unsurprising that the effect of aspect was more pronounced for this species than for ponderosa pine: 87% of all Douglas-fir regeneration, but only 52% of all ponderosa pine regeneration, was found on north aspects. In dry forests on the Colorado Front Range, cool, moist north aspects have greater potential for post treatment regeneration, provided a seed source and growing space are available within the residual overstory.

Fuels treatments appear to be acting as shelterwood regeneration treatments for ponderosa pine by reducing overstory density while maintaining a ponderosa pine seed source. In contrast, there was no relationship between abundance of post treatment Douglas-fir juveniles and time since treatment (Table 2), which implies treatments did not promote regeneration of this species. We acknowledge some potential for error in determining the germination dates of the seedlings. By taking the age from a single basal cross section from the ground surface as the true age, we potentially underestimated the age of some seedlings by missing the root collar (Telewski, 1993). This could have caused some advance regeneration to be mis-classified as germinating post-treatment, potentially introducing unknown bias into our analyses. However, the consistency of relationships between regeneration abundance and time since treatment throughout the model selection process lends confidence to our results (Tables B3 and B4). Ponderosa pine is known for infrequent episodic regeneration when mast years coincide with suitable climatic conditions for subsequent establishment on the Colorado Front Range (Brown and Wu, 2005; League and Veblen, 2006; Mooney et al., 2011; Savage et al., 1996; Shepperd et al., 2006). The significant relationship between abundance and time since treatment that we observed despite this species' proclivity toward episodic regeneration suggests treatments have created a regeneration environment that alleviates some of the limitations that contribute to the typical establishment pattern. The abundance of both advance and post treatment ponderosa pine regeneration were negatively correlated with overstory density (basal area or trees ha^{-1}, Table 2), which illustrates the well-understood principle that shade intolerant species regenerate in greater abundance under more open overstory conditions (Ertl, 2015; Francis et al., 2018; Gray et al., 2005; Zald et al., 2008). Our interpretation is that treatments disproportionately favored ponderosa pine because it is less shade tolerant than Douglas-fir (Boyden et al., 2005; Cannon et al., 2019; Chen, 1997; Rodman et al., 2020) and was therefore more limited by pretreatment overstory density.

Post treatment Douglas-fir regeneration also benefited from reduced overstory density (as suggested by the negative relationship with total overstory SDI), but was strongly positively related to conspecific SDI in the overstory (Table 3). The negative relationship with total overstory density was somewhat unexpected given Douglas-fir's tolerance for shade. However, seedling establishment niches may be defined by water availability more-so than light in drought conditions (Hill and Ex, 2020). It is possible root competition from mature trees inhibits seedling establishment in dry forests in our study area. A positive relationship between Douglas-fir regeneration and Douglas-fir overstory density has been observed in other treated Front Range conifer stands (Francis et al., 2018), and may reflect a seed source limitation for Douglas-fir in stands where treatments have shifted the overstory composition toward ponderosa pine, suggesting compositional changes are likely to persist through successive cohorts of trees. However, managers should nonetheless anticipate very abundant post treatment Douglas-fir regeneration under some conditions when this species is present in the overstory. About 5% of all plots had five times or greater than the average abundance of post treatment Douglas-fir seedlings, up to 13,343 trees ha^{-1} at the plot level. All of these high-density plots were on north aspects.

While Douglas-fir advance regeneration made up about half of all understory conifers sampled in this study (Table 1), it declined over time since treatment and this is more likely due to mortality than growth release. Release of advance regeneration following fuels treatments would potentially represent a worst-case scenario for fuel hazard development as these trees would have a head start in height growth over post treatment regeneration, in effect accelerating the development of fuel ladders to the canopy. By definition, advance regeneration abundance cannot increase over time following treatment: it can only persist or decline due to mortality or release. Although we encountered few dead stems in our plots, very small trees like those investigated in this study would not be expected to linger in a recognizable form for long after they died. We also observed only 18 total live or dead Douglas-fir saplings when we sampled, so it is unlikely advance regeneration declined because it grew into taller trees not measured in our regeneration plots. Lastly, we did not observe any obvious increase in the width of annual rings following the year of treatment in the seedlings aged for this study; we note, however, that release can sometimes be delayed (Kneeshaw et al., 2002), and that advance regeneration of Douglas-fir may yet be recruited into the overstory of treated stands. Future fuels management activities could improve treatment longevity by more effectively removing regeneration and reducing prevalence of advance regeneration, particularly by increasing the use of prescribed fire as a treatment tool (Battaglia et al., 2008).

The fact that we observed no trend in regeneration abundance with respect to treatment type is useful information for forest managers deciding how to implement fuels treatments. We anticipated mastication treatments would have greater surface fuel loading, but because the thinning treatments were followed by several different slash treatment methods (e.g. lop and scatter, pile and burn (Hunter et al., 2007; Jain et al., 2012)), our "thinning" treatment category likely encompassed a diversity of regeneration environments. Other research has found variable effects of mastication on conifer regeneration density (Battaglia et al., 2015) and growth (Roberts et al., 2005; Zabowski et al., 2000), and therefore on future stand development and fire potential (Reinhardt et al., 2010). Conifer regeneration abundance may be better predicted by a quantitative characterization of fuel loading such as mulch depth (Battaglia et al., 2015), or by aspect, residual overstory density, or species composition as indicated by our findings.

Our findings suggest that striving to meet desired conditions with respect to the historic range of variability for overstory density and species composition would further facilitate the creation of regeneration niches for ponderosa pine regeneration while limiting the seed source for Douglas-fir regeneration. Battaglia et al. (2018) found that ponderosa pine dominance in dry, mixed-conifer forests along the Colorado Front Range has decreased relative to pre-settlement overstory basal area proportions. And although fuels treatments in the Colorado Front Range montane zone seek to restore overstory density to within the historic range of variability in order to reduce wildfire hazard, recent research has indicated that treated forests are still about twice as dense as they were prior to European settlement (Cannon et al., 2018). While Battaglia et al. (2018) estimated pre-settlement basal area in ponderosa pine-dominated forests averaged 6.3–9.5 m^2 ha^{-1} in lower and upper montane forests, respectively, Cannon et al. (2018) observed that post treatment forests in both elevation zones and on both drier south aspects and wetter north aspects averaged 13.2–14.3 m^2 ha^{-1}. Observations of post treatment forest density from this study are similar to these values: the basal area in our plots averaged about 12 m^2 ha^{-1} on south aspects and 16 m^2 ha^{-1} on north aspects (Table 3). To better approximate historic conditions and improve treatment longevity, future treatments could focus on further reducing overstory density, increasing tree density variability between north and south aspects, and focus on removing Douglas fir.

5. Conclusions

The long-term outcomes of wildfire fuels reduction treatments depend on the tree species composition and density of the post treatment environment. Treatments that create conditions aligned with the ecological niches of seed-bearing trees in the residual stand are likely to result in abundant regeneration, reducing longevity of fire mitigation benefits. The high variability in understory conifer density we observed at the plot level highlights the importance of considering the outcomes of fuels treatments for regeneration at sub-stand scales in order to better understand how this variability will contribute to heterogeneous development of forest density, and therefore wildfire hazard, over time. In dry forests like the one we sampled, relatively cool, wet sites (i.e. north aspects in this study) have the potential for prodigious regeneration following fuels treatments because moisture is less limiting to tree establishment in these locations. Consequently, these sites may be poor candidates for fuels treatments and may be better included as "skips"

(Harrington, 2009) in silvicultural prescriptions to preserve dense forest habitats and refuges for Douglas fir on the landscape. If they are treated, they may need to be re-treated more frequently to maintain low fire hazard.

Managers are improving fuels treatment prescriptions by removing more Douglas-fir from the overstory (Cannon et al., 2018), which our results suggest will limit post treatment Douglas-fir regeneration while promoting niches for ponderosa pine regeneration. This will not only reduce immediate fire hazard, but also potentially shift the composition of forests away from Douglas-fir, thereby reducing future torching and promoting longer-term wildfire resistance. However, treatments could still further reduce tree density to approximate historic conditions (Cannon et al., 2018; Battaglia et al., 2018). Fuels treatments seeking to reduce crowning potential by opening up the canopy will inevitably precipitate some regeneration that may increase surface fire intensity in the short term. However, increased regeneration rates may nonetheless be consistent with longer-term goals of fuels and ecological restoration treatments that involve shifting dry, mixed-conifer forests toward more fire-adapted species by favoring ponderosa pine (Addington et al., 2018).

The modest levels of post treatment regeneration we observed reflect "background" regeneration rates for ponderosa pine on the Colorado Front Range. Much more abundant regeneration leading to rapid development of hazardous fuel conditions can occur when mast years for ponderosa pine coincide with favorable environmental conditions for seedling establishment (Savage et al., 1996; Tinkham et al., 2016). The authors note 2019 was a mast year for ponderosa pine on the Colorado Front Range. The stands we sampled may have much greater regeneration abundance following mast years, highlighting the importance of continued monitoring and potentially the need to implement maintenance treatments such as prescribed burning to counter the re-establishment of ladder fuels following fuels reduction treatments (Battaglia et al., 2008).

Dry, mixed-conifer forests on the Front Range are less productive, accumulate fuels more slowly, and experience more episodic tree recruitment (Addington et al., 2018) than, for example, ponderosa pine forests in the Black Hills where a 10-year return interval is suggested for fuels treatment maintenance using prescribed fire (Battaglia et al., 2008). However, the 15- to 20-year return interval for prescribed burning suggested by Hunter et al. (2007) for less productive sites on the Front Range may not be sufficient for sites such as those on wetter north aspects where we observed very high densities of Douglas-fir regeneration. Our study highlights the importance of identifying where these areas with high regeneration potential are located across the landscape and within stands to properly maintain treatment effectiveness over time.

CRediT authorship contribution statement

Kathleen Fialko: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Seth Ex:** Conceptualization, Methodology, Validation, Formal analysis, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Brett H. Wolk:** Conceptualization, Methodology, Resources, Data curation, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Understory vegetation sampling methods

Understory vegetation cover data were collected using ocular cover estimates in quadrats for herbaceous plants and line-intercept transects for shrubs (Fig. A1). The total percent cover of shrubs was estimated using the line-intercept method along a 15.24-meter (50-foot) transect (at a randomly selected azimuth) with plot center at 7.62 m (25 ft) (Colorado Forest Restoration Institute, 2016). Gaps were recorded where there was 15.24 cm (6 in.) or more of the transect without shrub cover. The percent cover of shrubs for the whole plot (% shrub cover/plot) was taken to be the cover along the entire transect (solid line in Fig. A1) and was included as a potential indicator of site quality in the analysis. To account for potential competitive or facilitative effects of shrubs on conifer regeneration, the percent cover of only the shrubs along the portion of the transect within the fixed 3.59-m (0.01 acres) radius regeneration plot was determined separately from the plot total. A 0.9-m (3-ft) buffer was added to account for any potential influence of nearby taller shrubs on the growing environment (i.e. shading), so that the percent cover of shrubs within and around the regeneration plot (% shrub cover/regeneration plot) was estimated from 3.05 to 12.19 m (10–40 ft) along the 15.24-m transect through plot center (dashed line in Fig. A1).

Percent cover of all herbaceous vegetation (graminoids and forbs) was estimated to the nearest percent in three 1-m^2 quadrats at 0, 7.62 m (25 ft), and 14.33 m (47 ft) along the left side of the 15.24-m transect through plot center. To determine total percent cover of all herbaceous vegetation at the plot level as a potential indicator of site quality (% herbaceous cover/plot), cover was averaged among the three quadrats (solid line box in Fig. A1). To describe herbaceous cover within just the regeneration plot as an indicator of potential competitive or facilitative effects (% herbaceous cover/regeneration plot), only data from the quadrat at plot center (7.62 m) was used (dashed line box in Fig. A1).

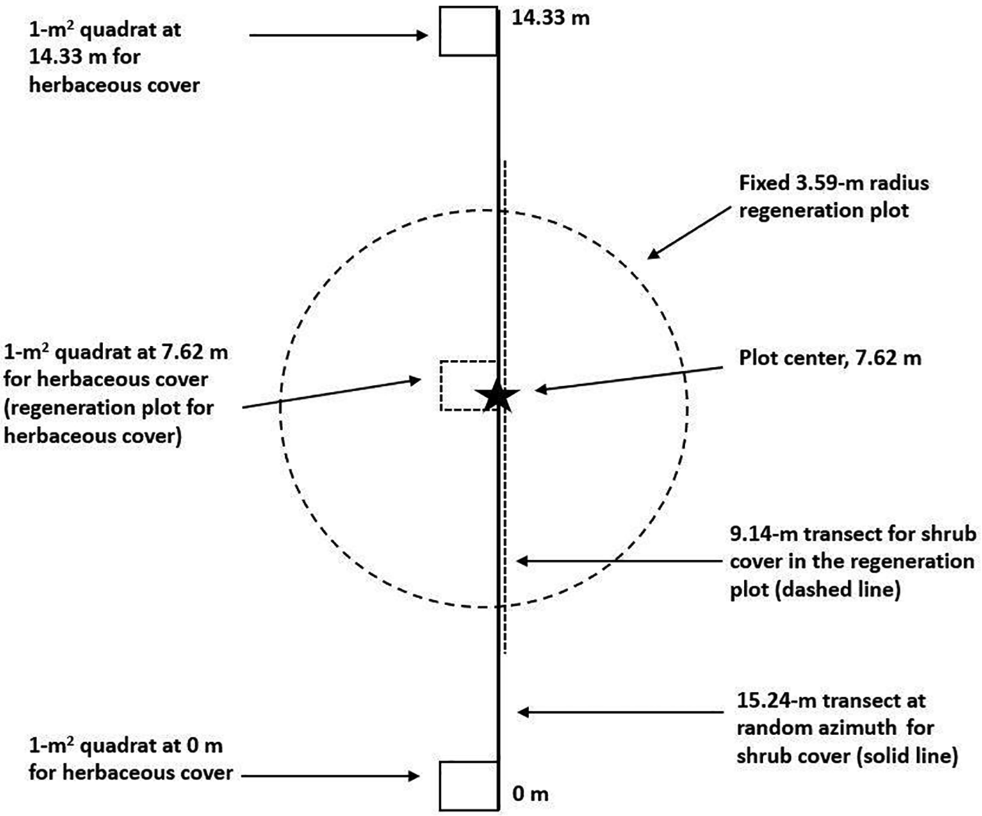

Fig. A1. Diagram of plot design with 15.24-m (50-ft) shrub cover transect, fixed radius regeneration plot, and three 1-m^2 herbaceous cover quadrats (scale approximate).

Appendix B. Model selection tables

Parameter estimates are interpreted as incidence rate ratios, such that values greater than 1 represent a percent increase in the response for every one-unit increase in the parameter, while values less than one represent a percent decrease in the response for every one-unit increase. Time since treatment (TST) was included in each model even when it was not significant. The incidence rate ratios for significant interactions are not interpretable by themselves.

Table B1
Stepwise model selection table for Douglas-fir advance regeneration with parameter estimates for each predictor included in the model, and their significance codes: 0.001 '***', 0.01 '**', 0.05 '*'. Maximum tree height was not included in this table because earlier model selection steps verified that it was not selected, so plots with missing values for this variable could be included here.

Model Step	Full	1	2	3	4	5	6	7	8	9	10	Final
Slope: Aspect Interaction	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.95	0.95*	0.95	0.95	0.95*
Aspect: Elevation Interaction	1.00	1.00	1.00	1.00	1.00	1.00	.	.	.	.	.	.
Slope	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Aspect	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Elevation	NA	NA	NA	NA	NA	NA	1.00	1.00	.	.	.	.
Douglas-fir BA	0.98	0.97	0.97	0.99	.	.	.	.	.	.	.	.
Douglas-fir SDI	1.17	1.18*	1.18*	1.17*	1.16***	1.16***	1.15***	1.15***	1.15***	1.13***	1.11***	1.10***
Douglas-fir TPH	1.00	0.00	1.00	.	.	.	.	.	.	.	.	.
Basal Area (BA)	0.92	0.93	0.93	0.93	0.924*	0.927*	0.93	0.94	0.93	964.00	.	.
Stand Density Index (SDI)	1.01	.	.	.	.	.	.	.	.	.	.	.
Trees ha^{-1} (TPH)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.	.	.
% Shrub/ Whole Plot	0.99	0.99	0.99	0.99	0.99	.	.	.	.	.	.	.
% Herbaceous/ Whole Plot	0.99	0.99	0.98	0.98	0.98	0.98	0.99	.	.	.	.	.
% Shrub/ Regeneration Plot	1.02	1.02	1.02	1.02	1.02	1.01	1.01	1.01	1.01	1.01	1.01	.
% Herbaceous/ Regeneration Plot	1.00	1.00	.	.	.	.	.	.	.	.	.	.
Time Since Treatment (TST)	0.69***	0.69***	0.69***	0.69***	0.69***	0.69***	0.69***	0.69***	0.69***	0.69***	0.70***	0.69***
AICc	733.7	731.3	729	726.7	724.4	722.2	720.4	718.8	717.4	716.6	716.6	716.6

Table B2
Stepwise model selection table for ponderosa pine advance regeneration with parameter estimates for each predictor included in the model, and their significance codes: 0.001 ‘***’, 0.01 ‘**’, 0.05 ‘*’. Slope, slope:aspect, and maximum tree height were not included in this table because earlier model selection steps verified that they were not selected, so plots with missing values for these variables could be included here.

Model step	Full	1	2	3	4	5	6	7	8	9	10	Final
Aspect: Elevation Interaction	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.	.	.
Aspect	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.36**	0.37*	0.46*
Elevation	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.00	.	.
Ponderosa pine BA	1.11	1.11	1.13	1.19	1.16	1.07	1.07	1.07	1.06	1.05	1.05	.
Ponderosa pine SDI	0.91	0.09	0.90	0.87	0.90	.	.	.	.	.	.	.
Ponderosa pine TPH	1.00	1.00	1.00	.	.	.	.	.	.	.	.	.
Basal Area (BA)	0.93	0.93	0.92	0.91	0.89**	0.89*	0.89**	0.89**	0.89**	0.89**	0.9**	0.92**
Stand Density Index (SDI)	0.99	0.99	.	.	.	.	.	.	.	.	.	.
Trees ha^{-1} (TPH)	1.00	1.00	1.00	1.00	.	.	.	.	.	.	.	.
% Shrub/ Whole Plot	1.00	.	.	.	.	.	.	.	.	.	.	.
% Herbaceous/ Whole Plot	1.05	1.05	1.05	1.05	1.05	1.05	1.02	1.02	.	.	.	.
% Shrub/ Regeneration Plot	1.01	1.01	1.01	1.01	1.01	1.01	1.01	.	.	.	.	.
% Herbaceous/ Regeneration Plot	0.97	0.97	0.97	0.97	0.98	0.98	.	.	.	.	.	.
Time Since Treatment (TST)	0.86*	0.86*	0.86*	0.86*	0.86*	0.86*	0.87	0.86*	0.87	0.86*	0.86*	0.88
AICc	351.3	349	346.7	344.5	343	342	341	340.2	339.5	338.4	336.4	336

Table B3
Stepwise model selection table for Douglas-fir post treatment regeneration with parameter estimates for each predictor included in the model, and their significance codes: 0.001 ‘***’, 0.01 ‘**’, 0.05 ‘*’. Maximum tree height was not included in this table because earlier model selection steps verified that it was not selected, so plots with missing values for this variable could be included here.

Model Step	Full	1	2	3	4	5	6	7	8	9	10	Final
Slope: Aspect Interaction	0.95	0.95	0.95	0.95	0.95	0.96	0.96	0.96	.	.	.	.
Aspect: Elevation Interaction	1.00	1.00	1.00	1.00	1.00	.	.	.	.	.	.	.
Slope	NA	NA	NA	NA	NA	NA	NA	NA	0.96*	0.96*	0.96*	0.96*
Aspect	NA	NA	NA	NA	NA	NA	NA	NA	0.25**	0.26**	0.25**	0.22***
Elevation	NA	NA	NA	NA	NA	1.00	.	.	.	.	.	.
Douglas-fir BA	0.83	0.84	0.90	0.91	0.91	0.91	0.90	0.90	0.89	0.90	.	.
Douglas-fir SDI	1.56*	1.55*	1.46*	1.44*	1.45**	1.46**	1.48**	1.50**	1.52**	1.52**	1.33***	1.31***
Douglas-fir TPH	1.00	1.00	.	.	.	.	.	.	.	.	.	.
Basal Area (BA)	1.14	1.13	1.09	1.06	1.07	1.07	1.08	1.09	1.09	1.08	1.03	.
Stand Density Index (SDI)	0.79	0.79	0.82	0.84	0.83	0.83	0.82*	0.81*	0.81*	0.81*	0.87	0.90*
Trees ha^{-1} (TPH)	1.00	1.00	1.00	.	.	.	.	.	.	.	.	.
% Shrub/ Whole Plot	1.01	.	.	.	.	.	.	.	.	.	.	.
% Herbaceous/ Whole Plot	1.04	1.04	1.04	1.04	1.03	1.02	1.02	1.02	1.02	.	.	.
% Shrub/ Regeneration Plot	0.98	0.99	0.99	0.99	0.99	0.99	0.99	.	.	.	.	.
% Herbaceous/ Regeneration Plot	0.99	0.99	0.99	0.99	.	.	.	.	.	.	.	.
Time Since Treatment (TST)	1.12	1.12	1.12	1.12	1.12	1.13	1.12	1.13	1.13	1.16	1.17	1.15
AICc	464.8	462.6	460.4	458.1	456	454	451.8	450	449.1	448.4	447.4	445.6

Table B4
Stepwise model selection table for ponderosa pine post treatment regeneration with parameter estimates for each predictor included in the model, and their significance codes: 0.001 ‘***’, 0.01 ‘**’, 0.05 ‘*’. Slope, slope:aspect, and maximum tree height were not included in this table because earlier model selection steps verified that they were not selected, so plots with missing values for these variables could be included here.

Model Step	Full	1	2	3	4	5	6	7	8	9	Final
Aspect: Elevation Interaction	1.00	1.00	1.00	1.00*	1.00*	1.00*	1.00*	1.00*	1.00	.	.
Aspect	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.23**	0.27**
Elevation	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.00	.
Ponderosa pine BA	0.95	0.95	0.95	0.94	0.96	.	.	.	.	.	.
Ponderosa pine SDI	0.99	.	.	.	.	.	.	.	.	.	.
Ponderosa pine TPH	1.01	1.01	1.01	1.01	1.01	1.01*	1.01*	1.01*	1.01*	1.01**	1.01*
Basal Area (BA)	1.07	1.08	1.08	1.08	.	.	.	.	.	.	.
Stand Density Index (SDI)	0.94	0.93	0.93	0.93	0.97	0.96	0.96	0.96	.	.	.
Trees ha^{-1} (TPH)	0.99	0.99	0.99	0.99	0.99*	0.99*	0.99*	0.99*	0.99**	0.99**	0.99**
% Shrub/ Whole Plot	0.99	0.99	0.99	0.99	0.99	0.99	.	.	.	.	.
% Herbaceous/ Whole Plot	1.00	1.00	1.00	.	.	.	.	.	.	.	.
% Shrub/ Regeneration Plot	1.01	1.01	1.01	1.02	1.02	1.01	1.00	.	.	.	.
% Herbaceous/ Regeneration Plot	1.00	1.00	.	.	.	.	.	.	.	.	.
Time Since Treatment (TST)	1.44	1.00**	1.44**	1.44*	1.43**	1.44**	1.43**	1.43**	1.44**	1.46**	1.41**
AICc	426.9	424.6	422.3	420	418	415.9	413.9	411.8	410.3	411.5	412.1

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