Forest restoration treatments increase native plant diversity but open the door to invasion in the Colorado Front Range

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Open Research Statement: All data and code to fully reproduce the analysis will be made public at www.github.com/admahood/thinned_comms and given a permanent digital object identifier upon acceptance.

Abstract

Forest thinning treatments are often done with objectives to re-establish historical forest structure and increase the system's resilience against future wildfires. But little is known about their long-term efficacy, and effects on understory plant composition. This is especially true in the Colorado Front Range (CFR). We used a before/after control/impact study design to assess the effects of forest restoration treatments on forest structure and understory plant composition one, five, and ten years after treatment. Five and ten years after treatments, treated areas had lower basal area and tree density, and higher quadratic mean diameter, consistent with treatment objectives, and had higher native cover and native richness, and graminoid cover. Species accumulation curves showed region-wide increases in native richness at five years, and further increases at 10 years, with a net increase of 47 native species in treated areas compared to 11 in untreated controls. However, treatments also had higher relative numbers of non-native plant species, and increased probability of non-native plant invasion. Native richness, native cover and graminoid cover were associated with stand structure and topography, while non-native invasions were more strongly associated with moisture deficit. This suggests that climate played a stronger role in constraining the introduction of species than treatment alone. In the CFR, forest restoration treatments can benefit the native understory, but also provide an opening for invasion in uninvaded sites. However, the overall impact of invasions was low after ten years.

Keywords: Fuel reduction treatments, understory diversity, ponderosa pine, invasive plants, thinning treatments

Introduction

Fire regimes are changing globally, with widespread documentation of increases in burned area (Abatzoglou and Williams, 2016), burn severity (Cansler and McKenzie, 2014; Parks *et al.*, 2016), and damage to infrastructure (Mietkiewicz *et al.*, 2020; Cook, 2021; Higuera *et al.*, 2023). In dry mixed conifer ecosystems in the western United states, the effects of fire exclusion (Kreider *et al.*, 2024) and timber harvesting (Naficy *et al.*, 2010) have exacerbated fire risk by altering the quantity and spatial arrangement of fuels. Land management agencies are implementing programs to mitigate the hazards posed by this increasing fire activity, in particular forest restoration treatments to restore historical fuel structure (Agee and Skinner, 2005; Stephens *et al.*, 2020; Hurteau *et al.*, 2024). These programs aim to reduce burn severity of future fires (Ritter *et al.*, 2022a) and to buffer to climate-driven declines in conifer resilience (Haffey *et al.*, 2018; Stanke *et al.*, 2021; Davis *et al.*, 2023). While fuel treatments are being widely proposed to reduce fire hazard and risk, not all forest types are significantly departed from historical structure. Here we focus on ponderosa pine dominated, dry mixed conifer forests that were historically characterized by frequent low and mixed severity fires (Battaglia *et al.*, 2018).

In forest types where historical structure has changed as a result of fire exclusion, tree thinning is frequently implemented to restore historical structure and reduce the potential for high severity fire impacts (Hessburg *et al.*, 2021). Thinning is done to reduce wildfire risk and potential for extreme wildfire behavior while retaining large, fire resistant trees (Knapp *et al.*, 2021; Ritter *et al.*, 2022b; Davis *et al.*, 2024). In addition to benefits for wildfire hazard, reducing overall stand density can enhance tree growth, reduce drought vulnerability, and promote biodiversity (Knapp *et al.*, 2021; McCauley *et al.*, 2022; Zald *et al.*, 2022; Rodman *et al.*, 2024). Despite the benefits of prescribed fire, implementation challenges continue to limit the scale of its application in the western US leaving forest managers to largely rely on thinning-only treatments. Over the past decade managers have also increasingly embraced thinning approaches that aim to create highly heterogeneous canopy structures through the deliberate creation of isolated trees, discrete tree groups, and non-treed openings (Larson and Churchill, 2012; Addington *et al.*, 2018), while reducing tree density and increasing mean canopy base height. These approaches result in stands that better reflect wildfire-resilient historical forest structures (Jeronimo *et al.*, 2019; Chamberlain *et al.*, 2023). Enhancing the heterogeneity of the horizontal canopy structure also increases the diversity of the understory light environment which may have implications for tree regeneration and cover and biodiversity of understory plant communities.

In forested ecosystems, understory plant species make up most of the diversity and are crucial components of ecosystem functions such as decomposition, water balance and nutrient cycling (Balandier *et al.*, 2022). The tree overstory interacts with the understory by controlling processes that include light availability, soil water availability and soil nutrient cycling (Coomes and Grubb, 2000; Balandier *et al.*, 2022). After forest restoration treatments, the understory plant community can be affected by disturbance from mechanical thinning (Korb, Fulé and Gideon, 2007; Nikooy *et al.*, 2020; Labelle *et al.*, 2022), increased surface fuels and fine woody debris (Wolk and Rocca, 2009), and increased spacing between trees (McConnell and Smith, 1970). A more open canopy increases light availability (Riegel, Miller and Krueger, 1992), belowground resources (Riegel, Miller and Krueger, 1992; Neal, 2007), and soil water content (Zou *et al.*, 2008). The increase in resource availability after a forest restoration treatment leads to a reassembly of the community as newly available niche space is filled. This can benefit native species that are adapted to open conditions, and meaningful changes to understory composition typically require tree canopy cover of less than 30-50% (Abella and Springer, 2015) or a basal area of less than 20 m^2 ha^{-1} (Demarest *et al.*, 2023), although this varies by the topographic context as well as temperature and moisture conditions. Immediate decreases in total plant abundance in the near-term, followed by increases in the long-term, are commonly observed (Metlen and Fiedler, 2006; Abella and Springer, 2015; Willms *et al.*, 2017; Hood, Crotteau and Cleveland, 2024), along with increases in plant diversity 3-5 years after treatment (McConnell and Smith, 1970; Nelson, Halpern and Agee, 2008; McGlone, Springer and Laughlin, 2009; Abella and Springer, 2015; Vernon *et al.*, 2023; Springer *et al.*, 2024).

Despite the observed benefits, there are concerns about forest restoration having unintended consequences, including the initiation of human-grass-fire cycles after treatment (Kerns *et al.*, 2020; Fusco *et al.*, 2021). There are non-native species capable of contributing to ecosystem transformation present across much of the United States (Fusco *et al.*, 2019), consistent observations of increases in non-native plant abundance after treatments (Nelson, Halpern and Agee, 2008; Willms *et al.*, 2017), and consistent observations of graminoids increasing with lower tree density (McConnell and Smith, 1970; Naumburg and DeWald, 1999; Fornwalt *et al.*, 2017). The increased resource availability that benefits native plants in the understory also provides colonization opportunities for non-native plants (Davis, Grime and Thompson, 2000), whose propagules may have been transported to the area during treatments. While non-native plants may remain at low levels of abundance following treatment (Hood, Crotteau and Cleveland, 2024; Springer *et al.*, 2024), there are also cases in which non-native abundance was minimal immediately after treatment, but then increased dramatically (McGlone, Springer and Laughlin, 2009). Exotic plant invasions are can be thought to proceed in stages, for example: stage 1) uninvaded; stage 2) present at low cover and having little ecological impact; stage 3) present and abundant enough to impact ecosystem function; stage 4) dominant and capable of causing ecosystem transformation (Brooks *et al.*, 2004). Progression through those stages can be sudden, and may or may not be in response to disturbance. Most analyses of thinning treatments on plant understories do not focus on the stage-based framework of invasion, and commonly report estimates of absolute cover or species richness at the plot scale (Abella and Springer, 2015; Willms *et al.*, 2017). While these metrics can characterize the impact of invasions, they are flawed in that they are scale-dependent (Gotelli and Colwell, 2001;

Thompson and Withers, 2003) and have limited comparability among habitats (Catford *et al.*, 2012). Occurrence of any exotic species can be used to differentiate from stage 1 (uninvaded), but there is no information on relative impact. Differentiating between stage 2 and 4 can be assessed in a way that is comparable across regions and systems with invasion rate, defined as the percentage of non-native species, and invasion impact, defined as the relative cover of non-native species (Catford *et al.*, 2012).

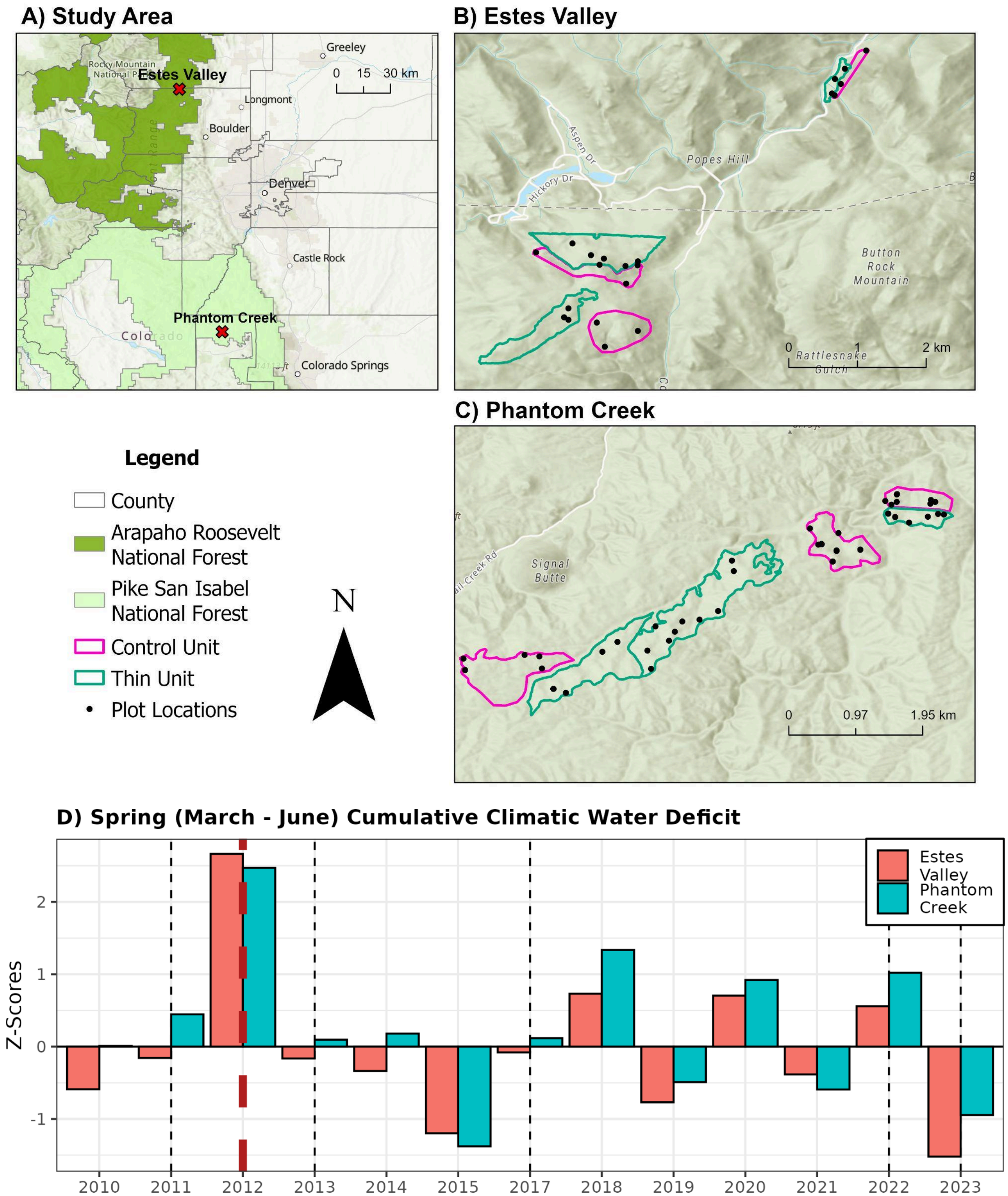
Regional differences in long-term effects of forest restoration treatments on the understory (Schwilk *et al.*, 2009) underscore the importance of understanding the effects of treatment on a regional level, rather than making broad generalizations across the entire western US. Near-term changes in abundance and composition of understory plants are typically realized 3-5 years after treatment, and then remain stable (Jang *et al.*, 2021; Hood, Crotteau and Cleveland, 2024). Forest restoration treatments lose their effectiveness due to ingrowth and increased ladder fuel due to regeneration, and through the accumulation of surface fuels that are deposited by litterfall from both understory and overstory plants (Hood *et al.*, 2020; Wasserman *et al.*, 2022). Dry mixed conifer ecosystems range from mesic to semi-arid to arid regions. Productivity is lower, masting events are less frequent (Wion *et al.*, 2023), and seedling mortality is higher (Rother, Veblen and Furman, 2015; Davis *et al.*, 2019), as aridity increases. In the more arid southwest understory composition has been observed to remain stable for the long term (> 10 years) (Laughlin *et al.*, 2008; Springer *et al.*, 2024), while in the more mesic northern systems they have returned to pre-treatment levels by year 20-23 (Jang *et al.*, 2021; Hood, Crotteau and Cleveland, 2024). The Colorado Front Range lies in the semi-arid part of this range, and therefore inferences from the more mesic Pacific Northwest and Northern Rocky Mountains, as well as the arid Southwest, may not hold. There have only been a handful of studies on the effects of thinning on understory plant composition in the CFR. They have found that immediate effects of mechanical thinning on understory plant composition are minimal (Briggs, Fornwalt and Feinstein, 2017; Demarest *et al.*, 2023), but with increased non-native species (Miller and Seastedt, 2009). Longer-term studies have observed increases in the abundance and species richness of both native and non-native plants 6-9 years after treatment (Fornwalt *et al.*, 2017; Demarest *et al.*, 2023). However, there is still little information available about how long forest restoration treatments remain effective in these systems, i.e. how long the canopy will remain open, and what is the rate of surface fuel accumulation.

Here, we studied the decadal effects of forest restoration treatments on forest structure and plant understory across two thinning projects using a before/after/control/impact (BACI) framework. Stand structure and plant understory composition were measured at 47 plots 1-2 years pre-, 1-2 years post-, 5 years post- and 10 years post-treatment. 24 plots were treated, 23 were untreated controls. Our aim was to investigate three research questions. 1) What were the immediate and long-term changes to surface fuels and forest structure as a result of treatments 2) What were the impacts of thinning on the overall plant functional group composition, diversity, and susceptibility to invasion of the understory and 3) How did climate, topography and stand structure interact to influence understory plant diversity and community composition in the long-term, and was this more informative than simply knowing whether or not an area was treated?

Methods

Study area

This study focuses on two sites: Estes Valley (2109-2573 m) and Phantom Creek (2511-2771 m). Both are in the upper montane zone and are dominated by ponderosa pine (*P. ponderosa*) and increasingly Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at higher elevations. Estes Valley includes three paired thin and control units that were treated in 2012 and monitored before treatments in 2011, and after treatments in 2012-2013, 2017, and 2022-2023 (**Figure 1b**). Phantom Creek also includes three paired thin and control units that were treated in 2011 and monitored before treatments in 2011, and after treatments in 2012, 2017, and 2023 (**Figure 1c**). All treatments were mechanical thinning, where a combination of hand crews and specialized machinery were used to remove small diameter trees (< 20 cm at breast height), increase spatial heterogeneity, and increase ponderosa pine dominance (Briggs, Fornwalt and Feinstein, 2017; Cannon *et al.*, 2018; Barrett *et al.*, 2021). Estes Valley units are located on Arapaho Roosevelt National Forest land in both the Big Thompson and St. Vrain watersheds. Phantom Creek units are in the Upper South Platte watershed in the Pike San Isabel National Forest. On average, Estes Valley receives 514 mm of annual precipitation and Phantom Creek receives 465 mm of annual precipitation (PRISM Climate Group, 2024). Moisture deficit during the study period for each site are shown in **Figure 1d**.



A) Study Area
Greeley
Rocky Mountain National P
Estes Valley
0 15 30 km
Longmont
Boulder
Denver
Castle Rock
Phantom Creek
Colorado
Colorado Springs
B) Estes Valley
Aspen Dr
Hickory Dr
Popes Hill
Button Rock Mountain
Rattlesnake Gulch
0 1 2 km
C) Phantom Creek
Signal Butte
0 0.97 1.95 km
Legend
County
Arapaho Roosevelt National Forest
Pike San Isabel National Forest
Control Unit
Thin Unit
Plot Locations
N
D) Spring (March - June) Cumulative Climatic Water Deficit
Z-Scores
2
1
0
-1
2010
2011
2012
2013
2014
2015
2017
2018
2019
2020
2021
2022
2023
Estes Valley
Phantom Creek

Figure 1: The study area. Panel A shows the broader location in Colorado. Colored outlines of treatment and control units and points for monitoring locations are in panels B (Estes Valley, Arapaho Roosevelt National Forest) and C (Phantom Creek, Pike San Isabel National Forest). Panel D is the annual cumulative climatic water deficit for monitoring locations, extracted for each plot, averaged by site (error bars are ± 2 standard deviations). The vertical dashed lines show the year of treatments (bold red), and years of sampling (black).

Field data collection

This study leverages common stand exam data which was collected by the United State Forest Service, and the Colorado Forest Restoration Institute for the Southern Rockies Landscape Conservation Cooperative using standard field protocols (USDA Forest Service, 2022). Plot centers were monumented in 2011 to ensure consistent repeat measurements 1 year pre-treatment and 1, 5, and 10 years post-treatment allowing for long-term monitoring of treatment effects. The Estes Valley and Phantom Creek projects included 12 treatment units, 47 plots, and 4 time steps totaling 268 observations (**Figure 1**). Randomly located plots were established within each treatment and control unit. From plot center, all overstory trees (> 1.37 m tall and diameter at breast height (DBH) > 12.7 cm) were surveyed within variable radius plots with a 10 basal area factor prism. Tree species, status (live/dead), and DBH were recorded for each tree. Tree seedlings (>4.5 ft, but <12.7 cm DBH) and saplings (< 1.37 m) were inventoried within a 2.5 m radius, 20 m^2 subplot around plot center. Understory cover was quantified with the line-point intercept method. All plants were identified to the species-level every 7.62 cm along four 7.5 m transects oriented from plot center in cardinal directions (0°, 90°, 180°, 270°). Six additional variables were measured only at ten years after treatment. These were fuel loads of fine woody debris (FWD), measured separately as 1-, 10-, and 100-hour fuels, coarse woody debris (CWD), measured as 1000-hour fuel load, litter and duff fuel load, sapling density, shrub height, and tree canopy cover.

Aggregation of field data

From our field-collected data, we calculated 6 stand structure metrics that could plausibly impact understory vegetation at each plot for each timestep: crown base height (CBH), quadratic mean diameter (QMD), basal area (BA), tree density, seedling density and cover of fine woody debris. We derived 9 metrics to characterize aspects of understory composition: total cover, total species richness, native cover, native species richness, invasion rate (non-native richness / total richness * 100), invasion impact (non-native cover / total cover * 100), forb cover, graminoid cover, and shrub cover.

Ancillary data

We acquired climate and topography data to incorporate into our statistical models (below). For climate, we calculated the 30 year normal of CWD (CWD_{norm}), the Z-scores of CWD for the spring (March - June) of sampling (CWD_s), and the Z-scores of CWD for the year of treatment (CWD_{trt}) for each plot. CWD_{norm} and CWD_{trt} were extracted from TopoTerra (Hoecker *et al.*, 2025). TopoTerra is derived from 4 km resolution TerraClimate (Abatzoglou *et al.*, 2018) and downscaled to 240 m via the gradient-plus-inverse distance squared method (Flint and Flint 2012) using Topofire (Holden *et al.*, 2019) as a template to capture fine-scale spatial variability in climatic water balance. Topofire is derived from a process-based model driven by topoedaphic features (aspect, slope angle, topographic position, soil water holding capacity), observations of biophysical variables (temperature, precipitation, insolation, and cloud cover). Because TopoTerra is not yet available for 2023, the last year of sampling, we derived CWD_s Z-scores from TerrraClimate and extracted those for each plot at each timestep. We considered 4km to be sufficient in this case because we expected the interannual variability in CWD to be much greater than the among-site variation within a given year, and furthermore TerraClimate at 4km has been used in other studies (Wion *et al.*, 2025) to represent interannual climate variability.

In addition to in situ measurements of slope, aspect and elevation, we acquired 30 m digital elevation models (DEM) from the shuttle radar topography mission using the *elevatr* R package (Hollister *et al.*, 2023) in order to calculate topographic indexes that we expected to be associated with understory vegetation, as well as to augment any field measurements that were missed. We used the DEMs to calculate heat load index (HLI) (McCune and Keon, 2002) using the *spatialEco* R package (Evans and Murphy, 2023), and folded aspect and the topographic wetness index (TWI) (Beven and Kirkby, 1979) using the R packages topmodel (Buytaert, 2022) and *topomicro* (Mahood, 2024).

Statistical analysis

Estimated marginal means

Estimated marginal means and confidence intervals for each metric of stand structure and understory composition at each time step for control and treated plots using the *emmeans* package (Lenth, 2025). These were estimated from linear mixed models created using the R package *glmmTMB* (Brooks *et al.*, 2017). Each model had site (Estes Valley or Phantom Creek), treatment, and time step as fixed effects, and plot nested within site as a random effect. Site was included as a fixed rather than random effect because random effects with less than six levels are known to produce biased estimates (Oberpriller, De Souza Leite and Pichler, 2022).

Change from pre-treatment

Having a BACI experimental design allowed us to calculate the difference from pre-treatment values for each metric we analyzed, and then test both whether the change from pre-treatment was significant, as well as testing for treatment effects on the change from pre-treatment, rather than just comparing means by timestep. Statistical tests on the difference from pre-treatment values rather than raw values account for the possibility of large differences in means among sites that can obscure treatment effects when only looking at means by timestep. We used one-sided Wilcoxon Rank Sum tests (Bauer, 1972) to test whether a given treatment by timestep combination changed significantly from pre-treatment. Treatment effects for changes from pre-treatment were calculated from linear mixed models that were fit with difference from pre-treatment as the response variable, and the same fixed and random effects as above.

For the six aspects of stand structure that were measured only at the ten-year time step (fuel loads of CWD, FWD, litter/duff, sapling density, tree canopy cover, and shrub height), we created generalized linear mixed models for each variable with site and treatment as fixed effects and plot as a random effect, estimated the marginal means, and used Wald Chi-square tests to assess significance (Fox and Weisberg, 2019).

Species accumulation curves

In order to assess how forest restoration treatments affected the regional species pools, we created species accumulation curves for each timestep and treatment combination, and estimated the total species pool using asymptotic richness estimators (Smith and Van Belle, 1984) using the vegan R package (Oksanen *et al.*, 2022). While species richness measured at the plot scale is a commonly used metric of alpha diversity, it has the problem of scale-dependency. Species accumulation curves are a way to overcome these issues (Gotelli and Colwell, 2001; Thompson and Withers, 2003). Extrapolating the curve to its asymptote yields an estimated species pool, or gamma diversity. The slope is analogous to beta diversity, and a gradual ascent to the asymptote indicates a high proportion of rare species.

Modeling the effect of treatments on understory plants

We used a mixed modelling approach to explore how much the treatment itself affects understory plant communities, versus how much the changes in forest structure resulting from thinning affect understory plant communities. We created mixed effects models for those understory metrics that had consistent treatment effects 5 and 10 years after treatment. These were P(invasion), Invasion rate, graminoid cover, forb cover, native richness and native cover (see results). The model for P(invasion) had a binomial error distribution, the models for native cover, graminoid cover and Invasion rate had beta error distributions, and the model for native species richness had a poisson error distribution. For each response variable, we created two models. The first model was a ‘naive’ model with treatment, time step and their interaction as predictors. The second model used AIC-based model selection procedures (Zuur *et al.*, 2009) to select the strongest predictors from metrics of stand structure (BA, QMD, tree density, seedling density, and FWD), topography (HLI, TWI, slope, and elevation) and water balance (CWD_{norm}, CWD_{trt} and CWD_{s}). Plot identity was used as a random effect in all models. Each candidate model was fit with maximum likelihood, candidate models were compared with AIC and diagnosed using tools from the DHARMa and performance packages (Lüdecke *et al.*, 2021;

Hartig, 2024), and the final model was refit with restricted maximum likelihood. Significance of the predictors for each final model was assessed using Wald Chi-squared tests using the R package *car* (Fox and Weisberg, 2019). We then compared the marginal R^2 (the variance explained by fixed effects (Nakagawa and Schielzeth, 2013)) for both sets of models to evaluate how well each set of predictors influenced each metric of understory plant composition.

Results

Stand structure and fuels changes

Treatment effects on changes from pre-treatment were statistically significant for QMD, BA and tree density at all post-treatment timesteps, and all three metrics remained near immediate post-treatment values five and ten years after treatment (**Figure 2**). Mean BA in treated plots was 18-22 m^2 ha^{-1}, which was 6.45 m^2 ha^{-1} below pre-treatment values on average. Mean tree density in treated plots ranged from 268-368 trees ha^{-1} after treatment, an average of 305 trees ha^{-1} lower than pre-treatment values. Mean QMD in treated plots was 31.6-33.6 cm, 3.29 cm higher than pre-treatment values, on average. It also increased from an average of 31.6 cm 1 year post-treatment to 33.6 cm ten years after treatment, an increase of 0.31 cm per year ($p<0.05$), in treated plots. Cover of fine woody debris was approximately 3% higher than pre-treatment values one and five years after treatment and was not different from pre-treatment at year ten (**Figure 2**). Crown Base Height did not have significant treatment effects, and was only significantly higher than pre-treatment in year five.

Seedling density had significant treatment effects for years five and ten (**Figure 2; Table 1**), but this was caused by a decrease in control plot post-treatment values. Untreated controls had an average of 7,420 seedlings/ha before treatments and 8,930 seedlings/ha in the year after treatments, and this declined to 1,830 and 1,740 seedlings/ha 5 and 10 years after treatment, respectively (**Table 2**). For those metrics that were measured only in year ten, fuel loads of CWD and FWD were higher in treated plots, while tree canopy cover and sapling density was lower than control plots (**Figure 4**).

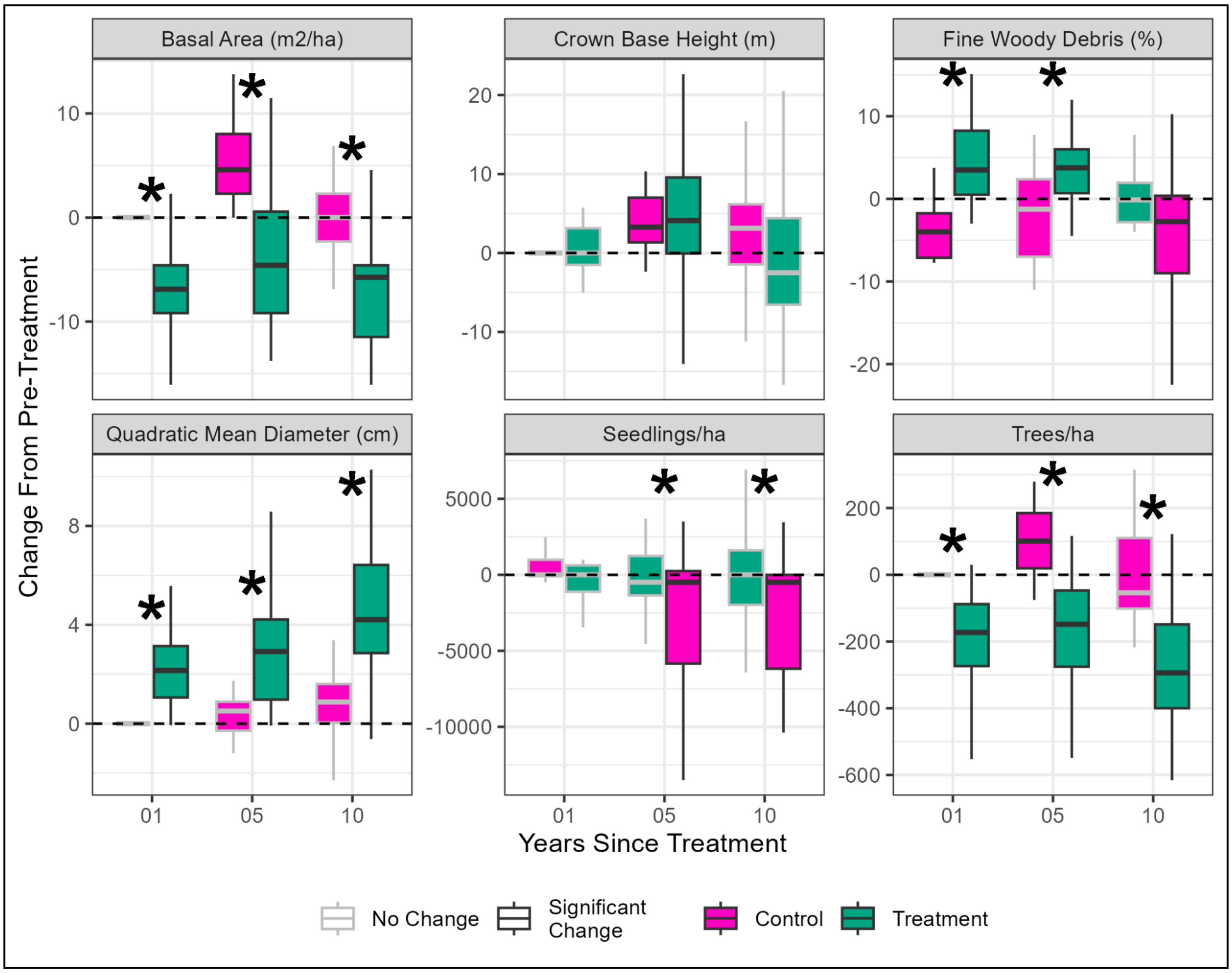


Figure 2. Change from pre-treatment for three stand structure metrics. Black outlines indicate that the difference from pre-treatment values was significant according to a one-sample Wilcoxon Rank Sum Test (each time step by treatment combination was tested individually). Stars indicate a significant treatment effect in a given timestep according to a linear mixed model. Y-axis units are indicated in panel titles.

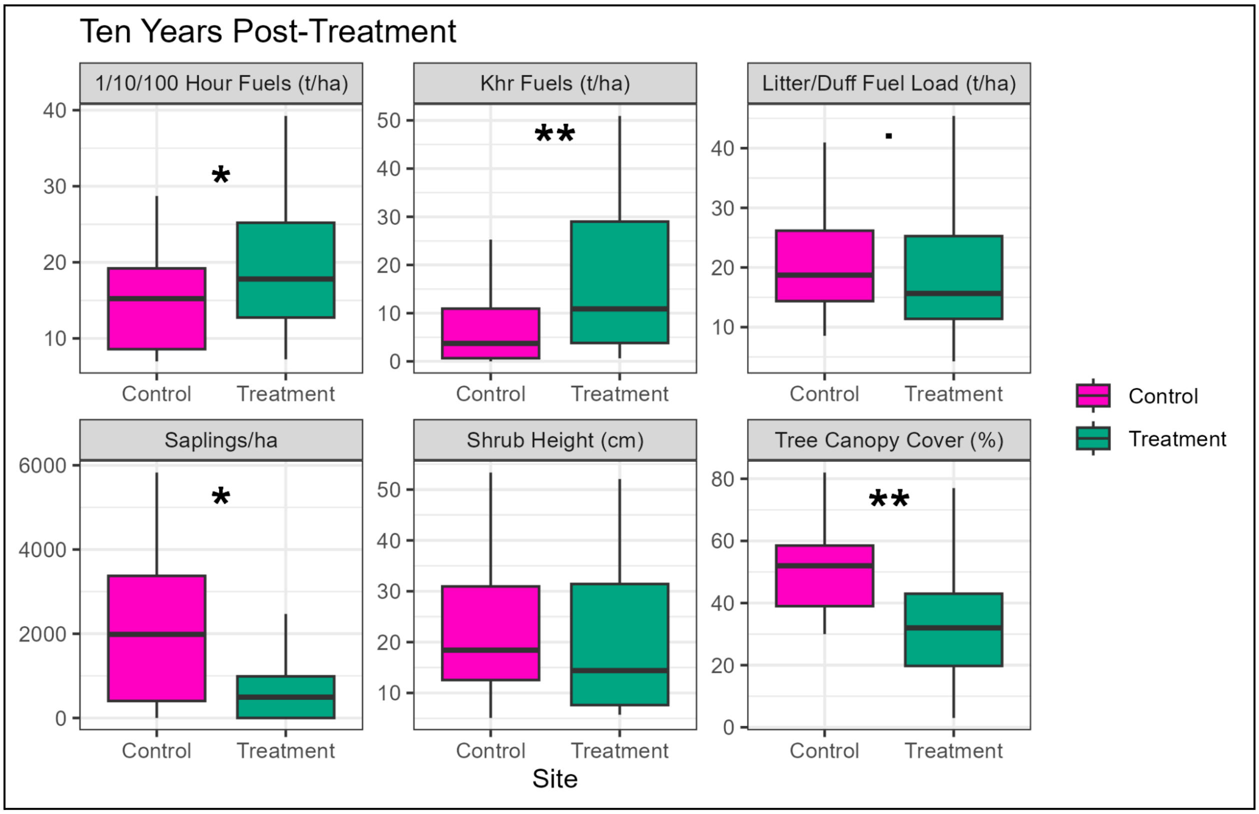


Figure 3. Mean comparisons for variables measured only ten years after treatment. Stars indicate significant differences from a linear mixed model (p < 0.1: ., p < 0.05: *, p < 0.01: **).

Table 1. Estimated marginal means for stand structure metrics at each time step, according to a generalized linear mixed model. Numbers in parenthesis are low and high 95% confidence intervals.

		Timestep			
Response	Treatment	Pre-Treatment	1 Year Post	5 Year Post	10 Year Post
Trees ha^{-1}	Control	609 (500, 718)	607 (497, 716)	749 (640, 859)	618 (508, 727)
	Treatment	583 (478, 688)	340 (235, 445)	369 (263, 475)	271 (165, 376)
Quadratic Mean Diameter	Control	29.3 (27, 32)	29.3 (27, 32)	29.2 (27, 31)	30 (28, 32)
	Treatment	29.2 (27, 31)	31.6 (29, 34)	32.3 (30, 35)	33.6 (31, 36)
Basal Area (m^2 ha^{-1})	Control	25.6 (22, 29)	25.4 (22, 29)	31.2 (28, 34)	26.3 (23, 29)
	Treatment	26.4 (23, 29)	18.8 (16, 22)	22.2 (19, 25)	18.1 (15, 21)
Fine Woody Debris (%)	Control	14.4 (11, 17)	7.84 (5, 11)	11 (8, 14)	9.33 (6, 12)
	Treatment	11 (8, 14)	15.3 (12, 18)	14.4 (12, 17)	9.36 (7, 12)
Crown Base Height (m)	Control	42 (36, 48)	42 (36, 48)	46 (40, 52)	44.3 (38, 51)
	Treatment	43.3 (37, 49)	45.1 (39, 51)	47.6 (41, 54)	43.3 (37, 50)
Seedlings ha^{-1}	Control	7,410 (4,140, 10,678)	8,930 (5,665, 12,204)	1,830 (0, 5,101)	1740 (0, 5,006)
	Treatment	3,550 (419, 6690)	3,270 (83, 6,448)	2,800 (0, 5,989)	3520 (337, 6,706)

Understory changes after treatments

One year after treatment, there was a decrease in total species richness for both control and treated plots and a decrease in shrub cover and total cover in treated plots (**Figure 4; Table 2**). Five years after treatment, there were increases in graminoid cover, total cover, total richness and invasion rate in the treated plots that were significantly greater than any increases that occurred in the control plots, and these increases remained in year ten. Total cover and total richness were also significantly increased from pre-treatment in treated plots 5 and 10 years after treatment, and were significantly higher than control plots.

Probability of invasion in both the control and treatment plots ranged from 0.2 or less in the pre- and 1 year post-treatment timesteps, and increased to 0.47 to 0.97 in the 5 and 10 year timesteps (**Table 2**). In treated plots, the differences between pre- and 1 year post-treatment timesteps and the differences between 5 and 10 year post-treatment timesteps were not significant, but all others were (**Table S1**). In control plots, the only significant differences were among the pre-treatment and ten year post-treatment timesteps, and among the 1 year post-treatment and the ten year post-treatment timesteps (**Table S1**).

There was little difference in the regional species pool estimations immediately before and after treatment, but native and exotic species pools increased after five years (**Figure 5**). Ten years after treatment, there were an estimated 209 species (from 149 pre-treatment) in treated areas, compared to 177 (from 165) in control plots (**Figure 5, Table 3**). The exotic species pool increased from an estimated 5 to 15 in treated areas, and from 7 to 10 species in control plots increased. Native species increased from 151 to 162 species in control plots, and from 140 to 187 in treated areas.

Table 2. Estimated marginal means of probability of invasion, invasion rate, invasion impact, total cover, total richness, graminoid cover, forb cover and shrub cover at each of the four timesteps in treated and control plots. Upper and lower ends of 95% confidence intervals are in parentheses.

		Timestep			
Response	Treatment	Pre-Treatment	1 Year Post	5 Year Post	10 Year Post
P(Invasion)	Control	0.24 (0.082, 0.53)	0.1 (0.022, 0.33)	0.52 (0.25, 0.77)	0.86 (0.62, 0.96)
	Treatment	0.18 (0.059, 0.43)	0.13 (0.039, 0.37)	0.89 (0.66, 0.97)	0.97 (0.82, 0.99)
Invasion Rate (%)	Control	1.58 (0.46, 2.7)	0.96 (0, 2.1)	2.65 (1.5, 3.8)	3.47 (2.4, 4.6)
	Treatment	1.09 (0.014, 2.2)	0.88 (0, 2)	6.66 (5.6, 7.8)	5.86 (4.8, 7)
Invasion Impact (%)	Control	0.27 (0, 1.9)	0.68 (0, 2.3)	1.25 (0, 2.9)	1.81 (0.18, 3.4)
	Treatment	1.82 (0.26, 3.4)	0.16 (0, 1.7)	1.99 (0.4, 3.6)	1.13 (0, 2.7)
Total Cover (%)	Control	20.47 (15, 26)	18.93 (13, 25)	32.36 (27, 38)	19.51 (14, 25)
	Treatment	18.56 (13, 24)	11.05 (5.7, 16)	37.79 (32, 43)	24.47 (19, 30)
Total Richness (%)	Control	35.26 (32, 39)	32.43 (29, 36)	36.04 (33, 40)	39.69 (36, 43)
	Treatment	31.88 (28, 35)	30.12 (27, 34)	38.76 (35, 42)	41.01 (38, 44)
Graminoid Cover (%)	Control	3.77 (1.4, 6.1)	3.75 (1.4, 6.1)	8.46 (6.1, 11)	4.09 (1.7, 6.4)
	Treatment	2.78 (0.52, 5)	2.87 (0.61, 5.1)	13.18 (11, 15)	7.16 (4.9, 9.4)
Forb Cover (%)	Control	2.75 (0.87, 4.6)	2.37 (0.49, 4.2)	5.08 (3.2, 7)	2.98 (1.1, 4.9)
	Treatment	1.93 (0.12, 3.7)	1.6 (0, 3.4)	7.88 (6, 9.7)	4.04 (2.2, 5.9)
Shrub Cover (%)	Control	9.46 (6.4, 12)	8.8 (5.8, 12)	12.01 (9, 15)	7.92 (4.9, 11)
	Treatment	8.69 (5.8, 12)	5.33 (2.4, 8.2)	13.53 (11, 16)	9.94 (7, 13)

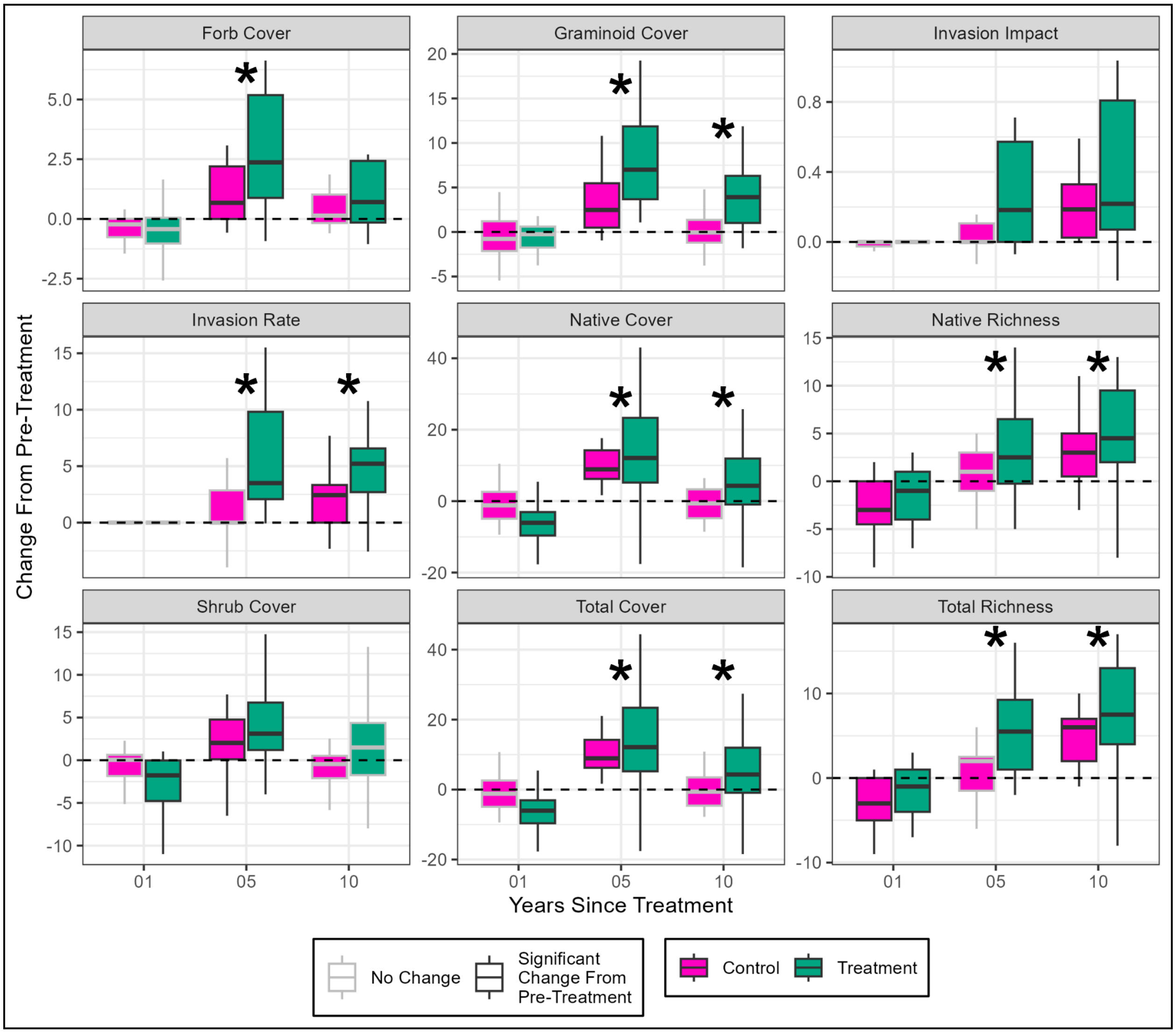


Figure 4. Change from pre-treatment. Dark outlines indicate that the change from pre-treatment values was significant according to a one-sample Wilcoxon Rank Sum Test (each timestep by treatment combination was tested individually). Stars indicate a significant treatment effect according to a linear mixed model. Y-axis units are indicated in panel titles.

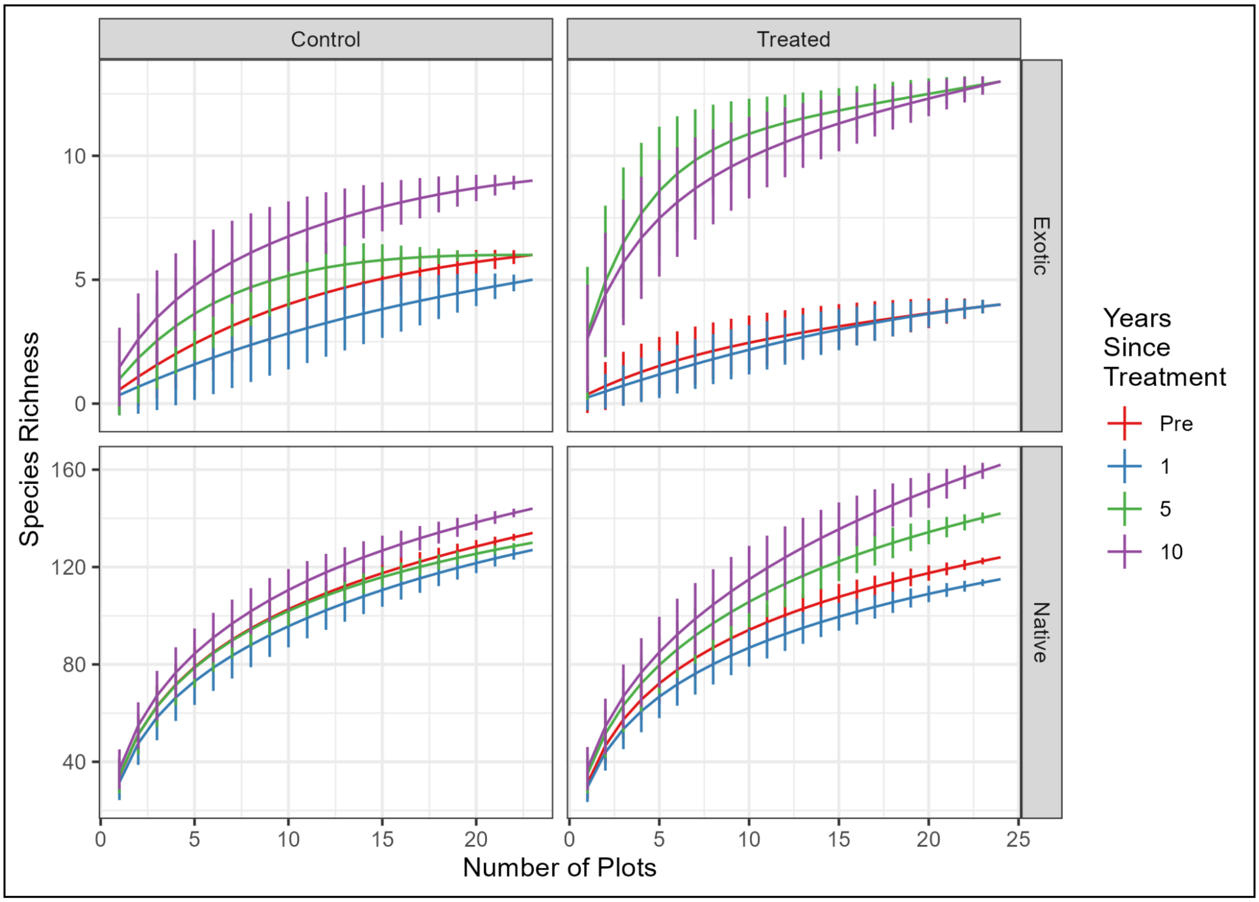


Figure 5. Species accumulation curves. Vertical bars represent the standard error of the estimated species count.

Table 3. Estimates of the regional species pool based on extrapolating the species accumulation curve to its asymptote. Standard errors are in parentheses.

	Treatment	Pre-Treatment	1 Year Post	5 Year Post	10 Year Post	10 year change
Non-native	Control	7 (1)	6 (1)	6 (1)	10 (1)	+3
	Treatment	5 (1)	5 (1)	14 (1)	15 (1)	+10
Native	Control	151 (6)	144 (8)	145 (5)	162 (7)	+11
	Treatment	140 (6)	130 (6)	161 (8)	187 (11)	+47
Total	Control	165 (7)	154 (9)	153 (6)	177 (8)	+12
	Treatment	149 (7)	140 (6)	181 (9)	209 (12)	+60

Associations of stand structure, topography and climate with understory vegetation

For all response variables, the variance explained by fixed effects (R^2_m) for the models informed by stand structure, topography and climate was greater than or equal to the variance explained by the "naive" models with treatment and timestep as predictors (**Table 4**). The difference in R^2_m values for the two model sets ranged from 0% to 40% of the variance explained. The stand structure model of native cover had an R^2_m of 0.35 while that of the naive model was 0.35. Native cover was positively associated with FWD, QMD, slope and TWI, and negatively associated with CWD_s (**Figure 6a, Table 5**). The stand structure model of native species richness had an R^2_m of 0.41 while that of the naive model was 0.088. Native species richness was negatively associated with CWD_s, HLI and tree density, positively associated with total vegetation cover, and had a hump-shaped relationship with CWD_{norm} (**Figure 6b, Table 5**). The forb cover model had an R^2_m of 0.76 for the informed model compared to 0.34 for the naive model. Forb cover was positively associated with total vegetation cover, negatively associated with tree density, CWD_s and HLI, and its relationship with CWD_{norm} was hump-shaped (**Figure 6c, Table 5**). The stand structure model of graminoid cover had an R^2_m of 0.54 while that of the naive model was 0.42. Graminoid cover was negatively associated with CWD_s, HLI and tree density, positively associated with BA, and had a hump-shaped relationship with CWD_{norm} (**Figure 6d, Table 5**). For P(Invasion), the stand structure model had an R^2_m of 0.56 while the naive model had an R^2_m of 0.30. P(Invasion) was negatively associated with CWD_s and CWD_{trt}, positively associated with total vegetation cover, and had a hump-shaped relationship with CWD_{norm} (**Figure 6e, Table 5**). For invasion rate, the stand structure model had an R^2_m of 0.86 while that of the naive model was 0.58. Invasion rate was negatively associated with CWD_s, CWD_{trt} and tree density, and positively associated with total vegetation cover (**Figure 6f, Table 5**).

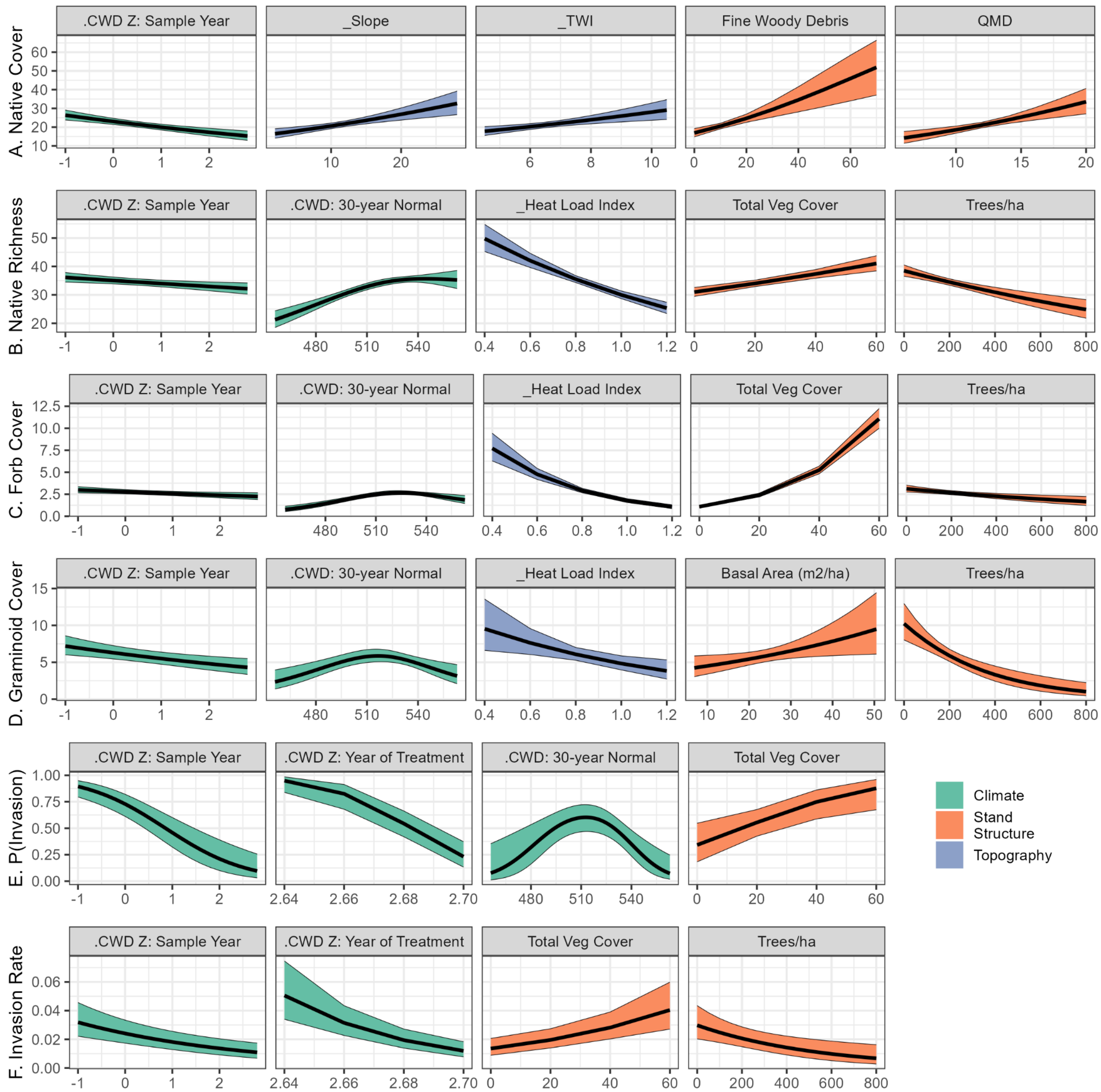


Figure 6. Partial effects of GLMMS. For each panel, the bold line represents the mean estimate of the partial effect, and the colored area surrounding the line is the 95% confidence interval.

Table 4. Variance explained by the fixed effects (Marginal R^2) for each generalized linear mixed model.

	Marginal R^2	
Response	Stand Structure, Topography, Climate	Treatment + Timestep
P(Invasion)	0.56	0.3
Invasion Rate	0.86	0.58
Graminoid Cover	0.54	0.42
Native Richness	0.41	0.088
Native Cover	0.35	0.35
Forb Cover	0.76	0.34

Table 5. Significance of generalized linear model coefficients as tested by a Wald chi-squared test.

	Treatment + Timestep Model		Stand Structure, Topography, Climate Model	
Response	Term	X^2	Term	X^2
Forb Cover	Timestep	169.97***	Total Cover	371.52***
	Treatment	0.45	CWD normal	10.23**
	Timestep x Treatment	31.06***	CWD(z) Sample Year	5.94*
			Heat Load	14.39***
			Tree Density	8.13**
Graminoid Cover	Timestep	225.08***	CWD normal	6.09*
	Treatment	1.99	CWD(z) Sample Year	10.89***
	Timestep x Treatment	32.79***	Heat Load	5.49*
			Tree Density	13.85***
			Basal Area	4.44*
Invasion Rate	Timestep	56.82***	Tree Density	7.62**
	Treatment	3.97*	CWD(z) Treatment Year	22.67***
	Timestep x Treatment	10.84*	CWD(z) Sample Year	17.89***
			Total Cover	14.95***
Native Cover	Timestep	210.98***	CWD(z) Sample Year	25.21***
	Treatment	0	Fine Woody Debris Cover	3.03.
	Timestep x Treatment	37.1***	Quadratic Mean Diameter	5.09*
			slope	4.25*
			Topographic Wetness	4.01*
Native Richness	Timestep	32.89***	CWD normal	26.87***
	Treatment	0.3	CWD(z) Sample Year	9.09**
	Timestep x Treatment	3.5	Heat Load	27.98***
			Tree Density	17.28***
			Total Cover	13.76***
P(Invasion)	Timestep	34.5***	CWD(z) Sample Year	26.73***
	Treatment	2.2	CWD normal	12.47**
	Timestep x Treatment	4.24	CWD(z) Treatment Year	24.21***
			Total Cover	8.21**

Discussion

This work adds to the growing consensus that forest restoration treatments can increase understory diversity (Vernon *et al.*, 2023; Springer *et al.*, 2024), while also increasing the probability of invasion (Willms *et al.*, 2017). The changes in forest structure brought on by forest restoration treatments remained largely unchanged ten years later (**Figure 2**). While the immediate effects on understory plant communities were minimal, after 5 years largely beneficial impacts on native plant cover and diversity were observed, and these benefits remained unchanged or increased after ten years (**Figure 4-5**). These outcomes were associated with increased QMD and lower BA and tree density (**Figure 6**)—common goals of mechanical thinning treatments (Larson and Churchill, 2012; Addington *et al.*, 2018). However, the treatments also resulted in invasions of non-native plants. These invasions became detectable after 5 years and remained at a low level of ecological impact. Given the low level of invasion detected it may be economically feasible to control, if necessary. Probability of invasion and invasion rate were less strongly associated with stand structure metrics than they were with climate (**Figure 6**), indicating that change in forest structure resulting from treatments may have less influence over non-native plant invasions than climate and the physical disturbance and propagule introduction associated with the act of treatment.

Treatment effects on forest structure unchanged after 10 years

Stands subjected to mechanical thinning treatments conducted in Estes Valley and Phantom Creek in 2011 had lower tree density and BA, and higher QMD than untreated controls, and these values remained near their immediate post-treatment values five and ten years after treatment (**Figure 2**) indicating that treatments remained effective in the long-term and showed minimal signs of returning to pre-treatment conditions. While treated plots remained significantly different from pre-treatment conditions, they still had higher tree density and BA, but similar QMD, than historical reconstructions. In CFR upper montane forests, historical reconstructions of QMD average 29.4 cm (Battaglia *et al.*, 2018). The treated plots studied here averaged 29.2 cm before treatment and 33.6 cm ten years after treatment. Basal area was reconstructed at 9.5 m^2 ha^{-1} and plots here were measured at 26.3 m^2 ha^{-1} before treatment and 18.1 m^2 ha^{-1} ten years after. Tree density was reconstructed at 163 trees ha^{-1}, and plots here averaged 582 trees ha^{-1} before treatment and 269 trees ha^{-1} ten years after treatment. Treatment prescriptions were variable due to differences in site conditions, regulations and treatment methods (Briggs, Fornwalt and Feinstein, 2017), so higher basal area and tree densities may be due to the treatment projects being situated on the higher end of the productivity gradient, rather than not being sufficiently thinned.

The primary mechanism by which treatments lose their effectiveness is for seedling, saplings and shrubs to grow in the newly opened canopies and create ladder fuels, or for an accumulation of surface fuels (Wasserman *et al.*, 2022). We did not detect any signs of increased ladder fuels. There were minimal changes in seedling density (**Figure 2**) and shrub cover (**Figure 4**), as well as lower sapling density in treated plots at year ten (**Figure 3**). Seedling density in untreated controls was much higher in pre- and post-treatment plots than in untreated controls, but then returned to similar levels in years five and ten (**Table 1**). Climatic water deficit was much higher than normal in the year of treatment, and there was only one wetter than normal year (2015) within five years of treatment (**Figure 1d**), so it is possible that there was a masting event in some of the control plots at or before the start of the pre-treatment monitoring, followed by a dieoff (Wion *et al.*, 2020). Prior research has found that warming temperatures and drought may inhibit regeneration in *P. ponderosa* and *P. menziesii* forests in the lower montane zone (Rother, Veblen and Furman, 2015), and so these forests in the upper montane zone are also likely to be vulnerable to regeneration failures (Davis *et al.*, 2019; Stevens-Rumann and Morgan, 2019). Lack of seedling and sapling regeneration may increase the longevity of treatment effectiveness, but also increases the likelihood of ecosystem type conversion if a crown fire does occur in spite of treatments (Stevens-Rumann and Morgan, 2019; Rodman *et al.*, 2020), whether that is due to extreme fire weather or ineffective treatment prescriptions. The only evidence we found of declining treatment effectiveness for these plots was increased surface fuel load. While the ground cover of fine woody debris returned to pre-treatment values by year ten (**Figure 2**), the fuel load of fine and coarse woody debris was significantly higher in treated plots than in untreated controls ten years post-treatment (**Figure 3**). Therefore, highlighting the importance of treatment maintenance when fuel loads exceed desired conditions.

In the more arid areas of western US dry mixed conifer forests, forest restoration treatments have been observed to make trees more resilient against drought (McCauley *et al.*, 2022), and enhance tree-level growth across sites spanning ponderosa pine's climatic niche, even during extreme drought (Knapp *et al.*, 2021; Zald *et al.*, 2022; Rodman *et al.*, 2024), and perhaps even increase carbon storage in the long-term (McCauley *et al.*, 2019; Doughty *et al.*, 2021). Our observations of increased QMD through time after treatment suggest that these findings likely hold true in the CFR as well.

Native species richness and cover was higher in treated plots

The understory plant communities were largely unchanged immediately after treatment, and this has been reported previously (Briggs, Fornwalt and Feinstein, 2017), followed by increased diversity in years five and ten. The contrast between species accumulation curves increasing from year five to ten and plot-level richness remaining constant is an artifact of the scale-dependency of species richness (Catford *et al.*, 2012). While similar numbers of species were encountered at each plot at timesteps five and ten, the particular species encountered at each plot were more likely to be different by year ten. The increase in plot-level native species richness may be explained by increased above- and below-ground resources available for utilization by the understory (McConnell and Smith, 1970; Riegel, Miller and Krueger, 1992; Zou *et al.*, 2008). The gradual curve to the asymptote in the native species accumulation curves (**Figure 4**) suggest that plots are diversifying by adding rare species (Gotelli and Colwell, 2001; Thompson and Withers, 2003). Therefore, the increased heterogeneity created by the treatments, along with spatial variation along resource gradients, may be creating suitable habitat for a wider range of species. Facilitation among native species allows the community to continue to assemble and diversify through time (Dovčiak and Halpern, 2010). In addition to spatial variation in resource gradients, some differences in observed species diversity were partially explained by temporal variation in water availability (**Figure 1d**). However, if this were the main driver we would also expect to see differences between timesteps five and ten for changes in native richness. Furthermore, while native richness had a negative association with CWD_s, it had stronger associations with HLI, total vegetation cover, CWD_{norm} and tree density (**Figure 6**), suggesting that higher richness values were more strongly influenced by the changes in stand structure than sample year climate.

Native cover and total vegetation cover were higher in treated units than untreated controls in years five and ten. While the effect size associated with CWD_s was smaller than those of the stand structure and topographic variables, the wettest CWD_s values were associated with a 75% increase in native cover over the drier year, and it had stronger statistical support (**Table 5**). So while these site and stand structure metrics strongly influence the potential cover of native plants, there is high year-to-year variation in cover, and this is to be expected in semi-arid systems with high interannual climate variability. Graminoid cover was higher than untreated controls in years five and ten (**Figure 4**). Higher graminoid cover may be desirable in cases where a return to historical frequent fire is desirable (Brown and Smith, 2000; Veblen, Kitzberger and Donnegan, 2000; Schoennagel, Sherriff and Veblen, 2011), but is also a potential concern due to worries about the establishment of a non-native grass-fire cycle (Kerns *et al.*, 2020; Fusco *et al.*, 2021). Most of the forb and graminoid species encountered here were native, and non-native cover was very low in all cases. Like native cover and richness, they were associated with cooler aspects and lower density stand metrics (**Figure 6; Table 5**). Forb cover was more strongly associated with aspect and productivity (for which total vegetation cover is a proxy), while graminoid cover was comparatively more strongly associated with stand metrics. They both had negative relationships with CWD_s that were weak, but with strong statistical support (**Table 5**), indicating that, like native cover, stand structure and topography are broad determinants of niche space, and interannual variability in abundance is associated with yearly fluctuations in temperature and moisture. There was no sign of a return to pre-treatment cover as has been found in more mesic dry mixed conifer systems (Jang *et al.*, 2021).

Introduced species richness remained constant after 5 years

Taken together, our data indicate that forest restoration treatments in the CFR can result in widespread introductions of non-native species in previously uninvaded areas. These new invasions were mostly detectable after five years and remained at very low values of relative cover (**Table 2; Figure 4**) indicating low ecological impact (stage 2 from the model of (Brooks *et al.*, 2004)). There were minimal changes in probability of invasion immediately after treatment, but it was higher in treated plots than it was in untreated controls in years five and ten (**Table 2**). Probability of invasion was strongly associated with CWD_s, CWD_{trt} and CWD_{norm}, as well as total vegetation cover. The strongest effects with the most statistical support were CWD_{trt} and CWD_a. The negative association with CWD_z suggests that annual fluctuations in climate drive interannual variability in abundance, and since these invasions were all at very low levels of impact (**Table 2**), many species may have been at very low population levels or remained dormant, or ungerminated in the seed bank (Faist, Stone and Tripp, 2015). The negative association with CWD_{trt} was strong, however at all the sites were treated during the same year, which had high CWD z-scores. So while the negative association between CWD_{trt} suggests that treatments conducted during abnormally hot and dry years will have a lower chance of being invaded, these results should be interpreted with caution, and more research across a broader range of treatment conditions is needed. The stand structure and climate variables explained more variation than just the naive model, indicating the role that climate played in constraining the introduction of species was stronger than the act of treatment alone. Control plots also had higher risk of invasion in the five and ten year timesteps, but less so than treatments (**Table 2**). Many of the non-native species we encountered were common across the western US (**Table S2**). Over the broader spatial scale of the western US, many of these species have a residence time of decades if not centuries, and may be in the midst of an ongoing invasion to fill out their potential range (Richardson and Pyšek, 2006; Wilson *et al.*, 2007; Rouget *et al.*, 2016). Treatments may be accelerating the broader invasion at a fine scale, and introductions in control plots could have been a result of spillover from introductions that occurred in nearby treatments. Little research that we are aware of exists on the topic of non-native species introductions in forest restoration treatments spreading to nearby areas in dry mixed conifer forests of the western US.

Analysis of species accumulation curves and extrapolated species pools yielded a regional species pool estimated at 10 introduced species across control plots and 15 in treated areas (**Figure 5**, **Table 3**). The overlap in species accumulation curves for years five and ten suggests that colonization by non-natives via the newly available resources unharnessed by resident the plant community have mostly taken place by the five year mark. After treatment there are newly available resources, including increased light from the opened canopy (McConnell and Smith, 1970), increased belowground water resources due to a reduction in competition from small trees that were removed (Riegel, Miller and Krueger, 1992), and the physical soil disturbance that results from the treatment aids in seed germination (Leffler *et al.*, 2016). This fluctuation in resources is likely to make the community more invisible (Davis, Grime and Thompson, 2000). Once the newly available resources have been harnessed, the invasions may slow down, especially in a diverse understory. High understory diversity is associated with higher resistance to invasion (McGlone, Sieg and Kolb, 2011), so the observed increases in native cover and richness indicate that the understory may be more resilient to the establishment of new non-native plants after the five year timestep. However, if newly arrived species have a competitive advantage for water or light, they may slowly overtake resident native species through time. If newly arrived species are more resilient to disturbance, they may quickly become dominant if a disturbance occurs after the species is established in low abundances but is well dispersed across the landscape.

Management implications

It has long been recognized that monitoring and control of invasive plants needs to be part of any forest restoration treatment prescription (Schwilk *et al.*, 2009). While there are long-term observations of non-native populations remaining stable after 20 years from similar treatment experiments in the northern Rockies (Hood, Crotteau and Cleveland, 2024) and southwest

(Springer *et al.*, 2024), there are also observations of dramatic increases in invasive populations within ten years of being at low-impact levels like those observed here. Subsequent changes in plant community composition may result from disturbance (e.g. fire, timber harvesting, and recreation), or competitive exclusion of natives by non-natives, which depends upon the invasion resistance of the resident community (McGlone, Sieg and Kolb, 2011). For example, *Bromus tectorum* is a species that is capable of building large seed bank reserves and has smoke-induced germination (Fenesi *et al.*, 2016; Naghipour *et al.*, 2016; Mahood, Koontz and Balch, 2023). It may be prevented from exceeding low levels of cover for long time periods due to interspecific competition from the resident community, and then quickly become dominant after a fire, but it can also increase abruptly without fire. Invasions of annual grasses like *B. tectorum* that have transformed areas of shrublands in the Great Basin formed the basis for the stage-based invasion framework proposed by Brooks *et al.* (2004), and there are observations suggesting this framework can also be applied to dry mixed conifer systems. In an example from a *P. ponderosa* forest in Arizona, McGlone *et al.* (2009) observed that *B. tectorum* was at low cover before (invasion stage 2) and after treatment from 1998-2002 (treatment was in 1999), then abruptly became dominant in 2005 without a subsequent disturbance (invasion stage 3). In another example from a *P. ponderosa* forest in New Mexico, *Bromus inermis* L., which was present in our plots and is common in the CFR, was observed to increase rapidly from low levels like those observed here (invasion stage 2) in 1997 to become the dominant understory species in 2008 (invasion stage 3) (Wion *et al.*, 2024). When those plots subsequently burned in 2011, non-native grass cover, which was mostly *B. inermis*, was associated with higher burn severity, suggesting a transition to stage 4.

Most of the observed changes in understory composition took place after five years and remained steady ten years after treatment. This is consistent with other studies, where the first 5 years after treatment saw changes in composition, and then the composition remained stable for 23 years (Jang *et al.*, 2021; Vernon *et al.*, 2023). The results here suggest that the time period between five and ten years after treatment is likely the most effective time to monitor and control invasive plants. The five to ten year window after treatment is a long enough period of time to reach the new equilibrium in productivity, and for non-native populations to become detectable. It is also short enough that invasive populations that establish after treatment are likely to still be small and manageable (Schuurman *et al.*, 2020) and before interspecific dynamics begin causing local extirpations. After ten years, it is unknown whether populations of introduced plants will continue to grow, or remain stable without further impacts.

It is important to understand the efficacy and impact of thinning-only forest restoration prescriptions. Literature reviews have largely supported the notion that forest restoration treatments reduce subsequent wildfire severity, however the available literature consistently shows greater severity reductions when thinning is paired with prescribed fire (Kalies and Yocom Kent, 2016; Davis *et al.*, 2023). However, in the CFR prescribed fires are less tractable due to high topographic complexity and relief, and the high prevalence of low-density residential development in forested areas (Ryan, Knapp and Varner, 2013). Lower tree density and BA, and higher QMD were associated with desirable outcomes of higher native cover, graminoid cover and native species richness following mechanical thinning (**Figure 6**). Here, desirable understory attributes were associated with stand structure attributes that are often targets for fire behavior goals, and invasion probability and impact were lower when treatment year climate was hotter and drier. Therefore, a potential management strategy to explore for CFR sites would be to prioritize mechanical thinning treatments in hot, dry years. Low severity prescribed fire to manage fine and coarse woody debris could be done in wet years 10 or more years after treatment while canopy structure is still near restoration targets, for those areas where it is tractable and permits are able to be obtained.

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Supplemental Tables and Figures

Table S1. Changes in probability of invasion among timesteps.

Treatment	contrast	odds.ratio	std.error	statistic	adj.p.value
Control	Pre / 1yr post	3	2.7	1.2	0.62
Control	Pre / 5yr post	0.29	0.23	-1.5	0.41
Control	Pre / 10yr post	0.051	0.047	-3.2	**0.0069**
Control	1yr post / 5yr post	0.098	0.091	-2.5	0.06
Control	1yr post / 10yr post	0.017	0.018	-3.8	**0.00088**
Control	5yr post / 10yr post	0.17	0.14	-2.1	0.14
Treatment	Pre / 1yr post	1.4	1.2	0.44	0.97
Treatment	Pre / 5yr post	0.028	0.027	-3.8	**0.00085**
Treatment	Pre / 10yr post	0.0076	0.0087	-4.3	**0.00012**
Treatment	1yr post / 5yr post	0.02	0.02	-4	**0.00039**
Treatment	1yr post / 10yr post	0.0053	0.0063	-4.4	**0.000058**
Treatment	5yr post / 10yr post	0.27	0.27	-1.3	0.55

Table S2. Non-native plants encountered.

FinalName	Family
Taraxacum officinale	Asteraceae
Cirsium arvense	Asteraceae
Tragopogon dubius	Asteraceae
Carduus nutans	Asteraceae
Lactuca serriola	Asteraceae
Cirsium vulgare	Asteraceae
Sisymbrium altissimum	Brassicaceae
Thlaspi arvense	Brassicaceae
Chenopodium album	Chenopodiaceae
Juncus compressus	Juncaceae
Nepeta cataria	Lamiaceae
Poa pratensis	Poaceae
Poa compressa	Poaceae
Bromus tectorum	Poaceae
Bromus inermis	Poaceae

Agrostis gigantea	Poaceae
Phleum pratense	Poaceae
Verbascum thapsus	Scrophulariaceae
Linaria vulgaris	Scrophulariaceae
Linaria dalmatica	Scrophulariaceae