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 restoration treatments in dry conifer forests of the western United States are often done with objectives to move current forest structure toward historical conditions and, in turn, increase the system's resilience to future wildfires. But little is known about their effects on understory plant composition, particularly over the long-term. This is especially true in the Colorado Front Range (CFR). We used a before/after control/impact study design to assess the effects of mechanical forest restoration treatments on forest structure, surface fuels and understory plant composition 1, 5, and 10 years after treatment. Five and 10 years after treatment, treated areas had lower basal area and tree density, and higher quadratic mean diameter, consistent with treatment objectives. Treated areas also had higher native understory plant cover and richness, and higher graminoid cover. Species accumulation curves showed treatment-wide increases in native richness at 5 years post-treatment, 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, though the overall level of invasion was low. Native richness, native cover and graminoid cover were more strongly associated with stand structure and topography, while non-native invasions were more strongly associated with moisture deficit. This suggests that climate played a greater role in enabling the introduction of species than changes in stand structure affected by treatment. In the CFR, forest restoration treatments can benefit the native understory, but also provide an opening for invasion in relatively uninvaded sites.

Keywords: Forest restoration treatments, understory diversity, ponderosa pine, non-native plants

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 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 severe wildfire risk by altering the quantity and spatial arrangement of fuels. Land management agencies are implementing programs to mitigate this risk, in particular via forest restoration treatments that move stands toward more open conditions similar to those that existed historically (Agee and Skinner, 2005; Stephens *et al.*, 2020; Hurteau *et al.*, 2024).

In western US dry conifer forest types, forest restoration treatments are commonly implemented via tree thinning (Hessburg *et al.*, 2021). Despite the benefits of prescribed fire, implementation challenges continue to limit the scale of its application, leaving forest managers to largely rely on thinning-only treatments. In addition to benefits for wildfire hazard, thinning treatments 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). 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, retaining large, fire-resistant trees, 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). After thinning-based forest restoration treatments, the understory plant community can be affected by physical disturbance during operations (Korb, Fulé and Gideon, 2007; Nikooy *et al.*, 2020; Labelle *et al.*, 2022), increased surface fuels (Wolk and Rocca, 2009), and increased canopy openness (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 can ultimately lead to a bolstering of the understory community as newly available niche space is filled. Native species that are adapted to open conditions can be among the primary beneficiaries, particularly if tree canopy cover is reduced to 30-50% or less (Abella and Springer, 2015) or if basal area is reduced to less than 20 m^2 ha^{-1} (Demarest *et al.*, 2023). Increases in native plant abundance are commonly observed by the time treatments are ~3-5 years old (Metlen and Fiedler, 2006; Abella and Springer, 2015; Willms *et al.*, 2017; Hood, Crotteau and Cleveland, 2024), as are increases in plant diversity (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 treatments having unintended consequences, including the invasion by non-native species and the initiation of human-grass-fire cycles (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). 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). Non-native plant invasions often 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). Most analyses of thinning treatments on plant understories commonly report estimates of absolute cover or species richness of non-native plants to assess non-native invasion (Abella and Springer, 2015; Willms *et al.*, 2017). While these metrics can characterize the impact of invasions, 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 non-native species can be used to differentiate from stage 1 (uninvaded), but there is no information on relative impact. Differentiating among stages 2 through 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.
Dry 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) in more arid locations. Understory plant communities can also remain more stable after treatment in the long term (> 10 years) (Laughlin *et al.*, 2008; Springer *et al.*, 2024) (Jang *et al.*, 2021; Hood, Crotteau and Cleveland, 2024). The Colorado Front Range lies in the semi-arid part of this range, where there have only been a handful of studies on the effects of thinning on understory plant communities, particularly over the long term (Miller and Seastedt, 2009; Briggs, Fornwalt and Feinstein, 2017; Fornwalt *et al.*, 2017; Demarest *et al.*, 2023). Additionally, there is little information available about how long forest restoration treatments remain effective in these systems, i.e. how long the canopy will remain open, and the rate of surface fuel accumulation (Fialko, Ex and Wolk, 2020).

Here, we studied the decadal effects of forest restoration treatments in the CFR on surface fuels, forest structure and understory plant communities across two thinning projects using a before/after/control/impact (BACI) framework. The treatments were in ponderosa pine dominated, dry conifer forests that were historically characterized by relatively frequent low and mixed severity fires (Battaglia *et al.*, 2018). Measurements were taken at 47 plots 1-2 years pre-, 1-2 years post-, 5 years post- and 10 years post-treatment. 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 functional group composition in the long-term?

Methods

Study area

This study focuses on two sites: Estes Valley (2109-2573 m) and Phantom Creek (2511-2771 m). These sites, and the plots within them, were established by Briggs, Fornwalt, and Feinstein (2017) in support of the Colorado Front Range Collaborative Forest Landscape Restoration Program's monitoring effort. The sites are in the 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 treatment and control units that were treated in 2011-2012 (**Figure 1b**); Phantom Creek includes three paired treatment and control units that were treated in 2011 (**Figure 1c**). All treatments were mechanical thinning, where hand crews and/or specialized machinery were used to remove small diameter trees (< 20 cm at breast height), increase tree 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 on 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**.

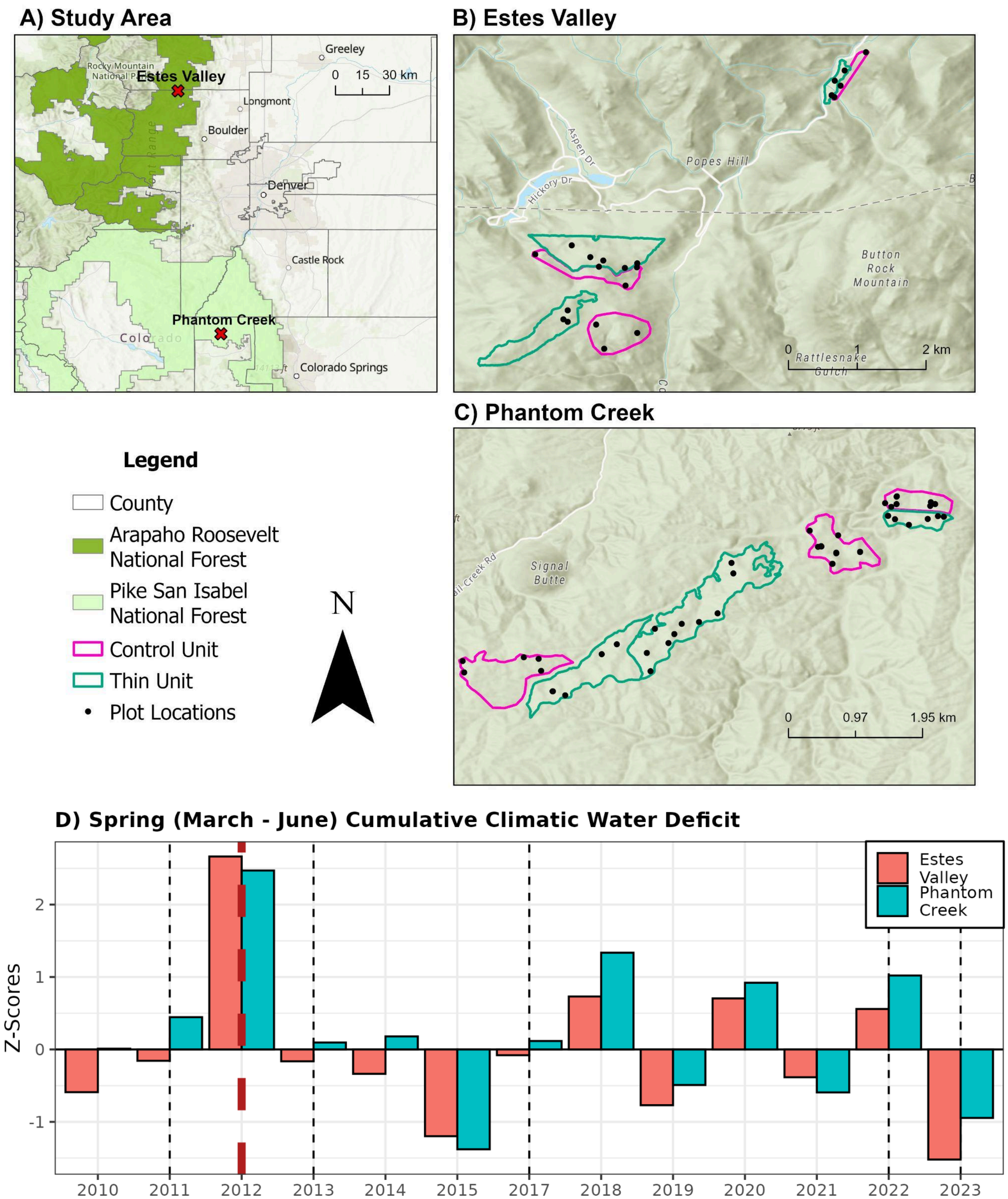

Figure 1: The study area. Panel A shows the broader location in Colorado. Colored outlines of treatment and control units and points for monitoring locations are in panels B (Estes Valley, Arapaho - Roosevelt National Forest) and C (Phantom Creek, Pike - San Isabel National Forest). Panel D is the annual 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 previously described data collected in 2011 (~1 y pre-treatment), 2012-2013 (~1 year post-treatment) and 2017 (~5 years post-treatment; Briggs, Fornwalt, and Feinstein 2017; Demarest et al. 2023), and builds upon them by adding data collected in 2022-2023 (~10 y post-treatment). Collectively, the data span 47 plots and 4 timesteps, totaling 268 observations (**Figure 1**). Plots were randomly located and permanently marked within each treatment and control unit. From plot center, all overstory trees (height > 1.37 m and diameter at breast height (DBH) > 12.7 cm) were surveyed within variable radius plots with a 10 ft^2 ac^{-1} (2.3 m^2 ha^{-1}) basal area factor prism. Tree species, status (live/dead), and DBH were recorded for each tree. Tree seedlings (< 1.37 m tall) were inventoried within a 20 m^2 circular subplot around plot center. For untreated controls, tree measurements were not conducted for the 1 year post-treatment timestep as they were assumed to be approximately identical to the pre-treatment timestep. Understory plant cover, as well as fuel cover (fine wood (1-, 10-, and 100-hour fuel), coarse wood (1000-hour fuel), and litter and duff), was quantified with the line-point intercept method. All plant species and fuels were identified every 7.62 cm along four permanently marked 7.5 m transects oriented from plot center in cardinal directions (0°, 90°, 180°, 270°). We also searched the entire plot to identify all understory plant species present but not documented along the transects.

Six additional variables were measured only at 10 years after treatment. These were fine wood, measured separately as 1-, 10-, and 100-hour fuel loads, coarse wood, measured as 1000-hour fuel load, litter and duff fuel load, sapling density, shrub height, and tree canopy cover. Fine wood fuel loading was estimated using the photoload technique (Keane and Dickinson 2007) in 1 square meter quadrats located at plot center, and 7.5 meters from plot center in each of the cardinal directions. Coarse wood was measured in a 0.004 ha circular plot around plot center. The diameters of both ends of the log were measured to the nearest 0.25 cm, and the length was measured to the nearest 0.25 cm. Litter and duff depth was measured at 3.05, 6.10, and 9.15 ft along the cardinal directions to the nearest 9.64 cm. Density of tree saplings (>1.37 m tall, but <12.7 cm DBH) was measured in a 0.002 ha subplot around plot center. Average shrub height was measured for each of the transects using the LPI method described above for understory plants. Canopy cover was collected at 75 evenly spaced intervals along a 22.86 meter N-S transect using a densitometer.

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 wood. We derived 10 metrics to characterize aspects of understory composition: the Shannon-Wiener diversity index (Shannon 1948), 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 at the scale of the treatment unit, we calculated the 30 year (1991-2020) 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 220 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), and 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 4 km 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 4 km has been used in other studies (Wion *et al.*, 2025) to represent interannual climate variability.

Because our CWD data was at the scale of the treatment unit, we used finer scale topographic data to account for topographic variation within pixels. 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 timestep for control and treated plots were calculated 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 timestep 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 whether treatment had a significant effect on the change from pre-treatment. 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 post-treatment 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 10-year timestep (fuel loads of coarse wood, fine wood, 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.

Compositional Change

We conducted two permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) tests to assess the change in community composition in response to treatments. For the first test we excluded the 5 and 10 year post-treatment timesteps and tested the differences between the pre- and 1 year post-treatment phases. For the second test, we used all data and tested the difference between the pre- and 1 year post-treatment timesteps grouped, and the 5 and 10 year post-treatment timesteps grouped. For both models, we had site and treatment as additional independent variables, and had 999 permutations per model.

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. In order to explore how the changes in structure that resulted from treatments affected the understory, we created mixed effects models for those understory metrics that had 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, timestep and their interaction as predictors. The second model was an 'informed' model that 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 fine wood), 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 to check for violations of assumptions, including normality of residuals, normality of random effects, linear relationship, homogeneity of variance, and multicollinearity (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 5 and 10 years after treatment (**Figure 2**). Mean BA in treated plots was 18-22 $m^2\ ha^{-1}$ post-treatment, which was 6.5 $m^2\ ha^{-1}$ 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 post-treatment, 3.3 cm higher than pre-treatment values, on average. QMD also increased in treated plots from an average of 31.6 cm 1 year post-treatment to 33.6 cm ten years after treatment, an increase of 0.3 cm year^{-1} ($p<0.05$). Cover of fine wood in treated plots was approximately 3% higher than pre-treatment values 1 and 5 years after treatment but was not different from pre-treatment at year 10 (**Figure 2**). Crown base height did not have significant treatment effects, and was only significantly higher than pre-treatment in year 5.

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

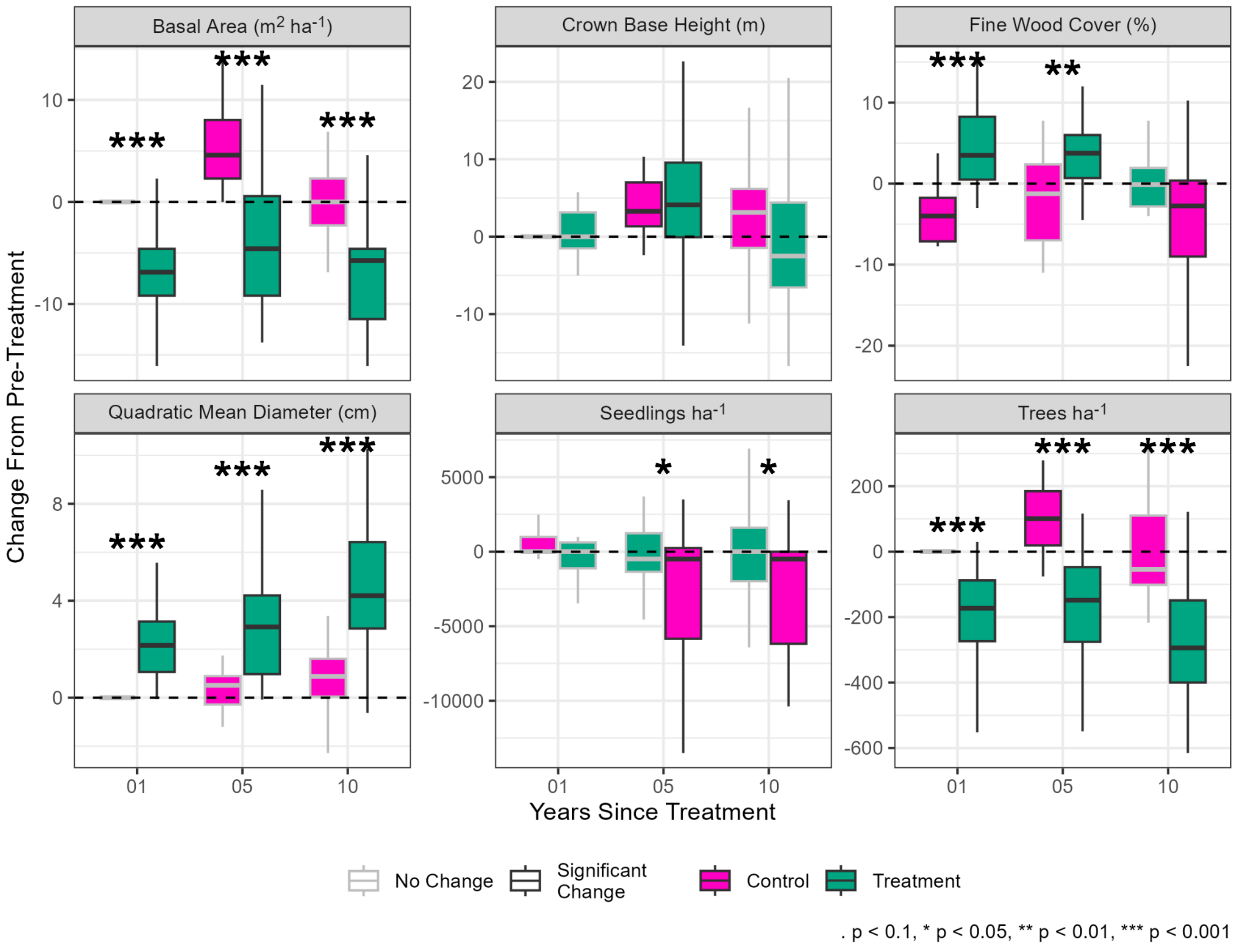

Figure 2. Change from pre-treatment for six stand structure metrics. Black outlines indicate that the difference from pre-treatment values was significant ($p < 0.05$) according to a one-sample Wilcoxon Rank Sum Test (each timestep by treatment combination was tested individually). Stars indicate a significant treatment effect in a given timestep according to a linear mixed model. Y-axis units are indicated in panel titles. Note that basal area, crown base height, quadratic mean diameter, seedling density, and tree density values are not available for control plots 1 year post-treatment because tree measurements were not conducted during this timestep.

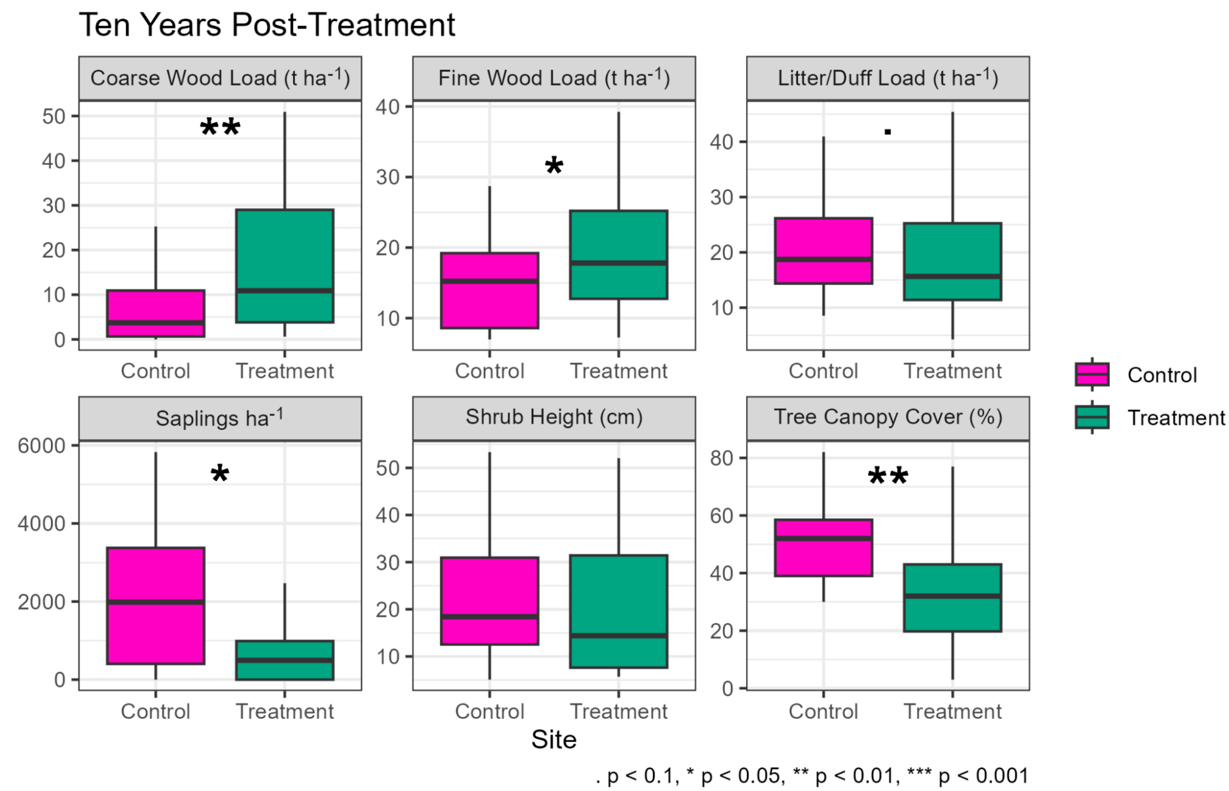

Figure 3. Mean comparisons for variables measured only ten years after treatment. Stars indicate significant differences from a linear mixed model.

Table 1. Estimated marginal means for stand structure metrics at each timestep, 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
Tree Density (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 (cm)	Control	29.3 (27, 32)	29.3 (27, 32)	29.2 (27, 31)	30.0 (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 Wood (%)	Control	14 (11, 17)	8 (5, 11)	11 (8, 14)	9 (6, 12)
	Treatment	11 (8, 14)	15 (12, 18)	14 (12, 17)	9 (7, 12)
Crown Base Height (m)	Control	42 (36, 48)	42 (36, 48)	46 (40, 52)	44 (38, 51)
	Treatment	43 (37, 49)	45 (39, 51)	47 (41, 54)	43 (37, 50)
Seedling Density (seedlings ha^{-1})	Control	7,410 (4,140, 10,678)	8,930 (5,665, 12,204)	1,830 (0, 5,101)	1,740 (0, 5,006)
	Treatment	3,550 (419, 6690)	3,270 (83, 6,448)	2,800 (0, 5,989)	3,520 (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 10. 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 10 year post-treatment timesteps, and among the 1 year post-treatment and the 10 year post-treatment timesteps (**Table S1**).

There was little difference in the regional species pool estimations immediately before and after treatment, but native and non-native species pools increased after 5 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 non-native 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 (count)	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)

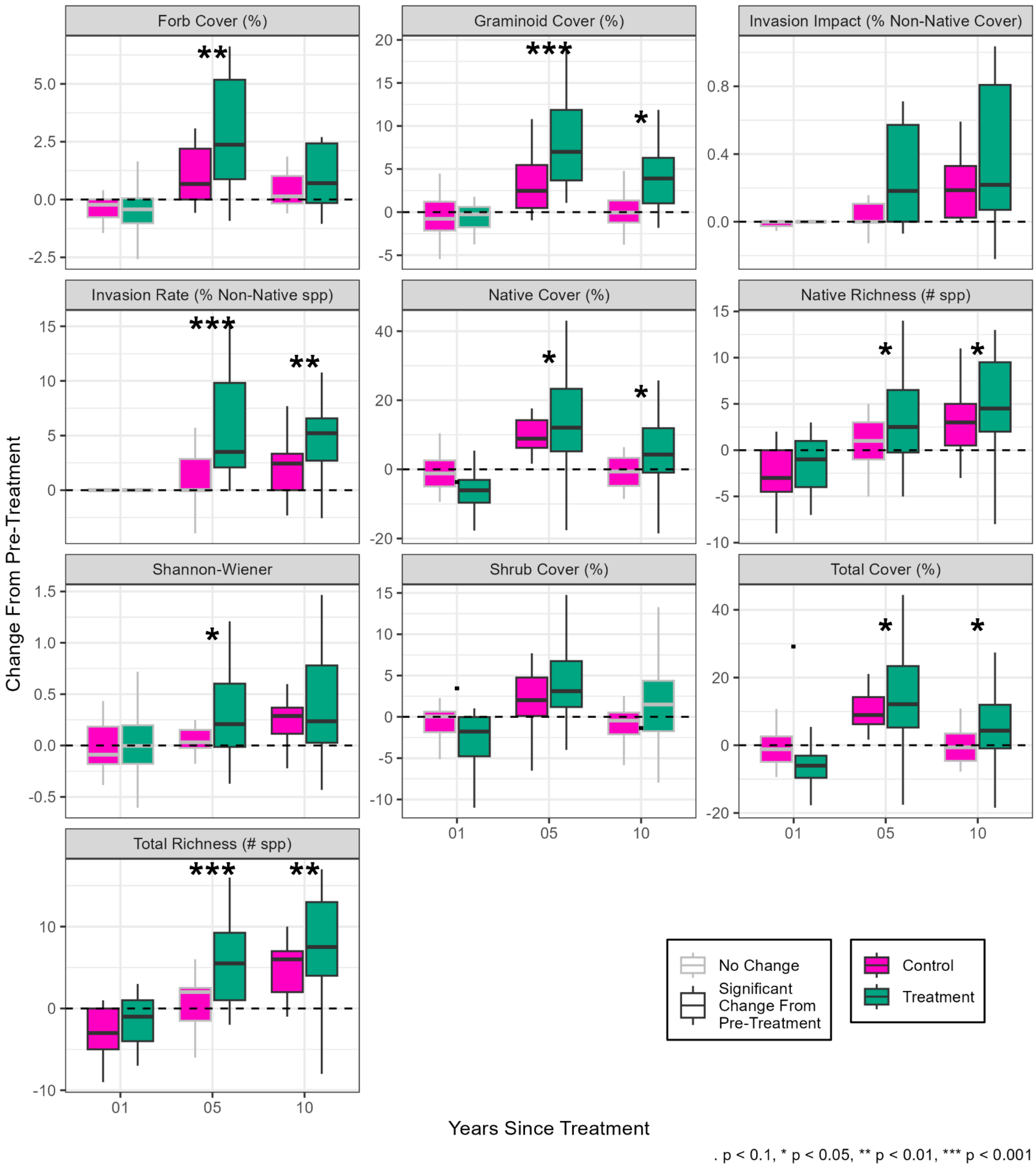
Forb Cover (%)
Graminoid Cover (%)
Invasion Impact (% Non-Native Cover)
Invasion Rate (% Non-Native spp)
Native Cover (%)
Native Richness (# spp)
Shannon-Wiener
Shrub Cover (%)
Total Cover (%)
Total Richness (# spp)
Change From Pre-Treatment
Years Since Treatment
01
05
10
No Change
Significant Change From Pre-Treatment
Control
Treatment
. p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Figure 4. Understory changes from pre-treatment. Dark outlines indicate that the change from pre-treatment values was significant ($p < 0.05$) according to a one-sample Wilcoxon Rank Sum Test (each timestep 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.

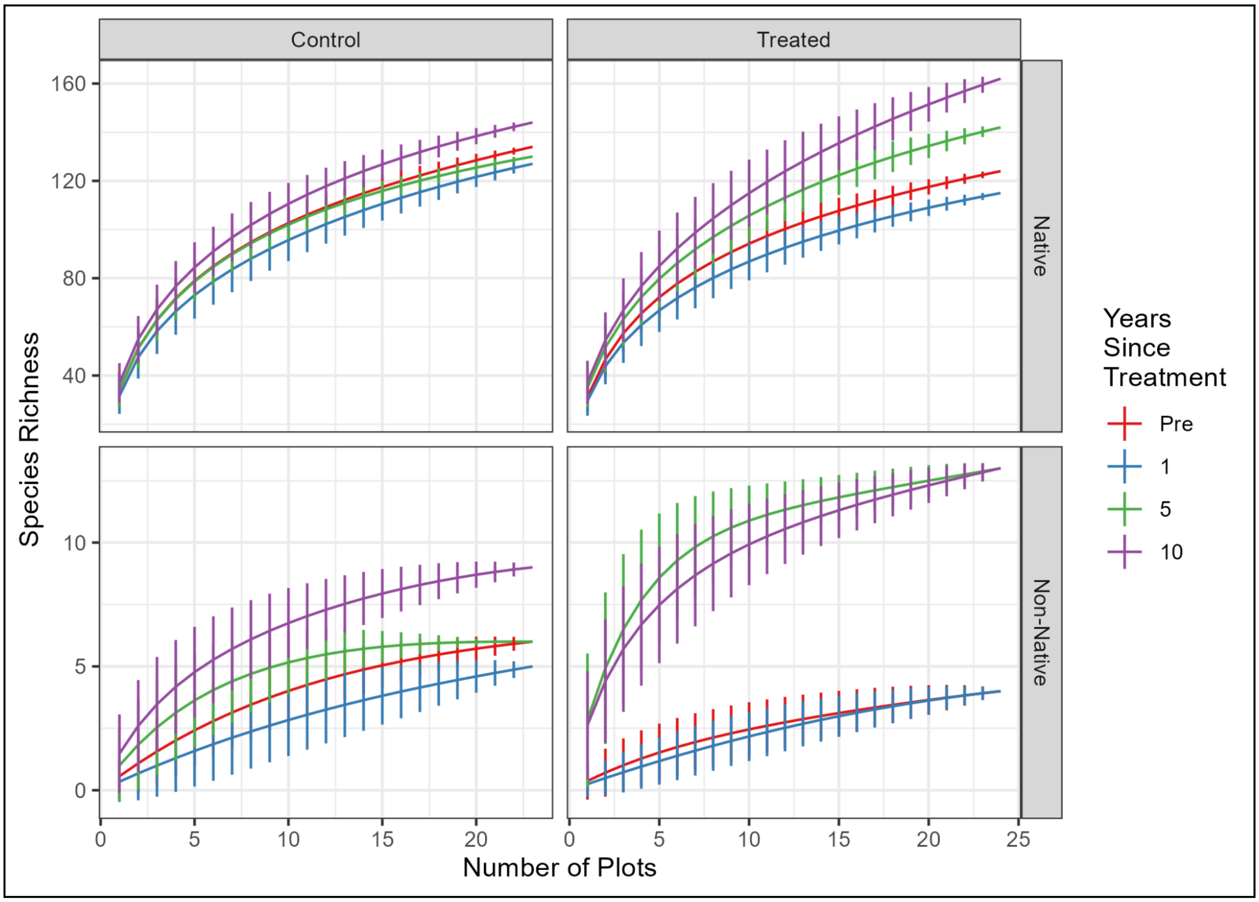

Figure 5. Species accumulation curves. Vertical bars represent the standard error of the estimated species count.

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)	9 (1)	+2
	Treatment	5 (1)	5 (1)	14 (1)	13 (1)	+8
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)	176 (8)	+11
	Treatment	149 (7)	140 (6)	181 (9)	208 (12)	+59

Compositional Change

Our PERMANOVA models indicated that the composition remained largely unchanged between pre-treatment and 1 year post-treatment timesteps, but changed significantly after 5 years (**Table 4**) but with a small effect size. Site (Estes Valley or Phantom Creek) was significant in both models and explained 11.6 - 12.8 percent of the variance. In the comparison of pre-treatment and 1 year post-treatment timesteps, both treatment and timestep were not significant. In the comparison of 5 and 10 year timesteps against pre- and 1 year post-treatment, both treatment and timestep were significant and explained 1.8 and 9.9 percent of the variance, respectively.

Table 4. PERMANOVA results. In the top table, community data was filtered to only pre- and 1 year post-treatment timesteps. In the bottom table, all timesteps were used, and the difference between both 5 and 10 year post-treatment timesteps against pre- and 1 year post-treatment were tested.

Comparison	Term	Df	Sum Of Squares	R^2	F	Pr(>F)
Pre-Treatment versus 1 Year Post-Treatment	Treatment	1	0.217	0.00878	0.948	0.454
	Site	1	3.17	0.128	13.9	0.001
	1 year post-treatment	1	0.248	0.0101	1.09	0.345
	Residual	92	21	0.853		
	Total	95	24.7	1		
Pre- & 1 Year Post-Treatment versus 5 & 10 Years Post-Treatment	Treatment	1	0.948	0.0178	4.33	0.001
	Site	1	6.14	0.116	28	0.001
	5-10 years post-treatment	1	5.24	0.0988	23.9	0.001
	Residual	185	40.5	0.763		
	Total	189	53.1	1		

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 5**). The difference in R^2_m values for the two model sets ranged from 0% to 40% of the variance explained. The informed 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 fine wood, QMD, slope and TWI, and negatively associated with CWD_s (**Figure 6a, Table 6**). The informed model of native species richness had an R^2_m of 0.41 while that of the naive model was 0.09. 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 6**). Forb cover 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 6**). The informed 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 6**). For P(invasion), the informed 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 6**). For invasion rate, the informed 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 6**).

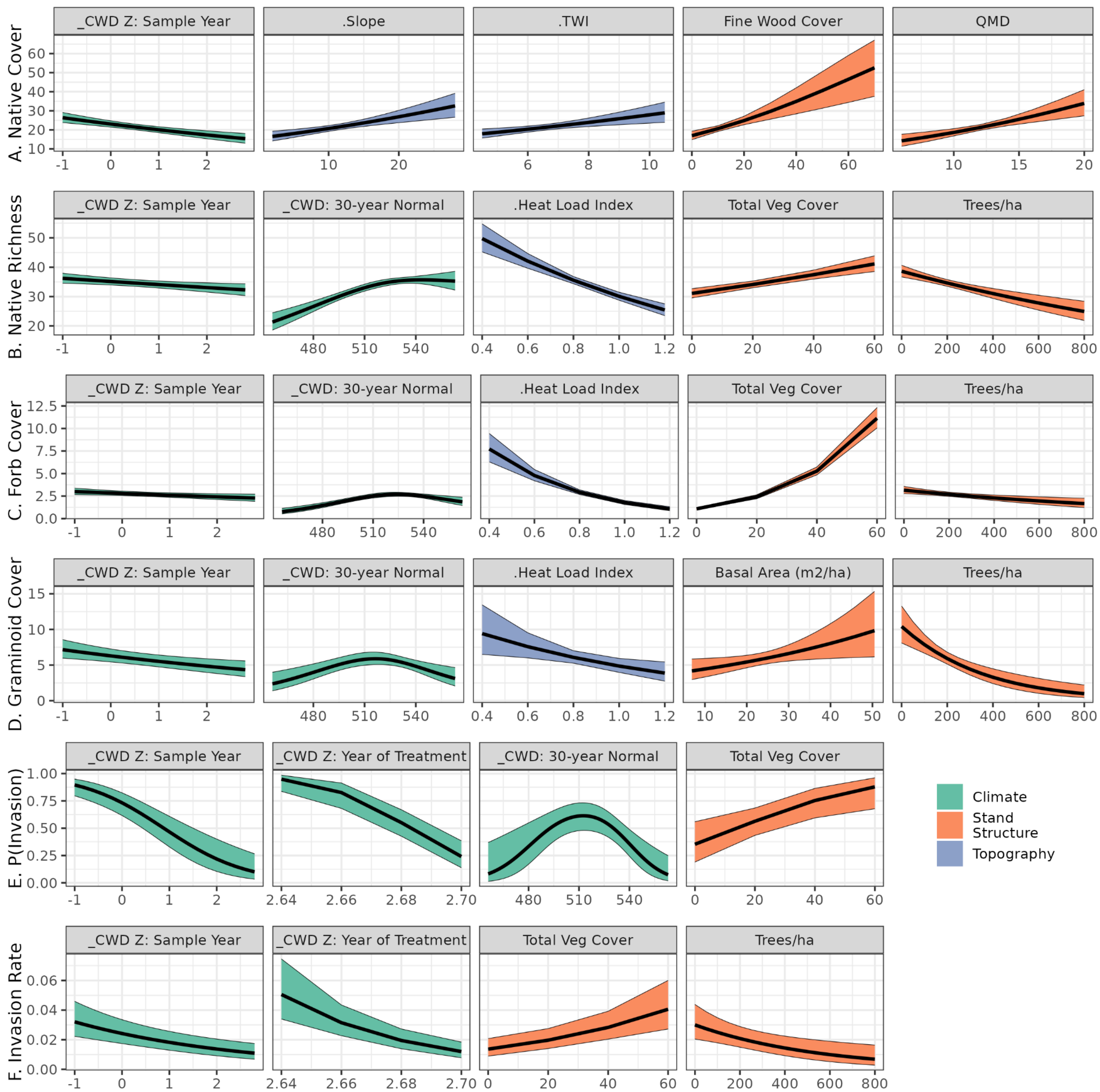

Figure 6. Partial effects of GLMMs. For each panel, the bold line represents the mean estimate of the partial effect, and the colored area surrounding the line is the 95% confidence interval.

Table 6. 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 Wood 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**

. $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Discussion

This work adds to the growing consensus that forest restoration treatments can benefit native understory plant communities(Vernon *et al.*, 2023; Springer *et al.*, 2024), while also increasing the probability of non-native plant invasion (Willms *et al.*, 2017). While the immediate effects of treatments on native understory plant cover and diversity were minimal, after 5 years largely beneficial impacts were observed, and these benefits remained unchanged or increased after 10 years (**Figure 4-5**). These outcomes were associated with greater QMD and lower BA and tree density (**Figure 6**)—common goals of restoration 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, but likely had a low level of ecological impact. Probability of invasion and invasion rate were less strongly associated with stand structure metrics than they were with climate (**Figure 6**) or with treatment per se, indicating that forest structure resulting from treatments may have less influence over non-native plant invasions than regional climate and the physical disturbance and potential for propagule introduction due to treatment.

Treatment effects on forest structure persisted for 10 years

Mechanical treatment at Estes Valley and Phantom Creek resulted in lower tree densities, lower BAs, and higher QMDs in treated plots relative to untreated controls. These values remained near their immediate post-treatment values 5 and 10 years after treatment (**Figure 2**), indicating that treatments showed minimal signs of returning to pre-treatment conditions. While treated plots remained significantly different from pre-treatment conditions, they still had higher residual tree density and BA, but similar QMD, than dendrochronological reconstructions of forest structure as it was just before Euro-American settlement (Battaglia *et al*, 2018). Plots treated here may have had higher targeted basal areas and densities than the regional averages, which may be due to the treatment projects being situated on the higher end of the productivity gradient. It is also possible that these treatments, which were among the first to occur during the 10-year lifetime of the Colorado Front Range Collaborative Forest Landscape Restoration Program, were constrained by decision documents that predated emerging research on historical forest structures and adaptively developing forest restoration objectives (Barrett et al 2021). 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.

The primary mechanism by which treatments lose their effectiveness is for seedlings, saplings and shrubs to grow in the newly opened canopies and create ladder fuels, or for surface fuels to accumulate (Wasserman *et al.*, 2022). We did not detect any signs of increased ladder fuels. There were minimal differences in seedling density (**Figure 2**) and shrub cover (**Figure 4**), as well as lower sapling density in treated plots at year 10 (**Figure 3**). Seedling density in untreated control plots was much higher than in treated plots in pre- and 1 year post-treatment, but not in years 5 and 10 (**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 5 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 (Rother, Veblen and Furman, 2015) (Davis *et al.*, 2019; Stevens-Rumann and Morgan, 2019). Lack of seedling and sapling regeneration may increase the longevity of treatment effectiveness. The only evidence we found of declining treatment effectiveness for these plots was increased surface fuel load. While the cover of fine wood returned to pre-treatment values by year 10 (**Figure 2**), the fuel load of fine and coarse wood was significantly higher in treated plots than in untreated controls 10years post-treatment (**Figure 3**).

Native species richness and cover were higher in treated plots

Native understory plant richness was largely unchanged immediately after treatment (also see Briggs, Fornwalt and Feinstein, 2017), but then increased in diversity in years 5 and 10 (**Figures 4, 5, Table S3**). Composition followed the same pattern (**Table 4**). The contrast between species accumulation curves increasing from year 5 to 10 and plot-level richness remaining constant is an artifact of the scale-dependency of species richness (Gotelli and Colwell, 2001; Thompson and Withers, 2003). While similar numbers of species were encountered at each plot at timesteps 5 and 10, the particular species encountered at each plot were more likely to be different by year 10. The gradual curve to the asymptote in the native species accumulation curves (**Figure 4**) suggest that plots are diversifying by adding new 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). 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). 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 5 and 10 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 5 and 10. 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 driest year, and it had stronger statistical support (**Table 6**). 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 5 and 10 (**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). Most of the forb and graminoid species encountered here were native, and non-native cover was very low in all cases. Forb cover was more strongly associated with aspect and total vegetation cover, 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 6**), 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 conifer systems (Jang *et al.*, 2021).

Non-native species richness remained constant after 5 years

Taken together, our data indicate that forest restoration treatments in the CFR can result in introductions of non-native species in previously uninvaded areas. These new invasions were mostly detectable after 5 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 5 and 10 (**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 model 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 5 and 10 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).

Analysis of species accumulation curves and extrapolated species pools yielded a regional species pool estimated at 10 non-native species across control plots and 15 in treated areas (**Figure 5**, **Table 3**). The overlap in species accumulation curves for years 5 and 10 suggests that colonization by non-natives via the newly available resources had mostly taken place by the 5 year mark. After treatment there are newly available resources, including increased light and water availability from the opened canopy (McConnell and Smith, 1970)(Riegel, Miller and Krueger, 1992), and increased bare soil from physical soil disturbance (Leffler *et al.*, 2016).

Management implications

It has long been recognized that monitoring and control of non-native plants need 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 abrupt increases in non-native populations within 10 years of being at low-impact levels like those observed here (McGlone *et al*, 2009; Wion *et al*, 2024) that proceeded in the stages outlined by Brooks *et al* (2004). In a *P. ponderosa* forest in Northern Arizona, McGlone *et al.* (2009) observed *B. tectorum* at low cover (stage 2) before and three years after treatment, followed by dominant levels of cover (stage 3)t 6 years after treatment without a subsequent disturbance. 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 (stage 2) in 1997 to become the dominant understory species in 2008 (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 5 years and remained steady 10 years after treatment. This is consistent with studies from other regions, where the first 5 years after treatment saw changes in composition, and then the composition remained stable for up to 23 years (Jang *et al.*, 2021; Vernon *et al.*, 2023). The time period between 5 and 10 years after treatment is likely the most effective time to monitor and control non-native plants, as it is a long enough period of time for the understory to reach the new equilibrium in productivity, and for non-native populations to become detectable. It is also short enough that non-native populations that establish after treatment are likely to still be small and manageable (Schuurman *et al.*, 2020). After 10 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.

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Supplemental Tables

Table S1. Differences 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
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