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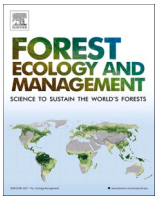

Mechanical forest restoration treatments stimulate understory plants in the Colorado Front Range

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ABSTRACT

Restoration efforts are underway in dry conifer forests across the western United States to increase their resilience to wildfire and other disturbances. Because such treatments typically decrease overstory density and homogeneity, they can also drive changes in the understory plant community. Past studies of post-treatment changes in understories have found variable results over short time frames and across regions, highlighting the need to study longer-term, region-specific responses. We investigated whether mechanical restoration treatments benefited understory plants in dry conifer forests of the Colorado Front Range, and what biotic and abiotic variables modified understory plant responses in treated areas. We analyzed data collected 1–2 years pre-treatment, 1–2 years post-treatment, and 4–6 years post-treatment in 168 plots, which were distributed across 8 sites and 16 pairs of treated and nearby untreated areas. Treatments were implemented by removing trees with heavy machinery or hand tools (i.e., thinning). By the time treatments were 4–6 years old, native understory plant cover was 1.7 times higher in treated compared to untreated plots, and native richness was 1.1 times higher. Heightened cover and richness values in treated plots were not driven by a single native plant functional group, but by a large portion of the native community; long-lived, graminoid, vegetatively spreading, and non-vegetatively spreading plants all had higher cover in treated plots, while short-lived, long-lived, forb, graminoid, and non-vegetatively spreading plants had higher richness in treated plots. Non-native plants showed 3.1 times higher cover and 4.4 times higher richness in treated compared to untreated plots at 4–6 years post-treatment, but were present at very low levels (e.g., $\leq$ 0.5% mean cover in either treatment). Greater native plant cover and richness at 4–6 years post-treatment were associated with lower overstory basal areas that resembled 19th-century forest structural conditions for the landscape. Contrary to expectations, a long-term measure of moisture availability (i.e., 30-year average climatic water deficit) was not a strong predictor of native cover or richness in treated plots 4–6 years post-treatment; rather, they were better predicted by moisture availability during the spring months prior to sampling. Overall, the consistent and enduring stimulation of cover and richness of native understory plants after mechanical treatments, with only limited invasion from non-native species, illustrates the important benefits of ongoing restoration activities in dry conifer forests of the Colorado Front Range.

1. Introduction

Maintaining and promoting native biodiversity is a key objective for natural resource managers (Noss et al., 1995; Rands et al., 2010). In many forests, understory plants are important targets for biodiversity conservation because they make up the overwhelming majority of plant diversity (Abella and Springer, 2015; Gilliam, 2007; Hart and Chen, 2006). Understory plants also form the foundation of forest food webs, provide habitat for wildlife, help protect soils from erosion, and affect forest development (Allen et al., 2002; Gilliam, 2007; Zuazo and

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Pleguezuelo, 2009).

In many dry conifer forests of the western United States (US), overstories have experienced considerable alterations since Euro-American settlement in the mid to late 1800s, which in turn are thought to have affected understory plant communities. Historically, dry conifer forests experienced relatively frequent, low- or mixed-severity fires that created and maintained a heterogenous but generally open overstory mosaic (Brown et al., 2015; Swetnam and Baisan, 1996; Veblen et al., 2000; Yocom-Kent et al., 2015). While historical forest understories remain poorly characterized, these overstory conditions likely fostered relatively productive and diverse native understories (Gildar et al., 2004; Keeling et al., 2006; Laughlin et al., 2011). In dry conifer forests, more open overstory conditions can be associated with higher levels of light, nutrients, and moisture available to understory plants, leading to higher understory abundance (Lindh, 2005; Riegel et al., 1992; Zou et al., 2008). Heterogeneous conditions, meanwhile, can support a wide variety of habitat niches, and therefore, high understory diversity (Burkle et al., 2015; Randall Hughes et al., 2007). More than 100 years of fire exclusion, logging, mining, and livestock grazing have produced modern forests with dense, contiguous canopies (Battaglia et al., 2018; Hagmann et al., 2021; Naficy et al., 2010; Rodman et al., 2019), and understories that are sparse and depauperate (Knapp et al., 2013; Laughlin et al., 2011). Such alterations in dry conifer forest overstories, along with rising temperatures and longer fire seasons due to climate change, have combined to drive increasingly severe wildfires in the past several decades (Hagmann et al., 2021; Singleton et al., 2019), with further consequences for understories (Lentile et al., 2007; Miller and Safford, 2020).

In recent decades, resource managers have implemented forest restoration treatments in dry conifer forests to move overstory stand structure towards fire-resilient states, such as those found historically (Churchill et al., 2013; Underhill et al., 2014). Treatments also aim to improve other degraded forest properties, such as native understory diversity and abundance. Restoration treatments using prescribed fire are often preferred as they reintroduce a key natural disturbance process. However, prescribed burns can be very difficult to implement for a variety of operational and social reasons, including perceived risk to human values and environmental laws such as the Clean Air Act (Ryan et al., 2013). Mechanical treatments, which employ chainsaws or heavy machinery to remove trees, have been widely used to meet overstory stand structure goals and mitigate risk of severe wildfire (Busse et al., 2009; Cannon et al., 2018; Schultz et al., 2012). However, we still have a limited understanding of many of the other impacts of mechanical treatments, and thus whether they are accomplishing the full suite of restoration goals.

Studies investigating how the understory plant community responds to mechanical restoration treatments in dry conifer forests have yielded mixed results with respect to the direction, magnitude, and timing of effect (Schwilk et al. 2009; Abella and Springer 2015; Willms et al. 2017). Changes in overall understory abundance and diversity were variable one to three years after treatment, with both increases and decreases commonly reported (Collins et al., 2007; Dodson et al., 2008; Wayman and North, 2007). In contrast, at four or more years post-treatment, understory abundance and diversity were often elevated relative to untreated or pre-treatment baselines (Carey and Wilson, 2001; Fornwalt et al., 2017; Kane et al., 2010; Lochhead and Comeau, 2012; Siegel and DeSante, 2003). Various functional groups, including those defined by nativity, growth form, or life strategy, were less often studied, and showed differing responses to treatment. For instance, cover sometimes increased with treatment for both forbs and graminoids (Fornwalt et al., 2017) or only forbs (Jang et al., 2021) or neither (Kane et al., 2010). Native species capable of spreading vegetatively by rhizomes or stolons were sometimes stimulated over longer post-treatment time frames (Wolk and Rocca, 2009), while short-lived species, which tend to thrive on disturbance, were sometimes unable to persist on longer times scales (Kane et al., 2010). However, where native plants benefited from treatment, non-native plants almost always did as well (Carey and Wilson, 2001; Fornwalt et al., 2017; Jang et al., 2021; Kane et al., 2010).

Mechanical restoration treatments in dry conifer forests have been implemented in many different places with varying conditions throughout the western US (Schwilk et al., 2009; Stephens et al., 2012), yet little is known about how biologically meaningful environmental gradients affect understory responses to treatments (Fornwalt et al., 2017; Jang et al., 2021; Kane et al., 2010). It is possible that variations in topography and climate may modify understory responses following treatment; cooler and wetter sites may be able to support more understory vegetation post-treatment than their warmer, drier counterparts (North et al., 2005). Examining how understory responses vary along gradients of climate (such as climatic water deficit) or topographic exposure to wind and insolation (such as topographic position index) could help resource managers understand how site conditions may change treatment outcomes. Additionally, treatments themselves can modify biotic gradients, intentionally altering overstories, depositing woody byproducts on the forest floor, changing litter and duff depth, and exposing bare soil, all of which can in turn influence understory plant germination and growth (Kane et al., 2010; Xiong and Nilsson, 1999). It is important to understand how these biotic gradients can affect the understory, considering that the specific prescriptions utilized can vary due to a multitude of factors such as pre-treatment stand conditions, logistical constraints, and local management preferences, and leave behind a wide range of post-treatment overstory and ground cover conditions (Jain et al., 2012; Lydersen et al., 2019).

In the Colorado Front Range of the western US, tens of thousands of hectares of ponderosa pine (*Pinus ponderosa)* dominated dry conifer forest have received mechanical restoration treatments in recent decades through collaboratives composed of federal, state, and local government agencies, water utilities, private land owners, and non-profit organizations, including the Colorado Front Range Landscape Restoration Initiative, Forests-to-Faucets, and the Upper South Platte Partnership (Jones et al., 2021; Underhill et al., 2014; Williams and Cannon, 2019). This study takes advantage of monitoring data collected by these collaboratives, leveraging pre-treatment and 1–2 and 4–6 year post-treatment data spanning a range of environmental conditions to investigate the following questions:

1. How have mechanical restoration treatments affected the biotic conditions that might influence the understory plant growing environment, including overstory and ground cover conditions?
2. How have mechanical restoration treatments affected cover and richness of understory plants within functional groups defined by nativity, as well as by growth form, life span, and reproductive strategy?
3. How do post-treatment native understory plant communities vary along biotic and abiotic environmental gradients, including those related to overstory and ground cover conditions, as well as to climate and topography?

2. Methods

2.1. Study area and study sites

We conducted our study at eight study sites within the dry conifer forests of the Colorado Front Range, three of which were established and initially measured by Briggs et al. (2017) (Fig. 1; Table 1). Site elevations ranged from 2062 to 3048 m. Hill slopes were moderately steep, averaging 26% and ranging from 5% to 63%. From 1991 to 2020, sites received an average of 471 to 601 mm of precipitation annually (PRISM Climate Group 2020). Precipitation peaks occurred during spring rain-snow showers (March to May) and again in late summer due to monsoonal thunderstorms (July to August) (PRISM Climate Group, 2020). Average annual temperature at the sites between 1991 and 2020

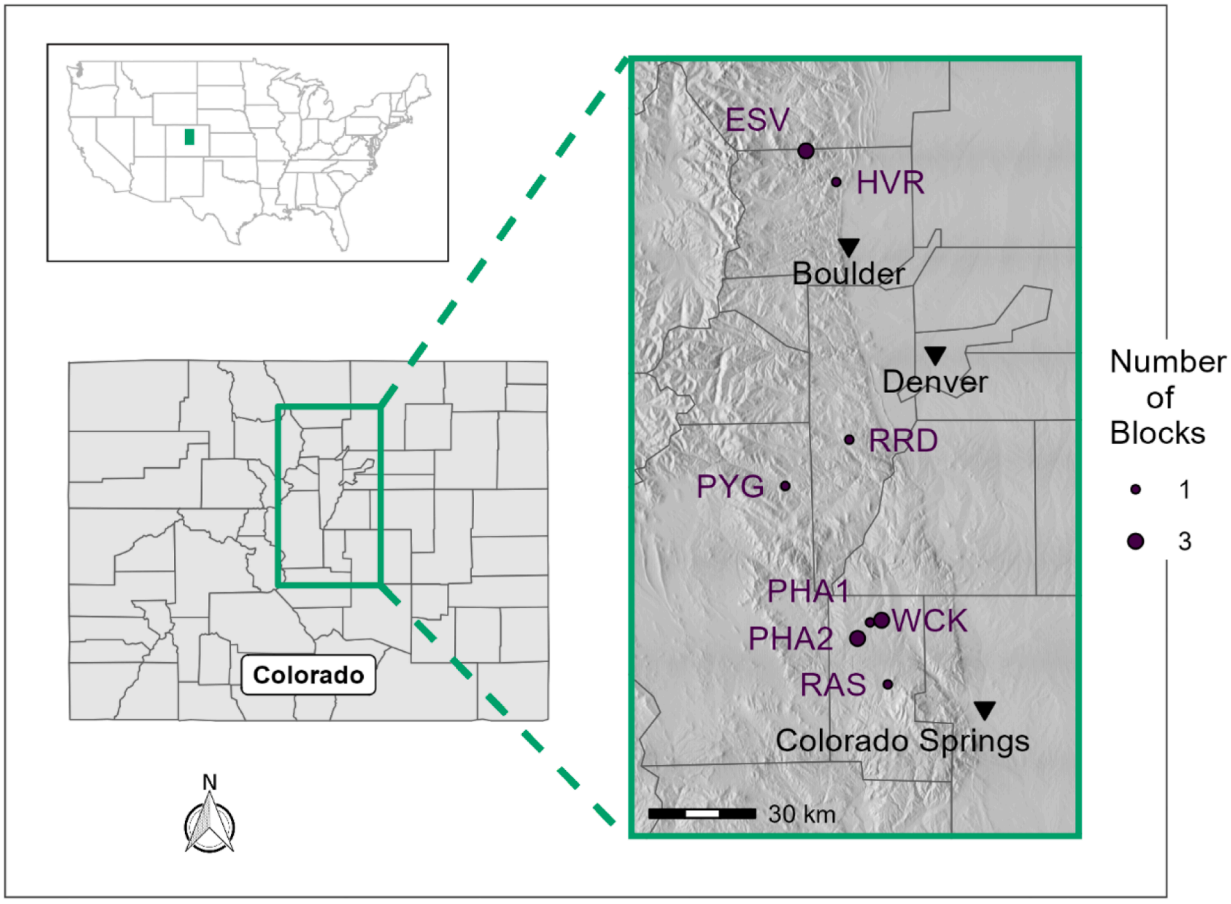

Fig. 1. Study area map. This map shows the study area in the Colorado Front Range, with study sites marked by purple circles. Nearby cities are labeled with black triangles. Sites include: Estes Valley (ESV), Heil Valley Ranch (HVR), Ridge Road (RRD), Payne Gulch (PYG), Phantom Creek 1 (PHA1), Phantom Creek 2 (PHA2), West Creek (WCK), Raspberry Mountain (RAS). We leveraged the Estes Valley, Heil Valley Ranch, and Phantom 1 sites from Briggs et al. (2017).

Table 1
Study site details. The number of plots and the hectares of treated and untreated areas are the totals for the site. Mean elevation was calculated from plot values. Sampling years reflect those for the 1–2 years pre-treatment, 1–2 years post-treatment, and 4–6 years post-treatment sampling periods. The sites Estes Valley, Heil Valley Ranch, and Phantom Creek 1 were leveraged from Briggs et al. (2017).

Site	Number of blocks	Number of plots	Treated area (Ha)	Untreated area (Ha)	Mean Elevation (m)	Sampling years	Treatment date	Treatment methods
Estes Valley	3	21	80	41	2362	2011, 2012 or 2013, 2017	Winter-Spring 2011/12	Trees cut with chainsaws; cut material piled and burned or masticated.
Heil Valley Ranch	1	8	70	128	2098	2011, 2013, 2017	Winter-Spring 2012/13	Trees cut with heavy machinery; cut materials removed or lopped and scattered
Phantom Creek 1	2	25	210	131	2670	2011, 2012, 2017	Summer 2011	Trees cut with heavy machinery; cut materials removed
Phantom Creek 2	3	36	140	73	2745	2015, 2018, 2021	Spring 2017	Trees cut with chainsaws and heavy machinery; tree boles removed; other cut materials left in place
Payne Gulch	2	24	30	16	2434	2016, 2018, 2021	Winter 2017	Trees cut with heavy machinery; cut materials removed
Raspberry	1	12	35	26	2982	2015, 2017, 2021	Winter 2015	Trees masticated
Ridge Road	1	12	36	26	2589	2015, 2017, 2020	Winter-Spring 2016/17	Trees cut with chainsaws and heavy machinery; tree boles left in place; other cut materials piled
West Creek	3	36	187	90	2607	2015, 2018, 2021	Fall 2016	Trees cut with heavy machinery; cut materials left in place

ranged from 3.6 to 8.7° C (PRISM Climate Group 2020). Soils underlying Front Range forests are often shallow, well-drained, coarse-gravelly, and slightly acidic, arising from granite, schist, or gneiss parent material (Moore, 1992; Peet, 1981; Veblen and Donnegan, 2005).

For all sites, ponderosa pine was the common component of forest overstories, and the sites spanned most of its elevational range (Peet,

1981). Ponderosa pine dominated in lower elevation sites, sometimes accompanied by Rocky Mountain juniper (*Juniperus scopulorum*). At intermediate elevations, open stands co-dominated by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) frequently occupied xeric, south-facing slopes, while denser stands with an even more significant Douglas-fir component were found on the cooler, mesic north-facing slopes (Battaglia et al., 2018; Kaufmann et al., 2006). At higher elevations, lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), Colorado blue spruce (*Picea pungens*), and limber pine (*Pinus flexilis*) co-occurred with ponderosa pine and Douglas-fir. Trembling aspen (*Populus tremuloides)* was sporadically present throughout the sites in moist meadows and drainages. Beneath the forest canopy, understory communities also varied with moisture, topography, and elevation (Peet, 1981). All understory plants at our sites are described in Supplementary Table 1. Ubiquitous forbs included common yarrow (*Achillea millefolium*), pineywoods geranium (*Geranium caespitosum*), and goldenrod (*Solidago* spp.), while common graminoids included sedge (*Carex* spp.), purple reedgrass (*Calamagrostis purpurascens*) and prairie Junegrass (*Koeleria macrantha*). Shrubs frequently occurring at our sites included kinnikinnick (*Arctostaphylos uva-ursi*), common juniper (*Juniperus communis*), and rose (*Rosa* spp.).

While the sites have varied land use histories, it is likely that they have experienced changes similar to those in many dry conifer forests of the western US, including logging since Euro-American settlement in the mid to late 19th century and near-total fire exclusion since the turn of the 20th century. A study spanning the entire Front Range detected evidence of past logging in 97% of plots, including in plots at some of our sites (Battaglia et al., 2018). Fire history studies in areas that overlapped many of our sites found evidence of dramatically reduced fire frequency since 1900 (Brown et al., 2015; Donnegan et al., 2001). It is also likely that most or all sites were grazed by domestic livestock during the settlement era, with grazing at some continuing well into the 20th century (Brown et al., 2015; Veblen and Donnegan, 2005).

We established the eight study sites on federal (Arapaho - Roosevelt and Pike - San Isabel National Forests of the USDA Forest Service), county (Boulder County), and private lands, in places where mechanical forest restoration treatments were being planned by land managers as part of multiple collaborative programs (Fig. 1). From 2011 to 2017, land managers delineated discrete forest treatment units (hereafter called treated units) within the sites according to local management priority and capacity. We simultaneously delineated nearby areas (within 1 km of treated units) with similar slope and aspect, but without plans for treatment, to serve as “controls” or reference areas (hereafter called untreated units). A treated unit and its paired untreated unit comprised a block. Each of the sites contained one to three blocks, for a total of 16 blocks (Table 1).

Land managers carried out mechanical restoration treatments at the sites between 2012 and 2017 (Table 1). Exact treatment prescriptions varied by unit, but common elements included reduction of basal area, creation of openings, creation of heterogeneity in tree group size and age, retention of old trees and snags, and preferential retention of ponderosa pine relative to other tree species (Dickinson et al., 2014; Underhill et al., 2014). Treatments were implemented by masticating trees or by cutting them with heavy machinery or chainsaws. Cut woody materials including tree boles, limbs, and branches were removed or left on site; materials left on site could be piled, piled and burned, lopped and scattered, or masticated.

2.2. Sampling design

We randomly placed sampling plots within the treated and untreated units of each block. Plots were at least 30 m away from a unit boundary to avoid boundary effects. We typically established 12 plots per block (6 in the treated unit and 6 in the untreated unit), although the number varied between 6 and 17 plots per block, dependent on block area. We established 180 plots in total. However, 12 plots were subsequently compromised by events like cutting in plots intended to be untreated or unplanned livestock grazing.

We employed a Before/After/Control/Impact (BACI) sampling design where each plot was measured before and after treatment. Sampling occurred 1–2 years before treatment, 1–2 years after treatment, and 4–6 years after treatment. Although sampling always occurred within these periods, the calendar years of sampling varied across sites based on the year of study site establishment, the year of treatment implementation, and the availability of field crews.

2.3. Understory plant and substrate measurements

Understory plant and substrate plots were circular with a fixed 406 m^2 area. We used the point intercept method to capture understory plant and substrate hits at observation points. The observation points were distributed along 11.3 m transects that radiated from plot center. Pilot plots at the Estes Valley, Heil Valley Ranch, and Phantom Creek 1 sites had 400 observation points distributed along four transects radiating in the cardinal directions, for all visits (Briggs et al. 2017). This protocol was subsequently adjusted slightly to increase plot coverage while decreasing sampling time; plots at all later sites had 200 observation points distributed along eight transects radiating in the cardinal and ordinal directions, for all visits. All plants and substrates hit below breast height were recorded. Plants were identified to species, with the exception of those in the genera *Carex*, *Solidago*, *Oreochrysum*, *Fragaria*, *Chenopodium*, *Rosa*, and *Euphorbia*; species in these genera could be challenging to distinguish and were consequently always identified to genus for consistency, even if species could be determined in a particular instance. Possible substrates included: litter and duff, rock, bare ground, moss and lichen, fine wood (dead woody material < 7.2 cm diameter), and coarse wood (dead woody material > 7.2 cm diameter). We also walked the entire plot and performed a full census of all understory plant species present. Plants that could not be identified to species (or genus in the above instances) in the field were collected outside the plot for identification in the lab. Plants were later classified into functional group categories defined by nativity (native or non-native to Colorado), growth form (forb, graminoid, or shrub), lifespan (short lived [annual or biennial] or long-lived [perennial]), and vegetative spread (vegetatively spreading [stoloniferous or rhizomatous] or non-vegetatively spreading) using information from the PLANTS database (USDA, NRCS 2020) and botanical keys (Ackerfield, 2015; Cronquist, 1972). For plants that were identified to genus (or coarser taxonomic resolution), if the genus contained members with varying categories within a functional group (e.g., the genus contained both native and non-native species), they were not classified for that group. We measured forest floor (litter and duff) depth at 3.0, 6.1, and 9.1 m along each of the cardinal transects.

We used these data to calculate substrate cover and understory plant cover and richness for each plot. Since one of the objectives of treatment was to promote dense and species-rich native plant communities, we calculated cover and richness for native and non-native species, then for native plants by growth form, lifespan, and vegetative spread categories. Percent cover was calculated by dividing the number of point intercept transect hits for each plant or substrate by the total number of points per plot, then multiplying by 100. For plants, because more than one species could be hit at each point due to layered vegetation, there was potential for cover to exceed 100%. We tallied all appropriate species encountered within a plot to calculate species richness for functional group categories.

2.4. Overstory measurements

Overstory plots were overlaid onto the same center point as understory plots. Overstory plots were variable in radius, as determined by a forestry prism, around the plot center point. We used a prism with a basal area factor (BAF) of 10 $ft^2\ ac^{-1}$ (2.3 $m^2\ ha^{-1}$) to determine whether a tree was in or out of the overstory plot. We then deemed all live trees in

the plot with a diameter at breast height (1.37 m; DBH) greater than 12.7 cm as overstory trees and tallied them. We subsequently calculated overstory basal area of the plot as a product of the number of overstory trees and the prism BAF.

2.5. Other measurements

At the center point of each plot, we recorded latitude, longitude, elevation, and dominant slope and aspect. For each plot we also calculated two climatic water deficit (CWD) variables. Climatic water deficit is a measure of unmet evaporative demand for water (i.e. the amount of water by which potential evapotranspiration exceeds actual evapotranspiration over a given time period). It incorporates monthly average temperature and precipitation (PRISM Climate Group, 2020), soil available water capacity (POLARIS; Chaney et al. 2019), and aspect, slope, and latitude. We calculated each CWD variable following the method in Lutz et al. (2010) and using R code from Redmond (2022). First, we calculated 30-year normal climatic water deficit (1991–2020) (hereafter average CWD), which represents long-term climatic conditions. Lower average CWD values indicate cooler-wetter conditions at a plot. We also calculated March-June climatic water deficit for the year of the 4–6 year post-treatment visit, then scaled and centered (i.e z-scored) it using the 30-year mean and standard deviation for each plot (hereafter final spring CWD z-score), to reflect how different the climate was in the 4–6 year post-treatment spring compared to springs over the last 30 years. Positive final spring CWD z-scores indicate warmer-drier March-June conditions at a plot than usual, while negative values indicate cooler-wetter conditions. Last, we calculated topographic position index (TPI) for each plot, which captures the difference between each plot's elevation and the mean elevation of its surroundings. TPI describes aspects of plot moisture and temperature conditions that would not be captured by CWD. For example, a low-lying drainage and adjacent ridge could have similar climate, soils, aspect, slope, and latitude (so, similar average CWD), but the drainage would likely be cooler and wetter. We defined the surroundings as a 450 m wide square centered on the plot as past research showed this was a useful scale in predicting tree regeneration in the southern Rocky Mountains (Rodman et al., 2020). To calculate TPI, we used 30 m digital elevation model data (U.S. Geological Survey, 2021) and the spatialEco package in R (Evans, 2021), following methods from Weiss (2001).

2.6. Data analyses

We used generalized linear mixed models (GLMMs) to investigate the effect of treatment and time-since-treatment on understory cover, richness, and biotic growing environment response variables. We carried these analyses out in R (R Core Team, 2021) using the *glmmTMB* package (Brooks et al., 2017). We incorporated data from 155 of the 180 original plots (78 treated and 77 untreated), as the 12 compromised plots made their entire blocks unusable. For each model, we selected the error distribution and link function most appropriate for the response variable: beta distribution for bare ground, fine wood, and coarse wood cover models; gamma distribution for plant cover models; Poisson or negative binomial distribution (if dispersion was especially high) for plant richness models; and Gaussian distribution for overstory basal area models (log transformed). Since gamma models are constrained to positive values in the response, for response variables with one or more zero observations, we followed Stahel's method (Stahel, 2002) to add a small value to each observation. We set treatment, time-since-treatment, and their interaction as the fixed effects in our GLMMs. We used a nested random effects term with four levels: site, block within site, unit within block within site, and sampling year within unit within block within site. The inclusion of unit and sampling year accounted for temporally repeated measures by capturing, respectively, the correlation between sampling periods (i.e., all the observations from a unit for all sampling years) and within a sampling period (i.e., all the observations from a unit in a particular year). The nested site, block, and unit terms accounted for potential correlation of observations across space. Significant ($\alpha = 0.050$) treatment by time-since-treatment interactions indicated that differences between treatments were not the same for all sampling periods. When interactions were significant, we conducted post-hoc comparisons to test for differences among treatments in each sampling period. We used the Tukey method for multiple comparisons to adjust P-values for these post-hoc tests, and noted both significant ($\alpha = 0.050$) and marginally significant ($\alpha = 0.100$) differences. All reported means are estimated marginal means from our models, and confidence intervals are based on variability in the fixed effects only. We assessed model fit and performed residual diagnostics with functions from the package *DHARMa* (Hartig, 2022). The non-native cover and short-lived cover variables had high proportions of zeros and diagnostics showed poor fit (Supplementary Document 1). However, we explored less compatible distributions and link functions for these variables, which yielded similar results.

We used Boosted Regression Trees (BRT) to explore how biotic and abiotic environmental gradients affected post-treatment native understory cover and richness (Elith et al., 2008). In order to focus on variation in longer-term treatment outcomes for the understory, we examined only data collected at 4–6 years after treatment and only data from treated plots. BRT analyses were also carried out in R, using the *dismo* package (Hijmans et al., 2021). Since block structure was not important for BRT analyses, we retained all plots for analysis except those which were compromised by unintended management (91 treated plots analyzed). The biotic growing environment variables related to treatment were residual basal area, forest floor depth, fine wood cover, coarse wood cover, and bare ground cover. To characterize abiotic environment, we used two climatic variables, average CWD and final spring CWD z-score, and one topographic variable, TPI. We added sample year to encompass yearly variations due to factors not captured by the other variables, including a change to the protocol for collecting cover data described in Section 2.3 and changes in personnel. Last, since some plots were visited outside of peak growing season in late spring or early fall, we included sample month to account for variation in cover as an effect of visit timing. Prior to modeling, we tested all variables for collinearity but did not find any highly correlated variable pairs (Pearson's $r > |0.7|$). For our cover model, we used a Gaussian loss function, 1000 trees, a tree complexity of 2, a learning rate of 0.0020, and a bag fraction of 0.5. For richness, we used a Poisson loss function, 1000 trees, a tree complexity of 2, a learning rate of 0.0022, and a bag fraction of 0.5. We determined model predictive ability outside the study dataset using 10-fold cross-validation (CV). We calculated R-squared values for each CV model and averaged them – these values measure how good the model was at predicting data not used to develop the model. We also calculated R-squared values for the final (non-CV) BRT models – these values measure how well the final model explained the data used to create it. After final models were fit, we calculated the relative influence (RI) of each predictor variable on the response. We then made partial dependence plots with the *pdp* package (Greenwell, 2017) to show individual relationships between the response and each predictor after controlling for the average effect of the other variables.

3. Results

We identified 356 unique understory plants over the course of this study (Supplementary Table 1). Of these plants, 300 were native and 34 were non-native, with 10 of the non-native species classified as noxious weeds in Colorado (Colorado Department of Agriculture, 2022), and 22 were of indeterminate nativity. We identified most plants to the species level (78.2% of observations), although some plants were identified to the genus level (21.2% of observations) or to a coarser taxonomic resolution (0.6% of observations).

3.1. Overstory and substrates

Of the variables related to the biotic growing environment for understory plants, the effect of treatment varied at different sampling periods for overstory basal area, fine wood cover, and bare ground cover, but not for forest floor depth or coarse wood cover (Table 2). Before treatment, basal area, fine wood cover, and bare ground cover values were similar in treated and untreated plots. Basal area was nearly halved by treatment, averaging 10.6 m^2 ha^{-1} in treated and 23.4 m^2 ha^{-1} in untreated plots at 1–2 years post-treatment ($p < 0.001$), with little alteration at 4–6 years post-treatment. Fine wood and bare ground covers were higher in treated plots compared to untreated plots at both post-treatment visits. At 4–6 years post-treatment, fine wood cover was on average 1.6 times higher in treated plots ($p = 0.001$) and bare ground cover was on average 2.4 times higher in treated plots ($p < 0.001$). Forest floor depth varied with time but not treatment, while coarse wood cover did not vary with either time or treatment.

3.2. Understory cover

Native plants dominated the overall plant cover in this study, comprising 98% of understory cover with known nativity status. As a whole, native cover reacted positively to treatment (Fig. 2; Table 3). Native cover was marginally higher in treated compared to untreated plots even before thinning ($p = 0.098$), which was unexpected since untreated units were selected to be similar to paired treated units. Native cover was similar in treated and untreated plots at 1–2 years post-treatment ($p = 0.689$). After 4–6 years post-treatment, native cover was 1.7 times higher in treated plots: on average, 24.1% cover occurred in treated versus 14.6% cover in untreated plots ($p < 0.001$).

Different growth forms of native plants responded differently to treatment in terms of cover (Fig. 2; Table 3). Before treatment, native shrub cover was 1.3 times higher in treated versus untreated plots ($p = 0.027$); this drove the marginal pre-treatment imbalance in native cover described above. After mechanical treatment, native shrub cover declined in treated plots such that cover was lower in treated plots 1–2 years after treatment ($p = 0.031$) due to reduced cover of the ubiquitous shrub common juniper. However, shrub cover rebounded and was similar between treatments at 4–6 years post-treatment ($p = 0.187$). Native graminoid cover was similar in treated and untreated plots before thinning ($p = 0.639$) and at 1–2 years post-treatment ($p = 0.187$). By 4–6 years after thinning, native graminoid cover was 2.1 times higher ($p < 0.001$) in treated than untreated plots. The treatment by time-since-treatment interaction was only marginally significant for native forb cover, suggesting differences between treatments were consistent across all sampling periods, even though cover appeared to be much higher in treated than untreated plots at 4–6 years post-treatment but comparable pre-treatment and at 1–2 years post-treatment.

Treatment-driven changes in cover of native plants with different life strategies varied (Fig. 2; Table 3). Short-lived natives made up a miniscule part of the cover in our plots (<1% cover in any plot), and the interaction between treatment and time-since-treatment was only marginally significant. Native vegetatively-spreading plants had roughly equal cover in treated and untreated plots prior to treatment and at 1–2 years post-treatment ($p = 0.524$ and $p = 0.645$, respectively), but cover was 2.5 times higher in treated than untreated plots at 4–6 years post-treatment ($p = 0.001$). Like short-lived plants, vegetatively-spreading plants were not abundant in general, averaging 1.1% cover in untreated plots and 2.7% cover in treated at 4–6 years post-treatment.

The other life strategy groups, native long-lived plants and native non-vegetatively spreading plants, made up the majority of plant cover in this study and shared similar patterns through time (Fig. 2; Table 3). Long-lived plants had marginally higher cover in treated that untreated plots before treatment ($p = 0.096$). Non-vegetatively spreading plants had 1.3-fold greater cover in treated than untreated plots prior to treatment ($p < 0.001$), again likely due to the pre-thinning prevalence of shrubs – most of which are non-vegetatively spreading – in treated plots. Both long-lived and non-vegetatively spreading plants had similar cover in treated and untreated plots 1–2 years after treatment, then had 1.6 and 1.4 times greater cover respectively in treated versus untreated plots at 4–6 years after restoration ($p < 0.001$ and $p = 0.001$, respectively).

The mean cover of non-native plants was minimal at all visits, but was 3.1 times higher in treated than untreated plots at the second post-treatment visit. Prior to thinning and 1–2 years post-treatment, non-native cover was comparable in treated and untreated plots (Fig. 2; Table 3). At 4–6 years post-treatment, non-native cover averaged 0.5% in treated and 0.2% in untreated plots ($p = 0.001$). Despite imperfect fit in the non-native species model, the low estimates of non-native cover are reasonable given that 92.2% of the non-native dataset was composed of zeros, and only 6 out of 441 plot visits over the whole study detected non-native cover greater than 5%. In 5 of these 6 plot visits, cheatgrass (*Bromus tectorum)* was the primary source of non-native cover, in the other, it was smooth brome (*Bromus inermis)*. Most plots with high non-native cover were found at Estes Valley or Heil Valley Ranch, the latter of which is a county open space with high human traffic.

3.3. Understory richness

Native species richness was slightly elevated in treated plots compared to untreated plots after restoration treatment, but not before (Fig. 3; Table 3). Before thinning, native richness was similar in treated and untreated plots ($p = 0.641$). At both 1–2 and 4–6 years post-treatment, native richness was 1.1 times higher in treated plots than untreated plots ($p = 0.019$ and 0.018, respectively). At 4–6 years post-treatment, treated plots averaged 33.1 native species while untreated plots averaged 28.9. Treatments favored many common native species

Table 2
GLMM results for growing environment variables. Model means (and 95% confidence intervals) of treatment metrics, 1–2 years before, 1–2 years after, and 4–6 years after restoration treatments in dry conifer forests of the Colorado Front Range for 78 treated and 77 untreated plots. Significant ($\alpha = 0.050$) p-values are shown in bold for the Treatment (**Tr**), Time-since-treatment (**Tst**), and interaction (**Tr × Tst**) terms. For variables where the treatment by time interaction was significant, pairwise comparisons between treatments were evaluated using estimated marginal means; within sampling periods, values sharing letters were not statistically different.

	1–2 yrs Pre		1–2 yrs Post		4–6 yrs Post		p- values		
	Untreated	Treated	Untreated	Treated	Untreated	Treated	Tr	Tst	Tr × Tst
Basal area (m^2/ha)	23.26[a] (18.1, 29.9)	20.5[a] (15.9, 26.3)	23.4[a] (18.2, 30.1)	10.7[b] (8.3, 13.8)	23.4[a] (18.2, 30.1)	10.6[b] (8.2, 13.6)	0.491	0.998	**< 0.001**
Forest floor depth (cm)	5.6 (4.9, 6.4)	5.3 (4.6, 6)	5.9 (5.2, 6.7)	5.2 (4.6, 5.9)	4.8 (4.3, 6.7)	4.1 (3.6, 4.7)	0.414	**0.004**	0.485
Bare ground (% cover)	4.8[a] (3.4, 6.9)	4.6[a] (3.2, 6.6)	3.8[a] (2.6, 5.5)	8.0[b] (5.7, 11.1)	4.4[a] (3.1, 5.5)	10.0[b] (7.2, 13.7)	0.728	0.216	**< 0.001**
Fine wood (% cover)	11.2[a] (8.9, 13.9)	11.1[a] (8.8, 13.8)	12.3[a] (9.8, 15.3)	22.1[b] (18.3, 26.5)	12.0[a] (9.6, 15.3)	17.5[b] (14.3, 21.3)	0.937	0.626	**< 0.001**
Coarse wood (% cover)	1.6 (1.2, 2.1)	1.8 (1.4, 2.3)	1.7 (1.3, 2.2)	2.3 (1.8, 3)	1.5 (1.1, 2.2)	2.2 (1.8, 2.9)	0.493	0.390	0.143

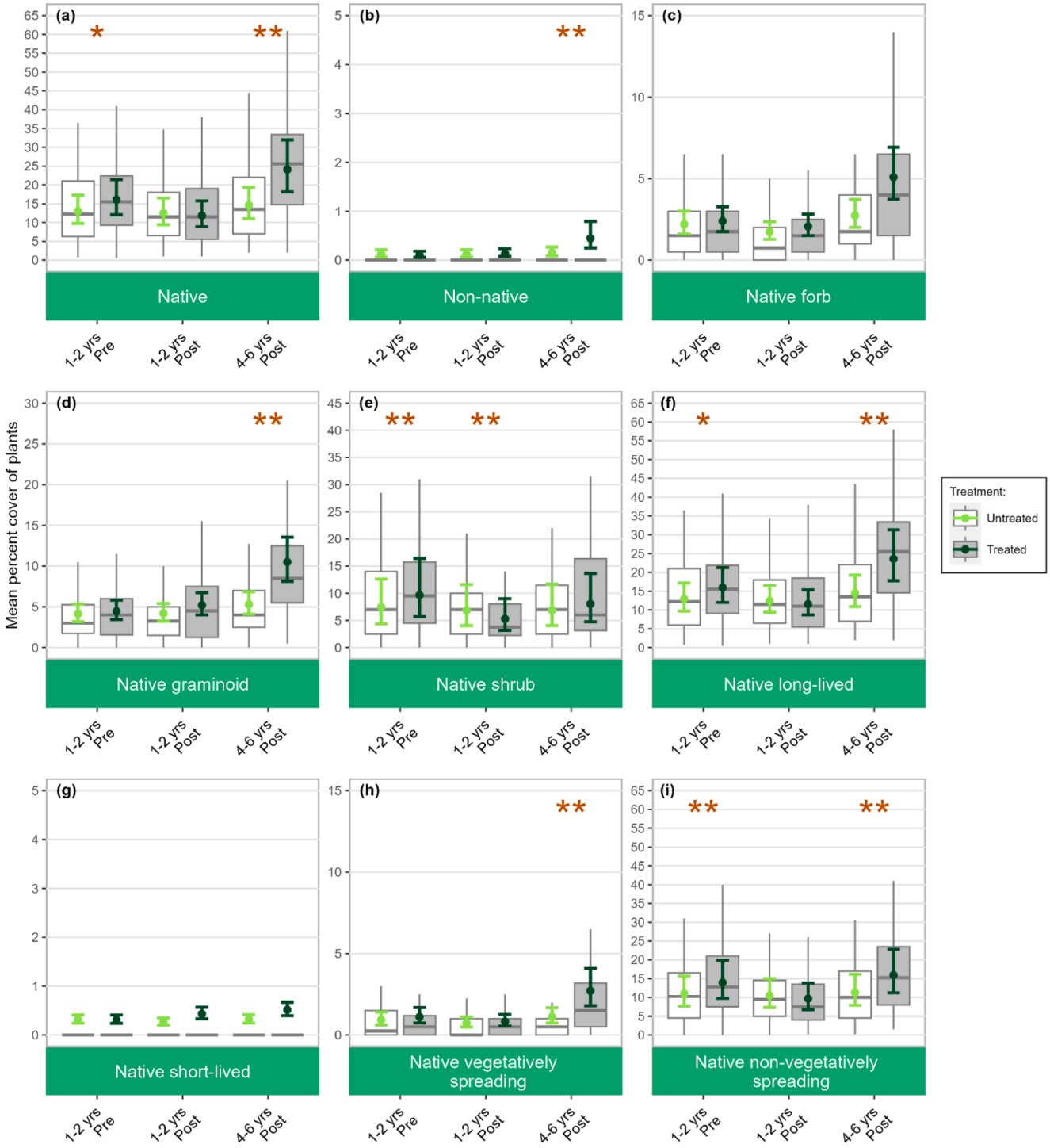

Fig. 2. Raw data (boxplots) and GLMM means and 95% confidence intervals (points and whiskers) for understory plant cover variables at 1–2 years before, 1–2 years after, and 4–6 years after restoration thinning treatments in dry conifer forests of the Colorado Front Range. For variables where the treatment by time interaction was significant, pairwise comparisons between treatments were evaluated using estimated marginal means. Orange stars indicate significant (**, $\alpha = 0.050$) or marginal (*, $\alpha = 0.100$) pairwise differences between treated and untreated plots for that sampling period. Boxplots do not include outliers, defined as values more than 1.5 times larger or smaller than the interquartile range.

including pygmyflower rockjasmine (*Androsace septentrionalis)*, bluebell bellflower *(Campanula rotundifolia)*, and eastern pasqueflower (*Pulsatilla patens)*, all of which were found in far more treated than untreated plots, despite being in similar numbers of plots before mechanical treatment.

Out of the three growth forms, treatment stimulated richness of native forbs and graminoids (Fig. 3; Table 3). Native forb richness was similar in treated versus untreated plots before thinning ($p = 0.670$), but was 1.2 times higher in treated plots at 1–2 years post-treatment ($p =$

Table 3
GLMM p-values of understory plant variables. Data were collected 1–2 years before, 1–2 years after, and 4–6 years after restoration treatments in dry conifer forests of the Colorado Front Range, in both treated and untreated plots. Significant ($\alpha = 0.050$) p-values are shown in bold for Treatment (**Tr**), Time-since-treatment (**Tst**) and their interaction (**Tr × Tst**).

Metric	Tr	Tst	Tr × Tst
Cover (%)			
Native	0.120	0.407	**0.008**
Non-native	0.642	0.708	**0.021**
Native forb	0.692	**0.036**	0.072
Native graminoid	0.646	0.127	**0.008**
Native shrub	**0.044**	0.738	**0.008**
Native long-lived	0.118	0.417	**0.007**
Native short-lived	0.955	0.504	0.076
Native vegetatively spreading	0.534	0.095	**0.009**
Native non-vegetatively spreading	**0.038**	0.756	**0.011**
Richness (species 406 m^2)			
Native	0.648	**0.001**	**0.007**
Non-native	0.826	**0.004**	**<0.001**
Native forb	0.676	**<0.001**	**0.012**
Native graminoid	0.546	0.116	**0.008**
Native shrub	0.982	0.279	0.832
Native long-lived	0.584	**0.002**	**0.034**
Native short-lived	0.806	**0.005**	**0.001**
Native vegetatively spreading	0.614	**0.002**	0.711
Native non-vegetatively spreading	0.519	**0.002**	**0.001**

0.023), and marginally higher in treated plots at 4–6 years post-treatment ($p = 0.054$). Native graminoid richness was comparable in treated versus untreated plots before thinning ($p = 0.536$), but was 1.1 times higher in treated plots at 1–2 years post-treatment ($p = 0.042$), and 1.2 times higher in treated plots at 4–6 years post-treatment ($p = 0.001$). Native shrub richness, meanwhile, did not exhibit a response to treatment, averaging ~ 4 species across all treatments and sampling periods.

Changes in richness of native plants with different life strategies varied (Fig. 3; Table 3). For long-lived, short-lived, and non-vegetatively spreading plants richness values were similar in treated and untreated plots prior to treatment. Non-vegetatively spreading plants had 1.1-fold higher richness in treated plots at 1–2 years post-treatment, and retained this increase at 4–6 years post-treatment ($p = 0.001$ and $p < 0.001$, respectively). Richness of short-lived plants was highest at the first post-treatment sampling period: treated plots had on average 2.4 times higher short-lived plant richness at 1–2 years post-treatment ($p < 0.001$), and 1.5 times greater richness in treated plots than untreated plots at 4–6 years post-treatment ($p = 0.023$). Long-lived species had similar richness in treated versus untreated plots at 1–2 years post treatment ($p = 0.120$) and an average of 1.1 times greater richness in treated plots at 4–6 years post-treatment ($p = 0.033$). Vegetatively spreading plant richness did not exhibit a response to treatment, but did vary slightly with time.

Non-native species richness responded positively to treatment. (Fig. 3; Table 3). Prior to treatment, treated and untreated plots had similar non-native richness ($p = 0.823$). Treated plots had 5.3 times higher non-native richness than untreated plots at 1–2 years post-treatment, and 4.4 times higher non-native richness at 4–6 years post-treatment ($p < 0.001$ and $p < 0.001$, respectively). While there were more non-native species in treated plots post-treatment, the average number of species was fairly low. Treated plots averaged 2.9 non-native species at 4–6 years post-treatment, which represented 8.1% of total richness at the average treated plot. Common dandelion (*Taraxacum officinale)* and Canada thistle (*Cirsium arvense)* were the non-native species whose presence in treated plots increased most substantially through time.

3.4. Native understory cover and richness along environmental gradients

BRTs identified overstory basal area as the most influential predictor of native understory cover in treated plots 4–6 years post-treatment (33% relative importance (RI)), and topographic position index and final spring CWD z-score as somewhat important (12% and 11% RI, respectively; Fig. 4). All other variables were much less influential (≤ 10% RI). The relationship between basal area and native understory cover showed strong non-linear thresholds. Cover predictions were high (~29% cover) under relatively open overstories with basal areas lower than ~10 m^2 ha^{-1}. At basal areas over ~10 m^2 ha^{-1}, cover predictions decreased steadily until leveling off to ~20% cover at basal areas over ~20 m^2 ha^{-1}(Fig. 5). TPI and native understory cover had a negative relationship, with the highest cover predictions at low TPI (i.e., relatively low areas of topography like a drainage or valley; Fig. 5). Our model predictions suggested a positive relationship between final spring CWD z-score and native understory cover, such that cover was predicted to be lower following cooler-wetter spring conditions (i.e., final spring CWD z-scores < 0) and higher following warmer-drier spring conditions (i.e., final spring CWD z-scores > 0). For the native understory cover BRT, the R-squared value was 0.14 in the cross-validation, and 0.47 using the full observed dataset.

Final spring CWD z-score and overstory basal area were the most influential predictors of native richness, with RI values of 28% and 20% respectively (Fig. 4). Richness was also influenced by TPI and fine wood cover (17% and 14% RI, respectively; Fig. 4). Final spring CWD z-score showed the opposite trend in prediction for richness as it did for cover. Plots with low z-scores (< 0, cooler-wetter spring conditions) had high predicted richness values (~35 species), while plots with high z-scores (> 0) had lower predicted richness (~31 species). The relationship between basal area and richness was similar to cover. Plots with low basal areas (< ~13 m^2 ha^{-1}) had high predicted richness values (~34 species), while plots with high basal areas (> ~20 m^2 ha^{-1}) had low predicted richness (~31 species). The relationship between TPI and richness was also similar to that with cover: the highest richness values were predicted in valley bottoms (i.e., lowest TPIs). Fine wood cover was not important for cover prediction, but had a mild effect on richness; high fine wood cover predicted lower understory richness. For the native richness BRT, R-squared values were 0.20 in cross-validation and 0.51 for the full observed dataset.

4. Discussion

4.1. Understory cover and richness

Maintaining and enhancing biodiversity has become a key concern in the global context of widespread habitat degradation and loss (Carey, 2003; Leclère et al., 2020; Rands et al., 2010). Restoration treatments in dry conifer forests of the western US can support biodiversity by improving ecosystem resilience to future disturbance and by reversing declines in native species abundance and richness due to changing land-use, altered disturbance regimes, or non-native species invasions (Noss et al., 2006; Palmer et al., 2016). Indeed, in this study in the dry conifer forests of the Colorado Front Range, we show that native understory plants overall and within many functional groups benefited from mechanical restoration treatments. These broad benefits were found across numerous sites, suggesting that our results may extend to other areas of this and similar dry conifer landscapes.

The benefits of mechanical restoration for native understory richness were evident just 1–2 years after treatment, and these early gains were maintained as of 4–6 years post-treatment (Fig. 3; Table 3). The 1–2 year post-treatment increase we documented contrasts with other studies that found negative or no changes (Briggs et al., 2017; Collins et al., 2007), while our long-term result is mirrored by other studies in dry conifer forests measuring richness at 4 years or more after treatment (Carey and Wilson, 2001; Kane et al., 2010). Moreover, native functional

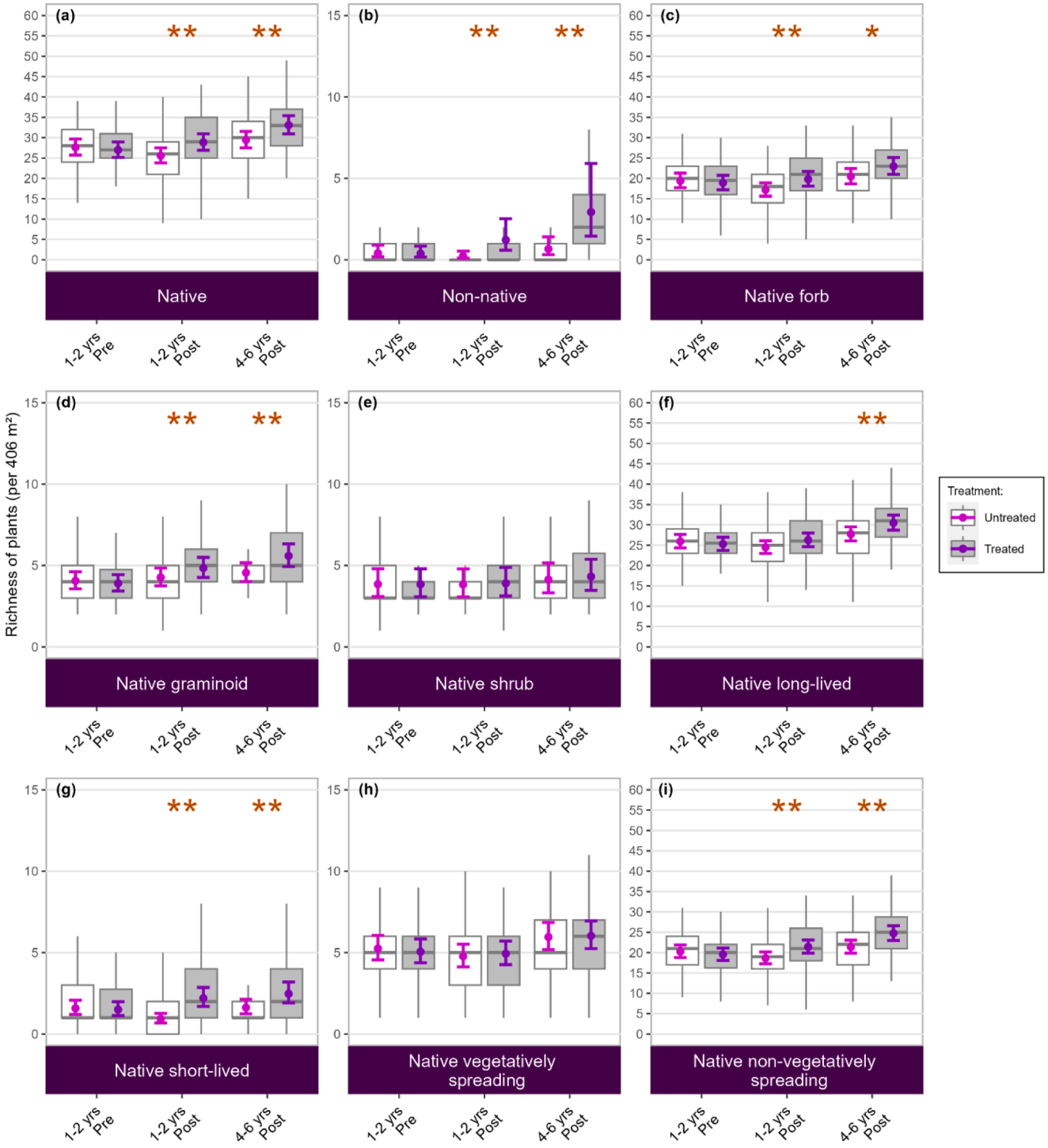

Fig. 3. Raw data (boxplots) and GLMM means and 95% confidence intervals (poimts and whiskers) for understory plant richness variables at 1–2 years before, 1–2 years after, and 4–6 years after restoration thinning treatments in dry conifer forests of the Colorado Front Range. For variables where the treatment by time interaction was significant, pairwise comparisons between treatments were evaluated using estimated marginal means. Orange stars indicate significant (**, $\alpha = 0.050$) or marginal (*, $\alpha = 0.100$) pairwise differences between treated and untreated plots for that sampling period. Boxplots do not include outliers, defined as values more than 1.5 times larger or smaller than the interquartile range.

groups that increased in richness at 1–2 years post-treatment usually retained these gains. This included some of the most common groups of plants in our study, such as: graminoids, long-lived and non-vegetatively spreading species, as well as less common plant groups like short-lived species. Native shrubs and vegetatively spreading species never showed heightened richness after treatment, however. In part this may be because these two groups are less diverse in this landscape and therefore there are fewer species available to recruit.

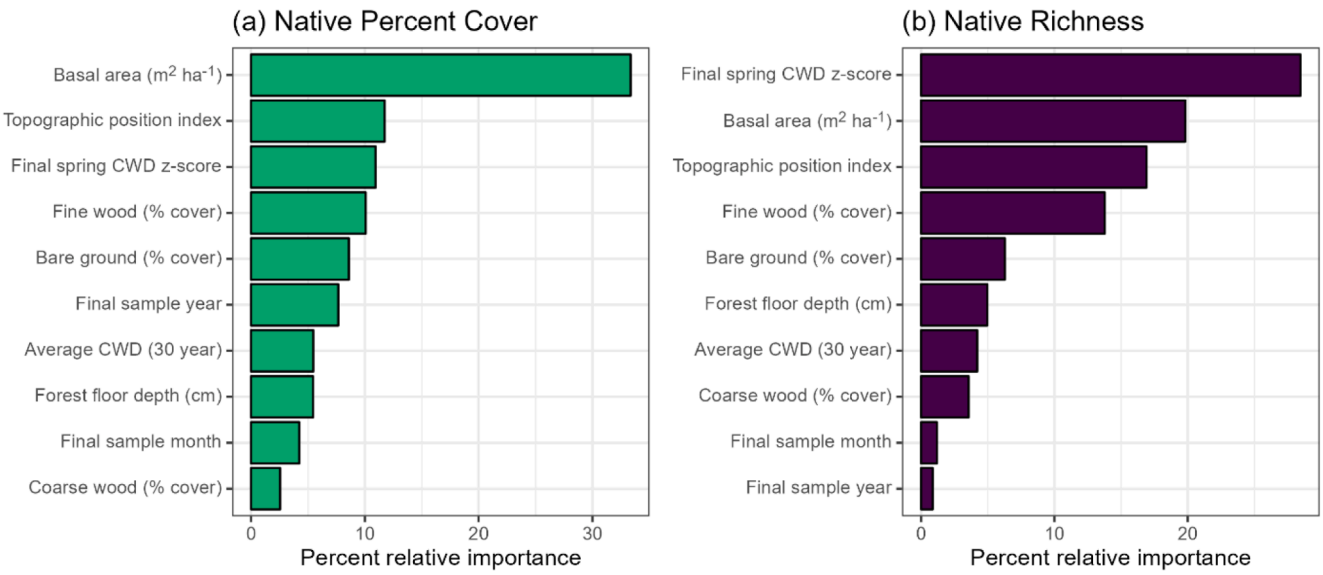

Fig. 4. Variable importance plots from boosted regression trees used to assess biotic and abiotic factors influencing native plant cover (a) and native plant richness (b). Relative importance values give the relative effect of each variable in predicting plant community responses at 4–6 years after restoration treatments in dry conifer forests of the Colorado Front Range at 91 treated plots.

While native richness was elevated in treated plots by the end of this study, the effect size was modest; treated plots had on average ~ 3 more species (12% higher richness) than untreated plots. This may be related to the overall influence of treatments on the conditions necessary for new plant establishment.. Generally speaking, our treatments minimally disturbed the forest floor: they did not alter forest floor depth or coarse wood cover, and only very mildly affected bare ground exposure, which is generally considered a prerequisite for establishment (Collins et al., 2007; Kane et al., 2010; Metlen and Fiedler, 2006). Furthermore, while overstory basal area was reduced by about half on average in our treated plots, overstory heterogeneity is also required to create a wide variety of niches to support more species (MacArthur and MacArthur, 1961; Naumburg and DeWald, 1999; Watt, 1947). A series of studies in the Colorado Front Range, which investigated some of the same sites in this study, found that restoration treatments increased overstory heterogeneity for at least some metrics and scales (Barrett et al., 2021; Briggs et al., 2017; Cannon et al., 2022, 2018), but it may be that the heterogeneity achieved was insufficient to strongly promote understory richness. Future exploration of whether greater overstory heterogeneity in treated areas is associated with higher understory species richness would provide insight into whether restoring this aspect of forest structure matters for understory diversity in modern, altered forests.

Native understory cover responded more slowly to mechanical restoration treatments than did richness, but by 4–6 years post-treatment, was invigorated in total and for about half of the functional groups we investigated (Fig. 2; Table 3). Somewhat surprisingly, given that heavy machinery was operating in many of the treated plots, native plants overall and within most functional groups had similar cover in untreated and treated plots 1–2 years after treatment, suggesting it did not significantly damage them. After 4–6 years, graminoids had approximately twice the cover in treated as untreated plots. Several studies measuring 4 + years post-thinning also found that mechanical treatment fostered heightened cover of graminoids (Fornwalt et al., 2017; Griffis et al., 2001; Lochhead and Comeau, 2012; Siegel and DeSante, 2003). Additionally, we examined trends by vegetative spreading status as treatments sometimes favor vegetatively spreading species (Wolk and Rocca, 2009). While vegetatively spreading species were still very uncommon on the landscape, they did have the greatest relative increase in cover of any native group, at 2.5 times the cover in treated plots at 4–6 years post-treatment. Vegetatively spreading plants may have had the edge in growth compared to the majority of native plants in our study – mainly bunchgrasses and small forbs – which would likely have to produce new individuals to greatly increase cover. The only native group which clearly did not improve in cover was the shrubs. However, this may be seen as a benefit for fire resilience as treatments often seek to reduce ladder fuels like shrubs (Churchill et al., 2013).

In this study, gains in native species were accompanied by gains in non-native richness and cover in treated plots by 4–6 years after treatment (Figs. 2 and 3; Table 3). While restoration treatments are critically needed to increase dry conifer forest resilience to wildfire and other disturbances, preventing non-native species proliferation in the process is also a high priority (Collins et al. 2007; Schwilk et al. 2009; Jang et al. 2021). Monitoring in treated areas should continue for non-native species like cheatgrass (a prolific seeder) and Canada thistle (a strong vegetative spreader) which showed a clear affinity for treated areas. Canada thistle in particular was identified as concerning in other forest mechanical treatment studies in Colorado (Fornwalt et al., 2018, 2017; Miller and Seastedt, 2009; Wolk and Rocca, 2009).

4.2. *Native understory cover and richness along environmental gradients*

Exploration of the biotic and abiotic drivers of understory responses showed that native understory cover in treated areas 4–6 years post-treatment was strongly linked to basal area, with mild linkages to topography and climate (Figs. 4 and 5). As expected, treated plots with low basal areas had markedly greater native understory cover than those with high basal areas. Interestingly, a review of thinning and burning treatments in conifer forests noted that several studies identified a basal area of 20 m^2 ha^{-1} as the threshold below which treatments begin to have an effect on understory cover (Abella and Springer, 2015), and this is what we found as well. We also found a second threshold: basal areas lower than 10 m^2 ha^{-1} all predicted very high native cover, but caution should be used in interpreting the effect of very low basal areas since very few plots had such conditions. Low basal areas may be associated with greater plant cover as more light is available for photosynthesis. Below-ground resources, which may be even more limiting than light in dry forest environments such as our study area, may also be more available (Coomes and Grubb, 2000). For example, some studies have

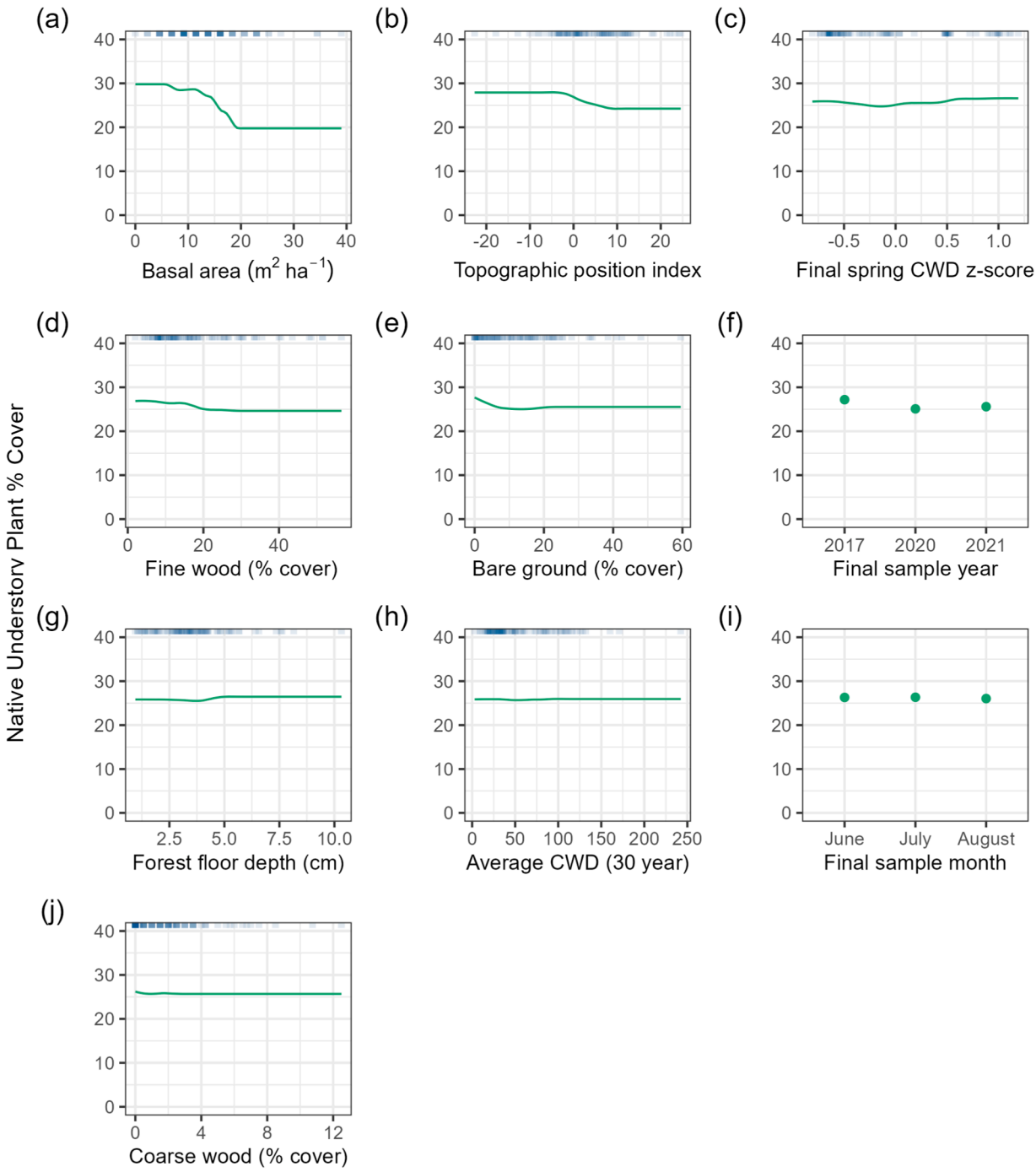

Fig. 5. Partial dependencies from boosted regression trees used to assess biotic and abiotic factors influencing native plant cover, showing individual relationships between cover and a single predictor after accounting for the average effect of the other predictors. Data were limited to longer-term (4–6 years post-treatment) effects of treatments in dry conifer forests of the Colorado Front Range at 91 treated plots. Each translucent blue mark at the top of each figure represents a single plot's value of the predictor. Darker areas of overlapping marks indicate a greater amount of data informing the percent cover BRT model.

found that areas of lower conifer density were associated with greater soil moisture (Zou et al., 2008) and that some methods of tree removal can increase plant-available nitrogen (Prescott, 2002; Rhoades et al., 2012). While treatments had a strong, albeit variable, impact on overstories as expected, treatment effects at the forest floor level were limited to mild increases in bare ground and fine wood. Furthermore, variation in these metrics was low, despite different treatment implementations (i.e., machinery versus chainsaws to fell trees, various woody debris handling methods) (Table 2). Given this, it is not surprising that forest floor variables were mostly unimportant in predicting native plant responses.

We originally expected that treated plots in warm-dry areas (high CWD or high TPI) would have low native understory cover after treatment due to heightened water stress. While TPI did negatively correlate with cover, this metric was of low importance compared to basal area, and average CWD was effectively uncorrelated. This may be because

plots in warm-dry (and cool-wet) locations have species assemblages that are well-suited to those conditions. Multivariate plant community analysis may help to determine if assemblages differ between warm-dry and cool-wet plots.

Final spring CWD z-score was also only somewhat influential for understory cover. Counterintuitively, predicted native cover was highest under the warmest and driest spring conditions. Notably, our sampling did not include any exceptionally warm and dry springs: the highest final spring CWD z-scores in our study years were only around one standard deviation away from the mean and therefore represent fairly mild differences. Therefore, it seems likely that relatively warm and dry spring conditions in the context of our study are more indicative of an earlier start to the growing season, rather than strong water stress. Growing seasons that started earlier may have given plants more time to grow prior to our sampling in mid-June through August.

In contrast to native understory cover responses, richness in treated

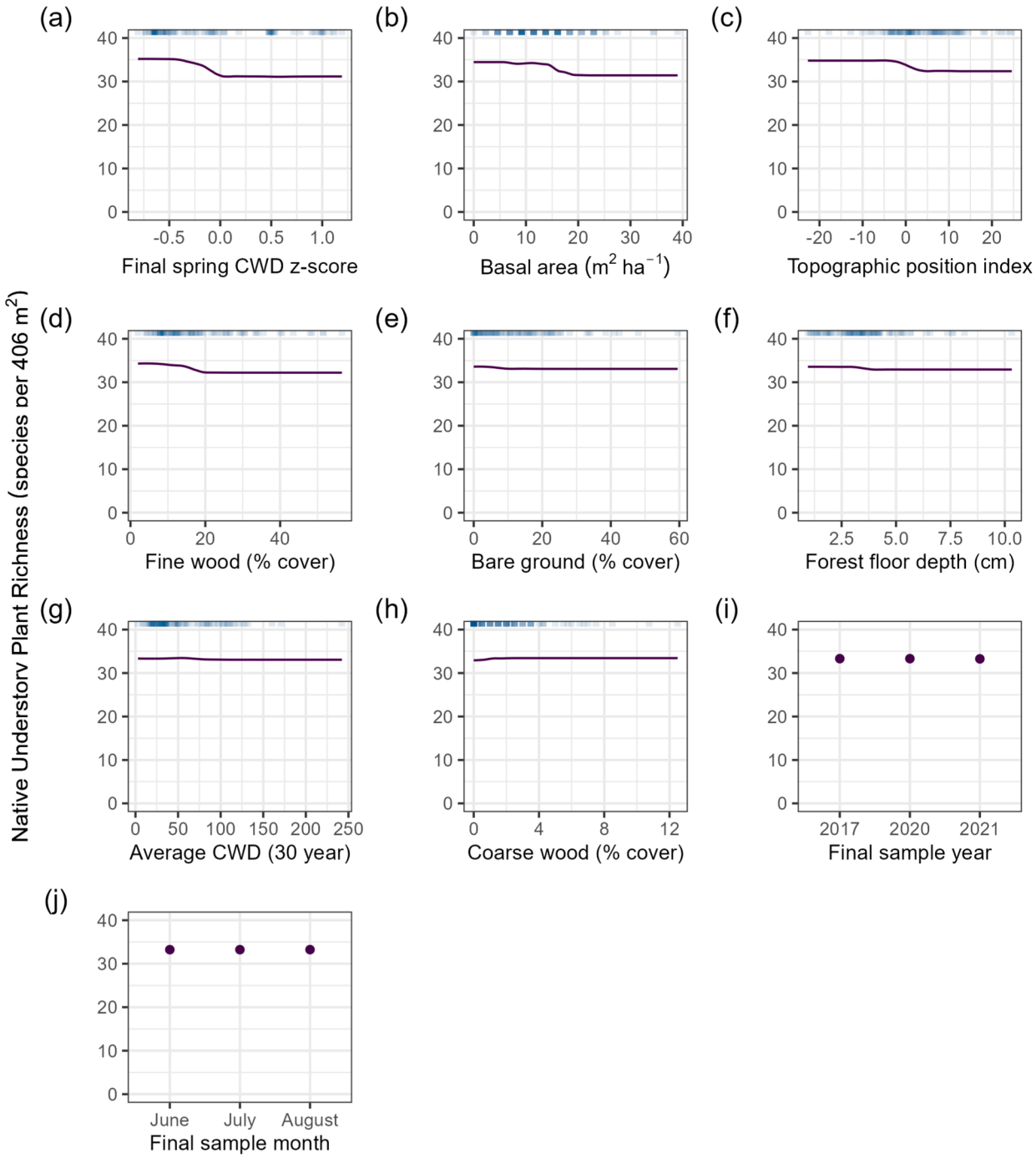

Fig. 6. Partial dependencies from boosted regression trees used to assess biotic and abiotic factors influencing native understory richness, showing individual relationships between richness and a single predictor after accounting for the average effect of the other predictors. Data were limited to longer-term (4–6 years post-treatment) effects in dry conifer forests of the Colorado Front Range at 91 treated plots. Each translucent blue mark at the top of each figure represents a single plot's value of the predictor. Darker areas of overlapping marks indicate a greater amount of data informing the richness BRT model.

plots at 4–6 years post-treatment was more strongly influenced by final spring CWD z-score than basal area (Figs. 4 and 6). As stated previously, spring conditions during our final sample years were never extreme, which makes it all the more interesting that final spring CWD z-score was the strongest predictor, implying that even small variations in spring conditions can affect native richness in treated areas. Relatively warm-dry springs in the 4–6 year post-treatment sampling year (positive final spring CWD z-score) were associated with lower richness predictions, as expected. While warmer-drier spring conditions might encourage earlier growth of established plants, they may not encourage survival of new germinants. For instance, species with small seeds, and therefore with less capacity to deal with water stress (Leishman and Westoby, 1994), may be less able to survive when temperatures are high and moisture is low. Low TPI values (low topographic areas) were also associated with high richness, but low average CWD values (cool-wet average conditions) were not. This may mean that while lower areas of topography can have lower temperature and greater humidity (Holden and Jolly, 2011), the more important characteristics of low areas may be lower wind exposure (Barry, 2008), or more diverse and abundant seed banks which allow more species to recruit (Ashton et al., 1998).

Basal area was the second most important predictor of native richness. Basal areas less than ~10 m^2 ha^{-1} produced the highest richness predictions, while dense stands at basal areas over ~20 m^2 ha^{-1} produced similar and low richness predictions. Greater richness at lower basal areas may be related to the relationship between overstory density and ranges of possible understory plant life strategies. Laughlin et al (2011) observed that modern dense forests with lower light, soil moisture, and nutrient availability restricted understory communities to species with high shade tolerance and conservative strategies to gaining and maintaining scarcer resources. They also found that understories measured between 1912–1938 that grew beneath more open overstories allowed for a wider array of life strategies reflected by a greater variety of leaf, seed, stem, and root characteristics. Thus, lower basal areas may encourage understory richness, at least when such areas area a component of overall heterogeneous overstory conditions.

4.3. Management implications

This study demonstrates that mechanical forest restoration treatments stimulated native understory plant cover and richness in dry conifer forests of the Colorado Front Range. The highest native cover and richness values were associated with overstory basal areas approximating the range of historical mean basal area for this region (Figs. 4–6). These findings support a core principle of ecological restoration: that native species are most likely to thrive when the conditions that shaped their evolution are restored (Palmer et al., 2016; Stephens et al., 2021). However, we do caution against interpreting this as evidence that there is a "best" residual basal area level; a key practice of ecological forest restoration in dry conifer forests is promoting heterogeneity in overstories (Addington et al., 2018). This study also helps address two practical questions for natural resource managers. Do "side effects" of mechanical treatments, like woody material inputs, bare ground exposure, or changes in forest floor depth, have a strong impact on native cover or richness? Despite varying treatment implementations, our treatments had little effect on such variables (Tables 1-2). Moreover, the changes that did occur had relatively little influence on the understory (Figs. 4–6). Together these results hint that understory plants may respond well to a variety of implementation strategies. Another concern when applying treatments across diverse landscapes is whether generally warm-dry areas like south-facing or low-elevation sites have different understory responses to treatment than cool-moist sites. As far as this study could determine, average CWD had no major impact on native cover or native richness in treated areas (Figs. 4–6); instead mechanical treatments consistently boosted both cover and richness across a range of conditions.

While restoration treatments benefited native understories as a whole, potential side effects of understory changes on other aspects of the ecosystem should also be considered. Increases in non-native species are a common side effect of disturbances, including restoration treatments. However, thinning restorations stimulate non-native species far less than the high-severity fires they are designed to mitigate against (Fornwalt et al., 2010; Griffis et al., 2001). Among restoration methods, mechanical treatment is often the least disruptive and provokes the smallest non-native species responses (Abella and Springer, 2015; McIver et al., 2013). Understory plants also provide crucial food and habitat structure for a variety of organisms (Tews et al., 2004). Treatments are likely to be mutually beneficial for understory plants and pollinating insects: flourishing understories in treated areas have been linked with higher bee or butterfly abundance or diversity, which are likely to translate to better pollination services (Davies, 2022; Waltz and Covington, 2004). Greater understory abundance or richness after treatments have been associated with greater overall bird and small mammal abundance or richness, although individual species may or may not benefit, so it is important to be aware of local wildlife species assemblages when planning treatments (Carey and Wilson, 2001; Latif et al., 2020; Siegel and DeSante, 2003).

It is unclear how long elevated cover and richness in treated areas might last, which may impact how frequently managers choose to treat stands. In the Colorado Front Range, studies have not extended past nine years (Briggs et al., 2017; Fornwalt et al., 2017; Wolk and Rocca, 2009). However, longer-term studies conducted elsewhere have found inconsistent results – a 12-year study in Arizona ponderosa pine forests found sustained higher herbaceous biomass in treated forest until a major drought event at 10 years into the study (Moore et al., 2006), while a 23-year study in Montana ponderosa pine and Douglas-fir forests found that richness and cover peaked at 5 years post-treatment then gradually fell back to pre-treatment levels (Jang et al., 2021). The current trajectory in our study shows heightened non-native species richness and cover, but the aforementioned Montana study found that non-native species cover also dissipated with time. Uncertain long-term trends emphasize the need to continue monitoring understory plants to further understand overall responses and functional group trajectories. Varying long-term results also underscore the value of adaptive management processes, like those employed by the collaboratives involved in this study, that conduct long-term monitoring to help inform future restoration treatments. Through continued monitoring, research, and refinement, ecological forest restoration has the potential to increase resilience and biodiversity in a world of climate change, intensifying disturbances, and increased human habitation in dry conifer forests (Hagmann et al., 2021; Radeloff et al., 2018; Suding, 2011; Warren et al., 2011).

CRediT authorship contribution statement

Arièl B. Demarest: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Visualization, Writing – original draft, Writing – review & editing. **Paula J. Fornwalt:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Brett H. Wolk:** Conceptualization, Methodology, Investigation, Resources, Project administration, Funding acquisition. **Kyle C. Rodman:** Methodology, Software, Formal analysis, Writing – review & editing. **Miranda D. Redmond:** Conceptualization, Methodology, Software, Writing – review & editing, Supervision.

Declaration of Competing Interest

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

Data availability

Data for this study are publicly available through the Forest Service Research Data Archive (Demarest et al., 2023).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121322.

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