THESIS

HOW DO ECOLOGICAL RESTORATION TREATMENTS AFFECT UNDERSTORY PLANT COMMUNITIES IN DRY CONIFER FORESTS OF THE COLORADO FRONT RANGE?

Submitted by

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ABSTRACT

HOW DO ECOLOGICAL RESTORATION TREATMENTS AFFECT UNDERSTORY PLANT COMMUNITIES IN DRY CONIFER FORESTS OF THE COLORADO FRONT RANGE?

Ecological restoration efforts are progressing in dry conifer forests across the western United States to increase resilience to fire and other disturbances. While such treatments primarily aim to create overstory change, impacts beyond the canopy should also be considered – such as effects on understory plants. Several studies have investigated outcomes of ecological restoration thinning treatments for understory plants, but few of these have examined effects across a landscape and at a time interval long enough for plants to potentially adjust to the disturbance. Additionally, none have investigated how specific aspects of treatment and local climate might interact to modify understory responses. In this study, we investigated the effects of ecological restoration thinning treatments on understory plant communities in dry conifer forests of the Colorado Front Range using a Before/After/Control/Impact study design. We collected data at 1-2 years pre-treatment, 1-2 years post-treatment, and 4-6 years post-treatment in 156 plots distributed across 8 sites, encompassing 15 treatment units and 15 nearby untreated areas. We found 1.6 times higher native understory plant cover and 1.1 times higher richness in treated compared untreated plots at 4-6 years after treatment. 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 community. Short- and long-lived, forb and graminoid, and vegetatively spreading and non-vegetatively spreading native plants all grew in cover. Both lifespans, forb, and non-vegetatively spreading native plants had heightened richness. Introduced plants showed 2.3 times higher cover and 3.9 times higher richness in treated plots compared to untreated, but were still present at very low levels. Greater native plant cover and richness were associated with lower basal areas that more closely resemble historical norms for the landscape. Thirty year average climatic water deficit (CWD) was not as strong of a predictor of native cover or richness as was a short-term relative measure, final spring CWD z-score, which describes how different the spring climatic conditions of the sampling year were from average conditions. Overall, the broad longer-term benefits to the native understory plant community that were found for numerous sites across the Colorado Front Range suggest that these results may generalizable to elsewhere on this and similar landscapes.

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TABLE OF CONTENTS

Chapter 1: How do ecological restoration treatments affect understory plant communities in dry conifer forests of the Colorado Front Range?

1. Introduction

In the shadow of the ongoing Anthropocene mass extinction, maintaining biodiversity has become a key challenge for natural resource managers worldwide (Noss et al. 1995; Rands et al. 2010; Braje and Erlandson 2013). In forest ecosystems, understory plants are important targets for biodiversity conservation because they often make up the overwhelming majority of plant diversity (Gilliam 2007; Abella and Springer 2015). Understory plants also form the foundation of forest food webs, provide habitat for wildlife, help protect soils from erosion, and alter disturbance patterns (Allen et al. 2002; Schwilk et al. 2009; Zuazo and Pleguezuelo 2009). Forest overstories compete with understory plants, and consequently, alterations in overstories often affect understory dynamics (Jameson 1967; Riegel et al. 1992; Callaway 1995; Coomes and Grubb 2000; Gilliam 2007; Laughlin et al. 2011a).

Overstories in many dry conifer forests of the western United States (US) have experienced considerable alterations since Euro-American settlement, due to c. 100 years of fire exclusion, logging, mining, and livestock grazing (Covington and Moore 1994; Keane et al. 2002; Naficy et al. 2010; Collins et al. 2011; Battaglia et al. 2018; Rodman et al. 2019). Historical fire regimes in dry conifer forests were generally characterized by low- or mixed-severity fire events burning at relatively frequent intervals on a scale of years to decades (Brown et al. 1999; Veblen et al. 2000; Schoennagel and Nelson 2011; Brown et al. 2015). An overall patchy distribution of fires and fire severities created heterogenous mosaics of vegetation (Brown and Sieg 1996; Swetnam and Baisan 1996; Yocom-Kent et al. 2015; Safford and Stevens 2017; Addington et al. 2018). Without periodic fires to consume fuels and thin out small trees, forests in some areas have accumulated high fuel loads beneath unusually dense, homogenous canopies (Covington and Moore 1994; Schwilk et al. 2009; Knapp et al. 2013; Battaglia et al. 2018). These overstory alterations have likely also affected understory communities. It is well known that increasing tree density reduces light, moisture, and nutrients available to understory plants, and there is also evidence to suggest that areas of uncharacteristically dense forest result diminish soil seed banks, understory abundance, and flowering vigor (Moir 1966; Coomes and Grubb 2000; Lindh 2005; Abella and Springer 2008; Laughlin et al. 2011a; Knapp et al. 2013). Increased forest homogeneity and curtailed disturbance regimes could also reduce or change the variety of habitat niches, and therefore, reduce understory diversity and alter community composition (Gildar et al. 2004; Randall Hughes et al. 2007; Burkle et al. 2015). Additionally, alterations in dry conifer forest overstories in some areas, along with rising mean annual temperatures and longer fire seasons associated with climate change, have combined to create increasingly large and severe wildfires in the past several decades (NOAA 2019; Singleton et al. 2019; Hagmann et al. 2021; Coop et al. 2022).

In response to the paired threats of increasing fire risk and uncharacteristic ecological changes, groups of stakeholders at local and national levels have taken action by implementing forest restoration treatments. Forest restoration treatments attempt to mitigate the risk of high-severity fire by reducing fuels, and to restore ecosystem function by emulating historical stand structures and reintroducing some level of disturbance (Churchill et al. 2013; Underhill et al. 2014; Safford and Stevens 2017). However, while such treatments are occurring at broad spatial scales throughout the western US, we still have limited understanding of how restoration treatments alter ecological properties and processes beyond the reduction of fire risk. A more comprehensive understanding is critical in evaluating the effectiveness of these treatments in accomplishing the full suite of restoration goals, including improving understory abundance and diversity. Given the essential roles that understory communities fulfill in forest ecosystems, restoration of dry conifer forest overstories may help improve ecosystem function and bolster biodiversity by benefitting understory plants (Abella and Springer 2015).

Though many studies have investigated how understory plants respond to thinning treatments in dry conifer forests in the western US, results have been mixed with respect to the direction, magnitude, and duration of effect (Schwilk et al. 2009; Abella and Springer 2015; Willms et al. 2017 and references therein). Studies measuring one to three years after treatment often found reductions in measures of overall plant abundance and variable changes in diversity (Metlen and Fiedler 2006; Collins et al. 2007; Wayman and North 2007; Dodson et al. 2008). This may be due to sudden alterations in growing conditions or plant damage during thinning operations. In contrast, at four or more years post-treatment, understory abundance and diversity (which was less commonly measured) were often elevated relative to control plots or pre-treatment baselines (Carey and Wilson 2001; Siegel and DeSante 2003; Kane et al. 2010; Lochhead and Comeau 2012; Fornwalt et al. 2017). Since plants of different functional groups (e.g., growth forms, lifespans, nativities, and spreading mechanisms) may have differing impacts on wildlife, fire behavior, native plant conservation, and understory recovery patterns, it is also valuable to analyze responses of different functional groups (Carey and Wilson 2001; Korb et al. 2003; Latif et al. 2020; Ibáñez et al. 2021). Though longer-term effects (i.e., 4+ years) of treatment have rarely been evaluated for different functional groups, forb and graminoid cover often increased post-treatment, and where native plants benefited from treatment, non-native plants usually did as well (Carey and Wilson 2001; Kane et al. 2010; Fornwalt et al. 2017; Jang et al. 2021).

Though forest restoration treatments often span large, heterogeneous landscapes, little is known about how biologically meaningful environmental gradients affect understories in treated areas (Kane et al. 2010; Fornwalt et al. 2017; Jang et al. 2021). Climatic water deficit (CWD), a holistic measure of plant water stress, has been shown to be strongly correlated with tree growth and distribution (Stephenson 1990; Lutz et al. 2010; Redmond et al. 2017), but few studies have associated CWD with understory plant dynamics (Crimmins et al. 2011; Dilts et al. 2015). CWD incorporates abiotic factors like temperature, precipitation, soil available water, hill slope, and aspect. The inclusion of topographic variables is particularly important in montane environments, where differences in topography are linked to variations in overstory characteristics, heat load, and disturbance regimes, which may modify understory responses (Peet 1981; Battaglia et al. 2018). If CWD is closely associated with understory responses, it could provide a new tool for natural resource managers to predict understory responses to treatment. Likewise, overstory conditions, ground cover conditions, and tree seedling abundance also present relevant biotic environmental gradients with potentially meaningful effects on understory plants. Since forest restoration treatments often attempt create spatial heterogeneity in forest structure, light conditions vary within treated areas (Churchill et al. 2013; Barrett et al. 2018; Cannon et al. 2019). Therefore measuring overstory gradients may aid understanding of how light conditions affect understory responses. Treatments may also alter forest floor (litter and duff) depth, deposit woody material, and expose bare soil; all of these changes may influence understory plant germination and growth (Xiong and Nilsson 1999; Wolk and Rocca 2009; Kane et al. 2010). Finally, tree seedling abundance may also be affected by the changes caused by treatment, but it is unclear if tree seedlings compete with other plants or instead facilitate them (Callaway 1995; Gilliam 2007; Kane et al. 2010). Overall, finer-level understanding of the effect of environmental gradients on understory responses to treatment may help land managers optimize prescriptions.

In the Colorado Front Range, tens of thousands of hectares in dry conifer forests received restoration treatments between 2010 and 2019 through collaboratives comprised of federal and local government agencies, water utilities, private land owners, and non-profit organizations, including the Front Range Collaborative Forest Landscape Restoration Program (FR-CFLRP), Forests-to-Faucets, and the Upper South Platte Partnership (Schultz et al. 2012; Underhill et al. 2014; Williams and Cannon 2019; Jones et al. 2021). Data collected by Front Range collaboratives provide the opportunity to examine the effects of restoration treatments on the understory across this broad and variable geography, then refine future treatments. This study leveraged pre-treatment and 1-2 and 4-6 year post-treatment data in order to investigate the following questions:

1. How have restoration treatments affected the biotic conditions that might influence the understory plant growing environment, including overstory basal area, forest floor depth, fine wood cover, coarse wood cover, bare ground cover, and tree seedling density?
2. How have restoration treatments affected abundance and richness of functional groups defined by nativity (native or non-native), growth form (graminoid, forb, or shrub), life span (short-lived or long-lived), and reproductive strategy (vegetative reproduction or reproduction from seed)?
3. How have understory plant responses to treatments varied along environmental gradients including CWD, overstory basal area, forest floor depth, fine wood cover, coarse wood cover, soil and gravel cover, and tree seedling density?

I hypothesized that restoration treatments may initially have little effect on understory plants, but after 4-6 years, treatments would increase abundance and richness of both native and non-native species, especially herbaceous forbs and graminoids, short-lived species, and vegetatively spreading (e.g., rhizomatous) species, while having no effect on shrubs. I hypothesized that abundance and diversity of understory plants would be greatest in areas with overstory basal areas similar to historical levels (~6.3 to 9.5 $m^2\ ha^{-1}$; Battaglia et al. 2018), low climatic water deficits, low forest floor depths, high bare ground abundance, and low woody material abundance.

2. Methods

2.1 Study Area and Study Sites

The study area and the eight study sites were located in dry conifer forests in the montane zone of the Colorado Front Range (**Figure 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 – 2020, sites received average annual precipitation from 471 to 601 mm (PRISM Climate Group 2020). Snow was the primary source of precipitation during winters, but a persistent snowpack was uncommon (Veblen and Donnegan 2006). Precipitation peaks occurred during spring rain-snow showers (March-May) and again in late summer due to monsoonal thunderstorms (July-August). Some sites experienced stronger monsoonal peaks than others, with sites to the South having greater monsoonality (PRISM Climate Group 2020). Long-term average annual temperature at the sites 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 (Peet 1981; Moore 1992; Veblen and Donnegan 2006).

Ponderosa pine (*Pinus ponderosa)* was the uniting component of forest overstories in the study sites, and the sites spanned most of its elevational range (Peet 1981; Huckaby et al. 2003). 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 blanketed the cooler, mesic north-facing slopes (Kaufmann et al. 2006; Battaglia et al. 2018). At higher elevations, lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), Colorado blue spruce (*Picea pungens*), and limber pine (*Pinus flexilis*) mingled with ponderosa pine and Douglas-fir. Trembling aspen (*Populus tremuloides)* appeared sporadically throughout the sites in moist meadows and drainages. Beneath the forest canopy, understory communities also varied with moisture, topography, and elevation (Peet 1981). Common understory plants at our sites are described in **Table 3.**

The sites were established prior to treatment, between 2011 and 2017 on federal (USDA Forest Service: Arapaho and Roosevelt National Forests, Pike and San Isabel National Forests), county (Boulder County), and private lands as part of multiple collaborative forest restoration programs (**Figure 1**). The sites have varied land use histories, but it is likely that most or even all have experienced logging and near-total fire suppression. Forest restoration treatments were carried out at these sites between 2012 and 2017, either mechanically or by hand. Exact treatment prescriptions varied by site, but common goals included: reduction of basal area, creation of openings, creation of heterogeneity in tree group size and age, retention of older trees and snags, and enlarging the proportion of ponderosa pine to Douglas-fir (Dickinson et al. 2014; Underhill et al. 2014; Cannon et al. 2018), all in accordance with historical ranges of variability for the area (Brown et al. 2015; Battaglia et al. 2018). Cut woody material including tree boles, limbs, and branches was variously handled. Material was removed in some cases and left on site in others; material left on site could be piled, piled and burned, scattered, or masticated. See **Table 1** for details about treatments.

2.2 Sampling Design

Forest treatment areas within our sites were delineated by land managers according to local management priority and capacity. Nearby areas (within 1 km of treatment areas) with similar slope and aspect, but without plans for treatment, were delineated to serve as control areas (hereafter called untreated units) for the treatment areas (hereafter called treated units). A treated unit and its matching untreated unit comprised a ”block. ” Each site contained one to three blocks in close proximity to each other (**Table 1; Figure 2**).

Plots were placed randomly within the treated and untreated units of each block. However, if a random plot location was within 30 meters of a unit boundary, a new randomly generated location was chosen in order to avoid boundary effects. Initially, 186 plots were established. A subset of 155 plots were used in the generalized linear mixed models analyses, due to events such as unplanned livestock grazing that compromised one unit within a block, making the whole block unusable. Since block structure was not important for Boosted Regression Tree analyses, all 174 uncompromised plots were used in those analyses. The number of plots per block varied from 6 to 17 (**Table 1**).

This study 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 exact years of sampling varied across sites based on the year of treatment implementation and the availability of field crews.

2.3 Plot Characteristic Measurements

At the center point of each plot, we recorded latitude, longitude, elevation, and dominant slope and aspect. Two climatic water deficit (CWD) values were calculated to capture climatic conditions at different time scales. Each CWD variable was calculated for each plot following the method in Lutz et al. (2010) and using R code from Redmond (2022). Data used to calculate CWD values were: monthly average temperature and precipitation (800 m resolution for average CWD, only 4 km resolution was available for final spring CWD z-score) from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group 2020), soil data from POLARIS used to calculate soil available water capacity (Chaney et al. 2019), and field measurements (aspect, slope, & latitude) used to calculate topographic influence on heat load. First, we calculated 30-year normal climatic water deficit (1991-2020) (hereafter average CWD), which represents long-term climatic conditions. We also calculated March – June climatic water deficit (hereafter final spring CWD) for the year of the 4-6 year post-treatment visit to describe climatic conditions leading up to final sampling. Final spring CWD was scaled and centered (i.e. z-score transformed) using the 30-year mean and standard deviation for each plot, 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.

2.4 Overstory and Tree Seedling Measurements

Overstory plots were variable in radius about a plot center point. A prism (basal area factor (BAF) 10) was used to determine whether a tree was “in” or “out” of the overstory plot. All trees with a diameter greater than 12.7 cm at breast height (1.37 m) were deemed overstory trees. Height, diameter at breast height (DBH), live or dead status, and species were recorded for all overstory trees within the variable-radius plot. Seedling fixed-radius plots were also overlaid at the center point. The area of these plots varied somewhat by protocol, but ranged from 20.2 – 40.5 m^2 (**Table 2).** Seedlings were defined as any tree under 1.37 m in height, and tallied by species.

2.5 Understory Plant and Substrate Measurements

Understory and substrate plots were circular, with a fixed 11.3 m radius (406 m^2), and were overlaid onto the same center point as overstory and tree seedling plots. We used the point intercept method to capture understory plant and substrate “hits” at 200 or 400 observation points per plot. The observation points were distributed along transects that radiated from plot center along either the cardinal or the cardinal and ordinal directions, depending on the monitoring protocol used (**Table 2**). Forest floor (litter + duff) depth was measured at 3.0, 6.1, and 9.1 m along each of the ordinal transects at a subset of 5 of the 8 sites. All plant species and substrates hit below breast height were recorded. Possible substrates included: litter and duff, rock, bare ground, moss and lichen, fine wood (woody material < 7.2 cm diameter) and coarse wood (woody material > 7.2 cm diameter). Surveyors also walked the entire plot and performed a full census of all understory plant species present. Plants that could not be identified in the field were collected outside the plot for identification in the lab. Plant species were later classified by growth form (forb, graminoid, or shrub), nativity (native or introduced to Colorado), lifespan (short-lived [annual and 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 relevant botanical keys (Cronquist 1972; Shaw 2008; Ackerfield 2015). Some plants could only identified to genus or to a coarser taxonomic resolution because key morphological characteristics were not available. For plants that were identified to genus, if the genus contained members with multiple levels within a functional group (e.g., both native and non-native) they were not classified for that group.

For each plot, we used field data to calculate substrate cover and understory plant cover and richness. Since one of the main objectives of treatment was to promote dense and species-rich native plant communities, we were particularly interested in responses of native versus introduced species, and functional groups within native plants. Therefore cover and richness were calculated for introduced and native species, then for native plants by growth form, lifespan, and vegetative spreading category. Percent cover was calculated by dividing the number of line-point intercept transect hits for each species or substrate by the number of intercepts per plot, then multiplying by 100 and summing as appropriate. 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%. Richness was calculated by tallying all understory species encountered within a plot either on transects or during the full-plot search.

2.6 Data Analyses

Generalized Linear Mixed Models (GLMMs) were used to investigate the effect of forest restoration treatment and time-since treatment on understory cover, richness, and growing environment variables.

GLMM approaches can effectively handle high-variance and non-normally distributed data that are common in ecological studies, and can accommodate non-independent observations such as our repeated measurements at the same plots over time (Ott and Longnecker 2010).

GLMM analyses were carried out in R (R Core Team 2021) using the *glmmTMB* package (Brooks et al. 2017) for 78 treated and 77 untreated plots. Understory Cover and richness were first assessed for each nativity status. Native plant cover and richness were then analyzed for each growth form, lifespan, and vegetative spreading category. For each model, we chose the error distribution and link function appropriate to the metric. Beta distributions were used for percent cover of bare ground, fine wood, and coarse wood. We used the gamma distribution with a log link to model plant cover variables and tree seedlings per hectare. Since gamma models do not support zero-values in the data, we followed Stahel's method (Stahel 2002) to add a small value to every observation so that all values were non-zero:

$$Cover_{adjusted} = Cover_{original} + c, \text{ where } c = \frac{(first\ quartile\ of\ non{-}zero\ subset\ of\ original\ data)^2}{(third\ quartile\ of\ non{-}zero\ subset\ of\ original\ data)}$$

We used the Poisson or negative binomial distribution with log links for understory richness models and tree basal area, since these distributions are appropriate for count data; negative binomial was used where dispersion in the data was especially high.

The fixed effects in our GLMMs were treatment, time-since-treatment, and their interaction. The random effects were random intercepts for site and block nested within site. These random effects allowed each site, and each block within a site, to have its own intercept in the model. This is a more sensitive way to discern treatment effect, as it allows variability in mean estimates for each site and block. Significant ($\alpha = 0.050$) treatment by time-since-treatment interactions indicated that the effect of treatment was not the same at every sampling period. To understand how the effect of treatment changed over time, we conducted post-hoc comparisons between treated and untreated groups within a sampling year to test for differences in estimated marginal means. P-values for these post-hoc tests were adjusted using the Tukey method for multiple comparisons. All reported means associated with p-values are model means. Marginal and conditional R^2 values were calculated as a measure of model fit using the *MuMIn* package (Bartoń 2022).

Boosted Regression Trees (BRT) were used to examine how native understory richness and cover varied along environmental gradients (Elith et al. 2008). BRTs build an ensemble of regression trees, where each tree is formed by finding which independent variables, and which splitting points within them, most improve prediction. In BRTs, trees are connected: the first tree represents an "initial guess" at the response variable value. Each subsequent tree takes the errors between the field observations and the predictions made by the previous tree, and predicts for those errors. Error calculation is controlled by a loss function appropriate to the data distribution; e.g. a Poisson loss function would be used for count data. The error predictions from each new tree are combined with the previous tree to make a new prediction of the response. A designated learning rate is set to "slow" the overall model's learning speed during this process, which combats over-fitting (i.e., creating a model that is so perfectly fit to the training dataset that it cannot be used to describe or predict any other dataset). By focusing on errors, BRTs identify and improve estimation of difficult-to-predict response values.

While GLMMs could also be used to explore the relationships between understory and environmental gradients, we chose BRTs for three reasons. First, we suspected the presence of non-linear relationships within our study system that would not be best modeled using a linear method like GLMM. For example, decreasing basal area generally allows more light for growth, but there could be a threshold past which too much light becomes detrimental due to elevated drought stress. Secondly, BRTs can handle large numbers of predictors, as well as correlation between predictors, without overfitting or losing prediction ability. This is very useful in the context of exploratory analysis, where the most important predictors are not necessarily known – more variables can be added to the model without losing predictive ability. Lastly, BRTs can not only show the relationship between a predictor and response, they can also rank variables against each other by their importance in predicting the response. This is especially useful information for natural resource managers looking to understand which variables have the strongest effect on desired outcomes. One downside to choosing BRTs is that they cannot handle the correlation between measurements in time series data; this means we were restricted to using the 4-6 year post-treatment data only, but this was acceptable since drivers of longer-term responses were more of interest.

BRT analyses were also carried out in R for 91 treated plots and 83 untreated plots, using the gbm.step & gbm.fixed functions from the *dismo* package, with partial dependence plots developed with the *pdp* package (Greenwell 2017; Hijmans et al. 2021). Native plant cover and native richness were the response variables; predictor variables represented different aspects of the growing environment. Treatments were described by the variables: basal area, forest floor depth, fine wood cover, coarse wood cover, and bare ground cover. Treatment status (untreated or treated) was also included to encompass any treatment effects that were not described by the other treatment-related variables. Two climatic variables were also used: average CWD and final spring CWD z-score (March-June of the 4-6 year post-treatment year). Tree seedling density was included in case of possible competition or facilitation of understory growth by young trees. Sample year was included to encompass yearly variations due to factors not captured by the other variables, including personnel and protocol changes.

Last, since some plots were visited outside of peak growing season in late spring or early fall, sample month was included to account for variation in cover as an effect of visit timing. For both BRT models, we used the rule-of-thumb number of trees: 1000 (Elith et al. 2008). Since learning rate affects the number of trees required to reach a final model, we chose the learning rate that regularly produced models with 1000+ trees. Interactions were modeled inherently as a result of the structure of decision trees, where the prediction for one response variable depends on the values of predictors higher up in the tree (De'ath 2007; Elith et al. 2008). We set tree complexity to 2, which limited the model to two-way interactions; important interactions were later identified using the method described in Elith et al. (2008). Bag fraction was chosen by trying three values (0.5, 0.625, and 0.75) and choosing the one which resulted in the model with the lowest root mean squared error (RMSE) during 10-fold cross-validation. For our cover model, we used a Gaussian loss function, a learning rate of 0.0024, and a bag fraction of 0.5. For richness, we used a Poisson loss function, a learning rate of 0.0021, and a bag fraction of 0.5. Model predictive ability outside the study dataset was determined using a 10-fold cross-validation (CV) process. This began by splitting the original data into ten equal parts ("folds"). Then ten CV models were created, each using a unique combination of nine of the folds to train the model and the last remaining fold to test the model. R-squared values were calculated for each CV model and averaged – these values measure how good the model was at predicting data not used to develop the model (i.e. how reliably could the model be applied to data from other locales). R-squared values were also calculated 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, the relative influence (RI) of each predictor variable on the response was calculated, based on number of times the variable was selected to create a tree split, and the improvement to the model as a result of those splits, averaged over all trees (Elith et al. 2008). Partial dependence plots were made to show individual relationships between the response and a single predictor after controlling for the average effect of the other variables. Interactions identified as relatively strong were also plotted, excepting any interactions involving a variable of very low importance in predicting the response (RI < 5%).

3. Results

In the course of this study, 367 unique understory plant species were identified, including 262 forbs, 64 graminoids, 38 shrubs, and 3 juvenile plants of undetermined growth form. Of these plants, 36 species were introduced, 10 of which were considered noxious weeds in Colorado (Colorado Department of Agriculture 2022). The three most common introduced species were *Taraxacum officinale* (dandelion), *Cirsium arvense* (Canada thistle), and *Tragopogon dubius* (yellow salsify). Most plants were identified to the species level (77.6% of observations), some plants could only be identified to the genus level (21.8% of observations) or were not identified at all (0.6% of observations). See **Table 3** for the most commonly encountered species; see **Supplementary Table 1** for list of all species.

3.1 Overstory, Substrates, and Tree Seedlings

Of the variables related to understory plant growing environment, the effect of treatment only significantly varied at different sampling periods for overstory basal area, fine wood cover and bare ground cover (**Table 4**). Basal area was similar in treated and untreated plots prior to treatment. Basal area was nearly halved by treatment, averaging 13.6 m^2 ha^{-1} in treated and 24.7 m^2 ha^{-1} in untreated plots ($p < 0.001$) at 1-2 years post-treatment, with little alteration at 4-6 years post-treatment. Fine wood cover and bare ground cover values were similar in untreated and treated plots before thinning, then modestly 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 21.0% in treated and 15.1% in untreated plots ($p < 0.001$) and bare ground cover was on average 10.0% in treated and 4.4% in untreated plots ($p < 0.001$).

Trends in tree seedling density, forest floor depth, and coarse wood cover did not show significant interactions between time and time-since-treatment. Only treatment was significant for coarse wood. Coarse wood cover was consistently and significantly different between treated and untreated plots at all sampling times, but the difference was very small: cover was on average 1.7% in untreated and 2.2% in treated plots ($p < 0.001$). Tree seedling density was significantly different over time, but treated and untreated plots had similar seedling densities: prior to treatment, seedling density was 6.0 seedlings ha^{-1} on average. This dropped over time to 3.7 seedlings ha^{-1} at 1-2 years post ($p = 0.005$) and 3.2 seedlings ha^{-1} at 4-6 years post ($p < 0.001$). Forest floor depth trends through time did not vary by treatment either: untreated plots had greater forest floor depth than treated plots at all sampling times, but overall, average forest floor depths decreased over time from 5.5 cm before treatment to 4.5 cm on average at 4-6 years after 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 (**Figure 4, Table 5**). Unexpectedly, given randomized plot placement, native cover was 1.2 times higher in treated (17.3%) compared to untreated plots (14.3%) even before thinning ($p = 0.036$). This was likely a result of an initial imbalance in native shrub cover prior to treatment. Native cover was similar in treated and untreated plots at 1-2 years post-treatment ($p = 0.894$). After 4-6 years post-treatment, native cover was 1.6 times higher in treated plots: on average, 25.0% cover in treated versus 15.5% cover in untreated plots ($p < 0.001$). This difference was not attributable to higher shrub cover in treated plots as was the case pre-treatment, since shrubs had similar cover in treated and control plots at this sampling period.

Different growth forms of native plants responded differently to treatment in terms of cover (**Figure 4, Table 5**). Native shrubs saw an immediate decline in treated relative to untreated plots, with effects persisting for 4-6 years after treatment. Before treatment, native shrub cover was 1.4 times higher in treated versus untreated plots ($p = 0.022$). After thinning, native shrub cover had declined in treated plots such that cover was similar between treatments at both 1-2 and 4-6 years post-treatment ($p = 0.114$ and $p = 0.152$, respectively). Native forb and native graminoid cover were similar in treated and untreated plots before thinning ($p = 0.286$ and $p = 0.367$, respectively) and at 1-2 years post-treatment ($p = 0.057$, and $p = 0.075$, respectively). Both native graminoids and forbs were thriving in treated plots by 4-6 years after thinning. Graminoid cover was 2.1 times higher in treated (9.9% cover) than untreated plots (4.8% cover; $p < 0.001$) and native forb cover was 1.9 times higher in treated (4.6% cover) than untreated plots (2.4% cover; $p < 0.001$). This invigorated native graminoid and native forb cover likely drove the trend of an overall increase in native cover at 4-6 years post-treatment.

Changes in cover of native plants with different life strategies varied (**Figure 4, Table 5**). Native short-lived and native vegetatively spreading plants had low cover on the landscape, but experienced similar boosts due to treatment. Both groups had roughly equal cover in treated and untreated plots prior to treatment (Figure XXX). Short-lived natives made up a miniscule part of the cover in our plots (< 1% cover in any plot), but still experienced a spike in cover in treated plots at 1-2 years post-treatment, with treated plots having 1.8 times higher cover than untreated plots ($p < 0.001$). Though still elevated at 4-6 years post-treatment, the proportion of short-lived plant cover was reduced, at 1.6 times higher cover in treated plots ($p < 0.001$). Vegetatively spreading plants responded to treatment more slowly than short-lived plants: cover was similar in treated and untreated plots at 1-2 years post-treatment ($p = 0.407$), but was 2.6 times higher in treated ($p < 0.001$) than untreated plots at 4-6 years post-treatment. Like short-lived plants, vegetatively-spread plants were not abundant in general, averaging 1.3% cover in untreated plots and 2.9% cover in treated.

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 also shared similar patterns through time (**Figure 4, Table 5**). Both had greater cover in treated than untreated plots prior to treatment, again likely due to the pre-thinning prevalence of shrubs – all of which are long-lived and most of which were non-vegetatively spreading in this study – 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 returned to greater cover in treated versus untreated plots at 4-6 years after restoration. Long-lived native cover was 1.2 times higher in treated previous to treatment, and 1.5 times higher in treated (26.0% cover) than untreated plots (16.9% cover, $p < 0.001$) at 4-6 years after treatment. Non-vegetatively spreading plants also had higher cover in treated than untreated plots at 4-6 years post-treatment, but cover was similarly high in treated relative to untreated plots pre-treatment and 4-6 years post-treatment: 1.3 times higher pre-treatment and 1.4 times higher at 4-6 years post-treatment.

The mean cover of introduced plants was minimal at all visits, but was higher in treated than untreated plots at the second post-treatment visit. Prior to thinning and 1-2 years post-treatment, introduced cover was comparable in treated and untreated plots (**Figure 4; Supplementary Table 1**). On average, introduced cover was 0.31% in treated and 0.13% in untreated plots at 4-6 years post-treatment ($p < 0.001$). Introduced cover was also very low: only 6 out of 441 samples taken over the course of the study had a combined introduced cover greater than 5%. In 5 of these, *Bromus tectorum* (cheatgrass) was the primary source of introduced cover, in the other, it was *Bromus inermis* (smooth brome).

3.3 Understory Richness

Native species richness was elevated in treated plots compared to untreated plots after thinning (**Figure 5; Table 5)**. Before thinning, native richness was similar in treated and untreated plots ($p < 0.552$). This changed after treatment: native richness was higher in treated versus untreated plots at both post-treatment sampling periods. At 1-2 years post-treatment, treated plots averaged 29.0 native species compared to 25.6 native species in untreated plots ($p < 0.001$). At 4-6 years post-treatment, treated plots averaged 33.2 native species while untreated plots averaged 29.5 ($p < 0.001$). Treatment favored common species like *Androsace septentrionalis, Campanula rotundifolia*, and *Pulsatilla patens*, all of which were found in far more treated than untreated plots, when they had been in similar numbers of plots before thinning. Treatment seemed to decrease occurrence for very few common species, but *Juniperus communis* was found in far fewer treated than untreated plots post-treatment, when it was in similar numbers of treated and untreated plots prior to treatment. Many less common species experienced changes in occurrence after treatment, but there were no obvious trends in the traits of those species: many were long-lived, non-vegetatively spreading plants, but this was also the most common type of plant on our landscape.

Out of the three growth forms, treatment only stimulated richness of native forbs (**Figure 5; Table 5)**. Native graminoid and shrub richness did not differ between treated and untreated plots at any sampling period, averaging 4.6 and 4.0, respectively, across all plots and sampling periods. Native forb richness was similar in treated versus untreated plots before thinning ($p = 0.536$), but after thinning, native forb richness was higher in treated plots. On average, treated plots contained 20.0 native forb species compared to 17.3 in untreated plots at 1-2 years post-treatment ($p = 0.001$), and 23.1 versus 20.1 species in treated compared to untreated plots at 4-6 years post-treatment ($p = 0.005$).

Changes in richness of native plants with different life strategies varied. Whether long- or short-lived, vegetatively spreading or non-vegetatively spreading, richness values were similar in treated and untreated plots prior to treatment. Vegetatively spreading plants continued to show no differences in richness at either post-treatment sampling period. Non-vegetatively spreading plants gained in richness in treated plots at 1-2 years post-treatment, and retained this increase at 4-6 years post-treatment. On average, non-vegetatively spreading plant richness was higher in treated plots (21.6 species) relative to untreated plots (18.7 species) at 1-2 years after treatment ($p < 0.001$), and at 4-6 years post-treatment (25.0 species vs 21.5 species, $p < 0.001$). Richness of short-lived plants echoed the results for cover of short-lived plants: a spike at 1-2 years post-treatment which was still present, but reduced, at 4-6 years post-treatment. At 1-2 years post-treatment, treated plots had on average 2.5 times the short-lived plant richness than untreated (~2.4 vs 1.0 species, $p < 0.001$). At 4-6 years post-treatment, this was reduced to 1.6 times greater richness in treated plots than untreated plots (~2.6 vs 1.7 species, $p < 0.001$). Long-lived species also had heightened richness in treated versus untreated plots at both post-treatment sampling periods: on average, 26.4 versus 24.5 species ($p = 0.040$) at 1-2 years post-treatment, and 27.8 versus 30.6 species at 4-6 years post-treatment ($p = 0.004$).

Introduced species richness was also higher in treated plots at both post-treatment sampling periods (**Figure 5; Table 5)**. Prior to treatment, treated and untreated plots had similar introduced richness ($p = 0.481$). At 1-2 years post-treatment, treated plots had an average of 1.4 introduced species while untreated plots had 0.3 ($p < 0.001$). At 4-6 years post-treatment, treated plots had an average of 3.1 introduced species compared to 0.8 in untreated plots ($p < 0.001$). Of the introduced species in this study, 10 of 36 were considered noxious weeds in Colorado (Colorado Department of Agriculture 2022). After thinning, *Taraxacum officinale* (dandelion) and *Cirsium arvense* (Canada thistle) colonized many more treated than untreated plots. Dandelion was found in 9% of untreated and 10% of treated plots before treatment, and 19% of untreated and 62% of treated plots 4-6 years after thinning. Canada thistle was present in 1% of untreated and 1% of treated plots before treatment, and 0% of untreated and 35% of treated plots 4-6 years after thinning.

3.4 Native Understory Cover and Richness Along Environmental Gradients

Boosted regression tree analysis identified overstory basal area as the most influential predictor of native understory cover with a relative influence (RI) of 49%. Final spring CWD z-score was the next most influential for native cover (15% RI), followed by fine wood cover (6 % RI). All other variables were much less influential (all < 5% RI) (**Figure 6**). The relationship between basal area and native cover showed strong non-linear thresholds. Native cover predictions were high (~30 % cover) in relatively open overstories with basal areas lower than ~ 10 m^2 ha^{-1}. At basal areas greater than 10 m^2 ha^{-1}, cover predictions decreased steadily until leveling off to ~15% cover at basal areas higher than ~20 m^2 ha^{-1}, representing relatively closed overstories (**Figure 7**). For final spring CWD z-score, values below zero (cooler-wetter spring conditions than usual) produced similarly low cover predictions, but when final spring CWD z-scores were above zero (indicating warmer-drier spring conditions than usual), cover grew with rising final spring CWD (**Figure 7**). There were two substantial interactions in the native cover BRT: between basal area and final spring CWD z-score, and between basal area and fine wood cover (**Figure 9**). Final spring CWD z-score had a stronger effect on native cover at lower basal areas, where combinations of low basal areas and high final spring CWD z-scores resulted in the highest predicted cover. When basal areas were high, fine wood cover had little effect on native understory cover. When basal areas were low, sparse fine wood cover resulted in the highest native cover predictions. For the native cover BRT, the R-squared value was 0.29 in the cross-validation, meaning that the model explained 29% of the deviance in understory cover when applied to data not used to train the model. The model explained 49% of the deviance in understory cover using the full observed dataset.

Overstory basal area and final spring CWD z-score were also the most influential predictors of native richness, with RI values of 35% and 21% respectively. However, richness was influenced by average CWD (10 % RI). Forest floor depth, fine wood cover, and bare ground cover were somewhat important for richness prediction, at 7% , 7%, and 6% RI respectively; all other variables in the native richness BRT had < 5% RI (**Figure 6**). The relationship between basal area and richness was less dramatic but similar to cover: plots with the lowest basal areas had the highest predicted richness values (~ 29 species), while plots with high basal areas greater than ~ 22 m^2 ha^{-1} had low predicted richness (~ 33 species). Final spring CWD z-score showed the opposite trend in prediction for richness as it did for cover: when final spring CWD z-score was less than zero, richness increased as final spring CWD z-score decreased (**Figure 8**). The relationship between richness and average CWD was similar: lower average CWD was associated with higher richness. The strongest interactions in the native richness BRT were between tree basal area and average CWD, and between tree basal area and final spring CWD z-score. When basal area was high, average CWD had little effect on species richness, but at low basal areas, low average CWD (cool-wet average site conditions) resulted in high richness predictions. Final spring CWD z-score also had a stronger effect on richness at lower basal areas, and similarly to average CWD, richness was highest at the lowest final spring CWD z-scores. For the native richness BRT, R-squared values were 0.17 in cross-validation and 0.40 for the full observed dataset.

4. Discussion

4.1 Understory Cover & Richness

Maintaining biodiversity has become a key concern in the global context of widespread habitat degradation and loss (Carey 2003; Rands et al. 2010; Leclère et al. 2020; The Convention on Biological Diversity 2022). Ecological restoration treatments can support biodiversity by improving ecosystem resilience and increasing native species abundance and richness following negative impacts due to changing land-use, altered disturbance regimes, or introduced species (Noss et al. 2006; Palmer et al. 2016). 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 ecological restoration treatments in terms of richness and cover, thereby supporting native plant biodiversity.

Benefits to native understory richness were evident shortly after ecological restoration treatment, and early gains in native richness were maintained as of 4-6 years post-treatment (**Figure 5; Table 5)**. Native richness as a whole was elevated in treated plots just 1-2 years after treatment, as was richness for four of seven native functional groups. This is in contrast to other studies that measured native richness within a similar time frame and found negative or no changes in richness (Collins et al. 2007; Briggs et al. 2017). It is interesting that Briggs et al. (2017), which analyzed early results from three sites which are also part of this study, did not find elevated native richness soon after treatment. This may be because Briggs et al. measured all plots in the first growing season after treatments, while in our study, some plots were measured in the second growing season. This may have provided more time for new species to establish post-treatment. Native richness remained heightened at 4-6 years post-treatment, a result mirrored by other studies in dry conifer forests measuring richness at 4 years or more after thinning (Carey and Wilson 2001; Kane et al. 2010). All functional groups that increased in richness at 1-2 years post-treatment, retained these gains. This included some of the most common types of plants in our study: long-lived and non-vegetatively spreading species, as well as less common groups like forbs and short-lived species. Native graminoids, shrubs, and vegetatively-growing species did not increase in richness, however. In part this may be because graminoids and shrubs are less diverse groups in this landscape and therefore there are fewer possible species available to gain.

While richness was elevated in treated plots in this study, the effect size was modest: treated plots had on average 3 more species (13% higher richness) than untreated plots. It is difficult to compare this number to other studies, given that richness depends non-linearly on the size of the area surveyed and different landscapes have different inherent levels of diversity (Francis and Currie 2003; Field et al. 2009; Dodson and Peterson 2010). Still, as native forbs were the only growth form with heightened richness, and forbs made up the least native cover in the study, it is likely that the increase in richness was subtle on the landscape from a human perspective. Limitations to new plant establishment may be related to soil seedbanks or the influence of treatment outcomes on growing conditions. Local seed banks may have lost richness where uncharacteristically dense and homogenous overstories limited the species which could survive and supply seed banks (Laughlin et al. 2011b; Knapp et al. 2013). The rapid rise in richness in treated plots suggests that local seed banks had at least some novel propagules readily available, perhaps from species with seeds able to persist for long periods or ruderal species with highly dispersible seeds (Spira and Wagner 1983; Hendry et al. 1994; Lang and Halpern 2007). However, a study in Oregon found that plants specific to forest meadows were the least likely of all species to be present in forest seed banks, mainly because of extremely small dispersal ranges (Lang and Halpern 2007). This suggests that forest meadow species may not be available to germinate in our treatments, despite newly improved aboveground conditions, thus limiting increases in richness. Additionally, studies which compare forest treatments of different treatment intensities, such as different levels of thinning or thinning versus prescribed burning, often find that gains in richness are higher with greater disturbance intensity (Dodson et al. 2008; Schwilk et al. 2009; Kane et al. 2010). Greater intensities of disturbance may provide stronger forest floor and overstory changes and interruption to competitive exclusion that allow more species of plants to establish (Huston 1979; Schwilk et al. 2009). This aligns with findings in our study that thinning treatments minimally disturbed the forest floor: they did not alter forest floor depth, and only very mildly increased bare ground exposure and fine wood cover. Furthermore, while overstory basal area was reduced by half on average in our study, in theory, overstory heterogeneity is also required to recreate the wider variety of niches historically available which could support more species (MacArthur and MacArthur 1961; Bazzaz 1975; Naumburg and

DeWald 1999; Allen et al. 2002; Battaglia et al. 2018). A series of studies, which investigated some of the same sites in this study, found that restoration treatment brought forest heterogeneity close to historical levels for at least some metrics and scales (Cannon et al. 2018; Barrett et al. 2021; Cannon et al. 2022). Future exploration of whether stand heterogeneity is associated with understory species richness would provide insight into whether heterogeneous forest structure matters for understory diversity in modern, altered forests which may have depauperate seed banks.

Native cover responded more slowly to treatment than did richness, but by 4-6 years post-treatment, thinning invigorated growth of native understory plants in total and across many functional groups (**Figure 4; Table 5)**. 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 cause significant damage to understory plants. After 4-6 years, graminoids and forbs each had approximately twice the cover in treated plots as untreated. Several studies measuring 4+ years post-thinning also found that treatment fostered heightened cover of graminoids (Griffis et al. 2001; Lochhead and Comeau 2012; Faist et al. 2015) or both graminoids and forbs (Siegel and DeSante 2003; Fornwalt et al. 2017). Short-lived natives increased in cover over the course of the study, but the differences in cover in treated versus untreated plots were smaller at 4-6 years compared to 1-2 years post-treatment, indicating that gains in short-lived species may be transitory. The lack of long-term establishment of these short-lived species implies that these may be ruderal and potentially require repeated disturbances to persist (Grime 2001). Additionally, we examined trends by vegetative spreading status as treatments can modify forest floor depth and 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 group, at 2.6 times the cover in treated plots at 4-6 years post-treatment. Forest floors were not deeper on average in treated plots in our study, but vegetatively-spreading plants may still have had the edge in growth compared to the majority of plants in our study – mainly bunchgrasses and small forbs – which would likely have to produce new individuals to greatly increase cover. The only group which did not improve in cover was the shrub functional group. This may be seen as a benefit for fire resilience as treatments often seek to reduce ladder fuels like shrubs (Churchill et al. 2013), but may have negative impacts for certain wildlife species (Latif et al. 2020). While increased herbaceous cover in treatments was associated with overall higher avian diversity in a Front Range study, two shrub-associated bird species were less abundant in treated areas due to reduced shrub cover (Latif et al. 2020). It is worth noting that other dry conifer restorations, even one within Colorado, did not result in reduced shrub cover (Carey and Wilson 2001; Siegel and DeSante 2003; Korb et al. 2020).

In this study, gains in native species were accompanied by higher introduced species richness and cover in treated plots by 4-6 years after treatment (**Figures 4 and 5; Table 5)**. Restoration thinning disturbs forest environments, and disturbance often increases invasion by introduced species, likely because of altered competitive interactions and resource availability (McIver et al. 2013; Ibáñez et al. 2021). The biotic resistance hypothesis holds that when native communities are diverse, invasion is less likely because more of the possible niches are occupied by natives, and this seems to be true in many systems (MacArthur 1955; Elton 1977; Beaury et al. 2020). However, though native species made up the majority of plant cover and richness by far in our study, introduced species also made gains. Heightened native and introduced species richness have been found together in many studies, a trend sometimes termed "the rich get richer" (Stohlgren et al. 2003). This may be because the same conditions that benefit native plants, such as greater light availability after thinning, also generally favor non-native plants (Catford 2012). Thinning treatments may still be the best option where some form of restoration is necessary for ecosystem resilience, but preventing introduced species is also a high priority: many studies comparing thinning to prescribed burning or thin-and-burn treatments found the lowest introduced species cover in thinning treatments (Collins et al. 2007; Schwilk et al. 2009 and references therein; Jang et al. 2021). Still, some introduced species in our study may warrant further monitoring: *Bromus tectorum* and *Cirsium arvense* were found in either many treated plots relative to untreated plots, or at very high cover in a few treated plots. Monitoring should be continued for these species, especially for *Cirsium arvense*, which was identified as concerning in other forest thinning studies in Colorado (Miller and Seastedt 2009; Wolk and Rocca 2009; Fornwalt et al. 2017; Fornwalt et al. 2018).

4.2 Native Understory Cover and Richness Along Environmental Gradients

Exploration into the drivers of understory responses found both expected and unanticipated relationships (**Figures 6-9)**. As expected, treatments significantly reduced overstory basal area, and overstory basal area was strongly linked with understory cover. Both recent and classic studies have found associations between tree canopy and understory abundance (Jameson 1967; Laughlin et al. 2005; Kane et al. 2010; Matonis and Binkley 2018; Jang et al. 2021). A recent study found that differences in native cover between treated and untreated areas were primarily explained by basal area differences (Jang et al. 2021). 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 treatment had an effect on understory cover, and this is what we found as well (Abella and Springer 2015). 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 the lowest basal areas since very few plots had such low tree cover. Average basal areas in treated vs untreated plots roughly aligned with these thresholds: ~ 13 m^2 ha^{-1} in treated and ~24 m^2 ha^{-1} in untreated plots. Lower basal areas may be associated with greater cover as more light is available for photosynthesis, thereby boosting plant growth. Below-ground resources may be limiting factors for plant cover, perhaps more so than light in arid environments (Coomes and Grubb 2000). Some studies have found that areas of lower conifer density were also associated with greater soil moisture (Simonin et al. 2006; Zou et al. 2008) and some thinning types can increase nitrogen available to understory plants (Prescott 2002; Kaye et al. 2005; Rhoades et al. 2012). Final spring CWD z-score was the next most important predictor of native cover. We originally expected that 30-year average CWD would be influential on the understory, particularly that typically warm-dry plots (high average CWD) would have lower cover due to harsher conditions for growth and establishment. However, average CWD was not important for native cover. This may be because warm-dry (and cool-wet) plots have species assemblages well suited to those conditions, or it could be that plants in the Front Range tolerate a wide range of 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 influential for the understory, and interacted with basal area. However, the relationship between final spring CWD z-score, basal area, and cover was somewhat counter-intuitive. Predicted native cover was highest at the lowest basal areas combined with the warmest and driest spring conditions. It is worth noting that the highest final spring CWD z-scores were only around one standard deviation away from the mean and therefore represent fairly mild relative warmth and dryness, and the difference in native cover predictions was small: ~28% versus ~32% cover. While treatments had a strong impact on overstories as expected, treatment effects at the forest floor level were limited to a mild increase (~6%) in soil/gravel and fine wood covers. While the many different types of woody debris handling methods could have combined to muddle any strong changes in forest floor, 95% confidence intervals were also very small, indicating low variation in these metrics (**Table 4**). Given the absence of strong changes in the forest floor, it makes sense that none of these predictors were identified as highly important to native cover (or richness) responses.

Many of the same drivers and patterns of native cover response also held true for native richness, although richness and cover responses diverged for CWD variables. As with cover, basal area was the most important predictor of richness, and basal areas of < 10 m^2 ha^{-1} produced the highest richness predictions, while dense stands at basal areas > 20 m^2 ha^{-1} produced similar and low richness predictions. This echoes several studies that found greater richness in more open dry conifer overstories (Laughlin et al. 2011; Matonis and Binkley 2018; Jang et al. 2021). 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 restricted understory communities to species with leaf, seed, root, and stem traits that indicated high shade tolerance and conservative strategies to gaining and maintaining scarcer resources. They also found that understories measured from 1912-1938 that grew beneath more open overstories allowed for a wider array of life strategies reflected by a greater variety of physical traits (Laughlin et al. 2011). Average CWD and final spring CWD z-score showed similar influences on richness predictions: richness was highest in cooler-wetter conditions, whether those reflected generally cool-wet plots (average CWD) or relatively cool-wet springs compared to the plot average (final spring CWD z-score). The interaction between final spring CWD z-score, basal area, and understory richness also showed the opposite trend from cover: where basal area was lowest, the lowest final spring CWD z-score (cooler-wetter than usual) predicted high richness. It makes sense that higher richness is maintained where spring conditions are good for germination and establishment: plentiful light tempered by a cooler, moister climate than usual.

4.3 Conclusions and Management Implications

This study demonstrates that ecological restoration thinning treatments stimulated understory plant cover and richness in 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 the

Front Range: 6.3 to 9.5 m^2 ha^{-1}. These findings support a core principal of ecological restoration: that native species are most likely to thrive when the conditions that shaped their evolution are restored (Churchill et al. 2013; Palmer et al. 2016; Stephens et al. 2020 Dec 2). The contribution of greater richness to improved biodiversity is clear, but higher plant cover in treated areas may imply higher genetic biodiversity and resilience if increased cover is the product of establishment of new, unique individuals (Allendorf et al. 2022). Genetic diversity is usually higher in larger populations of unique individuals and is strongly associated with adaptability and resilience to changing conditions, which is especially relevant due to climate change (Thompson et al. 2009; Reed et al. 2011; Allendorf et al. 2022). This study also addresses a practical question in targeting areas for treatment: do generally warm-dry areas like steep, south-facing slopes have different understory responses than cool-moist sites such as those on mild slopes or north faces? As far as this study could determine, average climate had no detectable impact on native cover and a mild effect on native richness; instead treatments were generally beneficial for cover and richness in spite of different average site conditions. Of course, water stress still affects plant richness and cover, as confirmed by our finding that final spring CWD z-score was predictive of richness and cover, so short-term climatic conditions should be accounted for when assessing the impact of treatment on understories.

While restoration treatments benefited native understories as a whole, the cascade of effects of understory changes on other aspects of the ecosystem should also be considered. Increases in introduced species are a common side effect of disturbances, including thinning treatments. However, thinning restorations stimulate introduced species far less than the high-severity fires they mitigate against (Griffis et al. 2001). Among restoration methods, thinning is often the least disruptive and provokes the smallest introduced species responses (McIver et al. 2013; Abella and Springer 2015; Willms et al. 2017). While the current trajectory in our study shows increasing introduced species richness and cover, a 23-year long study of dry conifer forest restoration in Montana found that introduced species cover dissipated with time (Jang et al. 2021). Managers may also consider whether increased herbaceous cover, and therefore plant connectivity and biomass, are desirable in terms of fire dynamics. However, on average, total understory cover in treated plots in this study was moderate at ~30% cover, most of it low-growing graminoids and forbs. 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 (Waltz and Covington 2004; Davies 2022). 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 species assemblages when planning treatments (Carey and Wilson 2001; Siegel and DeSante 2003; Latif et al. 2020).

It is unclear how long elevated cover and richness in treated areas might last in the Colorado Front Range, as studies in the region have not extended past nine years (Wolk and Rocca 2009; Briggs et al. 2017; Fornwalt et al. 2017). Studies looking at understories and thinning at even longer time scales have found inconsistent results – a 23-year study in Montana ponderosa/Douglas-fir forest found that richness and cover peaked at five years post-treatment then fell back to pre-treatment levels (Jang et al. 2021), while a 12-year study in Arizona ponderosa forests found sustained higher herbaceous biomass in treated forest until a major drought event at 10 years into the study (Moore et al. 2006). 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 employ 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 (Suding 2011; Warren et al. 2011; Wortley et al. 2013; Ummenhofer and Meehl 2017; Radeloff et al. 2018).

5. Figures and Tables

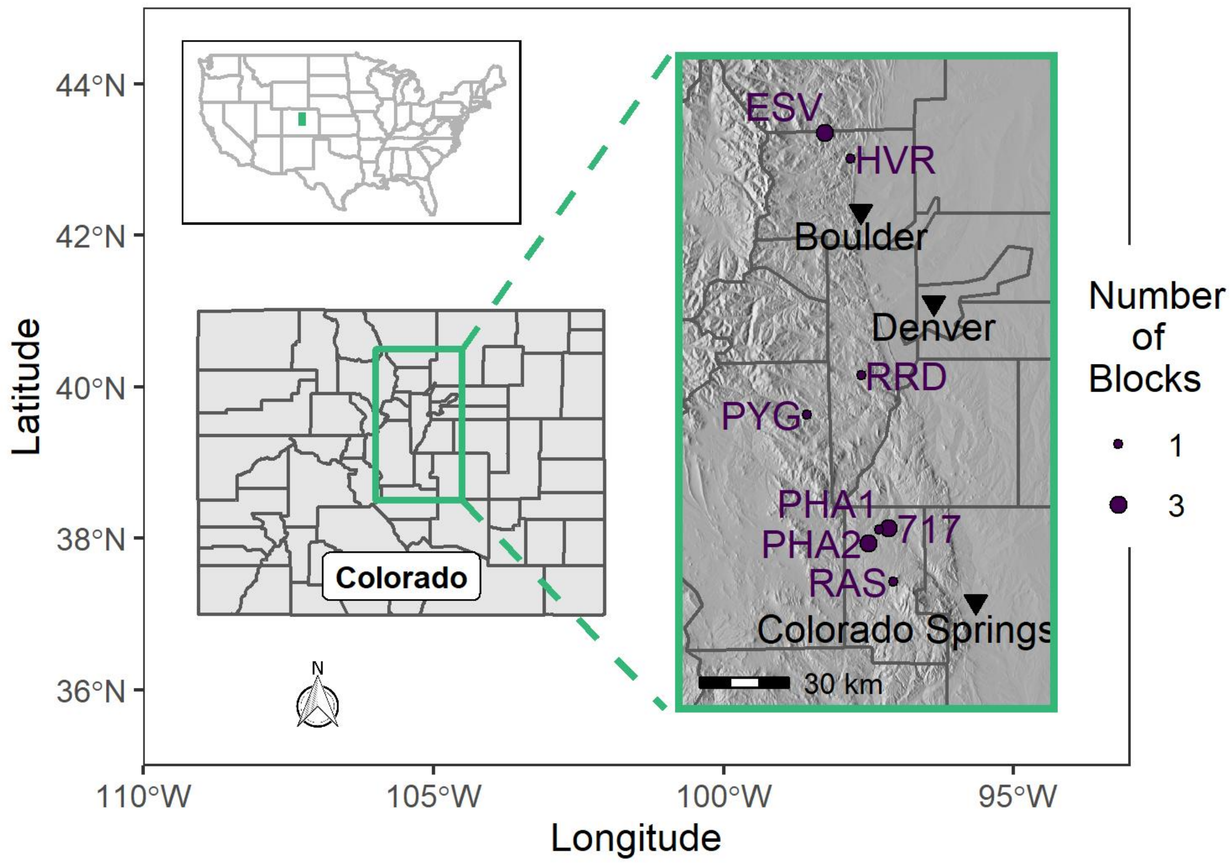

Figure 1. Study area map. This map shows the study area in the Colorado Front Range, with sites marked with purple circles. Cities are labeled in black. Sites include: Estes Valley (ESV), Heil Valley Ranch Open Space (HVR), Ridge Road (RRD), Payne Gulch (PYG), Phantom Creek 1 (PHA1), Phantom Creek 2 (PHA2), West Creek (717), Raspberry Mountain (RAS).

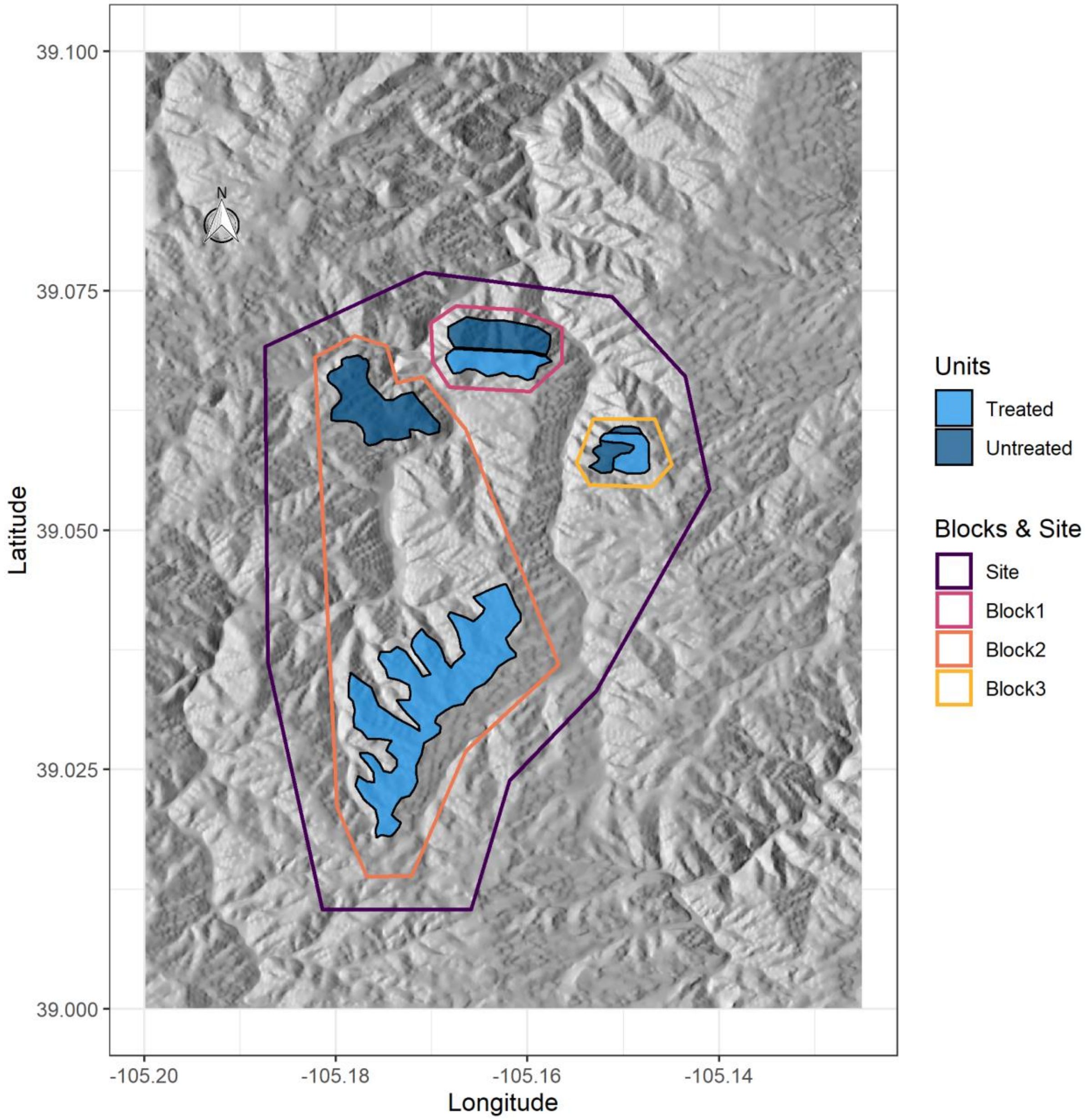

Figure 2. West Creek site, block, and unit map. This map demonstrates the nested structure of the study design. Each site consists of one to several blocks; each block contains a pair of forest units with similar characteristics, one treated unit and one untreated unit. Plots [not shown] were randomly placed within units. This figure shows the West Creek site; there were 8 sites in the study and 15 blocks.

Table 1. Site details. The number of plots is the total for the site.

Site	Number of plots	Number of blocks	Mean CWD (mm)	Mean Elevation (m)	Sampling date	Treatment date	Treatment methods
Estes Valley	21	3	76	2362	2011, 2012 or 2013, 2017	Winter/Spring 2011/12	Hand thinning with slash piled and burned, mastication
Heil Valley Ranch	8	1	145	2098	2011, 2013, 2017	Winter/Spring 2012/13	Mechanical thinning, with slash lopped and scattered
Phantom Creek 1	25	2	33	2670	2011, 2012, 2017	Summer 2011	Mechanical thinning, with slash removed
Phantom Creek 2	36	3	34	2745	2015, 2018, 2021	Spring 2017	Hand and mechanical thinning, with slash left on site
Payne Gulch	24	2	71	2434	2016, 2018, 2021	Winter 2017	Mechanical thinning, with slash removed
Raspberry	12	1	24	2982	2015, 2017, 2021	Winter 2015	Mastication
Ridge Road	12	2	97	2589	2015, 2017, 2020	Winter/Spring 2016/17	Hand and mechanical thinning, with slash piled and burned
West Creek	36	3	49	2607	2015, 2018, 2021	Fall 2016	Mechanical thinning, with slash left on site

Table 2. Differences in measurement techniques between protocols. Sites Estes Valley, Heil Valley Ranch, and Phantom Creek 1 used the SRLCC protocol. Phantom Creek 2 used the CFLRP protocol. Sites West Creek, Ridge Road, Payne Gulch, and Raspberry Mountain used the Mothership protocol.

Protocol	**CFLRP**	**Mothership**	**SRLCC**
Full plot area (m^2)	406	406	406
Number of understory transects	8	8	4
Number of intercepts per transect	25	25	100
Seedling plot area (m^2)	26.9	40.5	20.2

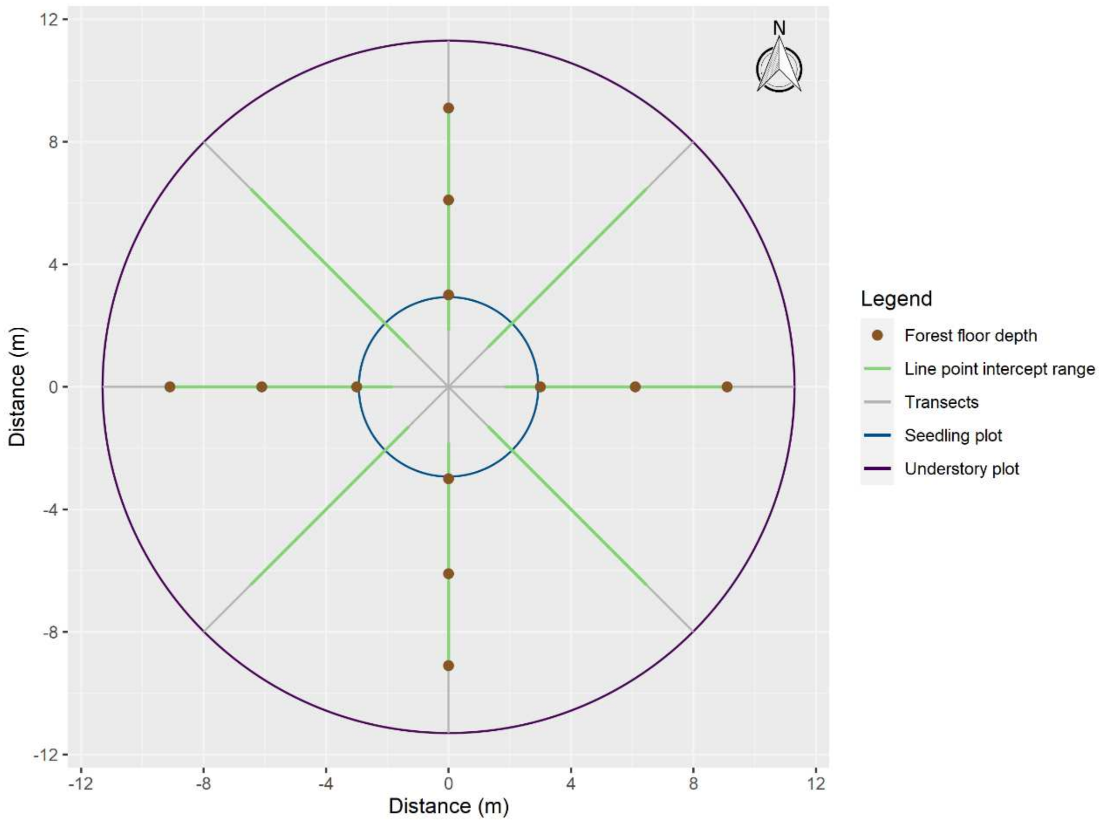

Figure 3. Simplified understory plot schematic. The number of transects and intercepts per transect varied by protocol, as did the radius of the seedling plot. Details on these variations can be found in **Table 2**.

Table 3. Plant species table. Plant species found in more than 40 plots in at least one sampling period, listed alphabetically by their scientific names. Some plants were identified to genus and may have higher plots counts due to the combination of several species under one genus.

			Number of Untreated Plots			Number of Treated Plots		
Common Name	**Scientific Name**	**Nativity, life span, vegetative spreading ability, growth form**	1-2 yrs Pre	1-2 yrs Post	4-6 yrs Post	1-2 yrs Pre	1-2 yrs Post	4-6 yrs Post
common yarrow	Achillea millefolium	Native, Long-lived, Vegetative growth, Forb	64	59	67	56	55	67
nodding onion	Allium cernuum	Native, Long-lived, Non-vegetative growth, Forb	50	41	53	60	58	67
small-leaf pussytoes	Antennaria parvifolia	Native, Long-lived, Vegetative growth, Forb	50	53	76	55	52	79
pygmyflower rockjasmine	Androsace septentrionalis	Native, Short-lived, Non-vegetative growth, Forb	52	18	39	49	50	60
Fendler's sandwort	Arenaria fendleri	Native, Long-lived, Non-vegetative growth, Forb	41	42	47	34	39	53
kinnikinnick	Arctostaphylos uva-ursi	Native, Long-lived, Non-vegetative growth, Shrub	74	76	76	71	71	74
purple reedgrass	Calamagrostis purpurascens	Native, Long-lived, Non-vegetative growth, Graminoid	66	64	66	61	63	61
sedge sp.	Carex sp.	Native, Long-lived, Both, Graminoid	81	82	83	90	82	91
bluebell bellflower	Campanula rotundifolia	Native, Long-lived, Non-vegetative growth, Forb	48	41	49	48	43	62
goosefoot sp.	Chenopodium sp.	Both, Both, Non-vegetative growth, Forb	2	1	27	18	43	53
fescue sp.	Festuca sp.	Both, Long-lived, Both, Graminoid	35	34	36	55	48	56
pineywoods geranium	Geranium caespitosum	Native, Long-lived, Non-vegetative growth, Forb	67	66	65	77	71	79
common juniper	Juniperus communis	Native, Long-lived, Non-vegetative growth, Shrub	69	67	72	75	68	68
prairie Junegrass	Koeleria macrantha	Native, Long-lived, Non-vegetative growth, Graminoid	63	61	65	76	65	81
mountain muhly	Muhlenbergia montana	Native, Long-lived, Non-vegetative growth, Graminoid	44	52	45	49	49	61
Fendler's ragwort	Packera fendleri	Native, Long-lived, Vegetative growth, Forb	42	39	45	48	48	56
bigflower cinquefoil	Potentilla fissa	Native, Long-lived, Non-vegetative growth, Forb	69	67	73	67	62	68
eastern pasqueflower	Pulsatilla patens	Native, Long-lived, Non-vegetative growth, Forb	51	50	51	52	55	57
rose sp.	Rosa sp.	Both, Long-lived, Non-vegetative growth, Shrub	51	53	57	46	38	43
spearleaf	Sedum	Native, Long-lived, Non-	52	57	55	48	52	48

stonecrop	lanceolatum	vegetative growth, Forb						
goldenrod sp.	Solidago sp.	Native, Long-lived, Both, Forb	73	71	74	83	76	86

Table 4. 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; n = 78 treated plots and n = 77 untreated plots. Significant (α = 0.050) p-values are shown in bold. For metrics where the treatment by time interaction was significant, pairwise comparisons between groups were evaluated using estimated marginal means; within sampling periods, values sharing letters were not statistically different.

Metric	**Untreated**			**Treated**			**Treatment**	**Time**	**Treatment x Time**
	1-2 yrs Pre	1-2 yrs Post	4-6 yrs Post	1-2 yrs Pre	1-2 yrs Post	4-6 yrs Post		**p-values**	
Basal area m^2 ha^{-1}	24.5 (22.2, 27.1)[a]	24.7 (22.4, 27.3)[a]	24.7 (22.4, 27.3)[a]	22.8 (20.6, 25.2)[a]	13.8 (12.3, 15.6)[b]	13.6 (12.1, 15.3)[b]	< 0.001	< 0.001	**< 0.001**
Tree seedlings ha^{-1}	6.8 (3.6, 12.9)	3.8 (2, 7.2)	2.9 (1.6, 7.2)	5.2 (2.8, 9.8)	3.6 (1.9, 6.8)	3.6 (1.9, 6.7)	0.786	< 0.001	0.254
Forest floor depth (cm)	5.6 (4.9, 6.3)	5.9 (5.2, 6.6)	4.8 (4.3, 6.6)	5.3 (4.7, 6)	5.2 (4.6, 5.9)	4.1 (3.7, 4.7)	0.002	< 0.001	0.453
Bare ground % cover	4.9 (3.4, 6.9)[a]	3.9 (2.7, 5.6)[a]	4.4 (3.1, 5.6)[a]	4.7 (3.3, 6.7)[a]	8 (5.7, 11.1)[b]	10 (7.3, 13.7)[b]	< 0.001	< 0.001	**< 0.001**
Fine wood % cover	14.2 (11.8, 16.9)[a]	15.5 (13, 18.4)[a]	15.1 (12.6, 18.4)[a]	14.3 (11.9, 17)[a]	25.3 (21.7, 29.1)[b]	21 (17.9, 24.4)[b]	< 0.001	< 0.001	**< 0.001**
Coarse wood % cover	1.7 (1.4, 2.1)	1.8 (1.5, 2.2)	1.5 (1.2, 2.2)	1.9 (1.6, 2.3)	2.4 (2, 2.9)	2.3 (1.9, 2.7)	< 0.001	0.157	0.265

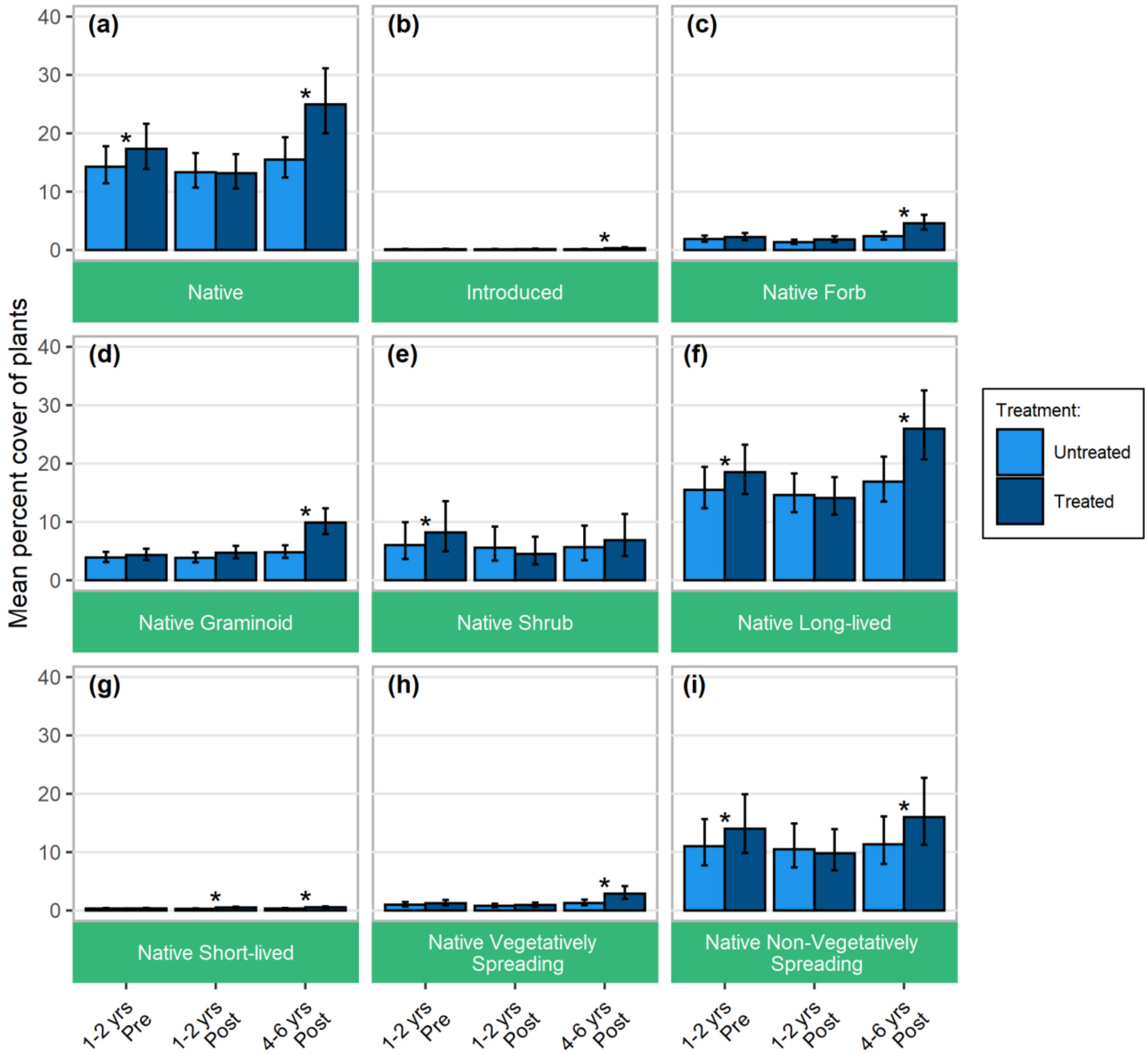

Figure 4. GLMM results for understory plant cover. Model means (and 95% confidence intervals) of understory percent cover 1-2 years before, 1-2 years after, and 4-6 years after restoration thinning treatments in dry conifer forests of the Colorado Front Range. Stars (*) indicate significant differences ($\alpha = 0.05$) between treated and untreated plots for that sampling period.

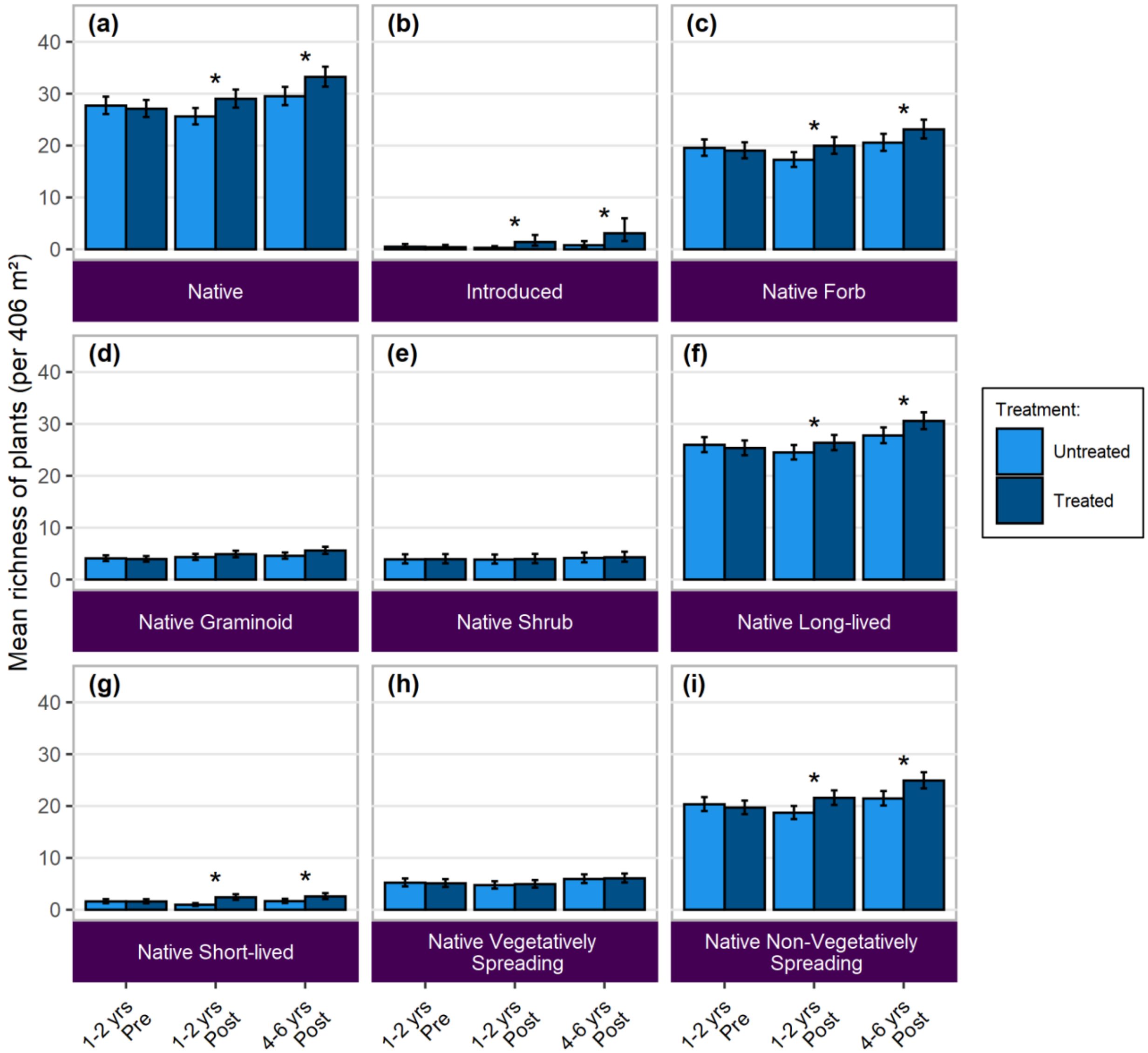

Figure 5. GLMM results for understory plant richness. Model means (and 95% confidence intervals) of understory richness 1-2 years before, 1-2 years after, and 4-6 years after restoration thinning treatments in dry conifer forests of the Colorado Front Range. Stars (*) indicate significant differences (α = 0.05) between treated and untreated plots for that sampling period.

Table 5. GLMM p-values for understory cover and richness analyses. Means (and standard errors) of understory plant metrics, 1-2 years after, and 4-6 years after restoration treatments in dry conifer forests of the Colorado Front Range; n = 78 treated plots and n = 77 untreated plots. Significant (α = 0.050) p-values for the Treatment x Time interaction are shown in bold.

Metric	**Treatment**	**Time**	**Treatment x Time**
		p-values	
Cover (%)			
Native	0.006	< 0.001	**< 0.001**
Introduced	0.004	< 0.001	**< 0.001**
Native Forb	0.003	< 0.001	**0.003**
Native Graminoid	< 0.001	< 0.001	**< 0.001**
Native Shrub	0.425	< 0.001	**< 0.001**
Native Long-lived	< 0.001	< 0.001	**0.001**
Native Short-lived	< 0.001	0.003	**< 0.001**
Native Vegetatively Spreading	0.001	< 0.001	**0.035**
Native Non-Vegetatively Spreading	0.002	< 0.001	**0.005**
Richness (species 406 m²)			
Native	< 0.001	< 0.001	**0.006**
Introduced	< 0.001	< 0.001	**< 0.001**
Native Forb	0.002	< 0.001	**0.010**
Native Graminoid	0.016	< 0.001	0.090
Native Shrub	0.635	0.263	0.973
Native Long-lived	0.013	< 0.001	**0.034**
Native Short-lived	< 0.001	0.006	**< 0.001**
Native Vegetatively Spreading	0.755	< 0.001	0.824
Native Non-Vegetatively Spreading	< 0.001	< 0.001	**0.001**

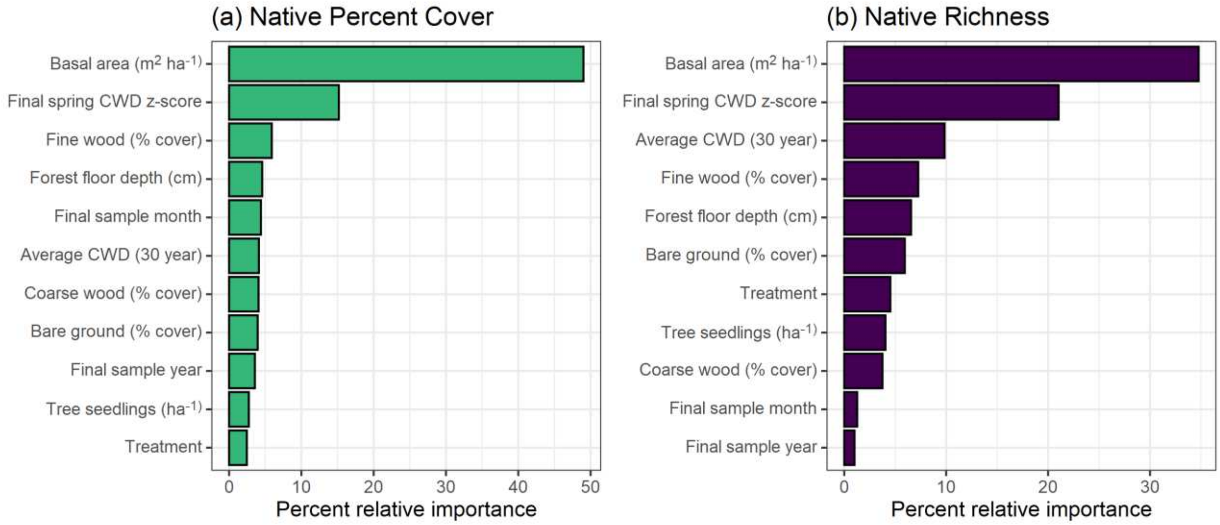

Figure 6. Relative influence plots. Relative influence of each variable in predicting percent cover (a) or richness (b) at 4-6 years after restoration treatments in dry conifer forests of the Colorado Front Range; n = 91 treated plots and n = 83 untreated plots.

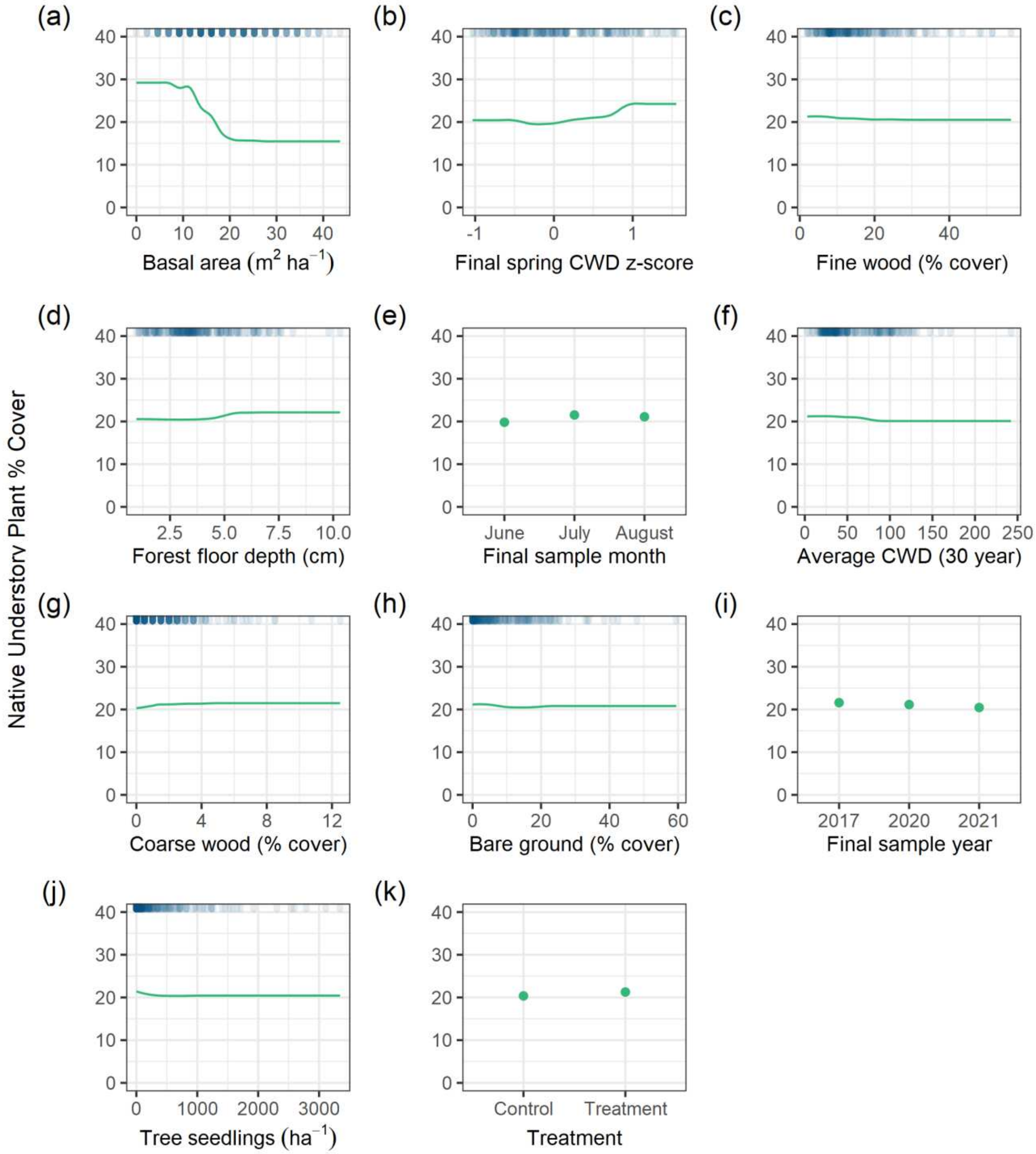

Figure 7. Native cover partial dependencies. Partial dependence figures show individual relationships between native understory cover and a single predictor after accounting for the average effect of the other predictors, at 4-6 years after restoration thinning treatments in dry conifer forests of the Colorado Front Range; n = 91 treated and n = 83 untreated plots. Each translucent blue mark at the top of each figure represents each plot's value of the predictor. Darker areas of overlapping marks indicate a greater amount of data informing the percent cover BRT model.

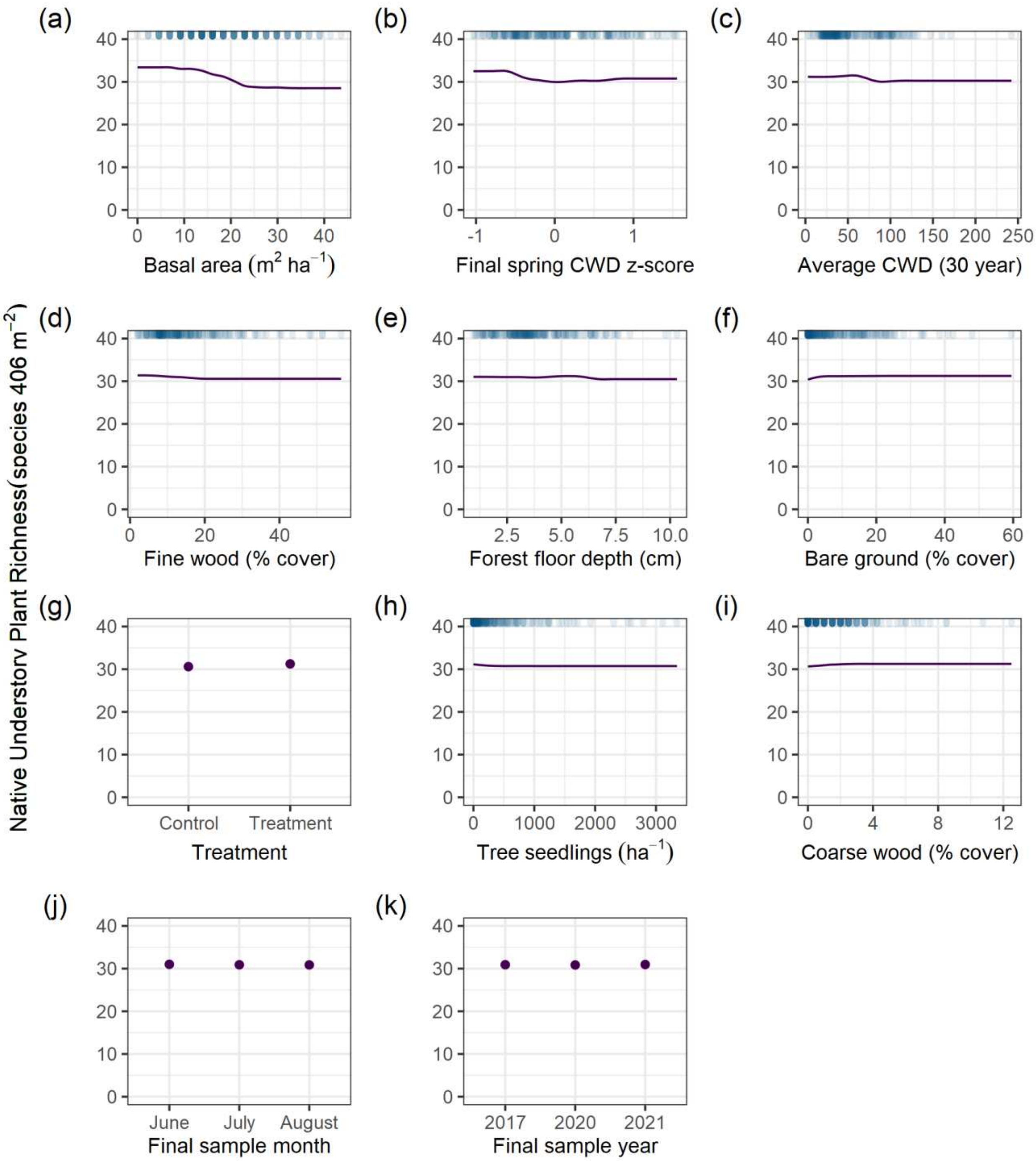

Figure 8. Native richness partial dependencies. Partial dependence plots show individual relationships between native understory richness (# species) and a single predictor after accounting for the average effect of the other predictors, at 4-6 years after restoration treatments in dry conifer forests of the Colorado Front Range; n = 91 treated and n = 83 untreated plots. Each translucent blue mark at the top of each figure represents each plot's value of the predictor. Darker areas of overlapping marks indicate a greater amount of data informing the richness BRT model.

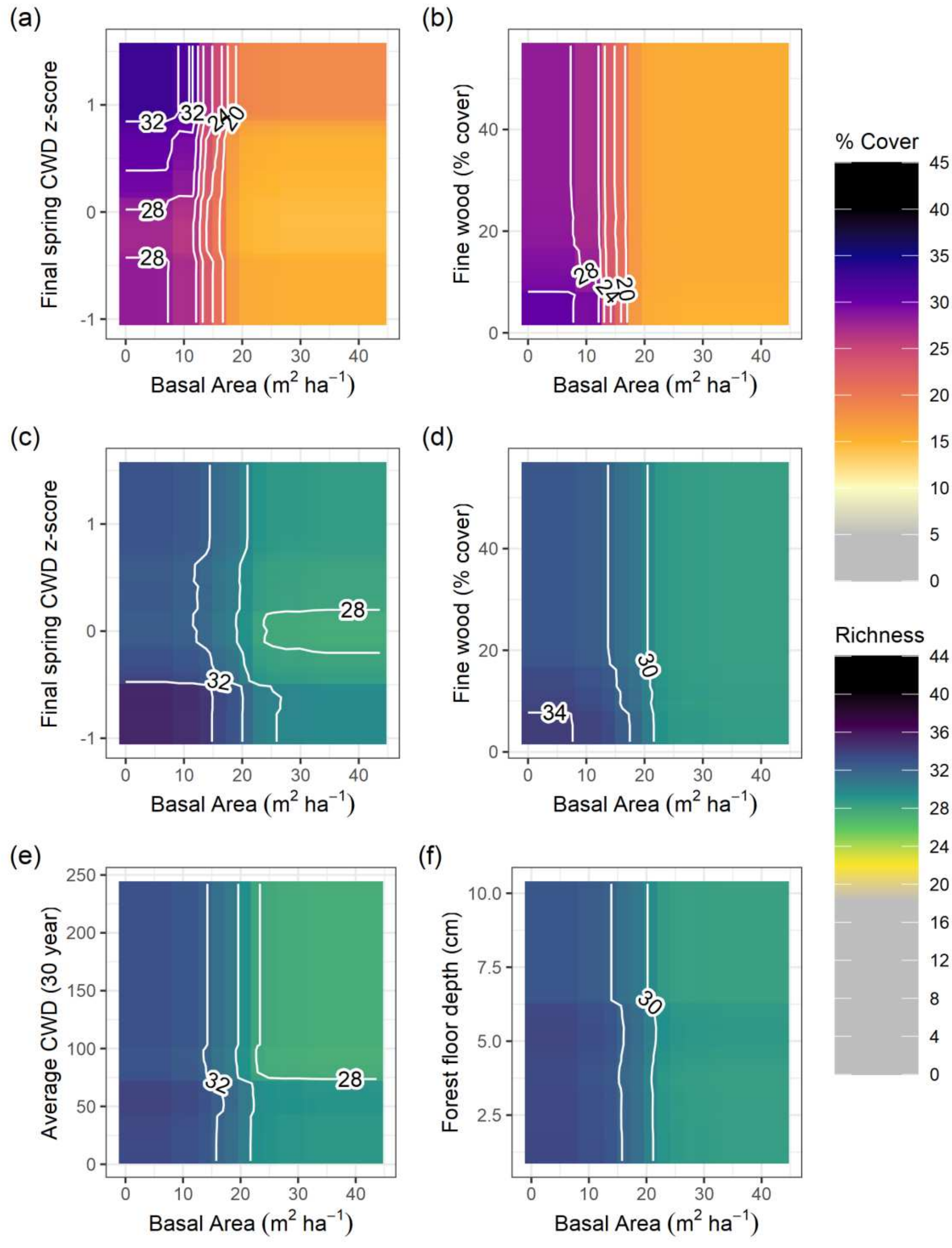

Figure 9. Variable interactions. Interactions between predictive variables at 4-6 years after restoration treatments in dry conifer forests of the Colorado Front Range; n = 91 treated and n = 83 untreated plots. Interacting variables are shown on the x and y axes; color fill indicates predicted values of either native understory cover (a-b) or richness (c-f). Interactions were shown only for variables of at least 5% relative importance. White contour lines aid in delineating differences in predictions.

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Appendix

Supplementary Table 1. Plant species found in at least one sampling period, listed alphabetically by their scientific names. Some plants were identified to genus and may have higher plots counts due to the combination of several species under one genus.

Common Name	Species	Nativity, life span, vegetative spreading ability, growth form	Number of Untreated Plots 1-2 yrs Pre	Number of Untreated Plots 1-2 yrs Post	Number of Untreated Plots 4-6 yrs Post	Number of Treated Plots 1-2 yrs Pre	Number of Treated Plots 1-2 yrs Post	Number of Treated Plots 4-6 yrs Post
Rocky Mountain maple	*Acer glabrum*	Native, Long-lived, Non-vegetative growth, Shrub	6	3	4	7	7	8
common yarrow	*Achillea millefolium*	Native, Long-lived, Vegetative growth, Forb	64	59	67	56	55	67
Letterman's needlegrass	*Achnatherum lettermanii*	Native, Long-lived, Non-vegetative growth, Graminoid	3	0	0	0	0	0
Columbia needlegrass	*Achnatherum nelsonii*	Native, Long-lived, Non-vegetative growth, Graminoid	0	2	2	1	1	1
sleepygrass	*Achnatherum robustum*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	2	0	0	0
crested wheatgrass	*Agropyron cristatum*	Introduced, Long-lived, Non-vegetative growth, Graminoid	0	0	0	0	0	1
rough bentgrass	*Agrostis scabra*	Native, Long-lived, Non-vegetative growth, Graminoid	4	0	1	2	2	9
stemless Indian parsley	*Aletes acaulis*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	0	0
Rocky Mountain Indian parsley	*Aletes anisatus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	2	0	0	1
sticky gilia	*Aliciella pinnatifida*	Native, Short-lived, Non-vegetative growth, Forb	2	1	1	4	0	4
nodding onion	*Allium cernuum*	Native, Long-lived, Non-vegetative growth, Forb	50	41	53	60	58	67
Geyer's onion	*Allium geyeri*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	1	2
alyssum	*Alyssum simplex*	Introduced, Short-lived,	0	0	0	0	1	0

		Non-vegetative growth, Forb						
Powell's amaranth	*Amaranthus powellii*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	2
annual ragweed	*Ambrosia artemisiifolia*	Native, Short-lived, Non-vegetative growth, Forb	1	0	0	1	2	0
Cuman ragweed	*Ambrosia psilostachya*	Native, Long-lived, Vegetative growth, Forb	0	0	0	2	0	3
western pearly everlasting	*Anaphalis margaritacea*	Native, Long-lived, Vegetative growth, Forb	2	0	3	4	0	4
big bluestem	*Andropogon gerardii*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	0	3	6
pygmyflower rockjasmine	*Androsace septentrionalis*	Native, Short-lived, Non-vegetative growth, Forb	52	18	39	49	50	60
Pacific anemone	*Anemone multifida*	Native, Long-lived, Vegetative growth, Forb	0	0	0	0	0	1
pearly pussytoes	*Antennaria anaphaloides*	Native, Long-lived, Vegetative growth, Forb	0	0	1	0	1	0
rush pussytoes	*Antennaria luzuloides*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	0	0
littleleaf pussytoes	*Antennaria microphylla*	Native, Long-lived, Vegetative growth, Forb	0	0	0	0	0	1
field pussytoes	*Antennaria neglecta*	Native, Long-lived, Vegetative growth, Forb	9	7	17	8	8	15
small-leaf pussytoes	*Antennaria parvifolia*	Native, Long-lived, Vegetative growth, Forb	50	53	76	55	52	79
rosy pussytoes	*Antennaria rosea*	Native, Long-lived, Vegetative growth, Forb	0	0	1	1	0	0
pussytoes sp.	*Antennaria sp.*	Native, Long-lived, Both, Forb	23	17	1	22	22	1
spreading dogbane	*Apocynum androsaemifolium*	Native, Long-lived, Vegetative growth, Forb	12	5	13	13	5	12
Colorado blue	*Aquilegia coerulea*	Native, Long-lived, Non-vegetative growth,	2	4	2	2	2	2

columbine		Forb						
spreadingpod rockcress	*Arabis ×divaricarpa*	Native, Long-lived, Non-vegetative growth, Forb	0	5	0	0	2	0
Drummond's rockcress	*Arabis drummondii*	Native, Long-lived, Non-vegetative growth, Forb	0	2	4	5	1	2
Fendler's rockcress	*Arabis fendleri*	Native, Long-lived, Non-vegetative growth, Forb	39	32	41	31	49	43
tower rockcress	*Arabis glabra*	Native, Short-lived, Non-vegetative growth, Forb	6	5	7	5	6	14
hairy rockcress	*Arabis hirsuta*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	9	0	4
rockcress sp.	*Arabis sp.*	Native, Long-lived, Non-vegetative growth, Forb	2	2	3	7	3	7
kinnikinnick	*Arctostaphylos uva-ursi*	Native, Long-lived, Non-vegetative growth, Shrub	74	76	76	71	71	74
Fendler's sandwort	*Arenaria fendleri*	Native, Long-lived, Non-vegetative growth, Forb	41	42	47	34	39	53
spreading sandwort	*Arenaria lanuginosa*	Native, Long-lived, Non-vegetative growth, Forb	1	1	1	1	0	2
heartleaf arnica	*Arnica cordifolia*	Native, Long-lived, Vegetative growth, Forb	0	0	1	1	3	1
foothill arnica	*Arnica fulgens*	Native, Long-lived, Vegetative growth, Forb	0	0	2	0	0	0
arnica sp.	*Arnica sp.*	Native, Long-lived, Both, Forb	0	0	0	1	0	0
field sagewort	*Artemisia campestris*	Native, Long-lived, Non-vegetative growth, Forb	3	2	2	3	4	5
prairie sagewort	*Artemisia frigida*	Native, Long-lived, Vegetative growth, Forb	14	14	13	25	22	36
white sagebrush	*Artemisia ludoviciana*	Native, Long-lived, Vegetative growth, Forb	30	27	27	40	35	44
aster sp.	*Aster sp.*	Native, Long-lived, Both, Forb	0	0	0	0	0	3
alpine	*Astragalus*	Native, Long-lived,	1	1	4	1	2	8

milkvetch	*alpinus*	Non-vegetative growth, Forb						
Laxmann's milkvetch	*Astragalus laxmannii*	Native, Long-lived, Non-vegetative growth, Forb	3	1	1	4	3	6
timber milkvetch	*Astragalus miser*	Native, Long-lived, Non-vegetative growth, Forb	10	11	11	1	5	6
Missouri milkvetch	*Astragalus missouriensis*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	0	0	0
Parry's milkvetch	*Astragalus parryi*	Native, Long-lived, Non-vegetative growth, Forb	6	3	2	7	9	6
Short's milkvetch	*Astragalus shortianus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	0	7
milk vetch sp.	*Astragalus sp.*	Both, Both, Both, Forb	1	0	0	6	1	3
Front Range milkvetch	*Astragalus sparsiflorus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	4
looseflower milkvetch	*Astragalus tenellus*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	2	1	1
ragleaf bahia	*Bahia dissecta*	Native, Short-lived, Non-vegetative growth, Forb	10	5	6	7	9	13
White River coraldrops	*Besseya plantaginea*	Native, Long-lived, Non-vegetative growth, Forb	0	6	6	0	5	6
pine dropseed	*Blepharoneuron tricholepis*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	0	5	6
blue grama	*Bouteloua gracilis*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	11	5	12
tasselflower brickellbush	*Brickellia grandiflora*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	1	1
field brome	*Bromus arvensis*	Introduced, Short-lived, Non-vegetative growth, Graminoid	0	0	0	0	1	2
rattlesnake brome	*Bromus briziformis*	Introduced, Short-lived, Non-vegetative growth, Graminoid	0	0	0	0	1	2
California brome	*Bromus carinatus*	Native, Short-lived, Non-vegetative growth, Graminoid	4	1	0	1	0	0

fringed brome	*Bromus ciliatus*	Native, Long-lived, Non-vegetative growth, Graminoid	6	9	16	4	16	21
smooth brome	*Bromus inermis*	Introduced, Long-lived, Vegetative growth, Graminoid	0	1	2	1	2	9
woolly brome	*Bromus lanatipes*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	2	0	0	1
Porter brome	*Bromus porteri*	Native, Long-lived, Non-vegetative growth, Graminoid	1	2	0	4	1	3
brome sp.	*Bromus sp.*	Both, Both, Both, Graminoid	0	0	0	0	1	2
cheatgrass	*Bromus tectorum*	Introduced, Short-lived, Non-vegetative growth, Graminoid	6	6	11	5	4	14
bluejoint	*Calamagrostis canadensis*	Native, Long-lived, Vegetative growth, Graminoid	1	0	0	0	0	0
purple reedgrass	*Calamagrostis purpurascens*	Native, Long-lived, Non-vegetative growth, Graminoid	66	64	66	61	63	61
Gunnison's mariposa lily	*Calochortus gunnisonii*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	0	0
mariposa lily sp.	*Calochortus sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
fairy slipper	*Calypso bulbosa*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	1	0	0
bluebell bellflower	*Campanula rotundifolia*	Native, Long-lived, Non-vegetative growth, Forb	48	41	49	48	43	62
nodding plumeless thistle	*Carduus nutans*	Introduced, Short-lived, Non-vegetative growth, Forb	1	0	3	2	9	18
sedge sp.	*Carex sp.*	Native, Long-lived, Both, Graminoid	81	82	83	90	82	91
wholeleaf Indian paintbrush	*Castilleja integra*	Native, Long-lived, Non-vegetative growth, Forb	3	1	2	6	5	5
Wyoming Indian paintbrush	*Castilleja linariifolia*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
giant red Indian	*Castilleja miniata*	Native, Long-lived, Non-vegetative growth,	0	1	2	0	0	4

paintbrush		Forb						
indian paintbrush sp.	*Castilleja sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	1	1
Fendler's ceanothus	*Ceanothus fendleri*	Native, Long-lived, Non-vegetative growth, Shrub	8	8	9	5	5	5
field chickweed	*Cerastium arvense*	Native, Long-lived, Vegetative growth, Forb	7	6	10	8	8	9
alderleaf mountain mahogany	*Cercocarpus montanus*	Native, Long-lived, Non-vegetative growth, Shrub	6	6	5	19	13	19
spotted sandmat	*Chamaesyce maculata*	Introduced, Short-lived, Non-vegetative growth, Forb	1	0	0	0	0	0
fireweed	*Chamerion angustifolium*	Native, Long-lived, Vegetative growth, Forb	6	4	9	9	11	27
goosefoot sp.	*Chenopodium sp.*	Both, Both, Non-vegetative growth, Forb	2	1	27	18	43	53
Canada thistle	*Cirsium arvense*	Introduced, Long-lived, Vegetative growth, Forb	1	0	0	2	12	31
prairie thistle	*Cirsium canescens*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
yellowspine thistle	*Cirsium ochrocentrum*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
meadow thistle	*Cirsium scariosum*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
thistle sp.	*Cirsium sp.*	Both, Both, Both, Forb	0	0	0	0	0	3
wavyleaf thistle	*Cirsium undulatum*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	1	3	5
bull thistle	*Cirsium vulgare*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	1	0	1
clematis sp.	*Clematis sp.*	Native, Long-lived, Non-vegetative growth, Forb	21	27	24	17	16	16
clematis sp.	*Clematis sp.*	Both, Long-lived, Both, Forb	0	0	0	0	0	1
maiden blue eyed Mary	*Collinsia parviflora*	Native, Short-lived, Non-vegetative growth,	8	5	13	4	2	11

		Forb						
tiny trumpet	*Collomia linearis*	Native, Short-lived, Non-vegetative growth, Forb	0	1	7	0	0	3
bastard toadflax	*Comandra umbellata*	Native, Long-lived, Vegetative growth, Forb	1	0	0	2	0	0
poison hemlock	*Conium maculatum*	Introduced, Short-lived, Non-vegetative growth, Forb	1	0	0	1	0	0
field bindweed	*Convolvulus arvensis*	Introduced, Long-lived, Vegetative growth, Forb	0	0	0	1	1	0
Canadian horseweed	*Conyza canadensis*	Native, Short-lived, Non-vegetative growth, Forb	0	0	1	1	8	5
summer coralroot	*Corallorhiza maculata*	Native, Long-lived, Vegetative growth, Forb	6	6	6	2	1	3
scrambled eggs	*Corydalis aurea*	Native, Short-lived, Non-vegetative growth, Forb	1	1	2	1	31	17
NA	*Cryptantha sp.*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
miner's candle	*Cryptantha virgata*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	2	1	6
gypsyflower	*Cynoglossum officinale*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	1	1
brittle bladderfern	*Cystopteris fragilis*	Native, Long-lived, Non-vegetative growth, Forb	8	2	2	8	5	5
Parry's oatgrass	*Danthonia parryi*	Native, Long-lived, Non-vegetative growth, Graminoid	4	9	0	4	11	3
oatgrass sp.	*Danthonia sp.*	Native, Long-lived, Non-vegetative growth, Graminoid	1	0	2	1	0	0
poverty oatgrass	*Danthonia spicata*	Native, Long-lived, Non-vegetative growth, Graminoid	3	0	0	3	1	1
shrubby cinquefoil	*Dasiphora fruticosa*	Native, Long-lived, Non-vegetative growth, Shrub	3	3	2	4	3	4
twolobe larkspur	*Delphinium nuttallianum*	Native, Long-lived, Non-vegetative growth,	1	0	0	0	0	0

		Forb						
mountain tansymustard	*Descurainia incana*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
western tansymustard	*Descurainia pinnata*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
herb sophia	*Descurainia sophia*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
golden draba	*Draba aurea*	Native, Long-lived, Non-vegetative growth, Forb	17	6	5	19	3	6
woodland draba	*Draba nemorosa*	Native, Short-lived, Non-vegetative growth, Forb	0	1	0	0	4	0
mountain draba	*Draba rectifructa*	Native, Short-lived, Non-vegetative growth, Forb	0	9	0	0	8	0
draba sp.	*Draba sp.*	Native, Both, Both, Forb	4	0	0	4	6	0
pretty draba	*Draba streptocarpa*	Native, Long-lived, Non-vegetative growth, Forb	13	7	18	22	25	32
American dragonhead	*Dracocephalum parviflorum*	Native, Short-lived, Non-vegetative growth, Forb	3	0	0	0	10	4
nylon hedgehog cactus	*Echinocereus viridiflorus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
Montana wheatgrass	*Elymus albicans*	Native, Long-lived, Vegetative growth, Graminoid	0	3	1	0	4	1
Canada wildrye	*Elymus canadensis*	Native, Long-lived, Non-vegetative growth, Graminoid	2	0	0	0	0	2
squirreltail	*Elymus elymoides*	Native, Long-lived, Non-vegetative growth, Graminoid	13	7	14	20	20	36
thickspike wheatgrass	*Elymus lanceolatus*	Native, Long-lived, Vegetative growth, Graminoid	0	0	0	1	0	1
slender wheatgrass	*Elymus trachycaulus*	Native, Long-lived, Non-vegetative growth, Graminoid	0	2	2	1	2	13
tall annual willowherb	*Epilobium brachycarpum*	Native, Short-lived, Non-vegetative growth, Forb	0	0	3	0	0	6

fringed willowherb	*Epilobium ciliatum*	Native, Long-lived, Non-vegetative growth, Forb	0	1	0	0	0	1
Parry's rabbitbrush	*Ericameria parryi*	Native, Long-lived, Non-vegetative growth, Shrub	0	0	0	0	0	1
bitter fleabane	*Erigeron acris*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
hoary fleabane	*Erigeron canus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	2	1
running fleabane	*Erigeron colomexicanus*	Native, Short-lived, Vegetative growth, Forb	0	0	0	0	3	0
cutleaf daisy	*Erigeron compositus*	Native, Long-lived, Non-vegetative growth, Forb	20	16	20	16	12	21
tall fleabane	*Erigeron elatior*	Native, Long-lived, Non-vegetative growth, Forb	1	0	1	4	0	1
trailing fleabane	*Erigeron flagellaris*	Native, Short-lived, Vegetative growth, Forb	1	4	3	4	9	10
beautiful fleabane	*Erigeron formosissimus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	3	1
fleabane sp.	*Erigeron sp.*	Native, Both, Both, Forb	0	0	1	2	2	2
aspen fleabane	*Erigeron speciosus*	Native, Long-lived, Non-vegetative growth, Forb	1	3	3	3	4	3
threenerve fleabane	*Erigeron subtrinervis*	Native, Long-lived, Non-vegetative growth, Forb	3	0	1	3	0	1
early bluetop fleabane	*Erigeron vetensis*	Native, Long-lived, Non-vegetative growth, Forb	9	7	5	15	15	18
winged buckwheat	*Eriogonum alatum*	Native, Long-lived, Non-vegetative growth, Forb	3	0	0	5	7	5
sulphur-flower buckwheat	*Eriogonum umbellatum*	Native, Long-lived, Non-vegetative growth, Forb	5	5	6	1	1	1
sanddune wallflower	*Erysimum capitatum*	Native, Short-lived, Non-vegetative growth, Forb	17	12	18	12	10	23
shy	*Erysimum*	Native, Short-lived,	0	0	0	1	0	0

wallflower	*inconspicuum*	Non-vegetative growth, Forb						
spurge sp.	*Euphorbia sp.*	Both, Both, Both, Forb	2	1	2	11	3	7
fescue sp.	*Festuca sp.*	Both, Long-lived, Both, Graminoid	35	34	36	55	48	56
strawberry sp.	*Fragaria sp.*	Native, Long-lived, Vegetative growth, Forb	47	43	48	49	45	47
elkweed	*Frasera speciosa*	Native, Long-lived, Non-vegetative growth, Forb	33	34	33	43	38	39
blanketflowe r	*Gaillardia aristata*	Native, Long-lived, Non-vegetative growth, Forb	3	3	3	4	5	7
northern bedstraw	*Galium boreale*	Native, Long-lived, Vegetative growth, Forb	12	10	14	10	10	11
spreading groundsmok e	*Gayophytum diffusum*	Native, Short-lived, Non-vegetative growth, Forb	3	0	4	1	0	8
pleated gentian	*Gentiana affinis*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	2	0	0
gentian sp.	*Gentiana sp.*	Native, Long-lived, Both, Forb	0	0	0	6	0	0
autumn dwarf gentian	*Gentianella amarella*	Native, Short-lived, Non-vegetative growth, Forb	12	5	4	23	9	10
pineywoods geranium	*Geranium caespitosum*	Native, Long-lived, Non-vegetative growth, Forb	67	66	65	77	71	79
eyed gilia	*Gilia ophthalmoides*	Native, Short-lived, Non-vegetative growth, Forb	0	1	0	0	2	0
western marsh cudweed	*Gnaphalium palustre*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	1	0	1
cudweed sp.	*Gnaphalium sp.*	Unknown, short-lived, Non-vegetative growth, Forb	0	0	1	0	0	5
curlycup gumweed	*Grindelia squarrosa*	Native, Short-lived, Non-vegetative growth, Forb	0	0	2	0	1	2
subalpine gumweed	*Grindelia subalpina*	Native, Short-lived, Non-vegetative growth, Forb	2	2	2	3	3	2
whiskbroom parsley	*Harbouria trachypleura*	Native, Long-lived, Non-vegetative growth,	13	13	12	12	9	6

		Forb						
Parry's dwarf-sunflower	*Helianthella parryi*	Native, Long-lived, Non-vegetative growth, Forb	11	10	4	7	10	9
common sunflower	*Helianthus annuus*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
little sunflower	*Helianthus pumilus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
needle and thread	*Hesperostipa comata*	Native, Long-lived, Non-vegetative growth, Graminoid	0	2	0	4	4	4
hairy false goldenaster	*Heterotheca villosa*	Native, Long-lived, Non-vegetative growth, Forb	27	25	29	34	26	47
bracted alumroot	*Heuchera bracteata*	Native, Long-lived, Non-vegetative growth, Forb	0	1	0	0	1	0
littleleaf alumroot	*Heuchera parvifolia*	Native, Long-lived, Non-vegetative growth, Forb	5	6	10	7	5	8
white hawkweed	*Hieracium albiflorum*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	0	0	1
yellow hawkweed	*Hieracium fendleri*	Native, Long-lived, Non-vegetative growth, Forb	5	5	5	9	9	10
hawkweed sp.	*Hieracium sp.*	Both, Long-lived, Non-vegetative growth, Forb	0	3	0	0	1	2
rockspirea	*Holodiscus dumosus*	Native, Long-lived, Non-vegetative growth, Shrub	0	0	1	0	0	0
foxtail barley	*Hordeum jubatum*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	0	1	5
barley sp.	*Hordeum sp.*	Both, Both, Non-vegetative growth, Graminoid	1	0	0	0	0	0
babyslippers	*Hybanthus verticillatus*	Native, Long-lived, Non-vegetative growth, Forb	0	3	0	0	0	0
NA	*Hymenopappus sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	1	0	0	0	0
scarlet gilia	*Ipomopsis aggregata*	Native, Short-lived, Non-vegetative growth,	12	10	16	17	16	23

		Forb						
fivepetal cliffbush	*Jamesia americana*	Native, Long-lived, Non-vegetative growth, Shrub	12	11	12	7	7	5
common juniper	*Juniperus communis*	Native, Long-lived, Non-vegetative growth, Shrub	69	67	72	75	68	68
prairie Junegrass	*Koeleria macrantha*	Native, Long-lived, Non-vegetative growth, Graminoid	63	61	65	76	65	81
prickly lettuce	*Lactuca serriola*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	8	1	4	17
Coulter's horseweed	*Laennecia coulteri*	Native, Short-lived, Non-vegetative growth, Forb	0	0	2	0	0	3
pineland horseweed	*Laennecia schiedeana*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	3	1
flatspine stickseed	*Lappula occidentalis*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
European stickseed	*Lappula squarrosa*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
field pepperweed	*Lepidium campestre*	Introduced, Short-lived, Non-vegetative growth, Forb	0	1	0	0	1	0
common pepperweed	*Lepidium densiflorum*	Introduced, Short-lived, Non-vegetative growth, Forb	0	1	0	0	1	1
mountain bladderpod	*Lesquerella montana*	Native, Long-lived, Non-vegetative growth, Forb	0	1	1	0	0	0
spike fescue	*Leucopoa kingii*	Native, Long-lived, Vegetative growth, Graminoid	5	6	7	6	10	8
beardless wildrye	*Leymus triticoides*	Native, Long-lived, Vegetative growth, Graminoid	0	0	0	0	0	1
dotted blazing star	*Liatris punctata*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	5	4	5
Dalmatian toadflax	*Linaria dalmatica*	Introduced, Long-lived, Vegetative growth, Forb	2	2	0	4	1	3
butter and eggs	*Linaria vulgaris*	Introduced, Long-lived, Non-vegetative growth,	1	0	1	1	2	7

		Forb						
twinflower	*Linnaea borealis*	Native, Long-lived, Vegetative growth, Shrub	4	1	3	2	2	2
Lewis flax	*Linum lewisii*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	0	0
narrowleaf stoneseed	*Lithospermum incisum*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	2	3
manyflowered stoneseed	*Lithospermum multiflorum*	Native, Long-lived, Non-vegetative growth, Forb	15	18	18	12	13	12
stoneseed sp.	*Lithospermum sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
twinberry honeysuckle	*Lonicera involucrata*	Native, Long-lived, Non-vegetative growth, Shrub	0	2	3	0	2	4
silvery lupine	*Lupinus argenteus*	Native, Long-lived, Non-vegetative growth, Forb	2	1	3	5	3	10
smallflowered woodrush	*Luzula parviflora*	Native, Long-lived, Vegetative growth, Graminoid	0	0	0	0	0	1
bristly wolfstail	*Lycurus setosus*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	0	1	0
Bigelow's tansyaster	*Machaeranthera bigelovii*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	3	2	11
hoary tansyaster	*Machaeranthera canescens*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	4
creeping barberry	*Mahonia repens*	Native, Long-lived, Vegetative growth, Shrub	4	4	5	1	1	1
feathery false lily of the valley	*Maianthemum racemosum*	Native, Long-lived, Vegetative growth, Forb	2	1	7	1	0	1
starry false lily of the valley	*Maianthemum stellatum*	Native, Long-lived, Vegetative growth, Forb	35	30	34	30	23	22
sweetclover	*Melilotus officinalis*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	1	0	1
prairie bluebells	*Mertensia lanceolata*	Native, Long-lived, Non-vegetative growth,	45	41	43	45	45	50

		Forb						
wild bergamot	*Monarda fistulosa*	Native, Long-lived, Vegetative growth, Forb	2	1	1	0	1	1
mountain muhly	*Muhlenbergia montana*	Native, Long-lived, Non-vegetative growth, Graminoid	44	52	45	49	49	61
green needlegrass	*Nassella viridula*	Native, Long-lived, Non-vegetative growth, Graminoid	3	3	1	2	2	1
catnip	*Nepeta cataria*	Introduced, Long-lived, Non-vegetative growth, Forb	0	0	0	0	2	1
Fendler's pennycress	*Noccaea fendleri*	Native, Long-lived, Non-vegetative growth, Forb	29	15	44	26	20	45
noccaea sp.	*Noccaea sp.*	Native, Both, Non-vegetative growth, Forb	3	9	2	1	7	0
tufted evening primrose	*Oenothera caespitosa*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
crownleaf evening primrose	*Oenothera coronopifolia*	Native, Long-lived, Vegetative growth, Forb	0	0	0	1	0	7
tulip pricklypear	*Opuntia phaeacantha*	Native, Long-lived, Non-vegetative growth, Shrub	0	1	0	0	1	1
plains pricklypear	*Opuntia polyacantha*	Native, Long-lived, Non-vegetative growth, Forb	3	2	0	2	0	0
prickly pear sp.	*Opuntia sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	0	3	0	0	0
sidebells wintergreen	*Orthilia secunda*	Native, Long-lived, Vegetative growth, Forb	1	3	4	3	5	2
yellow owl's-clover	*Orthocarpus luteus*	Native, Short-lived, Non-vegetative growth, Forb	1	0	2	0	0	0
roughleaf ricegrass	*Oryzopsis asperifolia*	Native, Long-lived, Non-vegetative growth, Graminoid	3	0	3	4	1	9
nodding locoweed	*Oxytropis deflexa*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
purple locoweed	*Oxytropis lambertii*	Native, Long-lived, Non-vegetative growth,	8	8	10	7	3	11

		Forb						
Nuttall's oxytrope	*Oxytropis multiceps*	Native, Long-lived, Non-vegetative growth, Forb	6	3	4	5	3	8
showy locoweed	*Oxytropis splendens*	Native, Long-lived, Non-vegetative growth, Forb	0	1	1	0	0	0
woolly groundsel	*Packera cana*	Native, Long-lived, Non-vegetative growth, Forb	25	26	26	37	35	40
Fendler's ragwort	*Packera fendleri*	Native, Long-lived, Vegetative growth, Forb	42	39	45	48	48	56
threetooth ragwort	*Packera tridenticulata*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	1	0
James' nailwort	*Paronychia jamesii*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
western wheatgrass	*Pascopyrum smithii*	Native, Long-lived, Vegetative growth, Graminoid	2	0	0	0	0	0
Canadian lousewort	*Pedicularis canadensis*	Native, Long-lived, Non-vegetative growth, Forb	4	4	4	7	4	8
giant lousewort	*Pedicularis procera*	Native, Long-lived, Non-vegetative growth, Forb	2	2	2	0	0	0
mountain ball cactus	*Pediocactus simpsonii*	Native, Long-lived, Non-vegetative growth, Shrub	4	0	4	12	5	7
sawsepal penstemon	*Penstemon glaber*	Native, Long-lived, Non-vegetative growth, Forb	18	14	19	25	22	42
upland beardtongue	*Penstemon saxosorum*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
sidebells penstemon	*Penstemon secundiflorus*	Native, Long-lived, Non-vegetative growth, Forb	5	1	4	12	10	13
NA	*Penstemon sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	0	6	0	0	0
Rocky Mountain penstemon	*Penstemon strictus*	Native, Long-lived, Vegetative growth, Forb	0	0	0	0	0	1
Front Range beardtongue	*Penstemon virens*	Native, Long-lived, Non-vegetative growth,	39	43	42	31	42	50

		Forb						
Whipple's penstemon	*Penstemon whippleanus*	Native, Long-lived, Non-vegetative growth, Forb	7	4	4	6	5	5
white phacelia	*Phacelia alba*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	2	0
Rocky Mountain phacelia	*Phacelia denticulata*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	6
silverleaf phacelia	*Phacelia hastata*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	3
varileaf phacelia	*Phacelia heterophylla*	Native, Long-lived, Non-vegetative growth, Forb	2	1	2	3	3	11
silky phacelia	*Phacelia sericea*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	0	0	0
timothy	*Phleum pratense*	Introduced, Long-lived, Non-vegetative growth, Graminoid	2	0	0	0	1	2
flowery phlox	*Phlox multiflora*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	1	1
prairie groundcherry	*Physalis hispida*	Native, Long-lived, Vegetative growth, Forb	0	0	0	0	1	0
husk tomato	*Physalis pubescens*	Native, Short-lived, Non-vegetative growth, Forb	0	1	0	0	0	0
mountain ninebark	*Physocarpus monogynus*	Native, Long-lived, Non-vegetative growth, Shrub	5	6	8	5	4	7
little ricegrass	*Piptatheropsis exigua*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	1	0	0
littleseed ricegrass	*Piptatheropsis micrantha*	Native, Long-lived, Non-vegetative growth, Graminoid	1	0	1	0	0	0
plains bluegrass	*Poa arida*	Native, Long-lived, Vegetative growth, Graminoid	0	1	0	0	0	0
Canada bluegrass	*Poa compressa*	Introduced, Long-lived, Vegetative growth, Graminoid	12	6	10	5	5	13
Cusick's bluegrass	*Poa cusickii*	Native, Long-lived, Non-vegetative growth,	0	0	1	0	1	3

		Graminoid						
muttongrass	*Poa fendleriana*	Native, Long-lived, Non-vegetative growth, Graminoid	21	21	22	25	29	37
glaucous bluegrass	*Poa glauca*	Native, Long-lived, Vegetative growth, Graminoid	0	2	1	0	1	0
wood bluegrass	*Poa nemoralis*	Native, Long-lived, Non-vegetative growth, Graminoid	2	3	3	0	4	4
fowl bluegrass	*Poa palustris*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	0	0	7
Kentucky bluegrass	*Poa pratensis*	Introduced, Long-lived, Vegetative growth, Graminoid	7	1	4	6	9	15
Sandberg bluegrass	*Poa secunda*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	2	2	2
bluegrass sp.	*Poa sp.*	Both, Both, Both, Graminoid	1	1	1	2	2	3
Tracy's bluegrass	*Poa tracyi*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	1	0	0	3
black bindweed	*Polygonum convolvulus*	Native, Short-lived, Non-vegetative growth, Forb	0	0	1	0	0	3
Douglas' knotweed	*Polygonum douglasii*	Native, Short-lived, Non-vegetative growth, Forb	1	1	0	2	1	5
broadleaf knotweed	*Polygonum minimum*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
Rocky Mountain polypody	*Polypodium saximontanum*	Native, Long-lived, Vegetative growth, Forb	1	0	0	2	0	0
elegant cinquefoil	*Potentilla concinna*	Native, Long-lived, Non-vegetative growth, Forb	0	2	4	1	9	10
bigflower cinquefoil	*Potentilla fissa*	Native, Long-lived, Non-vegetative growth, Forb	69	67	73	67	62	68
sticky cinquefoil	*Potentilla glandulosa*	Native, Long-lived, Vegetative growth, Forb	2	1	1	7	0	2
slender cinquefoil	*Potentilla gracilis*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	0	1

woolly cinquefoil	*Potentilla hippiana*	Native, Long-lived, Non-vegetative growth, Forb	40	34	37	44	41	46
beautiful cinquefoil	*Potentilla pulcherrima*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
cinquefoil sp.	*Potentilla sp.*	Native, Both, Non-vegetative growth, Forb	0	0	0	0	1	0
chokecherry	*Prunus virginiana*	Native, Long-lived, Non-vegetative growth, Shrub	12	15	15	5	6	5
alpine false springparsley	*Pseudocymopterus montanus*	Native, Long-lived, Non-vegetative growth, Forb	15	20	25	20	15	26
Wright's cudweed	*Pseudognaphalium canescens*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
Macoun's cudweed	*Pseudognaphalium macounii*	Native, Short-lived, Non-vegetative growth, Forb	3	0	0	2	2	2
cottonbatting plant	*Pseudognaphalium stramineum*	Native, Short-lived, Non-vegetative growth, Forb	0	0	1	0	0	1
bluebunch wheatgrass	*Pseudoroegneria spicata*	Native, Long-lived, Non-vegetative growth, Graminoid	10	0	2	5	0	2
woodland pinedrops	*Pterospora andromedea*	Native, Long-lived, Non-vegetative growth, Forb	4	2	4	5	1	1
Nuttall's alkaligrass	*Puccinellia nuttalliana*	Native, Long-lived, Vegetative growth, Graminoid	0	1	0	0	0	0
eastern pasqueflower	*Pulsatilla patens*	Native, Long-lived, Non-vegetative growth, Forb	51	50	51	52	55	57
antelope bitterbrush	*Purshia tridentata*	Native, Long-lived, Non-vegetative growth, Shrub	7	7	6	7	7	7
greenflowered wintergreen	*Pyrola chlorantha*	Native, Long-lived, Vegetative growth, Forb	15	10	12	17	4	5
wintergreen sp.	*Pyrola sp.*	Native, Long-lived, Vegetative growth, Forb	0	0	1	0	0	0
Gambel oak	*Quercus gambelii*	Native, Long-lived, Vegetative growth, Shrub	1	2	1	1	0	0

tadpole buttercup	*Ranunculus ranunculinus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	5	0	1	3
buttercup sp.	*Ranunculus sp.*	Native, Both, Both, Forb	2	0	0	1	0	0
skUnknownb ush sumac	*Rhus trilobata*	Native, Long-lived, Vegetative growth, Shrub	1	1	0	1	1	1
wax currant	*Ribes cereum*	Native, Long-lived, Non-vegetative growth, Shrub	28	27	30	39	37	43
whitestem gooseberry	*Ribes inerme*	Native, Long-lived, Non-vegetative growth, Shrub	0	1	2	4	6	8
gooseberry currant	*Ribes montigenum*	Native, Long-lived, Non-vegetative growth, Shrub	0	0	0	0	0	1
currant sp.	*Ribes sp.*	Native, Long-lived, Non-vegetative growth, Shrub	1	0	1	0	0	0
rose sp.	*Rosa sp.*	Both, Long-lived, Non-vegetative growth, Shrub	51	53	57	46	38	43
delicious raspberry	*Rubus deliciosus*	Native, Long-lived, Non-vegetative growth, Shrub	3	2	1	4	3	5
American red raspberry	*Rubus idaeus*	Native, Long-lived, Non-vegetative growth, Shrub	2	2	2	2	16	27
common sheep sorrel	*Rumex acetosella*	Introduced, Long-lived, Vegetative growth, Forb	0	0	0	0	0	1
dock sp.	*Rumex salicifolius mexicanus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
park willow	*Salix monticola*	Native, Long-lived, Non-vegetative growth, Shrub	0	0	2	1	1	3
Scouler's willow	*Salix scouleriana*	Native, Long-lived, Non-vegetative growth, Shrub	0	0	0	1	0	1
willow sp.	*Salix sp.*	Native, Long-lived, Non-vegetative growth, Shrub	1	1	1	0	2	1
red elderberry	*Sambucus racemosa*	Native, Long-lived, Non-vegetative growth, Shrub	0	0	0	0	0	1
yellowdot	*Saxifraga*	Native, Long-lived,	3	5	6	1	2	1

saxifrage	*bronchialis*	Non-vegetative growth, Forb						
little bluestem	*Schizachyrium scoparium*	Native, Long-lived, Non-vegetative growth, Graminoid	2	2	1	7	1	4
Britton's skullcap	*Scutellaria brittonii*	Native, Long-lived, Vegetative growth, Forb	15	13	16	21	15	24
spearleaf stonecrop	*Sedum lanceolatum*	Native, Long-lived, Non-vegetative growth, Forb	52	57	55	48	52	48
thickleaf ragwort	*Senecio crassulus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
desert ragwort	*Senecio eremophilus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	5	1
lambstongue ragwort	*Senecio integerrimus*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	0	3
openwoods ragwort	*Senecio rapifolius*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	0	1
Riddell's ragwort	*Senecio riddellii*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	1	1	0
tall ragwort	*Senecio serra*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	0	1	0
ragwort sp.	*Senecio sp.*	Both, Both, Both, Forb	1	3	1	1	0	2
broom-like ragwort	*Senecio spartioides*	Native, Long-lived, Non-vegetative growth, Forb	3	0	0	0	2	2
Wooton's ragwort	*Senecio wootonii*	Native, Long-lived, Non-vegetative growth, Forb	3	2	6	1	0	0
green bristlegrass	*Setaria viridis*	Introduced, Short-lived, Non-vegetative growth, Graminoid	0	0	0	0	1	0
russet buffaloberry	*Shepherdia canadensis*	Native, Long-lived, Non-vegetative growth, Shrub	2	2	2	6	4	3
sleepy silene	*Silene antirrhina*	Native, Short-lived, Non-vegetative growth, Forb	1	0	1	1	4	0
Drummond's campion	*Silene drummondii*	Native, Long-lived, Non-vegetative growth, Forb	4	0	8	3	2	14

bladder campion	*Silene latifolia*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
simple campion	*Silene scouleri*	Native, Long-lived, Non-vegetative growth, Forb	22	22	16	22	26	28
catchfly sp.	*Silene sp.*	Both, Both, Both, Forb	0	0	1	0	0	5
tall tumblemustard	*Sisymbrium altissimum*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
hoe nightshade	*Solanum physalifolium*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	0	2
cutleaf nightshade	*Solanum triflorum*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	3	5
goldenrod sp.	*Solidago sp.*	Native, Long-lived, Both, Forb	73	71	74	83	76	86
spiny sowthistle	*Sonchus asper*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	0	0	3	0
sand dropseed	*Sporobolus cryptandrus*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	1	0	0
starwort sp.	*Stellaria sp.*	Both, Both, Both, Forb	0	0	1	0	0	5
claspleaf twistedstalk	*Streptopus amplexifolius*	Native, Long-lived, Vegetative growth, Forb	0	0	0	0	0	1
common snowberry	*Symphoricarpos albus*	Native, Long-lived, Vegetative growth, Shrub	8	7	6	6	5	6
western snowberry	*Symphoricarpos occidentalis*	Native, Long-lived, Vegetative growth, Shrub	1	3	0	1	1	0
snowberry sp.	*Symphoricarpos sp.*	Native, Long-lived, Both, Shrub	0	0	3	4	0	1
smooth white aster	*Symphyotrichum porteri*	Native, Long-lived, Non-vegetative growth, Forb	16	6	3	10	6	9
aster sp.	*Symphyotrichum sp.*	Both, Long-lived, Both, Forb	0	0	3	0	0	2
common dandelion	*Taraxacum officinale*	Introduced, Long-lived, Non-vegetative growth, Forb	9	5	16	8	23	50
Fendler's meadow-rue	*Thalictrum fendleri*	Native, Long-lived, Non-vegetative growth, Forb	7	3	7	2	2	3
spreadfruit	*Thermopsis*	Native, Long-lived,	9	8	7	6	4	7

goldenbanner	*divaricarpa*	Vegetative growth, Forb						
field pennycress	*Thlaspi arvense*	Introduced, Short-lived, Non-vegetative growth, Forb	0	0	1	0	0	0
prairie spiderwort	*Tradescantia occidentalis*	Native, Long-lived, Non-vegetative growth, Forb	1	0	0	2	4	3
yellow salsify	*Tragopogon dubius*	Introduced, Short-lived, Non-vegetative growth, Forb	1	3	6	5	9	25
clasping Venus' looking-glass	*Triodanis perfoliata*	Native, Short-lived, Non-vegetative growth, Forb	0	0	0	0	1	0
spike trisetum	*Trisetum spicatum*	Native, Long-lived, Non-vegetative growth, Graminoid	0	0	0	1	0	0
forb sp.	*Unknown*	Unknown, Unknown, Unknown, Forb	4	4	8	4	27	12
graminoid sp.	*Unknown*	Unknown, Unknown, Unknown, Graminoid	6	2	4	5	4	3
plant sp.	*Unknown*	Unknown, Unknown, Unknown, Unknown	3	4	10	11	21	21
aster family sp.	*Unknown sp.*	Unknown, Unknown, Unknown, Unknown	0	2	1	0	2	4
mustard family sp.	*Unknown sp.*	Unknown, Unknown, Unknown, Unknown	0	0	1	0	0	0
grass family sp.	*Unknown sp.*	Unknown, Unknown, Unknown, Graminoid	0	0	2	0	0	4
dwarf bilberry	*Vaccinium cespitosum*	Native, Long-lived, Vegetative growth, Shrub	1	1	1	1	0	0
whortleberry	*Vaccinium myrtillus*	Native, Long-lived, Vegetative growth, Shrub	0	0	0	1	2	3
blueberry sp.	*Vaccinium sp.*	Native, Long-lived, Vegetative growth, Shrub	0	0	0	1	0	0
western valerian	*Valeriana occidentalis*	Native, Long-lived, Vegetative growth, Forb	1	0	0	0	0	0
common mullein	*Verbascum thapsus*	Introduced, Short-lived, Non-vegetative growth, Forb	3	1	5	7	13	32
American vetch	*Vicia americana*	Native, Long-lived, Vegetative growth, Forb	0	0	0	0	0	1
hookedspur	*Viola adunca*	Native, Long-lived,	0	1	0	0	2	0

violet		Non-vegetative growth, Forb						
Canadian white violet	*Viola canadensis*	Native, Long-lived, Vegetative growth, Forb	0	0	1	0	0	0
sixweeks fescue	*Vulpia octoflora*	Native, Short-lived, Non-vegetative growth, Graminoid	0	0	0	1	0	0
Oregon cliff fern	*Woodsia oregana*	Native, Long-lived, Non-vegetative growth, Forb	0	2	1	0	0	1
Rocky Mountain woodsia	*Woodsia scopulina*	Native, Long-lived, Non-vegetative growth, Forb	0	0	1	0	0	0
mule's ears sp.	*Wyethia sp.*	Native, Long-lived, Non-vegetative growth, Forb	0	0	0	0	0	1
soapweed yucca	*Yucca glauca*	Native, Long-lived, Vegetative growth, Shrub	4	4	4	14	8	14
mountain deathcamas	*Zigadenus elegans*	Native, Long-lived, Non-vegetative growth, Forb	3	2	4	1	4	9