Received: 8 May 2025 | Revised: 22 September 2025 | Accepted: 22 October 2025

DOI: 10.1002/ecs2.70521

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Vegetation Ecology

Understory plant species recruitment and expansion spur community shifts following forest restoration treatments

Arièl B. Demarest[1] | **Paula J. Fornwalt**[2] | **Brett H. Wolk**[3] | **Jennifer S. Briggs**[4] | **Judith D. Springer**[5]

[1]USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA

[2]USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA

[3]Colorado Forest Restoration Institute, Colorado State University, Fort Collins, Colorado, USA

[4]Colorado School of Mines, Golden, Colorado, USA

[5]Ecological Restoration Institute, Northern Arizona University, Flagstaff, Arizona, USA

Correspondence
Arièl B. Demarest
Email: ariel.demarest@usda.gov

Funding information
Boulder County Parks and Open Space; Colorado Forest Restoration Institute, Colorado State University; Rocky Mountain Geographic Science Center, US Geological Survey; USDA Forest Service, Rocky Mountain Research Station; USDA Forest Service, Collaborative Forest Landscape Restoration Program; USDA, Natural Resources Conservation Service; Upper South Platte Partnership; Southern Rockies Landscape Conservation Cooperative; Denver Water

Handling Editor: Jonathan D. Coop

Abstract

Restoration treatments have been implemented in many of the dry conifer forests of the western United States. By decreasing forest density and increasing forest heterogeneity, these treatments are generally effective at meeting their primary objective of reducing the risk of uncharacteristically severe wildfire. Treatments also commonly achieve a secondary objective of increasing overall native understory plant species richness and cover. However, it is less certain how treatments affect the recruitment, loss, and growth of individual understory plant species and, in turn, shape the composition of the understory plant community. We investigated these finer effects of forest restoration treatments on understory communities in the Colorado Front Range by collecting data pre-treatment and 1–2 years and 4–6 years post-treatment at 155 plots in treated and untreated areas. Treatments were implemented mechanically by cutting trees with heavy equipment or chainsaw; cut material was either removed, piled, piled and burned, scattered, or masticated. Species turnover analysis indicated that at 4–6 years post-treatment, losses of pre-treatment native species, as well as losses in the cover of pre-treatment native species, were attributable to background turnover rather than to treatment. Species turnover analysis also showed that the post-treatment recruitment of native species was greater in treated than untreated plots and that native species persisting from pre- to post-treatment contributed the most to the increased cover found in treated plots. Multivariate analysis demonstrated subtle but statistically significant differences in species composition in treated versus untreated plots after treatment. Indicator species analysis clarified which species contributed to post-treatment turnover and composition differences. No strong native or non-native indicator species were found for untreated plots at any sampling period, or for treated plots pre-treatment. However, at 4–6 years post-treatment, eight native species and two non-native species were strongly indicative of treated plots, most of which were open forest species. Based on these results, and our previous results that identified positive treatment effects on overall native cover and species richness, we conclude that mechanical forest restoration treatments benefited native understory plant communities in the Colorado Front Range both at broad and fine levels.

KEYWORDS

Colorado, dry conifer forests, forest restoration, indicator species, species composition, species turnover, understory plants

INTRODUCTION

Many dry conifer forests of the western United States were historically regulated by a wildfire regime composed of relatively frequent, low- to mixed-severity events (Hagmann et al., 2021; Hessburg et al., 2019; Hood et al., 2021). This historical regime created and maintained forest overstories with a generally open structure that was heterogeneous in tree size, age, and spatial arrangement (Hagmann et al., 2021; Hessburg et al., 2019; Hood et al., 2021). However, since Euro-American settlement, the interruption of historical wildfire regimes and other land use changes have allowed overstories in many dry conifer forests to become denser, more homogeneous, and in turn, more at risk of experiencing uncharacteristically severe wildfire (Allen et al., 2002; Hagmann et al., 2021; van Mantgem et al., 2013). Forest restoration treatments primarily aim to reduce this risk by creating more open, heterogeneous overstories inspired by historical conditions (Churchill et al., 2013).

The changes in dry conifer forest overstories and wildfire regimes since settlement have likely altered understory plant communities as well, and many forest restoration programs also have secondary goals focused on them (Stephens et al., 2020). Dense overstories limit the light transmitted to understories, which combines with the relatively arid nature of these forests to create dry shade, one of the most difficult growing conditions for plants (Coomes & Grubb, 2000). Homogenous overstories limit the variety of habitat niches, which may stifle understory diversity (Allen et al., 2002; MacArthur & MacArthur, 1961). Alterations in disturbance regimes, especially ca. 100 years of fire exclusion in many areas of the western United States, may limit the ability of early successional or disturbance-adapted species to persist (Knapp et al., 2013; Roxburgh et al., 2004). Restoration treatments that create open and heterogeneous overstories may promote understory plant recruitment and growth (Demarest, Fornwalt, et al., 2023; Dodson & Peterson, 2010); treatments may also affect understories by altering woody forest floor materials, exposing mineral soil, and changing soil moisture and nutrient availability (Kane et al., 2010; Rhoades et al., 2012).

Commonly, the success of forest restoration treatments at meeting understory goals is measured in a straightforward fashion: increased overall native plant richness and cover with a minimum of invasion by non-native species (Abella & Springer, 2015). Studies measuring responses to treatment after plant communities had time to recover from the initial disturbance and react to the new growing environment (~4 years) generally found increases in native plant richness and/or cover (Demarest, Fornwalt, et al., 2023; Fornwalt et al., 2017; Kane et al., 2010; Lochhead & Comeau, 2012; Springer et al., 2024). However, while overall richness and cover metrics concisely identify broad ecological trends, they may miss some finer aspects of plant community change. For example, post-treatment increases in overall native plant cover may be driven by just a few dominant species, which may or may not be desirable (Goodwin et al., 2018). Post-treatment increases in overall native richness may also hide species losses, which could be concerning if they are of sensitive, threatened, or endangered species, or if they reflect a shift in (as opposed to a broadening of) growing conditions (Hillebrand et al., 2018). Additionally, post-treatment increases in overall native richness and/or cover may not consistently translate into detectable changes in plant species composition.

Investigating plant species turnover, plant species composition responses, and individual plant species responses can provide a fuller understanding of how understories are affected when forests are manipulated by restoration treatments. Species turnover (i.e., species gain, loss, and persistence) has rarely been explicitly investigated in the context of dry conifer forest restoration, but it is likely that environmental shifts brought about by treatments may trigger both species gains and species losses (Dodson & Peterson, 2010). More investigations of plant species composition after restoration treatments have been conducted, and some identified whole-community changes due to treatment, while others did not (Jang et al., 2021; Laughlin et al., 2008; Wayman & North, 2007; Wolk & Rocca, 2009; Zald et al., 2020). However, even where species composition did not change after treatment, individual species benefiting from treatments were almost always identified. Building knowledge about which species do and do not thrive after treatment, and their traits, may help us understand how treatments will modify plant communities in different circumstances.

Tens of thousands of hectares of dry conifer forest have received restoration treatments in Colorado in the last two decades, and several studies have examined how these treatments altered coarse measures of understory plant species richness or abundance (Dannels et al., 2025; Fornwalt et al., 2017; Korb et al., 2020; Mahood et al., 2025; Wolk & Rocca, 2009). In our previous work using an understory plant dataset from multiple sites in the Colorado Front Range, we found that mechanically implemented (i.e., implemented with heavy machinery or chainsaws) treatments drove modest gains in overall native richness and more substantial gains in overall native cover, especially by 4–6 years post-treatment (i.e., native richness increased from ~29 to 33 species per plot and native cover increased from ~15% to 24%) (Demarest, Fornwalt, et al., 2023). Here, we analyzed species-level data to dive further into how restoration treatments modify native understory plant communities. We sought to discern (1, 2) how native species turnover contributed to the observed net increases in richness and cover following treatment, (3) whether native species turnover in treated areas was sufficient to alter species composition, and (4) which native species were most responsive to treatments. In our previous work, non-native species richness and cover were negligible pre-treatment, but likewise increased 4–6 years following treatment (i.e., non-native richness increased from ~0 to 3 species per plot and non-native cover increased from ~0% to 1%). Therefore, we also sought to discern (5) which non-native species drove these increases.

METHODS

Study area and study sites

We established our study area and eight study sites in the dry conifer forests of the Colorado Front Range, a mountain range that forms the easternmost edge of the southern Rocky Mountains (Figure 1; Table 1). Data from some or all of these sites have been previously analyzed in Briggs et al. (2017; three sites), Demarest et al. (2023; eight sites), and Mahood et al. (2025; two sites). Site elevations ranged from 2062 to 3048 m and hill slopes averaged 26%. Long-term average annual precipitation at the sites ranged from 471 to 601 mm, while long-term average annual temperature ranged from 3.6 to 8.7°C (PRISM Group, 2020). Soils were generally shallow, well-drained, and coarse-gravelly, arising from granite, schist, or gneiss parent material (Peet, 1981; Veblen & Donnegan, 2005).

Pinus ponderosa (ponderosa pine) was the uniting component of forest overstories in the study area, but *Pseudotsuga menziesii* (Douglas-fir) was also common, particularly at mesic sites. *Juniperus scopulorum* (Rocky Mountain juniper), *Pinus contorta* (lodgepole pine), *Picea engelmannii* (Engelmann spruce), *Picea pungens* (Colorado blue spruce), *Pinus flexilis* (limber pine), and *Populus tremuloides* (trembling aspen) were sometimes also present. While some understory plants were ubiquitous throughout the study area, such as upland *Carex* species (sedge) and *Juniperus communis* (common juniper), other predominant plants varied with moisture availability (Peet, 1981). At xeric sites, graminoids like *Poa fendleriana* (muttongrass) and *Leucopoa kingii* (spike fescue), forbs such as *Penstemon virens* (Front Range penstemon), *Campanula rotundifolia* (bluebell bellflower), and *Artemisia frigida* (fringed sage), and shrubs like *Ribes cereum* (wax currant) and *Cercocarpus montanus* (mountain mahogany) were common. At mesic sites, graminoids like *Calamagrostis purpurascens* (purple reedgrass) and *Koeleria macrantha* (prairie junegrass) mixed with forbs like *Fragaria* species (strawberry), *Achillea millefolium* (common yarrow), and *Antennaria parvifolia* (small-leaf pussytoes), and shrubs like *Rosa* species (rose) and *Arctostaphylos uva-ursi* (kinnikinnick).

Between 2011 and 2017, we established the eight study sites in landscapes where land managers were planning forest restoration treatments, including on federal (Roosevelt and Pike National Forests of the USDA Forest Service), county (Boulder County), and private lands (Figure 1). The sites had varied land use histories, but it is likely that most or even all have experienced logging, grazing, and near-total fire exclusion (Battaglia et al., 2018; Brown et al., 2015). Land managers selected discrete forest treatment areas within the sites according to local management priorities. We delineated nearby areas (within 1 km of treatment areas) with comparable slope, aspect, forest overstory structure, and other characteristics, but without plans for treatment, to serve as reference areas (hereafter called untreated units) for the treatment areas (hereafter called treated units). A treated unit and its paired untreated unit formed a block. The sites each contained one to three blocks, for a total of 16 blocks.

Land managers conducted restoration treatments at the treated units from 2012 and 2017 (Table 1). Exact treatment prescriptions varied, but common goals included reducing forest overstory basal area, creating forest openings, increasing the proportion of *Pinus ponderosa* trees relative to other tree species, and retaining old trees and snags (Addington et al., 2018; Cannon et al., 2018; Underhill et al., 2014). Treatments were implemented mechanically, either with heavy equipment or chainsaw. Cut woody material, including tree boles, limbs, and branches, was removed in some cases and left on site in others; material left on site was

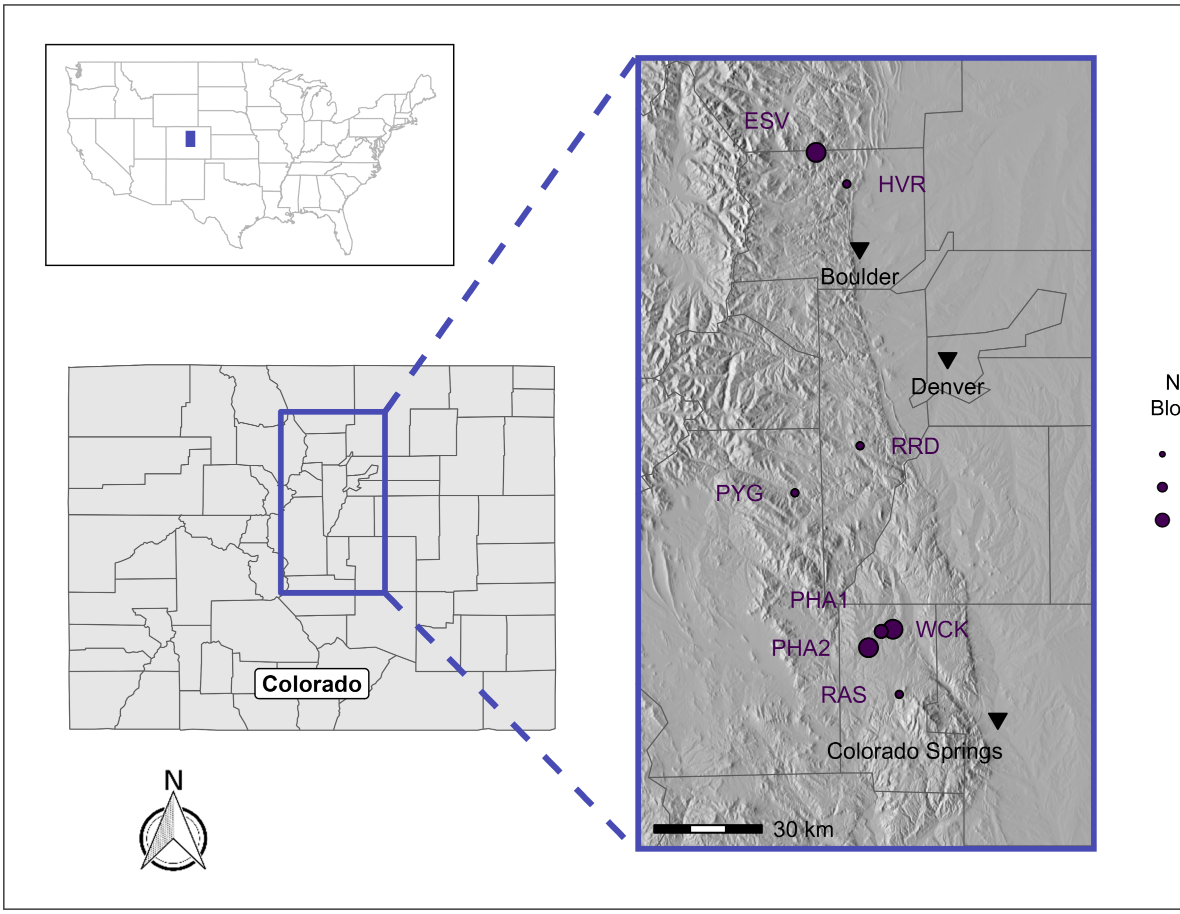

FIGURE 1 Location of the study area and the eight study sites in dry conifer forests of the Colorado Front Range, USA. Study sites are marked by purple circles. Major cities are labeled with black triangles. Sites include: Estes Valley (ESV), Heil Valley (HVR), Ridge Road (RRD), Payne Gulch (PYG), Phantom Creek 1 (PHA1), Phantom Creek 2 (PHA2), West Creek (WCK), and Raspberry Mountain (RAS). We adapted this map from Demarest, Fornwalt, et al. (2023).

piled, piled and burned, scattered, or masticated. On average, treatments at our sites reduced forest overstory basal area by ~50% (Table 1), doubled bare soil cover, increased fine woody material cover by ~50%, and had no detectable effect on coarse woody cover or forest floor depth (Demarest, Fornwalt, et al., 2023).

Data collection

We established 6 to 17 plots within each of the 16 blocks, for a total of 180 plots. However, some plots were subsequently compromised by events like unplanned livestock grazing or cutting in plots intended to be untreated; this reduced the usable block total to 15 and the plot total to 155 (78 treated, 77 untreated). The number of plots per block varied with block area. We randomly placed plots but located them at least 30 m away from a unit boundary to avoid boundary effects. We employed a Before-After-Control-Impact (BACI) sampling design where each plot was measured 1–2 years before treatment, 1–2 years after treatment, and 4–6 years after treatment; however, the specific years of sampling varied based on the year of study site establishment, the year of treatment implementation, and field crew availability.

We collected understory plant, substrate, and other data within circular 406-m^2 plots. We used the line-point intercept method to capture understory plant and substrate hits at observation points. Pilot plots at the Estes Valley, Heil Valley Ranch, and Phantom Creek 1 sites had 400 observation points distributed along four 11.3-m transects that radiated from plot center in the cardinal directions. This sampling protocol was subsequently adjusted slightly to increase plot coverage while decreasing sampling time; plots at all later sites had 200 observation points distributed along eight 11.3-m transects radiating in the cardinal and ordinal directions. We recorded all plant species and substrate hits below breast height. We also performed a full census of all understory plant species present in the plots. If we could not identify

TABLE 1 Description of the eight study sites in dry conifer forests of the Colorado Front Range.

Site	No. of blocks	No. of plots		Area (ha)		Average basal area		Sampling years	Treatment methods
		T	U	T	U	T	U		
Estes Valley	3	11	10	80	41	16.7	22.7	2011, 2012 or 2013, 2017	Cut with chainsaws; cut material piled and burned or masticated
Heil Valley	1	3	4	70	128	13.8	29.8	2011, 2013, 2017	Cut with heavy equipment; cut material removed (boles) and scattered (slash)
Payne Gulch	1	6	6	30	16	10.7	24.9	2016, 2018, 2021	Cut with heavy equipment; cut material removed
Phantom Creek 1	2	13	12	210	131	12.4	20.9	2011, 2012, 2017	Cut with heavy equipment; cut material removed
Phantom Creek 2	3	18	18	140	73	11.2	26.8	2015, 2018, 2021	Cut with chainsaws and heavy equipment; cut material removed (boles) and scattered (slash)
Raspberry Mountain	1	6	6	35	26	19.5	31	2015, 2017, 2021	Masticated
Ridge Road	1	3	3	36	26	5.4	26	2015, 2017, 2020	Cut with chainsaws and heavy equipment; cut material removed (boles) and piled (slash)
West Creek	3	18	18	187	90	18.2	22.8	2015, 2018, 2021	Cut with heavy equipment; cut material scattered

Note: "T" represents mechanically treated sites and "U" represents untreated sites. Average basal areas reflect values for the forest overstory at the 1–2 years post-treatment sampling period. Sampling years reflect those for the 1–2 years pre-treatment, 1–2 years post-treatment, and 4–6 years post-treatment periods.

a plant in the field, we collected it outside the plot for identification in the lab. We could only identify some plants to genus (or, rarely, to a coarser taxonomic resolution) because key morphological characteristics were not present; hereafter, these are also referred to as species. Taxonomy for understory plants follows the PLANTS Database (USDA NRCS, 2021). At the center of the plots, we recorded latitude, longitude, elevation, and dominant slope and aspect. All these data are publicly available (Demarest, Wolk, et al., 2023).

For each plot, we categorized plants in two ways, and then calculated six understory species turnover variables. First, we used Colorado plant keys (Ackerfield, 2015; Shaw, 2008) to classify plants into nativity categories, namely, native, non-native, or unknown. Plants of unknown nativity were those that were identified to genus, but the genus contained both native and non-native members. Second, we categorized native species at each post-treatment sampling period by turnover status relative to pre-treatment, namely, lost, gained, or persistent. For example, a species present in a plot pre-treatment and 1–2 years post-treatment, but not detected at 4–6 years post-treatment, would be categorized as persistent at 1–2 years post-treatment and lost at 4–6 years post-treatment. After classifications were complete, we calculated the richness of native gained, lost, and persistent species since pre-treatment for each plot and each post-treatment visit, as well as the change in cover for each category relative to the pre-treatment visit. Richness values were calculated by tallying all species present within a plot either on transects or during the full-plot search. Percent cover values were found by dividing the number of line-point intercept hits for each species by the number of observation points per plot, then multiplying by 100. Since more than one plant species could be hit at each observation point due to layered vegetation, there was potential for cover to exceed 100%.

Data analyses

We compared the richness and the change in cover of native persistent, lost, and gained understory species in treated versus untreated plots at different post-treatment sampling periods using generalized linear mixed models (GLMMs). We used *R* version 4.2.2 (R Core Team, 2022) and the *glmmTMB* package (Brooks et al., 2017) to create separate models for each richness and cover change turnover category (six models). We assessed model fit and performed residual diagnostics with functions from the package *DHARMa* (Hartig, 2022) (Appendix S1). We used Poisson or negative binomial error distributions with log links for richness models; negative binomial was used where overdispersion was evident in Poisson model diagnostics. To model change in cover, we used a Gaussian error distribution and identity link for variables with both positive and negative values (persistent cover), and a Tweedie error distribution and log link for the others (lost or gained cover). Tweedie models are constrained to positive values in the response variable, and so we eliminated zeroes by adding a small value to each observation following Stahel's method (Stahel, 2002), and we eliminated negatives by using absolute values (lost cover). We set treatment, time-since-treatment, and their interaction as predictor variables. We used a nested random effects term with four levels: site, block within site, unit within block within site, and sampling year within unit within block within site. The inclusion of unit and sampling year accounted for repeated measures by capturing the correlation between observations across time: both correlation within a sampling period (i.e., all the observations from a unit in a particular year) and between sampling periods (i.e., all the observations from a unit for all sampling years). The nestedness of the random effects term accounted for potential correlation of observations across space. We used Tukey-adjusted post hoc comparisons to examine any differences between treated and untreated plots within a sampling period ($p < 0.050$). All reported means are estimated marginal means from our models.

We used permutational multivariate analysis of variance, or PERMANOVA (Anderson, 2001), to detect differences in native understory species composition in treated and untreated plots ($p < 0.050$). PERMANOVA analyses were carried out separately for each sampling period using a plot-level compositional dataset that included cover values for all plant species that were present in a plot; for species that technically had 0% cover because they were not hit on a transect, we assigned them the minimum observable cover value (0.25% or 0.50% depending on sampling protocol). We employed the *adonis2* function in the *vegan* package in *R* (Oksanen et al., 2022; R Core Team, 2022). We measured plant community distances between plots using the Bray–Curtis dissimilarity index. We used 999 permutations and restricted permutations to within study blocks in recognition of block-specific differences. We tested for potential heterogeneity of dispersions between treated and untreated plots using the *betadisper* function from the *vegan* package (Appendix S1).

To visualize differences in native understory communities, we used nonmetric multidimensional scaling (NMDS) ordination of Bray–Curtis dissimilarity index values. To create our ordination, we employed the *metaMDS* function in the *vegan* package (Oksanen et al., 2022) using 999 permutations and the plot-level species composition dataset described above. We retained the smallest number of ordination dimensions that produced stress <0.200. While the ordination was conducted with all data, because of the large number of plots, we visualized community relationships by showing the unit (treated or untreated × three sampling periods) centroids separately for each block; compositionally similar treated and untreated units are closer together on the ordination figures.

We conducted indicator species analysis (ISA) to identify individual understory species strongly associated with treated or untreated plots in each sampling period. A species that is a strong indicator of a treatment shows both high specificity (a high proportion of the overall cover of a species is found within plots of a given treatment) and high fidelity (a high proportion of plots of a given treatment contain a species). For each species, we calculated indicator values for treated and untreated plots as the square root of the product of the species' specificity and fidelity using the *multipatt* function of the *indicspecies* package in *R* (De Cáceres & Legendre, 2009; R Core Team, 2022). We also used this function to assess treatment significance for each species based on a permutation test of indicator values (999 permutations). We were not able to incorporate the block structure of our study design as that was not an option in any indicator species package in R to our knowledge. We identified a species as a strong indicator of a treatment if it was significant ($p < 0.050$) and it had an indicator value >0.500 (Dufrêne & Legendre, 1997).

RESULTS

Questions 1 and 2: Native understory species turnover contributions to overall richness and cover

Of the three native species richness turnover categories, only the number of species gained post-treatment ever differed between treated and untreated plots, indicating that gained species alone drove overall post-treatment richness increases in treated areas (Figure 2). The number of species gained was 1.6 times higher in treated plots compared to untreated plots at both 1–2 years and 4–6 years post-treatment ($p < 0.001$ for both sampling periods), with an average of 10.7 species gained in treated plots versus 6.5 species gained in untreated plots at the final sampling period. Meanwhile, the number of lost species was similar in treated and untreated plots at both

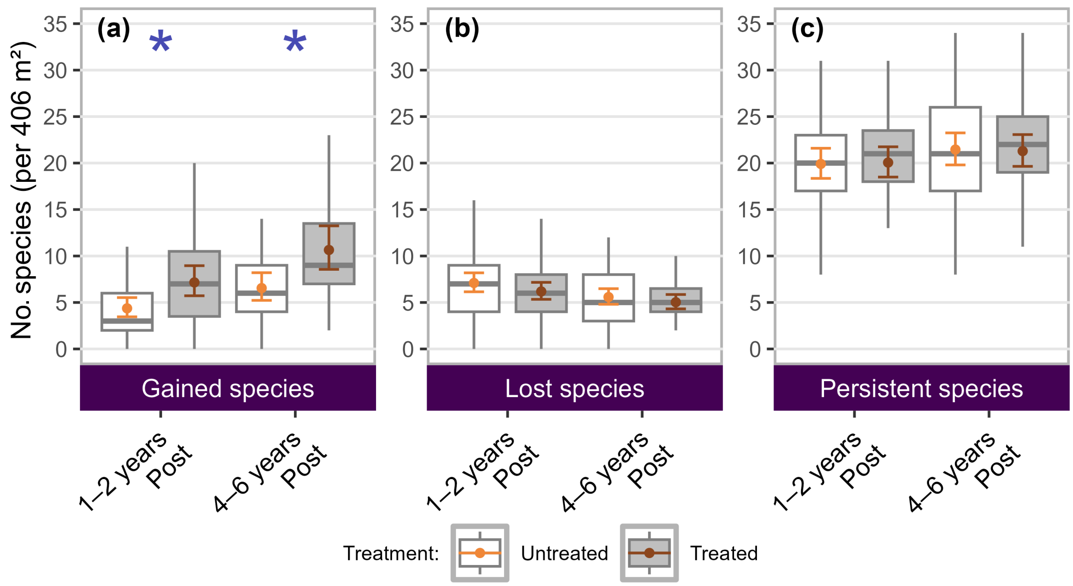

FIGURE 2 Raw data (box-and-whisker plots) and generalized linear mixed model (GLMM) estimates (point-and-whisker plots) for the number of gained, lost, or persistent native understory plant species per plot after treatment. Richness at 1–2 years and 4–6 years after forest restoration treatments in dry conifer forests of the Colorado Front Range was compared to pre-treatment richness. Box-and-whisker plots display the median (midline), the interquartile range (bottom and top lines), and the minimum and maximum values within 1.5 times of the interquartile range (whiskers); point-and-whisker plots display the mean (point) and the 95% CI (whiskers). Pairwise comparisons between treatments were evaluated using estimated marginal means. Blue stars indicate significant differences ($p < 0.050$) between treatments for that sampling period.

1–2 years and 4–6 years post-treatment ($p = 0.162$ and $p = 0.311$, respectively). Likewise, the numbers of persistent species did not differ between treated and untreated plots at either 1–2 years and 4–6 years post-treatment ($p = 0.890$ and $p = 0.888$ respectively). However, post-treatment species turnover could be extremely variable, with gains in species at a plot ranging from 0% to 200% and losses in species at a plot ranging from 0 to 71%.

Additionally, only gained and persistent species drove overall post-treatment increases in native cover in treated areas (Figure 3). The change in cover of gained species was similar in treated and untreated areas at 1–2 years post-treatment ($p = 0.102$), and 2.9 times greater in treated areas at 4–6 years after treatment ($p = 0.003$). In absolute terms, this change in cover was still small at an increase of 2.0% in treated areas. The change in cover of persistent species was not detectably different in treated and untreated areas at 1–2 years post-treatment ($p = 0.101$) but was 5.0 times higher in treated areas than untreated by 4–6 years after treatment on average ($p = 0.010$). Species losses did not lead to a strong change in cover for either treated or untreated areas at either post-treatment sampling period, with mean losses always less than 1.0% cover ($p = 0.206$ and 0.779 for 1–2 and 4–6 years post-treatment, respectively).

Question 3: Native understory species composition

PERMANOVA showed that native understory plant communities in treated and untreated plots were compositionally indistinguishable prior to treatment, but distinct at both post-treatment sampling periods (Table 2). While understory communities were detectably different in treated versus untreated plots at 1–2 years and 4–6 years post-treatment, treatment explained a small amount of the variation in species composition, as attested by low R^2 values for the Treatment term in these models. The differences identified by PERMANOVA were also generally reflected in the NMDS ordination (stress $= 0.162$, $k = 3$; Figure 4). Within many blocks, treated and untreated composition centroids increasingly diverged from each other in ordination space over time (e.g., Phantom Creek 2.3 and Ridge Road), although not in all blocks (e.g., Phantom Creek 1.1 and West Creek 3).

Questions 4 and 5: Individual native and non-native understory species

ISA identified a variety of indicator species associated with treated plots in our study, with strong indicators

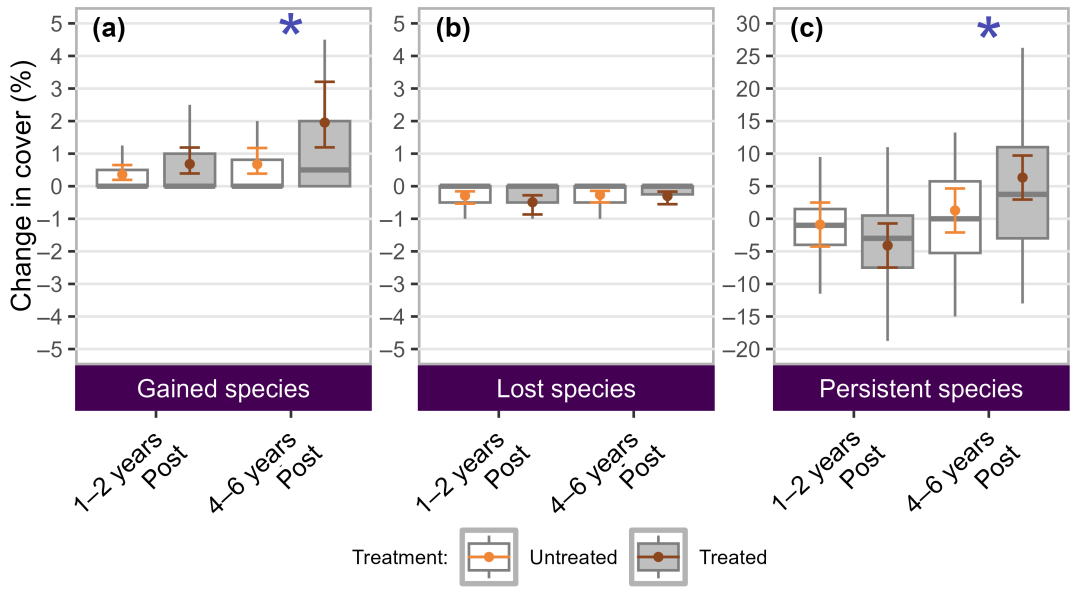

FIGURE 3 Raw data (box-and-whisker plots) and generalized linear mixed model (GLMM) estimates (point-and-whisker plots) for the change in cover of gained, lost, and persistent native understory plant species per plot after treatment. Cover at 1–2 years and 4–6 years after forest restoration treatments in dry conifer forests of the Colorado Front Range was compared to pre-treatment cover. Box-and-whisker plots display the median (midline), the interquartile range (bottom and top lines), and the minimum and maximum values within 1.5 times of the interquartile range (whiskers); point-and-whisker plots display the mean (point) and the 95% CI (whiskers). Pairwise comparisons between treatments were evaluated using estimated marginal means. Blue stars indicate significant differences ($p < 0.050$) between treatments for that sampling period.

TABLE 2 Permutational multivariate analysis of variance (PERMANOVA) test results for differences in native understory plant species composition at 1–2 years before, 1–2 years after, and 4–6 years after forest restoration treatments in dry conifer forests of the Colorado Front Range.

Source of variation	df	SS	R^2	F	p
1–2 years pre-treatment					
Treatment	1	0.22	0.01	0.98	0.157
Residual	154	33.93	0.99		
1–2 years post-treatment					
Treatment	1	0.41	0.01	1.83	0.003
Residual	153	34.36	0.99		
4–6 years post-treatment					
Treatment	1	0.95	0.03	4.47	0.001
Residual	154	32.55	0.97		

(indicator value >0.500, $p < 0.050$) found at both post-treatment sampling periods (Tables 3 and 4). Pre-treatment, no strong indicators were revealed for either treated or untreated plots. Even after treatment, strong indicators were not associated with untreated plots. At 1–2 years post-treatment, four native species were strong indicators of treated plots, and at 4–6 years post-treatment, eight native species were strong indicators of treated plots. Only one native species was a strong indicator at both post-treatment sampling periods: the short-lived forb, *Androsace septentrionalis* (pygmyflower rockjasmine). Most of the strong native indicator species in this study were forbs and graminoids, but one disturbance-loving shrub, *Rubus idaeus* (American red raspberry), was a strong indicator of treated plots at 4–6 years post-treatment. Of the 30 non-native species detected in our study, two were also strongly indicative of treated plots. At 1–2 years and 4–6 years post-treatment, *Taraxacum officinale* (common dandelion) was strongly associated with treated plots, as was *Cirsium arvense* (Canada thistle) at 4–6 years post-treatment.

DISCUSSION

In the Colorado Front Range and elsewhere in the western United States, dry conifer forest overstories have become denser and more homogeneous due to post-settlement changes in land use and wildfire regimes. Forest restoration programs have been underway to reduce overstory density and homogeneity, and consequently, the risk of uncharacteristically severe wildfire. Secondary forest restoration goals often include improvements beyond the forest overstory, such as the promotion of robust native understory plant communities. Previous analysis of our dataset, which was

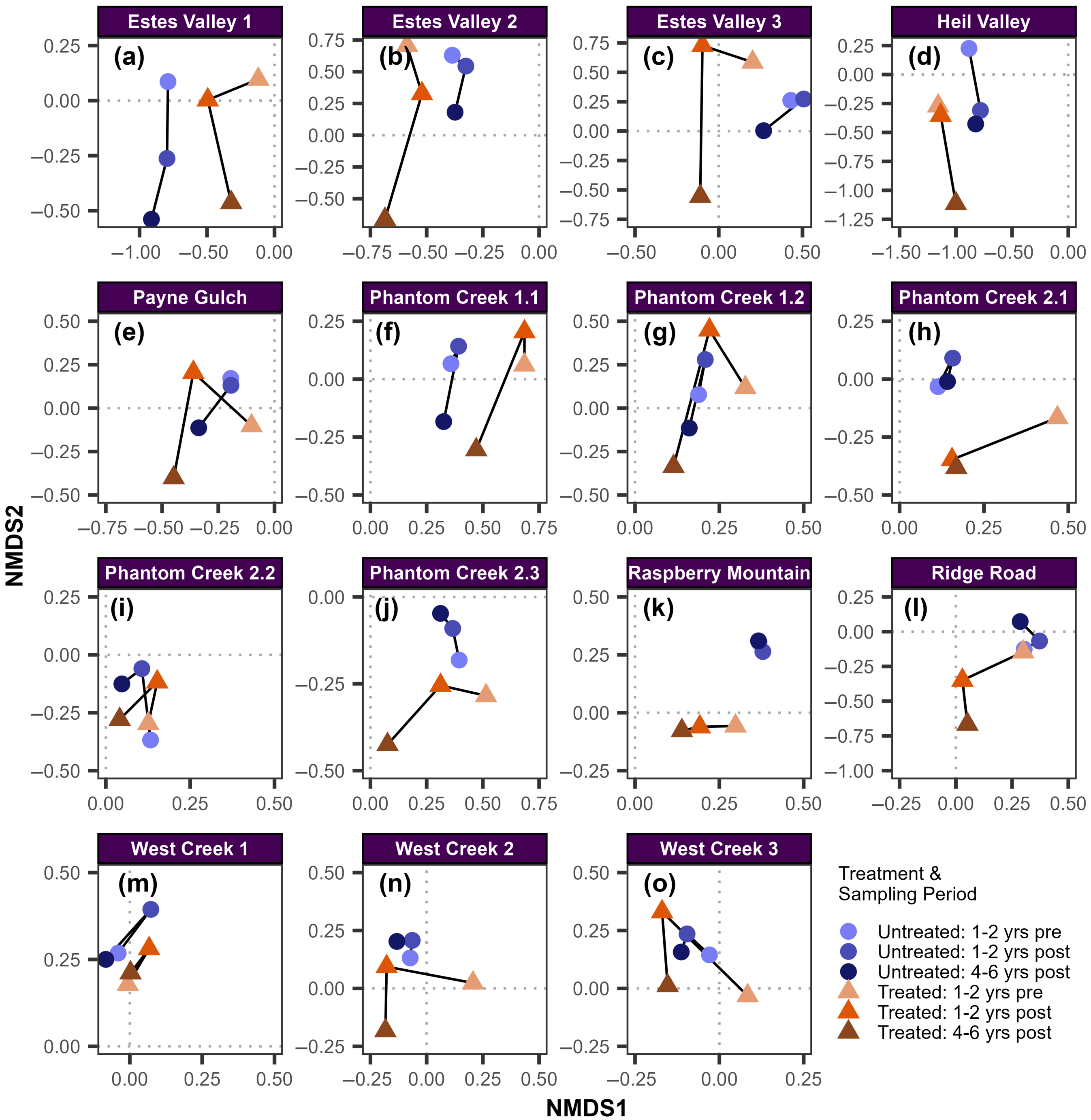

FIGURE 4 Native understory species composition in treated and untreated units over time, by block. Treated and untreated units at each sampling period are represented by unit centroids. Axes 1 (NMDS1) and 2 (NMDS2) are derived from a single nonmetric multidimensional scaling (NMDS) ordination of untransformed understory plant cover at 1–2 years before, 1–2 years after, and 4–6 years after forest restoration treatments in dry conifer forests of the Colorado Front Range.

collected across eight dry conifer forest sites in the Colorado Front Range, showed that mechanical forest restoration treatments led to heightened overall native understory species richness and cover by 4–6 years after treatment (Demarest, Fornwalt, et al., 2023). In this study, we used species-level data to investigate the nuances of these understory plant community reactions. We found that the richness increases in treated areas were not masking accompanying species losses and that persistent species were the primary drivers of the elevated cover in treated areas. We also determined that native understory communities were compositionally similar in treated and untreated areas prior to treatment but diverged post-treatment and that a small number of strong indicator species consistently

TABLE 3 Strong native indicator species (indicator value >0.500, *p* value < 0.050) associated with each sampling period and treatment for understory plant communities in dry conifer forests of the Colorado Front Range.

Treatment	Scientific name	Growth form	*p*	Specificity	Fidelity	Indicator value
1–2 years pre-treatment						
Untreated	No indicator species					
Treated	No indicator species					
1–2 years post-treatment						
Untreated	No indicator species					
Treated	*Androsace septentrionalis*	Forb	0.001	0.76	0.60	0.68
Treated	*Arabis fendleri*	Forb	0.011	0.61	0.62	0.61
Treated	*Allium cernuum*	Forb	0.028	0.59	0.68	0.63
Treated	*Corydalis aurea*	Forb	0.001	0.99	0.40	0.63
4–6 years post-treatment						
Untreated	No indicator species					
Treated	*Calamagrostis purpurascens*	Graminoid	0.039	0.64	0.77	0.71
Treated	*Carex* spp.	Graminoid	0.001	0.68	1.00	0.82
Treated	*Koeleria macrantha*	Graminoid	0.023	0.62	0.92	0.75
Treated	*Androsace septentrionalis*	Forb	0.011	0.58	0.68	0.63
Treated	*Antennaria parvifolia*	Forb	0.039	0.62	0.91	0.75
Treated	*Penstemon glaber*	Forb	0.009	0.65	0.46	0.54
Treated	*Artemisia frigida*	Forb	0.004	0.80	0.33	0.51
Treated	*Rubus idaeus*	Shrub	0.001	0.98	0.34	0.58

Note: Strong native indicator species only surfaced in treated plots, and only in the 1–2 years post-treatment and the 4–6 years post-treatment sampling periods; they did not surface in treated plots in the 1–2 years pre-treatment sampling period, or in untreated plots for any sampling period.

contributed to these richness, cover, and composition patterns across sites.

Questions 1 and 2: Native understory species turnover contributions to overall richness and cover

Previously, we found slightly greater native species richness in treated areas (~33 species per plot) compared to untreated areas (~29 species per plot) at 4–6 years post-treatment (Demarest, Fornwalt, et al., 2023). Here, we determined through our GLMM analyses that the modest size of this boost was solely a reflection of higher species recruitment rates in treated areas relative to untreated areas; that is, higher species gains were not simultaneously masking higher species losses in treated areas. Similar trends were documented following dry conifer forest restoration treatments in Washington (Dodson & Peterson, 2010). This lack of elevated species losses in treated areas suggests that treatments did not physically eliminate species or compromise species habitat niches, while elevated species gains suggest that treatments added niches. There are multiple potential explanations for why species gains were only modest following treatments. Mineral soil exposure can be a prerequisite for new species establishment in dry conifer forests (Hiers et al., 2007; Kane et al., 2010; Wayman & North, 2007), and so a primary explanation could be that the limited mineral soil exposure we observed following treatments (~10% in treated areas versus 4% in untreated areas at 4–6 years post-treatment) tempered new species recruitment (Demarest, Fornwalt, et al., 2023). Restoration projects that follow mechanical treatments with prescribed fire can expose more mineral soil and recruit a greater number of new species than mechanical treatments alone, as can wildfires that approximate the historical low- to mixed-severity fire regime (Dodson & Peterson, 2010; Fornwalt & Kaufmann, 2014; Kane et al., 2010; Wayman & North, 2007).

Our prior work also showed that treated areas had much higher native cover (~24%) than untreated areas (~15%) at 4–6 years post-treatment (Demarest, Fornwalt, et al., 2023), and here we showed that the expansion of persistent species was primarily responsible for this boost. Persistent species comprised the bulk of species in our plots post-treatment, and while it is almost always desirable to increase native biodiversity in anthropogenically altered ecosystems like our study area, retaining and promoting extant species is also important (Harrison et al., 2010;

TABLE 4 Strong non-native indicator species (indicator value >0.500, $p < 0.050$) associated with each sampling period and treatment for understory plant communities in dry conifer forests of the Colorado Front Range.

Treatment	Scientific name	Growth form	p	Specificity	Fidelity	Indicator value
1–2 years pre-treatment						
Untreated	No indicator species					
Treated	No indicator species					
1–2 years post-treatment						
Untreated	No indicator species					
Treated	*Taraxacum officinale*	Forb	0.001	0.86	0.30	0.50
4–6 years post-treatment						
Untreated	No indicator species					
Treated	*Taraxacum officinale*	Forb	0.001	0.80	0.62	0.70
Treated	*Cirsium arvense*	Forb	0.001	1.00	0.35	0.60

Note: Strong native indicator species only surfaced in treated plots, and only in the 1–2 years post-treatment and the 4–6 years post-treatment sampling periods; they did not surface in treated plots in the 1–2 years pre-treatment sampling period, or in untreated plots for any sampling period.

Stevens et al., 2019). As has also been posited for other dry conifer forests that received restoration treatments, we suspect that gains in the cover of persistent species were driven by vegetative growth of existing individuals, although the establishment of new individuals may also have played a meaningful role (Jang et al., 2021; Kane et al., 2010). While on average, persistent species gained cover in treated plots between pre-treatment and 4–6 years post-treatment, variability was high and persistent species lost cover in some plots. In these plots, shrubs like *Juniperus communis* contributed to the loss of cover the most. Shrubs in general grow more slowly than graminoids and forbs, prolonging their recovery from mechanical damage. Gained species also exhibited a greater increase in cover in treated plots compared to untreated plots between pre-treatment and 4–6 years post-treatment, but even in treated plots, the increase was small—gained species cover increased by just 2.0% on average.

Question 3: Native understory species composition

Our PERMANOVA analysis failed to detect a difference in native understory species composition in treated areas compared to untreated areas at the pre-treatment sampling period but did detect a difference at both post-treatment sampling periods. Even so, treatment explained very little of the overall compositional variation—R^2 values indicate that just 3% of the variability in species composition was attributable to treatment at 4–6 years after restoration. This subtlety aligns with our GLMM findings that most native species persisted within a plot over time and that native species gains and losses contributed very little to changes in native cover. Persistent species did often change considerably in cover, but it seems that this was not enough to have a strong effect on composition. This implies that other factors exerted more influence on composition than did treatment per se. Climate, disturbance history, soils, and other site factors have been known to affect species composition (Fontaine et al., 2006; Keith et al., 2010; Peet, 1981; Reikowski et al., 2022; Wilkin et al., 2021). Our NMDS analysis suggests that treatment effects on composition were quite strong in many of our blocks but not in all, leading us to wonder whether factors related to variations in treatment implementation might also be affecting composition. Indeed, the blocks where we highlighted particularly strong post-treatment divergence between treated and untreated centroids in ordination space (Phantom Creek 2.3 and Ridge Road) had more than 70% of the forest overstory basal area cut, while the blocks where we highlighted weak post-treatment divergence (Phantom Creek 1.1 and West Creek 3) had less than 20% of the forest overstory basal area cut (Demarest, Wolk, et al., 2023). Factors related to variations in treatment implementation have been identified as drivers of species composition in other restored dry conifer forests (Jang et al., 2021; Wayman & North, 2007; Wolk & Rocca, 2009), and we hope to explore this topic (as well as the effects of these factors on species turnover and individual species responses) in the future.

Questions 4 and 5: Individual native and non-native understory species

Indicator species analysis helped identify the major species responsible for post-treatment species turnover and compositional changes. Prior to treatment, our indicator species analysis detected no strong native indicators for treated or untreated areas, as expected. The abundance of strong native indicators for treated areas after treatment demonstrates that restoration clearly favored some species. At 1–2 years post-treatment, four strong native indicators surfaced, all of which are diminutive forbs. Two of the species were short-lived forbs that commonly thrive shortly after disturbance: *Corydalis aurea* (scrambled eggs) and *Androsace septentrionalis* (Fornwalt & Kaufmann, 2014; Laughlin & Fulé, 2008; Springer et al., 2018). At 4–6 years post-treatment, the eight strong native indicators included a mix of forbs, graminoids, and a single shrub. Most of these species prefer open forest conditions that would have been more common in historical Colorado dry conifer forests and that the treatments aim to promote, with two species (*Androsace septentrionalis* and *Rubus idaeus*) also strongly affiliated with disturbance (Fornwalt & Kaufmann, 2014; Laughlin et al., 2008; Laughlin & Fulé, 2008; Matonis & Binkley, 2018; Springer et al., 2018). Most also have traits for vigorous spread through vegetative growth (e.g., *Calamagrostis purpurascens* and *Carex* spp.), prodigious seed production (e.g., *Koeleria macrantha* and *Artemisia frigida*), or effective seed dispersal via wind or animals (e.g., *Antennaria parvifolia* and *Rubus idaeus*) (Anderson, 2008; Dixon, 2000; Fryer, 2011; McWilliams, 2003; Tesky, 1992; Tirmenstein, 1990). Springer et al. (2018) also noted that wind-dispersed understory species were often indicator species at 5 years post-wildfire in Arizona *Pinus ponderosa* forests treated for fuels reduction.

In contrast to the strong native indicators found in treated areas after treatment, untreated areas did not have any strong native indicator species at either post-treatment sampling period. This suggests that the restoration treatments did not have overwhelmingly negative effects on any native species. However, a few species, such as *Maianthemum racemosum* and *Pyrola chlorantha*, did surface as weak indicators of untreated areas, suggesting they may have been negatively impacted by treatment. These two uncommon species were lost following treatment from a large proportion of the few treated plots where they were originally found, but they were not usually lost from untreated plots. They are closed-forest species that may have been adversely affected by warmer, brighter conditions in treated areas (Ackerfield, 2015; Fornwalt et al., 2018).

Only two of the 30 non-native species were strong indicators of treated areas post-treatment, while none were strong indicators of untreated areas. This suggests that treatment did promote *Taraxacum officinale*, which was an indicator at both post-treatment periods, and *Cirsium arvense*, which was an indicator at 4–6 years post-treatment. These species are invasive in many regions of the world due to their ability to spread effectively: via copious wind-dispersed seeds for *Taraxacum officinale*, and via rhizomes, wind-dispersed seeds, and ant-dispersed seeds for *Cirsium arvense* (Alba-Lynn & Henk, 2010; Stewart-Wade et al., 2002). Two other non-native species, *Verbascum thapsus* (common mullein) and *Tragopogon dubius* (yellow salsify), nearly qualified as strong indicators of treatment at 4–6 years post-treatment as their indicator values were very close to the cutoff. While the encouragement of non-native species is often an undesirable outcome of forest restoration treatments, treatments are intended to reduce the risk of severe disturbances like high-severity fires, which can produce much stronger non-native plant responses (Fornwalt et al., 2010; Griffis et al., 2001; Jang et al., 2021; Reilly et al., 2020; Springer et al., 2024).

Conclusions

We previously showed that mechanical forest restoration treatments in dry conifer forests of the Colorado Front Range benefitted understories by increasing overall native richness and cover (Demarest, Fornwalt, et al., 2023). The species-level investigations presented here provide additional insight into the effects of restoration on understories. We found that whether native understory species were considered individually or as parts of a plant community, mechanical restoration provided a host of native understory "wins" that may have helped move conditions toward those historically created and maintained by low- to mixed-severity wildfire: treatments spurred native species gains without native species losses, and while some native species clearly thrived in treated areas, none seemed strongly disadvantaged. As is common with forest restoration treatments, we also found that mechanical restoration did favor some species of non-native plants. Overall, mechanical forest restoration treatments benefited native understory communities in the Colorado Front Range both at broad and fine levels.

AUTHOR CONTRIBUTIONS

All authors contributed to the conceptualization of the study. Fornwalt, Wolk, and Briggs acquired funding and developed and implemented the data collection methodology. Demarest, Fornwalt, and Wolk curated the data. Demarest conducted the formal data analysis and wrote the original draft of the manuscript with input from Fornwalt. All authors reviewed and edited the manuscript.

ACKNOWLEDGMENTS

We thank the members of the Colorado Front Range Landscape Restoration Initiative for their input and collaboration. We are grateful for the logistical support provided by J. Underhill, E. Biery, C. Oliver, D. Hattis, K. Zimlinghaus, A. Messing, C. Julian, C. Hansen, F. Quesada, N. Stremel, S. Spaulding, J. Staight, C. Cooley, J. Valladares, K. Morici, K. Warnick, E. Williams, A. Slack, K. Barrett, and R. Kolling. We are also grateful for the field assistance provided by D. Volz, C. Wilson, M. Wilson, K. Weimer, N. Wallace, J. Tucker-Jenks, M. Thomas, N. Teich, J. Swindon, B. Stouffer, A. Smith, A. Sherman, I. Richardson, M. Pierson, P. Pavlowich, K. Newton, C. Newcomb, S. Michl, A. Martin, B. Markle, B. Maillet, S. Lunt, E. LaPlante, T. Koski, M. Knuthson, T. Hunter, C. Heeney, R. Hatfield, R. Harris, A. Grinstead, A. Gilmore, R. Gelles, E. Garcia, A. Freundlich, K. Fialko, A. Faist, K. Evensen, E. Ertl, S. Elliott, K. Doyle, Z. Dickson-Hunt, C. Diaz, D. Diaz, B. del Rio, S. Corioso, M. Cook, C. Coggins, S. Chaplin, M. Cardoza-Reyes, H. Bergemann, H. Athanasakos, S. Asherin, and M. Abernathy. We graciously acknowledge funding for data collection and data management from the USDA Forest Service, Collaborative Forest Landscape Restoration Program; the Southern Rockies Landscape Conservation Cooperative; Boulder County Parks and Open Space; the Upper South Platte Partnership; Rocky Mountain Geographic Science Center, US Geological Survey; the USDA, Natural Resources Conservation Service; the USDA Forest Service, Rocky Mountain Research Station; the Colorado Forest Restoration Institute, Colorado State University; and Denver Water. Finally, we thank S. Crausbay and two anonymous reviewers for providing helpful feedback on earlier versions of this publication. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Demarest, Wolk, et al., 2023) are available from the USDA Forest Service Research Data Archive: https://doi.org/10.2737/RDS-2023-0048.

REFERENCES

Abella, S. R., and J. D. Springer. 2015. "Effects of Tree Cutting and Fire on Understory Vegetation in Mixed Conifer Forests." *Forest Ecology and Management* 335: 281–299. https://doi.org/10.1016/j.foreco.2014.09.009.

Ackerfield, J. 2015. *Flora of Colorado*, First ed. Fort Worth, TX: BRIT Press. https://doi.org/10.17348/jbrit.v13.i1.867.

Addington, R. N., G. H. Aplet, M. A. Battaglia, J. S. Briggs, P. M. Brown, A. S. Cheng, Y. Dickinson, et al. 2018. *Principles and Practices for the Restoration of Ponderosa Pine and Dry Mixed-Conifer Forests of the Colorado Front Range*. General Technical Report RMRS-GTR-373. Fort Collins, Colorado: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://doi.org/10.2737/RMRS-GTR-373.

Alba-Lynn, C., and S. Henk. 2010. "Potential for Ants and Vertebrate Predators to Shape Seed-Dispersal Dynamics of the Invasive Thistles *Cirsium arvense* and *Carduus nutans* in their Introduced Range (North America)." *Plant Ecology* 210: 291–301. https://doi.org/10.1007/s11258-010-9757-2.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. "Ecological Restoration of Southwestern Ponderosa Pine Ecosystems: A Broad Perspective." *Ecological Applications* 12(5): 1418–33. https://doi.org/10.2307/3099981.

Anderson, M. D. 2008. "*Carex rossii*." In *Fire Effects Information System [Online]*. Missoula, MT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Anderson, M. J. 2001. "A New Method for Non-parametric Multivariate Analysis of Variance: Non-parametric MANOVA for Ecology." *Austral Ecology* 26(1): 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Battaglia, M. A., B. Gannon, P. M. Brown, P. J. Fornwalt, A. S. Cheng, and L. S. Huckaby. 2018. "Changes in Forest Structure since 1860 in Ponderosa Pine Dominated Forests in the Colorado and Wyoming Front Range, USA." *Forest Ecology and Management* 422: 147–160. https://doi.org/10.1016/j.foreco.2018.04.010.

Briggs, J. S., P. J. Fornwalt, and J. A. Feinstein. 2017. "Short-Term Ecological Consequences of Collaborative Restoration Treatments in Ponderosa Pine Forests of Colorado." *Forest Ecology and Management* 395: 69–80. https://doi.org/10.1016/j.foreco.2017.03.008.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. "glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *The R Journal* 9(2): 378. https://doi.org/10.32614/RJ-2017-066.

Brown, P. M., M. A. Battaglia, P. J. Fornwalt, B. Gannon, L. S. Huckaby, C. Julian, and A. S. Cheng. 2015. "Historical (1860) Forest Structure in Ponderosa Pine Forests of the Northern Front Range, Colorado." *Canadian Journal of Forest Research* 45(11): 1462–73. https://doi.org/10.1139/cjfr-2014-0387.

Cannon, J. B., K. J. Barrett, B. M. Gannon, R. N. Addington, M. A. Battaglia, P. J. Fornwalt, G. H. Aplet, et al. 2018. "Collaborative Restoration Effects on Forest Structure in Ponderosa Pine-Dominated Forests of Colorado." *Forest Ecology and Management* 424: 191–204. https://doi.org/10.1016/j.foreco.2018.04.026.

Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. "Restoring Forest Resilience: From Reference Spatial Patterns to Silvicultural Prescriptions and Monitoring." *Forest Ecology and Management* 291: 442–457. https://doi.org/10.1016/j.foreco.2012.11.007.

Coomes, D. A., and P. J. Grubb. 2000. "Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments." *Ecological Monographs* 70(2): 171–207. https://doi.org/10.1890/0012-9615(2000)070[0171:IORCIF]2.0.CO;2.

Dannels, R., N. Kotlinski, S. Mueller, A. West Fordham, and B. Wolk. 2025. *Colorado Forest Management Activity Tracker (Forest Tracker) Report*. Fort Collins, Colorado: Colorado State Forest Service.

De Cáceres, M., and P. Legendre. 2009. "Associations between Species and Groups of Sites: Indices and Statistical Inference." *Ecology* 90(12): 3566–74. https://doi.org/10.1890/08-1823.1.

Demarest, A. B., B. H. Wolk, P. J. Fornwalt, K. J. Barrett, K. J. Warnick, J. S. Briggs, M. D. Redmond, K. C. Rodman, and J. A. Feinstein. 2023. *Understory Plant Community Data Collected before and after Mechanical Forest Restoration Treatments, Colorado Front Range*. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2023-0048.

Demarest, A. B., P. J. Fornwalt, B. H. Wolk, K. C. Rodman, and M. D. Redmond. 2023. "Mechanical Forest Restoration Treatments Stimulate Understory Plants in the Colorado Front Range." *Forest Ecology and Management* 548: 121322. https://doi.org/10.1016/j.foreco.2023.121322.

Dixon, J. M. 2000. "*Koeleria macrantha* (Ledeb.) Schultes (*K. alpigena* Domin, *K. cristata* (L.) Pers. pro parte, *K. gracilis* Pers., *K. albescens* auct. non DC)." *Journal of Ecology* 88(4): 709–726. https://doi.org/10.1046/j.1365-2745.2000.00483.x.

Dodson, E. K., and D. W. Peterson. 2010. "Dry Coniferous Forest Restoration and Understory Plant Diversity: The Importance of Community Heterogeneity and the Scale of Observation." *Forest Ecology and Management* 260(10): 1702–7. https://doi.org/10.1016/j.foreco.2010.08.012.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67(3): 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. "Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities." *PLoS Biology* 4(1): e1. https://doi.org/10.1371/journal.pbio.0040001.

Fornwalt, P. J., and M. R. Kaufmann. 2014. "Understorey Plant Community Dynamics Following a Large, Mixed Severity Wildfire in a *Pinus ponderosa – Pseudotsuga menziesii* Forest, Colorado, USA." *Journal of Vegetation Science* 25(3): 805–818. https://doi.org/10.1111/jvs.12128.

Fornwalt, P. J., C. C. Rhoades, R. M. Hubbard, R. L. Harris, A. M. Faist, and W. D. Bowman. 2018. "Short-Term Understory Plant Community Responses to Salvage Logging in Beetle-Affected Lodgepole Pine Forests." *Forest Ecology and Management* 409: 84–93. https://doi.org/10.1016/j.foreco.2017.10.056.

Fornwalt, P. J., M. E. Rocca, M. A. Battaglia, C. C. Rhoades, and M. G. Ryan. 2017. "Mulching Fuels Treatments Promote Understory Plant Communities in Three Colorado, USA, Coniferous Forest Types." *Forest Ecology and Management* 385: 214–224. https://doi.org/10.1016/j.foreco.2016.11.047.

Fornwalt, P. J., M. R. Kaufmann, and T. J. Stohlgren. 2010. "Impacts of Mixed Severity Wildfire on Exotic Plants in a Colorado Ponderosa Pine–Douglas-Fir Forest." *Biological Invasions* 12(8): 2683–95. https://doi.org/10.1007/s10530-009-9674-2.

Fryer, J. T. 2011. "*Antennaria parvifolia*." In *Fire Effects Information System [Online]*. Missoula, MT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Goodwin, M. J., M. P. North, H. S. J. Zald, and M. D. Hurteau. 2018. "The 15-Year Post-Treatment Response of a Mixed-Conifer Understory Plant Community to Thinning and Burning Treatments." *Forest Ecology and Management* 429: 617–624. https://doi.org/10.1016/j.foreco.2018.07.058.

Griffis, K. L., J. A. Crawford, M. R. Wagner, and W. H. Moir. 2001. "Understory Response to Management Treatments in Northern Arizona Ponderosa Pine Forests." *Forest Ecology and Management* 146(1–3): 239–245. https://doi.org/10.1016/S0378-1127(00)00461-8.

Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fulé, R. E. Keane, et al. 2021. "Evidence for Widespread Changes in the Structure, Composition, and Fire Regimes of Western North American Forests." *Ecological Applications* 31(8): e02431. https://doi.org/10.1002/eap.2431.

Harrison, S., E. I. Damschen, and J. B. Grace. 2010. "Ecological Contingency in the Effects of Climatic Warming on Forest Herb Communities." *National Academy of Sciences of the United States of America* 107(45): 19362–67. https://doi.org/10.1073/pnas.1006823107.

Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." https://doi.org/10.32614/CRAN.package.DHARMa.

Hessburg, P. F., C. L. Miller, S. A. Parks, N. A. Povak, A. H. Taylor, P. E. Higuera, S. J. Prichard, et al. 2019. "Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests." *Frontiers in Ecology and Evolution* 7: 239. https://doi.org/10.3389/fevo.2019.00239.

Hiers, J. K., J. J. O'Brien, R. E. Will, and R. J. Mitchell. 2007. "Forest Floor Depth Mediates Understory Vigor in Xeric *Pinus palustris* Ecosystems." *Ecological Applications* 17(3): 806–814. https://doi.org/10.1890/06-1015.

Hillebrand, H., B. Blasius, E. T. Borer, J. M. Chase, J. A. Downing, B. K. Eriksson, C. T. Filstrup, et al. 2018. "Biodiversity Change Is Uncoupled from Species Richness Trends: Consequences for Conservation and Monitoring." *Journal of Applied Ecology* 55(1): 169–184. https://doi.org/10.1111/1365-2664.12959.

Hood, S. M., B. J. Harvey, P. J. Fornwalt, C. E. Naficy, W. D. Hansen, K. T. Davis, M. A. Battaglia, C. S. Stevens-Rumann, and V. A. Saab. 2021. "Fire Ecology of Rocky Mountain Forests." In *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems* 287–336. Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-030-73267-7_8.

Jang, W., J. S. Crotteau, Y. K. Ortega, S. M. Hood, C. R. Keyes, D. E. Pearson, D. C. Lutes, and A. Sala. 2021. "Native and Non-native Understory Vegetation Responses to Restoration Treatments in a Dry Conifer Forest over 23 Years." *Forest Ecology and Management* 481: 118684. https://doi.org/10.1016/j.foreco.2020.118684.

Kane, J. M., J. M. Varner, E. E. Knapp, and R. F. Powers. 2010. "Understory Vegetation Response to Mechanical Mastication and Other Fuels Treatments in a Ponderosa Pine Forest." *Applied Vegetation Science* 13(2): 207–220. https://doi.org/10.1111/j.1654-109X.2009.01062.x.

Keith, R. P., T. T. Veblen, T. L. Schoennagel, and R. L. Sherriff. 2010. "Understory Vegetation Indicates Historic Fire Regimes in Ponderosa Pine-Dominated Ecosystems in the Colorado

Front Range." *Journal of Vegetation Science* 21(3): 488–499. https://doi.org/10.1111/j.1654-1103.2009.01156.x.

Knapp, E. E., C. N. Skinner, M. P. North, and B. L. Estes. 2013. "Long-Term Overstory and Understory Change Following Logging and Fire Exclusion in a Sierra Nevada Mixed-Conifer Forest." *Forest Ecology and Management* 310: 903–914. https://doi.org/10.1016/j.foreco.2013.09.041.

Korb, J. E., M. T. Stoddard, and D. W. Huffman. 2020. "Effectiveness of Restoration Treatments for Reducing Fuels and Increasing Understory Diversity in Shrubby Mixed-Conifer Forests of the Southern Rocky Mountains, USA." *Forests* 11(5): 508. https://doi.org/10.3390/f11050508.

Laughlin, D. C., and P. Z. Fulé. 2008. "Wildland Fire Effects on Understory Plant Communities in Two Fire-Prone Forests." *Canadian Journal of Forest Research* 38(1): 133–142. https://doi.org/10.1139/X07-118.

Laughlin, D. C., J. D. Bakker, M. L. Daniels, M. M. Moore, C. A. Casey, and J. D. Springer. 2008. "Restoring Plant Species Diversity and Community Composition in a Ponderosa Pine-Bunchgrass Ecosystem." *Plant Ecology* 197(1): 139–151. https://doi.org/10.1007/s11258-007-9367-9.

Lochhead, K. D., and P. Comeau. 2012. "Relationships between Forest Structure, Understorey Light and Regeneration in Complex Douglas-Fir Dominated Stands in South-Eastern British Columbia." *Forest Ecology and Management* 284: 12–22. https://doi.org/10.1016/j.foreco.2012.07.029.

MacArthur, R. H., and J. W. MacArthur. 1961. "On Bird Species Diversity." *Ecology* 42(3): 594–98. https://doi.org/10.2307/1932254.

Mahood, A. L., C. S. Stevens-Rumann, A. E. Rhea, S. M. Ritter, K. Barrett, P. J. Fornwalt, and D. M. Barnard. 2025. "Forest Restoration Treatments Increase Native Plant Diversity but Open the Door to Invasion in the Colorado Front Range." *Forest Ecology and Management* 593: 122881. https://doi.org/10.1016/j.foreco.2025.122881.

Matonis, M. S., and D. Binkley. 2018. "Not Just about the Trees: Key Role of Mosaic-Meadows in Restoration of Ponderosa Pine Ecosystems." *Forest Ecology and Management* 411: 120–131. https://doi.org/10.1016/j.foreco.2018.01.019.

McWilliams, J. 2003. "*Artemisia frigida*." In *Fire Effects Information System [Online]*. Missoula, MT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, R. O'Hara, P. Solymos, H. Stevens, et al. 2022. "Vegan: Community Ecology Package." https://doi.org/10.32614/CRAN.package.vegan.

Peet, R. K. 1981. "Forest Vegetation of the Colorado Front Range: Composition and Dynamics." *Vegetatio* 45(1): 3–75. https://doi.org/10.1007/BF00240202.

PRISM Group. 2020. "PRISM 30-Year Normals." https://prism.oregonstate.edu.

R Core Team. 2022. "R: A Language and Environment for Statistical Computing." https://www.R-project.org.

Reikowski, E. S., T. Refsland, and J. H. Cushman. 2022. "Ungulate Herbivores as Drivers of Aspen Recruitment and Understory Composition throughout Arid Montane Landscapes." *Ecosphere* 13(9): e4225. https://doi.org/10.1002/ecs2.4225.

Reilly, M. J., M. G. McCord, S. M. Brandt, K. P. Linowksi, R. J. Butz, and E. S. Jules. 2020. "Repeated, High-Severity Wildfire Catalyzes Invasion of Non-native Plant Species in Forests of the Klamath Mountains, Northern California, USA." *Biological Invasions* 22(6): 1821–28. https://doi.org/10.1007/s10530-020-02227-3.

Rhoades, C. C., M. A. Battaglia, M. E. Rocca, and M. G. Ryan. 2012. "Short- and Medium-Term Effects of Fuel Reduction Mulch Treatments on Soil Nitrogen Availability in Colorado Conifer Forests." *Forest Ecology and Management* 276: 231–38. https://doi.org/10.1016/j.foreco.2012.03.028.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. "The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence." *Ecology* 85(2): 359–371. https://doi.org/10.1890/03-0266.

Shaw, R. B. 2008. *Grasses of Colorado*. Boulder, CO: University Press of Colorado.

Springer, J. D., D. W. Huffman, M. T. Stoddard, A. J. Sánchez Meador, and A. E. M. Waltz. 2018. "Plant Community Dynamics Following Hazardous Fuel Treatments and Mega-Wildfire in a Warm-Dry Mixed-Conifer Forest of the USA." *Forest Ecology and Management* 429: 278–286. https://doi.org/10.1016/j.foreco.2018.06.022.

Springer, J. D., M. T. Stoddard, K. C. Rodman, D. W. Huffman, P. J. Fornwalt, R. J. Pedersen, D. C. Laughlin, et al. 2024. "Increases in Understory Plant Cover and Richness Persist Following Restoration Treatments in *Pinus ponderosa* Forests." *Journal of Applied Ecology* 61(1): 25–35. https://doi.org/10.1111/1365-2664.14538.

Stahel, W. A. 2002. *Statistische datenanalyse: eine einführung für naturwissenschaftler*. Braunschweig, Germany: Springer Vieweg Verlag.

Stephens, S. L., M. A. Battaglia, D. J. Churchill, B. M. Collins, M. Coppoletta, C. M. Hoffman, J. M. Lydersen, et al. 2020. "Forest Restoration and Fuels Reduction: Convergent or Divergent?" *Bioscience* 71(1): 85–101. https://doi.org/10.1093/biosci/biaa134.

Stevens, J. T., J. E. D. Miller, and P. J. Fornwalt. 2019. "Fire Severity and Changing Composition of Forest Understory Plant Communities." *Journal of Vegetation Science* 30(6): 1099–1109. https://doi.org/10.1111/jvs.12796.

Stewart-Wade, S. M., S. Neumann, L. L. Collins, and G. J. Boland. 2002. "The Biology of Canadian Weeds. 117. *Taraxacum officinale* G. H. Weber ex Wiggers." *Canadian Journal of Plant Science* 82: 825–853.

Tesky, J. L. 1992. "*Calamagrostis purpurascens*." In *Fire Effects Information System [Online]*. Missoula, MT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Tirmenstein, D. A. 1990. "*Rubus idaeus*." In *Fire Effects Information System [Online]*. Missoula, MT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Underhill, J. L., Y. Dickinson, A. Rudney, and J. Thinnes. 2014. "Silviculture of the Colorado Front Range Landscape Restoration Initiative." *Journal of Forestry* 112(5): 484–493. https://doi.org/10.5849/jof.13-092.

USDA NRCS [Natural Resources Conservation Service]. 2021. "The PLANTS Database." http://plants.usda.gov

van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. "Climatic Stress Increases Forest Fire

Severity across the Western United States." *Ecology Letters* 16(9): 1151–56. https://doi.org/10.1111/ele.12151.
Veblen, T., and J. Donnegan. 2005. *Historical Range of Variability for Forest Vegetation of the National Forests of the Colorado Front Range*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Region and the Colorado Forest Restoration Institute.
Wayman, R. B., and M. North. 2007. "Initial Response of a Mixed-Conifer Understory Plant Community to Burning and Thinning Restoration Treatments." *Forest Ecology and Management* 239(1–3): 32–44. https://doi.org/10.1016/j.foreco.2006.11.011.
Wilkin, K., L. Ponisio, D. L. Fry, B. M. Collins, T. Moody, and S. L. Stephens. 2021. "Drivers of Understory Plant Communities in Sierra Nevada Mixed Conifer Forests with Pyrodiversity." *Fire Ecology* 17(1): 30. https://doi.org/10.1186/s42408-021-00111-6.
Wolk, B., and M. E. Rocca. 2009. "Thinning and Chipping Small-Diameter Ponderosa Pine Changes Understory Plant Communities on the Colorado Front Range." *Forest Ecology and Management* 257(1): 85–95. https://doi.org/10.1016/j.foreco.2008.08.014.
Zald, H. S. J., B. K. Kerns, and M. A. Day. 2020. "Limited Effects of Long-Term Repeated Season and Interval of Prescribed Burning on Understory Vegetation Compositional Trajectories and Indicator Species in Ponderosa Pine Forests of Northeastern Oregon, USA." *Forests* 11(8): 834. https://doi.org/10.3390/f11080834.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Demarest, Arièl B., Paula J. Fornwalt, Brett H. Wolk, Jennifer S. Briggs, and Judith D. Springer. 2026. "Understory Plant Species Recruitment and Expansion Spur Community Shifts Following Forest Restoration Treatments." *Ecosphere* 17(1): e70521. https://doi.org/10.1002/ecs2.70521