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Mechanical thinning restores ecological functions in a seasonally dry ponderosa pine forest in the inland Pacific Northwest, USA

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A B S T R A C T

An increasingly important goal of federal land managers in seasonally dry forests of the western US is restoring forest resilience. In this study, we quantified the degree to which a thinning treatment in a dry forest of eastern Oregon restored aspects of forest resilience by focusing on key functional attributes of our study system. First, we measured several physiological responses of overstory trees that are associated with resilience, including radial growth, resin production, abundance of non-structural carbohydrates (NSC), and leaf area. Second, we investigated understory vegetation responses including species diversity, composition, and cover by growth form that influence fire behavior and resilience to disturbance. We found that tree radial growth was greater in trees in thinned stands beginning three years post-treatment. The abundance of key chemical compounds found in trees, including resin, starch, total NSC and sucrose did not differ between treatments; however, abundance of glucose plus fructose was lower in treated stands, suggesting mobilization and use of carbon reserves for foliar and wood production following thinning. We observed an increase in species richness and diversity within thinned stands three to four years after thinning, primarily due to the release of forbs and reestablishment of graminoids following ground disturbance. Here, we demonstrate that elements of forest resilience can be restored in dry forest systems via selective thinning to promote historical forest structure. In forests where thinning reduces stand density, vigorous overstory trees and increased herbaceous cover can help facilitate the re-establishment of low intensity surface fire regimes that maintain stable and persistent vegetative states. Understanding the ecological effects of fuel reduction treatments allows land managers to assess potential forest resiliency and adapt future treatments based on the observed results of previous activities.

1. Introduction

Ecological restoration of seasonally dry, fire prone forests ("dry forests") has been an important goal of U.S. Forest Service (USFS) managers for more than twenty years (O'Laughlin, 2005, Rains and Hubbard, 2002). In the early 2000s, both Congressional legislation (e.g., the Healthy Forest Restoration Act passed by Congress in 2003) and agency policy initiatives (e.g., the Healthy Forests Initiative established by President Bush in 2002) emphasized reduction of hazardous fuels to manage risk of large and severe wildfires (Abrams et al., 2016). More recently, federal policy for dry forests has evolved to emphasize restoring resilience of forest ecosystems (Selles and Rissman, 2020,

Sample, 2017, Bone et al., 2016). For instance, the Collaborative Forest Landscape Restoration Program (CFLRP) established by Congress in 2009 provides augmented funding for collaboratively designed forest resilience restoration treatments across high priority landscapes (Schultz et al., 2012). Revisions to National Forest Management Act (NFMA) regulations completed in 2012 require the USFS to use the best available scientific information to restore ecological resiliency, to monitor the effectiveness of treatments, and adapt treatments in light of new information (Brown and Nie, 2019).

Ecological resilience is defined by Holling (1973) as "a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between

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populations or state variables." Although this definition is conceptually robust, scientists and managers have struggled to develop specific measurements that reliably predict different systems' capacity to be resilient to disturbance (Nikinmaa et al., 2020, Standish et al., 2014). In this paper, we present results from a long-term monitoring effort designed to evaluate the degree to which mechanical thinning in the southern Blue Mountains of eastern Oregon promotes forest resilience. This research, co-produced with managers and stakeholder groups, takes a practical and functional view of ecological resilience. Specifically, we evaluate the degree to which thinning treatments restored aspects of resiliency by measuring ecosystem components associated with feedbacks that entrain recognizable and persistent vegetation states (North et al., 2022, Hood et al., 2016, Johnstone et al., 2016, Lindenmayer et al., 2016, Beisner et al., 2003).

Dry forests such as those found within our study area in eastern Oregon are characterized by strong feedbacks between overstory tree characteristics and surface vegetation. Historically, fine-scale tree mortality from chronic surface fire resulted in open stands with widely spaced shade intolerant and fire-resistant trees (Hagmann et al., 2021, Johnston, 2017). Sparse canopies allowed ample light to the forest floor which facilitated dominance by fast-regenerating herbaceous fuels that are ideal for carrying low intensity surface fire. Fire dynamics were drastically changed in our study area and throughout dry forests of the interior Pacific Northwest in the last decades of the 19th century for a variety of reasons. First, the late 1800s and early 1900s were unusually cool and moist. Second, European settlement changed how Indigenous people used fire on the landscape. Third, early forest rangers were charged with aggressively extinguishing fire starts in order to protect regeneration that was critical to early foresters' vision for sustained yield timber harvest. Finally, extensive unregulated grazing removed herbaceous fuel that carried surface fire (Mosgrove, 1980). Cool and moist conditions, fire suppression, and a lack of herbaceous fuel created ideal conditions for conifer regeneration, which initiated a new feedback that made forests much less suitable for surface fire (Hessburg and Agee, 2003). Instead, increasingly dense forests and shaded understories result in uncharacteristically severe drought-related mortality, wildfire, and susceptibility to biotic disturbance agents such as bark beetles (Bradford and Bell, 2017, Millar and Stephenson, 2015, Spies et al., 2006, Hessburg et al., 2005).

Given this knowledge of disturbance and successional dynamics in our study system, we gathered and analyzed data related to key overstory tree and understory vegetation characteristics in treated and untreated stands, specifically the health and vigor of overstory trees and the diversity and abundance of understory grasses, forbs and shrubs. Tree vigor has been identified as an important predictor of mortality (Cailleret et al., 2017, Dobbertin, 2005) and fuel treatments have been shown to enhance tree growth (Thomas and Waring, 2015), increase drought resistance (Vernon et al., 2018), increase late summer carbon assimilation (Tepley et al., 2020) and reduce susceptibility to bark beetle outbreaks (Hood et al., 2016). Other tree physiological characteristics, such as resin production, are important chemical defenses against bark beetles (Raffa and Smalley, 1995) and the mobilization of non-structural carbohydrates (NSC) facilitate growth during periods of stress and recovery following disturbance and seasonal change (Tixier et al., 2019, Iwasa and Kubo, 1997). Leaf area is associated with higher photosynthetic potential and thus serves as an indicator of tree vigor (Waring et al., 1980). Therefore, we hypothesize that reducing tree density via thinning will increase characteristics associated with forest resilience, including enhanced tree radial growth, increased leaf area and increased use of non-structural carbohydrates.

The understory vegetation community in dry forests is likely an important contributor to future stand resilience. Disturbance frequency and severity influences species abundance and selects for specific plant autecological traits. For example, a recent study in eastern Oregon found that plant groups with traits such as fire resistance were able to recover from prescribed fire treatments and persist following repeated burning (Kerns and Day, 2018). In the absence of fire, forest thinning may serve to stimulate the growth of grasses and forbs that would otherwise be suppressed under a closed canopy forest. Restoring forb and grass cover facilitates future low severity fire, especially when thinning treatments also reduce stand density and ladder fuels. Greater understory species diversity also creates ecological redundancy, which may make systems more resistant to change under future conditions (Drever et al., 2006). Therefore, we hypothesized that reduction in canopy cover would promote understory diversity and herbaceous cover, creating conditions for low-severity fires in the future and subsequently increasing the capacity of the system to rebound following disturbance.

2. Methods

2.1. Study area

We tested these hypotheses using data collected within the Marshall Devine Hazardous Fuel Reduction Project planning area at the south end of the Southern Blues CFLRP area on the Malheur National Forest (Fig. 1). The Southern Blues are one of 23 priority landscapes that currently receive funding under the CFLRP (Davis et al., 2018). Restoration treatments and multi-party monitoring of treatments within the Southern Blues CFLRP area are planned and implemented by the USFS in collaboration with the Blue Mountains Forest Partners (BMFP) and Harney County Restoration Collaborative (HCRC), stakeholder groups that convene local community leaders and representatives from conservation groups and the wood products industry (Butler et al., 2019). The Marshall Devine Project was one of the first of more than a dozen landscape-scale hazardous fuel reduction and forest resilience restoration projects completed with CFLRP funds.

The study area is dominated by gentle hills bisected by Trout Creek and Poison Creek which flow into the Great Basin from their source near the base of the Strawberry Mountains 50 km to the north. Elevations within the study area range from 1,433 to 2,012 m. The area receives an average of 612 mm of precipitation annually, 90% of which falls from October to May. Winters are cold—mean temperature is often below 0 °C between December and February. Summers are hot, with maximum daytime temperatures often in excess of 30 °C for consecutive weeks in July and August (PRISM, 2021). Lightning ignitions are common in July and August and prior to fire suppression practices beginning with the establishment of forest reserves in the late 1800s, mean fire return intervals for the area ranged from 10 to 12 years (Johnston et al., 2017).

The Marshall Devine area is dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), while Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and lodgepole pine (*Pinus contorta* Dougl. ex Loud) are occasionally found at the bottom of draws. Western juniper (*Juniperus occidentalis* Hook.) and mountain mahogany (*Cercocarpus ledifolius* Nutt.) are drought tolerant but fire sensitive species found in rocky, fuel-limited outcroppings or on the margins of forest and sage steppe (Johnson and Clausnitzer, 1992). Much of the widely spaced, old-growth ponderosa pine forest that historically dominated the area was removed by logging beginning in the 1920s. The area was used extensively as rangeland for cattle beginning in the 1880s, and grazing practices during this time led to dramatic reductions in native perennial grass cover and forb cover. There were significant reductions in grazing use between establishment of national forests in the Blue Mountains in 1907 and passage of the Taylor Grazing Act in 1934. Grazing remains an important use of the Marshall Devine planning area, and grazing levels have remained relatively constant since the 1950s (USDA, 2018).

2.2. Field data collection

Between late summer 2014 and early spring 2015, local timber operators mechanically thinned 2,900 ha within the planning area. The overall goals of the project were to increase forest resilience to fire disturbance and facilitate the return of episodic low-severity fire.
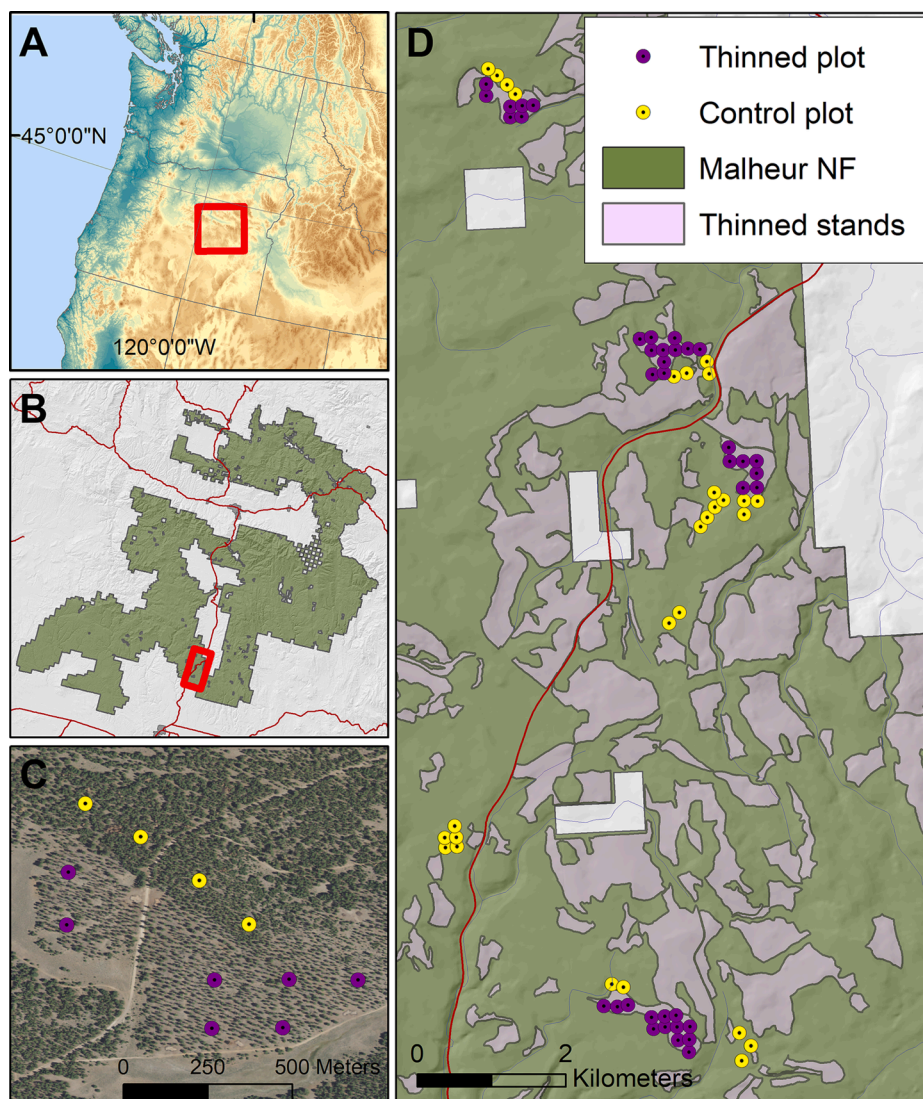
Fig. 1. Map showing the Marshall Devine study area within the Malheur National Forest located in eastern Oregon. Panel A shows the location of the southern Blue Mountains in the Pacific Northwest, USA. Panel B shows the location of the study area within the Malheur National Forest. Panel C shows an example of the arrangement of data collection plots in a thinning unit and adjacent untreated stands (note significant reductions in canopy cover in thinned portion of the stand). Panel D shows the location of all thinning plots and data collection plots within the study area.

Specific silvicultural objectives included thinning from below to reduce stand basal area from 35–46 m^2 ha^{-1} to 11.5–16 m^2 ha^{-1} (USDA, 2012). Between June and July 2014, before logging had commenced, we randomly selected four Marshall Devine treatment units and systematically located between 7 and 13 permanent 0.1 ha circular plots in each unit (total of 40 plots). We also selected three stands with similar slope, elevation, aspect and the same potential vegetation types as treatment stands and located an additional 23 plots to serve as controls for comparison with treatment plots (Fig. 1). Some control plots were located in unthinned portions of a stand where thinning had occurred and these plots were included in the same "strata" as thinned plots during statistical analysis to account for a lack of independence between treated and untreated units (i.e., split-plot design; see Table 1 and Methods section below). In 2015 (after logging had been completed) and in each subsequent year until 2019, we remeasured between 70% and 100% of all treated plots. We were unable to relocate two plots in thinned stands and those plots were excluded from subsequent analysis. In 2018, we remeasured control plots and also located and measured 18 additional control plots. The lack of balance between treated plots (n = 38) and untreated controls (n = 29) was largely due to an inability to locate additional unthinned stands with similar characteristics as thinned stands in the vicinity.

Table 1
Variables evaluated as potential explanatory variables for growth and resin flow mixed effect models.

Variable	Description
BAI 2018	Average basal area increment in 2018 (cm^2)
CBH	Crown base height – the lowest height above the ground of continuous live foliage (m)
CR	Crown ratio – the ratio of crown length to total tree height (%)
DBH	Diameter at breast height (cm)
DCH	Diameter at core height (cm)
Height	Height of tree (m)
Sample ID	Individual tree identifier
Strata	Sample unit that lumps together continuous treated and untreated stands
Unit	Sample unit in study area

2.3. Tree vigor

In August 2018, we randomly located one tree in each treatment and control plot (n = 66) to sample for select measures of tree vigor. Ponderosa pine made up 96% of plot basal area and all trees selected were ponderosa pine > 13 cm DBH (max = 97 cm, mean = 41 cm). We removed two 2.5 cm circular sections of bark and phloem using an arch

punch on either side of each tree. We affixed a 50 or 75 ml collection vial (depending on the size of the tree) below each wound. We revisited each tree approximately 24 h later and recorded the total amount of resin that had collected to the nearest 0.25 ml (Hood and Sala, 2015; Fig. 2). This measurement was converted to ml per hour in order to account for slight differences in total time that resin accumulated. Resin collection was completed between August 15 and August 16 because the literature suggests that resin flow in ponderosa pine peaks during the hottest part of the year (Hood and Sala, 2015). There was no measurable difference in cloud cover, precipitation, or temperature on these days.

At the same time as we recorded resin accumulation, we extracted a 12 × 127 mm core at breast height from each tree using a hand-powered increment borer for analysis of NSC content of current year (2018) bole sapwood. NSCs were analyzed as described in detail in Körner et al. (1995) and Wong (1990). Cores were placed in a cooler and chilled until microwaved in the laboratory to stop enzymatic activity. Samples were excised from cores using a thin metal blade, then dried and ground for analysis of sucrose, glucose plus fructose, starch and total NSC content using a 96-well microplate photometer (Multiskan FC, Thermo Scientific, Waltham, MA, USA). Photometric analysis is based on absorbance of samples at 340 nm in solution with reference to the absorbance of a glucose reference solution both before and after enzymatic treatments of sucrose digestion by invertase for 45 min and overnight starch digestion by amyloglucosidase. Glucose plus fructose content was determined from photometric analysis of sample solutions with no enzymatic treatment. Fifteen samples had insufficient material from that year's growth to perform extractions and these samples were discarded and not used in statistical analysis.

We returned to each tree in late October 2018 after radial growth of trees had ceased and extracted two 5.15 mm tree cores that intercepted the pith of the tree or that we estimated was within 15 rings of the pith. Each tree core was mounted in a wooden holder, sanded to fine polish, and visually crossdated using an existing ponderosa pine chronology from the area (Johnston et al., 2016; Stokes and Smiley, 1968). All ring widths were measured to 0.001 mm precision using a computer controlled Velmex or Acu-Gage linear measuring system (Velmex, Inc., Bloomfield NY; Acu-Gage Systems, Hudson NH). Crossdating accuracy was verified using COFECHA software (Grissino-Mayer, 2001). Each ring width was converted to basal area increment (BAI) from the pith (or estimated pith) outwards and inside-the-bark BAI was estimated for

each tree by averaging BAI from the two cores taken from each tree.

Tree leaf area varies as a function of sapwood at the base of the tree crown (Marshall and Waring, 1986; Waring et al., 1982). Therefore, we used measurements of crown base height, inside the bark diameter (calculated from the pith out), species and regional specific taper equations, and published sapwood-to-leaf-area ratios to estimate individual tree leaf area in fall 2018, the year of sampling (Fig. 2; Johnston et al., 2019, Walters and Hann, 1986, Waring et al., 1982, Waring et al., 1977).

2.4. Vegetation

Every year from 2014 to 2019, within each permanent plot, we located two 15.25 m transects beginning at plot center and extending to the edge of the plot along a random bearing. At 0.6 m intervals along the transect (total of 25 points per transect), we placed a slender 1 m long pin perpendicular to the forest floor and recorded the surface composition (the base of a plant, rock, litter, duff, bare ground, or woody debris) and up to three unique species of any plant encountered along the pin (Herrick et al., 2005). This procedure resulted in sampling up to 4 species at 50 different points within each plot. Species occurrences were later divided by the total number of points to estimate cover. We revisited each plot at approximately the same time in June or July in each measurement year so that species abundance and diversity was not strongly influenced by seasonal differences in vegetation or vegetation morphology (i.e., senesced herbaceous tissues).

2.5. Statistical analysis of tree response

We evaluated radial growth (basal area increment, n = 66) over time and between treatments by fitting linear mixed-effect models using R statistical software (R Core Team, 2021) and the nlme package (Pinheiro et al., 2022). All models included a nested random effect for sample and strata to account for individual tree responses and a lack of independence between paired sampling units. The final model also included weights (treatment & year) to address non-constant variance in the residuals across treatments and time. We tested a subset of models using combinations of tree characteristics and biologically reasonable interaction terms (Table 1). We used Akaike's information criterion (AIC) to find the simplest model with the most explanatory power (Zuur et al.,
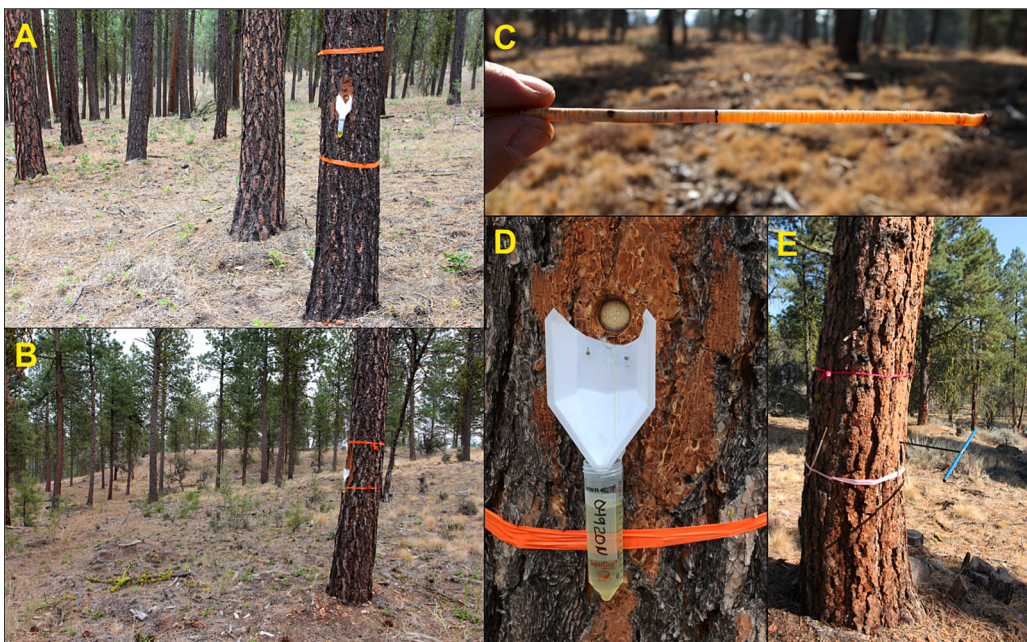

Fig. 2. Tree physiological response data collection. Panel A shows a randomly selected tree in unthinned control stand. Panel B shows a randomly selected tree in a thinned stand (note that trees in the thinned stand have significantly less competition). Panel C shows a close up of tree core (note the translucent sapwood, used to model leaf area). Panel D shows a close up of resin collection procedures. Panel E shows extraction of a 5.15 mm core from a randomly selected tree with a hand powered increment borer.

2009). Our final model included year in which basal area increment was measured to address year to year variation in growth, diameter at core height (DCH) to address variability in tree size and treatment to assess differences between treated and untreated stands. We checked for autocorrelation using ACF plots and included a first-order auto-correlation term to address temporal auto-correlation in the model. (Pinheiro and Bates, 2000). Growth differences in any given year between treatments were considered significant if estimated 95% confidence intervals did not overlap (α = 0.05).

To investigate the effect of fuel treatments on resin flow (n = 64) we created generalized additive models (GAMs) using R's mgcv package (Johnson, 2020, Wood, 2006). We tested a subset of models using combinations of tree characteristics (Table 1) to explain variation in resin flow expressed in milliliters per hour. Our final model included growth in the year of sampling (2018 BAI) to account for tree level growth differences, treatment to assess differences in thinned and unthinned stands, DBH to account for differences in tree size, and crown to base height to account for differences in photosynthetic potential. We used strata as a random effect and log transformed resin flow to ensure normality and homoscedasticity in the residuals. We chose a final model based on the lowest AIC and the lowest generalized cross-validation (GCV) scores. We used GAMs for modeling resin flow responses to treatments because the responses are likely to be non-linear (Johnston et al., 2019). GCV scores are useful because the cross-validation process can assess the predictive capacity of the model (Wood, 2011).

We evaluated treatment differences in non-structural carbohydrates (NSC; n = 37 for all models) including total NSC, starch, sucrose and glucose plus fructose, as well as leaf area (n = 66), by fitting separate linear mixed-effect models that included strata as a random effect. For all tree physiological response and leaf area models, we checked residual plots to assess normality and homoscedasticity assumptions in final models. Evaluation of treatment differences was based on non-overlapping 95% confidence intervals.

2.6. Vegetation analysis

To assess changes in vegetation diversity associated with thinning over the study period, we calculated species richness and Shannon index (Shannon, 1948) for each thinned plot in each year using the vegan package in R (Oksanen et al., 2019). We fit linear mixed effects models to compare richness and Shannon index over time in thinned plots (n = 40) using strata as a random effect and AIC for model selection. Our final model included measurement year to test variation across the study period and included weights (measurement year) to address non-constant variance in the residuals. We included a first-order auto-correlation term to address temporal auto-correlation in the time-series model and checked ACF plots (Pinheiro and Bates, 2000). Year to year differences were evaluated based on non-overlapping 95% confidence intervals. We also fit mixed effects models to test for differences in both species richness and Shannon index in thinned and unthinned plots in the year 2018 (n = 67) because it was the longest time since treatment (4 years) in which all plots in both thinned and unthinned stands were measured.

To test the effects of treatment on different plant types, we grouped all identified species by growth form (i.e. graminoid, forb, shrub) using the USDA plants database (USDA, 2021) and then tallied species richness and summed cover estimates across species within each growth form group for each plot. We fit linear mixed effect models for each growth form across plots (n = 67) with strata as the random effect to test for treatment differences in species richness and cover for each growth form. All models were checked for normality and homoscedasticity assumptions. Treatment differences were determined based on 95% confidence intervals that did not overlap zero. We also ran a post-hoc analysis comparing non-native cover between treatments using a mixed effect model with strata as a random effect to determine if any detected changes in vegetation composition were driven by non-native plant species.

To assess changes in community composition through time in only treated plots (2014–2018) and between treated and untreated plots 4 years after thinning (2018), we used nonmetric multidimensional scaling (NMDS) ordination of plots in species space using the vegan package in R. We achieved optimized 2-dimensional solutions using the Euclidian distance measure of species abundance between plots with 1,000 permutations (Kruskal, 1964). We then used a growth form (graminoid, forb, shrub) and native status trait matrix to overlay functional group abundance vectors using 'envfit' in vegan to assess the relationship between ordination axes and plant functional groups (McCune et al., 2002).

3. Results

3.1. Tree physiological responses

As predicted, we found evidence that thinning was associated with enhanced vigor of trees. After accounting for other factors that influence radial growth including the size of trees, there was no significant difference in the estimated mean radial growth between trees in treated and untreated stands in 2014 before thinning began or in the two years following thinning (Fig. 3). But three and four years after thinning was completed (2017–2018), basal area increment was 1000 mm² (95% CI = 208, 1803) and 1532 mm² (561, 2503) greater in treated compared to untreated stands respectively (Fig. 3).

Our GAM models indicate that resin flow was associated both with BAI and tree DBH (Table 2). We found no evidence that crown to base height influenced resin flow, nor was there a difference in resin flow between trees in treated and untreated stands (Table 2, Fig. 4A). Larger trees generally had higher resin flow than smaller trees although resin flow began to decline for trees exceeding 43 cm DBH (Fig. 4B). NSC content was generally lower in trees in treated stands than in trees in untreated stands, although most of these differences were statistically insignificant (Fig. 5). We found evidence that glucose plus fructose content was 0.70% (0.14, 1.25) lower in treated stands than untreated stands (Table 3). Mixed effect model results indicated that leaf area was strongly associated with tree size (DBH) and after accounting for size, we found evidence that thinning increased leaf area by 15.9 m² per tree (−0.30, 32.22), although confidence intervals slightly overlapped zero (Table 3, Fig. 6).

3.2. Vegetation analysis

Species richness and Shannon diversity increased over time following thinning (Fig. 7), with 5.6 (2.9, 8.2) more species in 2017 and 4.4 (2.7, 6.1) more species in 2018 compared to pre-treatment (Table 4). This resulted in a median of 3 more species in treated compared to untreated stands in 2018, although neither richness or diversity statistically differed that year (Fig. 8A & B). While we found no difference in forb richness with thinning, forb cover was 6.1% higher (0.87, 11.3) in treated compared to untreated stands in 2018 (Fig. 8C & D). Graminoid cover was also generally higher, while shrub cover was generally lower in treated stands, although we did not find strong statistical evidence of a treatment effect (Table 5; Fig. 8C & D). We also found no statistically significant difference in richness for graminoids and shrubs between treated and untreated stands in 2018 (Fig. 8C & D). A post-hoc analysis indicated that there was no difference in non-native species cover between thinned and unthinned stands (0.79%, 95% CI = −0.64, 2.21) in 2018, confirming that plants released from treated stands did not consist of non-native, invasive species (Table 5).

Box plots showing the range of values for cover (C) and species richness (D) by growth form in treated and untreated stands in 2018. Asterisks indicate results from mixed effect modeling that showed an increase in forb cover in treated stands 4 years post-treatment.

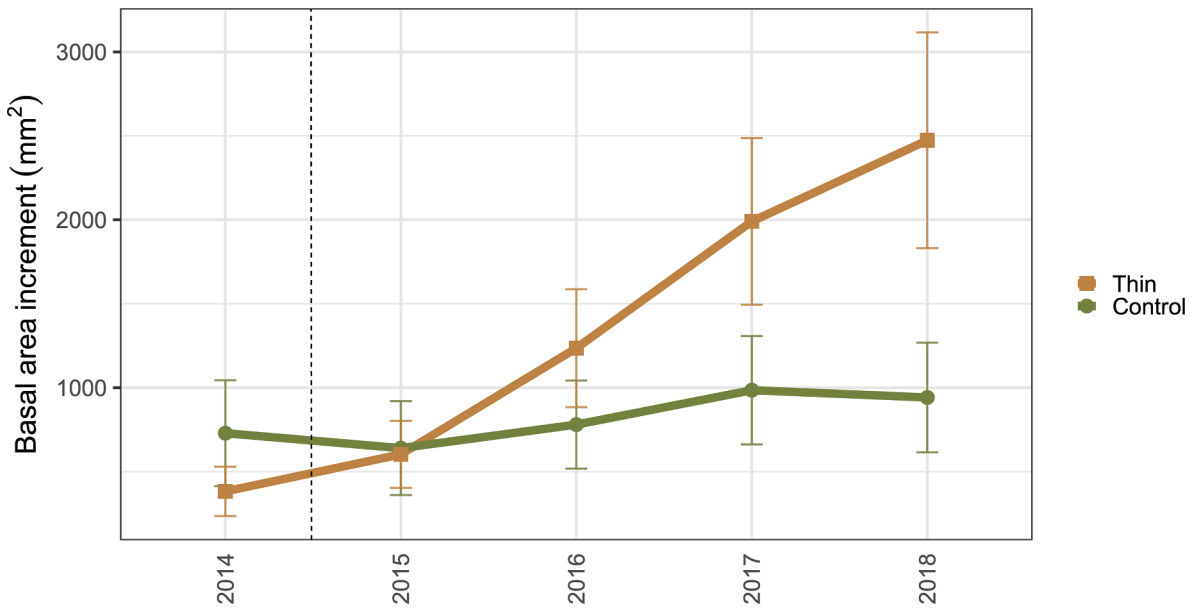The NMDS ordination of treated plots in species space over time

Fig. 3. Estimated mean basal area increment and confidence intervals (whiskers) for treated and untreated stands over the study period (2014–2018). Dashed line represents time of thinning treatment. Results from mixed effects models show that basal area increment was higher in treated stands 3 and 4 years after thinning.

Table 2

Parameter estimates and variation for GAM modeled resin flow (ml/hour) in 2018. Treatment differences are shown relative to untreated stands. Model estimates are shown on the original scale.

Predictors	Estimates	CI	P
Intercept	1.01	0.77–1.32	0.959
BAI 2018	1.00	0.99–1.00	0.006
Treatment	1.21	0.82–1.79	0.321
Smooth term (DBH)	20.85		<0.001
Smooth term (CBH)	2.72		0.677
Smooth term (Strata)	2.52		0.210

(2014–2018 convex hulls) yielded a 2-dimensional solution after 20 iterations with a final stress value of 0.103. The ordination indicated changes in species composition over time associated with treatment. Immediately following thinning (in 2015 and 2016), species composition was similar but more homogenous than plots were prior to treatment. Species composition three and four years after thinning (2017–2018) showed the greatest separation in plots in species space, indicating greater among-plot variation in plant communities (i.e., beta diversity, Fig. 9A). Forb abundance was correlated with axis 1 (r^2 = 0.33, p = 0.001) while graminoid abundance was correlated with axis 2 (r^2 = 0.17, p = 0.001). Shrub abundance was only marginally correlated with axis 1 (r^2 = 0.04, p = 0.04) indicating that thinned stands were
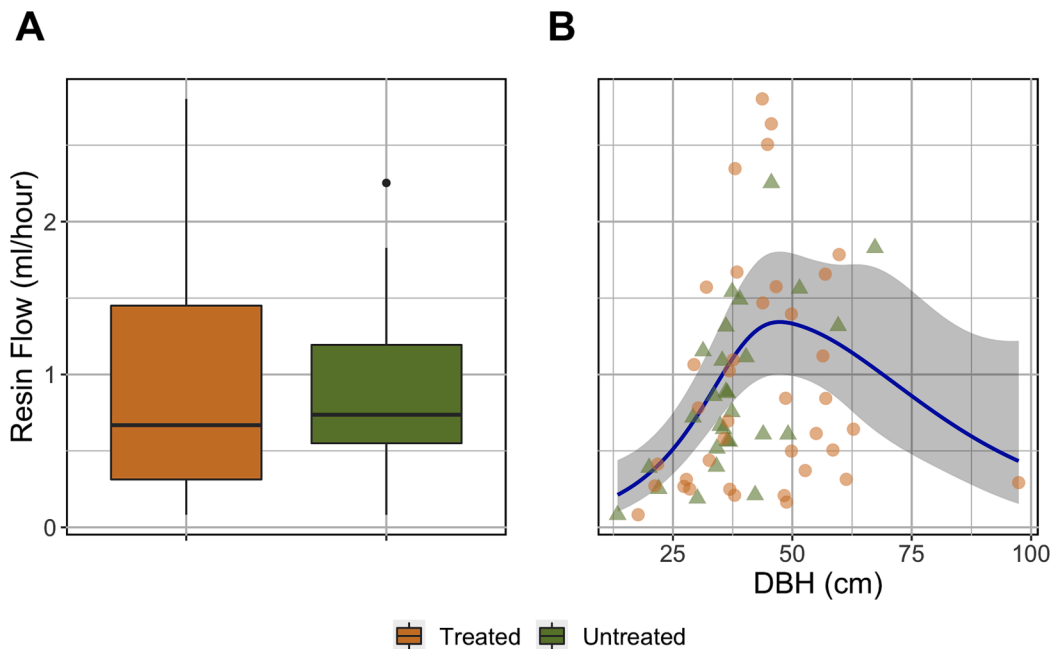

Fig. 4. Box plot of resin flow (ml/hour) for trees from treated and untreated stands in 2018 (A). Results from mixed effects models shows no difference between treatments 4 years after thinning. Response curve for mixed effect GAM model for resin flow in 2018 (B). The curve shows the predicted resin flow values as a function of tree size (DBH) after accounting for growth in 2018 and treatment. Model estimates are shown on the original scale, points show actual resin flow values.
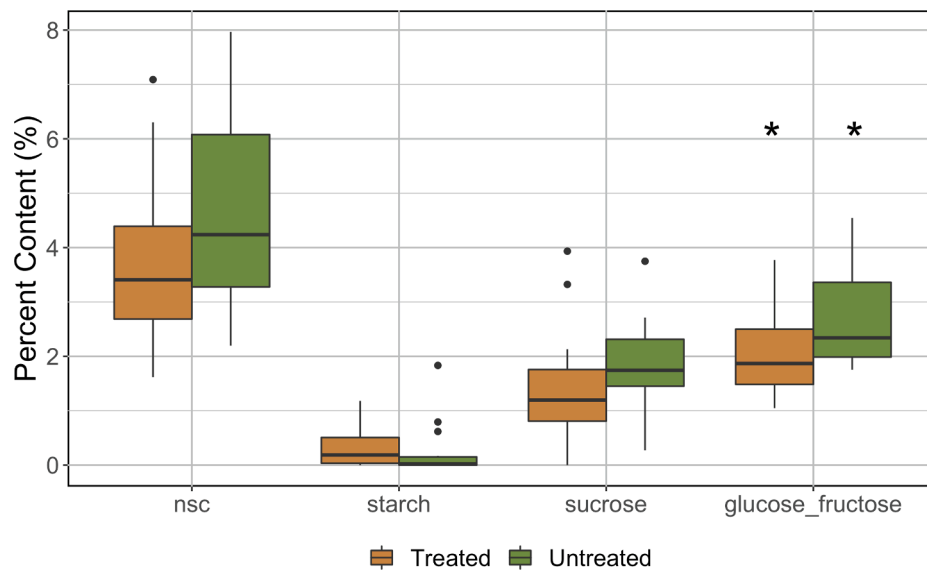
Fig. 5. Box plot of tree non-structural carbhohydrate (NSC) content by treatment in 2018 including total NSC, starch, sucrose and glucose plus fructose. Asterisks indicate results from mixed effect modeling that showed evidence of a difference in glucose plus fructose content 4 years post-treatment.

Table 3
Parameter estimates and variation for mixed effects models for non-structural carbohydrate content (total NSC, starch, sucrose, glucose plus fructose) and leaf area in 2018. Treatment differences are shown relative to the unthinned stands. Bold values indicate evidence of an effect at $\alpha = 0.05$.

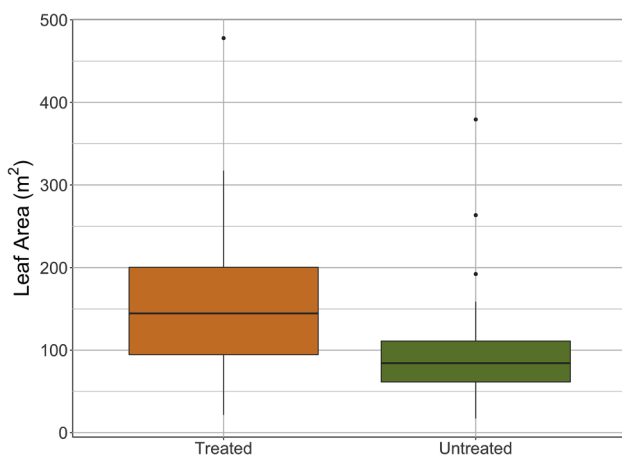| Response	Predictors	Estimates	CI	P
NSC	Treatment	−0.94	−2.02 to 0.14	0.085
Starch	Treatment	0.04	−0.24 to 0.32	0.793
Sucrose	Treatment	−0.53	−1.15 to 0.10	0.098
Glucose plus fructose	**Treatment**	**−0.70**	**−1.25 to −0.14**	**0.016**
Leaf Area	**DBH**	**6.03**	**5.44–6.62**	**<0.001**
	Treatment	15.96	−0.30 to 32.22	0.054

Fig. 6. Box plot of leaf area (m^2) estimates for trees in treated and untreated stands in 2018 (4 years post-treatment). Results from mixed effects modeling show that thinning increased leaf area, although confidence intervals slightly overlapped zero.

generally strongly associated with greater abundance of graminoids and forbs and less so for shrubs three and four years post-treatment (2017 and 2018).

Ordination of treated and untreated plots in 2018 yielded a 2-dimensional solution after 28 iterations with a final stress value of 0.129 and indicated some separation between treated and untreated stands

(Fig. 9B). Forb abundance was correlated with axis 2 ($r^2 = 0.3$, p = 0.001) while graminoid abundance was correlated with axis 1 ($r^2 = 0.11$, p = 0.028). Thinned plots were generally positively associated with forb and graminoid abundance vectors, while untreated plots were associated with the shrub abundance vector.

4. Discussion

This study provides evidence that mechanical thinning aids in restoring tree and understory vegetation conditions associated with forest resilience to disturbance. Similar to previous studies, we found that thinning promoted radial growth and thus vigor of retained ponderosa pine (Tepley et al., 2020), which is likely to confer resistance to future stress and disturbances such as drought, fire and insect outbreaks (North et al., 2022, Tepley et al., 2020, Vernon et al., 2018, McDowell et al., 2003). We also observed increased leaf area and decreased abundance of non-structural carbohydrates (i.e., mobilization of glucose plus fructose) in thinned stands, further indicating mobilization of resources to enhance growth of remaining trees. Strong leaf area responses to thinning may take more time to develop (McDowell et al., 2003) and although leaf area confidence intervals slightly overlapped zero, our observations provide evidence that augmented tree vigor can be achieved relatively quickly by thinning in seasonally dry inland Pacific Northwest forest systems. Similar to previous studies, we found that resin flow was largely a function of tree size and growth (BAI) (Johnson, 2020, McDowell et al., 2007). In contrast to studies from the southwest (McDowell et al. 2007, Kolb et al. 1998), we did not detect an increase in resin production following thinning. The lack of a strong resin production difference between treatments suggests that our sample size was too small, or that ponderosa pine in our study area prioritize production of primary defensive compounds, possibly at the expense of leaf, bole, and root growth. Taken together our results demonstrate that thinning makes more resources available to trees and permits trees to better mobilize resources for radial growth and leaf area (Woodruff and Meinzer, 2011).

The results of our vegetation community analysis suggest that thinning increases understory composition associated with resilient open-pine systems. Our statistical models showed a significant increase in understory species richness and diversity over time within thinned stands (Fig. 7). These differences took several years to develop following thinning, consistent with a disturbance response and increased resource availability following thinning. Our comparison of thinned and
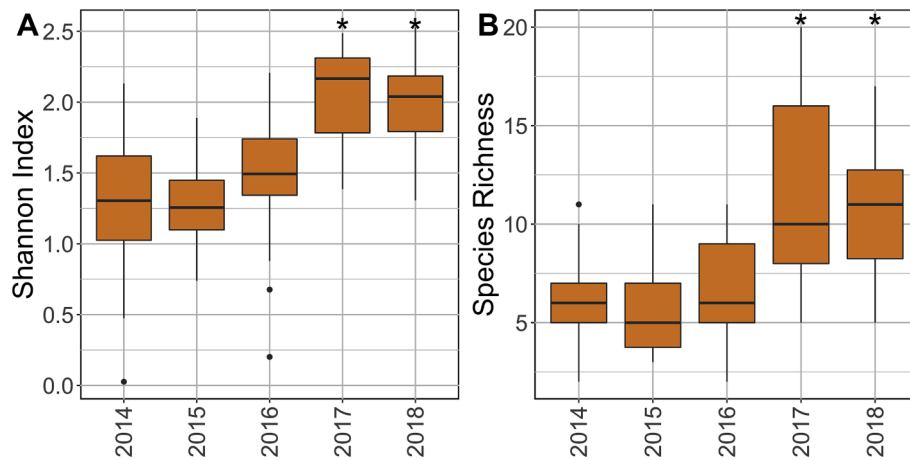
Fig. 7. Box plots showing range of plot-level values for Shannon Index (A) and Species Richness (B) over study period in treated stands. Asterisks denote differences from mixed effects modeling that showed both measures were higher 3 and 4 year post-treatment relative to pre-treatment values (2014).

Table 4
Estimated mean values by year for species richness from a mixed effect model. Asterisk denotes differences in mean values 3 and 4 post-treatment compared to pre-treatment (2014).

Year	Mean	SE	DF	CI
2014	6.1	0.54	4	4.6–7.6
2015	5.3	0.63	4	3.6–7.1
2016	6.5	0.57	4	4.9–8.1
2017	11.7*	0.96	4	9–14.3
2018	10.5*	0.66	4	8.6–12.3

Table 5
Parameter estimates and variation for mixed effects models for percent cover by growth form in 2018. Treatment differences are shown relative to the unthinned stands. Bold values indicate evidence of an effect at $\alpha = 0.05$.

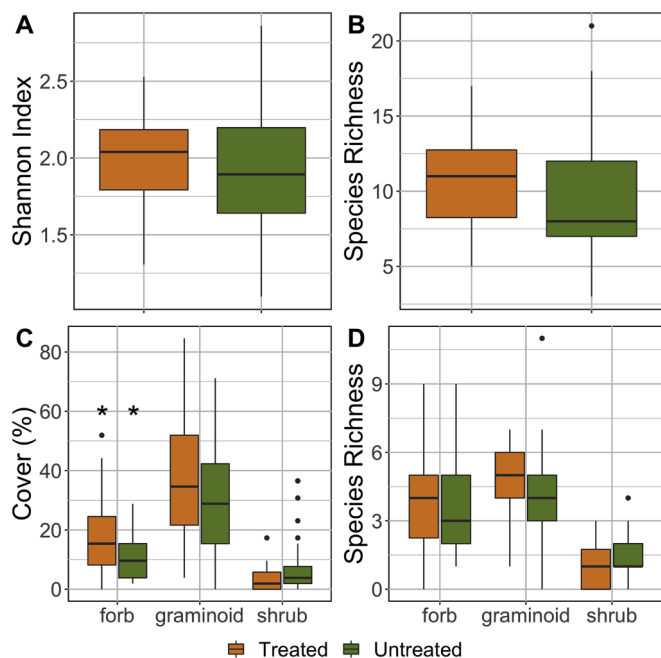| Response	Predictors	Estimates	CI	P
Forb cover	Treatment	6.1	0.87–11.3	**0.023**
Shrub cover	Treatment	−1.01	−4.7 to 2.7	0.59
Graminoid cover	Treatment	6	−3.7 to 15.7	0.22
Non-native cover	Treatment	0.79	−0.64 to 2.21	0.27

Fig. 8. Box plots showing the range of plot-level values for Shannon Index (A) and species richness (B) for all species, and percent cover (C) and species richness by growth form.

unthinned stands in a single year (2018) provided little evidence that thinning significantly increased overall richness or diversity, although thinned stands had significantly greater forb cover. The equivocal effects of thinning measured in a single year may be confounded by livestock grazing and native ungulate herbivory throughout the study area (Pekin et al., 2015). While understory patterns are emerging in treated stands, the effects of thinning may not be as simplistic as increasing overall diversity. Changes to vegetation in dry systems can be subtle and highly variable throughout space and time (Kerns and Day, 2018). Notably, we found no detectable increase in non-native vegetation cover following treatment, despite the presence of highly invasive *Bromus tectorum* within a study area with an extensive road system and significant ungulate use, which often serve as vectors for non-native vegetation species (Bartuszevige and Endress, 2008, Magee et al., 2008). A larger sample size or a larger area sampled may demonstrate an increase in non-native species in response to thinning where invasive species are abundant prior to treatment.

Ordination methods were well suited to illustrate relatively subtle shifts in species composition over time in thinned stands and between thinned and unthinned stands. Our ordinations showed that forb and graminoid abundance was associated with thinned stands while shrub abundance was associated with unthinned stands (Fig. 9), consistent with trends suggested by field measurements in 2018 (Fig. 8). Previous studies have also noted that reduction in stand basal area increases available water, nutrients and/or sunlight, which can stimulate flowering vegetation (Ares et al., 2009, Dodson et al., 2008, McDowell et al., 2007). It is possible that increases in forb cover were associated with ground-based logging activities, which create mineral soil seedbanks and scar seeds stimulating germination. Mechanical damage to shrubs from logging may account for the slight decline in shrub abundance consistent with other studies in the Blue Mountains (Metlen et al., 2004). The greater variability in plant communities observed across thinned stands implies greater beta diversity that may aid in the recovery of various plant functional groups and resilience of biodiversity across the landscape following future fire events (Drever et al., 2006). The observed increase in forb abundance associated with thinning at the local level will likely directly benefit a wide variety of species, particularly insect pollinators (Glenny et al., 2022) and wild herbivores (Vales et al., 2017).
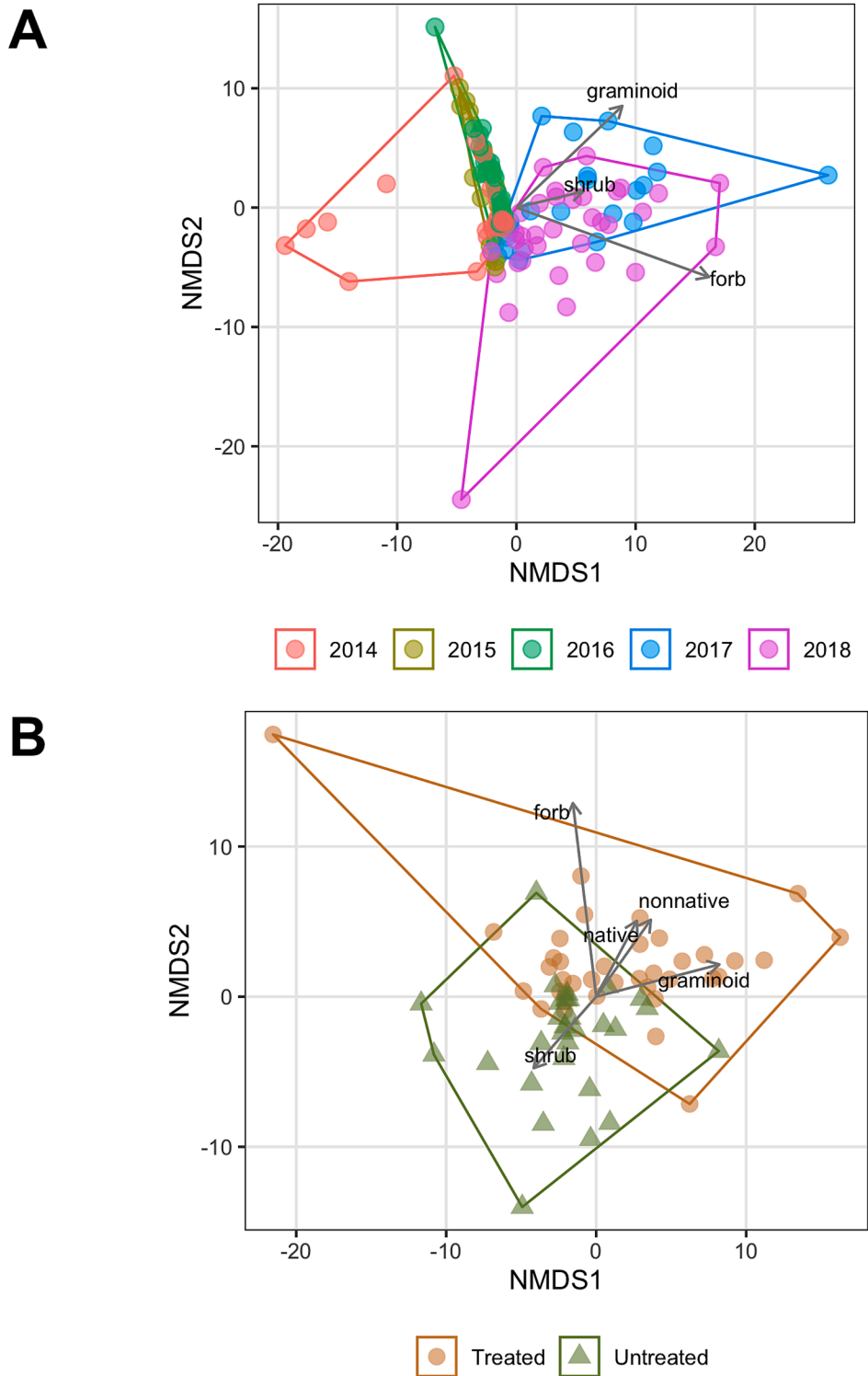
Fig. 9. Optimized 2-dimensional solution of an NMDS ordination for understory community composition for (A) treated plots throughout entire study period (2014–2018) and (B) a comparison of treated and untreated plots 4 years post-treatment (2018). Understory composition in treated plots, both over time and compared to untreated plots 4 years after thinning, is correlated with graminoid and forb abundance.

The increased presence of herbaceous vegetation in treated stands will likely also serve to propagate low intensity surface fire that can maintain desirable stand structure into the future (Stephens et al., 2021). A companion study of fuel loading in the Marshall Devine planning area (Johnston et al., 2021) demonstrated that thinning immediately reduced crown fire potential and that after an initial increase in fine fuels, modeled fire behavior was significantly reduced for several years. The present study demonstrates that thinning not only reduces fire hazard but initiates a cascade of tree and understory vegetation responses that simultaneously enhance residual tree resistance to disturbance, promote greater understory resilience to disturbance, and facilitate potential for low severity surface fire that reinforces structural changes initiated by selective thinning. Thinning does not simply help managers mitigate fire risk, it restores a suite of ecological functions that

make forests more resilient over time (Stephens et al., 2021). While our study area was not treated with prescribed fire, the reintroduction of fire is an important management tool that can restore historical fire regimes and achieve additional management goals (Kalies and Kent, 2016, Ryan et al., 2013).

Other studies have also investigated understory vegetation (e.g., Ares et al. 2009; Davis and Puettmann, 2009) or tree responses (e.g., Knapp et al., 2021; Hood et al., 2016) to thinning. This study is unique in that it synthesizes a wide variety of measurements of tree vigor and understory vegetation response within a functional framework to make inferences about treatment effects on forest resilience. While the geographic scope and sample size of our study are relatively small, we anticipate that a larger sample size across a broader area would result in less equivocal results and elucidate greater variability in responses in different biophysical environments. We encourage additional research that investigates multiple measurements of resilience and additional disturbances (i.e., fire) within a functional framework at broader spatial and temporal scales. Continued monitoring of a variety of metrics associated with forest resilience over time and space will strengthen the foundation for collaborative adaptive management of forest landscapes.

5. Conclusion

Effectively shifting restoration goals to the more holistic concept of ecological resilience requires the identification of conditions that can be easily measured and interpreted by land managers. In this study we evaluated several tree vigor correlates and understory vegetation characteristics that link processes that maintain forest resilience in dry, fire prone forests in eastern Oregon. Our results help scientists, managers, and stakeholders understand how these forests respond to fuel treatments and inform adaptive management. This study also highlights the value of long-term monitoring in understanding treatment effectiveness. Pine dominated forests are composed of relatively long lived trees and treatment responses can occur on time scales that would be difficult to observe without repeated measurement. Focusing on the functional attributes that maintain desirable forest conditions, and thus resilience, in addition to the structure, composition and processes that support it, is important for determining ecological effects within a collaborative adaptive management system (Lindenmayer et al., 2016).

CRediT authorship contribution statement

Michael J. Vernon: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft. **James D. Johnston:** Funding acquisition, Conceptualization, Project administration, Data curation, Formal analysis, Visualization, Writing - original draft. **Thomas D. Stokely:** Methodology, Writing – review & editing. **Becky A. Miller:** Conceptualization, Methodology, Data curation, Writing - review & editing. **David R. Woodruff:** Methodology, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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