Impacts of pre-fire forest structure and wildfire severity on understory vegetation and tree mortality

Principal investigator: Dr. Megan S. Matonis, The Ember Alliance (megan@emberalliance.org; 970-217-6473)

BCPOS Staff Sponsor: Nick Stremel

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EXECUTIVE SUMMARY

Exceptionally hot, dry, and windy conditions fueled the largest wildfire in Boulder County's recorded history—the Calwood Fire, which started on October 17, 2020, and burned about 10,000 acres. This wildfire offered an opportunity to assess post-fire understory response and relationships between forest structure and burn severity.

The Calwood Fire resulted in extremely diverse post-fire conditions due to high variability in topography and pre-fire forest structure and changing weather conditions during the incident. Non-native species rapidly responded to the wildfire. Basal area mortality exceeded 75% in many portions of Heil Valley Ranch, and some areas might remain unforested for decades to come. Areas that convert from forests to grasslands or shrublands can serve as diverse habitat and moderate future wildfire behavior. Large-scale thinning and prescribed burning treatments on Heil Valley Ranch slightly reduced soil and vegetation burn severity. Burn severity declined on the fire's northern flank as it encountered lower fuel loads and higher crown base heights in areas prescribed burned from 2014-2016. However, expectations of fuel treatment performance should be

moderated when weather conditions are exceptionally hot, dry, and windy. The most important predictor of soil and vegetation burn severity was day of the incident due to a dramatic decrease in energy release component between the first and second day of the Calwood Fire. This research suggests that:

- Continual monitoring the next few years is important to assess patterns in native and non-native species response.
- Integrated weed management might be necessary to reduce the abundance of non-native species across Heil Valley Ranch.
- Post-fire assessments of burn severity should include measurements of both soil and vegetation burn severity to fully understand post-fire ecosystem changes.
- Substantially reducing overstory density, using prescribed burns to reduce activity fuels, and intentionally linking fuel treatment projects together can enhance ecosystem resilience to wildfires.

ABSTRACT

A combination of extreme fire weather conditions, unplanned ignitions, and dense forest conditions have resulted in unprecedented wildfire behavior in northern Colorado. I sampled understory vegetation in 12 mosaic-meadows created or expanded by forest thinning on Heil Valley Ranch to assess the response of understory vegetation to the 2020 Calwood Fire. I measured stand density, scorch height, crown scorch/consumption, and fuel loads at 44 plots distributed across the central and eastern portion of Heil Valley Ranch to explore impacts of pre-fire forest structure on burn severity. Understory plant cover and richness increased after the Calwood Fire, with non-native species showing a strong, positive response to post-fire conditions. Forest structure had a marginal impact on vegetation and soil burn severity due to exceptionally dry and

windy conditions during the first day of the Calwood Fire. However, there was evidence that several linked prescribed burns from 2014-2016 reduced soil and vegetation burn severity and are an important management strategy for restoring ponderosa pine ecosystems and enhancing their resilience to wildfire.

INTRODUCTION

Historical and current conditions in frequent-fire ponderosa pine ecosystems

Prior to Euro-American settlement, many ponderosa pine ecosystems were characterized by open, spatially contiguous grasslands with scattered tree groups. Such ecosystems were common along the Colorado Front Range, especially on dry, south-facing slopes and in areas adjacent to grasslands where surface fires occurred every 1–25 years (Veblen et al. 2000; Gartner et al. 2012; Brown et al. 2015; Addington et al. 2018). Mosaic-meadows in ponderosa pine woodlands and forests varied in shape from discrete patches to sinuous, interconnected areas weaving among tree groups (Lydersen et al. 2013; Matonis and Binkley 2018; Clyatt et al. 2016).

The juxtaposition of mosaic-meadows and scattered tree groups made environmental conditions highly variable in ponderosa pine ecosystems and created environmental niches for a wide array of plant and animal species (Naumburg and Dewald 1999; Kalies et al. 2012). Mosaic-meadows supported 5-6 times more understory cover or biomass than areas under tree canopies and 2.5 to 5 times greater understory richness (Moore et al. 2006; Abella and Springer 2008; Laughlin et al. 2008; Laughlin et al. 2011). Graminoids, forbs, and shrubs in mosaic-meadows provided fine fuels that carried frequent, low-severity surface fires (Belsky and Blumenthal 1997; Gartner et al. 2012).

Ponderosa pine savannas are relatively uncommon today. Weather conditions favorable to tree regeneration and human management, including fire suppression and livestock grazing, have resulted in tree encroachment and fragmentation of mosaic-meadows over the past 150 years

(Addington et al. 2018). Tree density has increased more than 4-fold in ponderosa pine ecosystems along the Front Range of Colorado and Wyoming (Battalgia et al. 2018), and areas in these ecosystems are 3.7 times more likely to have trees than grassy openings compared to historical conditions (Dickinson 2014).

Increasingly dense ponderosa pine forests have higher risk of active crown fires, which in turn impacts post-fire recovery of these ecosystems. High-severity wildfires in ponderosa pine ecosystems can result in extreme overstory mortality, slow regeneration, extensive post-fire erosion, habitat loss for some plant and animal species, and invasion by non-native plant species (Benavides-Solorio et al. 2005; Fornwalt et al. 2010; Chambers et al. 2016; Rother and Veblen 2016; Rew and Johnson 2017).

Extreme fire behavior is increasing along the Colorado Front Range

A combination of extreme fire weather, unplanned ignitions, and dense forest conditions have resulted in unprecedented wildfire behavior in northern Colorado. Climate change has increased wildfire risk by lengthened fire seasons and increasing the prevalence of hot and dry conditions (Parks et al. 2016). Wildfires along the Colorado Front Range greatly impact human lives and highly valued resources due to rapid development in the wildland-urban interface (Haas et al. 2014).

Exceptionally hot, dry, and windy conditions fueled the state's three largest wildfires in 2020, as well as the largest wildfire in Boulder County's recorded history—the Calwood Fire. The Calwood Fire started on October 17, 2020, and burned about 10,000 acres (Appendix Figure A.1). The energy release component on October 17th was higher and 1000-hour fuel moisture was lower than any observation from 2006-2017 in the area (Figure 1). The Calwood Fire destroyed 26 structures and triggered evacuation orders for nearly 5,000 residents (Boulder County Sheriff's Office 2021).

Forest management to restore historical conditions and mitigate fire behavior

Forest management to reduce the risk of active crown fires is a priority for managers along the Colorado Front Range (Underhill et al. 2014). Thinning and/or prescribed burning are utilized to reduce the density of trees, retain tree groups separated by mosaic-meadows, and increase availability of fine, flashy fuels in the understory (Reynolds et al. 2013; Underhill et al. 2014; Addington et al. 2018). Fuel reduction through thinning and/or prescribed burning can be consistent with restoration of historical forest structure when prescriptions intentionally address within stand heterogeneity (Addington et al. 2018; Stephens et al. 2021). Restoration treatments that involve prescribed burning and substantial reductions in tree density can enhance understory cover and richness by altering resource availability and reducing competition with overstory trees (Moore et al. 2006; Laughlin et al. 2008; Wolk et al. 2008; Sabo et al. 2009). Thinning and prescribed burning can lower the incidence of torching, active crown fires, and post-fire tree mortality (Martinson and Omi 2013; Kalies and Kent 2016; Ritter et al. 2020). Thinning and prescribed burning can still lower crown fire activity despite higher fire rate of spread due to the abundance of fine-flashy fuels and higher mid-flame windspeeds (Banerjee 2020; Stephens et al. 2021).

Research objectives and hypotheses

This project explored the impacts of forest structure and wildfire severity on understory vegetation and tree mortality following the 2020 Calwood Fire at Heil Valley Ranch. My research centered on four key research questions:

1. How did understory vegetation respond the first year following the Calwood Fire and was this response impacted by treatment history? *Hypothesis:* The Calwood Fire would change

understory plant composition relative to pre-fire conditions by increasing the relative abundance of non-native species.

2. Did wildfire strengthen or dampen the relationship between understory cover and richness and competition from overstory trees? *Hypothesis:* Burning of mosaic-meadows would flatten the relationship between understory cover and richness and overstory competition by exposing bare mineral soil and mobilizing nitrogen near the base of trees, thereby creating opportunities for understory plant colonization near overstory trees.

3. How did pre-fire forest structure impact vegetation and soil burn severity[1]? *Hypothesis:* Scorch height, tree mortality, and soil burn severity evaluated by the Interagency Burned Area Emergency Response (BAER) Team would be greater in untreated stands with higher tree density and lower crown base heights.

4. How do field-based estimates of fire effects correlate with BAER soil burn severity? *Hypothesis:* Litter/duff depth, litter cover, scorch height, and overstory basal area mortality would be correlated with each other and with BAER soil burn severity, but these relationships would show high variation due to different sensitivities of soils and vegetation to wildfire intensity and residence time and different assessment methodologies.

Anticipated value

This project addressed two priority research topics for Boulder County Parks & Open Space (BCPOS): (1) examine post-fire recovery at Heil Valley Ranch, and (2) study existing conditions

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[1] Fire severity is a general term referring to loss of organic matter aboveground and belowground due to wildland fire. Following Kelley (2009) and Parsons et al. (2010), I use the term soil burn severity to refer to loss of organic matter in the soil, measured by variables such as litter/duff depth and litter cover; vegetation burn severity to refer to the effects of fire on vegetation, measured by variables like crown scorch/consumption and overstory tree mortality; and ecosystem response to refer to changes in post-fire ecosystem composition and processes, measured by variables like understory plant cover and richness.

and compare pre-fire data to post-fire conditions. Evaluating soil burn severity, vegetation burn severity, and ecosystem response are important for guiding post-fire management to stabilize soils, minimize erosion, reduce hazards such as fire-created snags, and support vegetative recovery (Parsons et al. 2010). Findings from my research will help natural resource managers monitor the colonization and spread of non-native species and determine if integrated weed management is necessary to support the recovery of native species. This research can inform future projects to mitigate fire hazards by determining whether thinning and burning treatments resulted in lower overstory mortality. It is important to assess tree mortality from wildfires because of impacts on microhabitat conditions, forest carbon and water cycling, wildlife habitat, and seed sources (Hood and Varner 2019). Data is currently available on soil burn severity for the Calwood Fire, but soil burn severity is not always correlated with tree mortality (Kelley 2009; Whittier and Gray 2016).

METHODS

Site description

The study was conducted at Heil Valley Ranch, which has been owned and managed by the BCPOS Department since the early 1990s. Topography is highly variable due to several steep valleys running through the property—Marietta Canyon and Plumey Canyon from east to west and Geer Canyon Creek from north to south. Elevations range from 5,515 to 8,095 feet. Soils are mainly coarse textured and shallow. About two-thirds of the property contains forests and woodlands dominated by ponderosa pine (*Pinus ponderosa*), with Rocky Mountain juniper (*Juniperus scopulorum*) and Douglas-fir (*Pseudotsuga menziesii*) occurring as minor components depending on soil moisture (BCPOS 1996).

The mean fire return interval for ponderosa pine ecosystems on Heil Valley Ranch was 9 years (range of 3-23 years) prior to 1860 (Brown et al. 2015). Six wildfires burned Heil Valley Ranch between 1988-2020, but only the 2020 Calwood Fire burned across the western and central portion of the property (Table 1; Appendix Figure A.1). The Calwood Fire impacted about 70% of the property, with 19% of this area burning at high severity according to the BAER burn severity assessment (Arapaho-Roosevelt National Forests 2020; Appendix Figure A.2). Over the past several decades, BCPOS has conducted thinning and prescribed burn projects across 1,395 acres of Heil Valley Ranch to reduce fire risk and restore historic forest conditions (Figure 3).

Fieldwork methodology for fire effects on understory plants

In fall 2021, I measured understory conditions in eight mosaic-meadows in the Wapiti treatment unit and four in the PA7 treatment unit (Figure 2). I defined mosaic-meadows as treeless areas that were created or expanded by thinning and had at least 33 feet between boles of edge trees. The Wapiti unit was thinned in 2010 and prescribed burned in 2014, and the PA7 unit was thinned in 2013. Mosaic-meadows in the Wapiti unit burned on the first day of the Calwood Fire (October 17th), and those in the PA7 unit burned the second day of the fire. I revisited eight of the nine mosaic-meadows that I sampled in 2014; one meadow was unusable for this research due to post-fire salvage logging. I added sample locations in the PA7 unit because sampling at the Wapiti unit in 2014 occurred before the prescribed burn, and I wanted to see if post-fire understory conditions differed between mosaic meadows that were thinned vs thinned and burned.

I collected data at similar times of the year in 2014 and 2021 to control for phenological differences in the emergence of understory plants

Table **2**). Maximum temperature and minimum relative humidity in August 2021 were similar to average conditions from 2001-2017, but precipitation was almost half the typical amount.

Conditions in August 2021 were warmer and drier than the first period of understory sampling in August 2014

Table **2**).

Within each mosaic-meadow, I aligned transects from north to south starting 16.4-feet back from the northern-most edge tree. I sampled understory vegetation and abiotic conditions in a total of 67 1-m2 quadrats at 16.4-feet increments along each transect, with 5 to 7 quadrats/transect depending on the size of the mosaic-meadow. I visually estimated cover of understory species, rocks, litter/duff, woody debris with diameter >1 inch, and bare ground, measured litter/duff depth at nine equally spaced locations/quadrat, measured the distance to the bole of the three nearest overstory trees with diameter at breast height ≥3.9 inches, and estimated percent crown scorch/consumption for nearby trees. I calculated the Hegyi index to quantify competition from overstory trees by combining diameter and distance following Naumburg and DeWald (1999):

$$\text{Hegyi index} = \Sigma \text{dbh} / (\text{dist.} + 1) \tag{1}$$

where dist. is the distance from quadrat to tree bole. Higher values of the Hegyi index indicate larger and closer trees and therefore greater competition to understory plants.

I followed the PLANTS database for nomenclature of understory plant species (USDA NRCS 2021). Vegetative characteristics were insufficient for species-level identification for the genus *Antennaria*, *Carex*, *Chenopodium*, *Juncus*, *Penstemon*, *Rumex*, and *Solidago.*

Statistical analysis for fire effects on understory plants

I quantified relationships among understory cover, competition from overstory trees, vegetation burn severity (crown scorch/consumption), and soil burn severity (post-fire litter depth) with linear multilevel models and Poisson multilevel models for understory richness. Models included a random intercept for quadrats nested within mosaic-meadows to account for autocorrelation. I used Dirichlet regression to estimate the impact of overstory competition on the relative cover and richness of native vs non-native species; these models did not include a random intercept due to the difficulty of fitting random effects for this class of model. Analyses with litter/duff depth excluded three outliers with depth >2.5 inches.

I used Akaike's Information Criteria (AIC) to compare fit between intercept-only (i.e., null) models and those with different combinations of dependent variables, seeking models that reduced AIC by >5. I assessed significance of variables with Wald chi-squared at an alpha of 0.10, conducted pairwise comparisons with the Tukey method and Bonferroni adjusted *p*-values, and calculated 90% confidence intervals for fixed-effects using semi-parametric bootstrapping.

I used non-metric multidimensional scaling (NMDS) on Bray-Curtis dissimilarity values to compare understory composition among disturbance histories (thinned, thinned + prescribed burned + Calwood Fire, and thinned + Calwood Fire) and three classes of average crown scorch/consumption (low: <40%; moderate: 40-70%; high: >70%). I relativized cover for each species by the total cover/quadrat, excluded rare species occurring in 3 or fewer quadrats, and eliminated outlying quadrats with Bray-Curtis dissimilarity values >2.3 standard deviations above the average value following recommendations of McCune and Grace (2002).

I tested the null hypothesis of no difference in understory species composition among disturbance histories and crown scorch/consumption with permutational MANOVA on Bray-Curtis distances. I included mosaic-meadow as a random effect in the model, computed *p*-values by comparing the pseudo-*F* value against that obtained from 1,000 random permutations, and conducted multilevel pairwise comparison.

Analysis were conducted in R v 4.0.3 (R Core Team 2020) using the packages *lme4* (Bates et al. 2015), *nlme* (Pinheiro et al. 2020), *car* (Fox and Weisberg 2019), *multcomp* (Hothorn et al. 2008), *DirichletReg* (Maier 2021), *vegan* (Oksanen et al. 2020), and *pairwiseAdonis* (Martinez Arbizu 2020).

Fieldwork methodology for fire effects on overstory trees

I estimated fire effects on overstory trees at 44 variable-radius plots distributed across the central and eastern portion of Heil Valley Ranch (Figure 3). About 70% of these plots burned on the first day of the Calwood Fire (October 17th). Thirty-seven of these plots were sampled by BCPOS staff prior to the Calwood Fire as part of ongoing forest monitoring. I stratified sampling to achieve relatively equal sample sizes in low and moderate BAER burn severity classes; very few monitoring plots experienced high BAER soil burn severity (Appendix Figure A.2).

I measured stand density, scorch height, and crown scorch/consumption in variable radius plots using a 10 basal area factor prism. I estimated probability of tree mortality based on diameter at breast height and crown scorch/consumption following Steele et al. (1996) and Powell (2012). In total, I measured scorch height, canopy base height, crown scorch, and crown consumption on 265 trees (97% ponderosa pine and 3% Douglas-fir) across the 44 plots. Within four 1-m^2 quadrats/plot, I visually estimated cover of understory plants, rocks, litter, woody debris with diameter >1 inch, and bare ground, measured litter/duff depth at nine equally spaced locations/quadrat, and estimated 1-, 10-, and 100-hr fuel loads using the photoload method (Keane and Dickinson 2007). I measured diameter and length of course woody debris with diameter >3 inches within a 37-foot radius plot to estimate 1000-hr fuel load. I only included 1000-hr fuels that were obviously present prior to the Calwood Fire based on evidence of scorch. I calculated the average BAER soil burn severity rating in a 90 m x 90 m area around each overstory plot, treating soil burn severity as a continuous variable ranging from 0 (none to very low) to 4 (high).

Methodology for assessing impacts of stand-scale variables on tree-, plot-, and landscape-scale fire effects

Fire behavior is affected by fuel and topographic characteristics at a variety of scales, so I included estimates of canopy cover and canopy bulk density from the 2019 LANDFIRE Remap in the vicinity of each plot (LANDFIRE 2019). I calculated average canopy fuel characteristics in an irregularly shaped 65-acre area around each plot with a width of 0.3 miles (Appendix Figure A.4), which corresponds to the distance at which estimates of soil and vegetation burn severity become spatially independent (Appendix Figure A.3) and is within the size range of treatment units on Heil Valley Ranch (2 - 153 acres). I also assessed the relationship between BAER soil burn severity and topography, fuel characteristics, and disturbance history across the entire Calwood Fire burned area (see

Table **3** for description and source of independent variables).

To assess the general quality of LANDFIRE data prior to analysis, I conducted minimum travel time analyses with FlamMap version 6.1 (Finney 2006) using weather conditions recorded at the Sugarloaf RAWS on October 17th, 2020. Predicted and observed fire perimeters were similar at 2 hours and at 9 hours and 41 minutes into the Calwood Fire, providing confidence in the accuracy of canopy bulk density and canopy cover estimates for this area (Appendix Figure A.5).

Statistical analysis for tree-, plot-, and stand-scale effects on soil and vegetation burn severity

I used binomial generalized linear models to quantify relationships between stand conditions and tree-level mortality, plot-level percent basal area (BA) mortality, percent tree/acre mortality, and average crown scorch/consumption and linear models for tree-level and plot-level scorch height. Models of tree-level mortality and scorch included a random intercept for trees nested plots to account for autocorrelation. I compared model fit using AIC, seeking models that resulted in the greatest reduction in AIC relative to the null, intercept-only model. I assessed significance of variables with F-values for non-multilevel models and Wald chi-squared for multilevel models at an alpha of 0.10. I used non-parametric Kruskal-Wallis one-way ANOVA and pairwise Wilcox tests to compare stand conditions and estimates of soil and vegetation burn severity among treatment histories. I calculated 90% confidence intervals for fixed effects using parametric bootstrapping for non-multilevel models and semi-parametric bootstrapping for multilevel models.

I used maximum likelihood estimation of spatial simultaneous autoregressive error models to assess the impact of topography, fuel characteristics, and disturbance history on soil burn severity across the entire Calwood Fire burned area. This approach accounted for the high degree of spatially autocorrelation in independent and dependent datasets. I conducted the analysis at the scale of 30-, 150-, 300-, and 450-meter pixels to identify the minimum scale at which residuals became spatially independent, in this case, at a resolution of 300 m x 300 m. I excluded pixels that had >33% cover of grasslands and shrublands, leaving a total of 312 pixels for analysis. I standardized independent variables with the z transformation to facilitate comparison of variable importance. Moran's I was not significant for residuals from the final model, indicating adequate incorporation of spatial autocorrelation.

Analysis were conducted in R v 4.0.3 (R Core Team 2020) using the packages *lme4* (Bates et al. 2015), *nlme* (Pinheiro et al. 2020), *car* (Fox and Weisberg 2019), *multcomp* (Hothorn et al. 2008), *ciTools* (Haman and Avery 2020), *gstat* (Pebesma 2004), and *spatialreg* and *spdep* (Bivand et al. 2013).

RESULTS

Native and non-native species rapidly responded to conditions created by the Calwood Fire

I identified 36 native and 11 non-native understory plant species in the Wapiti unit in 2014 before the Calwood Fire and 38 native and 16 non-native species in the Wapiti unit after the Calwood Fire in 2021 (Table 4; Appendix Tables A.1 and A.2). Most species were relatively uncommon; 57% of species occurred in fewer than 10% of quadrats in 2014 and 40% of species occurred in fewer than 10% of quadrats after the Calwood Fire in the Wapiti unit

Year	Incident name	Total fire size (acres)	Area of Heil Valley burned (acres)
1988	Lefthand Canyon Fire	3,460	90
2000	Mountain Ridge Fire	18	8
2004	Overland Fire	3,230	600
2005	Lykins Fire	35	20
2006	Elk Mountain Fire	2,570	11
2020	Calwood Fire	10,105	4,150

Table 2. Dates of understory research and weather data recorded at the Sugarloaf RAWS near Heil Valley Ranch in August 2001-2017, 2014, and 2021.

Year(s)	Understory sample dates	August average daily maximum temperature (°F)	August average daily minimum humidity (%)	August total precipitation (inch)
2001-2017	N/A	83	24	1.6
2014	August 11-14	80	26	1.7
2021	August 17-31	84	22	0.9

Table 3. Topography, fuel characteristics, and disturbance history impacted average BAER soil burn severity across the Calwood Fire. Areas with >33% cover of grasslands and shrublands were excluded. Results are presented for the spatial error model with the lowest AIC and significant predictors (alpha = 0.05). Parameter estimates indicate the change in predicted average soil burn severity associated with 1-standard deviation increase in the independent variable.

	Observed values		**Output from spatial error model**			
Independent variable	**Range**	**Standard deviation**	**z-value**	**Parameter estimate**	**95% CI**	**Data source**
General burn conditions						
Day of burn	1 - 8	1.2	-12.8	-0.33	-0.38 - -0.28	NIFC 2021
Topography (average in 300 x 300 m area)						
Elevation (ft)	5,820 - 8,423	592	N/S			LANDFIRE 2019
Slope (degrees)	5.1 - 36.1	6.3	-3.1	-0.10	-0.16 - -0.04	LANDFIRE 2019
Daily solar radiation (Watt hour/m2)	1,184 - 3,617	437	6.3	0.17	0.12 - 0.22	ArcGIS Area Solar Radiation tool
Fuel conditions (average in 300 x 300 m area)						
Canopy cover (%)	4 - 53	9.4	8.6	0.23	0.18 - 0.29	LANDFIRE 2019
Canopy bulk density (100 * kg/m3)	1.1 - 11.3	1.7	N/S[a]			LANDFIRE 2019
Distance from fuel breaks (roads/trails) (feet)	97 - 4,604	1,217	4.1	0.14	0.07 - 0.21	OpenStreetMap (2021) and ArcGIS Near tool
Disturbance history (percent of 300 x 300 m area)						
Thinned between 2003-2017	0 - 100	25	N/S			BCPOS
Prescribed burned between 2003-2017	0 - 100	19	-4.4	-0.13	-0.18 - -0.07	BCPOS
Burned by wildfire between 2000-2006	0 - 100	16	N/S			NIFC 2021

[a]Canopy bulk density was significant only if canopy cover were excluded from the model due to high correlation between these variables. The AIC value was lower for the model with canopy cover than that with canopy bulk density.

Table 4(Table 4). The most common species in the Wapiti unit after the Calwood Fire were native species smooth white aster (*Symphyotrichum porteri*), timber oatgrass (*Danthonia intermedia*), Canada toadflax (*Nuttallanthus canadensis*), sedges (*Carex* spp), and rough bentgrass (*Agrostis scabra*) and non-native Canada bluegrass (*Poa compressa*).

The absolute cover of native species was higher than non-native species before the Calwood Fire, but native and non-native cover were the same after the fire (Figure 4; Appendix Table A.3). Native richness was higher than non-native richness before and after the fire. The average cover of non-native species increased from 6% pre-fire to 23% post-fire, and average richness increased from 2 species/m^2 to 3-4 species/m^2. The Calwood Fire resulted in a significant decline in the relative cover of native graminoids, which dominated understory cover prior to the fire (Figure 5). Relative richness by functional group was not altered by the Calwood Fire (Figure 5).

Cover of non-native species and richness of native species were affected by the severity of wildfire. Cover of non-native species was higher in areas with higher litter/duff depth, which is indicative of less surface fuel consumption (Figure 6); this relationship was not significant for native species. Overall litter/duff depth were almost three-times lower after the Calwood Fire than before (Appendix Table A.3). Richness of native species increased with percent crown scorch of surrounding overstory trees, but non-native richness did not (Figure 7).

Composition of the understory community varied before and after the Calwood Fire at the Wapiti unit. Composition also varied between the Wapiti unit and the PA7 unit regardless of burn status, suggesting underlying differences in site conditions (Appendix Figure A.6). The composition of mosaic-meadows varied based on crown scorch/consumption and litter/duff depth (Figure 8). Sorrel (*Rumex* spp), cheatgrass (*Bromus tectorum*), and mountain muhly (*Muhlenbergia montana*) were associated with lower soil and vegetation burn severity, and common mullein (*Verbascum thapsus*) and curlycup gumweed (*Grindelia squarrosa*) were associated with higher burn severity.

Wildfire did not alter the relationship between overstory competition and overall understory cover and richness but did alter the relationship between overstory competition and relative richness and cover of native vs. non-native understory plants

Understory cover declined with increasing competition from overstory trees regardless of disturbance history at a rate of 9% with each 5-point increase in the Hegyi index (Figure 9). Average understory cover was about 1.3 times higher in locations burned by the CalWood Fire than pre-burn conditions regardless of competition from overstory trees. Understory richness was not significantly related to competition from overstory trees pre- or post-fire in the Wapiti treatment area; however, richness declined with increasing competition in the PA7 treatment area (Figure 9). Species responding to increases in competition from overstory trees included timber oatgrass (*Danthonia intermedia*), sleepy silene (*Silene antirrhina*), and common mullein, and those benefiting from lower competition included sorrel species (*Rumex* spp) and hairy false goldenaster (*Heterotheca villosa*) (Appendix Figure A.6).

Competition from overstory trees did not influence the relative cover and richness of native vs. non-native understory plants prior to the Calwood Fire. However, native species dominated over non-native in areas with more competition from overstory trees after the Calwood Fire (Figure 10). Litter/duff depth increased with the proximity and size of overstory trees in 2014 but decreased with the proximity and size of overstory trees after the Calwood Fire (Figure 11).

Pre-fire forest structure had relatively minor impacts on overstory mortality and moderate effects on soil burn severity after the Calwood Fire

Over half of the trees that I sampled (55%) were dead or near death due to the Calwood Fire. Percent BA mortality varied from 0 to 100% (average of 55%) across the 44 plots. Plots-burning at high severity[2] were distributed across Heil Valley Ranch on both the first and second day of the Calwood Fire. Clusters of high-severity plots were located along the steep west-facing slope above the Linchen Loop Trail and across the center the Wapiti burn unit (Figure 3).

The probability of a tree being dead after the Calwood Fire decreased with increasing crown base height (CBH), increased with slope, and increased with crown bulk density of the surrounding 65-acre area (Figure 12). The probability of mortality was higher for trees burned on the first day of the Calwood Fire than those burned on the second day. The influence of CBH on tree survival was particularly pronounced in stands with lower BAER soil burn severity. Trees were likely to die regardless of CBH under high soil burn severity, and trees were unlikely to die regardless of CBH under low soil burn severity. However, the probability of mortality dropped from an average of 50% for trees with a CBH of 1 feet to 2% for trees with a CBH of 25 feet under moderate soil burn severity (Figure 13).

Average scorch height—an indicator of fire behavior—varied from 1 to 56 feet (average of 22 feet) and was significantly lower in plots that were thinned and burned than plots that were untreated or only thinned prior to the Calwood Fire (Figure 14). Average scorch height was positively related to slope and crown bulk density of the surrounding 65-acre area (Appendix Figure A.7; Appendix Table A.6). These relationships were stronger on the first day of the incident. Average scorch height was not significantly related to average crown base height, but average crown base height was higher in stands that were thinned and burned than those that were untreated or only thinned (Appendix Table A.5).

[2] The Fire Effects Information System of the U.S. Forest Service defines high-severity fire as areas with 75% BA mortality, moderate severity as 25-75% BA mortality, and low severity as <25% BA mortality (FEIS 2021).

Percent BA mortality and tree/acre mortality were not significantly related to any measurements of forest structure or topography (Appendix Table A.6). Average BA mortality tended to be higher in untreated plots (69%) than those that were thinned (48%) or thinned and burned (45%) prior to the Calwood Fire, but these differences were not significant due to high variation within treatments (Figure 14).

Across the entire Calwood Fire burned area, average BAER soil burn severity increased with canopy cover, exposure to solar radiation (i.e., higher values on south-facing slopes than north-facing slopes), and distance from roads and trails, decreased with percent area previously prescribed burned, and decreased with slope (Table 3). Predictions were higher on the first day of the burn and lower on subsequent days. Day of the incident and canopy cover had the greatest impacts on predicted soil burn severity. Elevation, percent area previously thinned, and percent area previous burned by wildfire were not significant predictors of average soil burn severity.

Metrics of vegetation and soil burn severity were highly correlated

Plot-level estimates of soil burn severity (percent litter cover and litter/duff depth) were strongly correlated with BAER estimates of soil burn severity (Figure 15). Increasing litter/duff depth was associated with decreases in BAER soil burn severity up until about 0.15 inches, past which BAER soil burn severity stayed about 2.0 (i.e., low severity). Estimates of vegetation burn severity (percent BA and trees/acre mortality, crown scorch/consumption, and scorch height) were positively correlated[3]. Basal area mortality increased linearly with scorch height from 0 to 25 feet, past which basal area mortality approached 100% for most plots. The correlation between BAER soil burn severity and vegetation burn severity exceeded the correlation between plot-level soil

[3]Estimates of tree mortality were calculated from diameter and average crown scorch/consumption but were not calculated using measurements of scorch height.

burn severity and vegetation burn severity, partly because estimates of BAER soil burn severity incorporated changes in “greenness” (i.e., vegetation mortality) using remote sensing data.

DISCUSSION

How did understory vegetation respond the first year following Calwood Fire and was this response impacted by treatment history?

Total cover and richness of understory plant communities often increase the first few years following wildfire by altering competition, increasing nutrient and light availability, and stimulating germination for some species (Hunter et al. 2006; Abella 2009; Sabo et al. 2009; Abella and Fornwalt 2015). The richness and cover of non-native plant species and richness of native plant species was higher 10 months after the Calwood Fire. It is unlikely that differences in growing-season weather accounted for higher plant cover and richness in 2021. Conditions were hotter and drier in August 2021 than August 2014, and lower, not higher, understory richness and cover are observed during dry years (Moore et al. 2006; Sabo et al. 2009).

The cover of native graminoids significantly declined after the Calwood Fire, a pattern observed after other severe wildfires in ponderosa pine forests in Arizona and Colorado (Griffis et al. 2001; Fornwalt and Kaufmann 2014). Rough bentgrass (*Agrostis scabra*), timber oatgrass, and mountain muhly (*Muhlenbergia montana*) were associated with pre-fire conditions at Heil Valley Ranch (Appendix Figure A.6). Mountain muhly significantly declined in areas burned at high severity following the 2002 Hayman Fire (Fornwalt and Kaufmann 2014), but this species responded favorably to low-severity prescribed burning in Arizona (Moore et al. 2006).

Wildfires can create opportunities for new species to establish that were not present prior to the fire (Abella and Fornwalt 2015). The Calwood Fire created opportunities for some native plant species, as evidenced by higher species richness after the Calwood Fire at the Wapiti unit and increasing native species richness with percent overstory crown scorch/consumption. At the Wapiti unit, I observed nine native species after the Calwood Fire that were not present prior to the fire (Appendix Table A.2). Silverleaf phacelia (*Phacelia hastata*) and Clasping Venus' looking-glass (*Triodanis perfoliate*) were frequent new-comers after the fire (present in >30% of quadrats).

The Calwood Fire increased the relative cover of non-native species, as is often observed the first few years after wildfires (Hunter et al. 2006; Abella and Fornwalt 2015; Rew and Johnson 2017). Common non-native species in burned areas across the Intermountain West include cheatgrass, Japanese brome (*Bromus japonicus*), Canada thistle (*Cirsium arvense*), common dandelion (*Taraxacum officinale*), prickly lettuce (*Lactuca serriola*), Kentucky bluegrass (*Poa pratensis*), and common mullein (McGlone and Egan 2009; Rew and Johnson 2017). I observed all these species before and after the Calwood Fire, except for Canada thistle which was only observed after the fire. Common mullein, Canada bluegrass (*Poa compressa*), goosefoot (*Chenopodium* spp), and cheatgrass were particularly associated with post-fire conditions at Heil Valley Ranch (Appendix Figure A.6).

Higher richness and cover of non-native species are often associated with higher burn severity (Hunter et al. 2006; McGlone and Egan 2009; Abella and Fornwalt 2015). However, Hunter et al. (2006) observed negative relationships between non-native species cover and bare soil exposure at the scale of 1-m^2. Cover of native and non-native graminoids can decline in areas experiencing greater duff consumption from wildfires due to destruction of roots and rhizomes (Armour et al. 1984). Cover of non-native species was lower in areas with lower litter/duff depth and therefore less-severe fire behavior after the Calwood Fire (Figure 6). Non-native sorrel species and cheatgrass (*Bromus tectorum*) were particularly associated with higher litter/duff depth after the

Calwood Fire, but common mullein was associated with lower post-fire litter/duff depth. Common mullein is abundant in the seed bank at Heil Valley Ranch (Wolk et al. 2008) and often responds to high-severity fire that increases the cover of bare ground (Moore et al. 2006; Sabo et al. 2009)

Impacts of wildfire can overshadow the impacts of thinning and/or prescribed burning on the establishment of non-native species (Hunter et al. 2006), but multiple disturbances over a short period of time can also increase the potential for non-native species colonization (Sabo et al. 2009). Compounding disturbances at Heil Valley Ranch did not appear to exacerbate cover and richness of non-native species; non-native richness and cover were comparable between areas that were thinned and burned and those that were only thinned prior to the 2021 Calwood Fire. However, post-fire understory conditions at the Wapiti and PA7 units are not completely comparable due to potential site differences independent of disturbance history.

Monitoring understory cover and richness over time will be important to assess the spread and dominance of non-native species at Heil Valley Ranch. Understory cover, richness, and composition can continue fluctuating 10 years after a wildfire (Abella and Fornwalt 2015). Differentiation of understory communities by burn severity can increase over time; cover of non-native species did not differ by fire severity for the first 2 years following the 2002 Hayman Fire, but cover was higher in areas burned with moderate and high-severity 3 to 5 years after the fire (Fornwalt et al. 2010).

<u>Did wildfire strengthen or dampen the relationship between understory cover and richness and competition from overstory trees?</u>

Richness and cover of understory plants are spatially linked to competition from overstory trees (Naumburg and Dewald 1999; Abella and Springer 2008; Matonis and Binkley 2018). Contrary to my hypothesis, wildfire did not flatten the relationship between understory cover and competition from overstory trees. Post-fire richness of understory plants showed a stronger negative relationship with increasing overstory competition at the PA7 unit but not at the Wapiti unit. The relationship between overstory competition and relative cover and richness of native vs. non-native plants was altered by the Calwood Fire. Relative cover of non-native plants decreased with increasing overstory competition after the Calwood Fire, but there was no pattern prior to the fire. Relative abundance of native species might have increased near overstory trees due to exposure of bare mineral soil and nitrogen mobilization near the base of trees (Hille and Stephens 2005; Gundale et al. 2006).

The restoration of mosaic-meadows is important for increasing understory biodiversity and stimulating production of fine fuels (Laughlin et al. 2011; Churchill et al. 2013; Matonis and Binkley 2018). However, large mosaic-meadows might create an opportunity for non-native species colonization the first few years after severe wildfires, particularly in areas with abundant non-native vegetation prior to the fire (Fornwalt et al. 2010). Causal factors explaining changes in relative cover and richness of native vs. non-native plants with spatial patterns of overstory trees warrant more research.

How did pre-fire forest structure impact soil and vegetation burn severity?

Wildfires provide an opportunity to assess the influence of fuel treatments on fire behavior and ecosystem response. Fuel treatments, particularly thinning and burning, can reduce fire intensity and post-fire tree mortality (Martinson and Omi 2013; Kalies and Kent 2016). The impact of fuel treatments on fire behavior can be marginal when wildfires burn under extremely hot, dry conditions and when treatments fail to substantially lower tree density and increase crown base heights (Martinson and Omi 2013; Ziegler et al. 2017).

The Calwood Fire burned under exceptionally dry and windy conditions, so the marginal impact of forest structure on fire behavior was not surprising. The strongest predictor of burn severity at the tree-, plot-, and landscape-scale was the date when an area burned during the Calwood Fire, with severity being consistently higher on the first day of the incident. Relative humidity in afternoon (1200-1800) increased from an average of 20% on October 17th to 95% on October 18th and energy release component dropped from an average of 62 to 42. Forest structure did not greatly vary between the treated and untreated areas that I sampled. Average crown base heights were higher in treated areas, but basal area and tree density did not differ among untreated and treated plots. It is possible that differences among treatments were greater than I observed; I targeted sampling at locations with trees and did not collect enough data to summarize conditions at the stand-scale.

The influence of pre-fire forest structure on burn severity varied among the tree-, plot-, and landscape-scale. Tree-level mortality was influenced by canopy base height and local canopy bulk density, particularly under low burn severity. Fire behavior can vary at the scale of individual trees due to the influence of crown base height on torching, substantial variation in duff, litter, and fine fuel loads at the scale of 1-2 meters, and the impact of adjacent trees on convective cooling (Martinson and Omi 2013; Vakili et al. 2016; Ritter et al 2020). Canopy bulk density within a 65-acre area impacted tree-level mortality and plot-level scorch height, but plot-level tree density and basal area did not, potentially due to a mismatch between plot-level measurements and processes influencing fire behavior at the stand-level.

At the landscape-scale, lower soil burn severity was associated with prescribed burning and lower canopy cover. BCPOS conducted prescribed burns on 415 acres between 2014-2016, creating an area with reduced fuel loads about 1.9-miles long and 0.6-miles wide. The negative relationship between percent area prescribed burned and soil burn severity suggests that the Wapiti and Overland prescribed burns moderated fire behavior even under hot, dry, and windy conditions the first day of the Calwood Fire. Overstory mortality also decreased as the fire spread northwards into the Wapiti and Overland prescribed burns (Figure 3).

Slope had a surprisingly negative impact on soil burn severity across the Calwood Fire. Visual inspection of the pairwise relationship between slope and burn severity indicate a parabolic relationship, with burn severity increasing with slope until about 20 degrees and then declining with steeper slopes (Appendix Figure A.8). Similar findings were observed by Estes et al. (2017). This pattern might be explained by correlation between steep slopes and cover of boulders, the location of suppression activities, and the orientation of the fire head and flanks relative to steep slopes. Soil burn severity was low along some of the steepest slopes on the northwest edge of the Calwood Fire near CO Highway 7.

How do field-based estimates of soil and vegetation burn severity relate to soil burn severity evaluated by the Burned Area Emergency Response (BAER) Team?

Soil and vegetation burn severity are often correlated, but there can be substantial variation due to different sensitivities of soils and vegetation to wildfire intensity and residence time and different assessment methodology (Kelley 2009; Parsons et al. 2010). Whittier and Gray (2016) found that basal area mortality and BAER soil burn severity were positively correlated, but BAER soil burn severity tended to be lower than vegetation burn severity. I also found that BAER soil burn severity was correlated with average scorch height, canopy scorch/consumption, and basal area mortality, but only one of my plots was classified as high BAER soil burn severity even though 16 of my 44 plots had high vegetation burn severity (>75% basal area mortality). This finding does not suggest inaccuracies in the BAER soil burn severity map but demonstrates that BAER soil burn severity is not an analog for vegetation burn severity.

Measuring crown scorch/consumption to predict post-fire tree mortality is important for assessing vegetation burn severity. Measurements of average scorch height were not linearly related to overstory mortality after the Calwood Fire, and high variability has been observed between scorch height and tree mortality (Martinson and Omi 2013).

Management implications

The Calwood Fire resulted in extremely diverse post-fire conditions due to high variability in topography and pre-fire forest structure and changing weather conditions during the incident (

Figure **16**). Non-native species rapidly responded to the wildfire and might require integrated weed management to reduce their abundance across the landscape. Continual monitoring the next few years is important to assess patterns in native and non-native species response. Post-fire assessments should include field measurements of soil burn severity, such as litter/duff depth, and measurements of vegetation burn severity, particularly crown scorch/consumption and tree mortality, to fully understand post-fire ecosystem changes.

Basal area mortality exceeded 75% in many portions of Heil Valley Ranch, and some areas might remain unforested for decades to come. Areas that convert from forests to grasslands or shrublands can serve as diverse habitat and moderate future wildfire behavior (Parks et al. 2015). Large-scale thinning and prescribed burning treatments on Heil Valley Ranch slightly reduced soil and vegetation burn severity. Substantially reducing overstory density, using prescribed burns to reduce activity fuels, and intentionally linking fuel treatment projects together can enhance ecosystem resilience to wildfires, although expectations of fuel treatment performance should be moderated when weather conditions are exceptionally hot, dry, and windy. Treatments that achieve fuel treatment and ecosystem restoration objectives, particularly those that include prescribed burning, have a higher likelihood of protecting lives and property and creating diverse habitat conditions across the landscape (Kalies and Kent 2016; Stephens et al. 2021).

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TABLES

Table 1. Wildfires burning portions of Heil Valley Ranch between 1988-2020. Acreage is based on fire perimeters from the National Interagency Fire Center (2021). Fire perimeters are displayed in Appendix Figure A.1.

Year	Incident name	Total fire size (acres)	Area of Heil Valley burned (acres)
1988	Lefthand Canyon Fire	3,460	90
2000	Mountain Ridge Fire	18	8
2004	Overland Fire	3,230	600
2005	Lykins Fire	35	20
2006	Elk Mountain Fire	2,570	11
2020	Calwood Fire	10,105	4,150

Table 2. Dates of understory research and weather data recorded at the Sugarloaf RAWS near Heil Valley Ranch in August 2001-2017, 2014, and 2021.

Year(s)	Understory sample dates	August average daily maximum temperature (°F)	August average daily minimum humidity (%)	August total precipitation (inch)
2001-2017	N/A	83	24	1.6
2014	August 11-14	80	26	1.7
2021	August 17-31	84	22	0.9

Table 3. Topography, fuel characteristics, and disturbance history impacted average BAER soil burn severity across the Calwood Fire. Areas with >33% cover of grasslands and shrublands were excluded. Results are presented for the spatial error model with the lowest AIC and significant predictors (alpha = 0.05). Parameter estimates indicate the change in predicted average soil burn severity associated with 1-standard deviation increase in the independent variable.

	Observed values		**Output from spatial error model**			
Independent variable	**Range**	**Standard deviation**	**z-value**	**Parameter estimate**	**95% CI**	**Data source**
General burn conditions						
Day of burn	1 - 8	1.2	-12.8	-0.33	-0.38 - -0.28	NIFC 2021
Topography (average in 300 x 300 m area)						
Elevation (ft)	5,820 - 8,423	592	N/S			LANDFIRE 2019
Slope (degrees)	5.1 - 36.1	6.3	-3.1	-0.10	-0.16 - -0.04	LANDFIRE 2019
Daily solar radiation (Watt hour/m^2)	1,184 - 3,617	437	6.3	0.17	0.12 - 0.22	ArcGIS Area Solar Radiation tool
Fuel conditions (average in 300 x 300 m area)						
Canopy cover (%)	4 - 53	9.4	8.6	0.23	0.18 - 0.29	LANDFIRE 2019
Canopy bulk density (100 * kg/m^3)	1.1 - 11.3	1.7	N/S[a]			LANDFIRE 2019
Distance from fuel breaks (roads/trails) (feet)	97 - 4,604	1,217	4.1	0.14	0.07 - 0.21	OpenStreetMap (2021) and ArcGIS Near tool
Disturbance history (percent of 300 x 300 m area)						
Thinned between 2003-2017	0 - 100	25	N/S			BCPOS
Prescribed burned between 2003-2017	0 - 100	19	-4.4	-0.13	-0.18 - -0.07	BCPOS
Burned by wildfire between 2000-2006	0 - 100	16	N/S			NIFC 2021

[a]Canopy bulk density was significant only if canopy cover were excluded from the model due to high correlation between these variables. The AIC value was lower for the model with canopy cover than that with canopy bulk density.

Table 4. Richness of native and non-native species and common species identified pre- and post-fire at the Wapiti treatment unit and post-fire at the PA7 unit. Scientific and common names follow the PLANTS database (USDA NRCS 2021).

	Num. of quadrats	**Num. of non-native species**	**Num. of native species**	**Percent of species occurring in <10% of quadrats**	**Common species occurring in >66% of quadrats**
Wapiti unit pre-fire (2014)	50	11	36	57%	Timber oatgrass (*Danthonia intermedia*) Sedge (*Carex* spp)
Wapiti unit post-fire (2021)	44	16	38	40%	Smooth white aster (*Symphyotrichum porteri*) Timber oatgrass (*Danthonia intermedia*) Canada toadflax (*Nuttallanthus canadensis*) Sedge (*Carex* spp) Rough bentgrass (*Agrostis scabra*) Canada bluegrass (*Poa compressa*)*
PA7 unit post-fire (2021)	23	14	41	47%	Field chickweed (*Cerastium strictum*) Canada bluegrass (*Poa compressa*)*

*Non-native species

FIGURES

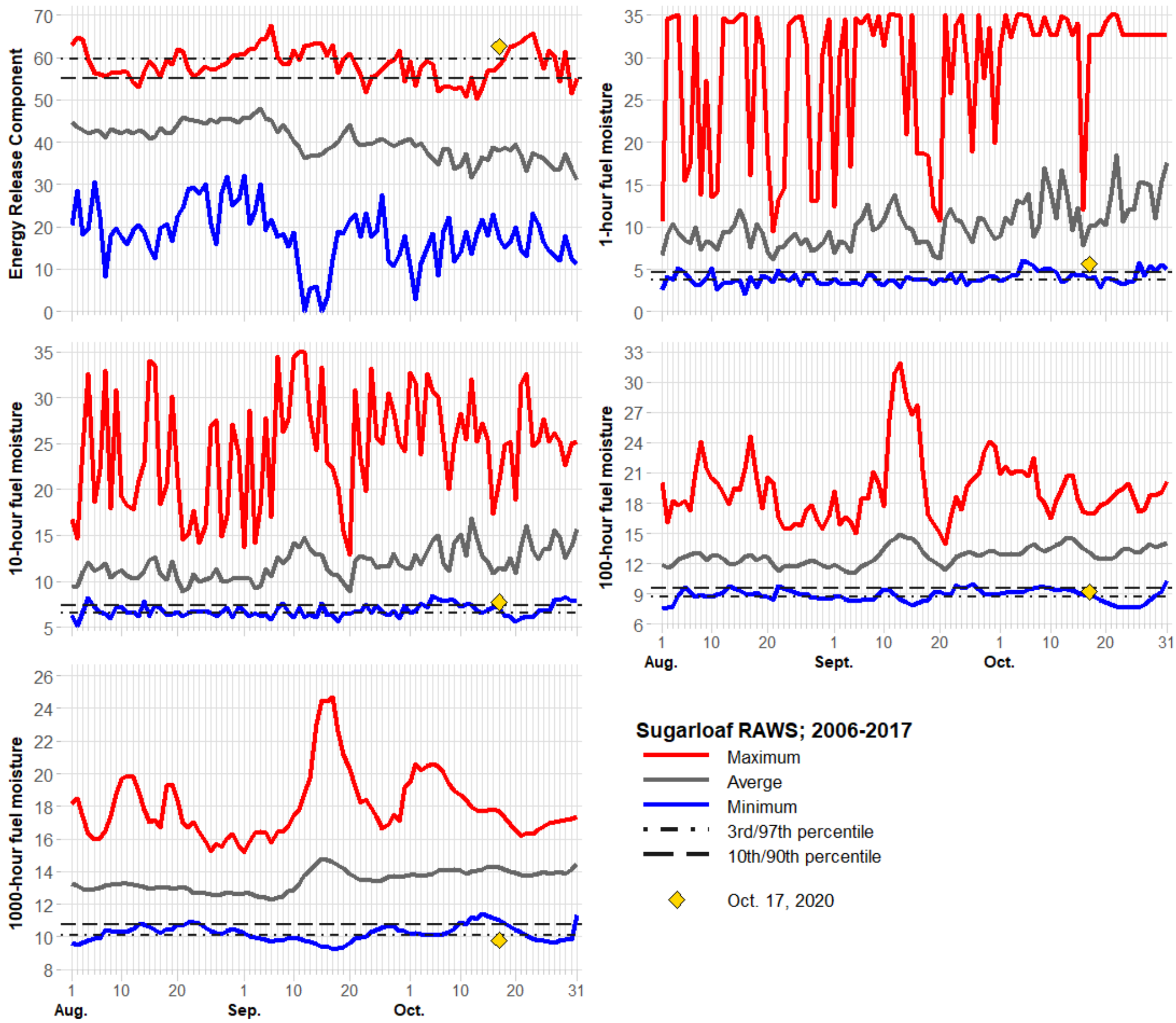

Figure 1. Energy release components (ERC) and fuel moistures were extreme on the first day of the Calwood Fire (October 17, 2020) relative to baseline conditions recorded at the Sugarload RAWS near Heil Valley Ranch. ERC was higher and 1000-hr fuel moisture was lower than any observations on October 17th from 2006-2017.

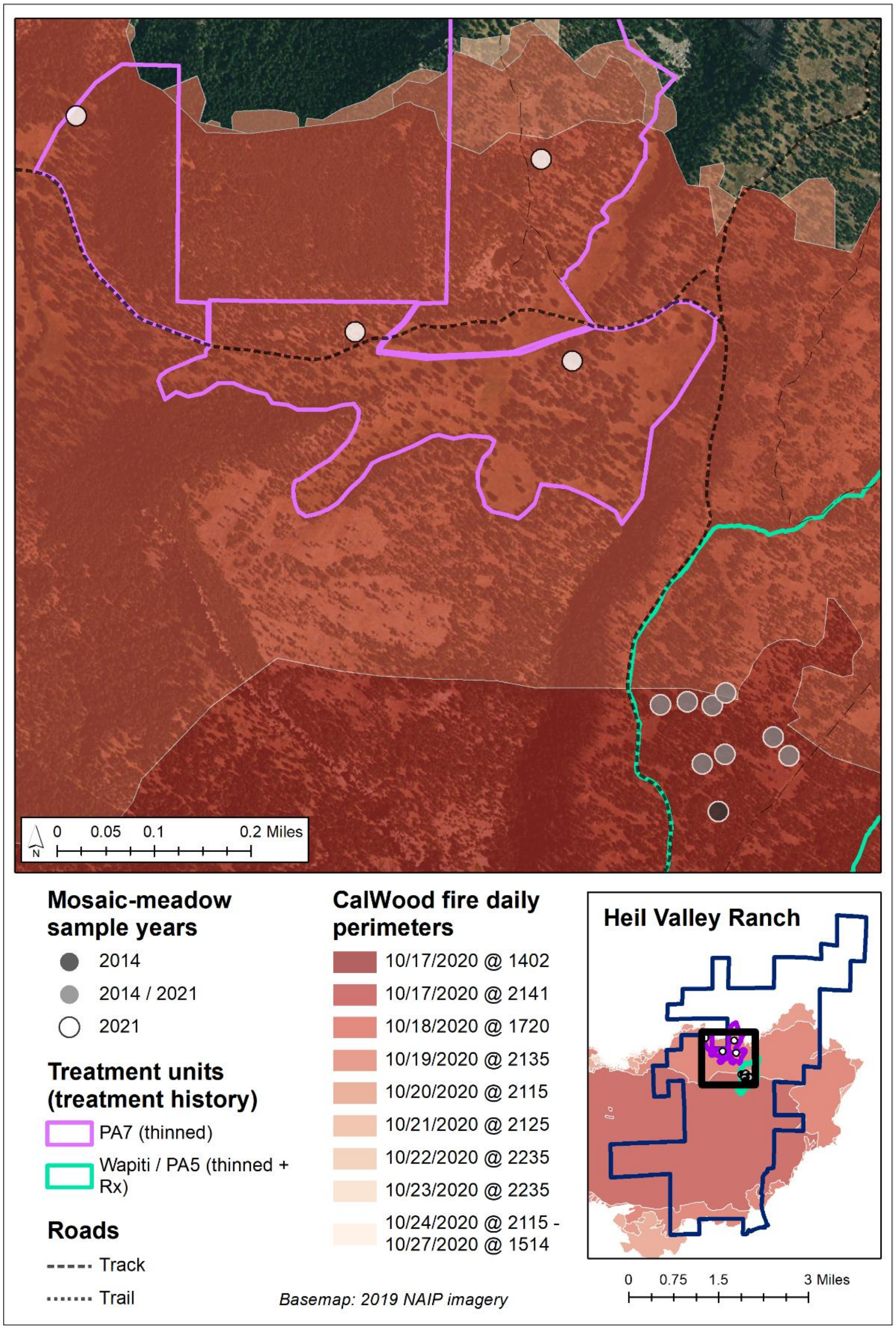

Figure 2. Location of mosaic-meadows where I sampled understory plant richness, cover, and composition in 2014 and 2021. One mosaic-meadow from 2014 could not be resampled because the area was salvaged logged after the Calwood Fire and before sampling in August 2021.

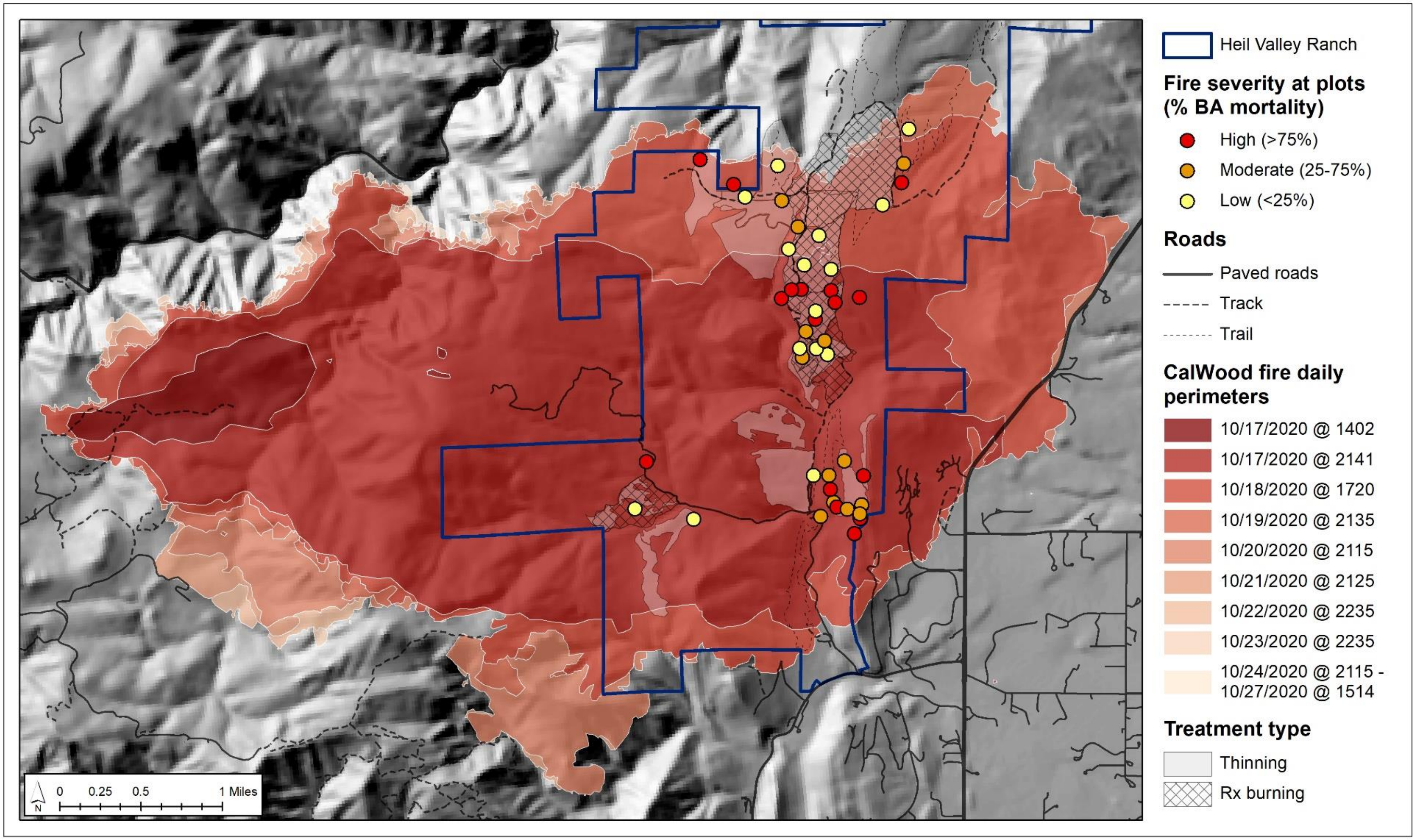

Figure 3. Location of plots where I sampled overstory density, tree characteristics, and fuel loads. I stratified sample locations across BAER soil burn severity categories (Appendix Figure A.2). Colors of plot locations indicate estimates of vegetation burn severity based on basal area mortality and cutoffs established by the USDA Forest Service Fire Effects Information System (FEIS 2021).

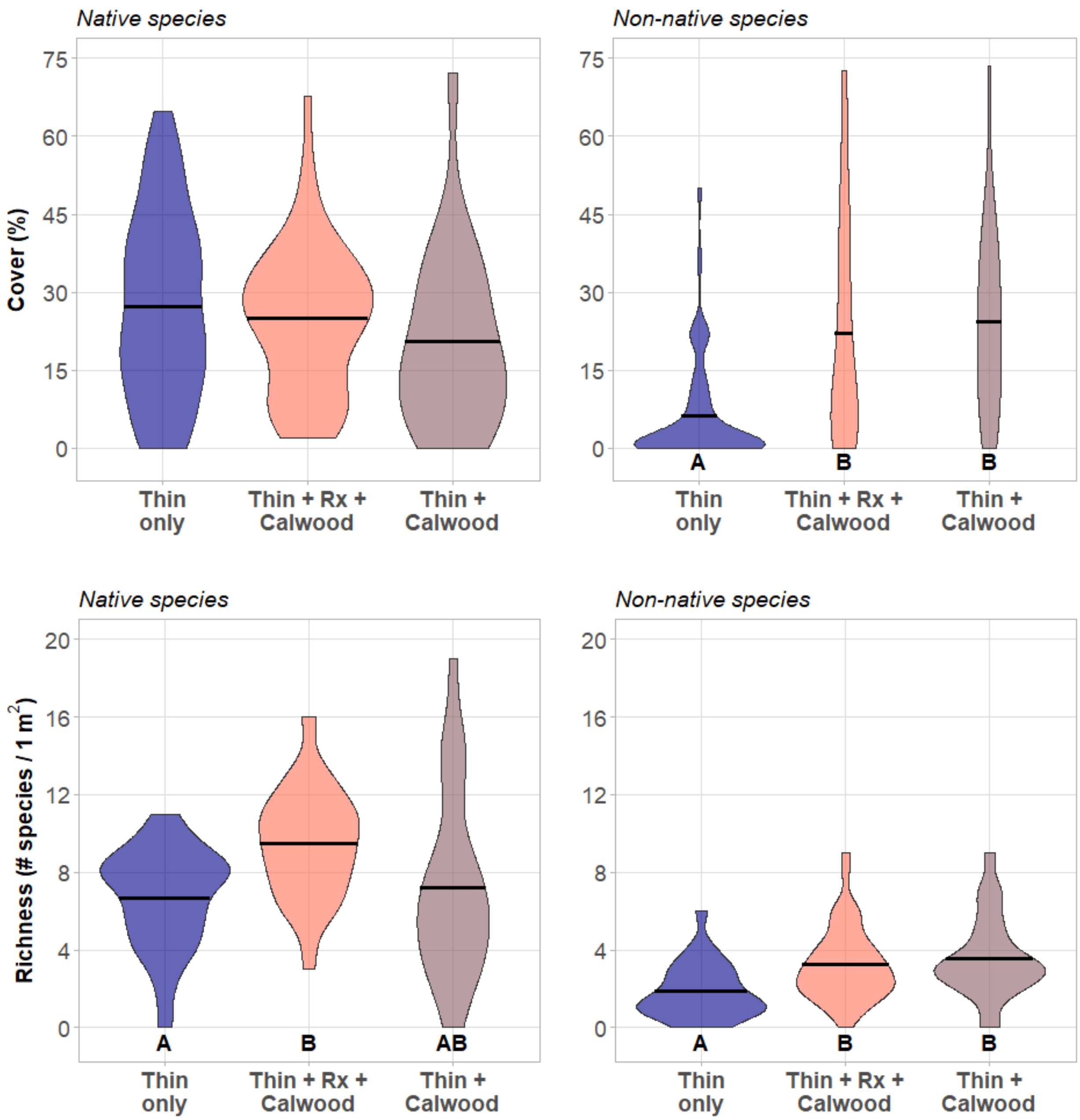

Figure 4. Average cover of native and non-native plant species and the richness of non-native plants were significantly higher in 2021 following the Calwood Fire than areas that had only been thinned in 2014. Width of the violin plot indicates the relative density of quadrat-level observations by disturbance history. Horizontal lines indicate average values by treatment, and letters indicate significant pairwise comparisons. See Appendix Table A.3 for Type II Wald X^2 values.

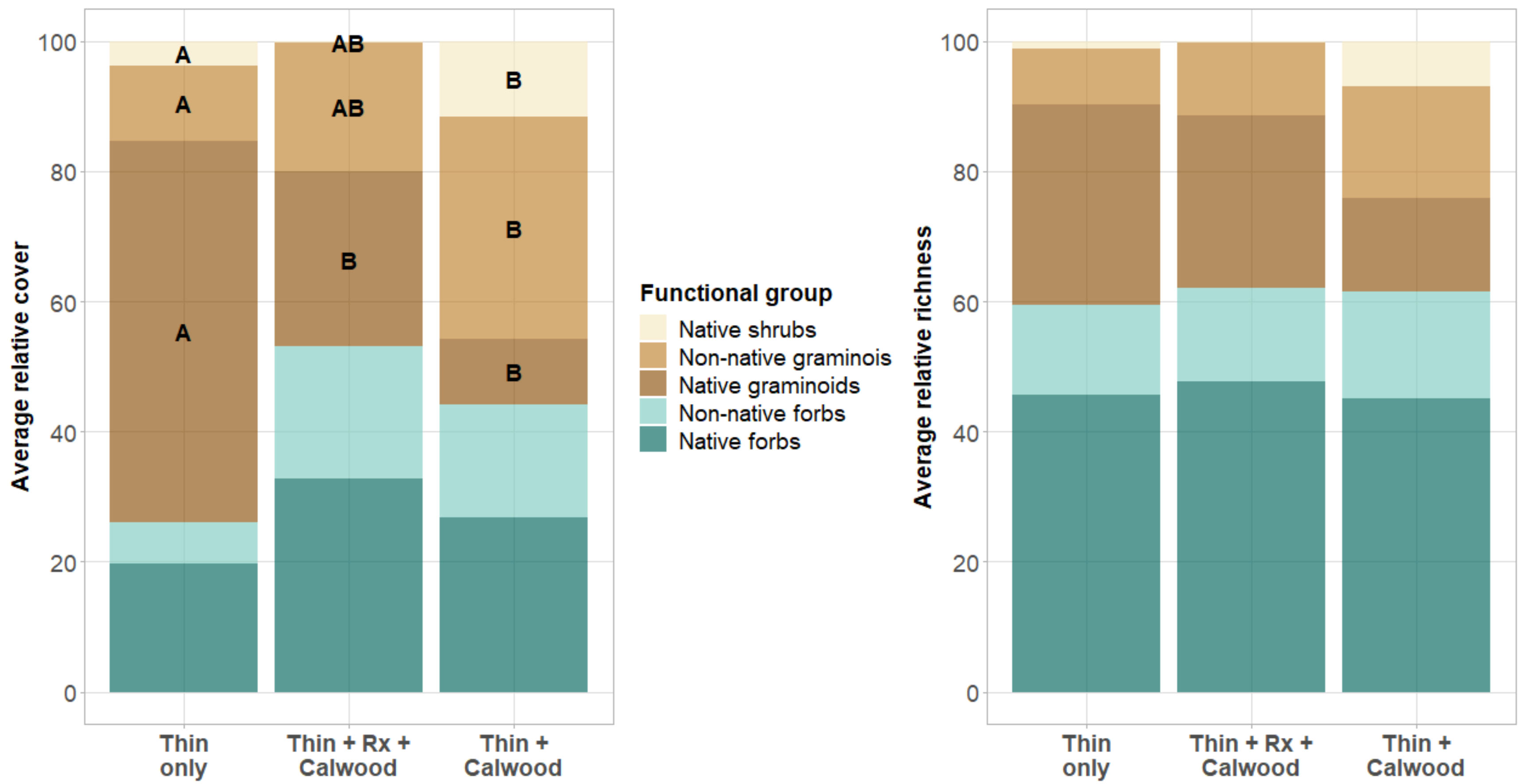

Figure 5. Relative cover varied among disturbance history for native graminoids, non-native graminoids, and native shrubs. Relative cover of native graminoids was notably lower in burned areas. Average relative richness did not differ by disturbance history. Letters indicate significant pairwise comparisons by functional group. See Appendix Table A.3 for Type II Wald X^2 values.

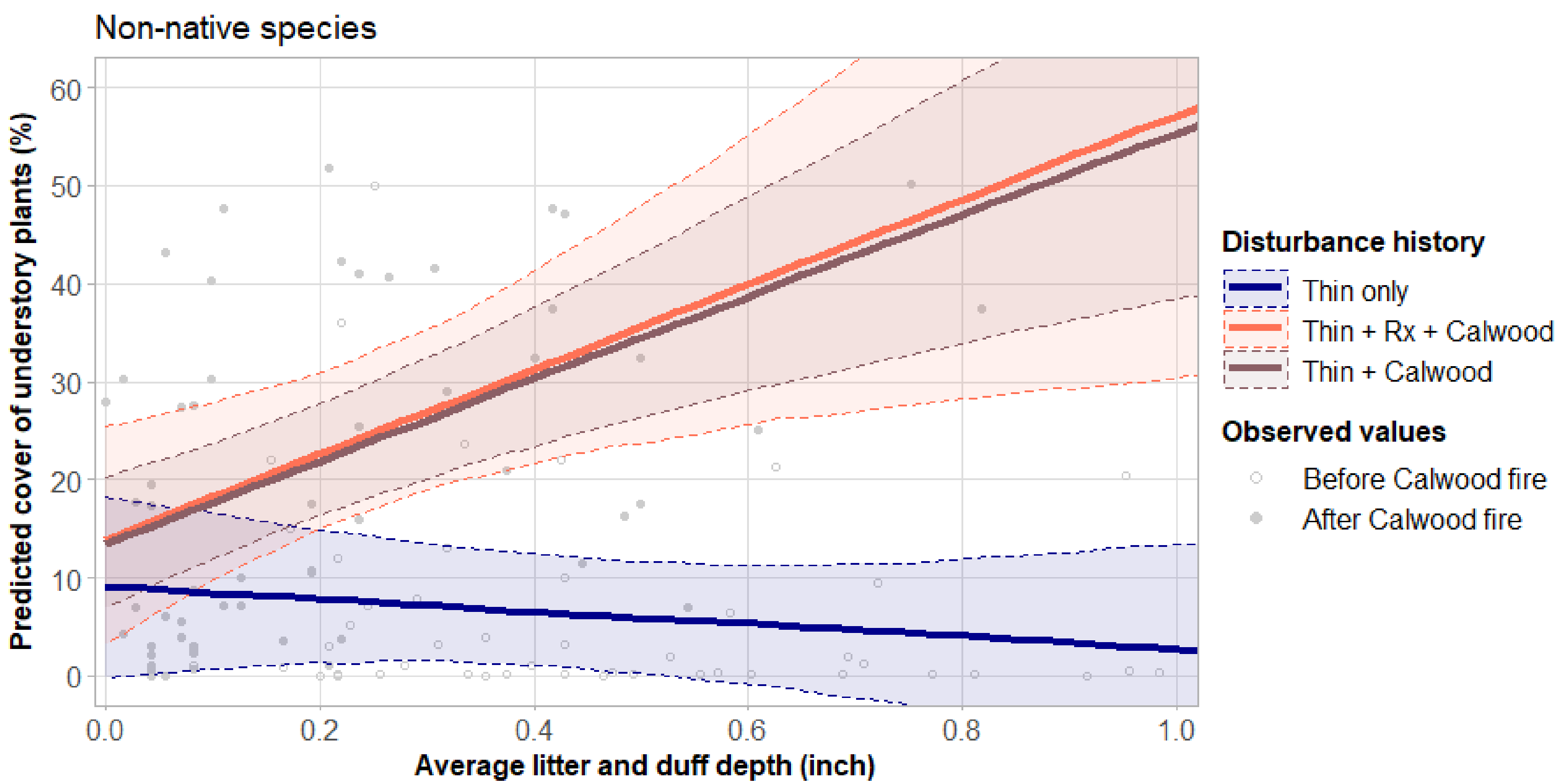

Figure 6. The cover of non-native species decreased with increasing litter/duff depth prior to the Calwood Fire but increased with litter/duff depth after the fire. Shaded areas indicate 90% confidence intervals for fixed effects. See Appendix Table A.4 for Type II Wald X^2 values.

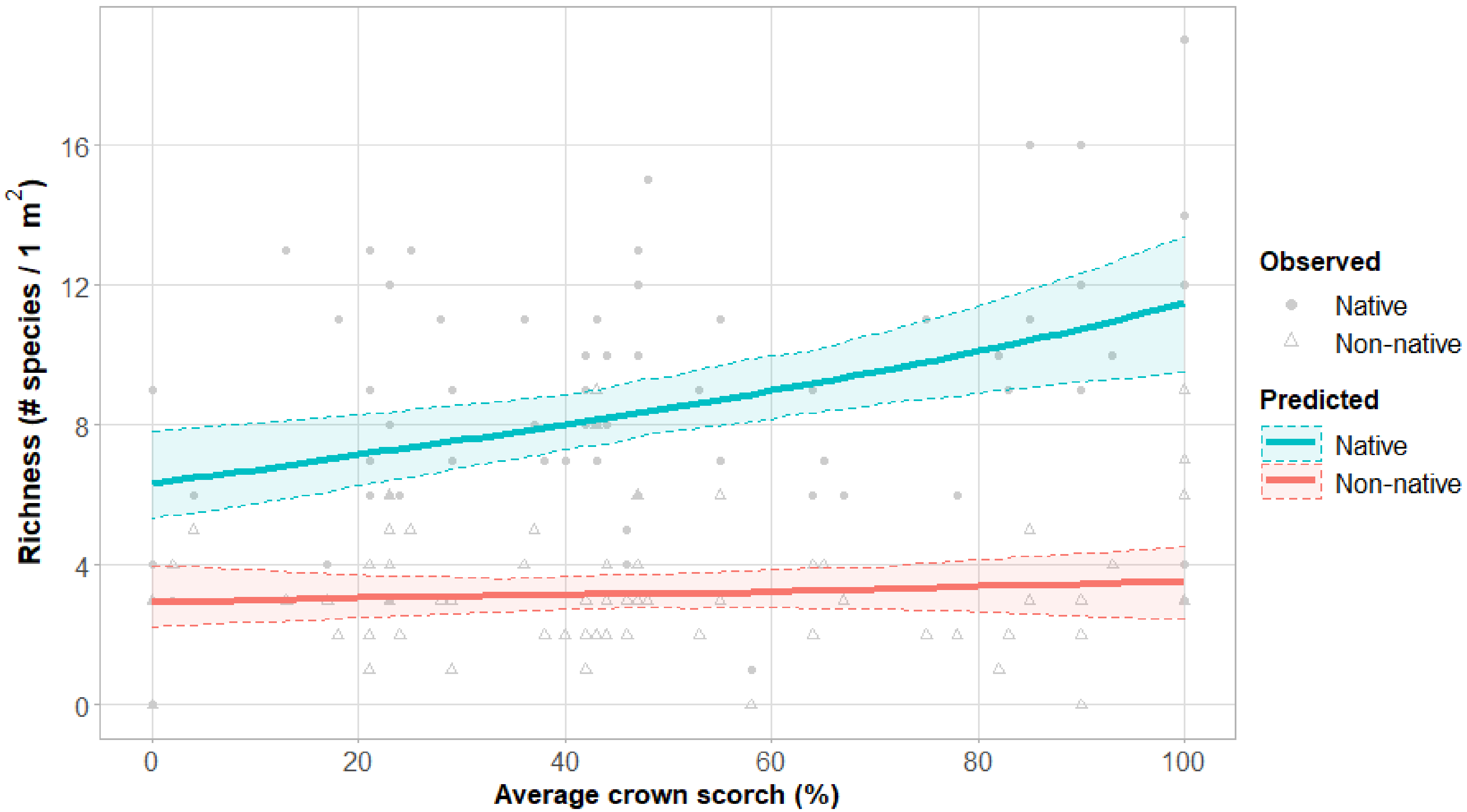

Figure 7. The richness of native species increased with increasing crown scorch/consumption of adjacent trees, but richness of non-native species did not. Shaded areas indicate 90% confidence intervals for fixed effects. See Appendix Table A.4 for Type II Wald X^2 values.

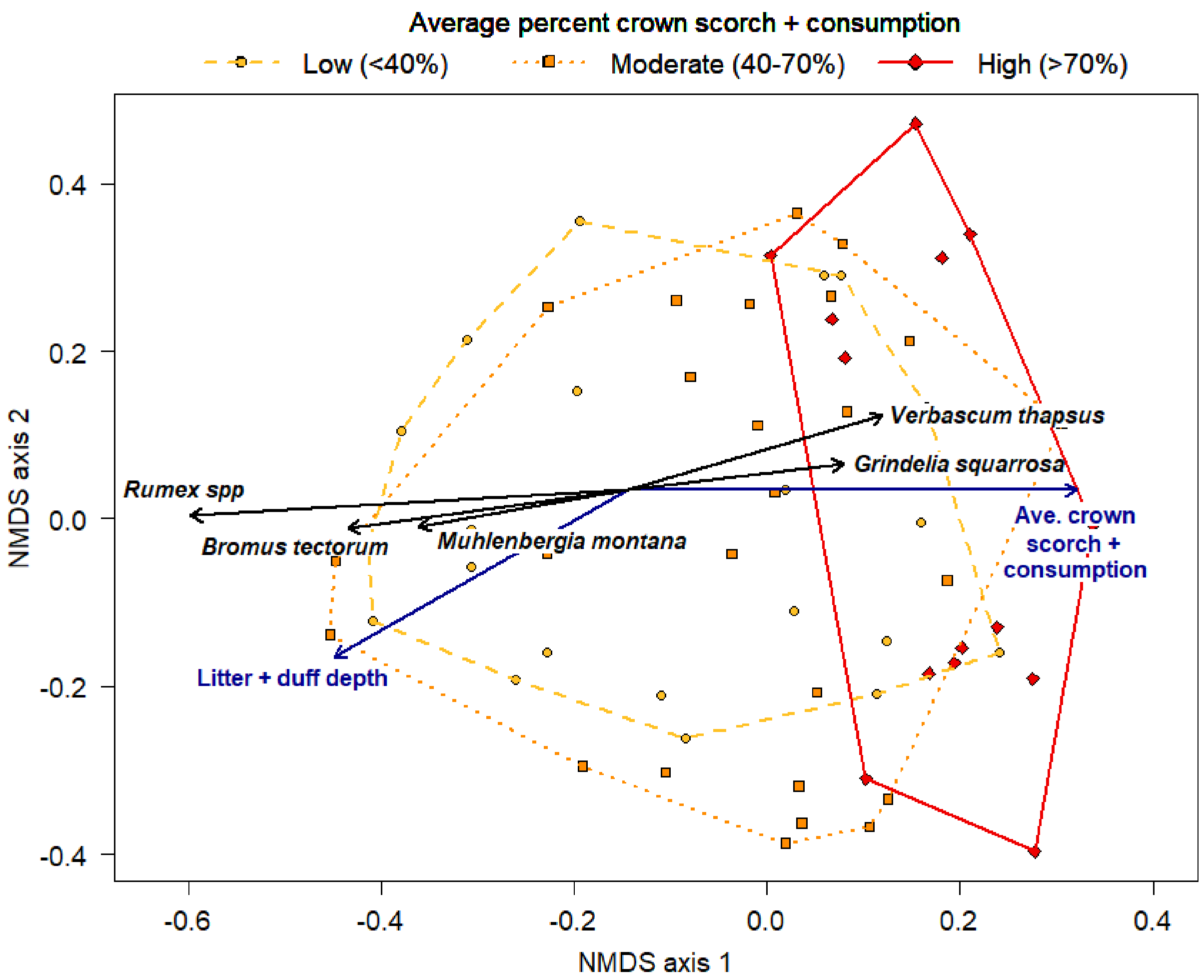

Figure 8. The composition of understory plant communities varied between plots with a high percent of crown scorch/consumption and those with a low to moderate percent of crown scorch/consumption after the Calwood Fire (F-value=2.8, p=0.01). The first NMDS axis was rotated to align with average crown scorch/consumption and was strongly correlated with litter/duff depth (r^2=0.19, p<0.001). Five species were strongly correlated with the first NMDS axis (r^2>0.10, p<0.05), indicating their association with higher average crown scorch/consumption or with higher litter/duff depth. Four-dimensional ordination resulted in a stress value of 0.12.

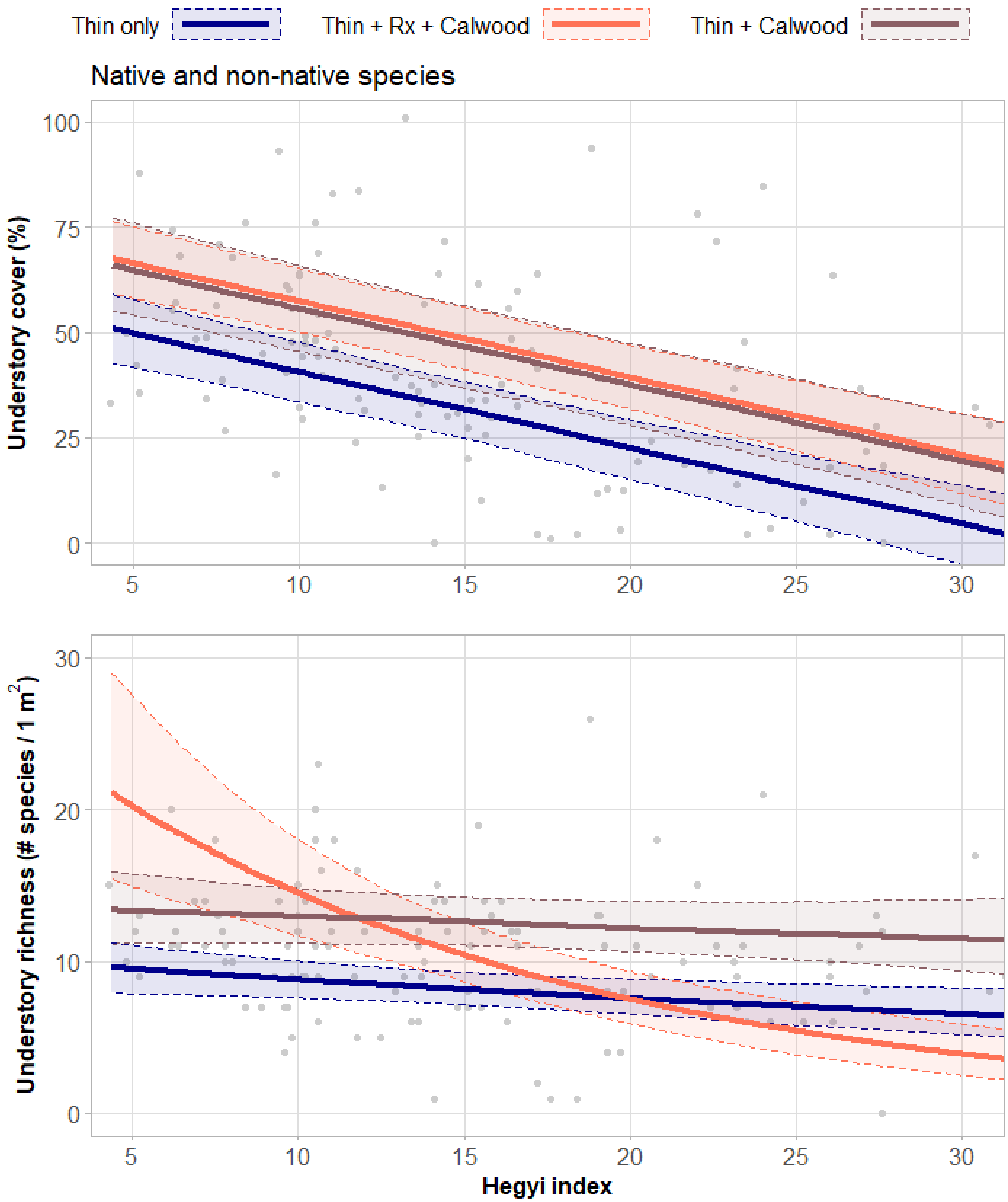

Figure 9. Cover of understory plants decreased with a higher degree of competition from overstory trees (i.e., higher Hegyi index) regardless of disturbance history. Richness showed a negative relationship with overstory competition only in areas that were thinned and burned in the PA7 treatment unit. Shaded areas indicate 90% confidence intervals for fixed effects, and grey dots indicate observed values. See Appendix Table A.4 for Type II Wald X^2 values.

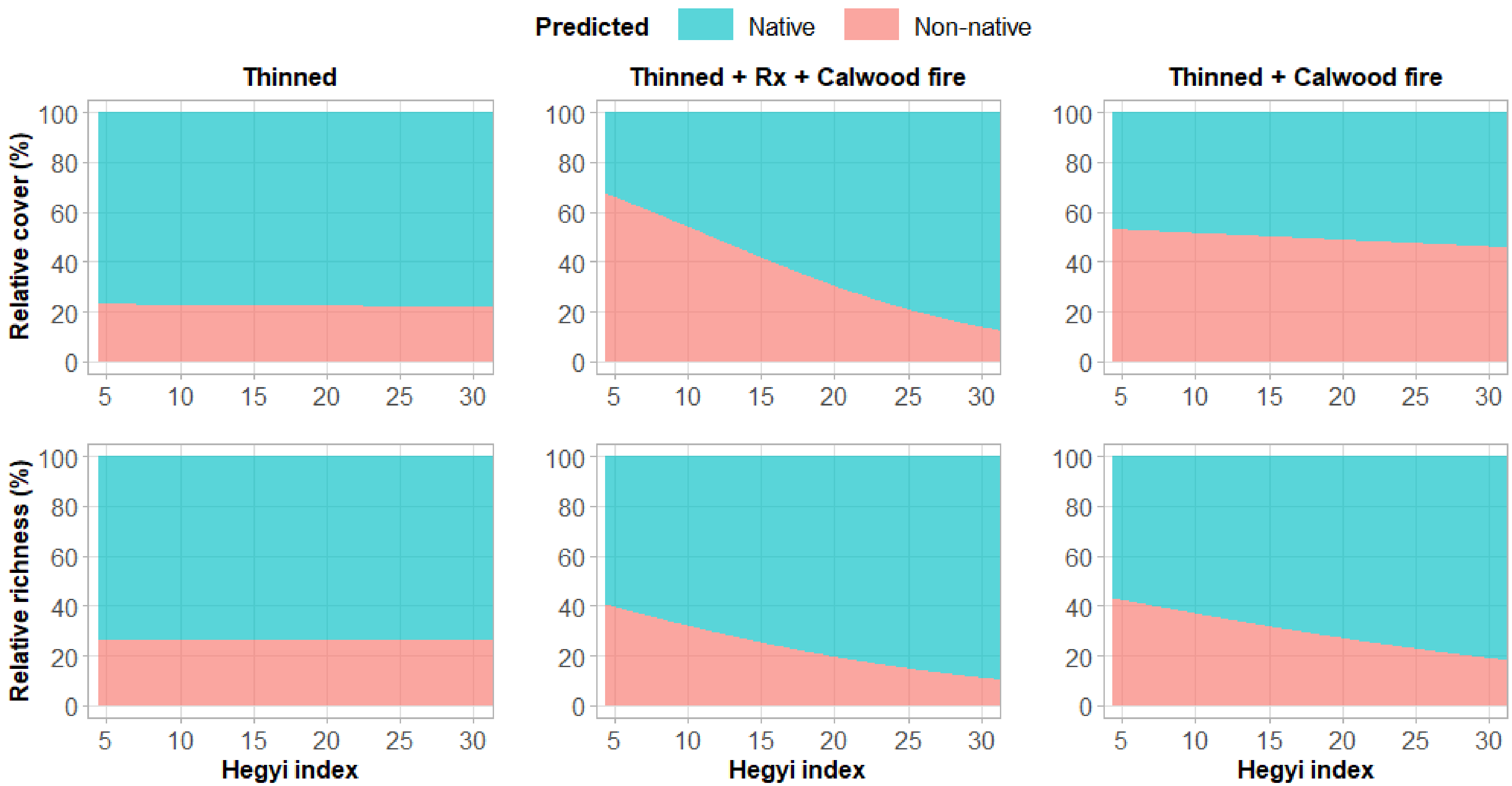

Figure 10. The relative richness and cover of native species increased with competition from overstory trees relative to non-native species in areas burned by the Calwood Fire. See Appendix Table A.4 for Type II Wald X^2 values.

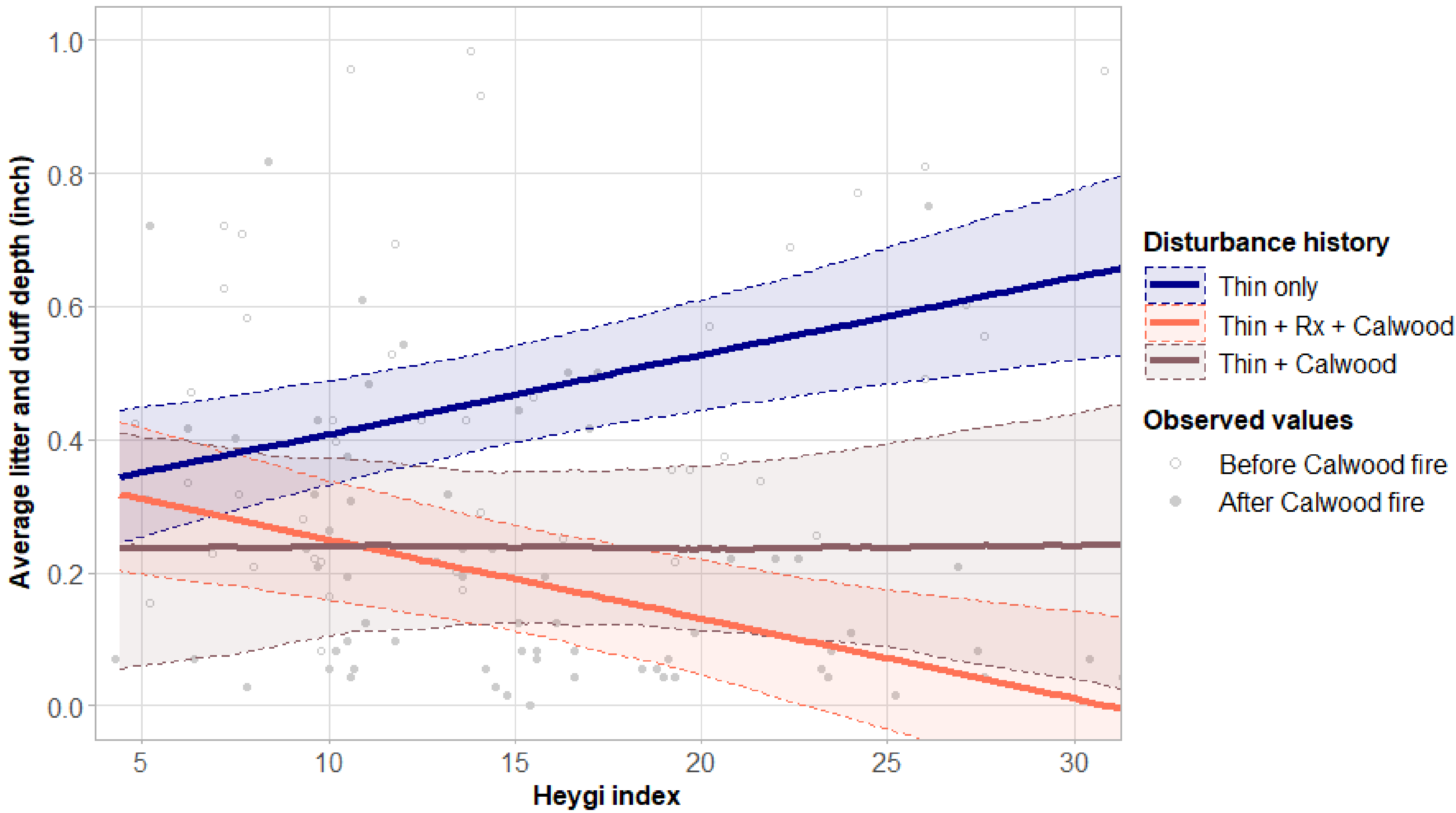

Figure 11. Litter/duff depth was higher before the Calwood Fire than after. Litter/duff depth increased with proximity and size of overstory trees (i.e., Heygi index) before the fire and decreased with the Heygi index after the fire at the Wapiti site. See Appendix Table A.4 for Type II Wald X^2 values.

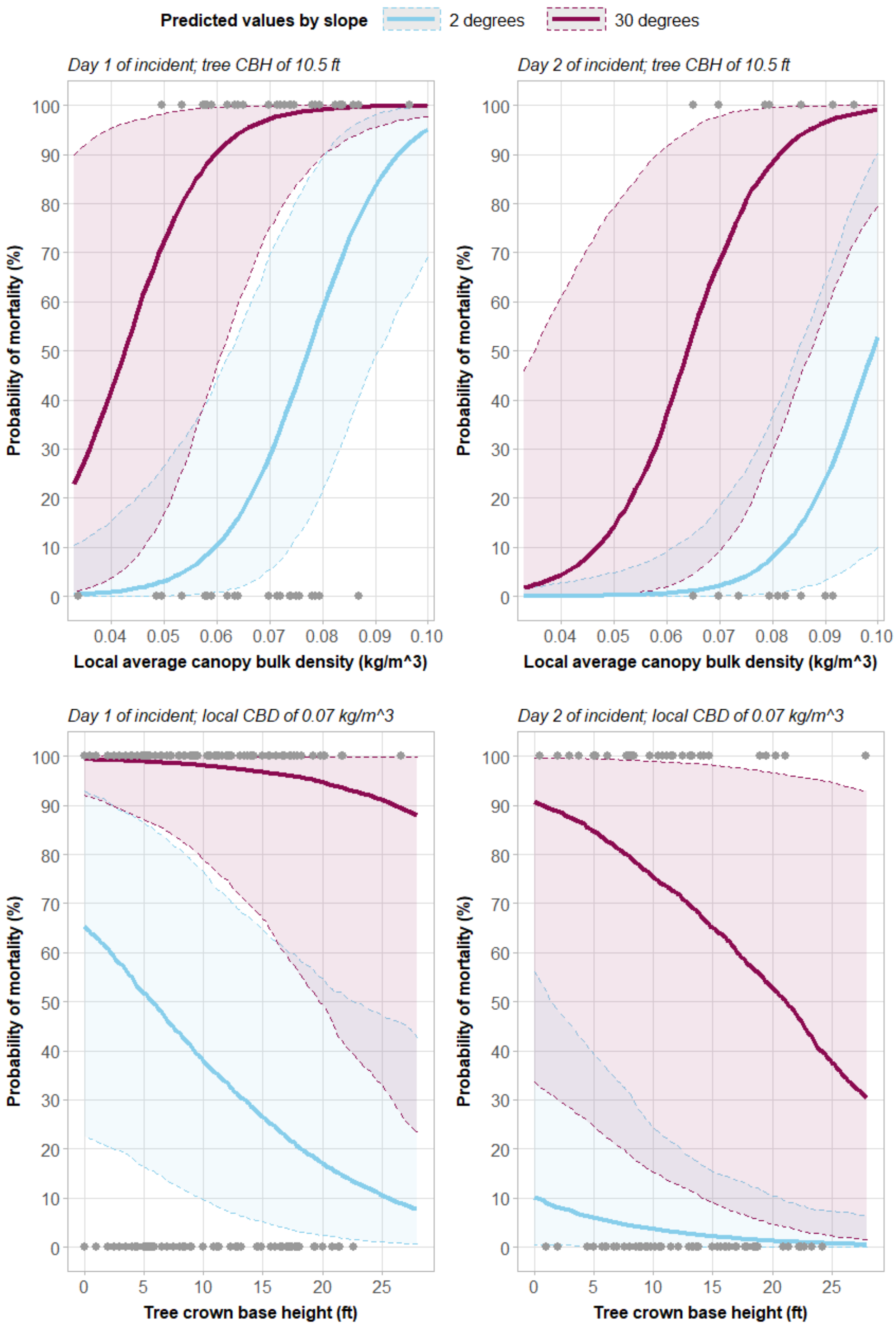

Figure 12. The probability of tree mortality after the Calwood Fire decreased with increasing crown base height, increased with slope, increased with crown bulk density of the surrounding 65-acre area, and decreased the second day of the Calwood Fire. Shaded areas indicate 90% confidence intervals for fixed effects and indicate high uncertainty in parameter estimates, particularly for slope. Grey dots indicate observed values. See Appendix Table A.6 for Type II Wald X^2 values.

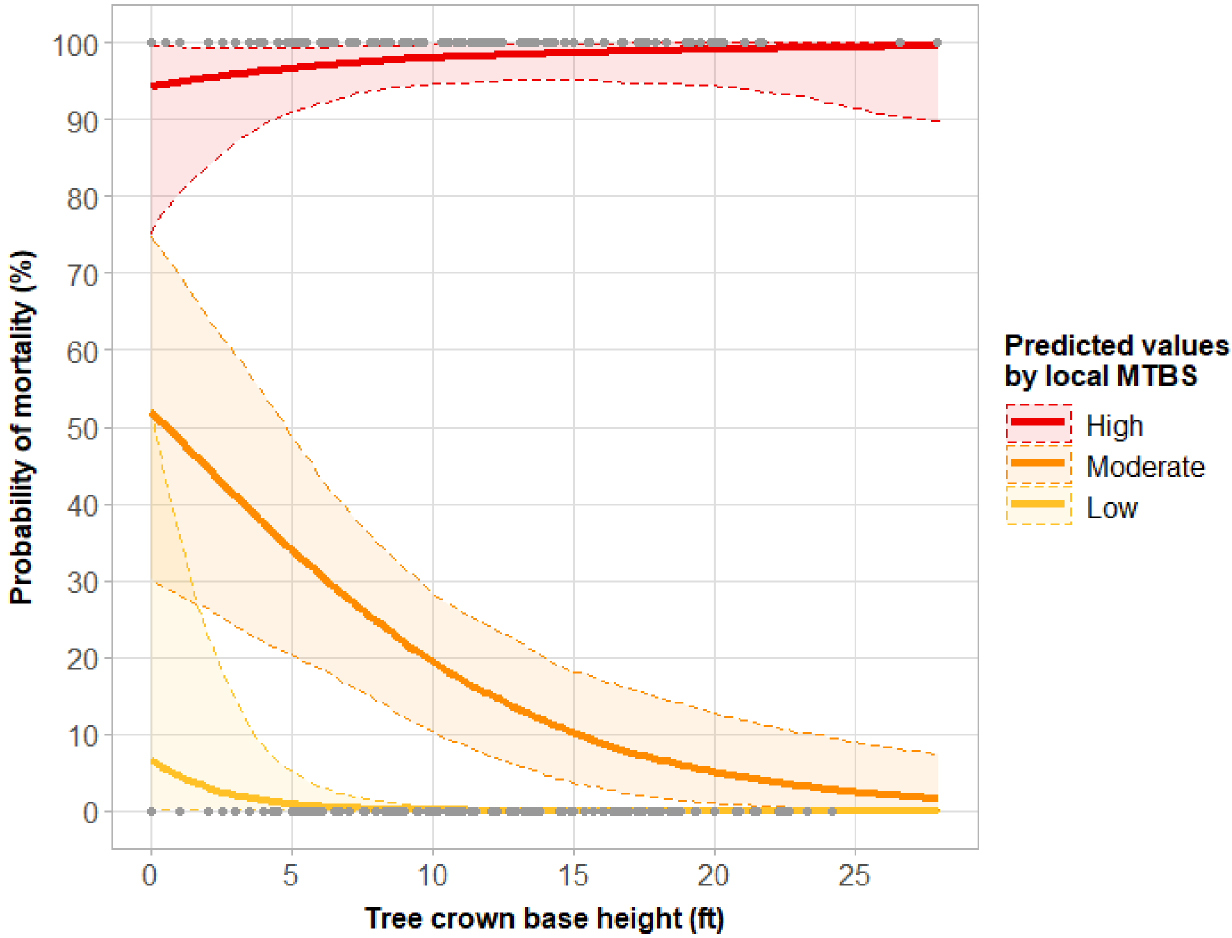

Figure 13. Increasing crown base height decreased the probability of mortality in stands that experienced lower BAER soil burn severity. Shaded areas indicate 90% confidence intervals for fixed effects, and grey dots indicate observed values. See Appendix Table A.6 for Type II Wald X^2 values.

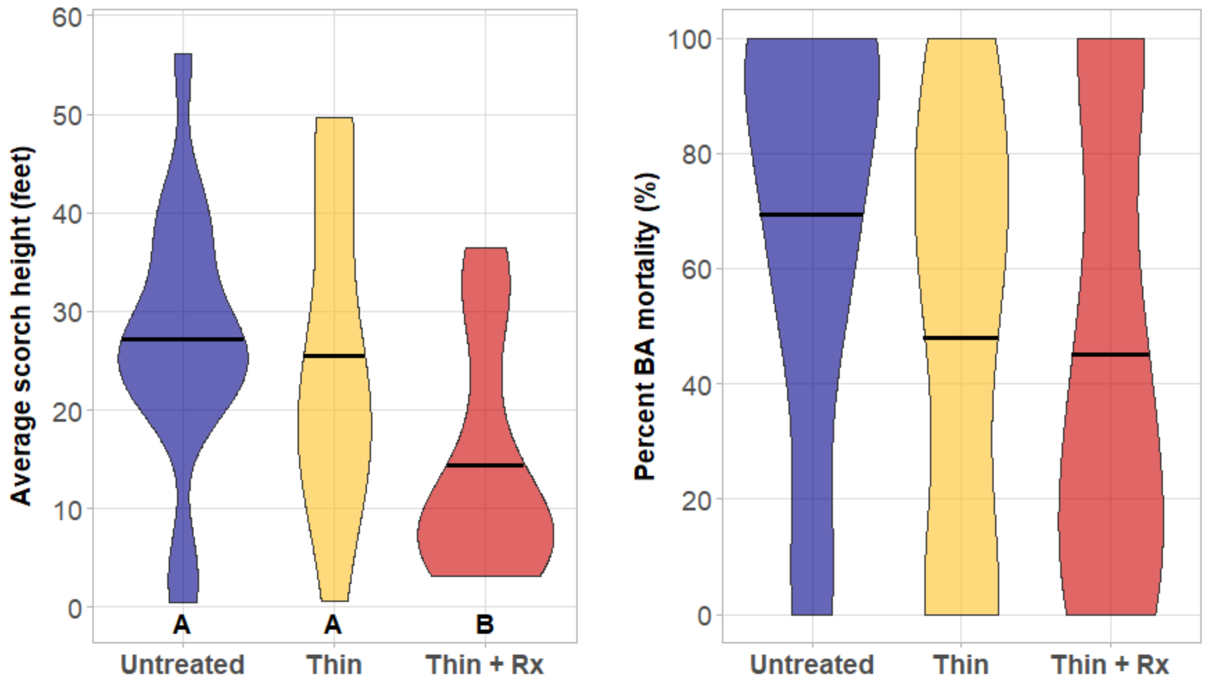

Figure 14. Average scorch height was significantly lower in areas that were thinned and burned prior to the Calwood Fire, but percent BA mortality was not significantly different among treatment histories. Width of the violin plot indicates the relative density of plot-level observations. Horizontal lines indicate average values by treatment, and letters indicate significant pairwise comparisons. See Appendix Table A.5 for Kruskal–Wallis X^2 values.

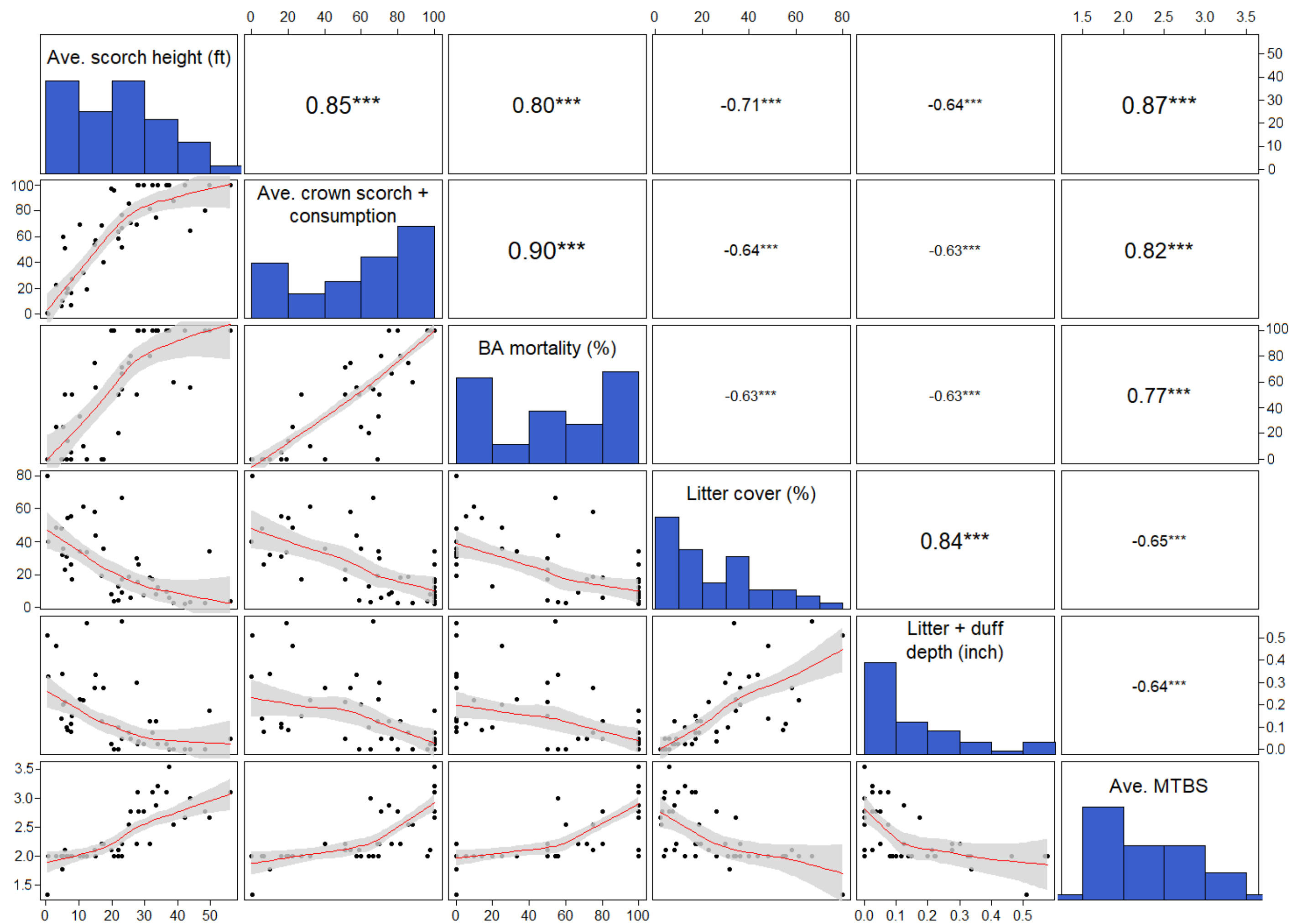

Figure 15. Metrics of soil and vegetation burn severity were highly correlated based on the Spearman correlation coefficient. Red lines indicate local moving regression relationships and grey areas indicate 95% confidence intervals. Tree-level crown scorch/consumption and diameter were used to estimate tree mortality, so the strong relationship between average crown scorch/consumption and percent BA mortality is not surprising.

Figure 16. The Calwood Fire resulted in highly variable soil and vegetation burn severity within stands (top) and across the landscape (bottom) conditions due to high variability in topography and pre-fire forest structure and changing weather conditions during the incident.

Appendix: Impacts of pre-fire forest structure and wildfire severity on understory vegetation and tree mortality

TABLES

Table A1. Occurrence of non-native species identified pre- and post-fire at the Wapiti treatment unit and post-fire at the PA7 unit. Scientific and common names follow the PLANTS database (USDA NRCS 2021).

Common name	**Scientific name**	**Life form**	**Wapiti unit pre-fire (2014)**	**Wapiti unit post-fire (2021)**	**PA7 unit post-fire (2021)**
Japanese brome	*Bromus japonicus*	G	X	X	X
Cheatgrass	*Bromus tectorum*	G	X	X	X
Nodding plumeless thistle	*Carduus nutans*	F	X		X
Goosefoot	*Chenopodium* spp	F		X	X
Canada thistle	*Cirsium arvense*	F		X	X
Bull thistle	*Cirsium vulgare*	F			X
Field bindweed	*Convolvulus arvensis*	F		X	
Common St. Johnswort	*Hypericum perforatum*	F		X	
Prickly lettuce	*Lactuca serriola*	F	X	X	X
Dalmatian toadflax	*Linaria dalmatica*	F	X	X	X
Sweetclover	*Melilotus officinalis*	F		X	
Canada bluegrass	*Poa compressa*	G	X	X	X
Kentucky bluegrass	*Poa pratensis*	G	X	X	X
Black bindweed	*Polygonum convolvulus*	F		X	
Sorrel	*Rumex* spp	F	X	X	X
Common dandelion	*Taraxacum officinale*	F	X	X	X
Yellow salsify	*Tragopogon dubius*	F	X	X	X
Common mullein	*Verbascum thapsus*	F	X	X	X

[a]G = graminoid. F = forb.

Table A2. Occurrence of native species identified pre- and post-fire at the Wapiti treatment unit and post-fire at the PA7 unit. Scientific and common names follow the PLANTS database (USDA NRCS 2021).

Common name	**Scientific name**	**Life form[a]**	**Wapiti unit pre-fire (2014)**	**Wapiti unit post-fire (2021)**	**PA7 unit post-fire (2021)**
Common yarrow	*Achillea millefolium*	F	X	X	X
Rough bentgrass	*Agrostis scabra*	G	X	X	X
Nodding onion	*Allium cernuum*	F	X	X	X
Cuman ragweed	*Ambrosia psilostachya*	F	X	X	X
Pussytoes	*Antennaria* spp	F	X		
Kinnikinnick	*Arctostaphylos uva-ursi*	S	X	X	
Prairie sagewort	*Artemisia frigida*	F			X
White sagebrush	*Artemisia ludoviciana*	F	X	X	X
Drummond's milkvetch	*Astragalus drummondii*	F			X
Bluebell bellflower	*Campanula rotundifolia*	F	X	X	X
Sedge	*Carex* spp	G	X	X	X
Fendler's ceanothus	*Ceanothus fendleri*	S			X
Field chickweed	*Cerastium strictum*	F	X	X	X
Canadian horseweed	*Conyza canadensis*	F	X	X	X
Timber oatgrass	*Danthonia intermedia*	G	X	X	
Slimleaf panicgrass	*Dichanthelium linearifolium*	G	X	X	
Heller's rosette grass	*Dichanthelium oligosanthes*	G	X		
Squirreltail	*Elymus elymoides*	G	X		X
Fringed willowherb	*Epilobium ciliatum*	F		X	
Spreading fleabane	*Erigeron divergens*	F			X
Trailing fleabane	*Erigeron flagellaris*	F	X		X
Sanddune wallflower	*Erysimum capitatum*	F		X	
Idaho fescue	*Festuca idahoensis*	G		X	
Rocky Mountain fescue	*Festuca saximontana*	G	X	X	X
Blanketflower	*Gaillardia aristata*	F	X	X	X
Stickywilly	*Galium aparine*	F		X	
Pineywoods geranium	*Geranium caespitosum*	F	X	X	X
Curlycup gumweed	*Grindelia squarrosa*	F	X	X	X

Common name	Scientific name	Life form[a]	Wapiti unit pre-fire (2014)	Wapiti unit post-fire (2021)	PA7 unit post-fire (2021)
Whiskbroom parsley	*Harbouria trachypleura*	F	X	X	X
Hairy false goldenaster	*Heterotheca villosa*	F	X	X	X
Rush	*Juncus* spp	G			X
Prairie Junegrass	*Koeleria macrantha*	G	X	X	X
Silvery lupine	*Lupinus argenteus*	F			X
Prairie bluebells	*Mertensia lanceolata*	F	X	X	X
Pony beebalm	*Monarda pectinata*	F	X	X	X
Mountain muhly	*Muhlenbergia montana*	G	X	X	X
Canada toadflax	*Nuttallanthus canadensis*	F	X	X	
Twistspine pricklypear	*Opuntia macrorhiza*	S	X		
Slender yellow woodsorrel	*Oxalis dillenii*	F	X	X	
Woolly groundsel	*Packera cana*	F			X
Penstemon	*Penstemon* spp	F		X	X
Silverleaf phacelia	*Phacelia hastata*	F		X	X
Sunbright	*Phemeranthus parviflorus*	F	X	X	X
Douglas' knotweed	*Polygonum douglasii*	F		X	X
Bigflower cinquefoil	*Potentilla fissa*	F	X		X
Wright's cudweed	*Pseudognaphalium canescens*	F	X		
Delicious raspberry	*Rubus deliciosus*	F			X
Little bluestem	*Schizachyrium scoparium*	G	X	X	X
Britton's skullcap	*Scutellaria brittonii*	F			X
Sleepy silene	*Silene antirrhina*	F	X	X	X
Goldenrod	*Solidago* spp	F	X	X	X
Smooth white aster	*Symphyotrichum porteri*	F	X	X	X
Clasping Venus' looking-glass	*Triodanis perfoliata*	F		X	X
Neckweed	*Veronica peregrina*	F		X	X

[a]G = graminoid. F = forb. S = shrub.

Table A.3. Comparisons of understory conditions by disturbance history based multi-level models accounting for autocorrelation of quadrats within mosaic-meadows. Tukey's Honest Significant tests are presented for significant pairwise comparisons at an alpha of 0.10.

Independent variable	**Type II Wald X^2 (p-value)**	**Mean (significant pairwise comparisons among disturbance histories)**		
		Thin (n=50)	**Thin + Rx + Calwood (n=44)**	**Thin + Calwood (n=23)**
Litter/duff depth (inch)	19.1 (<0.001)	1.4 (A)	0.5 (B)	0.6 (B)
Cover of all plants (%)	7.4 (0.02)	33 (A)	47 (B)	45 (AB)
Cover of native plants (%)	N/S	27	25	21
Cover of non-native plants (%)	16.2 (<0.001)	6 (A)	22 (B)	24 (B)
Richness of all plants (spp / 1 m^2)	15.5 (<0.001)	9 (A)	13 (B)	11 (AB)
Richness of native plants (spp / 1 m^2)	12.6 (0.002)	7 (A)	9 (B)	7 (AB)
Richness of non-native plants (spp / 1 m^2)	11.7 (0.003)	2 (A)	3 (B)	4 (B)
Relative cover of native forbs (% of total cover)	N/S	20	33	27
Relative cover of non-native forbs (% of total cover)	N/S	6	20	17
Relative cover of native graminoids (% of total cover)	19.6 (<0.001)	59 (A)	27 (B)	10 (B)
Relative cover of non-native graminoids (% of total cover)	4.7 (0.09)	12 (A)	20 (AB)	34 (B)
Relative cover of native shrubs (% of total cover)	5.2 (0.07)	4 (AB)	0 (A)	12 (B)
Relative richness of native forbs (% of total spp)	N/S	46	48	45
Relative richness of non-native forbs (% of total spp)	N/S	14	14	16
Relative richness of native graminoids (% of total spp)	N/S	31	26	14
Relative richness of non-native graminoids (% of total spp)	N/S	9	11	17
Relative richness of native shrubs (% of total spp)	N/S	1	0	7

Table A.4. Relationships among understory vegetation and competition from overstory trees (i.e., Hegyi index), disturbance history, litter/duff depth, and crown scorch/consumption. Results only presented for models with ΔAIC value >-5.0 relative to the intercept-only (i.e., null) model and with variables significant at an alpha of 0.10. Analyses with litter/duff depth excluded three outliers with litter/duff depth > 2.5 inches.

Independent variable	**Dependent variable(s)**	**Direction of relationship**	**Type II Wald X^2 (p-value)**	**ΔAIC**	**Model form**
Litter/duff depth (inch)	Disturbance history	"-" Thin + Rx + Calwood "-" Thin + Calwood	18.7 (<0.001)	-5.1	Linear + random effect for meadow
	Hegyi index		N/S		
	Disturbance history x litter/duff depth (inch)	"+" Thin "-" Thin + Rx + Calwood N/S Thin + Calwood	16.9		
Cover of all understory plants (%)	Disturbance history	"+" Thin + Rx + Calwood "+" Thin + Calwood	9.2 (0.01)	-47.9	Linear + random effect for meadow
	Hegyi index	"-"	47.1 (<0.001)		
Cover of all understory plants (%)	Disturbance history	"+" Thin	7.2 (0.03)	-39.7	Linear + random effect for meadow
	Litter/duff depth (inch)		2.7 (0.10)		
	Disturbance history x litter/duff depth (inch)	"-" Thin "+" Thin + Rx + Calwood "+" Thin + Calwood	15.7 (<0.001)		
Cover of non-native plants (%)	Disturbance history	"+" Thin + Rx + Calwood "+" Thin + Calwood	19.3 (<0.001)	-44.6	Linear + random effect for meadow
	Litter/duff depth (inch)		6.3 (0.01)		
	Disturbance history x litter/duff depth (inch)	"-" Thin "+" Thin + Rx + Calwood "+" Thin + Calwood	12.0 (0.002)		

Independent variable	**Dependent variable(s)**	**Direction of relationship**	**Type II Wald X^2 (p-value)**	**ΔAIC**	**Model form**
Richness of all understory plants (# spp / quad)	Disturbance history	"+" Thin + Calwood	16.8 (<0.001)	-29.2	Poisson + random effect for meadow
	Hegyi index		10.8 (<0.001)		
	Disturbance history x Hegyi index	"N/S" Thin "N/S" Thin + Rx + Calwood "-" Thin + Calwood	14.1 (<0.001)		
Richness of native plants (# spp / quad)	Average crown scorch + consumption (%)	"+"	9.0 (0.003)	-5.1	Poisson + random effect for meadow
Relative cover of native vs. non-native plants	Disturbance history	"+" Thin + Rx + Calwood for non-natives "+" Thin + Calwood for non-natives	30.2 (<0.001)	-32.9	Dirichlet regression
	Hegyi index	"-" for non-natives	5.4 (0.07)		
	Disturbance history x Hegyi index		8.6 (0.07)		
Relative richness of native vs. non-native plants	Disturbance history		22.5 (<0.001)	-37.9	Dirichlet regression
	Hegyi index	"-" for non-natives	15.3 (<0.001)		
	Disturbance history x Hegyi index	"+" Thin for natives "+" Thin + Rx + Calwood for natives "N/S" Thin + Calwood for natives	9.7 (0.046)		

Table A.5. Comparisons of overstory and surface fuel conditions by disturbance history after the 2020 Calwood Fire based on non-parametric Kruskal-Wallis one-way ANOVA and Wilcox tests for pairwise comparisons with an alpha of 0.10.

Independent variable	**X^2 (p-value)**	**Mean (significant pairwise comparisons among treatment histories)**		
		Untreated (n=16)	**Thin only (n=11)**	**Thin + Rx (n=17)**
Total BA (ft^2/acre)	N/S	61.3	50.9	65.3
Total trees/acre	6.3 (0.04)	121 (AB)	42 (B)	130 (A)
Average DBH (inch)	12.1 (0.002)	14.7 (A)	18.2 (B)	12.2 (A)
Average crown base height (ft)	8.1 (0.02)	6.6 (A)	9.4 (AB)	11.2 (B)
Local average canopy bulk density (kg/m^3)	N/S	0.073	0.067	0.078
Local average canopy cover (%)	N/S	32	30	35
Percent BA mortality (%)	N/S	69	48	45
Percent TPA mortality (%)	N/S	74	52	52
Average scorch height (ft)	7.0 (0.03)	27.2 (A)	25.6 (A)	14.4 (B)
Average BAER soil burn severity[a]	N/S	2.5	2.3	2.3
Percent litter cover (%)	N/S	21	24	31
Litter/duff depth (inch)	N/S	0.1	0.2	0.1

[a]Average value in an irregularly shaped 65-acre area with a width of 0.3 miles (Appendix Figure A.4).

[b]Average soil burn severity from the Interagency BAER Team within a 90 x 90 m area around each plot, treating soil burn severity as a continuous variable ranging from 0 (none to very low) to 4 (high).

Table A.6. Relationships between plot- and tree-level vegetation burn severity and pre-fire forest structure. Results only presented for models with ΔAIC value >-5.0 relative to the intercept-only (i.e., null) model and with variables significant at an alpha of 0.10. Non-significant variables were included if their interaction was significant.

Independent variable at the plot-level	**Dependent variable(s)[1]**	**Direction of relationship**	**F-value (p-value)**	**ΔAIC**	**Model form**
BA mortality (%)	None				Binomial
TPA mortality (%)	None				Binomial
Average crown scorch and consumption (%)	None				Binomial
Average scorch height (ft)	Day of incident	"-" Day 2	9.3 (0.004)	-12.8	Linear
	Treatment	"-" Thin + burn	7.0 (0.003)		
	Local CBD (100 * kg/m^3)	"+"	7.2 (0.01)		
	Slope (degrees)	"+"	3.4 (0.07)		
Independent variable at the tree-level	**Dependent variable(s)**	**Direction of relationship**	**Type II Wald X^2 (p-value)**	**ΔAIC**	**Model form**
Tree status (live vs fire-killed)	Day of incident	"-" Day 2	4.6 (0.03)	-7.0	Binomial + random effect for plot
	Crown base height (ft)	"-"	3.5 (0.06)		
	Slope (degrees)	"+"	5.0 (0.02)		
	Local CBD (100 * kg/m^3)	"+"	5.8 (0.02)		
Tree status (live vs fire-killed)	Crown base height (ft)	"-"	4.6 (0.03)	-49.5	Binomial + random effect for plot
	Local BAER soil burn severity	"+"	29.1 (<0.001)		
	Crown base height (ft) x local BAER soil burn severity	"+"	3.9 (0.05)		

Independent variable at the tree-level	**Dependent variable(s)[1]**	**Direction of relationship**	**Type II Wald X^2 (p-value)**	**ΔAIC**	**Model form**

Scorch height	Day of incident	"-" Day 2	9.3 (0.002)	-26.5	Linear + random effect for plot
	Treatment	"-" Thin + burn	15.9 (<0.001)		
	Local CBD (100 * kg/m^3)	"+"	4.7 (0.03)		
Scorch height	Crown base height (ft)	"-"	N/S	-44.6	Linear + random effect for plot
	Local BAER soil burn severity	"+"	74.7 (<0.001)		
	Crown base height (ft) x local BAER soil burn severity	"+"	5.6 (0.02)		

[1]Possible independent variables included day of the Calwood Fire, slope, treatment history, average BAER soil burn severity, and pre-fire basal area, trees per acre, average diameter, average crown base height, local crown bulk density, and local canopy cover.

FIGURES

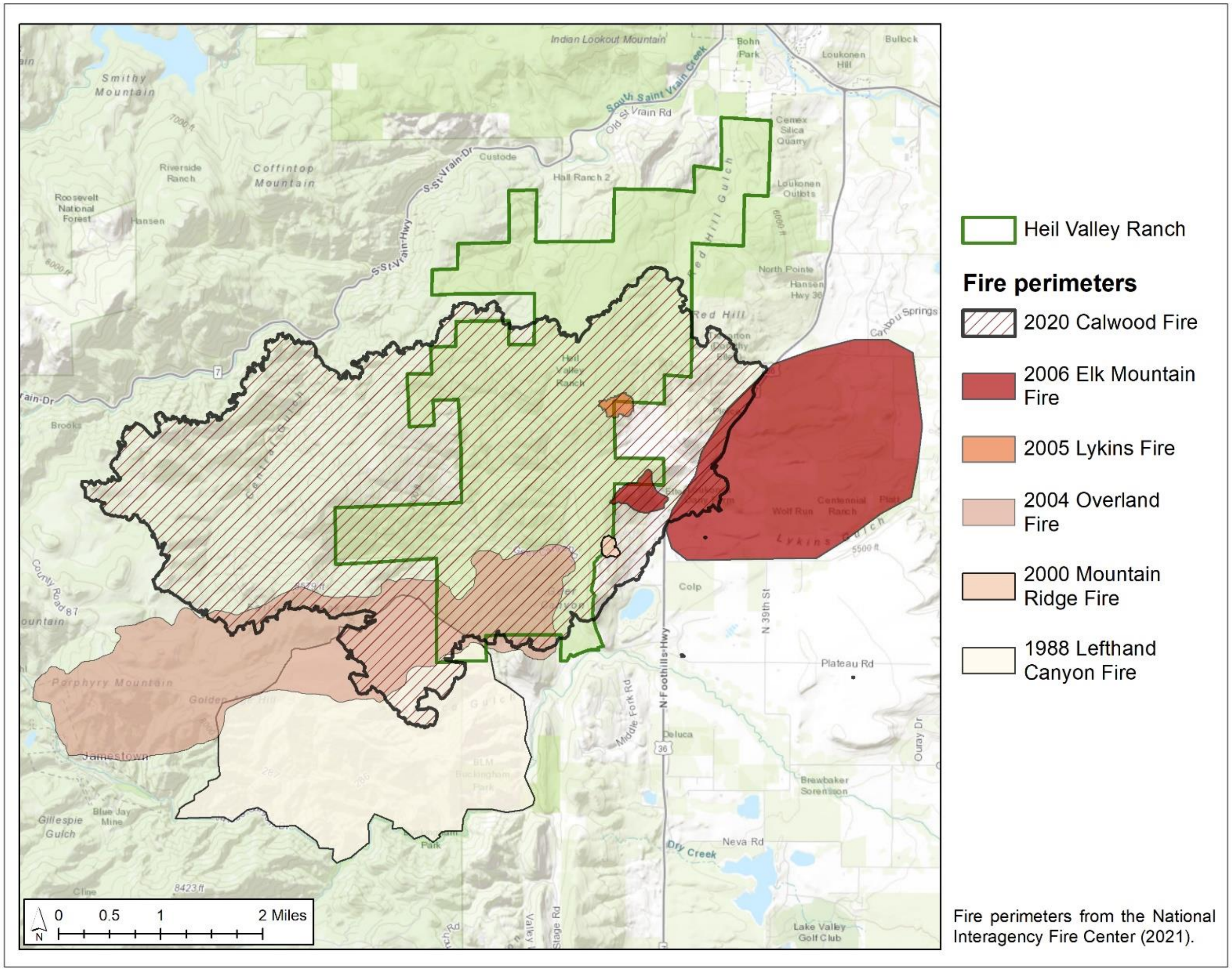

Figure A.1. Six fires burned portions of Heil Valley Ranch between 1988-2020, with the Calwood Fire being the largest and burning the greatest proportion of the property. Data based on fire perimeters from the National Interagency Fire Center (NIFC 2021).

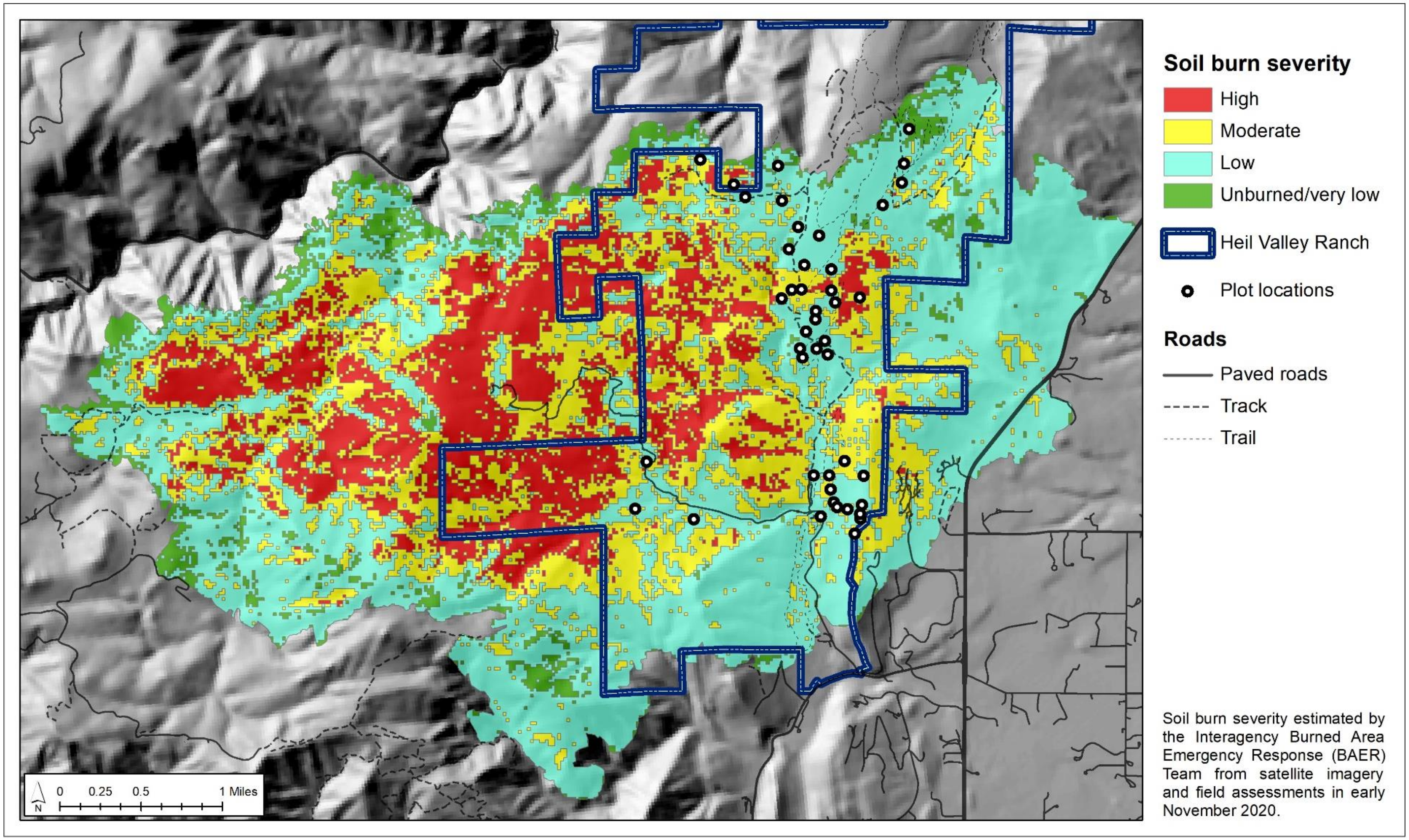

Figure A.2. Soil burn severity estimated by the Interagency Burned Area Emergency Response (BAER) Team in early November 2020 (Arapaho-Roosevelt National Forests 2020; BAER 2020). Soil burn severity is based on soil exposure, with high severity classified as areas with near total consumption of pre-fire ground cover and surface organic matter; moderate severity as areas with up to 80% consumption; low severity as areas with only light char on surface fuels; and unburned/very low severity as areas with completely intact canopy and surface litter.

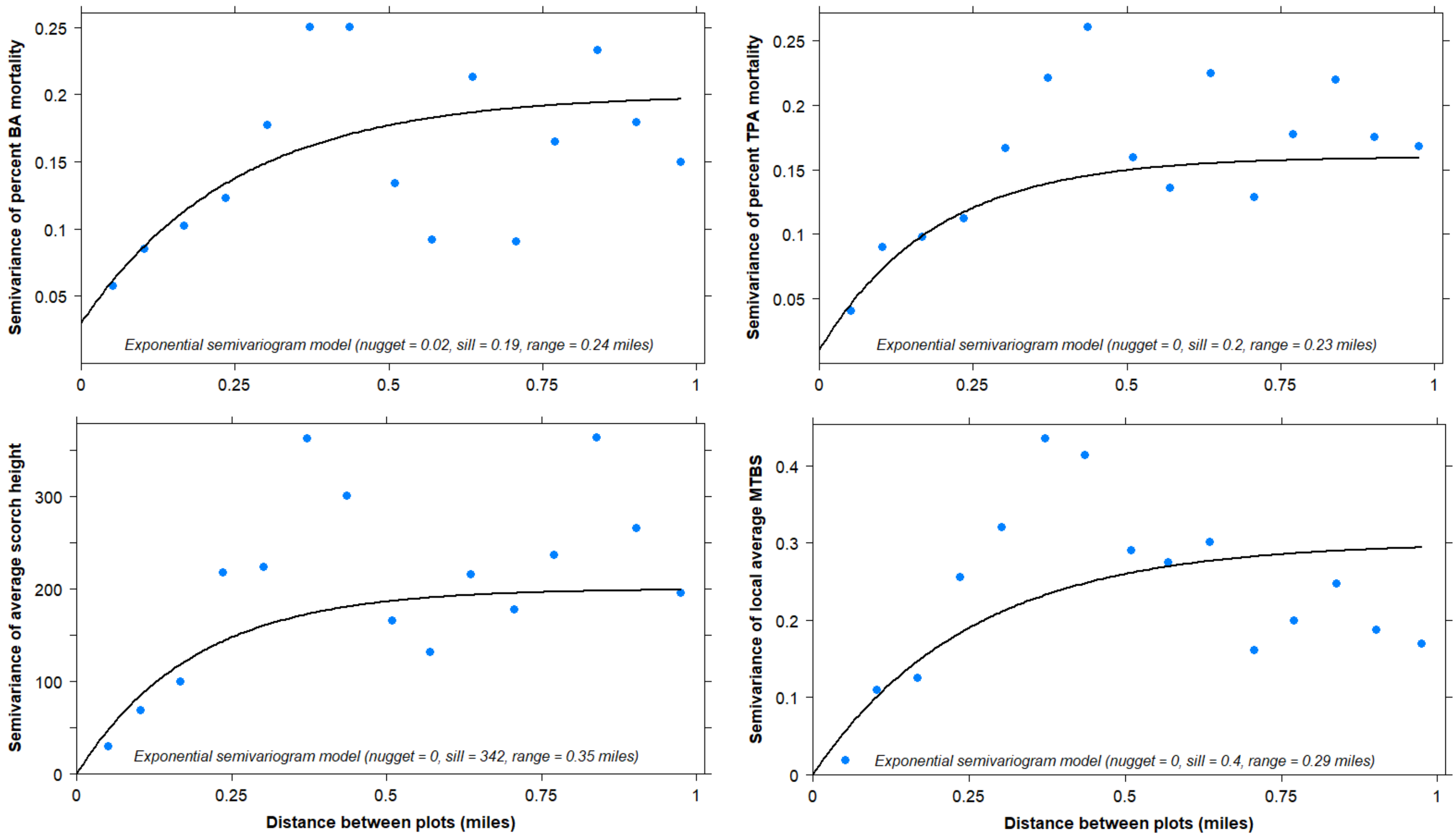

Figure A.3. Semi-variograms depicting spatial dependencies of soil and vegetation burn severity. The range indicates the distance at which burn severity measurements become spatially independent of each other.

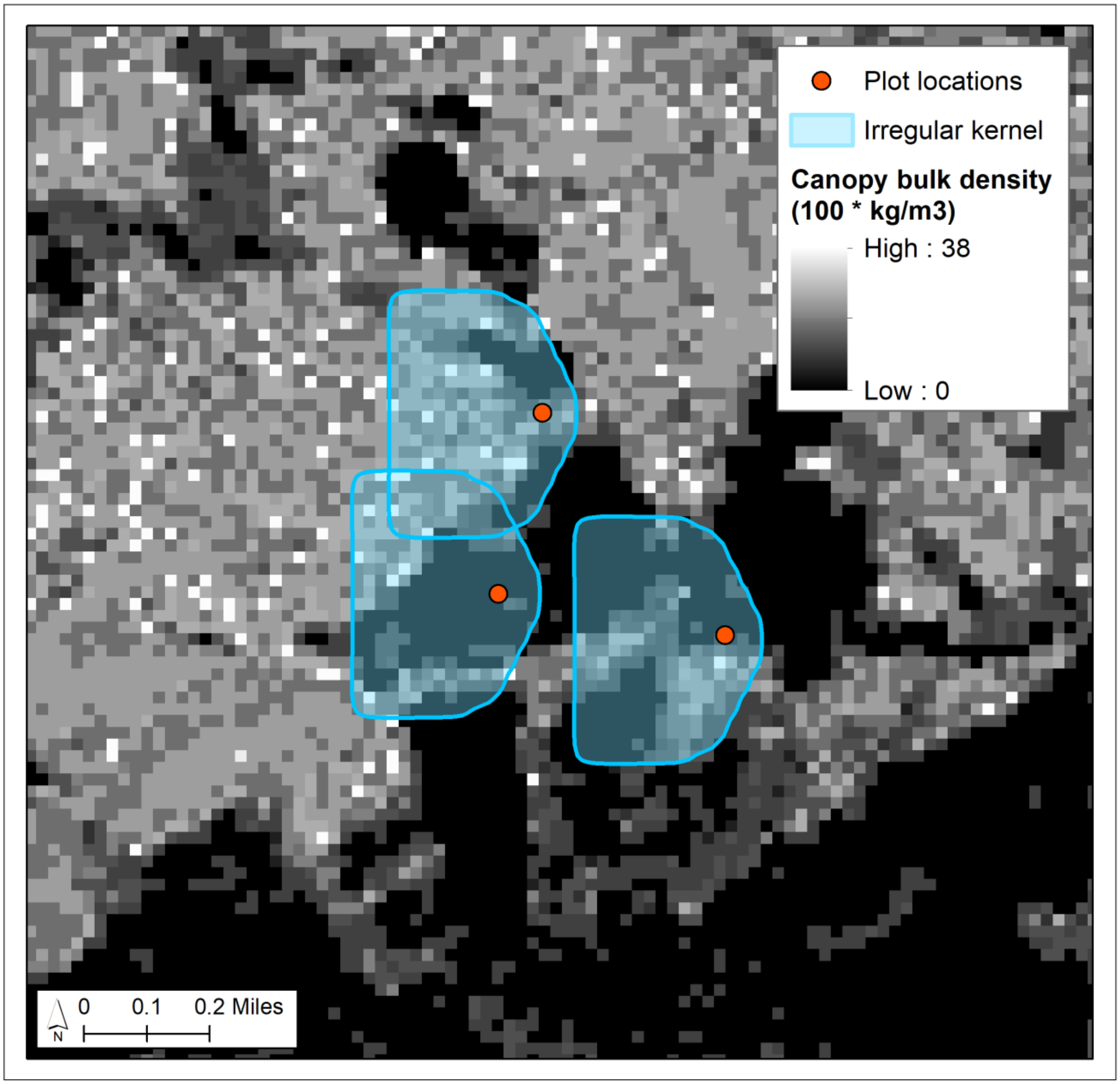

Figure A.4. I estimated average crown bulk density and canopy cover in a 65-acre area with a width of 0.3 miles based on the semi-variance range of soil and vegetation burn severity (Appendix Figure A.2). The shape of the area was irregular to account for the greater impact that forest conditions to the west of my plots would have on fire behavior than conditions east of the plots due to the strong westerly winds observed during the Calwood Fire. Crown bulk density and canopy cover estimates came from LANDFIRE Remap for 2019 (LANDFIRE 2019).

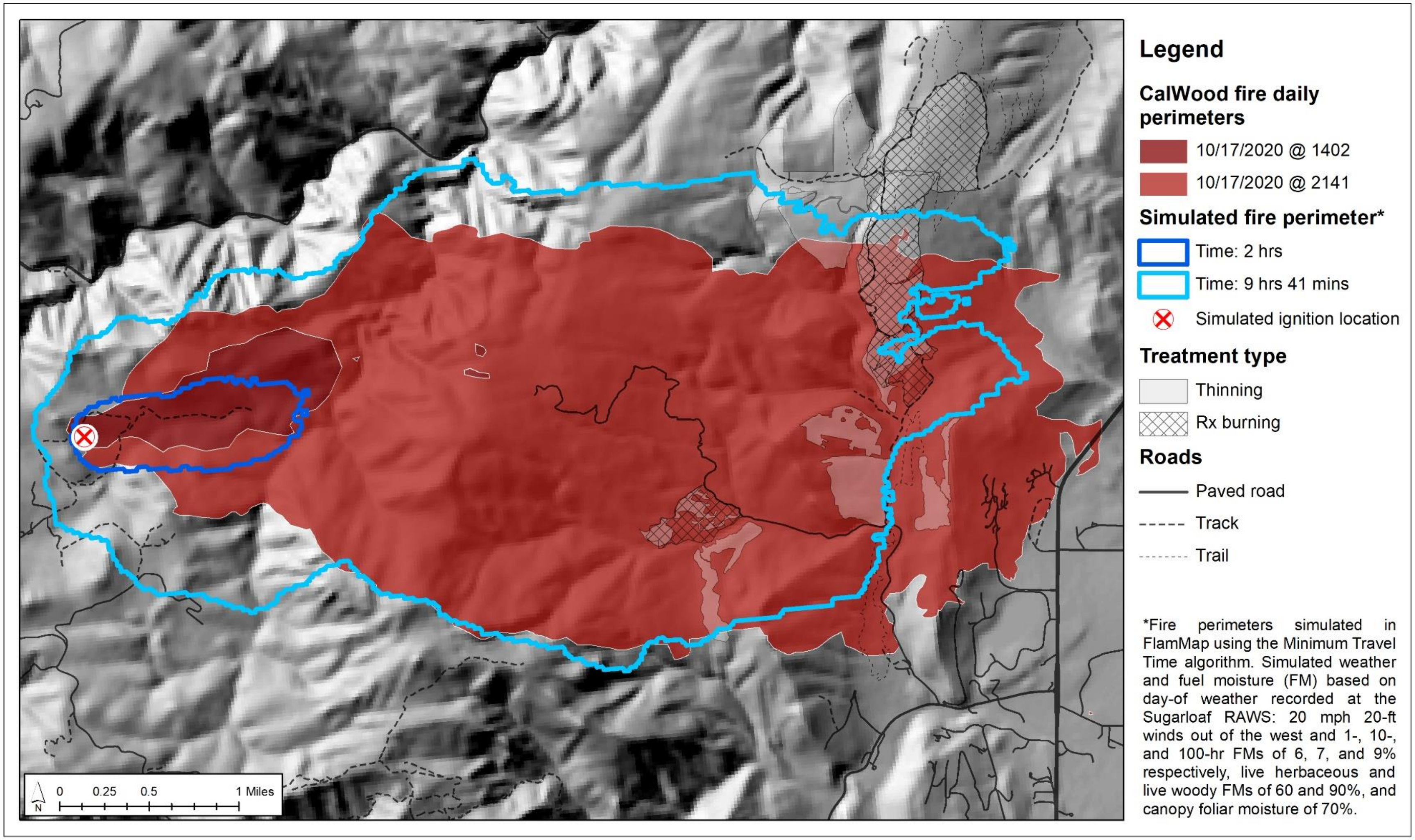

Figure A.5. Minimum travel time perimeters predicted by FlamMap closely approximated actual fire perimeters observed for the Calwood Fire at 2 hours and 9 hours and 41 minutes into the incident (NIFC 20201. The simulated ignition location was approximated based on the observed fire perimeter. Weather and fuel moisture conditions were based on observations at the Sugarloaf RAWS on October 17, 2020. I simulated 20-foot wind speeds of 20 mph; average gusts between 1200 and 1800 on October 17, 2020, were 28 mph and sustained speeds were 8 mph.

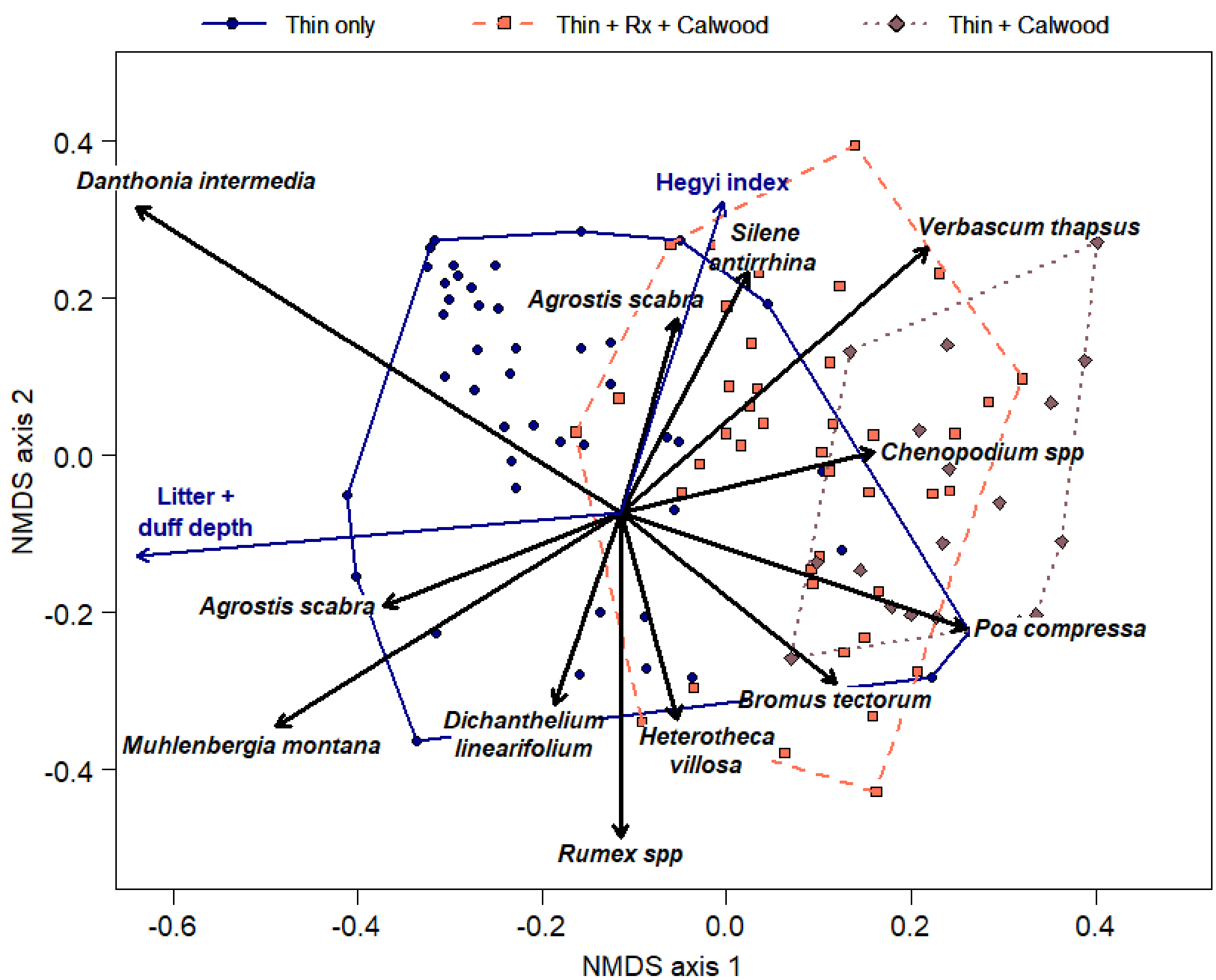

Figure A.6. The composition of understory plant communities was significantly different among all disturbance histories (F-value=12.5, p=0.03). The first NMDS axis was rotated to align with disturbance history and the second axis to align with the Hegyi index. The first axis was strongly correlated with litter/duff depth (r^2=0.19, p<0.001) and the second axis with the Hegyi index (r^2=0.12, p=0.002). Twelve species were strongly correlated with the first and second NMDS axes (r^2>0.10, p<0.05). Four-dimensional ordination resulted in a stress value of 0.14.

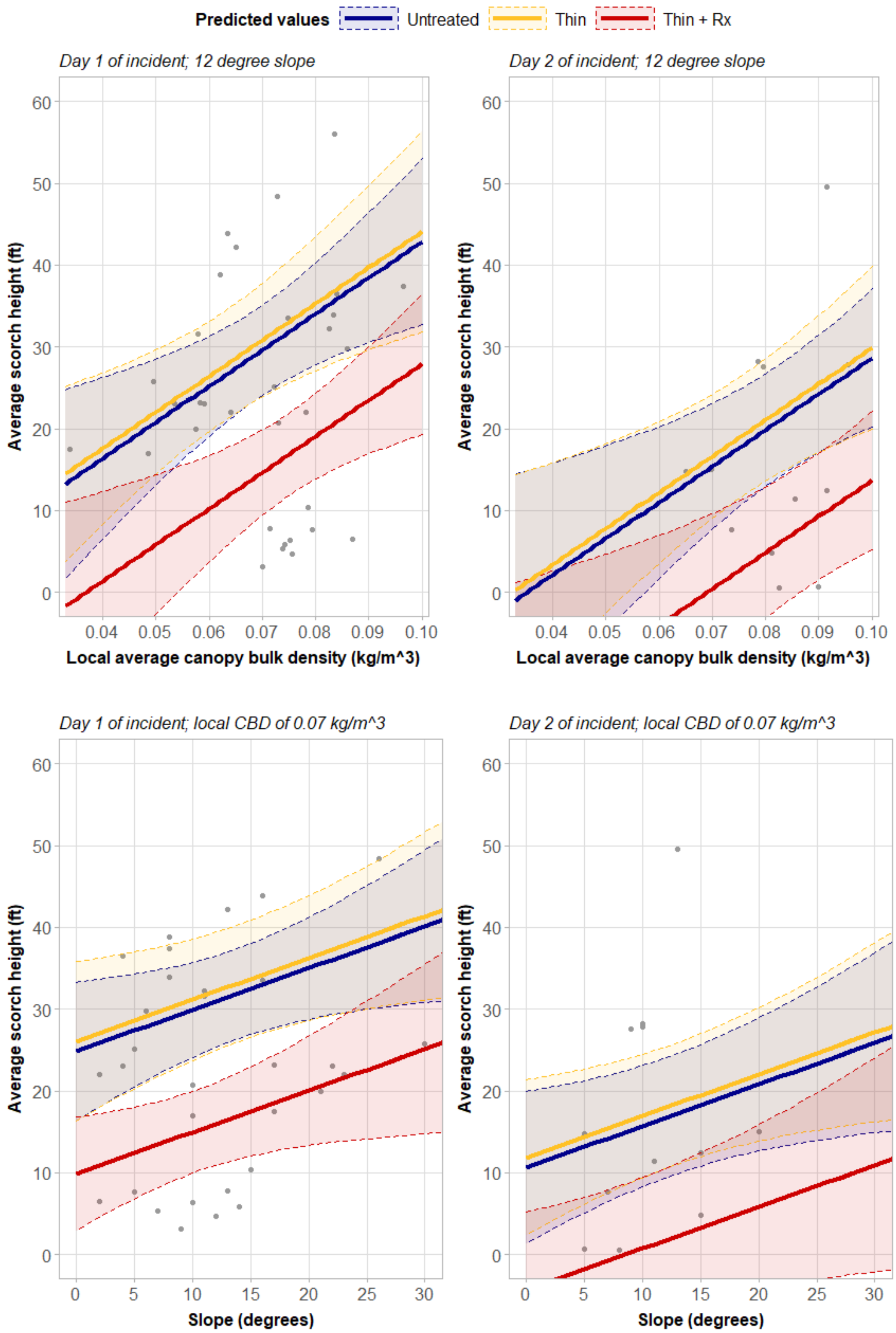

Figure A.7. Average scorch height was lower in areas that had been thinned and prescribed burned prior to the Calwood Fire. Scorch height increased with crown bulk density of the surrounding 65-acre area and with slope. Average scorch height was lower on the second day of the Calwood Fire. Shaded areas indicate 90% confidence intervals for fixed effects, and grey dots indicate observed values. See Appendix Table A.6 for Type II Wald X^2 values.

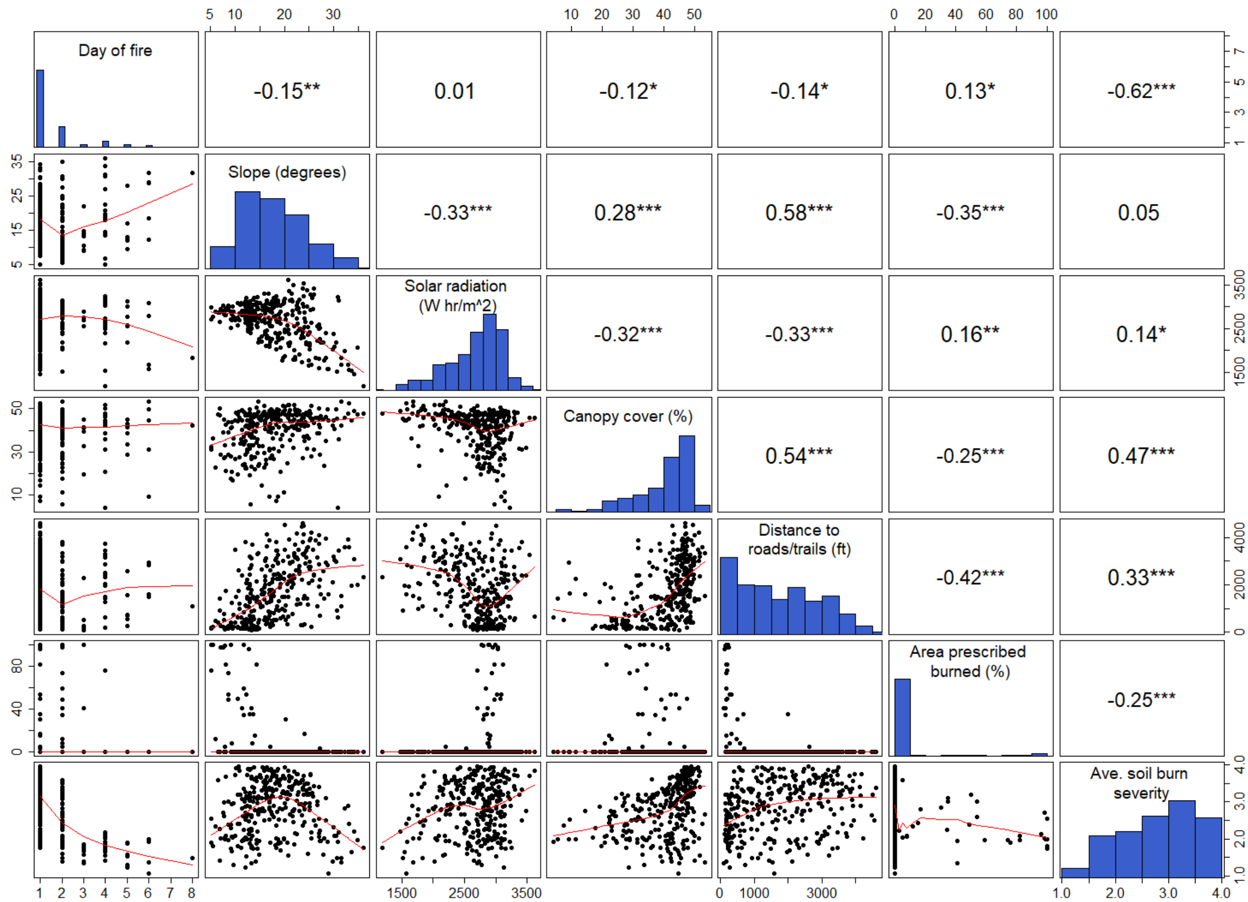

Figure A.8. Spearman correlation coefficients among average BAER soil burn severity and independent variables significant in the spatial error model for the entire area burned by the Calwood Fire at the scale of 300 x 300 m.