THESIS

EFFECTS OF DISTURBANCE ON TREE LEVEL RESISTANCE IN PONDEROSA PINE TREES ALONG THE COLORADO FRONT RANGE

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ABSTRACT

EFFECTS OF DISTURBANCE ON TREE LEVEL RESISTANCE IN PONDEROSA PINE TREES ALONG THE COLORADO FRONT RANGE

Forest restoration treatments are being implemented across ponderosa pine systems along the Colorado Front Range with goals of reducing risk of catastrophic wildfire, returning forest structure to historical conditions, and increasing ecosystem resilience and resistance in the face of climate change. While there are studies monitoring effects of thinning and wildfires on forest structure across the Front Range, few studies assess the effects of disturbances from wildfires and thinning treatments on tree-level resistance. Here we examined forest stand structure, growth, and defense characteristics in response to treatments and wildfires through the collection of plot level data, tree-level characteristics, and tree cores. We sampled 160 plots in areas that experienced thinning treatments between 2007-2012, were burned by low-severity wildfires (2012 Hewlett Gulch and High Park Fire, 2010 Fourmile Canyon Fire and Dome Fire, 2012 Flagstaff Fire, 2012 Waldo Canyon Fire), or that were untreated and unburned (hereafter "control"). Our findings reveal that tree growth and resin duct size significantly increased following thinning treatments. Relative resin duct area and duct density were significantly higher in trees following wildfire compared to trees that experienced thinning or to those trees within control plots. Control plots exhibited the highest mean basal area and stand density index, coupled with the lowest quadratic mean diameter, indicating high inter-tree competition, which both thinning and low-severity wildfire helped alleviate. Overall, our results highlight the beneficial impacts of both thinning and low-severity wildfire on mature ponderosa pine trees by enhancing their resistance to future disturbance, such as bark beetle outbreaks and drought.

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Colorado State University Colorado State University acknowledges, with respect, that the land we are on today is the traditional and ancestral homelands of the Arapaho, Cheyenne, and Ute Nations and peoples. This was also a site of trade, gathering, and healing for numerous other Native tribes. We recognize the Indigenous peoples as original stewards of this land and all the relatives within it. As these words of acknowledgment are spoken and heard, the ties Nations have to their traditional homelands are renewed and reaffirmed. CSU is founded as a land-grant institution, and we accept that our mission must encompass access to education and inclusion. And, significantly, that our founding came at a dire cost to Native Nations and peoples whose land this University was built upon. This acknowledgment is the education and inclusion we must practice in recognizing our institutional history, responsibility, and commitment.

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Introduction

Forests across western North America are increasingly susceptible to more frequent and severe disturbances such as wildfire and bark beetle outbreaks due to climate change (Fettig et al., 2014; Westerling et al., 2006; Williams et al., 2013). The escalating concern regarding tree mortality throughout western North America stems from a combination of factors such as drought stress, insect outbreaks, an abundance of surface and ladder fuels, and direct and indirect effects of climate change, all of which are altering disturbance regimes (Allen et al., 2010; Hessburg et al., 2021). These disturbances, ranging from wildfires and insect outbreaks to severe droughts, serve as catalysts for significant change in structure and composition of forest ecosystems. For example, bark beetles target specific host species changing species dominance, while wildfires may cause a shift from forest to non-forested landscapes (Bentz et al., 2010; Coop et al., 2020). Faced with these novel climatic conditions, forest ecosystems, such as ponderosa pine (*Pinus ponderosa*) forests, which historically experienced frequent, low to mixed severity fire, are now experiencing more severe wildfires and bark beetle outbreaks (Addington et al., 2018; Negrón & Popp, 2004; Raffa et al., 2008).

Climate change is impacting a forest's ability to resist, or remain relatively unchanged by these disturbances (Folke et al., 2004; Johnstone et al., 2016). In much of the western US, forest managers face the challenge of increasing ecosystem resistance and resilience amidst climate change and shifting disturbance regimes. Historically, fire within ponderosa pine forests burned at low to moderate severity every 7 to 50 years (Brown et al., 2020), typically occurring in late summer to fall during drier than average years, and often preceded by 2 to 3 years of wetter than average conditions (Mckinney, 2019). Warmer and drier conditions can induce tree stress, potentially leading to mortality in the absence of fire, or increase susceptibility to fire induced mortality. Additionally, wetter than average years can contribute to greater understory fuel accumulation, further exacerbating fire risk (Mckinney, 2019). Short term projections of future fire frequency and severity in montane forest ecosystems indicate high risk of high-severity fire, whereas long term projections remain variable, due to precipitation fluctuations (Rocca et al., 2014). Nevertheless, previous land use practices such as logging, grazing, and fire suppression have altered ponderosa pine forest structure and composition, resulting in increased stand density, fuel loads, and heightened vulnerability to catastrophic wildfires (Cannon et al., 2018). These lasting effects, coupled with climate change, have transformed forest structure, leading to high stand density, high competition among trees, and homogeneity of tree size and age across these dry forests (Battaglia et al., 2018), emphasizing the urgent need to reduce risk and severity of future disturbances like wildfire (Addington et al., 2018; Cannon et al., 2018).

Currently, forest restoration treatments such as fuels reduction or mechanical thinning, represent management techniques that attempt to mitigate risk of catastrophic wildfire by reducing tree density and fuel loads in accessible, high priority areas (Stephens et al., 2021). Thinning treatments often aim to increase stand or landscape scale resistance to disturbance, as well as decrease competition among trees, enhance wildlife habitat, and promote tree vigor (North et al., 2022). Fuels reduction treatments aim to reduce surface fuels, increase the height to live crown ratio, decrease crown density, and retain large diameter trees of fire-resistant species (Agee & Skinner, 2005). Despite numerous studies monitoring the effects of these thinning treatments on forest structure (e.g. Cannon et al., 2018; Graham et al., 2004; Stephens et al., 2009), there are few studies evaluating the success of increasing tree-level resistance to future disturbance following these treatments and wildfires.

Ponderosa pine is an ecologically important species found throughout western North America. Ponderosa pine favor sunny conditions, warmer temperatures, and can survive low to mixed severity fire due to physiological adaptations such as thick bark (Brown & Smith, 2000). A less explored characteristic of ponderosa pine is that of resin. Inducibility of resin, or capability of forming resin in pine trees has been found to vary due to complex interactions within genetic factors and local adaptations to climatic conditions (Vázquez-González et al., 2019). Allocation of resources within essential ponderosa pine life functions of reproduction, growth, and defense have been found to have stronger tradeoffs depending on environmental stressors such as site productivity and climatic gradients (Gonzalez et al., 2023).

The growth differentiation balance hypothesis (GDBH) can help explain this trade off in allocation of carbon, as it predicts plants will allocate more resources to defense rather than growth when resources are scarce (Herms & Mattson, 1992). Previous research has provided evidence supporting the predictions of the GDBH on conifer species throughout the northern hemisphere. Lorio (1986) was one of the first to investigate this hypothesis by examining interactions between southern pine beetle and its host pines such as loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*), and slash pine (*Pinus elliottii*), suggesting the balance between growth and defense processes influence their susceptibility to insect attack. Specifically, he hypothesized that trees that grow faster may produce lower levels of resin, making them more attractive for southern pine beetle infestation. Other studies have shown that drought-stressed Scots pine (*Pinus sylvestris*) trees allocated more carbon to resin production compared to irrigated trees (Rissanen et al., 2021). Similarly, with maritime pine (*Pinus pinaster*), Zas et al. (2020) found a negative correlation between resin flow and growth. Most recently, Ferrenberg et al. (2023) examined growth differentiation responses in live and bark beetle killed ponderosa pine trees sampled from the Gila national forest in New Mexico, and found that trees conformed to predictions of the GDBH and variation in the rate of this trade-off accurately distinguished trees killed by bark beetles from those that survived beetle outbreaks. Tree-level and stand-level characteristics may offer insights into how resources are allocated among ponderosa pine trees. Nonetheless, growth and defense metrics can serve as indicators of tree vigor and function as factors for assessing the susceptibility to mortality resulting from drought and bark beetle infestation (Cailleret et al., 2017; Hood & Sala, 2015).

Resin is a significant defense mechanism against bark beetles in ponderosa pine trees as resin ducts, or resin canals, facilitate the movement of resin throughout the tree via the secondary xylem delivering resin to seal fire wounds and pitch beetles out to prevent entry to the cambium layer (Bär et al., 2019; Hood et al., 2020). Resin is comprised of complex chemical compounds acting as both physical and chemical defenses against bark beetles (Hood et al., 2015; Raffa, 2014). While few studies have examined the effects of thinning treatments on defense metrics, available evidence suggests that treatments that reduce stand density can bolster resistance to bark beetles and drought due to increased growth and defenses (Fettig et al., 2014; Hood et al., 2016; Tepley et al., 2020). Previous studies have also demonstrated that trees with larger or more resin ducts have stronger defense mechanisms, diminishing the likelihood of insect-caused mortality (Gaylord et al., 2013; Kane & Kolb, 2010; Zhao & Erbilgin, 2019). A study from ponderosa pine systems in Montana specifically, indicated an increase in defense measures among trees within a wildfire burn perimeter eight years post-fire (Hood et al., 2015). Findings from another recent study examining tree vigor metrics of sugar pine (*Pinus lambertiana*) and white fir (*Abies lowiana*) following thinning and prescribed fire treatments in California suggest that thinning can promote or sustain growth through drought periods, and prescribed fire can stimulate resin duct production in sugar pine (Bernal et al., 2023).

Studies that have examined treatments including thinning, prescribed fire, and combined thinning then prescribed fire, have found that BAI does not increase in trees within burned areas, but increases in trees within thinned and combined treatments (Bernal et al., 2023; Hood et al., 2016). Hood et al. (2015) observed a marked surge in resin duct area and duct production immediately following historic wildfires compared to unburned areas. Numerous investigations have analyzed growth and defense metrics before and after beetle outbreaks, comparing metrics in trees that died from bark beetle attacks to those that resisted them (Kane & Kolb, 2010; Ferrenberg et al., 2014; Zhao & Erbilgin, 2019). These studies consistently reveal that trees with larger resin duct size and production prior to bark beetle outbreaks have a higher chance of survival. Additionally, studies have explored the impact of drought on resin ducts (Gaylord et al., 2013) and competition effects on growth and resin ducts (Slack et al., 2017), consistently indicating smaller resin ducts in stressed trees from competition or drought. Although the majority of resin duct studies have been conducted in ponderosa pine forests in Montana, Utah, and Arizona (Hood et al., 2015; Hood et al., 2016; Kane & Kolb, 2010), little is known on if these patterns will persist in ponderosa pine of the Colorado Front Range, where growing sites are of particularly low quality by comparison.

We utilized a range of thinning treatments implemented on multiple federal, county, and city lands across the Front Range, as well as wildfires that burned on these lands to examine tree responses in ponderosa pine dominated forests. Due to lack of historic prescribed fire treatments along the Front Range, we are considering low severity burned areas within wildfires as an analog to prescribed fire. We collected 291 tree cores to measure tree-level resistance using resin duct metrics such as resin duct size, production, total duct area, total duct density, and relative duct area along with ring width data and Basal Area Increment (BAI) with three primary objectives:

1. To analyze changes in forest structural characteristics in mechanically thinned stands, stands burned in low-severity wildfire, and control stands.
2. To examine the impact of stand-level characteristics on growth and defense mechanisms.
3. To examine the influence of tree-level characteristics on growth and defense mechanisms.

These findings offer valuable insights for both researchers and managers regarding the efficacy of thinning treatments and low-severity fires in enhancing tree-level resistance in ponderosa pine forests along the Colorado Front Range. As potential management strategies such as mechanical thinning or prescribed fire will become more prevalent in the coming years, understanding their impacts on surviving trees is paramount. Moreover, gaining insight into how ponderosa pine trees allocate carbon within dry, rocky, and resource-constrained environment of the Colorado Front Range can help elucidate the tradeoffs proposed by the GDBH. Ultimately, by examining the effects of disturbances from thinning and wildfire on tree level resistance, we can better understand growth and defense tradeoffs among trees and can give insight into future management and research directions.

Methods

Study Area

We collected stand structure and composition data from one hundred and sixty plots within ponderosa pine stands in the Arapaho-Roosevelt and Pike national forests, Boulder City Open Space and Mountain Parks (OSMP), and Boulder and Larimer County lands (Figure 1). Ponderosa pine stands suitable for sampling were identified as greater than 50% of live ponderosa pine trees. Plots were categorized into one of three treatment types: 1) unburned/untreated, 2) thinning treatment (thin), and 3) low-moderate severity wildfire (fire). Thinning treatments and wildfire boundaries and dates were identified from City of Boulder OSMP, Boulder County, and USFS Geodata Clearinghouse GIS data layers and filtered to include only treatments and wildfires >10 years old. Control plots were in unburned and untreated stands. Thinning treatments were in stands unburned by wildfire but treated between 2007-2012. Low-severity wildfire plots were untreated prior to wildfire and sampled on a gradient of fire caused tree mortality, with plots ranging from 17% to 77% mortality.

Low-severity burned areas were located in the 2012 High Park Fire (35,322 ha), 2012 Hewlett Gulch Fire (3,110 ha), 2010 Fourmile Canyon Fire (2,501 ha), 2010 Dome Fire (58 ha), 2012 Flagstaff Fire (121 ha) and 2012 Waldo Canyon Fire (7,384 ha). These fires accumulated combined losses of 768 houses and 3 human lives, and the cost to fight them totaled more than 46.7 million dollars with many more costs associated with post-fire remediation (Bounds & Snider, 2010; Graham et al., 2012; Miller et al., 2017). Low-severity wildfire plots were identified where there was evidence of at least one wildfire induced tree death, and greater than 50% of live trees remaining were ponderosa pine. We avoided areas with evidence of additional treatments either post-fire or those mechanically treated areas with multiple re-entries in the last

20 years. Where possible, the same plots established by Stevens-Rumann and Fornwalt (2018) were used. We also used a complimentary dataset of sites and tree cores collected by Negrón (2021, 2022) on the Arapaho-Roosevelt and Pike national forests. The plots located in the northern and southern regions of the Arapaho-Roosevelt national forest were designated as AR north and AR south, respectively, while those within the Pike national forest were labeled as Pike (Table 1). Plots were randomly distributed across thinning treatments, wildfire boundaries, or control areas and established at least 100m from one another. Elevation ranged from 1886-2906m (Table 1).

Field Data Collection

Forest structure characteristics were measured from 160, 0.04-ha circular plots. Elevation, aspect, slope, and GPS coordinates were recorded at plot center. For every tree in the plot, we recorded species type, diameter at breast height (DBH), and status (live, dead by bark beetle, dead by fire). Tree cores were taken at approximately 1.37m off the ground, or the location of DBH, with a 5mm wide increment borer from the two closest live dominant or co-dominant trees to plot center to reduce selection bias. We extracted two cores from each tree cored on sides parallel to the slope to get a subsample of the tree, allowing for an average of growth and defense metrics. For each tree cored, we measured tree-level characteristics such as height and lowest live branch using a laser rangefinder, as well as canopy cover at both cardinal and subcardinal directions around the tree using a densitometer. This resulted in 291 suitable trees cored to be analyzed for growth and defense metrics: 100 trees from thin plots, 97 trees from control plots, and 94 trees from fire plots (Table 1). Since I used a complimentary dataset from Negrón (2022, 2021), this didn't result in the two trees cored per plot as some plots only contained suitable ponderosa pine core suitable analysis. Additionally, certain tree cores had to be excluded from the analysis due to damage that hindered accurate dating.

Tree growth and defense measures

Tree cores were processed at CSU using standard dendrochronological techniques to examine ring width relationships (Stokes & Smiley, 1996). Cores were mounted on wooden mounts, sanded with progressively finer grits using belt and hand sanders, and dated under a microscope. After processing, we scanned each core to create a high-resolution image (1200 dpi). From these scanned images, annual growth rate measurements (±0.001 mm y-1) were collected and analyzed through the ring width measurement software using CooRecorder 9.8 and Cdendro, resulting in ring width files (RWL) for each core (Cybis Electronic, CDendro, and CooRecorder V.9.8). Cores were crossdated and quantitatively validated using ring width series in xDateR, a shiny app for crossdating tree ring data in the dPLR package in R (Bunn, 2008, 2010). Outputs from xDateR included series intercorrelation (site level similarities) and mean sensitivity (annual variability in ring width) (Table 1). Ring width measurements were averaged by tree since there were two cores collected for each tree. We calculated annual growth using BAI (mm^2) through the bai.out function in the dPLR package in R for each tree from 2000-2022 (Bunn, 2008, 2010). BAI is widely used and preferred over raw ring width measurements as it can provide an estimate of wood production by accounting for age and size differences across trees (Biondi & Qeadan, 2008; Visser et al., 2023).

Defense measurements of resin ducts were collected for each core through the ImageJ software following the methods and R code outlined in Hood et al. (2020). This methodology allows for measurement of individual resin duct areas within tree rings. The first step of the R code adds calendar years to the year which each resin duct was formed to produce initial CSV output files. The second step of the R code compiles these individual CSV files into a new CSV file containing years and duct area measurements for each core. The third step of the R code computes unstandardized resin duct metrics using the CSV file created in step two. The fourth step of the R code produces standardized resin duct metrics by combining the CSV files and RWL files for each core. This CSV output file contains five resin duct metrics of resin duct size (mm²), resin duct production (number/year), total resin duct area (mm²/year), resin duct density (duct production/ring area), and relative resin duct area (%), as well as ring width (mm) and ring area (mm²). Since we had two cores per tree, the last step of the R code allows for resin duct metrics from multiple cores to be combined by tree, as core area and duct area is summed by tree, and mean resin duct size is averaged.

Data Analysis

R (version 4.2.1) was used for all analyses (R Core Team 2022). To understand forest structural changes from thinning treatments and wildfires, we calculated plot level (n=160) tree characteristics of Basal Area (BA), Quadratic Mean Diameter (QMD), and Stand Density Index (SDI) using the equations from Curtis and Marshall (2000), and Long and Shaw (2005). To understand differences in stand structural characteristics such as BA (m^2/ha), QMD (cm), and SDI (tpha), we used a one-way analysis of variance (ANOVA), with treatment type as the predictor variable, after testing for assumptions of normality and equal variances. When overall differences were detected (α=0.05), we used a Tukey's HSD test to identify pairwise differences between them.

To assess the impact of stand-level characteristics on growth and defense mechanisms, we used a generalized linear mixed model (GLMM) examining the impact of year, treatment type (control, fire or thin), site productivity (via heat load index), stand structure (via SDI), and interaction effects of treatment type and pre or post disturbance on BAI and resin duct metrics from 2000-2022 for each tree, totaling 6,480 annual measurements (n=6,480). Year was included to capture temporal autocorrelation among the cores, and site and tree were included as nested random effects to account for spatial autocorrelation. Heat load index (HLI) was determined using the equations from Mccune & Keon (2002), as this index ranges in values from 0 to 1, with wetter and cooler conditions approaching 0, and dryer and hotter conditions approaching 1.

To assess the influence of tree-level characteristics on growth and defense mechanisms, we used a GLMM to examine the effect of canopy cover (%), height (m), and live crown ratio (%) on annual BAI and resin duct metrics from 2019-2022 across 184 trees (n=736). Since measurements of tree-level characteristics were only collected in 2023, we included tree ID was included as a random effect to average BAI and resin duct metrics over the preceding four years.

Results

Forest structural characteristics

Stand structure differed amongst treatment groups across 160 plots (n=160). BA (F=52.88, P<0.0001) and SDI (F=83.43, P<0.0001) were significantly lower in thin and fire areas compared to control areas. The opposite pattern was observed for QMD (F= 39.66, P<0.0001) (Table 2, Figure 2). Wildfire plots had the lowest mean BA and SDI, and control plots had the highest mean SDI, BA and lowest QMD. Thinned plots had the highest mean QMD.

Stand-level characteristics on growth and defense

Our GLMM examined the impacts of treatment type, pre- and post-treatment, year, site productivity via HLI, stand structure via SDI, and interactions between treatment type and pre- and post-treatment, on growth and defense metrics (Table 3, Figure 3, 4). Out of 291 trees, we collected annual BAI and resin duct measurements from 2000 to the year of collection (n=6,480). For BAI, we found a significant interaction between thinning and post-treatment. Trees in thinned areas showed significant increases (P<0.0001) in BAI while trees in areas that experienced wildfire did not. SDI also appeared as having a statistically significant (P<0.0001) negative impact on BAI. For duct size, we also found a significant interaction between thinning and post-treatment, as trees in thinned areas showed significant increases (P<0.0001) in duct size while trees in burned areas did not. Increased SDI showed decreases in BAI, meaning as stand density increases, tree growth decreases. Trees in thinned areas showed increases in BAI and duct size following treatment. For duct density, trees experiencing wildfire appeared statistically significant (P<0.0001), meaning duct density increases following wildfires holding all else constant. Relative duct area showed predictor variables of HLI (P=0.0301), SDI (P=0.0064), and the effect of wildfire appearing as statistically significant (P<0.0001). Relative duct area decreases in areas with high HLI, high SDI, and increases in areas following wildfire holding all else constant. Duct production increased following the effects of both fire (P=0.0365) and thinning (P<0.0001), and decreased as SDI (P=0.0007) increases. Total duct area also increased following effects of both fire (P=0.0412) and thinning (P<0.0001), and decreased as SDI (P<0.0001) increases. Year was found significant in 5 out of 6 of our models (P<0.0143) as we would expect to see growth and resin duct correlations by year due to climate variations.

Tree-level characteristics on growth and defense

Our GLMM examined the effects of tree-level characteristics such as canopy cover, height, and live crown ratio, on growth and defense metrics (Table 4, Figure 5). Since we averaged the previous four years of BAI and resin duct measurements from 184 trees, this totaled 736 measurements (n=736). We found significant increases in BAI (P=0.0265), duct size (P=0.0246), and total duct area (P=0.0277) in trees with larger live crown ratios. Height showed significant positive impacts on BAI (P=0.0073), and a marginally significant impact on duct density (P=0.0644). Trees with taller heights and larger live crown ratios exhibited increased BAI. Additionally, as the live crown ratio increased, both BAI, duct size, and total duct area also increased. Canopy cover did not appear statistically significant in any of our six models.

Discussion

This study demonstrated that trees' growth and defense mechanisms, significantly increase following thinning and low-severity wildfire in ponderosa pine stands. Consistent with prior findings, we demonstrated that thinning and low-severity fire can effectively enhance tree resistance to disturbances by increasing growth through reductions in stand density (Bottero et al., 2017; Fettig et al., 2014; Hood et al., 2016). In our sites across the Front Range, increases in growth occurred 6-13 years after disturbance in thinned areas and low-severity burned areas within wildfires, similar to prescribed fire studies elsewhere (Figure 3; Bernal et al., 2023; Hood et al., 2016). Moreover, our findings from our burned plots are consistent with previous research examining tree growth response immediately following prescribed fire, suggesting that trees show initial reductions in growth in the short-term (1-3 years) following fire (Collins et al., 2014; Knapp et al., 2021; Sala et al., 2005) and increase in the mid-term (3-10 years) following a period of reduced growth (Anning & McCarthy, 2013; Valor et al., 2013). These variations in tree growth following fire are highly dependent on time since fire and site characteristics (Wenderott et al., 2022), which we can observe in this longer time since fire window (11-13 years) of our study.

Our analyses of tree responses within wildfires that burned throughout the entire fire season from May (Hewlett Gulch Fire) June, July (High Park Fire, Flagstaff Fire and Waldo Canyon Fire), September (Fourmile Canyon Fire) to October (Dome Fire), have revealed significant increases on four out of five resin duct metrics. Specifically, wildfire has resulted in increased relative duct area, total duct area, duct density, and duct production when compared to trees in control sites. This aligns with findings from previous prescribed fire studies where prescribed burns were conducted in the shoulder season (November to April), suggesting that fires occurring within the fire and growing season do not hinder growth more substantially and still enhance defense mechanisms. Resin duct metrics have shown corresponding relationships to stand-level predictors: BAI and duct size increased after the effects of thinning, while relative duct area and duct density increased after the effects of wildfire. Moreover, duct production and total duct area increased after the effects of both thinning and wildfire. Compared to control sites, trees following these disturbance effects demonstrate enhancements across growth and defense metrics.

Interestingly, thinning significantly increased resin duct size on our sites, whereas the effect of fire on resin duct size was not statistically significant, similar to burn only treatments in other studies (Hood et al., 2016). Treatments, especially thinning and thinning and burning, are associated with heightened resistance and survivability against bark beetle attacks or drought (Bernal et al., 2023; Gaylord et al., 2013; Hood et al., 2015; Zhao & Erbilgin, 2019). Given that resin duct size is important for bark beetle defense, with larger ducts indicating higher resistance, the significant increase observed following thinning suggests its importance as a proactive tool for mitigating future bark beetle mortality. Though fire did not increase resin duct size, the reintroduction of fire on these landscapes is equally important for stand and landscape scale processes (Addington et al., 2020) and does not increase the likelihood of bark beetle invasion (Hood et al., 2015).

Our results reinforce findings of others that show reducing BA and SDI through thinning typically leads to increases in BAI (Kolb et al., 2007) and resin duct area (Hood et al., 2016). Thinning also led to increases in duct production, total duct area and duct size, showing the importance of reducing stand density for both growth and defense. By reducing BA and SDI, thinning and wildfire mitigate tree to tree competition, compared to control areas. Reduced competition allows for increased abundance and access to resources such as water and light (Oliver & Larson, 1996), thus this corresponded to increases in growth and defense responses by trees (Hood et al., 2016; Zhang et al., 2019).

Furthermore, our analyses revealed that tree-level metrics such as live crown ratio and tree height significantly influence BAI, duct size and total duct area. This observation is intuitive, as taller trees with larger live crowns exhibit increased growth and duct production due to their competitive advantage for light resources over smaller trees. While we expected an increase in canopy cover to show decreased growth and resin duct establishment, canopy cover was not statistically significant in any of our models. Canopy cover did show a slight negative relationship in BAI, duct size and relative duct area which we would expect, however this was not significant. Perhaps the trees we sampled across our plots had taller heights and higher live crown ratios due to the selection of dominant and codominant trees closest to plot center. Or our sampling methods were not robust enough to pick up differences and more observations around individual trees would have resulted in significant differences. Nonetheless, increasing canopy openings have multiple benefits at the stand scale by reducing fuel continuity (Ritter et al. 2020), and at the tree-level by decreasing competition for resources such as light and water, and improving growth and defense mechanisms in residual trees (McDowell et al., 2006; Vernon et al., 2018; Young et al., 2023).

The GDBH predicts that in times of limited resources, trees prioritize allocating carbon towards defense mechanisms rather than growth, but that both increase to a point as resources become more available (Herms & Mattson, 1992). Our study shows that thinning treatments and wildfire reduce stand density and tree-level competition, leading to increases in resource availability, allowing trees to invest more in both growth and defense. We found that certain physical characteristics at the tree-level, such as height and live crown ratio, are predictors of tree vigor. Despite observing significant increases in BAI, duct size, and total duct area, it's possible that trees still face tradeoffs in carbon allocation, perhaps towards below-ground mechanisms or reproduction instead of growth and resin production.

Previous work has noted phenotypic variation in the tradeoff between growth and defense strategies among surviving ponderosa pine trees following a bark beetle outbreak. Surviving trees exhibit advantages in defense production that accumulate over time, enhancing their resistance to natural enemies (Ferrenberg et al., 2023). Additionally, other studies in pine species have provided support for the GDBH, as evidenced by the tradeoff of carbon allocation observed in resin (Rissanen et al., 2021), growth (Zas et al., 2020), and reproduction (Redmond et al., 2019). Our study area, characterized by rocky, dry forests along the Colorado Front Range, likely experiences limited resource availability. Despite disturbances that reduce competition and increase resource availability, ponderosa pine trees in this environment likely do not fully optimize their carbon allocation toward growth and defense mechanisms. Further investigation is needed to understand how site characteristics, such as climatic and resource gradients, interact with local characteristics, such as stand density, influence growth and defense allocation strategies. This variability in allocation strategies influences tree-level resistance to future disturbances such as drought and bark beetle outbreaks, highlighting the complex interplay among growth, defense, and resource availability in shaping forest dynamics.

Overall, our study has revealed significant differences in tree growth and defense responses to disturbance effects from wildfire and thinning compared to control site trees. These differences are largely attributable to high competition. Increased competition resulting from fire suppression likely explains many of these stand structure differences, such as negative relationships among growth and resin duct stimulation in denser stands (Battaglia et al., 2018; Dickinson, 2014), as both treatments and low-severity wildfire help reduce tree to tree competition. Our findings underscore the importance of retaining healthier trees with larger live crown ratios and taller heights following thinning treatments, given their demonstrated association with increased BAI, duct size and total duct area, which are all crucial components of tree-level resistance to future stressors.

Results from our study emphasize the importance of forest management for a multitude of ecological goals. Although these thinning treatments were focused primarily on reducing fuels and risk of high-severity fire, it is crucial to acknowledge that wildfires are just one of several potential disturbances, with drought and insect outbreaks commonly occurring in ponderosa pine forests as well. Our research illustrates that fuels reduction management strategies and low-severity fire increase resistance to multiple future disturbances. The findings demonstrate that mechanical treatments with goals of low-density ponderosa pine stands enhance tree-level resistance to future disturbances, and low-severity fire also confers resistance across several metrics.

When thinking about wildfire, it is essential to shift our perspective from solely measuring the total area burned to evaluating the ecological value of areas burned at low to moderate severity, which aligns more closely with historical fire regimes. Wildfires have the capacity to treat larger areas more rapidly than any mechanical thinning or prescribed fire treatments. Areas burned at low to moderate severity offer increased ecological benefits for surviving trees, as evidenced by our findings.

Management Implications

With trends of increasing wildfire size and severity (Abatzoglou et al., 2021), the implementation of treatments such as thinning and prescribed burning are crucial for mitigating future fire risk in communities nestled within forested regions across western North American forests (Prichard et al., 2021). This study emphasizes the importance of treatments like mechanical thinning or prescribed fire to create diverse stand structure conditions. This approach offers multiple benefits including fuels reductions and reduced catastrophic wildfire risk as demonstrated in other studies (Addington et al., 2018; Crotteau & Keyes, 2020; Ritter et al., 2023). Additionally, it enhances tree-level resistance to future disturbances as demonstrated here. Beyond curtailing catastrophic wildfire risk, other studies have exhibited that thinning and wildfire also have additional ecological benefits such as maintaining native understory plants (Fornwalt & Kaufmann, 2014), promoting native pollinator species (Gelles et al., 2022), and benefitting avian biodiversity (Latif et al., 2020).

The Colorado Front Range landscape has been identified as having ‘high risk’ firesheds within the wildfire crisis strategy framework due to prevailing environmental conditions and community exposure (US Forest Service, 2022). This designation under the initial wildfire crisis strategy has resulted in increased funding allocations with the aim of advancing the pace and scale of forest health treatments over the next decade (US Forest Service, 2022). However, the reintroduction of prescribed fire into Front Range forests still presents many challenges ranging from substantial fuel loads and proximity to the wildland-urban interface, to constraints related to agency personnel and resources, permitting processes, weather windows, and smoke management (Addington et al., 2020). Yet, reintroducing fire into these forests is essential for meeting objectives of fostering healthier and more resilient forest ecosystems. Consequently, our findings suggest that thinning treatments that reduce tree to tree competition have multiple ecological benefits that go beyond reducing wildfire severity, and should continue to be implemented. We recommend forest restoration treatments that consider historical disturbance patterns while implementing adaptive strategies, to fortify ecosystem resilience and bolster resistance against an array of disturbances exacerbated by climate change.

Limitations and Future Research

This study has several limitations. First, this study does not account for the intensity of thinning treatments. We addressed this by tallying stumps from thinned plots, but this does not fully account for the importance of varying sizes in trees within a stand or changes in canopy cover. Second, the true level of tree resistance to future disturbance remains uncertain. Our results suggest an enhancement in tree resistance to future disturbance following thinning or low-severity fire due to these associated changes in tree physiology. However, to truly understand how these management actions impacted resistance to disturbance, we would need to sample following bark beetle outbreak, drought, or fire to discern differences in internal tree structure between affected and unaffected trees. Lastly, this study examines an 8-10-year post disturbance effect, and little is known about the continued tree benefit to these management and disturbance actions.

Future studies could delve into how climate relationships influence carbon allocation versus resin duct production following disturbance effects from thinning and wildfire. Understanding climate's role in tree resource allocation could explain potential variations in growth or resin duct production. We didn't examine some top-down drivers like climate which may explain some of this variability. We also didn't examine how seasonality of fire could influence growth and defense mechanisms following disturbance. Ferrenberg et al. (2023)

demonstrated that combining measures such as mean annual temperature, total annual precipitation, and mean annual drought severity significantly enhances models' predictive ability regarding tree growth in response to climate. Gonzalez et al. (2023) found that hotter and drier conditions resulted in stronger tradeoffs for ponderosa pine vital functions. Coupled with high density stands, such conditions could display more complex tradeoffs within growth, defense, and reproduction. Additionally, we didn't examine several bottom-up drivers like soil moisture and site temperature which could also explain variability and warrants further investigation.

Future research examining which resin duct metric is the most useful or important when assessing tree-level resistance to bark beetles is important for understanding physiological responses. Our findings suggest three resin duct metrics have similar relationships to stand and site level predictors, but identifying the most pertinent metric for resisting bark beetle outbreaks is invaluable for subsequent research. Hood and Sala (2015) identified resin duct size and total duct area as the most robust predictors of resin flow, both of which escalate with tree growth. Resin flow fundamentally influences the beetle's capacity to successfully bore into the tree, yet it is extremely difficult to predict due to the extensive variability among resource availability, competition, and species-specific responses to environmental conditions. Individual tree characteristics such as xylem sap flow (water use), tree water status, and resin exudation would further enrich physiological research into the tradeoffs between growth and defense that trees allocate carbon to. A metric encompassing the effects of growth and resin combined with tree- and stand-level characteristics would provide a more dependable estimate of resistance to bark beetles.

Conclusions

Studies investigating the impacts of disturbance from thinning and fire are of increasing importance as we see larger, more frequent disturbances across western North America. It is imperative for managers to understand how management actions influence resistance to future disturbances like insect outbreaks or drought. In high risk firesheds that are slated for more treatments, this research is important in elucidating the impacts of thinning and fire on residual surviving trees. An examination of burned landscapes, extending beyond high-severity patches, enriches comprehension of the potential ecological benefits of wildfires, particularly where they burn at low to moderate severity. This work highlights that thinning and wildfire alter forest stand structure, which in part leads to greater tree-level resistance and growth. Thinning and low-severity fire are important tools for enhancing resistance to future disturbances, beyond just wildfires, in ponderosa pine trees.

Tables and Figures

Table 1: Plot information and tree core characteristics within the Arapaho-Roosevelt national forest (AR North, AR South) and Pike national forest. Standard errors are included in parentheses.

Location	**AR North**			**AR South**			**Pike**		
Treatment	**Control**	**Thinned**	**Wildfire**	**Control**	**Thinned**	**Wildfire**	**Control**	**Thinned**	**Wildfire**
Plots	21	15	16	19	20	16	18	19	16
Elevation Range (m)	2401-2631	2058-2718	1942-2470	1886-2721	1934-2726	1818-2568	2535-2841	2445-2868	2703-2906
BA mean (m²/ha)	29.91 (2.73)	21.35 (2.62)	15.76 (1.83)	37.76 (4.42)	21.50 (1.53)	12.06 (0.84)	22.12 (2.84)	18.53 (2.64)	12.44 (1.07)
QMD mean (cm)	22.38 (1.22)	26.64 (1.36)	30.76 (1.61)	24.28 (1.12)	31.86 (1.20)	26.68 (1.54)	23.29 (1.36)	31.62 (1.18)	29.38 (1.21)
SDI mean (tpha)	1152 (157)	467 (108)	200 (38)	1116 (180)	231 (32)	294 (61)	665 (112)	217 (52)	196 (42)
Canopy cover (%)	79.2 (14.2)	33.8 (6.1)	22.2 (4.0)	41.3 (7.2)	33.9 (5.7)	30.2 (5.4)	50 (8.7)	16 (2.7)	23.8 (4.2)
Cores	31	31	31	33	35	31	33	34	32
Mean DBH of trees cored (Range)	32.1 (11.9-58.4)	31.1 (20.1-46.0)	36.6 (19.8-72.8)	29.8 (21.5-47.8)	38.7 (22.1-57.7)	33.5 (14.5-50.6)	29.5 (20.1-44.2)	34.6 (21.1-47.0)	36.0 (21.3-54.4)
Series Intercorrelations	0.556	0.561	0.492	0.574	0.551	0.484	0.513	0.516	0.436
Mean Sensitivity	0.121	0.132	0.192	0.108	0.112	0.174	0.189	0.169	0.163

Table 2: Summary table showing results from One-way ANOVA test of significance for each stand structure variable (BA, QMD, SDI) among treatment type

Response Variable	Df	Sum of Squares	Mean of Squares	F-value	P-value
BA	2	290974	145487	1120	<0.0001
QMD	2	56988	28494	852.1	<0.0001
SDI	2	713912963	356956482	1722	<0.0001

Table 3: Generalized linear mixed model inputs and outputs predicting growth and defense metrics at the stand scale. Defense metrics include resin duct size, production, total area, density, and relative duct area. Values in bold indicate significance based on α=0.05.

Response Variable	Predictor Variables	Coefficient estimate	Standard error	p-value
BAI	Fire	-89.310	64.520	0.1673
	Thin	-35.630	62.500	0.5690
	Pre_Post	-27.230	21.640	0.2084
	HLI	201.200	302.700	0.5068
	SDI	**-0.199**	**0.048**	**<0.0001**
	Year	**5.335**	**1.350**	**<0.0001**
	Fire * Pre_Post	-10.830	22.220	0.6289
	Thin * Pre_Post	**179.100**	**22.200**	**<0.0001**
Duct Size	Fire	0.0004	0.0010	0.7190
	Thin	-0.0004	0.0010	0.6648
	Pre_Post	0.0005	0.0005	0.2943
	HLI	-0.0025	0.0045	0.5840
	SDI	**-0.000003**	**0.0000007**	**<0.0001**
	Year	0.00002	0.00003	0.4829
	Fire* Pre_Post	-0.0004	0.0005	0.4901
	Thin* Pre_Post	**0.0015**	**0.0005**	**0.0036**
Duct Production	Fire	-0.1171	0.3007	0.6973
	Thin	-0.3510	0.2920	0.2302
	Pre_Post	-0.1394	0.1369	0.3089
	HLI	-1.9900	1.3960	0.1552
	SDI	**-0.0007**	**0.0002**	**0.0007**
	Year	**0.0279**	**0.0085**	**0.0011**
	Fire * Pre_Post	**0.2944**	**0.1407**	**0.0365**
	Thin * Pre_Post	**0.6683**	**0.1405**	**<0.0001**
Total Duct Area	Fire	-0.0016	0.0099	0.8717
	Thin	-0.0117	0.0097	0.2265
	Pre_Post	-0.0048	0.0045	0.2859
	HLI	-0.0449	0.0462	0.3322
	SDI	**-0.00003**	**0.000007**	**<0.0001**
	Year	**0.0008**	**0.0003**	**0.0020**
	Fire * Pre_Post	**0.0094**	**0.0046**	**0.0412**

	Thin * Pre_Post	**0.0261**	**0.0048**	**<0.0001**
Duct Density	Fire	0.0346	0.0540	0.5224
	Thin	-0.0245	0.0527	0.6423
	Pre_Post	0.0187	0.0352	0.5949
	HLI	-0.0359	0.2411	0.8819
	SDI	-0.00003	0.00004	0.3808
	Year	**0.0064**	**0.0022**	**0.0034**
	Fire * Pre_Post	**0.1562**	**0.0362**	**<0.0001**
	Thin * Pre_Post	-0.0475	0.0361	0.1888
Relative Duct Area	**Fire**	**0.5834**	**0.2344**	**0.0133**
	Thin	0.0141	0.2292	0.9511
	Pre_Post	0.2202	0.1604	0.1699
	HLI	**-2.2870**	**1.0490**	**0.0301**
	SDI	**-0.0005**	**0.0002**	**0.0064**
	Year	**0.0245**	**0.0100**	**0.0143**
	Fire * Pre_Post	**0.8467**	**0.1650**	**<0.0001**
	Thin * Pre_Post	-0.0230	0.1647	0.8888

Table 4: Generalized linear mixed model inputs and outputs predicting growth and defense metrics at the tree-level scale. Values in bold indicate significance based on α=0.05.

Response Variable	Predictor Variables	Coefficient estimate	Standard error	p-value
BAI	Canopy Cover	-0.0921	0.6078	0.8796
	Height	**39.8179**	**14.6493**	**0.0073**
	Live Crown Ratio	**6.4753**	**2.8913**	**0.0265**
Duct Size	Canopy Cover	-0.0000009	0.00001	0.9465
	Height	0.0002	0.0002	0.3696
	Live Crown Ratio	**0.00008**	**0.00003**	**0.0246**
Duct Production	Canopy Cover	0.0013	0.0047	0.7821
	Height	-0.0538	0.0644	0.4050
	Live Crown Ratio	0.0204	0.0127	0.1102
Total Duct Area	Canopy Cover	0.00005	0.0001	0.7278
	Height	-0.0012	0.0022	0.5720
	Live Crown Ratio	**0.0009**	**0.0004**	**0.0277**
Duct Density	Canopy Cover	0.0005	0.0014	0.7388
	Height	0.0278	0.0150	0.0649
	Live Crown Ratio	-0.0024	0.0029	0.4158
Relative Duct Area	Canopy Cover	-0.0019	0.0061	0.7628
	Height	0.0248	0.0592	0.6755
	Live Crown Ratio	0.0016	0.0117	0.8886

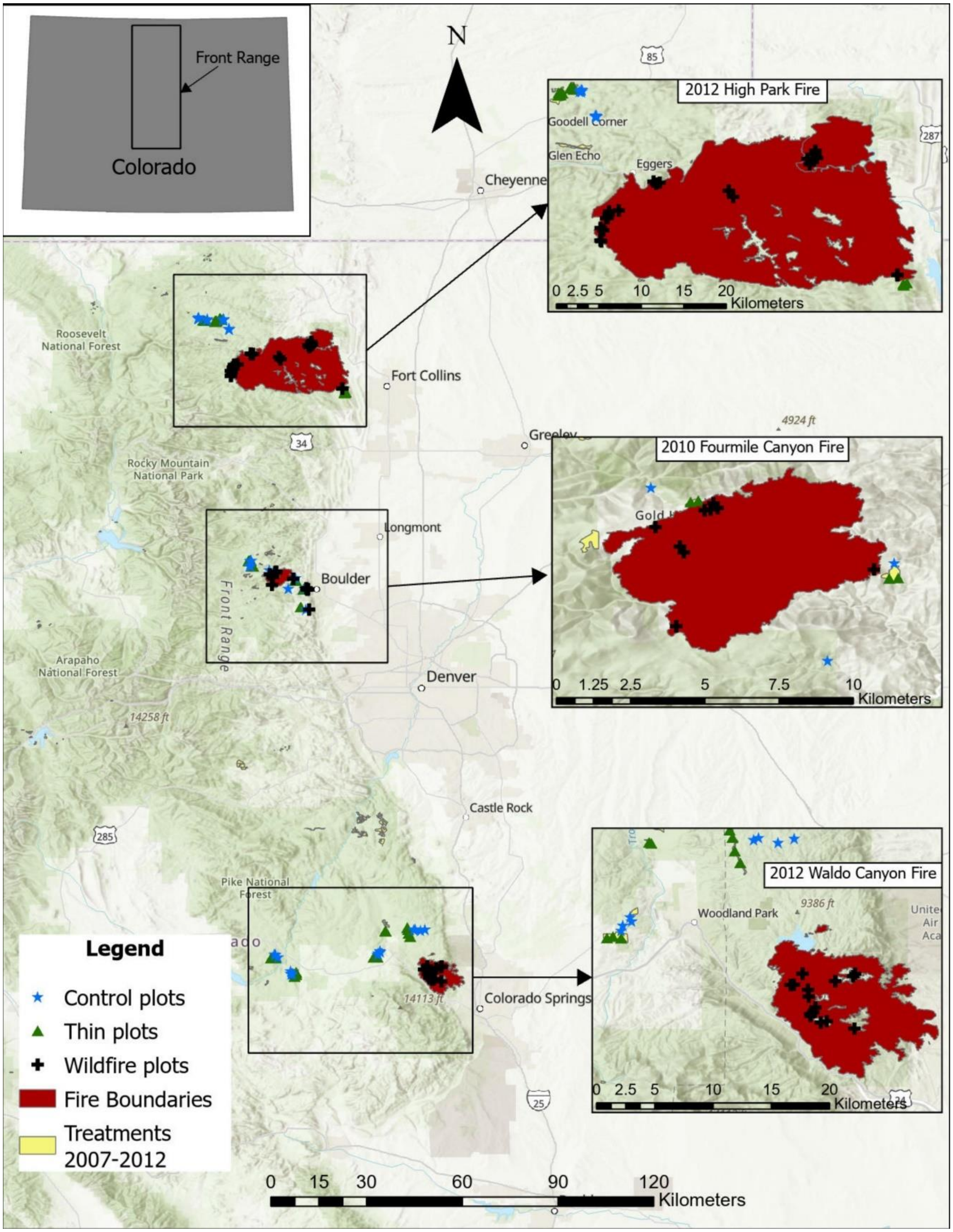
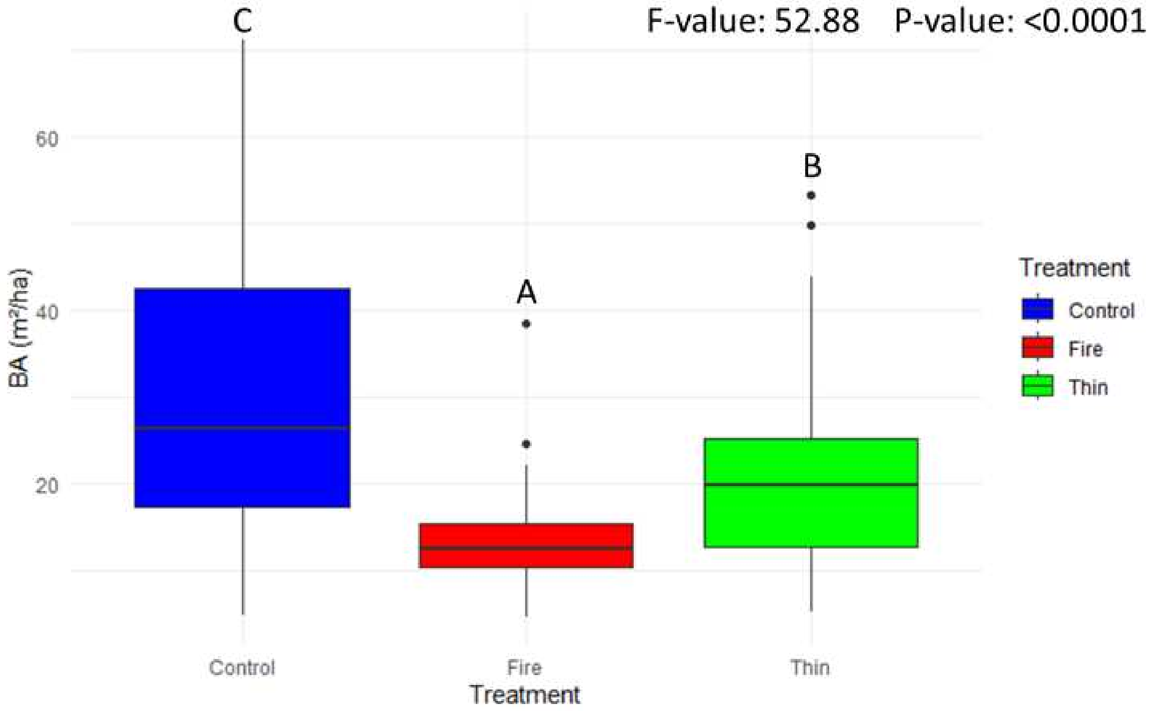
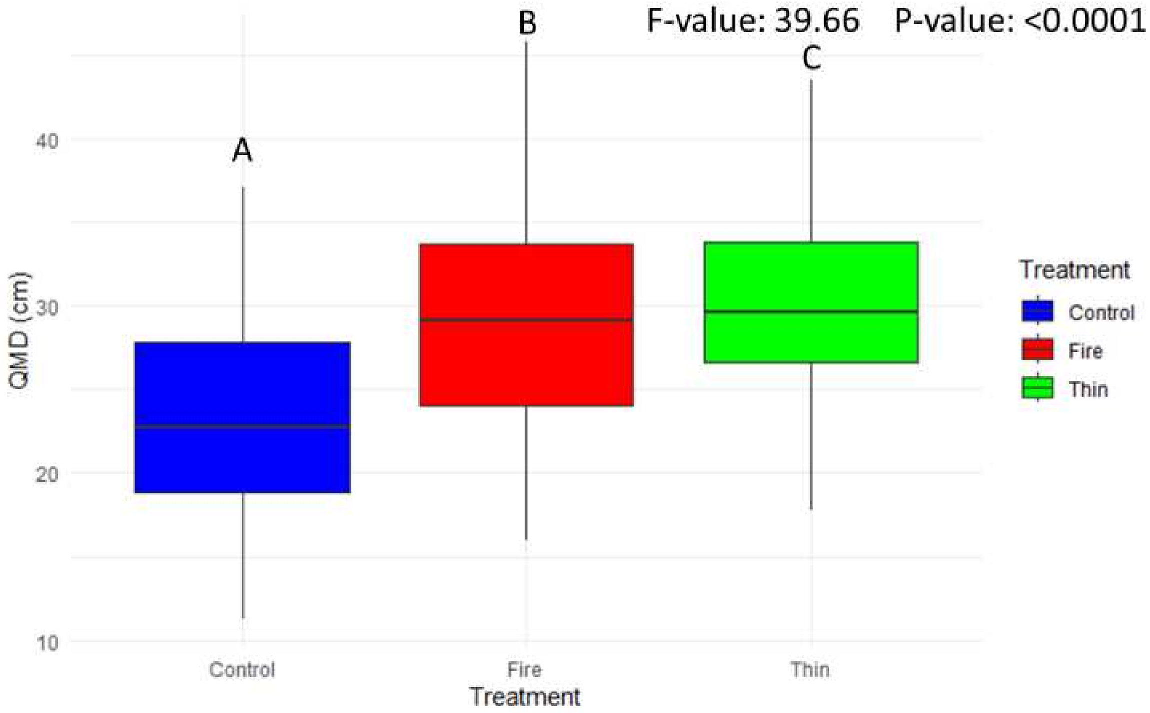


Figure 1: Map showing plot locations (blue star, green triangle, black cross), High Park Fire, Fourmile Canyon Fire, Waldo Canyon Fire boundaries (maroon), and thinning treatment boundaries (yellow). Inset maps showing fire boundaries and surrounding treatment and control plots.

a)


F-value: 52.88 P-value: <0.0001
C
B
A
BA (m²/ha)
60
40
20
Treatment
Control
Fire
Thin
Control
Fire
Thin
Treatment

b)


F-value: 39.66 P-value: <0.0001
B
C
A
QMD (cm)
40
30
20
10
Treatment
Control
Fire
Thin
Control
Fire
Thin
Treatment

c)

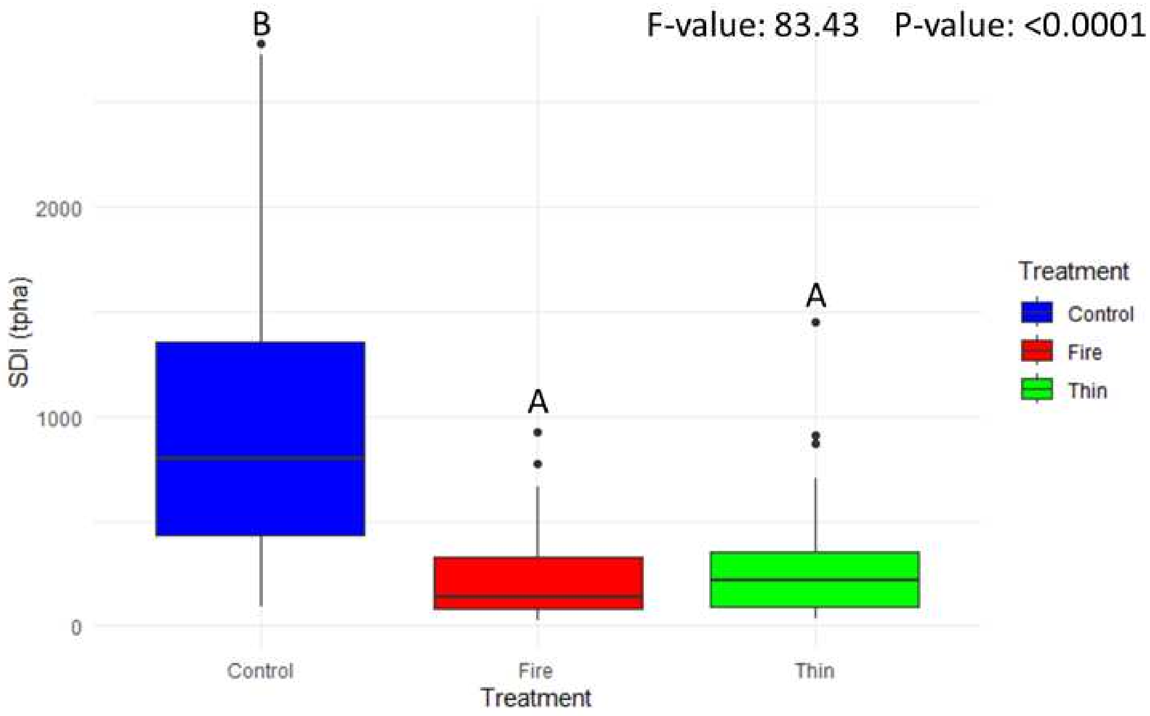


Figure 2: Boxplot showing BA (a), QMD (b), and SDI (c) by Treatment. Results of Tukey HSD test assessing significance of difference between pairs of group means (p<0.05) shown by different letters.

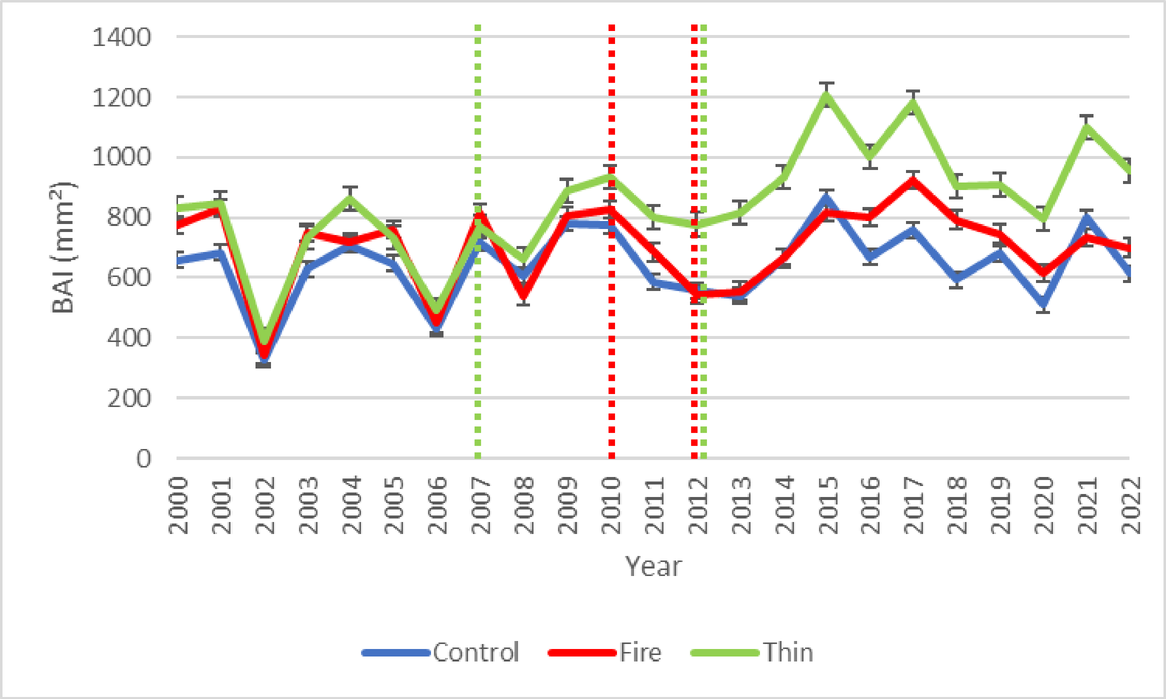
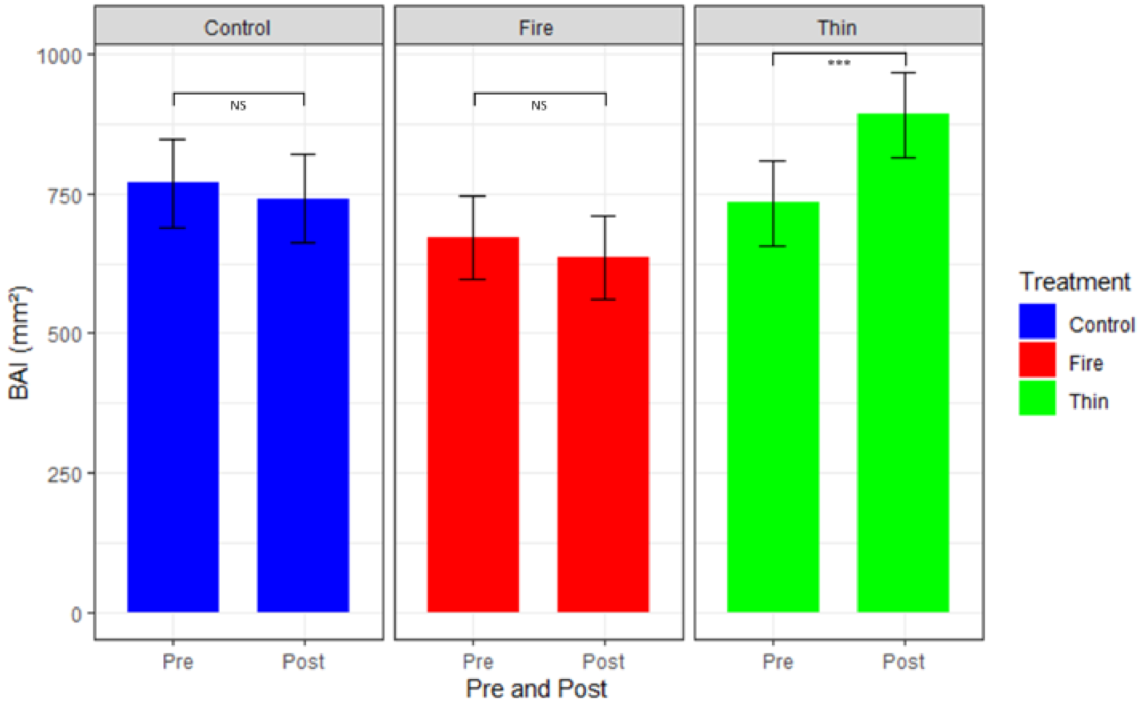


Figure 3: Average basal area increment (BAI) in mm² over time by treatment type. Dashed colored lines bracket the range of years in which treatments (green) and wildfires (red) occurred.

a)



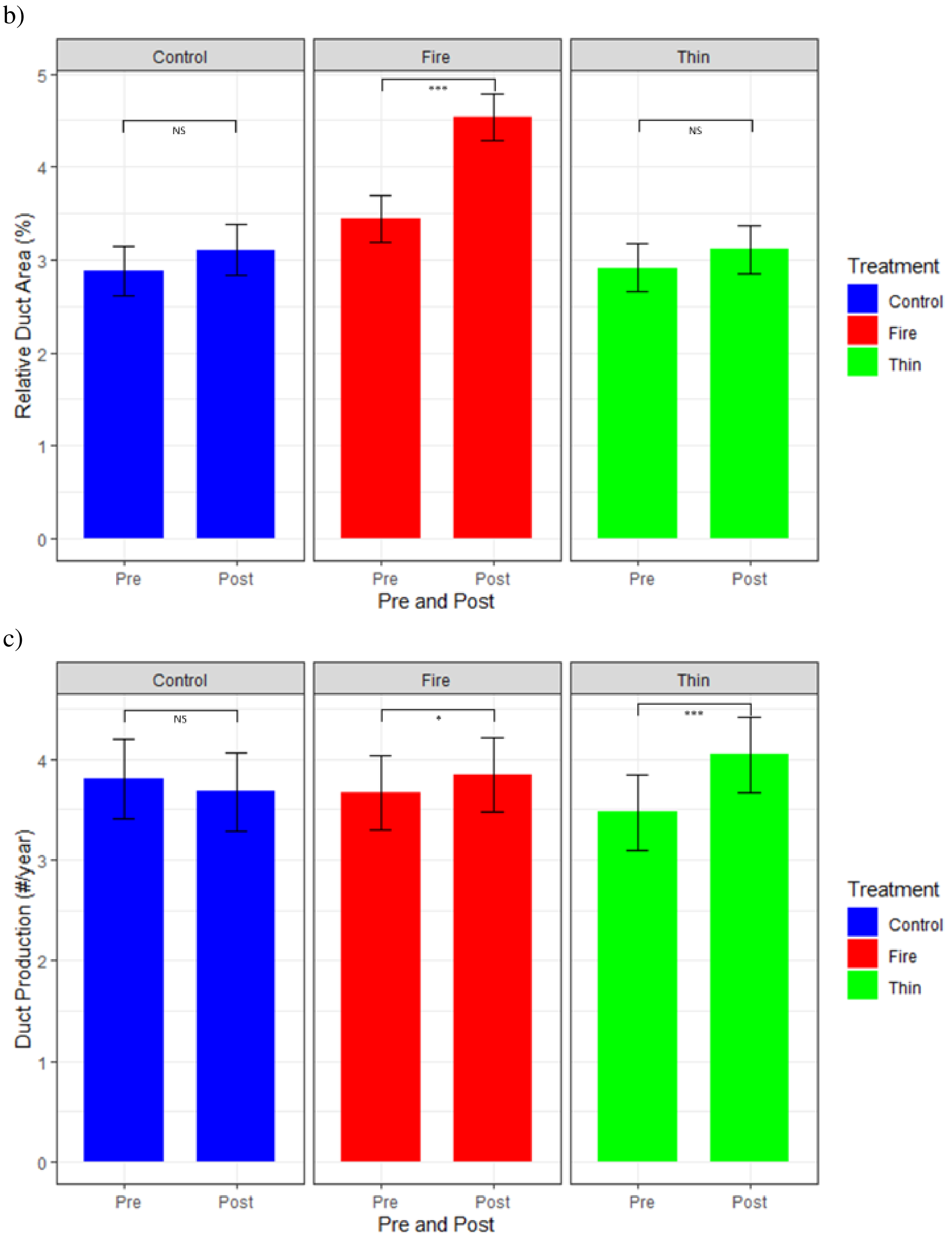
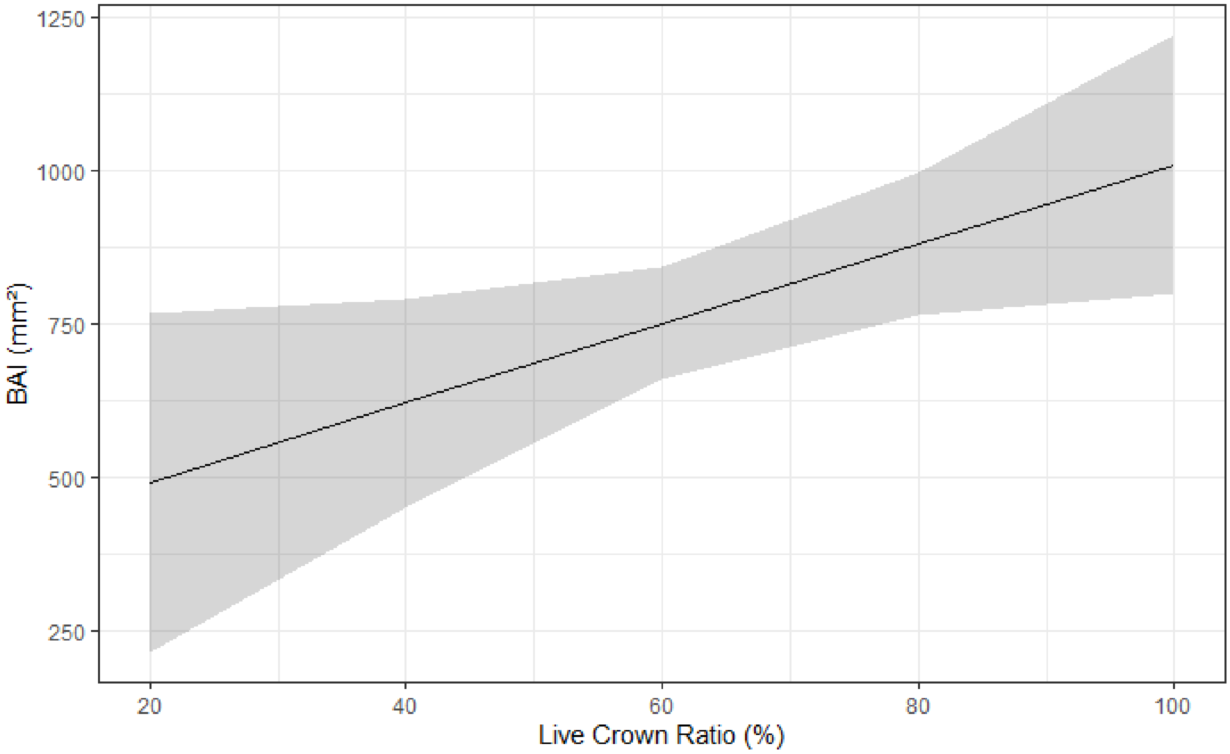
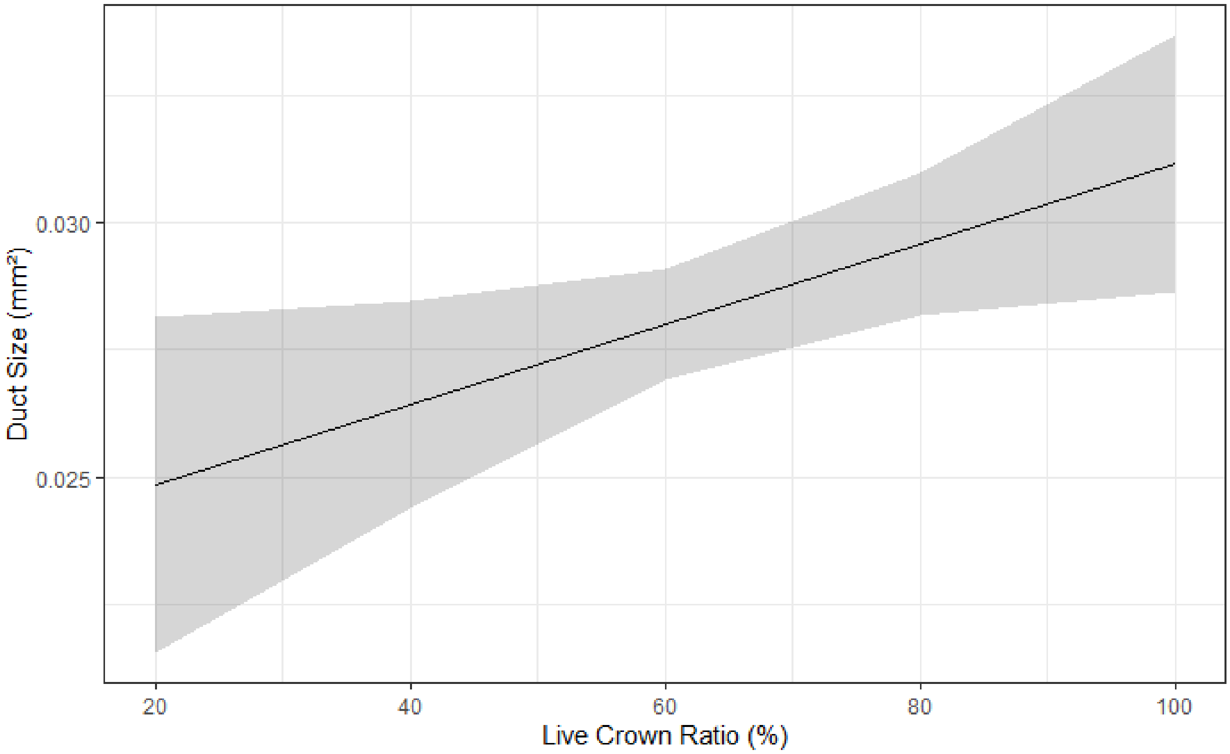


Figure 4: Bar graphs illustrating the results from our GLMM analyzing the effects of thinning and fire on BAI (a), relative duct area (b), and duct production (c). Significance levels indicated as 'NS' (No Significance), '*' (<0.05), '**' (<0.01), '***' (<0.001). BAI (a) shows greatest increase following thinning. Relative duct area (b) shows greatest increase following wildfire. Duct production (c) shows significant increases following both thinning and wildfire.

a)


1250
1000
750
500
250
BAI (mm²)
20
40
60
80
100
Live Crown Ratio (%)

b)


0.030
0.025
Duct Size (mm²)
20
40
60
80
100
Live Crown Ratio (%)

c)

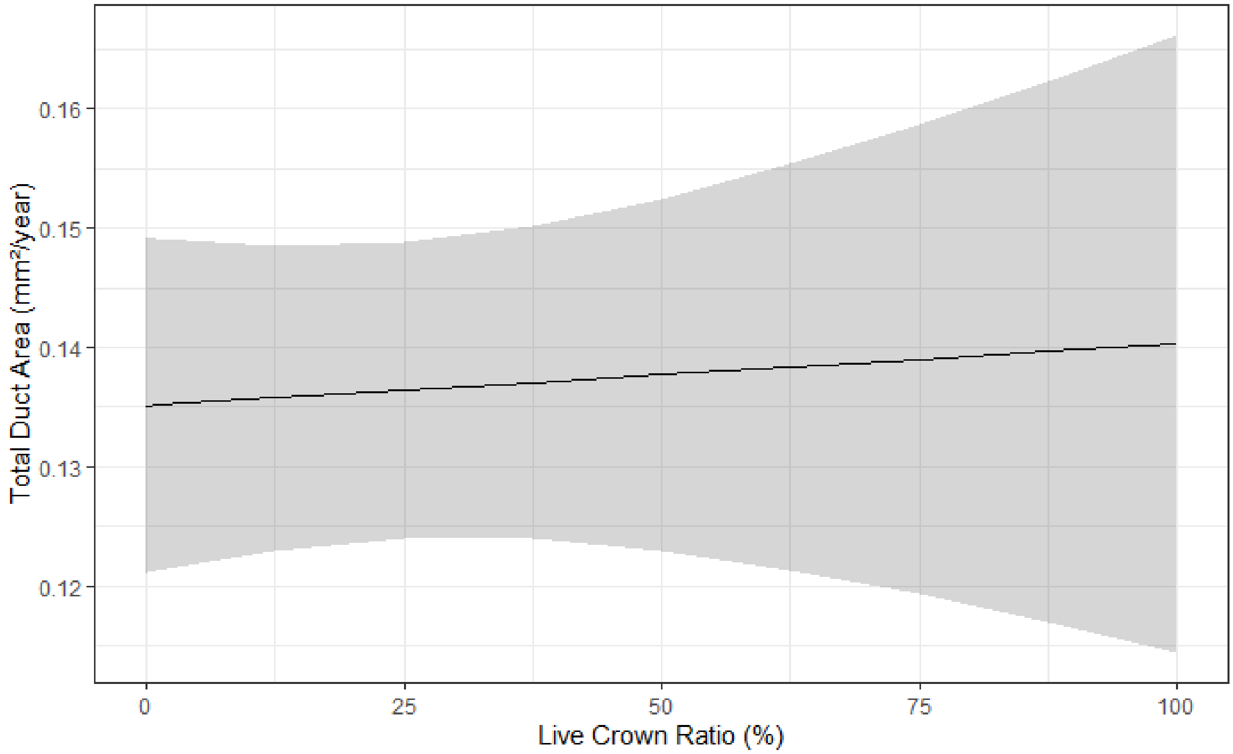


Figure 5: Partial dependence plots visualizing the average impact of live crown ratio values on BAI (a), duct size (b), and total duct area (c). BAI (a) and duct size (b) show the strongest positive relationships of live crown ratio, meaning as live crown ratio increases, BAI and duct size increase. Total duct area (c) shows a weaker positive relationship of live crown ratio.

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