POST-FIRE EFFECTS IN CHAPARRAL AND OAK ECOSYSTEMS OF NORTHERN CALIFORNIA

By

Abigail M. Jones

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Forestry, Watershed, and Wildland Sciences

Committee Membership

Dr. Jeffrey M. Kane, Committee Chair

Dr. Harold S. J. Zald, Committee Member

Dr. Rosemary L. Sherriff, Committee Member

Eamon A. Engber, Committee Member

Dr. Erin C. Kelly, Graduate Coordinator

December 2021

ABSTRACT

POST-FIRE EFFECTS IN CHAPARRAL AND OAK ECOSYSTEMS OF NORTHERN CALIFORNIA

Abigail M. Jones

The issue of wildfires, hazard fuels management, and post-fire tree mortality has become an increasingly common topic in the western United States. This thesis is composed of two studies, with the first study, Chapter 1, examining fuel treatment effectiveness and the second study, Chapter 2, striving to characterize post-fire mortality in oaks.

Prior to wildfire, fuel reduction projects may take place to decrease the likelihood of high severity fire around human infrastructure and communities. Within California's chaparral ecosystems, common treatment types include hand-thinning, prescribed burning, mechanical mastication, and mechanical mastication followed with prescribed burning. Because chaparral has a longer historical fire return interval and these ecosystems do not need frequent fire disturbance, the efficacy of these treatment types is debated. Our study had the rare opportunity to collect data on fine woody fuel loading, shrub density, and vegetation both immediately before and one year following wildfire in northern California's Whiskeytown National Recreation Area. Using these comparisons, our goal was to determine the post-fire response of each treatment type and determine an effective fuels treatment in chaparral to mitigate fire behavior, while maintaining

ecosystem integrity and supporting native species habitat. The severity of the wildfire was moderate across the study site and did not differ among treatments. Post-fire live shrub density and live shrub height also were not influenced by treatment type, but oak dominated sites had greater live shrub density after wildfire. Fine woody fuel loading levels differed by treatment type, with prescribed burned units having the greatest levels in both chaparral and oak sites. Fine woody fuel consumption was lowest in hand-thinned units. Total plant species richness increased in all treatment types following wildfire, largely driven by an increase in exotic species, as native plant cover decreased and exotic species cover increased across all treatments. This study suggests that areas of chaparral may need to be retreated sooner than this timeframe to reduce fire severity. However, retreating these systems may not be economically feasible and it remains unclear if treatments will meet fuel and fire behavior objectives.

Land managers are concerned about post-fire mortality of trees and rely on statistical models of tree mortality in post-fire decision making. While many studies have evaluated the accuracy of these models in conifers, the performance of these models on hardwood species, specifically oak species, has been understudied. Models, such as FOFEM and FVS-FFE, can help land managers to predict which trees will die following fire and can help in hazard tree removal and post-fire salvage logging operations. These models, however, have been exclusively developed using western United States conifer species, bringing into question the veracity of these models for hardwood species. The purpose of this study was to test current mortality models using observations from wildfire and prescribed burn sites in northern California for two oak species, California

black oak (*Quercus kelloggii*) and canyon live oak (*Quercus chrysolepis*). Our findings suggest that both modeling approaches performed well, but Random Forest was better at predicting probability of mortality for an imbalanced dataset. When using imbalanced datasets, logistic regression can underpredict mortality, which can have negative repercussions for land managers dealing with recently burned ecosystems containing oaks.

ACKNOWLEDGEMENTS

This project was supported by the National Park Service Fire Reserve Fund (Task Agreement #P17AC01263) and the Joint Fire Science Program (20-1-01-10). I would like to thank my graduate committee, Jeffrey Kane, Eamon Engber, Harold Zald, and Rosemary Sherriff for their feedback and support. I would particularly like to thank my advisor, Dr. Jeff Kane, for his patience, encouragement, and overall willingness to teach throughout my academic journey. I would also like to thank Caroline Martorano for the collaboration and support throughout this process. I would like to thank Jennifer Gibson and Andrew Spain for providing data from previous years and prescribed burning information. Lastly, this project would not have been possible without the diligent work and eagerness to learn from field technicians Grace Rhoades, Raul Barajas-Ramirez, and Chris Belko.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1: FUEL TREATMENT EFFECTIVENESS TO WILDFIRE IN CHAPARRAL STANDS OF NORTHERN CALIFORNIA

ABSTRACT

Fuel reduction treatments are commonly used within fire prone wildlands to reduce the risk of wildfire to human communities. Within California's chaparral ecosystems, a variety of treatments are commonly used to minimize fire intensity and support fire suppression efforts. This study examines the post-wildfire response of vegetation and fuel loading within areas that were treated 15 years prior to wildfire in Whiskeytown National Recreation Area in northern California. Treatment types included hand-thinning, mechanical mastication, mechanical mastication + spring prescribed burning, and spring prescribed burning only. The study site contained 10 blocks, five of which were chaparral dominated and five oak dominated blocks. All blocks contained one or two units for each treatment and each unit contained one or two sample plots. Burn severity, fuel loading, and understory vegetation data were collected following wildfire within each plot to determine the effect of treatment type and vegetation type (chaparral or oak dominated). The severity of the wildfire was moderate across the study site and did not differ among treatments. Post-fire live shrub density and live shrub height also were not influenced by treatment type, but oak dominated sites had greater live shrub density after wildfire. Fine woody fuel loading levels differed by treatment type, with prescribed burned only units having the greatest levels in both chaparral and oak sites.

Fine woody fuel consumption was lowest in hand-thinned units. Total plant species richness increased in all treatment types following wildfire, largely driven by an increase in exotic species, as native plant cover decreased and exotic species cover increased across all treatments. Ultimately, the lack of strong differences in burn severity and fine woody fuel loading among treatment types was likely due to the length of time since treatment (15 years). This study suggests that areas of chaparral may need to be retreated sooner than this timeframe to reduce fire severity. However, retreating these systems may not be economically feasible and it remains unclear if treatments will meet fuel and fire behavior objectives. Additionally, due to the potential for expanding exotic species, more frequent treatments will likely be problematic for land managers attempting to manage native plant populations and maintain ecosystem integrity.

INTRODUCTION

Fire is an important ecological process that maintains and promotes biodiversity and ecosystem services in California's chaparral shrublands (Keeley 2002). Vegetation associated with chaparral is both resilient to and dependent upon infrequent, high severity wildfires, making this an important component in maintaining the high endemism found in these ecosystems (Keeley and Keeley 1988, Keeley 1991). Chaparral is characterized by unique features that contribute to its flammability, such as a contiguous canopy layer with dense twigs and leaves which contain volatile oils, supporting high intensity crown fires with rapid rates of spread (Quinn and Keeley 2006). Historical fire return interval estimates for California's chaparral range from 30 to 100 years (Keeley and Davis 2007), and many of these shrub species rapidly regenerate following wildfires via seed or basal sprouting (Horton and Kraebel 1955).

Over the past few decades, expansion of the wildland urban interface (WUI) coupled with anthropogenically-altered fire regimes in areas containing chaparral ecosystems poses substantial challenges toward protecting human communities from high severity wildfires. In recent decades, much of the new housing development in California has occurred within the WUI (Hammer et al. 2007), exacerbating the risks to human lives and property during wildfires (Radeloff et al. 2018). High human population densities are also associated with an increase in human-caused fires (Keeley 2001, Syphard et al. 2007). Climate change-related warmer and drier conditions have increased fuel availability and the ability to ignite and spread fire (Abatzoglou and Williams 2016).

These combined circumstances have contributed toward increases in wildfire size and frequency in chaparral ecosystems (Syphard et al. 2009), prompting managers to rapidly expand the implementation of fuel treatments without a sufficient understanding of their effectiveness to mitigate fire behavior and effects, such as exotic species and biological diversity.

Many fuel treatment options, such as prescribed burning, mechanical mastication, or hand-thinning, are commonly used to reduce hazardous fuels in chaparral ecosystems, but each treatment has benefits and drawbacks that are not fully understood. Prescribed burning in chaparral and its effectiveness as a fuel treatment is debated (Keeley and Fotheringham 2001, Keeley 2002), partially due to the variability in fuel consumption associated with prescribed burning conditions (Knapp et al. 2005). Prescribed burning requires highly trained staff, appropriate weather and air quality conditions, and often faces societal challenges (Yoder et al. 2004, Ryan et al. 2013). Because of these barriers to prescribed burning, managers often opt for the use of manual thinning or mechanical mastication treatments instead. Mechanical mastication is an increasingly common treatment used in chaparral that reduces fuel bed depth and vertical continuity by converting the live, contiguous shrub layer to a compacted layer of dead surface fuels (Jain et al. 2007, Kane et al. 2009). While the altered fuel structure from mastication can be effective at reducing crown fire risk (Rothermel 1991), the substantial increase in dead surface fuels can lead to undesired surface fire behavior (Kreye et al. 2014). Additionally, much of the dead surface fuels generated from mastication can persist for over a decade (Reed et al. 2020, Martorano et al. 2021). Hand-thinning of chaparral, which entails removal of shrubs by fire crews using chainsaws, can be a less disruptive option than mastication in more sensitive ecological areas. Hand-thinning is a more labor-intensive treatment in chaparral ecosystems but has shown to be effective in the short-term through substantially reducing shrub height (Kane et al. 2010).

Most fuel treatments applied in chaparral ecosystems will also involve tradeoffs in their impacts on understory vegetation. For example, prescribed burning outside of historic wildfire conditions can have negative effects on species composition. Native soft-seeded annual species may experience higher levels of seed mortality from prescribed burning in the winter or spring when soil moisture is elevated (Le Fer and Parker 2005). Hand-thinning is effective at reducing shrub cover in chaparral and oak woodlands but has been associated with increased cover of exotic annual plants, perhaps due to the associated increase in sunlight and changes in soil moisture and temperature (Perchemlides et al. 2008). The deep woody fuel layer following mechanical mastication can lead to increased residence time once burned with temperatures exceeding lethal limits of roots and seeds under drier soil conditions (Busse et al. 2005, Busse et al. 2010). Yet, mastication followed by prescribed burning has also been found to increase plant biodiversity by exposing mineral soil and increasing light availability to support plant establishment (Kane et al. 2010). Mastication treatments can maintain lower shrub cover compared to prescribed burning treatments depending on burn severity but can also support higher densities of exotic annual grasses (Perchemlides et al. 2008, Wilkin et al. 2017).

Increases in the amount of area treated combined with increasing fire activity may contribute to type conversion of chaparral to exotic grasslands (Keeley et al. 2005, Dickens and Allen 2014). However, information about fuel treatment and wildfire interactions and their effect on understory vegetation has not been adequately examined. Historically, intact chaparral stands have largely resisted the invasion of exotic species by maintaining a thick, closed canopy that inhibits herbaceous understory plant growth (Brooks et al. 2004, Keeley et al. 2005). Disturbances, such as wildfires or fuels treatments, that result in shrub removal in chaparral stands can increase the risk of type conversion to exotic annual grasslands if subsequent disturbances occur in short succession (Zedler et al. 1983, D'Antonio and Vitousek 1992). Once exotic annual grasses have sufficiently established, their high surface area-to-volume ratios, earlier seasonal drying, and high horizontal fuel continuity promote a positive feedback effect that increases the probability of a subsequent fire (Brooks et al. 2004). The resultant increase in fire frequency prevents shrubs from regenerating because they require a longer recovery time than exotic annual grasses, therefore perpetuating self-sustaining conditions for the newly established exotic annual grasses (Keeley 2001, Brooks et al. 2004, Dickens and Allen 2014).

Land managers often seek fuel reduction treatments that have greater longevity of effectiveness to reduce the cost of fuels management by decreasing the need to repeat treatments as frequently. Prior studies that examined the longevity of fuel treatment effectiveness in chaparral have varied widely. Masticated and prescribed burn treatments in chaparral have exhibited a short duration of effectiveness, showing similar levels of live woody fuel cover as the control units within 10 years following treatment, while slower shrub recovery in masticated only treatments may indicate a longer duration of effectiveness (Brennan and Keeley 2017, Wilkin et al. 2017). The longevity of effectiveness of different treatments also depends on whether species are resprouting species or non-resprouting species (obligate seeders). Faster recovery of live woody fuels in masticated and prescribed burn sites is likely due to the stimulation of obligate seeder shrub species by fire (Stephens et al. 2009, Kane et al. 2010). This stimulation can eventually lead to live shrub recovery that may reduce the longer-term effectiveness of mastication and prescribed burn treatments in comparison to mastication only and hand-thinning treatment types (Martorano et al. 2021), potentially requiring subsequent treatments to maintain effectiveness. More knowledge detailing the duration of fuel treatment effectiveness is necessary for land management planning purposes.

In 2018, the Carr Fire burned through a previously established experimental fuel treatment site in Whiskeytown National Recreation Area of northern California. The original study was implemented in 2002 to examine the immediate effects of four different fuel treatment types: mechanical mastication, prescribed burning, mechanical mastication followed by prescribed burning and hand thinning on understory vegetation in chaparral and oak woodland stands (Bradley et al. 2006). In 2018, the study site was serendipitously resurveyed shortly before the wildfire to examine the longer-term effectiveness of these treatments on both understory vegetation and fuels (Martorano et al. 2021).

The current study expands upon this earlier work by examining the direct long-term effectiveness of fuel treatments following a wildfire. While some studies have examined fuel treatments in chaparral or shrublands, there are currently no previous studies that we are aware of that have examined fuel treatment effectiveness to wildfire in chaparral stands. In 2019 and 2020, the Whiskeytown National Recreation Area study site was resurveyed following the Carr Fire to examine the impacts of 15-year-old fuel treatments on fire effects in chaparral and oak woodlands. Specifically, this study examined the effects of fuel treatments on: 1) wildfire burn severity; 2) post-wildfire live and dead surface fuels; and 3) native and exotic understory plants. This study provides a unique opportunity to examine the effects of 15-year-old fuel treatments following wildfire. Results from this study can be used to assist management decisions within chaparral stands in northern California that are adjacent to human communities in the wildland-urban interface.

MATERIALS AND METHODS

Site Location

The study site encompasses 18.2 ha within Whiskeytown National Recreation Area in Shasta County, along the southeastern boundary of the Klamath Mountains in northern California. Elevation ranges from 381 to 457 m with slopes ranging from 1% to 40%. Whiskeytown National Recreation Area has a Mediterranean climate with hot, dry summers and cool, rainy winters. Summer (May through October) temperatures are often as high as 38°C, while winter (November through March) temperatures occasionally fall below freezing. Average annual precipitation is 1,524 mm, with 70% falling between November and March (PRISM, 2019). In 2018, the year the Carr Fire burned, annual precipitation was 1,101 mm, and in 2019 was 2,271 mm. Soils in the study site location are either Boomer gravelly loam (15 to 30% slopes) or Neuns very stony loam (8 to 50% slopes) (NRCS 2020).

The overstory of this study site was comprised primarily of California black oak (*Quercus kelloggii*) Newb. and knobcone pine (*Pinus attenuata*) Lemmon, with a less common overstory of canyon live oak (*Quercus chrysolepis*) Liebm., gray pine (*Pinus sabiniana*) D. Don, and interior live oak (*Quercus wislizeni*) A DC. Pre-fire shrub species predominantly included whiteleaf manzanita (*Arctostaphylos viscida*) Parry, toyon (*Heteromeles arbutifolia*) (Lindl.) M. Roem., and poison oak (*Toxicodendron diversilobum*) (Torr. & A. Gray) Greene (Bradley et al. 2006). Common native perennial herbaceous plants at this site included Hartweg's odontostomum (*Odontostomum hartwegii*) Torr., wild hyacinth (*Dichelostemma multiflorum*) (Benth.) A. Heller, and Tolmie star tulip (*Calochortus tolmiei*) Hook. & Arn. The most common annual grasses include Rattail sixweeks grass (*Festuca myuros*) L., silver hairgrass (*Aira caryophyllea*) L., and nit grass (*Gastridium phleoides*) (Nees & Meyen) E.E. Hubb.

The Carr Fire, which burned through the study site, was a human-caused fire that burned 92,936 ha in 2018. This fire is currently ranked as the ninth most destructive (CalFire 2021a) and the twelfth largest wildfire in California state history (CalFire 2021b). Over half of this fire burned as high severity, leading to eight fatalities and the loss of 1,079 structures (CalFire 2018). A total of 97% of Whiskeytown National Recreation Area burned, and the National Park Service lost numerous structures (National Park Service 2020). The Carr Fire burned through the study area on July 26 - 27, 2018. The fire spotted across a narrow finger of Whiskeytown Lake in the vicinity of the study site and spread laterally into the study area. Firefighting was conducted by handcrews and bulldozers in and adjacent to the study area (but did not result in observable direct impacts in any of our plots), in an unsuccessful attempt to hold the spot from progressing to the south.

Experimental Design

In 2002, a complete randomized block design was implemented within the study site containing ten blocks (Figure 1) divided based on similar slope, aspect, and vegetation characteristics (hereafter referred to as vegetation type), which were broadly classified as oak dominated or chaparral dominated stands. Prior to treatment, oak stands had overstory trees (primarily California black oak and knobcone pine) with a mid-story shrub component. Chaparral units were mostly composed of whiteleaf manzanita, toyon, and poison oak with occasional knobcone pine in the overstory. There were five oak blocks and five chaparral blocks. Each block was subdivided into treatment units which ranged in size from 0.01 to 0.15 ha. Within each block, one or two units were treated with one of the following five treatment types: hand thinned, prescribed burned in the spring (Spring Burn), mechanically masticated (Mast), mechanically masticated and spring burned (Mast + Rx), or no treatment (Control).

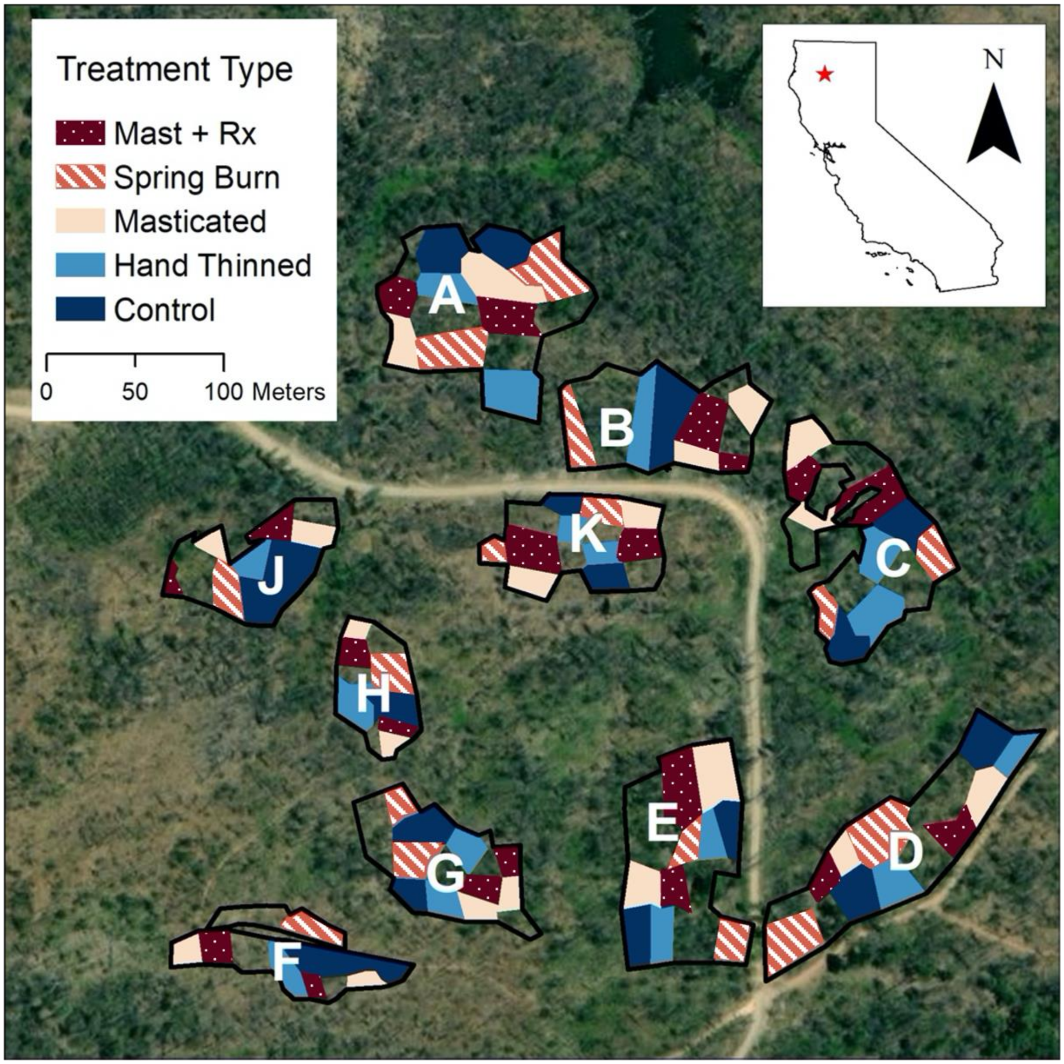


Figure 1. Experimental fuel treatments applied to chaparral and oak stands in Whiskeytown National Recreation Area of northern California. Layout of experiment is subdivided by vegetation type blocks and treatment type. Within each block were one or two treatment units, designated by color. Within each treatment unit there were two vegetation plots where data was collected. The inset locator map shows the boundary of the Carr Fire in California. Chaparral dominated vegetation type was present in blocks F, H, J, K, while the oak dominated type was present in blocks B, C, D, E, G. Block A was split up into half chaparral dominated and half oak dominated units.

Mechanical mastication was completed in November of 2002 using a North Tree Fire International ASV Posi-Track with an industrial brushcutter. Machine operators attempted to minimize soil disturbance and compaction by operating the masticator over chipped surfaces only when soils were dry. It was the goal of the mastication treatments to reduce understory shrub density and small trees less than three or four meters tall by 60-95% (Bradley et al. 2006). Hand thinned treatments were implemented in February and March of 2003 by fire crews with chainsaws. Heavy hand-thinning was conducted, to mimic the shrub reduction that took place in masticated units. Once cut, brush was carried outside of the experimental site and pile burned.

All prescribed burning was independently applied in the spring within each designated treatment unit. Approximately half of the prescribed burning was conducted from April 8, 2003 to April 10, 2003, while the remaining burns were completed on May 15, 2003. All prescribed burn units were ignited using drip torches with strip and spot ignition patterns. Soil moisture during the burns was recorded as "very high" (0.3-0.4 kPa tension). Air temperature ranged from 15°C to 22°C, while relative humidity ranged from 34% to 73%. Wind speed averaged about 3 km/hr with maximum speeds of 10 km/hr. Fires were low intensity surface fires, reaching a maximum surface fire temperature of 104°C. Shrubs were generally killed but not consumed from these burns. In the Mast + Rx units surface fires were much hotter with an average temperature of 347°C resulting in higher mortality in the overstory (Bradley et al. 2006).

Within each treatment unit, two 4 m^2 vegetation plots were randomly assigned and established. In total, there were 87 treatment units with 176 vegetation plots. The southwest corner of each treatment unit was established as the starting coordinate. Random numbers were generated to establish vegetation plot locations using an x and y coordinate system. This x and y coordinate system provided the distance to the edge of the treatment unit for each vegetation plot. Each vegetation plot was oriented to the north and were marked using plastic stakes. Most plastic stakes were consumed in the Carr Fire, so their locations were estimated using the original coordinates and replaced in 2019 with new stakes.

Data Collection and Analysis

To examine how fuel treatment type affected vegetation burn severity and substrate burn severity, categories were assigned along each fuel transect (Figure 2) using the National Park Service Fire Monitoring Handbook, form FMH-21 (National Park Service 2003), except that the order of burn severity classifications were reversed so that they logically ranged from 1 (unburned) to 5 (high severity). Transects were 4.6 m in length. During post-fire data collection, the proportion of each transect by burn severity classification were quantified and recorded. For example, if all parts of a plant were consumed and the only remaining pieces were deeply charred, this received a vegetation burn severity classification of 5 (high severity). Burn severity data was summarized by calculating a weighted value proportional to the distance of each burn severity category along each transect to represent the average burn severity across treatment types.

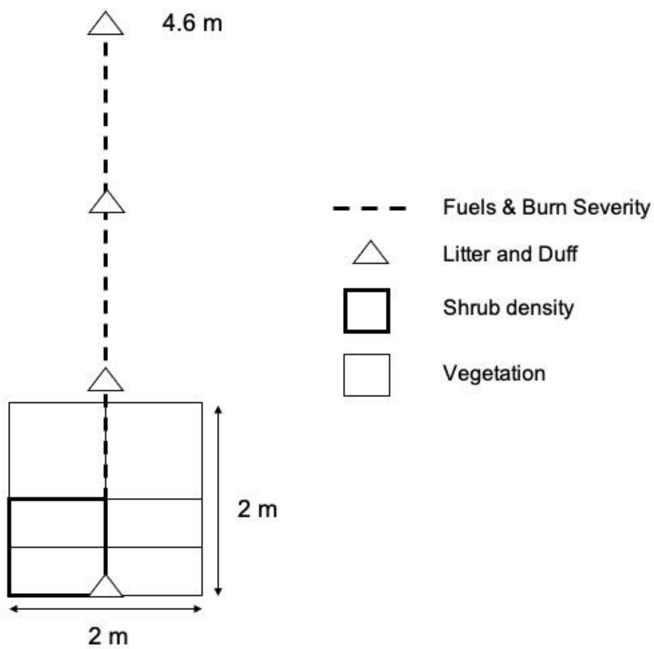


Figure 2. Illustration of vegetation plots showing sample methods for vegetation, shrub density, fuels, and burn severity data.

The planar intercept method (Brown 1974) was used to estimate dead surface fuel loading before and after the wildfire to compare fine woody fuel loading among treatment types. A transect with a length of 4.6 m was used to collect burn severity along with fuel loading and depth data starting at the base of the vegetation plot and running north through the center of the vegetation plot. Litter depth and duff depth, a fermentation and humus layer, were recorded at 0 m, 1.83 m, 3.66 m, and 4.57 m. One-hour fuels (dead woody material with a diameter less than 6.35 mm) and 10-hour fuels (dead woody material with a diameter between 6.35 mm and 25.4 mm) were counted along the first 1.8 m of the transect. One hundred-hour fuels (dead woody material with a diameter between 2.54 cm and 7.62 cm) were counted along the first 3.7 m of the transect. Standing dead shrub fuels that directly crossed the planar intercept transect were separately tallied and recorded as 1 hour, 10 hour, and 100 hour standing dead fuels. This allowed for separate analyses to be performed on fuel loading between standing dead shrubs and surface fuels. The diameter of all 1000 hour fuels (dead woody material with a diameter greater than 7.62 cm) along the entire transect was measured, and the decay class (sound or rotten) and species were recorded.

Fuel loading for each time-lag class was calculated separately for fine woody fuels (1 – 100 hour; Equation 1) and coarse woody fuels (1000 hour; Equation 2) (Brown 1974). Equation 3 was used to calculate the slope correction factor (*c*).

Equation 1: *1 - 100 Hour Fuel Load* $(\frac{Mg}{ha}) = \frac{1.234 \times n \times d^2 \times s \times a \times c}{l}$

Equation 2: *1,000 Hour Fuel Load* $(\frac{Mg}{ha}) = \frac{1.234 \times \Sigma d^2 \times s \times a \times c}{l}$

Equation 3: $c = \sqrt{1 + (\frac{Percent\ Slope}{100})^2}$

Preexisting values from Brown (1974) were used to complete fuel loading calculations. The variable *n* refers to the number of woody particles (total count) that intersected the transect for a given time-lag class. For specific gravity (*s*), a value of 0.48 was used for 1 and 10 hour fuels, 0.40 for 100 hour fuels, 0.40 for sound 1000 hour fuels, and 0.30 for rotten 1000 hour fuels. For squared average diameters (d^2), a value of 0.1 cm, 2.5 cm, and 25.8 cm were used for 1 hour, 10 hour, and 100 hour fuels, respectively. For 1000 hour fuels, diameters were measured in the field. Values for the non-horizontal correction factor (*a*) were 1.13 for 1 hour, 10 hour, and 100 hour and 1.00 for rotten and sound 1000 hour fuels. Mean surface fine woody fuel loading was calculated by taking the sum of 1 hour, 10 hour, and 100 hour fuels of each plot and averaged within each treatment unit.

To examine the shrub response to wildfire among fuel treatment types, all live shrubs within the first 1 m^2 area of each plot (Figure 2) were recorded, with heights measured for the first 5 individuals of each species closest to the southwest corner of the quadrat. Live shrub density and live shrub height were calculated for each plot and averaged at the treatment unit level. Tree and shrub canopy cover were estimated using a densiometer held at hip height in the center of the vegetation plot. The number of points intercepted by the canopy was counted (96 was the total possible number of points on a densiometer). Four canopy cover measurements in each cardinal direction were recorded, averaged, and multiplied by 1.04 (Lemmon 1956).

To study understory vegetation response to wildfire among fuel treatment types, all plants were identified within a 2 × 2 m vegetation quadrat in 2020, further subdivided into four 0.5 × 1 m quadrats. The Jepson Manual (Baldwin et al. 2012) and local plant lists from Whiskeytown National Recreation Area were used to help with identification to species level. Each understory species was recorded along with type (forb, grass, shrub), nativity, and percent cover was estimated to the nearest 1% within each quadrat.

All statistical analyses were conducted in the R environment (R Development Core Team 2021). A linear mixed effects model approach using the *lme4* (Bates et al. 2015) package was used to test all response variables including burn severity, fuel loading, shrub density and shrub height, and species richness with predictor variables of treatment type (Mast, Mast + Rx, hand-thinned, spring burned), year (pre-fire or post-fire), edge distance, and vegetation type (oak or chaparral). The random effects structure of all candidate models included plot nested within block, and fixed effects included treatment type, vegetation type, and edge distance (only for species richness). All response variables were averaged and analyzed at the block level (n = 10). Each variable, including treatment type, year (pre-wildfire vs. post wildfire), and vegetation type (oak dominated or chaparral dominated), was tested individually as well as in additive and interactive models. Species richness, the number of unique species present, was calculated in a 1 m^2 area and modeled using a mixed effects model distributed by treatment type, vegetation type (oak or chaparral), and year (pre or post fire). The relationship of species richness with canopy cover, burn severity, and litter to test for significance was modeled using linear regression.

Akaike Information Criteria (AIC) was calculated for all candidate mixed effects models to select the best explanatory and least complex model (Burnham & Anderson 1998). The model with the lowest AIC value with the fewest explanatory variables was considered as the most informative. Following model selection from AIC criteria, a post-hoc pairwise analysis was performed using a Tukey HSD test in the *emmeans* package (Lenth 2018) to further examine differences between treatment types within selected models.

RESULTS

Burn Severity

All treatment types experienced moderate burn severity (Table 1), with similar observed values for both substrate and vegetation severity measures among treatments or vegetation types ($P > 0.2$). While not statistically significant, hand thinned units in the chaparral type had the lowest substrate burn severity (2.8) and vegetation burn severity (3.1), while the Mast units had the highest (substrate = 3.8, vegetation = 3.9). The average difference between vegetation types was only 0.28. Differences in severity among treatment types within oak stands were subtle, with no noteworthy trends.

Table 1. Burn severity (mean ± SE) by treatment type and vegetation type. Burn severity values ranged from unburned (1) to heavily burned (5).

Vegetation Type	Burn Severity	Control	Hand Thinned	Mast	Mast + Rx	Spring Burn
Chaparral	Substrate	3.7 (0.3)	2.8 (0.3)	3.8 (0.2)	3.6 (0.2)	3.6 (0.3)
	Vegetation	3.5 (0.3)	3.1 (0.2)	3.9 (0.2)	3.8 (0.2)	3.8 (0.3)
Oak	Substrate	3.9 (0.2)	3.7 (0.2)	3.9 (0.3)	3.5 (0.2)	3.8 (0.3)
	Vegetation	3.7 (0.3)	3.4 (0.3)	3.6 (0.3)	3.3 (0.4)	3.8 (0.3)

Fuels

After wildfire, live shrub density and height decreased but treatment type had no effect on either variable. While there were no significant differences among treatments compared to the control, there were slight differences between the oak and chaparral vegetation types ($\chi^2 = 5.51$, $P < 0.02$; Figure 3). Average live shrub density within chaparral dominated units was about 8 shrubs per m^2, while average live shrub density within oak stands was about 13 shrubs per m^2. The lowest live shrub density was observed in the Mast units within the chaparral vegetation type (about 6 shrubs per m^2). The greatest average live shrub density was in the Mast units in oak stands (about 16 shrubs per m^2).

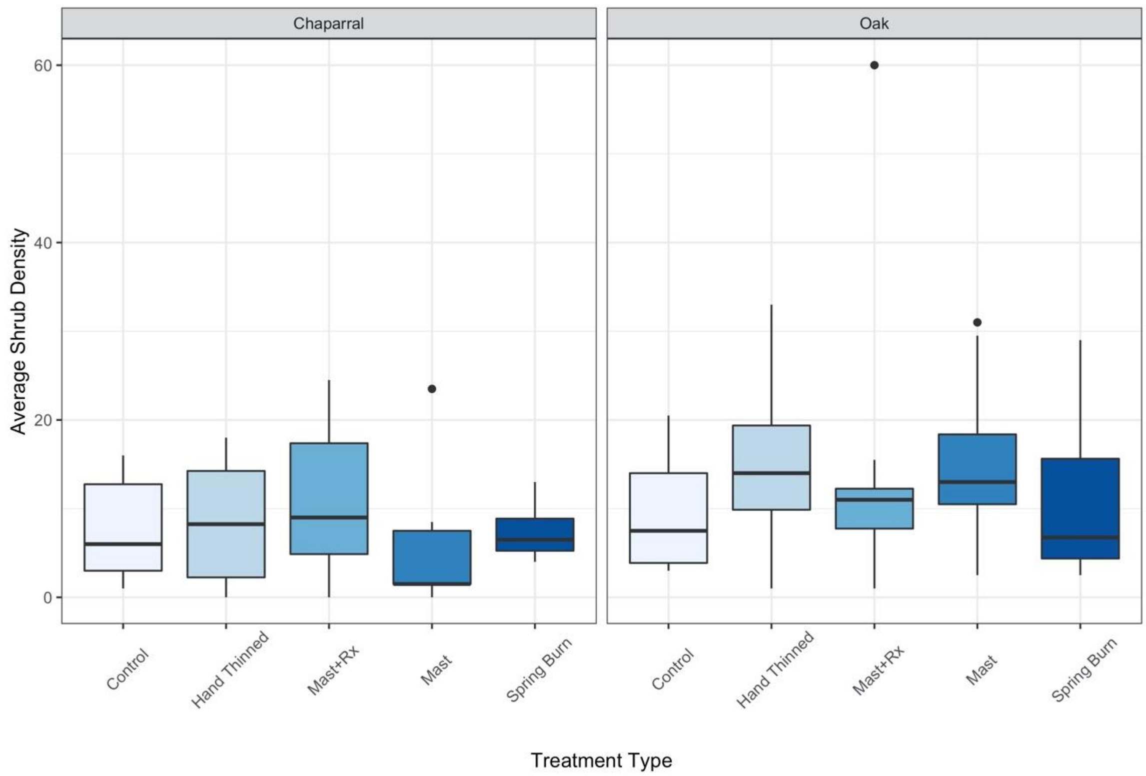


Figure 3. Average post-wildfire live shrub density per meter squared by treatment type and vegetation type.

Fine woody fuel loading expectedly decreased following wildfire across all treatments and initial differences among treatment types prior to wildfire were not maintained one year after wildfire (Table 3). Fine woody fuel loading varied by treatment type (χ^2 = 47.98, P < 0.0001) and by the interaction of treatment type and year (χ^2 = 16.89, P < 0.002). Before the wildfire, fine woody fuel loading was 48 to 73% greater in the Mast units compared to the other treatment types in the chaparral vegetation type and 13 to 53% greater in the control units in the oak vegetation type compared to other treatment types. Following wildfire, fine woody fuel in the Mast units was reduced by 80 and 87% for the chaparral and oak stands, respectively. The lowest change in fine woody fuels was in the hand-thinned units with a 14% decrease in oak and a 20% decrease in chaparral stands. Following wildfire, fine woody fuel loads in chaparral stands in both Mast units and Mast + Rx units were significantly lower than in spring burned units (t = -2.95, P < 0.03 and t = -3.80, P < 0.002 respectively). Litter depths varied by treatment type (χ^2 = 11.7, P < 0.02), vegetation type (χ^2 = 21.7, P < 0.0001), and year (χ^2 =334.1, P < 0.0001). Both before and after the wildfire, litter depths were generally higher in the oak stands than in the chaparral units (Table 2, Table 3). The oak dominated Mast units had the greatest litter depth (4.0 cm) prior to wildfire, and experienced the greatest reduction following wildfire.

Table 2. Litter depth and fine woody fuel loading (mean ± SE) by time-lag class (1-100 hr) before wildfire (2018) by treatment type (including hand-thinned, masticated only (Mast.), masticated and burned (Mast + Rx), and prescribed burn only (spring burn) and vegetation type (chaparral or oak).

Vegetation Type	Category	Control	Hand Thinned	Mast	Mast + Rx	Spring Burn
Chaparral	Litter (cm)	2.0 (0.3)	1.9 (0.6)	2.4 (0.3)	1.8 (0.2)	2.8 (0.5)
	1-hr (Mg/ha)	0.4 (0.1)	0.2 (0.1)	0.3 (0.1)	0.2 (0.0)	0.2 (0.0)
	10-hr (Mg/ha)	2.1 (0.6)	1.7 (0.4)	5.6 (1.3)	2.1 (0.5)	2.8 (0.8)
	100-hr (Mg/ha)	1.6 (0.9)	1.6 (0.6)	7.5 (2.5)	3.8 (1.2)	3.9 (2.2)
	Fine woody fuels (Mg/ha)	4.1 (1.1)	3.5 (0.9)	13.4 (3.5)	6.1 (1.4)	7.0 (2.7)
Oak	Litter (cm)	2.5 (0.3)	3.2 (0.5)	4.0 (0.3)	3.1 (0.3)	3.4 (0.3)
	1-hr (Mg/ha)	0.5 (0.1)	0.3 (0.1)	0.3 (0.1)	0.2 (0.1)	0.3 (0.1)
	10-hr (Mg/ha)	4.4 (0.8)	1.8 (0.3)	4.2 (0.7)	2.4 (0.5)	3.4 (0.5)
	100-hr (Mg/ha)	7.1 (2.0)	3.6 (1.0)	5.9 (1.2)	5.2 (1.7)	5.0 (1.4)
	Fine woody fuels (Mg/ha)	12.0 (2.5)	5.7 (1.2)	10.4 (1.7)	7.9 (1.9)	8.8 (1.7)

Table 3. Litter depth and fine woody fuel loading (mean ± SE) by time-lag class (1-100 hr) after wildfire (2019) by treatment type (including hand-thinned, masticated only (Mast.), masticated and burned (Mast + Rx), and prescribed burn only (spring burn) and vegetation type (chaparral or oak).

Vegetation Type	Category	Control	Hand Thinned	Mast	Mast + Rx	Spring Burn
Chaparral	Litter (cm)	0.8 (0.2)	0.5 (0.1)	0.5 (0.1)	0.4 (0.1)	0.4 (0.1)
	1-hr (Mg/ha)	0.2 (0.1)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)
	10-hr (Mg/ha)	1.0 (0.3)	1.1 (0.4)	0.9 (0.3)	1.0 (0.3)	2.2 (0.9)
	100-hr (Mg/ha)	0.5 (0.4)	1.6 (0.7)	0.7 (0.3)	0.0 (0.0)	1.8 (0.6)
	Fine woody fuels (Mg/ha)	1.7 (0.5)	2.8 (1.0)	1.8 (0.5)	1.1 (0.3)	4.3 (1.3)
Oak	Litter (cm)	0.7 (0.2)	1.1 (0.2)	1.1 (0.2)	1.1 (0.1)	1.1 (0.2)
	1-hr (Mg/ha)	0.2 (0.1)	0.2 (0.0)	0.3 (0.0)	0.2 (0.0)	0.2 (0.0)
	10-hr (Mg/ha)	1.2 (0.3)	1.0 (0.3)	1.5 (0.3)	1.4 (0.4)	1.7 (0.4)
	100-hr (Mg/ha)	2.6 (0.7)	3.7 (1.2)	0.3 (0.3)	2.5 (0.7)	3.5 (1.1)
	Fine woody fuels (Mg/ha)	3.9 (0.9)	4.9 (1.3)	2.1 (0.4)	4.1 (0.9)	5.4 (1.4)

Understory Vegetation

Species richness increased following wildfire across all treatments but differences among treatments were modest and varied between vegetation types (Table 4 and Table 5). Total species richness varied by year (χ^2 = 306.7, P < 0.0001), the interaction of treatment type and year (χ^2 = 30.1, P < 0.0001), and the interaction of vegetation type and year (χ^2 =86.9, P < 0.0001). Changes in species richness following wildfire ranged from two fewer species in the chaparral dominated hand-thinned units to 13 more species in the spring burned units in oak stands. Pre-wildfire chaparral units had about four more plant species than the oak stands, while post-wildfire oak stand had about three more plant species than chaparral stands. The control and hand-thinned units in post-wildfire chaparral stands had the greatest difference compared to the other treatment types, with five fewer plant species in the hand-thinned units than in the control units (t ratio = 3.54, P = 0.0042). Exotic species richness levels were highest in the control units of both chaparral and oak stands after the fire. Within oak stands following fire, the Mast + Rx treatments had fewer exotic species than the control (t ratio = 2.75, P = 0.0492), while the other treatments showed no difference from the control.

Table 4. Native, exotic, and total species richness (mean ± SE) per m^2 before wildfire (2018).

Vegetation Type	Origin	Control	Hand Thinned	Mast	Mast + Rx	Spring Burn
Chaparral	Native	8.2 (0.7)	11.1 (0.6)	10.7 (0.6)	10.5 (0.6)	9.7 (0.6)
	Exotic	2.9 (0.7)	4.0 (0.3)	2.9 (0.4)	3.9 (0.3)	2.7 (0.7)
	Total	11.1 (1.1)	15.1 (0.7)	13.6 (0.8)	14.5 (0.7)	12.3 (1.1)
Oak	Native	7.4 (0.6)	8.1 (0.7)	8.1 (0.9)	7.4 (0.5)	6.1 (0.6)
	Exotic	1.3 (0.4)	1.7 (0.5)	1.8 (0.4)	1.8 (0.4)	0.6 (0.3)
	Total	8.6 (0.9)	9.8 (1.1)	9.9 (1.2)	9.2 (0.8)	6.7 (0.8)

Table 5. Native, exotic, and total species richness (mean ± SE) per m^2 after wildfire (2020).

Vegetation Type	Origin	Control	Hand Thinned	Mast	Mast + Rx	Spring Burn
Chaparral	Native	12.2 (0.7)	9.3 (0.8)	10.8 (0.8)	10.9 (0.8)	12.1 (0.9)
	Exotic	5.9 (0.5)	3.7 (0.3)	4.6 (0.4)	4.0 (0.4)	5.4 (0.4)
	Total	18.1 (1.0)	13.0 (0.9)	15.4 (1.0)	14.9 (1.0)	17.5 (1.0)
Oak	Native	13.3 (0.7)	13.4 (0.7)	12.6 (0.6)	12.3 (0.5)	13.6 (0.7)
	Exotic	6.3 (0.4)	5.6 (0.2)	5.7 (0.3)	5.0 (0.3)	6.2 (0.4)
	Total	19.6 (0.8)	18.9 (0.7)	18.2 (0.7)	17.3 (0.6)	19.8 (0.8)

Total species richness decreased with increasing canopy cover. Species richness was best modeled with the interaction of canopy cover and vegetation type (Figure 4, canopy cover: t ratio = -2.67, P = 0.009; vegetation type: t ratio = 4.68, P < 0.0001; canopy cover × vegetation type: t ratio = -5.23, P < 0.0001). Litter depth and burn severity were both poor predictors of species richness (litter: t ratio = -1.06, P > 0.05; vegetation burn severity: t ratio = -0.68, P > 0.05; substrate burn severity: t ratio = - 0.06, P > 0.05).

Treatment type had no effect on total plant cover (both native and exotic species), but native cover decreased and exotic cover increased in all treatment types two years following wildfire (Figure 5). Total plant cover varied by year (χ^2 = 43.2, P < 0.0001) and vegetation type (χ^2 =19.4, P < 0.0001). Prior to wildfire, native cover was 6.6% to 8.1% greater than exotic species cover in chaparral sites and 6.2% to 11.2% greater in oak stands. The only exception was in the hand thinned units and Mast units within chaparral sites, the exotic species percent cover was 1.9% and 2.6% greater than native cover, respectively. Exotic species cover after wildfire ranged from 9.6% to 25.1% greater than native species cover in chaparral sites and 0.4% to 8.3% in oak stands. Exotic species cover, when analyzed separately, differed significantly by treatment type (χ^2 = 23.0, P < 0.0001), vegetation type (χ^2 = 25.3, P < 0.0001), year (χ^2 = 165.3, P < 0.0001), and the interaction of treatment type and vegetation type (χ^2 = 10.4, P < 0.04). The highest post-wildfire exotic cover was found in Mast and Mast + Rx (32.8% and 32.1% respectively) units within chaparral stands, while the lowest post-wildfire exotic cover values were in Spring burned oak stands (11.3%). Chaparral stands had greater exotic species cover than oak stands by about 10%. Spring burn was the only treatment type that was not significantly different from the control in its levels of exotic species cover both before and after wildfire in chaparral stands (t < 0.6, p > 0.9).

Live shrub cover decreased and grass cover increased after wildfire in all treatment types (Figure 6). Forb cover increased slightly in chaparral sites but more in oak stands. Grasses accounted for most of the plant cover after wildfire in all treatment types but were highest in the Mast and Mast + Rx units in chaparral sites. Exotic grass levels were greater in chaparral sites than oak stands after wildfire.

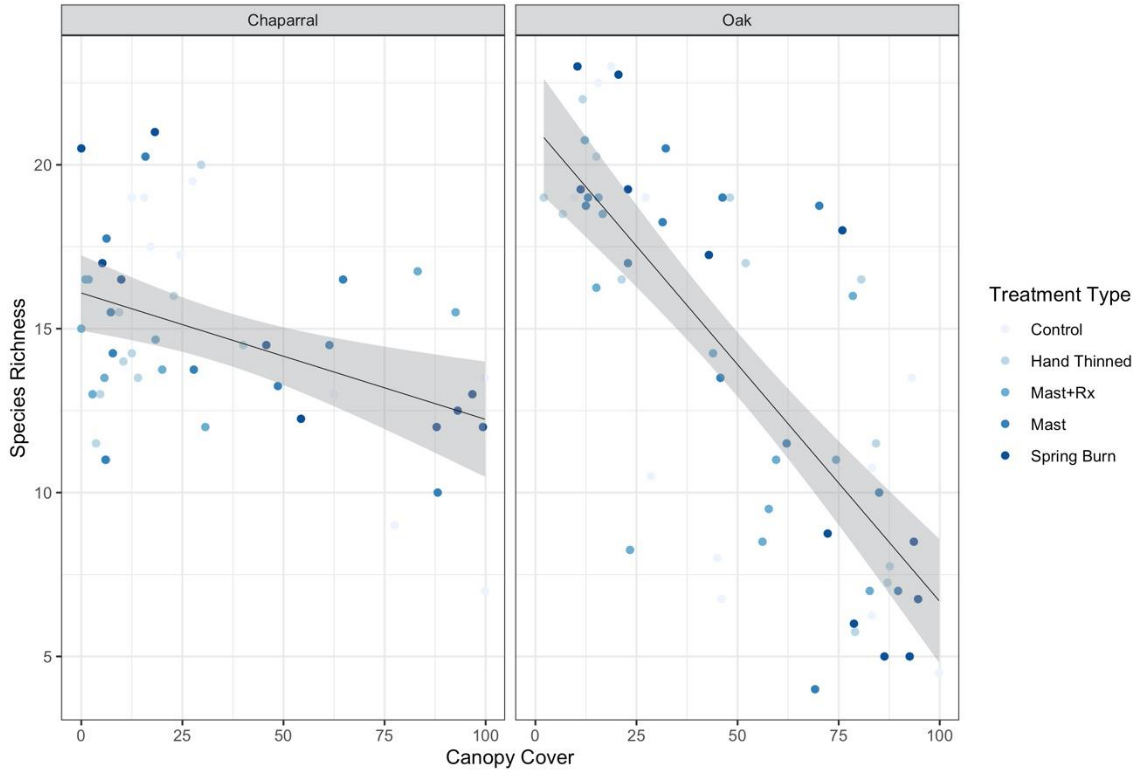


Figure 4. Relationship between average species richness (per m^2) and canopy cover (%) by treatment type and vegetation type.

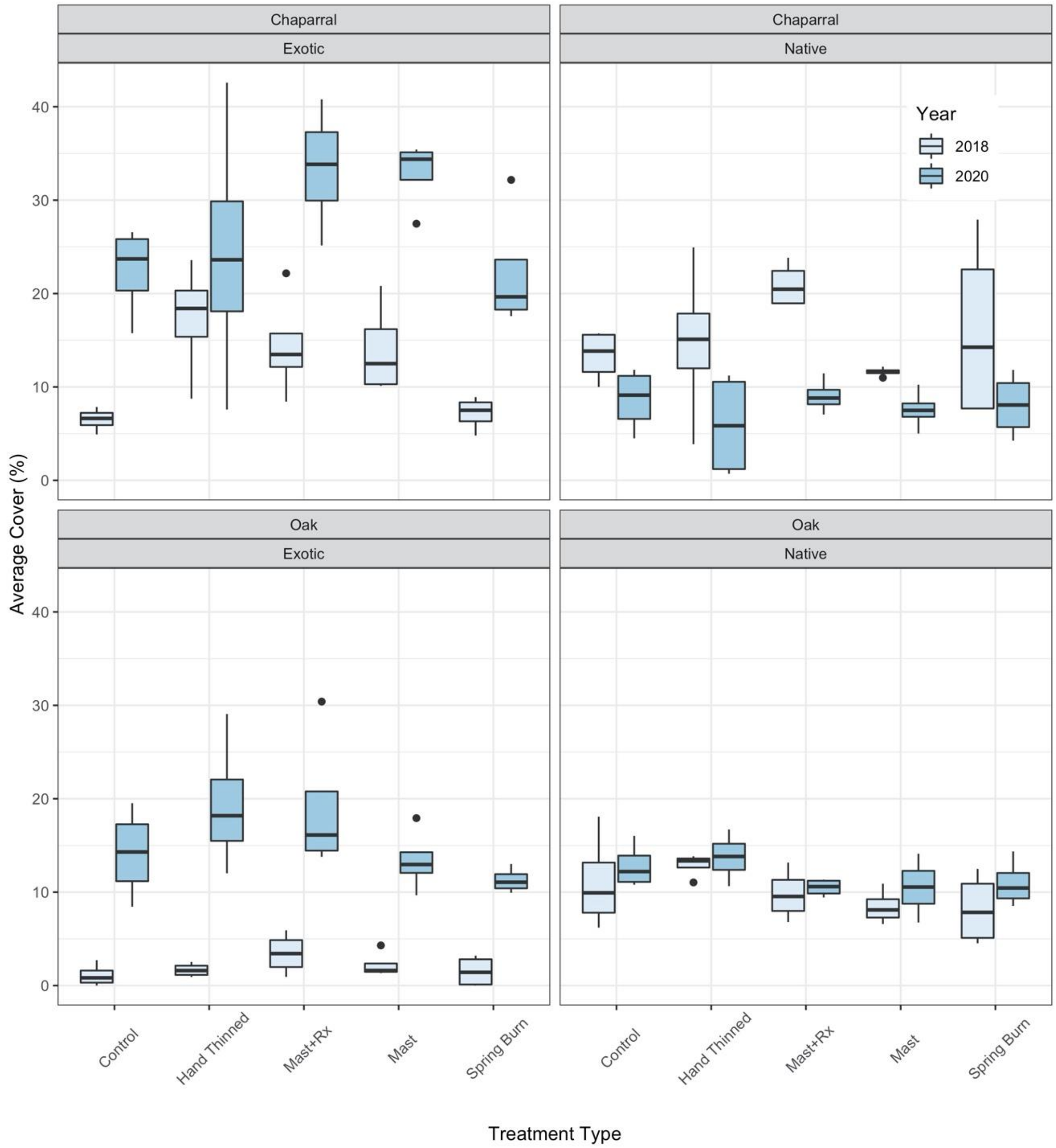


Figure 5. Average percent cover (per m^2) of exotic species and native species before (2018) and after (2020) wildfire by treatment type and vegetation type.

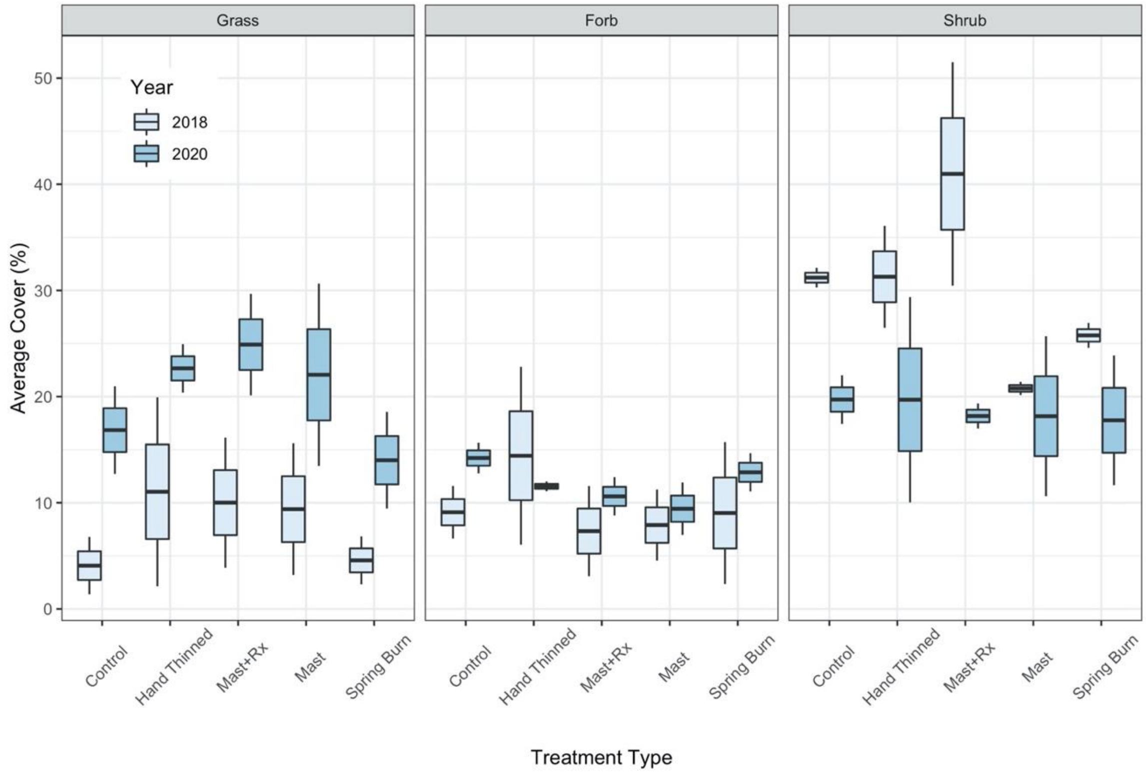


Figure 6. Average percent cover (per m^2) of grass, forb, and shrub lifeforms before (2018) and after (2020) wildfire by treatment type.

DISCUSSION

With increasing wildfires combined with warmer and drier climates, land managers in chaparral ecosystems often rely on fuel treatments to limit negative impacts from wildfire, but sufficient information on the longevity of treatment effectiveness is not well understood. To our knowledge, this study represents the first to observe the long-term (15 years) effectiveness of commonly used fuel treatments in chaparral ecosystems when directly exposed to a wildfire. While there were differences between control sites and treated areas prior to the wildfire, all fuel treatments had relatively consistent responses following wildfire based on multiple measures of fuels and vegetation. Changes in severity, fuel loading, and vegetation were more distinct between vegetation type (chaparral or oak) than by treatment type. Our findings of limited long-term effectiveness of fuel treatments in chaparral vegetation types in northern California, while somewhat unexpected, provide managers with more information to assess the utility of these treatments to meet management goals.

Burn Severity

All treatments were largely ineffective in reducing burn severity compared to untreated stands. This finding was unexpected at our site since pre-wildfire fuel structure and loading for some treatments were far below control levels (Martorano et al. 2021). It is likely that the prolonged time since treatment (15 years) resulted in sufficient fuel recovery to limit any observable reduction in fire severity. The lack of effectiveness of fuels treatments to modify fire behavior and effects in chaparral stands has been suggested, with previous observations of fires carrying easily through young stands (e.g. Dunn 1989, Conrad and Weise 1998, Moritz 2003).

While time since treatment in our study may have been too long to affect burn severity within treated areas, the small treatment units utilized in our study may have limited reductions in fire severity. Treatment sizes used for this study, which ranged from 0.01 to 0.15 ha, may have been too small to influence fire intensity regardless of treatment type. Information on size of treatments necessary for effectively reducing fire behavior is generally limited, and even more so in chaparral ecosystems. Previous studies that have examined the effectiveness of treatments in forested areas to wildfire found that edge areas experienced similar fire effects to untreated areas (Agee and Skinner 2005, Safford et al. 2009). Treatment sizes in these two studies were also substantially larger (5-194 ha) than the units in our study. If fuel treatments are not sufficiently large enough, they may not be effective at reducing fire behavior, and thus fire severity (Graham et al. 2004; Agee and Skinner 2005).

Fuels

Treatment differences in shrub height and density prior to wildfire did not result in distinct post-fire shrub responses. Prior to wildfire, spring burned units had greater shrub cover than Mast units, even 15 years after treatment implementation. Following wildfire, however, differences were greatly diminished, and shrub cover was only 1% greater in spring burned units than in Mast units in chaparral stands. It is possible that there may have been sufficient seed banks and resprouting species present, which would contribute to diminished differences following wildfire. Although not statistically significant, both before and after wildfire the Mast units had the lowest average shrub density in chaparral vegetation types. This may have been from the mastication process killing underground root structures of resprouting species, as well as mastication debris inhibiting seed germination of obligate seeders.

Post-wildfire fine woody fuel loading differed among fuel treatment types, with spring burned units having significantly greater fine woody fuel loading than both the Mast and Mast + Rx units. Spring burned units had a relatively low reduction in fine woody fuels following the wildfire and had the greatest post-wildfire fine woody fuel levels in chaparral sites. This difference was likely due to an overall lack of shrub mortality or consumption in the initial prescribed burning treatment, leaving unconsumed fuels within the units. One study in northern California found that prescribed burning in chaparral sites reduced shrub fuels for a shorter time than mastication over a 10-year period (Wilkin et al. 2017). This study, along with our results suggest that it is possible that prescribed burning may need to be done more often than mastication to maintain effectiveness in terms of shrub recovery and height.

Lower post-fire fine woody fuel loading (i.e. greater consumption) in Mast units was expected due to elevated fine woody fuel levels 15 years after treatment compared to control units (Martorano et al. 2021). Although not statistically significant, post-wildfire Mast units had the highest average vegetation and substrate burn severity, as well as the greatest reduction in fine woody fuels and a slightly decreased live shrub density compared to other treatment types and the control units.

Vegetation

Treatment type did not strongly influence post-wildfire species richness, likely because treatments did not substantially reduce fire behavior or fire severity. There was a significant increase in exotic plant species cover and richness (mostly grasses) and a noticeable decline in native plant species cover and richness, particularly in chaparral stands, in all treatment types after wildfire. Annual precipitation was 49% above average the year following the Carr Fire, possibly contributing to a stronger exotic species response. Following wildfire, shrub cover decreased the most in our study, while forb plant cover amounts barely changed from pre-wildfire levels, and grass cover increased drastically. These changes are consistent with previous studies and are similarly concerning given that exotic grasses are often associated with slower recovery of shrublands and increase vulnerability to type conversion to exotic annual grasslands (Zedler et al. 1983, D’Antonio and Vitousek 1992, Davis et al. 2001, Dickens and Allen 2014).

The increase in exotic species cover following wildfire was expected, since exotic species often colonize burned areas more quickly than native species (Dickens and Allen 2014). In the pre-wildfire study, hand-thin and Mast + Rx units in chaparral stands had the greatest increase in exotic species cover over 15 years (Martorano et al. 2021). Following wildfire, differences in exotic species cover between treatment types remained significant. Spring burned units within both oak stands and chaparral stands were the only treatments that had significantly lower exotic species compared to other treatments including the control units. The lower exotic species cover in spring burned units, similar to the low levels of fuel reduction in spring burned units, could be from the low intensity prescribed burns that took place during the original treatment implementation. Exotic species often benefit from disturbed areas with increased sunlight and water (D'Antonio and Vitousek 1992), allowing them to rapidly spread. In the chaparral stands two years following treatment, spring burned treatments were the least successful at reducing shrub cover as compared to the other treatments (Martorano et al. 2021), limiting disturbed area and amount of sunlight available to understory species. Additionally, a low intensity prescribed burn likely failed to kill underground root structures of shrubs, allowing shrub recovery and more intact native species than units that experienced more intense vegetation removal treatments, such as mastication.

Shrub dominance prior to wildfire shifted to exotic grasses after wildfire. In a study in southern California during the first five years following wildfire, over 75 species of exotic plants were recorded, with exotic plant cover peaking in the second year after wildfire (Keeley et al. 2005). The strongest factor that affected the presence of exotic plants following wildfire was postfire recovery of woody plant canopy, with less woody plant canopy came increased exotic plant species. In our study, out of all treatment types in the chaparral units, hand-thinned treatments resulted in the lowest increase in exotic grasses following wildfire, while the spring burned units had the lowest overall post-fire exotic grass cover. With decreased canopy cover, our study found increased exotic species cover. These results suggest that chaparral stands are possibly more vulnerable than oak stands to post-wildfire exotic species invasion and that Mast and Mast + Rx treatments may negatively impact the native chaparral plant communities more so than hand-thinning and spring burning. It is likely that reduced canopy cover promotes exotic invasion when disturbed (Keeley et al. 2005). From these findings, it can be inferred that treatments that are more effective at disturbing and removing canopy cover can increase risk for invasion of exotic species.

Implications

The time since treatment for this study (15 years) was likely too long to maintain fuel loading effectiveness due to shrub and understory recovery. This strongly suggests that follow-up treatments may need to be administered within 15 years of treatment. Previous studies have recommended retreatment of areas every 10 to 20 years (Wilkin et al. 2017). Our study, which was within this timeframe, suggests that this is likely too long, and that more frequent retreatment would be needed to maintain treatment efficacy. The timeframe in which previous studies (Brennan and Keeley 2015, Wilkin et al. 2017) show shrubs recovering within 10 years following treatments is an indicator of how frequently these areas would need to be treated. Retreating areas every 10 years, however, may be too frequent to maintain the health and integrity of a chaparral ecosystem. Disturbances at too high of a frequency is one of the greatest threats to chaparral ecosystems (Franklin et al. 2014), and could support the further invasion of exotic species, rather than the recovery of native herbaceous and shrubby plants, leading to a possible replacement of chaparral shrublands with exotic annual grasses (Zedler et al. 1983, Brooks et al. 2004, Keeley and Brennan 2017, Syphard et al. 2019). Chaparral sites need anywhere from 5 to 15 years to recover from fire disturbance (Zedler 1995). Fuel treatments, such as mastication and prescribed fire, which may result in expansion of non-native species (Brennan and Keeley 2017, Potts and Stephens 2009, Coulter et al. 2010), especially when followed by wildfire. Our results suggest that hand-thinning treatments may be the most effective at reducing consumption and limiting exotic grasses.

Repeated disturbances, such as fuel treatments of shrublands, especially at a rate greater than an ecosystem’s historic disturbance interval (in this case 30 to 100 years) will likely lead to a continued expansion of exotic species and a higher potential for type conversion to exotic annual grasslands (Fried et al. 2004). Implications from our study suggest that frequent maintenance is necessary to maintain the effectiveness of fuel treatments in chaparral, with the possible repercussion of type conversion to exotic annual grasslands. Frequent treatment will likely increase exotic species cover, potentially resulting in positive fire feedback cycles which would also be problematic for the wildland urban interface. Because of this, we suggest that fuel treatments in chaparral are generally not compatible with maintaining ecosystem integrity, and therefore, should be used in areas where type conversion is acceptable to land managers and focused on areas surrounding infrastructure and human communities or for fuel breaks to aid in fire suppression.

LITERATURE CITED

Abatzoglou, J.T., & Williams, A.P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*, 113(42), 11770-11775.

Agee, J.K. & Skinner, C.N. (2005). Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*, 211(1-2), 83-96.

Baldwin, B.G., Goldman, D., Keil, D.J., Patterson, R., & Rosatti, T.J. (2012). The Jepson Manual Vascular Plants of California, Thoroughly Revised and Expanded. University of California Press, Los Angeles, USA.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software*, 67(1), 1–48.

Bradley, T., Gibson, J., & Bunn, W. (2006). Fuels management and non-native plant species: an evaluation of fire and fire surrogate treatments in a chaparral plant community. Final Report to the Joint Fire Science Program.

Brennan, T.J., & Keeley, J.E. (2017). Impacts of mastication fuel treatments on California, USA, chaparral vegetation structure and composition. *Fire Ecology*, 13(3), 120-138.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., & Pyke, D. (2004). Effects of Invasive Alien Plants on Fire Regimes. *BioScience*, 54(7), 677.

Brown, J.K. (1974). Handbook for inventorying downed woody material. USDA Forest Service, General Technical Report INT-16. United States Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. Ogden, Utah, USA.

Burnham K.P., & Anderson D.R. (1998). Model Selection and Inference: A Practical Information-Theoretic Approach. Springer, New York, New York, USA.

Busse, M.D., Hubbert, K.R., Fiddler, G.O., Shestak, C.J., & Powers, R. F. (2005). Lethal soil temperatures during burning of masticated forest residues. *International Journal of Wildland Fire*, 14, 267-276.

Busse, M.D., Shestak, C.J., Hubbert, K.R., & Knapp, E.E. (2010). Soil physical properties regulate lethal heating during burning of woody residues. *Soil Science Society of America Journal*, 74, 947-955.

CalFire (2018). CalFire Green Sheet: Burn Over Fatalities July 26, 2018, Carr Incident 18-CA-SHU-007808, 18-CA-SHU-007962, California Northern Region.

CalFire (2021a). Top 20 Most Destructive California Wildfires. https://www.fire.ca.gov/media/t1rdhizr/top20_destruction.pdf

CalFire (2021b). Top 20 Largest California Wildfires. https://www.fire.ca.gov/media/4jandlhh/top20_acres.pdf

Conrad, S.G., & Weise, D.R. (1998). Management of fire regime, fuels, and fire effects in southern California chaparral: lessons from the past and thoughts for the future. Pages 342-350 *in* Teresa L. Pruden and Leonard A. Brennan (eds.). Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20. Tall Timbers Research Station, Tallahassee, FL.

Coulter, C.T., Southworth, D., & Hosten, P.E. (2010). Prescribed fire and post-fire seeding in brush masticated oak-chaparral: Consequences for native and nonnative plants. *Fire Ecology*, 6(2), 60-75.

D'Antonio, C.M. & Vitousek, P.M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23, 63-87.

Davis, M.A. & Pelsor, M. (2001). Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters*, 4(5), 421-428.

Dickens, S.J.M., & Allen, E.B. (2014). Exotic plant invasion alters chaparral ecosystem resistance and resilience pre- and post-wildfire. *Biological Invasions,* 16, 1119-1130.

Dunn, A.T. (1989). The effects of prescribed burning on fire hazard in the chaparral: toward a new conceptual synthesis. Pages 23-24 *in* N.H. Berg (technical coordinator). Proceedings of the symposium on fire and watershed management. General Technical Report PSW-109, U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Franklin, J., Regan, H.M., & Syphard, A.D. (2014). Linking spatially explicit species distribution and population models to plan for the persistence of plant species under global change. *Environmental Conservation,* 41, 97-109.

Fried, J.S., Torn, M.S. and Mills, E. (2004). The impact of climate change on wildfire severity: a regional forecast for northern California. *Climatic Change*, 64(1), 169-191.

Graham, R.T., McCaffrey, S. & Jain, T.B., (2004). *Science basis for changing forest structure to modify wildfire behavior and severity*. United States Department of Agriculture Forest Service, Rocky Mountain Research Station.

Hammer, R.B., Radeloff, V.C., Fried, J.S., & Stewart, S.I. (2007). Wildland-urban interface housing growth during the 1990s in California, Oregon, and Washington. *International Journal of Wildland Fire*, 16(3), 255.

Horton, J.S. & Kraebel, C.J. (1955). Development of vegetation after fire in the chamise chaparral of southern California. *Ecology*, 36, 244-262.

Jain, T.B., Graham, R.T., Sandquist, J., Butler, M., Brockus, K., Cobb, D., Sup-Han, H., Halbrook, J., Denner, R., & Evans, J.S. (2007). Restoration of northern Rocky Mountain moist forests: Integrating fuel treatments from the site to the landscape. Gen. Tech. Rep. PNW-GTR-733. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station.

Kane, J.M., Varner, J.M., & Knapp, E.E. (2009). Novel fuelbed characteristics associated with mechanical mastication treatments in northern California and south-western Oregon, USA. *International Journal of Wildland Fire*, 18(6), 686-697.

Kane, J.M., Varner, J.M., Knapp, E.E., & Powers, R.F. (2010). Understory vegetation responses to mechanical mastication and other fuels treatments in a ponderosa pine forest. *Applied Vegetation Science*, 13(2), 207-220.

Keeley, J.E. & Keeley, S.C. (1988). Chaparral. *North American Terrestrial Vegetation.*, 165-207. M. G. Barbour and W. D. Billings (eds). New York: Cambridge University Press.

Keeley, J.E. (1991). Fire management for maximum biodiversity of California chaparral. In Nodvin, S. C.; Waldrop, T. A. (Eds), Fire and the Environment: Ecological and Cultural Perspectives. Gen. Tech. Rep. SE-69. (pp. 11-14). Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station.

Keeley, J.E. (2001). Fire and invasive species in Mediterranean-climate ecosystems of California. Pages 81-94 in: K.E.M. Galley and T.P. Wilson, editors. Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Tall Timbers Research Station, Tallahassee, Florida, USA.

Keeley, J.E., & Fotheringham, C.J. (2001). History and management of crown-fire ecosystems: A Summary and Response. *Conservation Biology*, 15(6), 1561-1567.

Keeley, J.E. (2002). Fire management of California shrubland landscapes. *Environmental Management*, 29(3), 395-408.

Keeley, J.E., Baer-Keeley, M., & Fotheringham, C.J. (2005). Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications*, 15, 2109-2125.

Keeley, J.E. & Davis, F.W. (2007). *Terrestrial Vegetation of California.* Pages 339-366 in: M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, editors. University of California Press, Los Angeles, USA.

Keeley, J.E. & Brennan T.J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, 169, 1043-1052.

Knapp, E.E., Keeley, J.E., Ballenger, E.A., & Brennan, T.J. (2005). Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fires in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*, 208, 383-397.

Kreye, J.K., Brewer, N.W., Morgan, P., Varner, J.M., Smith, A.M., Hoffman, C.M., & Ottmar, R.D. (2014). Fire behavior in masticated fuels: a review. *Forest Ecology and Management*, 314, 193-207.

Le Fer, D. & Parker, V.T. (2005). The effect of seasonality of burn on seed germination in chaparral: the role of soil moisture. *Madroño*, 52(3), 166-174.

Lemmon, P.E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science*, 2(4), 314-320.

Lenth, R.V. (2018) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.0

Martorano, C.A., Kane, J.M., Engber, E.A., & Gibson, J. (2021). Long-term fuel and understory vegetation response to fuel treatments in oak and chaparral stands of northern California. *Applied Vegetation Science*, 24, e12551.

National Park Service (2003). Fire Monitoring Handbook. Boise (ID). Fire Management

Program Center, National Interagency Fire Center.

National Park Service (2020). The Carr Fire at Whiskeytown. https://www.nps.gov/whis/carrfire.htm.

Perchemlides, K.A., Muir, P.S., & Hosten, P.E. (2008). Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in Southwestern Oregon. *Rangeland Ecology & Management*, 61(1), 98-109.

Potts, J.B. & Stephens, S.L. (2009). Invasive and native plant responses to shrubland fuel reduction: Comparing prescribed fire, mastication, and treatment season. *Biological Conservation*, 142(8), 1657-1664.

PRISM [PRISM Climate Group]. (2019). PRISM Climate Data. <http://prism.oregonstate.edu>. Oregon State University, Corvallis, Oregon, USA (accessed 26 October 2019).

Quinn, R.D. & Keeley, S.C. (2006). *Introduction to California Chaparral*. University of California Press, Berkeley, California, USA.

R Development Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radeloff, V.C., Helmers, D.P., Kramer, H.A., Mockrin, M.H., Alexandre, P.M., Bar-Massada, A., Butsic, V., Hawbaker, T.J., Martinuzzi, S., Syphard, A.D. & Stewart, S.I. (2018). Rapid growth of the US wildland-urban interface raises wildfire risk. *Proceedings of the National Academy of Sciences*, 115(13), 3314-3319.

Reed, W.P., Varner, J.M., Knapp, E.E., Kreye, J.K. (2020). Long-term changes in masticated woody fuelbeds in northern California and southern Oregon, USA. *International Journal of Wildland Fire*, 29, 807-819.

Rothermel, R.C. (1991). *Predicting behavior and size of crown fires in the Northern Rocky Mountains* (Vol. 438). US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Ryan, K.C., Knapp, E.E., & Varner, J.M. (2013). Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the Environment*, *11*(s1), e15-e24.

Safford, H.D., Schmidt D.A., & Carlson, C.H. (2009). Effects of fuel treatments on fire severity in an area of wildland–urban interface, Angora Fire, Lake Tahoe Basin, California. *Forest Ecology and Management*, 258, 773-787.

Stephens, S.L., Moghaddas, J. J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., McIver, J.D., Metlen, K. Skinner, C.N., & Youngblood, A. (2009). Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecological Applications*, 19(2), 305-320.

Syphard, A.D., Radeloff, V.C., Keeley, J.E., Hawbaker, T.J., Clayton, M.K., Stewart, S.I., & Hammer, R.B. (2007). Human influence on California fire regimes. *Ecological Applications*, 17(5), 1388-1402.

Syphard, A.D., Radeloff, V.C., Hawbaker, & T.J., Stewart, S.I. (2009). Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conservation Biology*, 23(3), 758-769.

Syphard, A.D., Brennan, T.J., & Keeley, J.E. (2019). Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Diversity and Distributions*, 25, 90-101.

USDA NRCS [United States Department of Agriculture, Natural Resources Conservation Science]. (2020). National Cooperative Soil Survey (NCSS) Soil Characterization. <https://nrcs.maps.arcgis.com/apps/webappviewer/index.html?id=956154f98fc94edeaa2dbad99bb224af> Accessed April 12, 2020.

Wilkin, K.M., Ponisio, L.C., Fry, D.L., Tubbesing, C.L., Potts, J.B., & Stephens, S.L. (2017). Decade-long plant community responses to shrubland fuel hazard reduction. *Fire Ecology*, *13*(2), 105-136.

Yoder, J., Engle, D., & Fuhlendorf, S. (2004). Liability, incentives, and prescribed fire for ecosystem management. *Frontiers in Ecology and the Environment*, *2*(7), 361-366.

Zedler, P.H., Gautier, C.R., & McMaster, G.S. (1983). Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology*, 64, 809-818.

Zedler, P.H. (1995). Fire frequency in southern California shrublands: biological effects and management options. Pages 101-112 *in* J.E. Keeley and T. Scott, editors. *Brushfires in California wildlands: ecology and resource management*. International Association of Wildland Fire, Missoula, Montana, USA.

CHAPTER 2: ADVANCING POST-FIRE TREE MORTALITY MODELS TO LIMIT FIRE-INDUCED OAK MORTALITY

ABSTRACT

Post-fire tree mortality modeling is an important and commonly used tool among land managers aiming to predict mortality, particularly in prescribed burn planning and hazard tree removal following wildfire. Current models may not adequately predict mortality for many oaks and other hardwood species and lack the ability to predict resprouting response. The goal of the study was to predict tree mortality and resprouting in two oak species, California black oak (*Quercus kelloggii)* and canyon live oak (*Q. chrysolepis*) following wildfire and prescribed fire in northern California. The objectives of this study were: 1) to quantify bark thickness for both species across two sites with different fuel structures; 2) to compare post-fire mortality model performance based on a logistic regression and random forest model approaches; and 3) to examine the relationships of tree diameter and fire effects (bole char and severity measures) to predict post-fire basal resprouting. California black oak expectedly had thicker bark than canyon live oak, and bark thickness was greater in open grass sites versus shrub dominated sites for California black oak trees. Both modeling approaches performed well, but Random Forest was better at predicting probability of mortality for an imbalanced dataset. Basal resprouting was best predicted by bole char height, diameter, and vegetation burn severity. There was a greater resprouting response at the wildfire site (Whiskeytown),

than at the prescribed burned site (Shasta), but no differences were found between the two species' resprouting response. Our results suggest that when using imbalanced datasets, logistic regression can underpredict mortality, which can have negative repercussions for land managers dealing with recently burned ecosystems containing oaks.

INTRODUCTION

Oak woodlands and forests are regarded as ecologically and culturally important ecosystems (e.g., Long et al. 2016). In the western US, a century of fire exclusion has led to dense forest conditions, compositional shifts, and substantial fuel accumulation, resulting in a decline in the integrity and persistence of many oak ecosystems. In the prolonged absence of fire, oaks often become overcrowded and outcompeted by shade tolerant species (Hunter and Barbour 2001), eventually leading to oak mortality (Schriver et al. 2018, Knight et al. 2020). Reintroduction of low intensity prescribed fire in long unburned stands often does not sufficiently reduce competition of shade tolerant species and can further reduce oak vigor (Cocking et al. 2014). Some managers have observed increased mortality in large oaks following low severity fire (E. Engber, *personal communication*). While higher severity fire can be more effective in killing competitors, this typically requires the top-killing of large legacy oaks (Cocking et al. 2014). Managers interested in reintroducing prescribed fire and retaining large legacy oaks are hindered in their planning efforts due in part to limitations in predicting post-fire tree mortality.

Models of post-fire tree mortality are frequently used to inform land management and planning decisions regarding the application of prescribed fire, hazard tree removal, and post-wildfire treatments to better meet management objectives. The First Order Fire Effects Model (FOFEM 6.5, Lutes 2019) and the Fire and Fuels Extension of the Forest Vegetation Simulator (FVS-FFE; Rebain et al. 2010) are software programs that use published logistic regression equations to help predict tree mortality based on tree size and fire damage. Despite the importance of understanding post-fire tree mortality, the performance of logistic regression models is highly variable among species (e.g., Kane et al. 2017, Cansler et al. 2020). Models that under or overestimate post-fire tree mortality can result in the development of ineffective prescriptions that fail to meet management objectives. For example, if a model underpredicts post-fire tree mortality during the planning process of a prescribed burn, land managers may burn under conditions that contribute to undesired mortality.

The original post-fire tree mortality model was developed by Ryan and Reinhardt (1988) based on observations of seven conifer species, which was modified by Ryan and Amman (1994) and later expanded to a wider range of tree species. This model uses tree size, bark thickness, and crown volume scorch to predict whether a tree will live or die following fire. The use of crown volume scorch as a factor has limitations for deciduous trees, such as oaks, that lose their leaves seasonally and only allow a short window to observe crown scorch. Bark thickness estimates for the Ryan and Amman model are calculated by multiplying the species-specific multiplier by observed measures of diameter at breast height. For some genera, a single bark thickness multiplier value is usually applied across multiple species (e.g., oaks) that does not reflect the known variation in bark thickness, within and among species (Jackson et al. 1999). Inaccurate estimates of bark thickness may contribute to poor model performance.

Many oak species, along with other hardwood trees, respond to fire by resprouting, which is not quantitatively incorporated in most post-fire tree mortality models. Resprouting, for many oaks, is the primary method of reproduction following fire and likely varies among species (McDonald 1990). Many trees identified as "dead" in most post-fire tree mortality models often resprout. Oaks can often survive complete crown scorch by resprouting from the base or by producing epicormic sprouts from dormant buds in the crown of the tree (Plumb 1980, Plumb and McDonald 1981). Understanding the post-fire resprouting response of oaks could help land managers in their efforts to support conservation and oak recovery projects.

Most post-fire mortality models use logistic regression to predict tree mortality by classifying each tree as live or dead. A limitation of using logistic regression is the requirement of selecting a probability of mortality threshold, which land managers must change to reflect their management goals (Ganio and Progar 2017). Additionally, using logistic regression on imbalanced datasets can substantially underpredict tree mortality when there are much fewer dead trees than live trees in the model (Shearman et al. 2019). An alternative approach to using logistic regression is a classification algorithm called Random Forest (Breiman 2001), a statistical method that uses a random set of observations and a random selection of predictor variables to classify a tree as live or dead. The other observations, not used in the model, are used to assess error. The balanced Random Forest algorithm (Chen et al. 2004) uses an equal number of observations for living trees and dead trees to resolve the issue of imbalanced classes commonly seen in logistic regression models and helps prevent overfitting the data (Breiman 2001). A recent study comparing post-fire tree mortality model performance in longleaf pine (*P. palustris*) found that the Random Forest approach was much better at predicting dead trees from an unbalanced dataset than the logistic regression approach (Shearman et al. 2019). While the Random Forest approach holds promise, it has not been examined for other species, including oaks.

The goal of this study was to improve our ability to predict post-fire tree mortality in California black oak (*Quercus kelloggii*) and canyon live oak (*Quercus chrysolepis*) in recently burned sites of northern California. The first objective was to determine if the relationship between tree diameter and bark thickness varied by species and site. Second, this study developed new post-fire mortality models based on tree and fire characteristics and then compared model performance between a logistic regression approach and the random forest approach for both species. Lastly, we examined the basal resprouting response for each species and determined if factors such as burn severity, diameter, or species were associated with basal resprouting. Improving our understanding and prediction of post-fire oak mortality and resprouting response will assist land managers in pre- and post-fire planning.

MATERIALS AND METHODS

Site Location

The first study site was located in the 2018 Carr Fire perimeter in Whiskeytown National Recreation Area of northwestern California (40°38’36.6014” N, 122°35’53.9225” W). The second study site was within three prescribed burn units (40°46’36.3603” N, 122°20’35.6059 W) on Shasta Trinity National Forest land adjacent to Shasta Lake. The Shasta Lake site was burned in 2013 and again in 2019. Within the Whiskeytown National Recreation Area site (hereafter “Whiskeytown”), the majority of the Carr Fire burned as a high severity fire. A range of burn severities were sampled across the entire recreation area, from unburned to high severity. The prescribed burning sites at Shasta Lake was within the Northwoods units and was predominantly a low severity prescribed burn, with occasional areas of higher severity. Average elevation of sampling at Whiskeytown is 369 m, and about 424 m at Shasta Lake. Both Whiskeytown and the Shasta Lake sites are characterized as having a Mediterranean climate with hot, dry summers and cool, rainy winters. Summer (May through October) temperatures often reach as high as 35°C at Shasta Lake and 38°C at Whiskeytown, while average winter (November through March) temperature reaches 0°C at Shasta Lake and 3°C at Whiskeytown. Average annual precipitation was 1,600 mm at Whiskeytown and 1,727 mm at Shasta Lake, with 70% falling between November and March (Western Regional Climate Center 2021). The year prior to sampling at both Whiskeytown and Shasta Lake experienced greater than average precipitation (22.2 inches more at Whiskeytown and 23.6 inches more at Shasta Lake, PRISM 2021, Western Regional Climate Center 2021). Overstory trees at Whiskeytown were predominantly California black oak (*Q. kelloggii* Newb.), knobcone pine (*P. attenuata* Lemmon), canyon live oak (*Q. chrysolepis* Liebm.), gray pine (*P. sabiniana* D Don.), and interior live oak (*Q. wislizeni* A DC). The Shasta Lake site was primarily composed of ponderosa pine (*P. ponderosa* Dougl. ex. Laws), gray pine, California black oak, and canyon live oak. Additionally, Whiskeytown had a greater shrub presence while the Shasta site's understory is mostly grasses and forbs. The Shasta site was largely dominated by fuel model TL6 (moderate load broadleaf litter, moderate spread rate and flame length), while the Whiskeytown site was mostly SH2 (moderate load dry climate shrub, woody shrubs and shrub litter, fuelbed depth about 1 foot, no grass, low spread rate and flame length), intermixed with occasional TU5 (very high load, dry climate shrub, heavy forest litter with shrub or small tree understory, spread rate and flame moderate) and TL6 (USGS Landfire 2021).

Experimental Design and Data Collection

Bark Thickness

Bark thickness measurements were taken from 30 trees of both species at each site for a total of 120 trees across a range of sizes (0 to 10 cm, 10 to 20 cm, 20 to 30 cm, 30 to 40 cm, 40 to 50 cm, and 50 cm and above) in unburned areas adjacent to burned sites used for the tree mortality study. Bark thickness was measured using a bark gauge on ridges and within furrows and averaged for the bark thickness estimate. Two measurements were taken for each tree at breast height (1.37 m) from each side of the tree parallel to the slope. From this data, species-specific bark thickness models were developed for California black oak and canyon live oak to generate estimates to use in post-fire mortality models. To create the best linear model for predicting bark thickness, diameter at breast height, species, site and their interactions were considered in candidate models. Akaike Information Criteria (AIC) was used to determine the best explanatory model, and the model with the lowest AIC value was considered as the most informative. Models within two AIC values of the lowest were deemed as equally informative (Burnham & Anderson 1998), but models with lower complexity (fewer explanatory variables) were ultimately selected as the best model. Following model selection from AIC criteria, a post-hoc pairwise analysis was performed using a Tukey HSD test in the *emmeans* package (Lenth 2018) to further examine differences among predictor variables and their interactions of the top model. Predicted bark thickness estimates were generated using the predict function in R (R Core Team 2019) for all trees used in the post-fire tree mortality portion of the study.

Post-fire Mortality Model Development and Comparison

California black oak and canyon live oak were surveyed across a spectrum of tree size and burn severity classes to construct and assess post-fire mortality models. Tree size was based on diameter at breast height and included the following size classes: 0 to 10 cm, 10 to 20 cm, 20 to 30 cm, 30 to 40 cm, and >50 cm. Burn severity classes were based on the Fire Monitoring Handbook burn severity classification guide (National Park Service 2003), and included the following classes: 1 (unburned), 2 (scorched), 3 (lightly burned), 4 (moderately burned), and 5 (heavily burned). Substrate and vegetation burn severity were separately recorded within a 2-m radius plot around each tree. We strived to collect a minimum of three trees per size class and burn severity class, but some larger trees in more extreme burn severity classes were more challenging to find. A total of 122 California black oak and 133 canyon live oak were surveyed from the Carr Fire site, and 96 California black oak and 93 canyon live oak trees were surveyed from the Shasta sites (Table 6). Tree status was recorded with a classification of alive (survived fire or epicormically resprouted from the crown), total kill (dead aboveground with no resprouting), or top-killed (dead aboveground but basal resprouting). Maximum bole char height was used to represent a proxy for fire intensity and tree damage. Most models incorporate crown scorch to predict post-fire mortality, but unlike most conifers, deciduous trees lose their leaves annually, meaning information on crown volume scorch is commonly unavailable or impractical to sample immediately following wildfire or fall prescribed fires. Maximum bole char height was measured using a laser rangefinder as the upper limit of the tree bole that was visibly blackened from fire.

Table 6. Total number and status of all California black oak and canyon live oak sampled at Whiskeytown National Recreation Area (WHIS) and Shasta National Forest (Shasta) in northern California. Live trees survived the fire and had live canopy, dead trees were trees which had no live canopy or any form of resprouting (basal or epicormic), and top-killed trees had no live canopy but had basal resprouts.

Species	Site	Total Trees	Live Trees	Dead Trees	Top-killed Trees
California black oak	WHIS	122	68	10	44
	Shasta	96	75	1	20
Canyon live oak	WHIS	133	73	4	56
	Shasta	93	85	0	8

Logistic regression models were developed to predict the probability of post-fire tree mortality based on tree diameter, maximum bole char height, soil burn severity, vegetation burn severity, and predicted bark thickness values. Because previous studies suggest that bark thickness is one of the most important characteristics in determining tree mortality (van Mantgem and Schwartz 2003, Michaletz and Johnson 2007, Lawes et al. 2011, Brando et al. 2012), candidate models compared whether the use of a predicted bark thickness for each tree improved model performance. Trees with probabilities greater than 0.5 were considered dead, while less than 0.5 were considered alive. AIC was used to determine the best explanatory model, and the model with the lowest AIC value was considered as the most informative. Models with variance inflation factor (VIF) greater than two were excluded.

A Random Forest modeling approach was also used to predict probability of tree mortality. All variables tested in the logistic regression model development were also used in the Random Forest model. Variable importance of the Random Forest model was assessed through partial dependence plots and calculating the mean decrease in accuracy when a variable is removed from the model.

Post-fire model comparisons were tested to compare probability of mortality predictions between model types. Probability of mortality was assessed at the individual tree level for both oak species using logistic regression in base R software and Random Forest modeling in the *randomForest* package available in R (R Core Team 2019). Due to the low number of total killed trees, both total killed and top-killed trees were considered dead for the sake of analysis. Sensitivity (the proportion of correctly classified dead trees), specificity (proportion of correctly classified live trees), accuracy (proportion of correctly classified dead and live trees), and area under the receiver operator characteristic (AUC) curve (Hosmer and Lemeshow 2000) were examined to assess model performance for each species and model approach.

Resprouting Response

The resprouting response of each surveyed tree at both Whiskeytown and Shasta were measured one year after the fire. The number of basal sprouts was recorded for each tree, along with maximum basal sprout height, average basal sprout height, and average basal diameter of the resprouts. To incorporate as many of these variables as possible, total resprout basal area was calculated by multiplying the average area of each resprout by the total number of resprouts for each individual tree. This served as a representative measure of basal resprout biomass for each tree. Basal area of resprouts was modeled using Random Forest to test for the relative importance of burn severity, tree diameter, bark thickness, bole char height, species, and site location in predicting post-fire resprouting basal area. Variable importance was used to determine the best model by selecting the variables with the highest variable importance.

RESULTS

Bark Thickness

Bark thickness values were best predicted using diameter ($\chi^2 = 8.0$, $P < 0.0001$), species ($\chi^2 = 2.3$, $P < 0.03$), and site location ($\chi^2 = -3.0$, $P < 0.003$) in an additive model. There was an overall positive relationship between diameter and bark thickness for both species and site location ($r^2 = 0.39$). California black oak had 0.17 cm thicker bark than Canyon live oak. Differences in bark thickness between the two sites was most pronounced for California black oak, with the greatest differences occurring in larger diameter trees (Figure 7). The Shasta site had 0.26 cm and 0.17 cm thicker bark than at the Whiskeytown site for California black oak and canyon live oak, respectively.

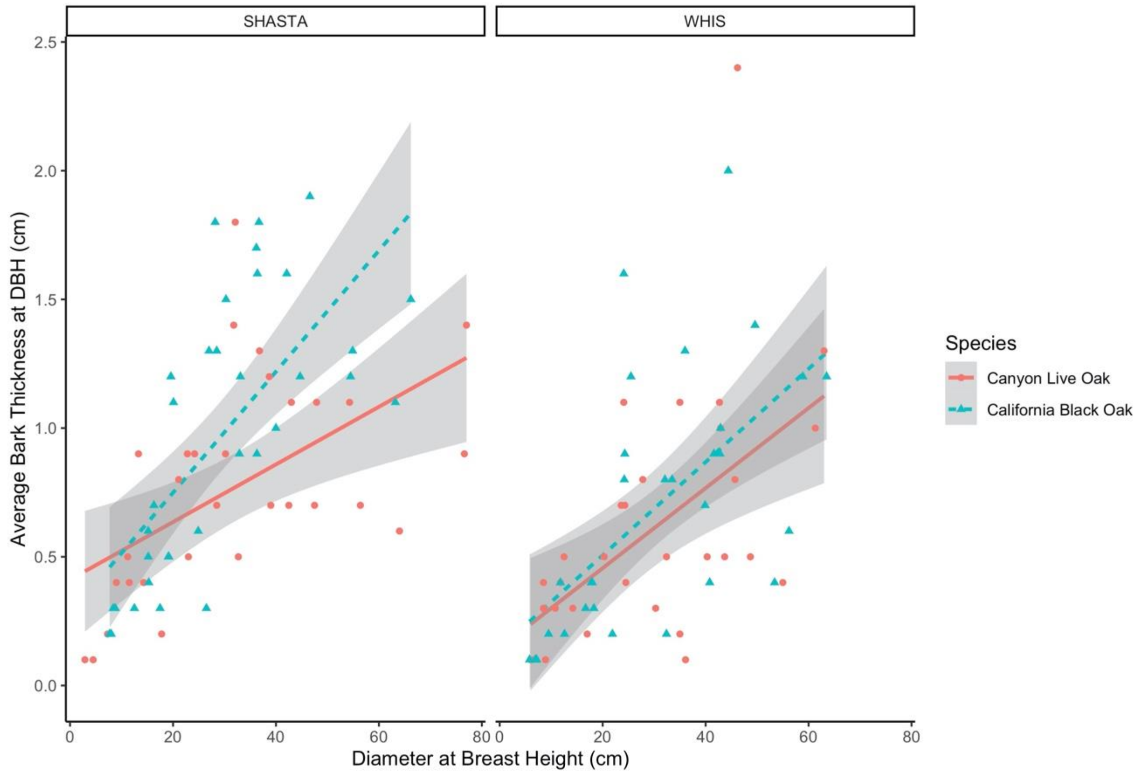


Figure 7. Relationship between diameter at breast height (DBH) and average bark thickness for California black oak and canyon live oak at both the Shasta and Whiskeytown (WHIS) study sites in northern California.

Post-fire Mortality Model Development and Comparison

Overall, there was a low number of total killed trees that were surveyed, particularly at the Shasta site. There was only one total killed California black oak at the Shasta site, with a size of 17.3 cm. Of the remaining California black oak at the Shasta site, the average diameter of top-killed trees was 13.8 cm, while surviving California black oak were on average 31.7 cm. At the Whiskeytown site, the average size of California black oak trees that were total killed was 21.1 cm, while the average size of trees that were top-killed was 17.8 cm, and surviving California black oak were on average 28.9 cm. As for canyon live oak at the Shasta site, average diameter of top-killed trees was 11.2 cm and live trees was 25.5 cm. There were no surveyed total killed canyon live oak at the Shasta site. At the Whiskeytown site, top-killed trees were on average 22.7 cm in diameter, while total-killed trees averaged 22.8 cm, and live trees were 30 cm.

Canyon live oak mortality was best predicted using an additive model that included bark thickness ($p < 0.0001$, $z = -3.38$) and soil burn severity ($p < 0.0001$, $z = 7.10$), while California black oak mortality was best predicted using an additive model that included bark thickness ($p < 0.0001$, $z = -5.12$), soil burn severity ($p < 0.0001$, $z = 4.33$) and bole char height ($p < 0.003$, $= 2.94$). Diameter and vegetation burn severity were less informative. For both species, probability of mortality decreased with greater diameter or bark thickness and increased with greater bole char height and soil burn severity (Figure 8).

As for Random Forest models, variable importance plots showed all factors as being important predictors for probability of mortality in California black oak trees. Diameter, maximum bole char height, and predicted bark thickness were the top three most important variables, while soil burn severity and vegetation burn severity were less important variables in predicting probability of mortality. Variable importance plots of Random Forest models for canyon live oak trees showed soil burn severity as being the most important variable, followed by vegetation burn severity and maximum bole char height. Tree diameter and predicted bark thickness were least important in predicting canyon live oak probability of mortality.

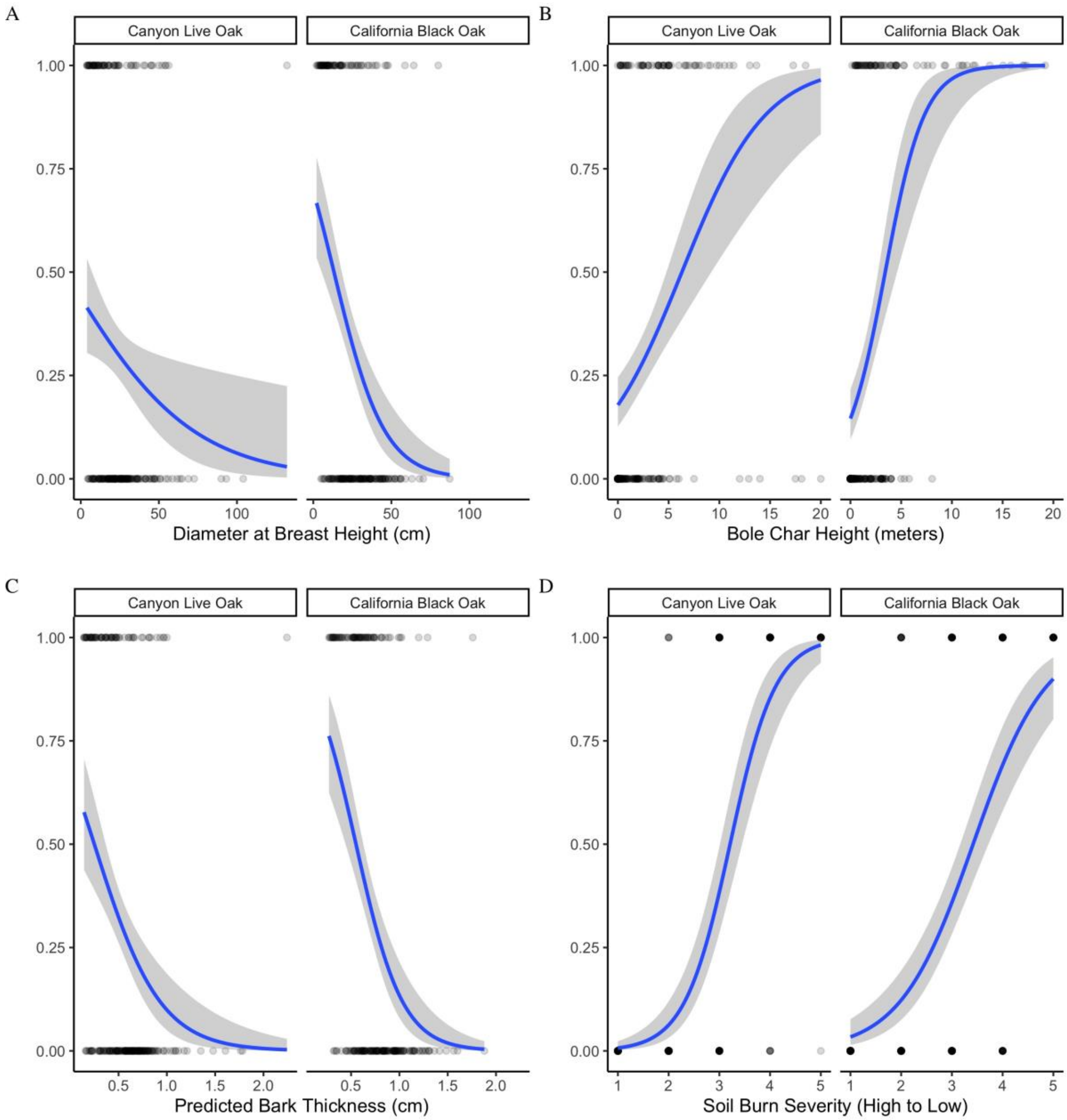


Figure 8. Logistic regression fits of explanatory variables (diameter at breast height (A), bole char (B), predicted bark thickness (C), soil burn severity (D)) with probability of mortality for trees by species at both the Shasta and WHIS locations.

Both logistic regression and Random Forest model approaches performed well when predicting post-fire oak mortality. All Random Forest models had 2 to 11% greater accuracy than the logistic regression models (Table 7). Specificity levels at the Shasta site, where there were only 29 dead trees (1 total killed and 28 top-killed, Table 6), were greater in Random Forest models than in logistic regression. Based on AUC values, logistic regression models performed better than random forest models at Whiskeytown for California black oak (AUC of logistic regression = 0.94 and AUC of random forest = 0.91), and at Shasta for canyon live oak (AUC of logistic regression = 0.93, AUC of random forest = 0.88; Table 7).

Table 7. Assessment of model performance of logistic regression (LR) and random forest (RF) models for each species at both the Whiskeytown (WHIS) and Shasta study sites. Sensitivity is the proportion of correctly classified dead trees, specificity is the proportion of correctly classified live trees, and accuracy is the overall proportion of correctly classified trees. AUC is the area under the reciever operator curve and CI is the 95% confidence interval.

Species	Site	Model	Sensitivity	Specificity	Accuracy	AUC	CI
California black oak	WHIS	LR	0.89	0.82	0.85	0.94	0.78-0.91
	WHIS	RF	0.94	0.96	0.95	0.91	0.90-0.98
	Shasta	LR	0.48	0.97	0.86	0.89	0.78-0.93
	Shasta	RF	0.86	1.00	0.97	0.91	0.91-0.99
Canyon live oak	WHIS	LR	0.92	0.90	0.91	0.95	0.85-0.95
	WHIS	RF	0.95	0.92	0.93	0.97	0.88-0.97
	Shasta	LR	0.13	0.99	0.91	0.93	0.84-0.96
	Shasta	RF	0.50	0.99	0.95	0.88	0.88-0.98

Regardless of the modeling approach, specificity was greater than sensitivity at the Shasta site, and the opposite was generally true for Whiskeytown (Table 7). Specificity of logistic regression models for California black oak were greater for thicker bark trees (0.8 cm and greater) than thinner bark trees, while sensitivity and specificity for canyon live oak using logistic regression models were generally inconsistent, ranging from 0 to 1. Random Forest models for canyon live oak had the greatest specificity (greater than 0.83) across all bark thickness categories, while California black oak had the greatest overall sensitivity levels (greater than 0.67).

Resprouting Response

Most trees basally resprouted following fire (97%). When modeled using random forest, resprouting response was best predicted by bole char height, tree diameter, and vegetation burn severity (Figure 9). Vegetation burn severity was slightly more informative than soil burn severity. Basal area of resprouts was positively correlated with vegetation burn severity (Figure 10). Bole char height was more influential in predicting resprouting basal area than diameter and vegetation burn severity, so the greatest levels of resprouting response were in trees less than 20 cm in diameter that had a bole char height greater than 5 m (Figure 11b). Larger trees in higher severity burns had 0.20 m^2/tree more resprout basal area than smaller trees in higher severity burns (Figure 11a). There were minimal differences in resprout basal area between species, but there was a slightly greater resprouting response at the Whiskeytown site than at the Shasta site.

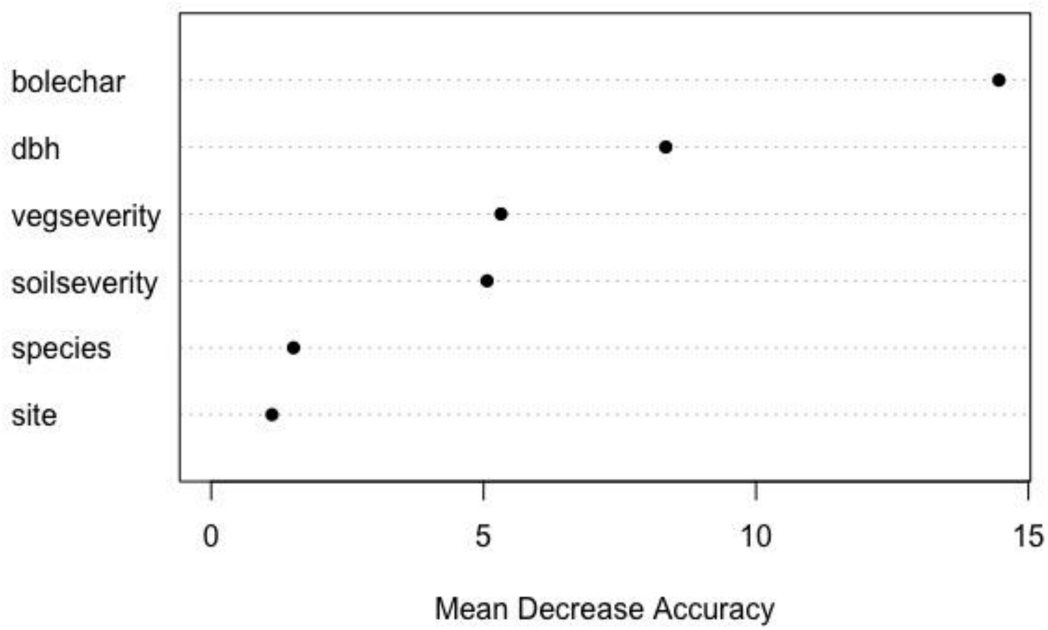


Figure 9. Variable importance for predicting resprout basal area in California black oak and canyon live oak at Whiskeytown and Shasta sites modeled with Random Forest. Mean decrease accuracy symbolizes how much accuracy a model loses when a variable is removed.

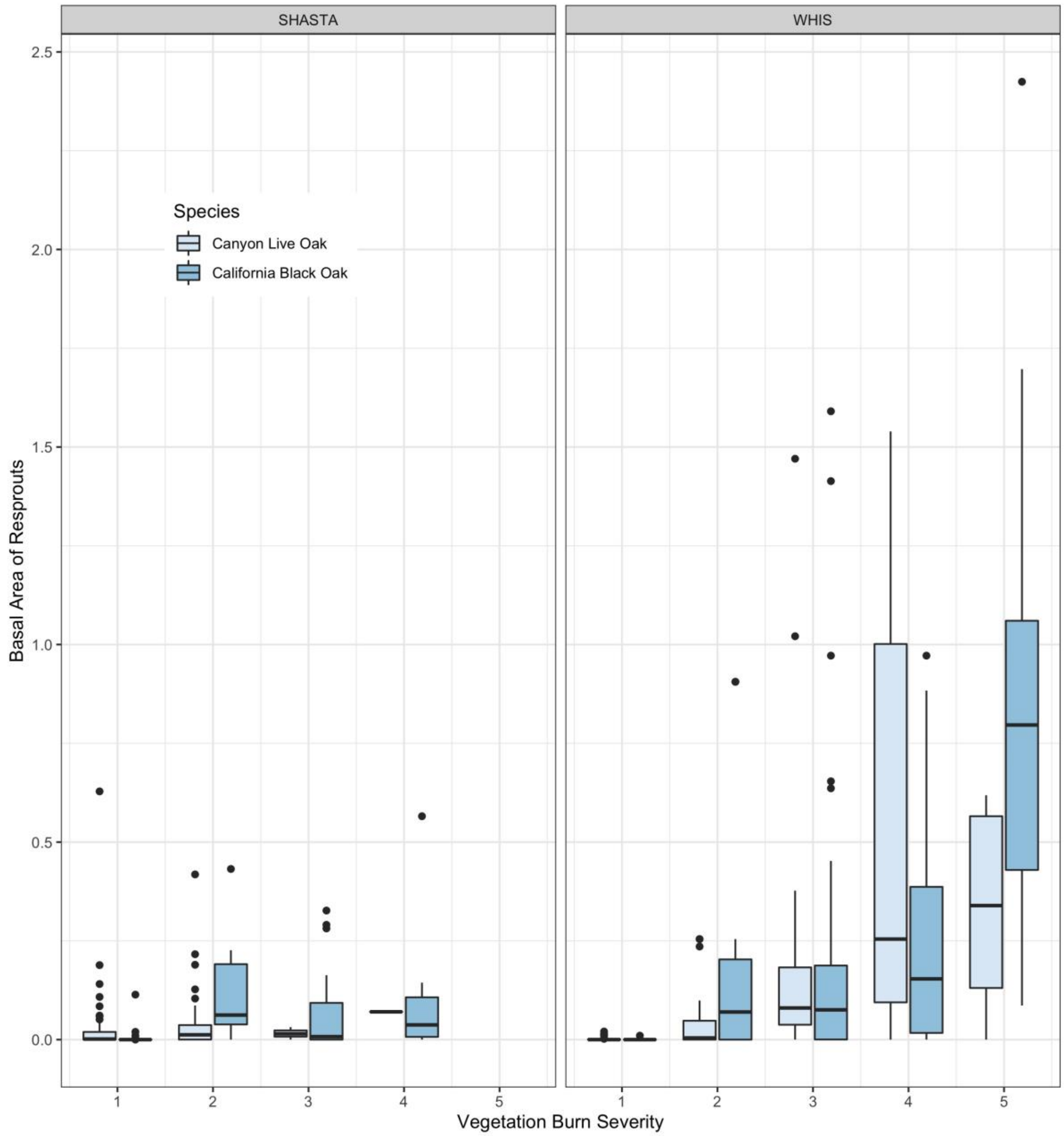
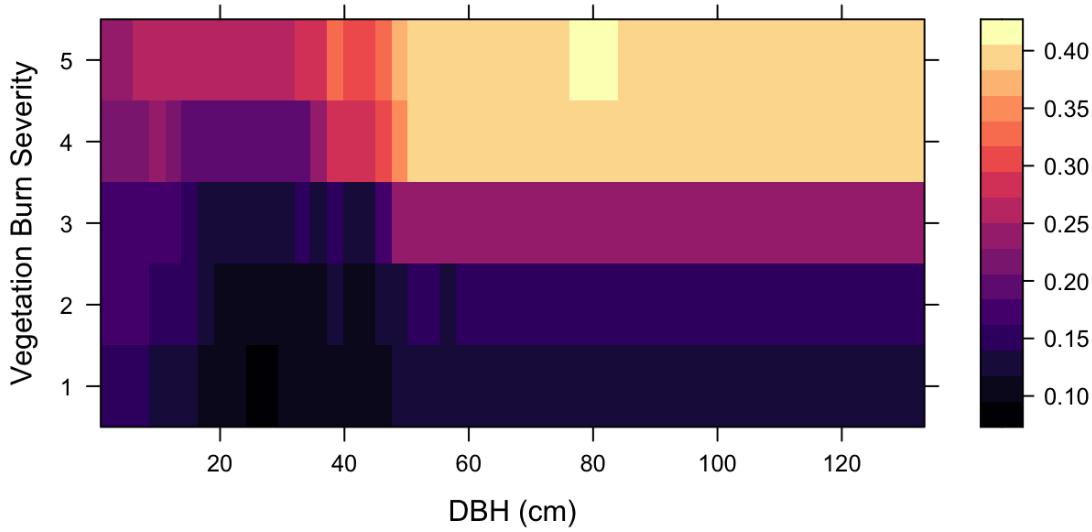


Figure 10. Basal area of basal resprouts (m^2/tree) by vegetation burn severity classes (1 = unburned, 5 = heavily burned) and site (SHASTA = Shasta, WHIS = Whiskeytown). Basal area resprouting response was greatest in higher vegetation burn severity classes.

a)



b)

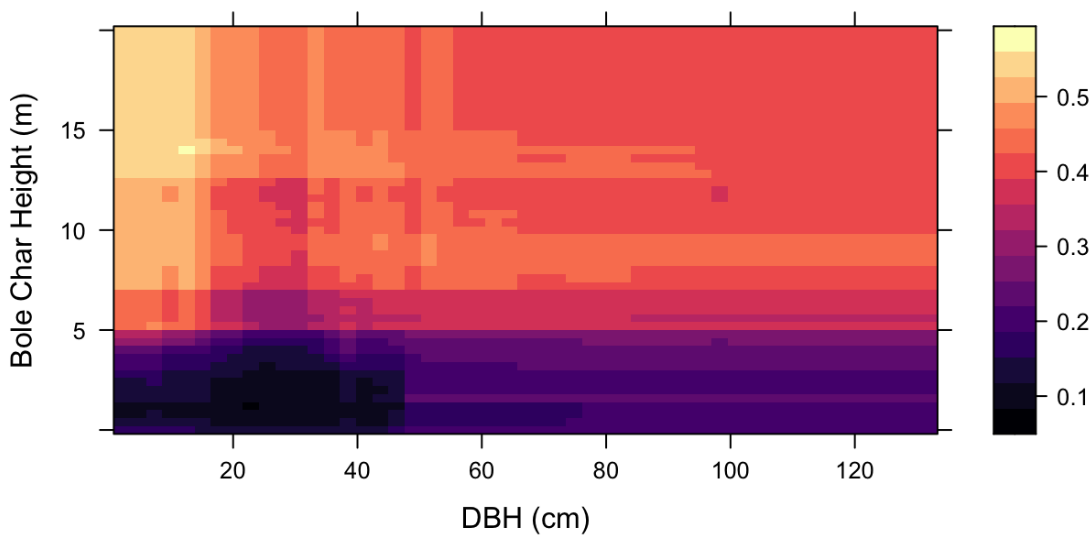


Figure 11. Partial dependence plots of a) diameter at breast height (DBH) and vegetation burn severity, and b) DBH and bole char height. Color bar represents resprout basal area (m^2/tree).

DISCUSSION

Informative and accurate post-fire oak mortality models are necessary to effectively anticipate changes following fire to aid management decisions. The findings of this study advance these efforts by examining post-fire tree mortality in California black oak and canyon live oak of northern California. The relationship of bark thickness and tree size were not static across sites, a result with potential implications that may affect post-fire tree mortality predictions. It was also demonstrated that measures of bole char and soil severity can provide an adequate substitute to crown scorch when predicting post-fire tree mortality in oaks. This study is the first to compare model performance between the traditional logistic regression and Random Forest approaches in a non-coniferous species. Logistic regression and random forest models both performed well in predicting tree mortality for these two oak species following both prescribed fire and wildfire. The Random Forest approach was slightly better at predicting mortality but incorporation of its use by managers may be limited without the development of decision support tools that facilitate integration of this approach. Lastly, this study developed a post-fire basal resprouting model for the two oaks species. Resprouting was surprisingly consistent across sites and species but was best predicted by vegetation burn severity, bole char height, and tree diameter. The finding of this study advances our post-fire tree mortality and resprouting in two oak species of northern California, with possible implications for other oak and angiosperm tree species in fire-prone ecosystems.

Bark Thickness

California black oak had slightly thicker bark than canyon live oak, which was expected and is consistent with previous findings (Baldwin et al. 2012, Kidd and Varner 2019). More interestingly, there were clear differences in bark thickness between study sites. While both species had greater bark thicknesses at the Shasta site, differences in California black oak trees between sites were more pronounced. This finding suggests that bark thickness may not simply be an allometric relationship with tree size (e.g., DBH) for a given species and that other site level factors may contribute to differential allocation to bark.

The observed bark thickness differences between sites may be due to edaphic and climatic differences and their collective influence on historical fire regimes. Greater bark thickness has been found for trees of the same species in more fire prone areas compared to less fire prone areas (Stephens and Libby 2006, Lawes et al. 2013, Schafer et al. 2015, Kidd and Varner 2019). In certain pines, such as Monterey pine (*P. radiata*), basal bark thickness within areas of historical fire use by Native Americans was greater than in areas with no evidence of historical fire use (Stephens and Libby 2006). While there were limited differences in the recent fire history of both sites (Shasta and Whiskeytown) examined in this study (FRAP 2021, MTBS 2021), there were pronounced differences in the fuel structures and presumably their historical fire regime types. The Shasta site is characterized by open ponderosa pine stands with a dense layer of grass and forbs in the understory that would have historically experienced more frequent, low severity fire prior to fire exclusion. The Whiskeytown site is characterized by overstory pines and a dense shrubby understory with the capability to support less frequent, high severity fires. The lighter understory fuels of the Shasta site may have allowed trees to experience lower intensity fires that, over time, supported bark growth by selecting for thicker bark trees. It is also possible that bark thickness differences between sites was associated with slightly greater annual precipitation amounts at the Shasta sites than at the WHIS sites (Western Regional Climate Center 2011). Trees growing in sites with higher precipitation may be able to allocate a greater portion of carbon to bark synthesis compared to drier sights. However, more information on the sources of variation in bark thickness among sites is needed so that they can be better integrated into bark thickness prediction equations, given its importance to post-fire tree mortality modeling (van Mantgem and Schwartz 2003, Brando et al. 2012).

Post-fire Mortality Model Development and Comparison

Our results indicate that bole char height, burn severity, and bark thickness were important factors in predicting post-fire probability of mortality for both species in logistic regression models. Along with crown volume scorch, bole char height is a commonly used indicator of fire injury to predict mortality (Peterson 1985, Stephens and Finney 2002). A previous study found that bole char height and bark thickness were the most important factors in predicting probability of top-kill amongst both conifer and broadleaved tree species (Catry et al. 2010). Similar to our study, Catry et al. (2010) found increased probability of top-kill in trees with thinner bark thickness and greater fire injuries. Including additional factors of fire intensity such as burn severity in mortality models may be useful for deciduous tree species in which measuring crown volume scorch is challenging or not possible due to leaf senescence.

Our results show that the logistic regression mortality model performed well, particularly in terms of specificity, accuracy, and AUC values. The lowest accuracy level for logistic regression was 0.85. Sensitivity values for logistic regression were very low for both species at the Shasta sites. At the WHIS site, where the dataset was slightly more balanced due to a greater number of dead trees available for sampling, sensitivity was improved, but still much lower than specificity levels. Our findings are contrary to a previous study that found lower specificity and higher sensitivity levels, even within two oak species (*Q. kelloggii* and *Q. gambelii*; Kane et al. 2017). These contrasting results are likely from both studies having imbalanced datasets, with Kane et al. (2017) having sampled disproportionally more dead trees than live trees, and our study sampling disproportionally more live trees than dead trees. These results further support previous findings that logistic regression models perform less well with imbalanced datasets (Ganio and Progar 2017, Shearman et al. 2019).

As expected, random forest models performed slightly better than logistic regression when datasets were imbalanced and contained very few dead tree observations. At the Shasta site, where the number of dead trees sampled was very low, specificity levels were nearly perfect for random forest models and very good for logistic regression models for both species, while sensitivity levels were lower for both random forest and logistic regression. Similar to Shearman et al. (2019), our study found that in the case of imbalanced datasets, logistic regression models were biased towards overpredicting live trees and underpredicting dead trees, while the random forest model was better suited for more accurate predictions and improved sensitivity levels.

A benefit of using Random Forest rather than logistic regression models includes minimizing the issue of imbalanced datasets (Chen et al. 2004). Our results supported the notion that Random Forest models perform better than logistic regression with imbalanced datasets. An additional benefit of Random Forest is that it does not need to meet the assumptions of logistic regression. A potential limitation of many datasets may be sample size, since data collection is time consuming and resources are often limited. One assumption of logistic regression is that the sample size must be sufficiently large enough. Our sample size was relatively small, with a total of 444 trees collected from two sites. While greater sample sizes are preferred, Random Forest may perform better than logistic regression with smaller datasets.

Resprouting Response

Consistent with previous studies that have examined post-fire oak responses (Taylor 2010, Hammett et al. 2017, Nemens et al. 2018), resprouting in California black oak and canyon live oak was vigorous following fire. In our study, post-fire basal resprouting of both oak species was influenced strongly by bole char height and vegetation burn severity, two indicators that are associated with fire intensity. Our results also align with previous studies (Cocking et al. 2014, Nemens et al. 2018) which found greater resprouting responses from both species in areas of higher burn severity.

Tree diameter was also a significant factor in predicting resprouting response, with greater resprouting levels in larger trees. Our results of greater resprouting levels in larger trees contradict previous studies in oaks which found that in resprouting trees, while survivorship increased with tree size, resprouting ability declined (McCreary et al. 1991; Vesk 2006). While many factors contribute towards a tree's resprouting capabilities, the amount of nonstructural carbohydrates allocated towards resprouting is important (Dietze et al. 2014). A previous study found a positive correlation between overall tree biomass and mean annual nonstructural carbohydrates (Furze et al. 2019), which could explain our findings of greater resprouting responses in larger diameter trees.

Implications

Bark thickness, an important tree defense measure that is commonly used as a predictor for post-fire mortality, differed between species and sites in our study. These findings support the need to account for bark thickness variation within and among oak species, rather than as a fixed estimate that is used for all oak species and sites. Implications from our findings indicate that site-specific diameter and bark thickness relationships may need to be developed, especially within areas where historical fire regimes may differ. The use of general equations or species multipliers to estimate bark thickness may reduce the accuracy of post-fire mortality models.

Our study found that bole char height and substrate or vegetation burn severity provided good alternatives to crown volume scorch in mortality models. This has important implications for predicting the post-fire mortality of deciduous trees for which managers do not have crown volume scorch data. This leads to better decision making and planning for prescribed burning conditions and post-fire rehabilitation.

Both logistic regression and Random Forest model approaches performed well in terms of mortality predictions, but Random Forest was slightly better. Logistic regression approaches are the most commonly used method to predict post-fire mortality, and with many circumstances resulting in imbalanced datasets, this can underpredict the number of dead trees or live trees depending on the dataset. To better predict and account for post-fire mortality, we suggest the use of random forest over logistic regression modeling, but the approach that land managers use should depend on the level of accuracy desired. Logistic regression still may be preferred since established decision support tools use this approach and managers may not be familiar with the Random Forest approach. Drawbacks of Random Forest modeling include the inability to test hypotheses. Random Forest models do not provide p-values or coefficients for formulas to be used by land managers, therefore, not lending itself to decision-making the way that logistic regression does.

Most post-fire tree mortality models, like FOFEM, do not consider differences in resprouting following fire, but our results suggest that resprouting response is not uniform. Resprouting following fire has significant implications for post-fire recovery, rehabilitation, erosion control, and persistence of resprouting species. There is currently a need for integration of post-fire resprouting with tree mortality models. We suggest that tools for predicting post-fire mortality among trees beyond conifers should continue to be developed and enhanced.

LITERATURE CITED

Baldwin, B.G., Goldman, D., Keil, D.J., Patterson, R., & Rosatti, T.J. (2012). The Jepson Manual Vascular Plants of California, Thoroughly Revised and Expanded. University of California Press, Los Angeles, USA.

Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M., & Putz, F.E. (2012). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, 18 (2), 630-641.

Breiman, L. (2001). Random Forests. Machine learning, 45, (1) 5-32.

Cansler C.A., Hood S.M., van Mantgem P.J., & Varner J.M. (2020) A large database supports the use of simple models of post-fire tree mortality for thick-barked conifers, with less support for other species. *Fire Ecology*, 16, 25.

Catry, F.X., Rego, F., Moreira, F., Fernandes, P.M. and Pausas, J.G. (2010). Post-fire tree mortality in mixed forests of central Portugal. *Forest Ecology and Management*, *260*(7), 1184-1192.

Chen, C., Liaw, A., & Breiman, L. (2004). Using Random Forest to learn imbalanced data. Dept. Statistics, Univ. California, Berkeley, CA, Tech. Rep, 666.

Cocking, M.I., Varner, J.M., & Knapp, E.E. (2014). Long-term effects of fire severity on oak-conifer dynamics in the southern Cascades. *Ecological Applications*, 24, 94-107.

Dietze, M.C., Sala, A., Carbone, M.S., Czimczik, C.I., Mantooth, J.A., Richardson, A.D., Vargas, R. (2014). Nonstructural carbon in woody plants. *Annu Rev Plant Biol*, 65 (65), 667-687.

Furze, M.E., Huggett, B.A., Aubrecht, D.M., Stolz, C.D., Carbone, M.S., Richardson, A.D. (2019). Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *New Phytol.*, 221 (3), 1466-1477.

Ganio, L.M. & Progar, R.A. (2017). Mortality predictions of fire-injured large Douglas-fir and ponderosa pine in Oregon and Washington, USA. *Forest Ecology and Management*, 390, 47–67.

Hammett, E.J., Ritchie, M.W., & Berrill, J.P. (2017). Resilience of California black oak experiencing frequent fire: regeneration following two large wildfires 12 years apart. *Fire Ecology*, 13, 91-103.

Hosmer, D.W. & Lemeshow, S. (2000). Interpretation of the fitted logistic regression model. *Applied Logistic Regression*. John Wiley and Sons Press. New York.

Hunter, J.C. & Barbour, M.G. (2001). Through-growth by *Pseudotsuga menziesii*: A mechanism for change in forest composition without canopy gaps. *Journal of Vegetation Science*, 12, 445-452.

Jackson, J.F., Adams, D.C., & Jackson, U.B. (1999). Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. *The American Naturalist*, 153, 614-632.

Kane, J. M., van Mantgem, P.J., Lalemand, L.B., & Keifer, M. (2017). Higher sensitivity and lower specificity in post-fire mortality model validation of 11 western US tree species. *International Journal of Wildland Fire*, 26, 444-454.

Kidd, K.R. & Varner, J.M. (2019) Differential relative bark thickness and aboveground growth discriminates fire resistance among hardwood sprouts in the southern Cascades, California. *Trees,* 33, 267-277.

Knight, C.A., Cogbill, C.V., Potts, M.D., Wanket, J.A., & Battles, J.J. (2020). Settlement-era forest structure and composition in the Klamath Mountains: reconstructing a historical baseline. *Ecosphere*, 11, 23.

Lawes, M.J., A. Richards, J. Dathe, & J.J. Midgley. (2011). Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology*, 212 (12), 2057-2069.

Lawes M.J., Midgley J.J., & Clarke P.J. (2013) Costs and benefits of relative bark thickness in relation to fire damage: a savanna/forest contrast. *Journal of Ecology* 101, 517–524.

Long, J.W., Anderson, M.K., Quinn-Davidson, L., Goode, R.W., Lake, F.K., & Skinner, C.N. (2016). Restoring California black oak ecosystems to promote tribal values and wildlife. General Technical Report PSW-252. United States Department of Agriculture Forest Service, Albany, CA, p 110.

Lutes, D.C. (2019). FOFEM 6.5 User Guide. Rocky Mountain Research Institute.

McDonald, P.M. (1990). Quercus kelloggii Newb., California black oak. In: Burns R.M., Honkala, B.H., tech. coords. Silvics of North America. Volume 2, Hardwoods. Agriculture Handbook. 654. Washington, DC: U.S. Department of Agriculture, Forest Service, 661-671.

McCreary, D.D., Tietje, W.D., Schmidt, R.H., Gross, R., Weitkamp, W.H., Willoughby, B.L. and Bell, F.L. (1991). Stump sprouting of blue oaks in California. *General technical report PSW-US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station (USA)*.

Michaletz, S.T., & Johnson, E.A. (2007). How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research*, 22 (6), 500-515.

National Park Service. (2003). Fire Monitoring Handbook. Boise (ID). Fire Management Program Center, National Interagency Fire Center.

Nemens, D.G., Varner, J.M., Kidd, K.R., & Wing, B. (2018). Do repeated wildfires promote restoration of oak woodlands in mixed-conifer landscapes? *Forest Ecology and Management*, 427, 143-151.

Peterson, D.L. (1985). Crown scorch volume and scorch height: estimates of postfire tree condition. *Canadian Journal of Forest Research*, *15*(3), 596-598.

Plumb, T.R. (1980). Response of oaks to fire. Ecology, management, and utilization of California oaks. General Technical Report PSW-44. United States Department of Agriculture Forest Service, Berkeley, CA, 202-215.

Plumb, T.R. & McDonald, P.M. (1981). Oak management in California, Vol. 54. US Dept. of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.

PRISM [PRISM Climate Group]. (2019). PRISM Climate Data. <http://prism.oregonstate.edu>. Oregon State University, Corvallis, Oregon, USA (accessed 20 August 2021).

Rebain, S.A., Reinhardt, E.D., Crookston, N.L., Beukema, S.J., Kurz, W.A., Greenough, J.A., Robinson, D.E., & Lutes, D.C. (2010). (Revised 2015). The Fire and Fuels Extension to the Forest Vegetation Simulator: Updated Model Documentation. U.S. Department of Agriculture, Forest Service, Forest Management Service Center.

Ryan, K.C., & Amman, G.D. (1994). Interactions between fire-injured trees and insects in the greater Yellowstone area. *In* Plants and their Environments: Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem, 16–17 September 1991, Yellowstone National Park, Wyoming. *Edited by* D.G. Despain. Tech. Rep. NPS/NRYELL/NRTR. US Department of the Interior, National Park Service, Natural Resources Publication Office, Denver, Colo. pp. 259-271.

Ryan K.C. & Reinhardt, E.D. (1988). Predicting postfire mortality of seven western conifers*. Canadian Journal of Forest Research*, 18, 1291-1297.

Schafer J.L., Breslow B.P., Hohmann M.G., & Hoffmann W.A. (2015) Relative bark thickness is correlated with tree distributions along a fire frequency gradient. *Fire Ecology*, 11, 74-87.

Schriver, M., Sherriff, R.L., Varner, J.M., Quinn-Davidson, L., & Valachovic, Y. (2018). Age and stand structure of oak woodlands along a gradient of conifer encroachment in northwestern California. *Ecosphere*, 9, e02446.

Shearman, T.M., Varner, J.M., Hood, S.M., Cansler, C.A., & Hiers, J.K. (2019). Modelling post-fire tree mortality: Can Random Forest improve discrimination of imbalanced data? *Ecological Modelling*, 414, 108855.

Stephens, S.L., and Finney, M.A. (2002). Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *Forest Ecology and Management*, 162(2-3), 261-271.

Stephens, S.L., Libby, W.J., (2006). Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California. *Journal of Biogeography*, 33, 648–652.

Taylor, A.H. 2010. Fire disturbance and forest structure in an old-growth Pinus ponderosa forest, southern Cascades, USA. *Journal of Vegetation Science*, *21*(3), 561-572.

USGS (2021). Landfire data distribution site. Landfire.gov.

van Mantgem, P. & Schwartz, M. (2003). Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. F*orest Ecology and Management*, 178 (3), 341-352.

Vesk, P.A. (2006), Plant size and resprouting ability: trading tolerance and avoidance of damage? *Journal of Ecology*, 94, 1027-1034.

Western Regional Climate Center, 2011. Remote Automated Weather Station (RAWS) data. <http://www.raws.dri.edu/> (accessed October, 2019).

CHAPTER 1 APPENDIX

Appendix A. National Park Service form FMH-21 was used to standardize burn severity. Values were reversed for this study with heavily burned as 5 and unburned as 1.

	Unburned	Scorched	Lightly Burned	Moderately Burned	Heavily Burned
Substrate	Not burned	Litter partially blackened; duff nearly unchanged; wood/leaf structures unchanged	Litter charred to partially consumed; upper duff layer may be charred but the duff layer is not altered over the entire depth; surface appears black; woody debris is partially burned; logs are scored or blackened but not charred; rotten wood is scorched to partially burned	Litter mostly to entirely consumed, leaving coarse, light colored ash; duff deeply charred, but underlying mineral soil is not visibly altered; woody debris is mostly consumed; logs are deeply charred, burned-out stump holes are common	Litter and duff completely consumed, leaving fine white ash; mineral soil visibly altered, often raddish; sound logs are deeply charred, and rotten logs are completely consumed. This code generally applies to less than 10% of natural or slash burned areas
Vegetation	Not burned	Foliage scorched and attached to supporting twigs	Foliage and smaller twigs partially to completely consumed; branches mostly intact	Foliage, twigs, and small stems consumed; some branches still present	All plant parts consumed, leaving some or no major stems/trunks; any left are deeply charred

CHAPTER 2 APPENDIX

Appendix B. Summary of logistic regression model coefficients for California black oak.

Model Input	Coefficient Standard estimate error (β)	Standard Error	P-value
Predicted bark thickness	-5.55921	1.08493	$2.99e^{-07}$
Substrate burn severity	1.07912	0.24917	$1.48e^{-05}$
Maximum bole char height	0.28193	0.09604	0.00333

Appendix C. Summary of logistic regression model coefficients for canyon live oak.

Model Input	Coefficient Standard estimate error (β)	Standard Error	P-value
Predicted bark thickness	-3.6803	1.0889	0.0007
Substrate burn severity	2.4232	0.3415	1.28e-12