

MECHANISMS AND SPATIAL PATTERNS OF BARK BEETLE-ASSOCIATED
MORTALITY FOLLOWING VARIABLE DENSITY THINNING TREATMENTS IN
A SIERRA MIXED-CONIFER FOREST

By

Alexis Bernal

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 & Wildland Sciences

Committee Membership

Dr. Jeffrey Kane, Committee Chair

Dr. Eric Knapp, Committee Member

Dr. Harold Zald, Committee Member

Dr. Rick Zechman, Graduate Coordinator

July 2019

ABSTRACT

MECHANISMS AND SPATIAL PATTERNS OF BARK BEETLE-ASSOCIATED MORTALITY FOLLOWING VARIABLE DENSITY THINNING TREATMENTS IN A SIERRA MIXED-CONIFER FOREST

Alexis Bernal

Long-term trends of tree mortality have increased over the last several decades, coinciding with above-average temperatures, high climatic water deficits, and bark beetle outbreaks. With the anticipation that drought and bark beetles may increase with climate change, uncertainty exists over the appropriate treatments that could ensure the future sustainability of forest resources and the ecosystem services that forests provide. Conventional thinning treatments are used to reduce stand density, with the assumption that reductions in competition can alleviate drought stress and enable trees to resist bark beetle attack. Alternative thinning treatments may also reduce stand density, but have a greater focus on increasing spatial heterogeneity. Variable density thinning is a management method intended to mimic the spatial heterogeneity that was present in mixed-conifer forests prior to logging and fire exclusion. Although the added benefits of increasing spatial heterogeneity include biodiversity, wildlife, recreation, and restoration, information is lacking on the effects that these treatments have on tree resistance to disturbances.

Since 2012, the Sierra Nevada experienced widespread tree mortality coinciding with severe drought conditions and bark beetle outbreak. This provided a unique opportunity to explore the mechanisms driving bark beetle-associated mortality following variable density thinning treatments in the central Sierra Nevada. Using dendrochronological methods, we modeled the relationship between drought resistance and bark beetle-associated mortality to evaluate if reductions in competition enhance tree resistance to bark beetles. We also determined if structural elements within variable density thinning treatments influenced the level and spatial pattern of bark beetle-associated mortality. By exploring these relationships, our findings could provide a greater understanding on the underlying mechanisms that drive mortality to disturbances and also provide information to help develop prescriptions for enhancing resistance to drought and bark beetles.

ACKNOWLEDGEMENTS

Funding for this project was provided by the United States Department of Agriculture Forest Service – Pacific Southwest Research Station, Joint Fire Sciences Program, and the USDA Hispanic Serving Institute (CAMBIO program). I would like to thank my graduate committee members Jeffrey Kane, Eric Knapp, and Harold Zald for their endless support and valuable insight through the entirety of this project. Jeff, your dedication as an educator and as a researcher have inspired me deeply over the last two years. Thank you for helping me become a better scientist. Eric, words cannot explain how grateful I am for the opportunity to work with such a brilliant person and to conduct research in this very special place you have managed. Harold, I am so thankful for your passion to dive deeper into all issues related to forest ecology and hope that I take that same enthusiasm as I move forward in my career. This project could not be possible without the support of many dedicated and diligent field technicians, including Jessie Avitia, Alicia Abrego, Emily Hoeft, and Austen Thibault. I also want to extend my deepest gratitude to my friends who have guided and supported me throughout this endeavor: Bob Carlson, Caroline Martorano, Cerena Brewen, Andre Sanchez, Chance Callahan, Gabriel Goff, James Lamping, Robert Muma, and Micah Wright. And to my biggest cheerleader, Fred Ackerman, thank you for believing in this project and believing in my ability to get it done.

TABLE OF CONTENTS

ABSTRACT.....	ii
MECHANISMS AND SPATIAL PATTERNS OF BARK BEETLE-ASSOCIATED MORTALITY FOLLOWING VARIABLE DENSITY THINNING TREATMENTS IN A SIERRA MIXED-CONIFER FOREST	ii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vii
LIST OF APPENDICES	xi
CHAPTER 1: EFFECTS OF THINNING ON RESISTANCE TO DROUGHT AND BARK BEETLE-ASSOCIATED MORTALITY IN A SIERRA MIXED-CONIFER FOREST	1
ABSTRACT.....	1
INTRODUCTION	3
MATERIALS AND METHODS.....	8
Study Area	8
Data Collection	11
Subject tree sampling	11
Estimating competition	12
Estimating tree vigor	13
Drought resistance	14
Statistical analyses	16
RESULTS	19
Sugar pine mortality.....	19
Sugar pine drought resistance	21
White fir mortality	23

White fir drought resistance.....	25
DISCUSSION	29
REFERENCES	34
CHAPTER 2: MECHANISMS AND SPATIAL PATTERNS OF BARK BEETLE- ASSOCIATED MORTALITY FOLLOWING VARIABLE DENSITY THINNING TREATMENTS IN A SIERRA MIXED CONIFER FOREST.....	46
ABSTRACT.....	46
INTRODUCTION	48
MATERIALS AND METHODS.....	51
Study Site	51
Stand Maps	53
Data Collection	53
Stand Structures	55
Data Analysis	56
Spatial patterns of mortality.....	57
RESULTS	59
White fir mortality	59
Sugar pine mortality.....	61
Spatial patterns of mortality.....	64
DISCUSSION	68
REFERENCES	73
CONCLUSION.....	83
APPENDICES CHAPTER 1	85
APPENDICES CHAPTER 2	92

LIST OF TABLES

Table 1 Summary of logistic regression inputs and outputs to predict probability of sugar pine mortality. Coefficients > 0.50 suggest resistance to bark beetle-associated mortality. Values in bold were significant based on an alpha level of 0.05 while AUC represents the area under the receiver operating characteristic curve, with values closer to 1 suggesting higher model accuracy.	20
Table 2 Generalized linear model inputs and outputs predicting average growth ratio of live sugar pine over the duration of drought. Values in bold indicate significance based on an alpha level of 0.05 and variance inflation factor (VIF) describes multi-collinearity potential of each parameter with values less than 2 indicating low collinearity.	23
Table 3 Summary of logistic regression inputs and outputs to predict probability of white fir mortality. Coefficients > 0.50 suggest resistance to bark beetle-associated mortality. Values in bold suggest significance based on an alpha level of 0.05. AUC represents the area under the receiver operating characteristic curve, with values closer to 1 suggesting higher model accuracy.	25
Table 4 Generalized linear model inputs and outputs predicting average growth ratio of live white fir over the duration of drought. Values in bold indicate significance based on an alpha level of 0.05 and variance inflation factor (VIF) describes multi-collinearity potential of each parameter with values less than 2 indicating low collinearity.	28
Table 5 Summary of model inputs predicting the proportion of white fir mortality and model performance metrics. K indicates the number of parameters in the model. Δ AIC indicates the difference between AIC values from a given model and the top-rated model. AIC weight suggests the probability that a given model is the best model in comparison to all model being evaluated. Log likelihood describes the fit of estimated coefficients to observed data, with higher values suggesting a better fit.	60
Table 6 Summary of model inputs predicting the proportion of sugar pine mortality and model performance metrics. K indicates the number of parameters in the model. Δ AIC indicates the difference between AIC values from a given model and the top-rated model. AIC weight suggests the probability that a given model is the best model in comparison to all model models evaluated. Log likelihood describes the fit of estimated coefficients to observed data, with higher values suggesting a better fit.	63

LIST OF FIGURES

Figure 1 Location of Stanislaus-Tuolumne Experimental Forest, including delineation of unit boundaries. UTB = unthinned/burned, UTUB = unthinned/unburned, LVB = Low variability thin/burned, LVUB = low variability thin/unburned, VDB = Variable density thin/burned, VDUB variable density thin/unburned. 9

Figure 2 Aerial photos from 2012 depicting each of the three treatments within our study at Stanislaus-Tuolumne Experimental Forest. Panel A is an unthinned plot, showing high tree density and a relatively homogeneous tree distribution. Panel B is a low variability thinning plot, showing lower competition than the unthinned treatments with an even distribution of trees. Panel C is variable density thinning treatment, showing a similar amount of competition as low variability thinning, but exhibits clumps of trees and openings. Source: United States Department of Agriculture National Agriculture Imagery Program, 2012. 10

Figure 3 Possible resistance ratio (vigor during drought/vigor pre-drought) patterns over time from Year (x) through the drought. Growth and resin duct metrics pre-drought are assumed to be relatively consistent ($Vigor_{x-1} = Vigor_x$), while growth and resin duct metrics during drought can shift in three different ways. Trees with growth and resin duct metrics that decline relative to pre-drought conditions exhibit resistance ratios < 1 and indicate a lack of resistance to drought. If trees show growth and resin duct metrics equal to than pre-drought conditions, resistance ratios are equal to 1 and indicate maintained resistance. When growth and resin duct metrics are greater than pre-drought conditions, trees exhibit resistance ratios > 1 and indicate enhanced drought resistance. 16

Figure 4 Average growth and average resin duct size (defense) ratio of live and dead sugar pine in the year prior to mortality of dead trees. Error bars represent bootstrapped 95% confidence intervals around the mean. Dotted red lines represent static drought resistance (growth or defense during drought = growth or defense pre-drought), while confidence intervals > 1 suggest enhanced resistance and confidence intervals < 1 suggest lack of resistance. 20

Figure 5 Competition, as measured by the Hegyi index, surrounding live sugar pine across treatments. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned. Letters denote significant differences in competition among treatments as determined by pairwise comparisons of permutation tests adjusted for multiple comparisons with a Bonferroni correction. 21

Figure 6 Response curves of model predicting growth ratio of live sugar pine over the duration of drought, with competition measured using the Hegyi Index. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned,

LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned. 23

Figure 7 Average growth ratio of live and dead white fir in the year prior to mortality of dead trees. Error bars represent bootstrapped 95% confidence intervals around the mean. Dotted red lines represent static drought resistance (growth during drought = growth pre-drought), while confidence intervals > 1 suggest enhanced resistance and confidence intervals < 1 suggest lack of resistance. 25

Figure 8 Competition, as measured by the Hegyi index, surrounding live white fir across treatments. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned. Letters denote significant differences in competition among treatments as determined by pairwise comparisons of permutation tests adjusted for multiple comparisons with a Bonferroni correction. 26

Figure 9 Response curves of model predicting growth ratio of live white fir over the ... 28

Figure 10 Locations of variable density thinning units within the Stanislaus-Tuolumne Experimental Forest. Unit boundaries superimposed on aerial photos provided by the United States Department of Agriculture National Agriculture Imagery Program, 2012. 52

Figure 11 Map of predicted tree locations from LiDAR data and actual locations of trees. Panel A depicts underestimation of tree counts, panel B depicts overestimation of tree counts, and panel C depicts poor estimations of tree locations. 55

Figure 12 Response curves from top logistic regression models predicting the proportion of white fir mortality across different scales, with black dots representing observed values. Numbers in top left corner indicate distance (m) from plot center. 61

Figure 13 Response curves from top logistic regression models predicting the proportion of sugar pine mortality across different scales, with black dots representing observed values. Numbers in top left corner indicate distance (m) from plot center. 64

Figure 14 Pooled estimates of spatial patterns of bark beetle-associated mortality between observed dead white fir (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($gd, d - gd, l_{observed} > gd, d - gd, l_{random}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. 66

Figure 15 Pooled estimates of spatial patterns of bark beetle-associated mortality between observed dead sugar pine (red line) and mortality patterns generated by complete

spatial randomness (gray). Deviations of observed values above the gray area ($gd, d - gd, lobserved > gd, d - gd, lrandom$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. 67

LIST OF APPENDICES

Appendix A Summary of paired white fir samples found for analysis.....	85
Appendix B Summary of paired sugar pine samples found for analysis.	86
Appendix C Competition for live and dead trees across treatments. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned.	87
Appendix D A description of resin duct variables measured from sugar pine tree cores.	88
Appendix E Spearman's rank correlation coefficient matrix. Values in bold indicate p-value < 0.05.....	89
Appendix F Average sugar pine growth and resin duct size ratio ($\pm 2SE$) for live and dead white fir during the year preceding mortality of dead counterparts.	90
Appendix G Summary of average growth ratio ($\pm 2 SE$) for live and dead white fir during the year preceding mortality of dead counterparts.	91
Appendix H Number of plots containing bark beetle-associated mortality of white fir or sugar pine.	92
Appendix I Summary of effect size for top logistic regression models predicting proportion of white fir mortality across different scales.....	93
Appendix J Summary of effect size for top logistic regression models predicting proportion of sugar pine mortality across different scales.....	94
Appendix K Individual unit estimates of spatial patterns of bark beetle-associated mortality between observed dead white fir (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($gd, d - gd, observed > gd, d - gd, random$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. Plots without patterns of random mortality did not contain an adequate sample of dead trees to generate simulation envelopes and were removed from the pooled estimate of $g(r)$	95
Appendix L Individual unit estimates of spatial patterns of bark beetle-associated mortality between observed dead sugar pine (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area	

$(gd, d - gd, lobserved > gd, d - gd, lrandom)$ indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. Plots without patterns of random mortality did not contain an adequate sample of dead trees to generate simulation envelopes and were removed from the pooled estimate of $g(r)$ 96

CHAPTER 1: EFFECTS OF THINNING ON RESISTANCE TO DROUGHT AND BARK BEETLE-ASSOCIATED MORTALITY IN A SIERRA MIXED-CONIFER FOREST

ABSTRACT

Over recent decades, substantial increases in tree mortality and unprecedented bark beetle outbreaks has occurred during severe drought conditions. With compounding disturbances such as these expected to increase in frequency and intensity with climate change, managers must develop creative ways to promote resistance in forests. While thinning is often used to increase growing space and improve tree health, treatments that enhance spatial heterogeneity may provide an alternative approach to promoting resistance to disturbances. Variable density thinning is a management method that can also reduce competition, but residual trees are intended to mimic the spatial heterogeneity that was present in forests historically. However there exists little research evaluating how forests treated with variable density thinning respond to drought and bark beetles. This study quantifies the relationship between drought resistance and bark beetle-associated mortality. We also evaluate whether reductions in competition affect the capacity of trees that survived bark beetle-associated mortality to withstand prolonged drought conditions. We conducted a paired-tree experiment to compare drought resistance characteristics between trees that died from bark beetle-associated mortality and trees that survived. We randomly chose 40 live and recently dead sugar pine (*Pinus*

lambertiana), along with 48 live and recently dead white fir (*Abies concolor*) to determine the effects of competition on drought resistance. Measuring resistance by comparing growth and defense (i.e. average resin duct size) during and before drought, we evaluated how drought resistance influenced resistance to bark beetle-associated mortality. Our results suggest that trees which succumbed to bark beetle-associated mortality exhibited low drought resistance via lower growth in the year preceding tree mortality than trees that survived ($p = 0.01$ for sugar pine and $p = 0.02$ for white fir). We also found that drought resistance of sugar pine that survived bark beetle-associated mortality was negatively associated with competition ($p < 0.01$). Live sugar pine within the lowest levels of competition had the highest drought resistance, showing a 2% increase in growth ratio relative to the first year of drought. Although competition and tree size was also negatively related to live white fir drought resistance ($p < 0.01$ and $p = 0.02$, respectively), year of drought appeared to have the strongest influence on growth ratio. Despite growth reductions over time, live white fir with the lowest levels of competition still had 21% higher growth ratio relative to pre-drought conditions. Our results suggest that reducing competition may be an effective way of enhancing drought resistance. Therefore, thinning treatments characterized by varying levels of spatial variability may provide pathways toward promoting resistance to bark beetle-associated mortality.

INTRODUCTION

Forested ecosystems are already experiencing the effects of climate change, showing vulnerability to drought and other agents of mortality (Allen et al. 2010). Over recent decades, increases in temperature-driven drought stress and high water deficits coincided with elevated rates of tree mortality (van Mantgem and Stephenson 2007, van Mantgem et al. 2009). Although trees avoid drought-induced mortality by restricting transpiration, doing so weakens host defenses (McDowell et al. 2011) and creates opportunities for bark beetles to colonize and kill host trees (Bentz et al. 2010). Greater frequency and intensity of disturbances under climate change may amplify the interactions between drought and bark beetles, potentially altering forest ecosystems in unanticipated directions.

The effects of compounding disturbances may be mitigated if forests maintain their ability to resist drought and bark beetle outbreak. Resistance is defined as the capacity to withstand disturbance by maintaining physiological performance during the disturbance (Lloret et al. 2011). Whether a tree is resistant to mortality from drought and bark beetles can be related to several physiological metrics. Growth is a commonly used surrogate of tree vigor and can serve as a proxy of mortality risk from drought and bark beetle attack (Waring et al. 1980, Mitchell et al. 1983, Larsson et al. 1983). Declines in radial growth generally precede tree mortality, with the longevity and strength of those declines varying by contributing agents of mortality (Cailleret et al. 2016). Severe drought conditions lead to strong but short-term declines in tree growth, while bark beetle

outbreaks are associated with weak growth signals and abrupt tree death (Cailleret et al. 2016).

Although growth reductions relate to bark beetle-associated tree mortality, tree defense measures can be better related to resistance from bark beetles than growth (Kane and Kolb 2010, Hood and Sala 2015). Resin defenses represent the potential carbohydrate capacity that a tree has to resist bark beetle-associated mortality. Resin flow is a common metric of tree defense, but is highly variable among environmental conditions, genetics, and season (Lombardero et al. 2000, Perrakis et al. 2011, Moreira et al. 2015). Resin ducts are an important constitutive defense system that store and deploy oleoresins to physically or chemically inhibit insect attack (Franceschi et al. 2005), with resin ducts showing a stronger relationship to bark beetle resistance than resin flow (Hood and Sala 2015). A tree's capacity to resist beetle attack increases with greater investment in resin ducts (Kane and Kolb 2010, Ferrenberg et al. 2014), with declining investments increasing tree mortality during severe drought conditions (Gaylord et al. 2013).

Although thinning and prescribed fire are conventional treatments designed for restoration or fuel hazard reduction, they may also potentially mitigate tree mortality due to drought and bark beetles. By focusing on reducing stand density, these treatments may alleviate water stress and create sufficient resources to resist bark beetles (Coops et al. 2009, Fettig et al. 2012, Stark et al. 2013). While thinning can increase resistance to bark beetle attack by enhancing growth and resin duct characteristics under water stress (Hood et al. 2015, Hood et al. 2016), prescribed fire produces more mixed effects on tree resistance. In pines (*Pinus* spp.), prescribed fire can stimulate resin flow and resin duct

production (Perrakis and Agee 2006, Hood et al. 2015), but effects vary with season of burn and fire intensity (Perrakis et al. 2011, Hood et al. 2016). Short-term reductions in tree growth may follow prescribed fire (Busse et al. 2000, Collins et al. 2014) and temporarily increase secondary mortality from bark beetles (Breece et al. 2008).

Although these treatments may enhance resistance characteristics, residual stands can lack spatial complexity that maintains resistance over time (North et al. 2009, Fettig et al. 2012).

Increasing spatial complexity by incorporating ecological processes that influence stand structure may be a more effective approach to enhancing long-term forest resistance (Franklin et al. 2007). Stand structure partly arises from disturbance legacies, reflecting interactions amongst agents of mortality, species composition, and spatial variability (Franklin et al. 2002). Also known as biological legacies, structures developed and maintained by disturbances exhibit characteristics that help evade, resist, or recover from disturbances (Perry and Amaranthus 1997). Prior to logging and fire suppression, forests characterized by high frequency, low- and mixed-severity fire regimes exhibited mosaics of individual trees, clumps of trees, and openings (ICO) (Larson and Churchill 2012, Churchill et al. 2013). Manipulating forests to reflect these more heterogeneous structures may confer greater resistance to natural disturbances (Turner et al. 1989, Churchill et al. 2013, Seidl et al. 2016).

Variable density thinning (VDT) is an alternative pathway towards reducing stand density similar to other conventional thinning methods, while increasing spatial heterogeneity. Intended to mimic ICO structures, VDT increases variation in tree density

and shifts species composition and size classes (Knapp et al. 2017). However, there is limited research comparing its efficacy with conventional thinning methods. Although conventional thinning and VDT may reduce competition, maintaining clumped trees within VDT might retain highly competitive environments that reduce tree vigor within those clumps. Given the recent unprecedented drought (2012-2015) in California (Griffin and Anchukaitis 2014), where substantial tree mortality occurred in areas with greater climatic water deficit and highly competitive environments (Young et al. 2017), the potential impacts of retaining relatively dense clusters within stands is a cause for concern. With climate projections for California suggesting future increases in summer temperatures and losses in snow accumulation (Cayan et al. 2008), potential water deficits may have drastic impacts on forested ecosystems. Using an ongoing variable density thinning study within the central Sierra Nevada, we can evaluate if spatial variability influences resistance to drought and bark beetle-associated mortality by addressing the following questions: 1) Does drought resistance vary between trees that died from bark beetle-associated mortality and those that survived and 2) How do reductions in competition affect drought resistance in trees that survived bark beetle-associated mortality?

While we expect trees that died from bark beetle-associated mortality to show declines in growth and defense before succumbing to mortality, we expect trees that survived to show enhanced drought resistance during that same time period. We expect reductions in competition from variable density thinning and thinning with low spatial

variability will have equivalent effects on tree growth and defense, effectively maintaining drought resistance over time.

MATERIALS AND METHODS

Study Area

Our study site consisted of a 100 ha mixed-conifer forest located within the Stanislaus-Tuolumne Experimental Forest in the central Sierra Nevada of California (38°10'22"N, 120°00'00"W; **Figure 1**). At an elevation of 1740 m to 1900 m, stands at this site are composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and incense-cedar (*Calocedrus decurrens*). Four years prior to the onset of drought (2008 – 2011), average temperature ranged from 8.7 °C to 9.9 °C and precipitation ranged from 90.6 cm – 160.4 cm (PRISM, 2019). During the extended drought from 2012 to 2015, average temperature was 15 % higher than average (range = 10.6 – 11.4 °C) and precipitation was 44 % lower than average (range = 36.6 – 115.6 cm).

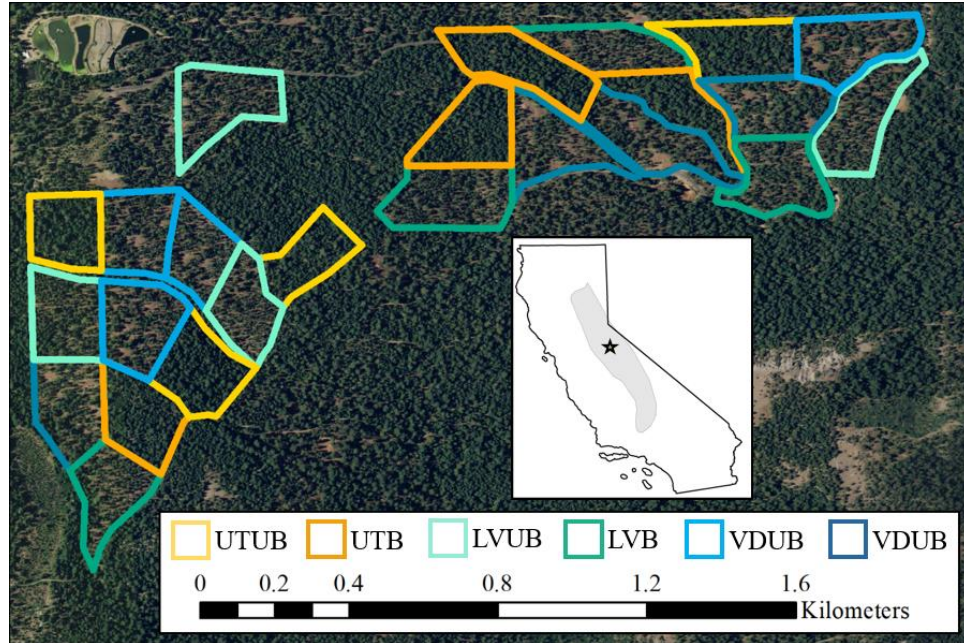


Figure 1 Location of Stanislaus-Tuolumne Experimental Forest, including delineation of unit boundaries. UTB = unthinned/burned, UTUB = unthinned/unburned, LVB = Low variability thin/burned, LVUB = low variability thin/unburned, VDB = Variable density thin/burned, VDUB variable density thin/unburned.

Since the 1920s, fire exclusion increased tree density at our study site and shifted compositional dominance towards shade-tolerant species and smaller-sized diameter classes (Knapp et al. 2013). In 2009, the United States Department of Agriculture Forest Service initiated a variable density thinning (VDT) experiment to restore these forests toward historical stand structures prior to logging and fire exclusion. In 2011, three different thinning treatments (unthinned, low variability, and VDT) were applied across 24 (4 ha) units (Knapp et al. 2017). To assess the ecological impacts of spatial variability in stand structure, both thinning treatments contained similar basal area, size class

distribution, and species composition but differed in the spatial arrangement of trees

(Figure 2).

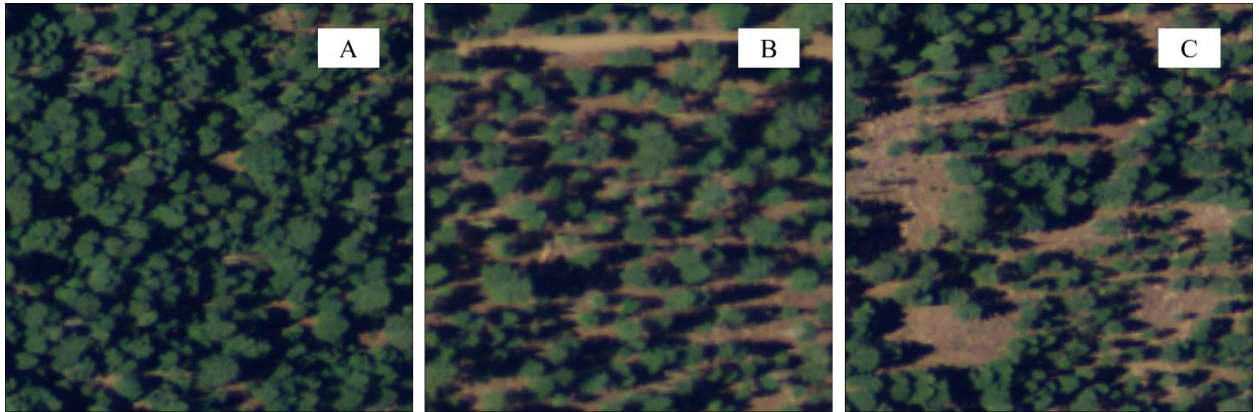


Figure 2 Aerial photos from 2012 depicting each of the three treatments within our study at Stanislaus-Tuolumne Experimental Forest. Panel A is an unthinned plot, showing high tree density and a relatively homogeneous tree distribution. Panel B is a low variability thinning plot, showing lower competition than the unthinned treatments with an even distribution of trees. Panel C is variable density thinning treatment, showing a similar amount of competition as low variability thinning, but exhibits clumps of trees and openings. Source: United States Department of Agriculture National Agriculture Imagery Program, 2012.

In each VDT unit, five gaps were created ranging from 0.04 – 0.2 ha within in areas dominated by shade-tolerant species or with root disease present. The remainder of each VDT unit was divided into groups of similar-sized trees and thinned to low ($27.5 \text{ m}^2 \text{ ha}^{-1}$), medium ($50.5 \text{ m}^2 \text{ ha}^{-1}$), or high ($73.5 \text{ m}^2 \text{ ha}^{-1}$) basal area. In each low variability thinned unit, residual trees were evenly spaced, leaving 0.5-crown widths between neighbors. In both thinning treatments, large vigorous trees with healthy crowns were left on site regardless of thinning guidelines. In November of 2013, the area was ignited using a spot-ignition pattern with a headinh and backing fire to burn half of the replicates for each thinning treatment. During this time, the study site experienced fairly high relative

humidity (32-57%) and fuel moisture in 1 hr (11-19%), 10 hr (11-19%), 100 hr (13-18%) and 1000 hr (18-22%) timelag classes, resulting in a lower-intensity prescribed fire (Knapp et al. 2017). In total, there were six different treatments including unthinned – unburned (UTUB), unthinned – burned (UTB), low variability thin – unburned (LVUB), low variability thin – burned (LVB), variable density thin – unburned (VDUB), and variable density thin – burned (VDB). Each treatment was replicated 4 times, totaling 24 units across our site.

Data Collection

Subject tree sampling

To determine the effect of competition across treatments on tree resistance to drought and bark beetle attack, we conducted a paired-tree experiment that compared growth and defense characteristics between trees that died from bark beetle-associated mortality and trees that survived. To select subject trees within each unit, we randomly chose grid points from a pre-existing 30 m grid and conducted a 15 m radius search to select recently dead sugar pine and white fir. We defined “recently dead” as trees that exhibited characteristics of decay consistent with mortality within the last four years, including intact dead needles, fine branches, and major limbs (Raphael and Morrison 1987). Once we located a suitable tree, we removed enough bark to confirm bark beetle activity by identifying larval galleries of fir engraver (*Scolytus ventralis*) on white fir and mountain pine beetle (*Dendroctonus ponderosae*) on sugar pine. To control for other biotic agents of mortality, we excluded trees that showed signs of pathogens not

associated with fir engraver and mountain pine beetle (Paine et al. 1997). We also excluded trees that showed signs of abiotic agents of mortality such as mechanical damage, lightning scars, and severe fire injuries. When a tree satisfied these criteria, we paired it with a live intraspecific tree of similar size (≤ 7 cm difference in diameter at breast height, DBH) and similar environmental conditions (≤ 40 m distance between trees). With each selected pair, we recorded species, status (dead or live), and DBH (cm). We repeated this process for all random points, until we selected eight pairs for each species in each treatment. A combination of low tree mortality and restrictive experimental design criteria led to reduced sampling in some treatments, totaling 48 pairs of white fir and 39 pairs of sugar pine (**Appendix A, Appendix B**).

Estimating competition

To evaluate how reductions in competition affect drought resistance, we estimated competitive environments around each subject tree. We delineated competitive environments by establishing a nested 20 m fixed-radius plot around each subject tree. With the subject tree as plot center, we recorded the species, status, DBH, and distance to subject tree (m) of competitor trees within each plot. Competitor trees were included in a plot if it had a DBH ≥ 10 cm and were within 5 m of plot center, a DBH ≥ 25 cm and were within 10 m of plot center, and a DBH ≥ 45 cm within 20 m of plot center. Because of its stronger correlation with growth across multiple species (Contreras et al. 2011), we used the Hegyi index to estimate the competitive environment for each tree:

$$Competition = \sum_{j=1}^n \frac{DBH_j}{DBH_i \times (D_{ij} + 1)}$$

Where DBH_j is the DBH of the competitor tree, DBH_i is the DBH of the subject tree, and D_{ij} is the distance between the subject tree and competitor. This index estimates the weighted contribution of each competitor tree based on its relative size and distance from the subject tree (Hegyi 1974, Biging and Dobbertin 1992). Because our data did not meet the assumptions of a linear model, we used a permutation t-test adjusted with a Bonferroni correction factor to compare competition amongst treatments and competition between paired dead and live trees. Preliminary analysis showed that competition did not vary between paired live and dead trees (**Appendix C**).

Estimating tree vigor

To discern the effects of treatment on growth, we conducted tree ring analyses for each subject tree. Using an increment borer, we extracted one 5 mm wide core from each live and dead tree at approximately DBH (1.37 m) and allowed each core to dry prior to mounting them on wood blocks. Once mounted, we progressively sanded each core with 80- to 600-grit sandpaper with an orbital sander, upon which we manually sanded each core with 800- to 1500-grit sandpaper. After processing, we scanned each core to create a high-resolution image (1200 dpi) and saved them as .jpg files for analysis. Each scanned image was imported into WinDendro (Regent Instruments, Quebec, Canada), where we assigned annual ring boundaries and measured ring widths (0.1 cm year^{-1}). We created a cross-dated master chronology for all live trees of each species with possible errors assessed using ring width series in COFECHA (Grissino-Mayer 2001). Using this master chronology, we cross-dated the ring width series of each dead tree and estimated the year of mortality. None of our subject trees died before 2012, and a majority of sugar pine and

white fir died in 2016 (53% and 58%, respectively). We assumed the last annual growth ring for each dead sample represented the year of mortality, but it is possible the actual year of mortality is later than reported due to mortality occurring prior to the initiation of radial growth or absent tree rings that were unaccounted. Outputs from COFECHA included series intercorrelation (site level similarities) and mean sensitivity (annual variability in ring width). Tree ring series for sugar pine had an intercorrelation of 0.464 and a mean sensitivity of 0.280, while white fir had an intercorrelation of 0.532 and a mean sensitivity of 0.198.

In addition to growth, we quantified defense characteristics from sanded cores of sugar pine only since white fir do not contain xylem resin ducts. Using scanned core images and ImageJ (Schneider et al. 2012), we estimated mean resin duct size (mm^2), resin duct production (number year^{-1}), total resin duct area ($\text{mm}^2 \text{ year}^{-1}$), resin duct density (number mm^{-2}), and relative resin duct area (%) (**Appendix D**). Preliminary analysis indicated high correlations (**Appendix E**) amongst average duct size, total duct area, resin duct production, duct density, and relative duct area. Therefore, we focused our analyses only on average duct size because this metric shows a strong association with resin flow (Hood and Sala 2015).

Drought resistance

We defined drought resistance in sugar pine and white fir as the ability to maintain or increase growth (ring width year^{-1}) during drought years (2012 – 2016) relative to growth prior to drought (2007 – 2011) and expressed growth resistance as a ratio (Lloret et al. 2011). While resources are limited under normal conditions, we

expected trees adapted to dry environments would optimize resource allocation, resulting in relatively static growth patterns over time (Herms and Mattson, 1992). Under severe drought conditions, reduced resource availability may have led to declines in tree growth, resulting in growth less than pre-drought years. This would result in growth ratio < 1 , indicating a lack of drought resistance (**Figure 3**). It is possible that reductions in competition, such as those produced with thinning treatments, negated the effects of drought. This condition may result in tree growth equal to or greater than pre-drought conditions, resulting in growth ratio ≥ 1 or an indication of drought resistance. For sugar pine, we also defined drought resistance as the ability to maintain resin duct size during drought years relative to pre-drought measures and expressed defense resistance as a ratio. Because resin duct size is correlated with growth (Hood and Sala 2015), we expected resin duct size to follow similar patterns to growth ratio. Live trees may have had more years of growth than their dead counterparts, potentially leading to higher resistance ratios amongst live trees than dead ones. To avoid an unbalanced dataset, we adjusted samples from each live tree to match the years of growth preceding mortality of its dead counterpart.

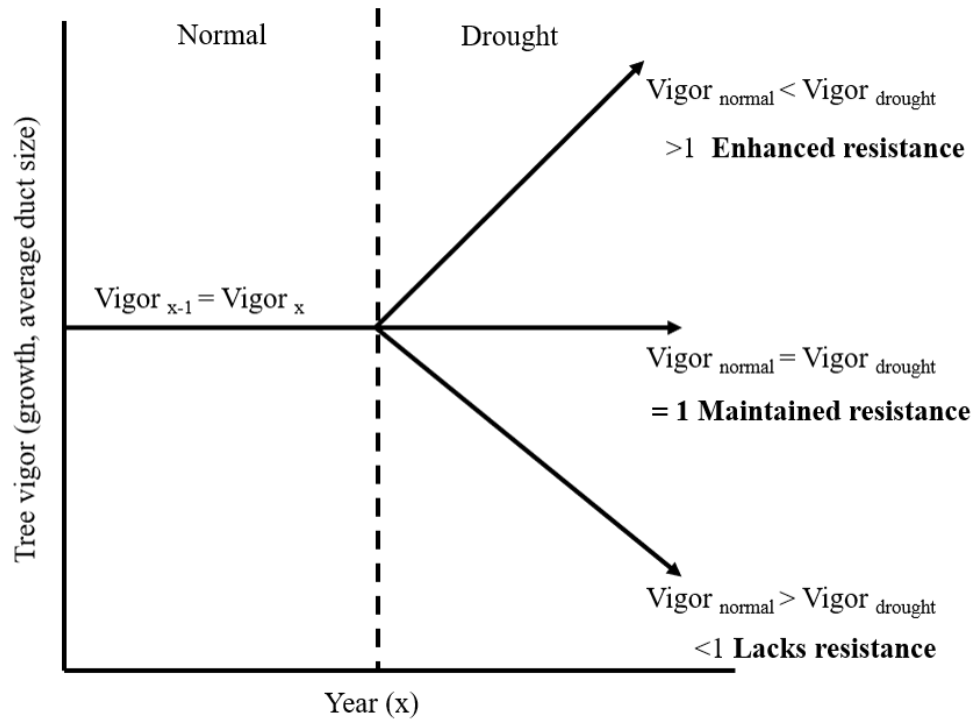


Figure 3 Possible resistance ratio (vigor during drought/vigor pre-drought) patterns over time from Year (x) through the drought. Growth and resin duct metrics pre-drought are assumed to be relatively consistent ($Vigor_{x-1} = Vigor_x$), while growth and resin duct metrics during drought can shift in three different ways. Trees with growth and resin duct metrics that decline relative to pre-drought conditions exhibit resistance ratios <1 and indicate a lack of resistance to drought. If trees show growth and resin duct metrics equal to than pre-drought conditions, resistance ratios are equal to 1 and indicate maintained resistance. When growth and resin duct metrics are greater than pre-drought conditions, trees exhibit resistance ratios > 1 and indicate enhanced drought resistance.

Statistical analyses

To assess differences in drought resistance between trees that died from bark beetle-associated mortality and those that survived, we bootstrapped 95% confidence intervals for each mean growth and defense ratio to determine levels of drought resistance (1000 permutations) using the *boot* package in R (Canty and Ripley 2017, R Development Core Team 2018). We then conducted logistic regression models to predict

the probability of bark beetle resistance based on growth ratio (sugar pine and white fir) and duct size ratio (sugar pine only) in the year preceding mortality of dead counterparts. With outputs from our logistic regression models, we used the following formula to convert coefficients to estimate probability of resistance:

$$\text{Probability of resistance} = \frac{1}{1 + e^{-(\beta x_1 + \beta x_2 + \beta x_3 \dots \beta x_n)}}$$

Where β is the coefficient of variable x_n and response values ≥ 0.5 indicating bark beetle resistance. We also report the area under the receiver operating characteristic curve to assess how well our parameters distinguished between our binary (live or dead) data.

To determine how reductions in competition affected drought resistance in trees that survived bark beetle-associated mortality, we used generalized linear models for each species in R. Using a log link function in the gamma distribution family, we created separate models predicting drought resistance ratio of growth (sugar pine and white fir) and defense (sugar pine only). We used competition (Hegyi index) and year of drought as our response variables. To account for differences in tree size amongst live trees, we also included DBH as a covariate in our models. Before interpreting model coefficients, we accounted for multicollinearity by determining if explanatory variables had a variance inflation factor ≥ 10 (Burnham and Anderson 1998). Since preliminary analysis suggested that none of our variables exceeded this threshold, we included all variables in our models.

With outputs from all of our generalized linear models, we used the following formula to convert coefficients to estimate growth and defense ratio:

$$Resistance\ ratio = e^{(\beta x_1 + \beta x_2 + \beta x_3 \dots \beta x_n)}$$

Where β is the coefficient of variable x_n and ratio \geq indicating drought resistance. To evaluate effect size, we rescaled our variables by standardizing observations with the following formula:

$$Standardized\ observation = \frac{x - \bar{x}}{s(x)}$$

Where x is the observed value, \bar{x} is the mean of all observed values, and $s(x)$ is the standard deviation of all observed values.

RESULTS

Sugar pine mortality

Metrics of drought resistance had variable associations with sugar pine resistance to bark beetle-associated mortality. In the year prior to tree mortality, dead sugar pine exhibited a lower growth ratio in comparison to live counterparts during the same year ($p = 0.01$, **Figure 4**). While dead sugar pine maintained drought resistance [0.58 – 1.06] in the year preceding tree mortality, they showed an 18% decline in growth relative to pre-drought conditions (**Appendix F**). Not only did live trees show enhanced drought resistance [1.06 – 1.41] during the same year, they had a 23% increase in growth relative to pre-drought conditions. Our model indicates that lower drought resistance in the year preceding tree mortality was an indicator of bark beetle susceptibility, with growth ratio positively associated with bark beetle resistance (**Table 1**). When average duct size was used as a metric of drought resistance, dead and live sugar pine similarly maintained drought resistance (**Figure 4**). Although dead and live trees showed increases in duct size relative to pre-drought conditions (14% and 10%, respectively), our model did not detect differences between dead and live sugar pine ($p = 0.67$).

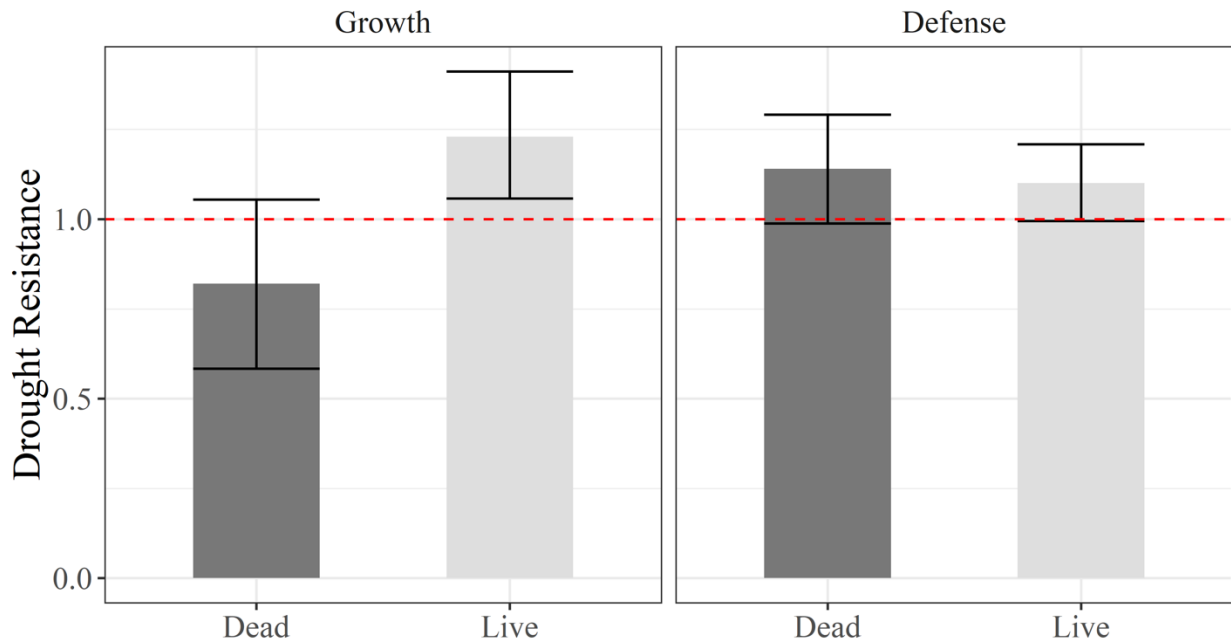


Figure 4 Average growth and average resin duct size (defense) ratio of live and dead sugar pine in the year prior to mortality of dead trees. Error bars represent bootstrapped 95% confidence intervals around the mean. Dotted red lines represent static drought resistance (growth or defense during drought = growth or defense pre-drought), while confidence intervals > 1 suggest enhanced resistance and confidence intervals < 1 suggest lack of resistance.

Table 1 Summary of logistic regression inputs and outputs to predict probability of sugar pine mortality. Coefficients > 0.50 suggest resistance to bark beetle-associated mortality. Values in bold were significant based on an alpha level of 0.05 while AUC represents the area under the receiver operating characteristic curve, with values closer to 1 suggesting higher model accuracy.

Model inputs	Coefficient	Standard error	p-value	AUC
Growth ratio	0.74	0.43	0.01	0.73
Duct size ratio	0.43	0.63	0.67	0.54

Sugar pine drought resistance

Competition surrounding live sugar pine varied among treatments (**Figure 5**), with all thinning treatments showing reduced competition in comparison to UTUB. Competition was the lowest in VDUB relative to all treatments ($p = 0.03$), with live sugar pine surrounded by 58% lower competition than UTUB. VDB, LVUB, and LVB showed equivalent levels of competition ($p = 1.00$), averaging 30 to 42% reductions in competition relative to UTUB ($p = 0.03$). Although UTB did not reduce competition relative to UTUB ($p = 1.00$), live sugar pine in UTB showed similar levels of competition in comparison to VDB, LVUB, and LVB.

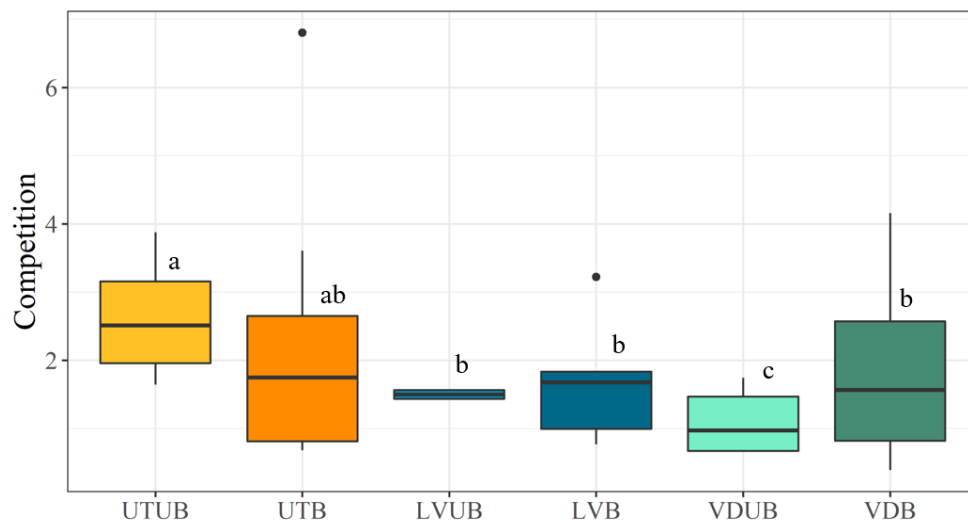


Figure 5 Competition, as measured by the Hegyi index, surrounding live sugar pine across treatments. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned. Letters denote significant differences in competition among treatments as determined by pairwise comparisons of permutation tests adjusted for multiple comparisons with a Bonferroni correction.

Drought resistance in live sugar pine decreased under higher levels of competition, with growth ratio declining as the drought progressed (**Figure 6**). Increased competition was associated with 28% declines in growth ratio ($p < 0.001$, **Table 2**), and live trees showed a 27% lower average growth ratio in 2014 than in 2012 ($p = 0.007$). Despite reductions, trees with the lowest levels of competition recovered during the last two years of drought, showing 2% higher growth ratio compared to 2012. Conversely, live sugar pine with the highest levels of competition showed declining drought resistance over the entire duration of drought, with 24% lower growth ratio in 2016 compared to 2012. When drought resistance was measured with average duct size ratio, our models did not detect an effect of competition on drought resistance ($p = 0.18$).

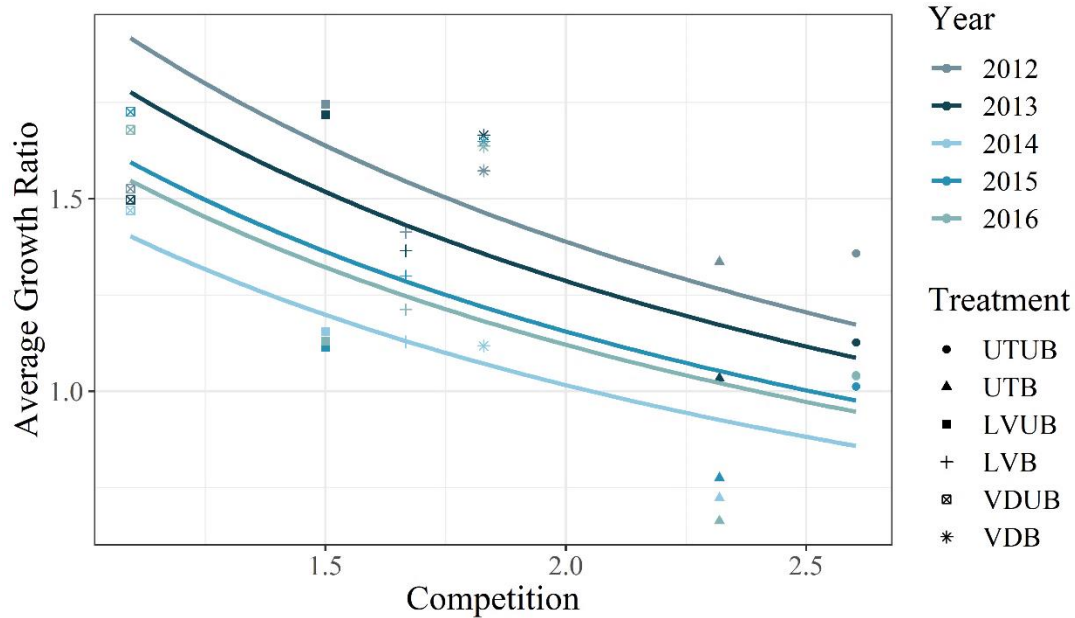


Figure 6 Response curves of model predicting growth ratio of live sugar pine over the duration of drought, with competition measured using the Hegyi Index. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned.

Table 2 Generalized linear model inputs and outputs predicting average growth ratio of live sugar pine over the duration of drought. Values in bold indicate significance based on an alpha level of 0.05 and variance inflation factor (VIF) describes multi-collinearity potential of each parameter with values less than 2 indicating low collinearity.

Parameter	Coefficient	Standard error	p-value	VIF
Average competition	0.72	0.07	<0.001	1.02
Year 2013	0.92	0.10	0.473	1.00
Year 2014	0.73	0.10	0.007	-
Year 2015	0.83	0.10	0.091	-
Year 2016	0.81	0.10	0.052	-
Average DBH	0.99	0.01	0.161	1.02

When growth was used as a metric of drought resistance, live white fir exhibited a higher growth ratio in the year prior to mortality of its dead counterpart ($p = 0.02$, **Figure 7**). While dead white fir maintained drought resistance $[0.75 - 1.00]$ in the year preceding tree mortality, they showed a 12% decline in growth relative to pre-drought conditions (**Appendix G**). Although live trees also maintained drought resistance $[1.00 - 1.25]$ during the same year, they had a 12% increase in growth relative to pre-drought conditions. Our model indicated that lower drought resistance in the year preceding tree mortality is an indicator of bark beetle susceptibility, with growth ratio positively associated with bark beetle resistance (**Table 3**).

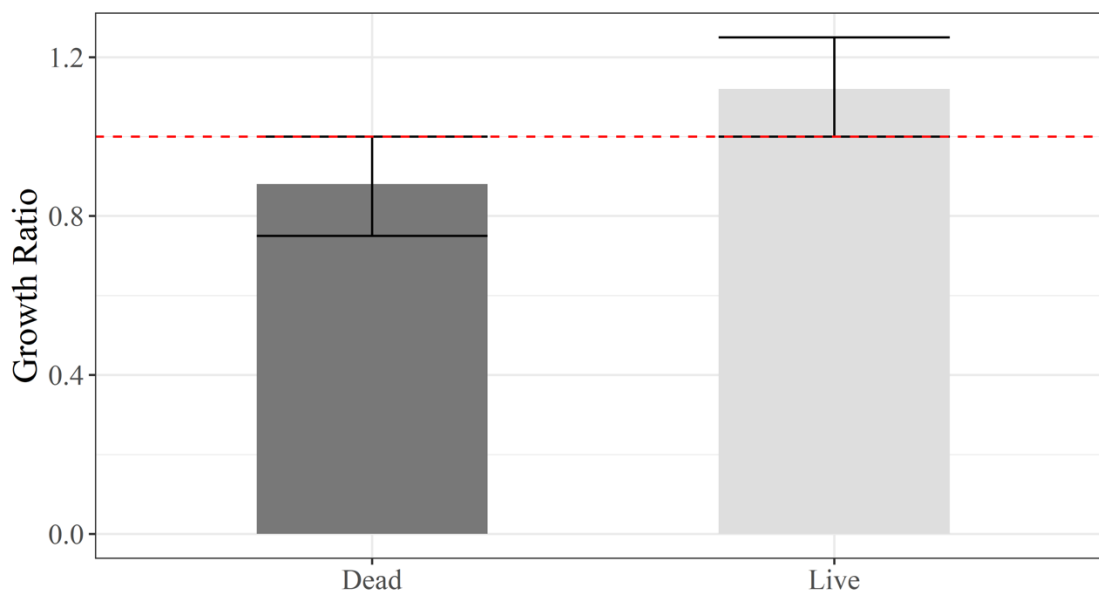


Figure 7 Average growth ratio of live and dead white fir in the year prior to mortality of dead trees. Error bars represent bootstrapped 95% confidence intervals around the mean. Dotted red lines represent static drought resistance (growth during drought = growth pre-drought), while confidence intervals > 1 suggest enhanced resistance and confidence intervals < 1 suggest lack of resistance.

Table 3 Summary of logistic regression inputs and outputs to predict probability of white fir mortality. Coefficients > 0.50 suggest resistance to bark beetle-associated mortality. Values in bold suggest significance based on an alpha level of 0.05. AUC represents the area under the receiver operating characteristic curve, with values closer to 1 suggesting higher model accuracy.

Model inputs	Coefficient	Standard error	p-value	AUC
Growth ratio	0.77	0.50	0.02	0.67

White fir drought resistance

Competition surrounding live white fir varied among treatments (**Figure 8**), with all thinning treatments showing reduced competition in comparison to UTUB.

Competition was the lowest in VDUB relative to all treatments ($p = 0.03$), with live white fir surrounded by 62% lower competition than UTUB. VDB, LVUB, and LVB showed equivalent levels of competition ($p = 1.00$), averaging 22 to 55% reductions in competition relative to UTUB ($p = 0.03$). UTB did not reduce competition relative to UTUB ($p = 1.00$), and had 33 to 52% higher competition than all thinning treatments ($p = 0.03$).

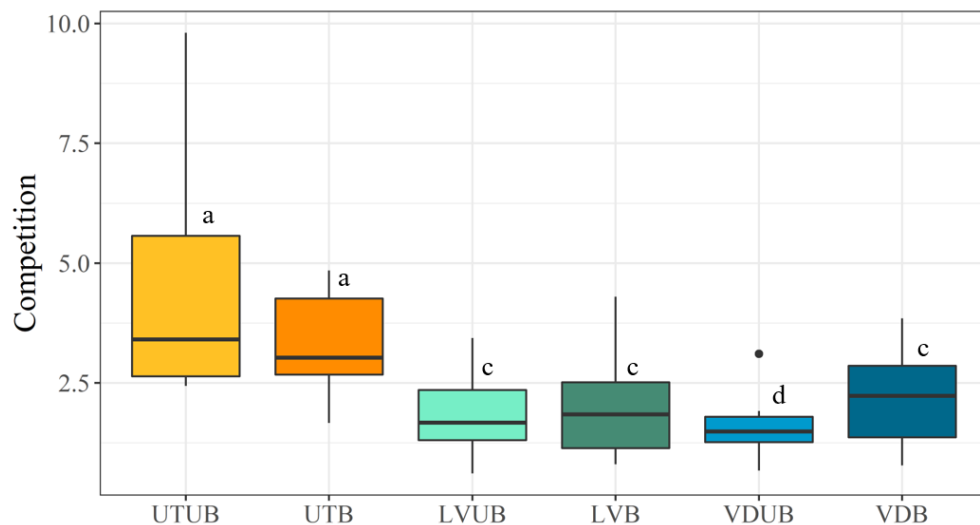


Figure 8 Competition, as measured by the Hegyi index, surrounding live white fir across treatments. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned. Letters denote significant differences in competition among treatments as determined by pairwise comparisons of permutation tests adjusted for multiple comparisons with a Bonferroni correction.

Drought resistance in live white fir decreased under higher levels of competition, with growth ratio declining as the drought progressed (**Figure 9**). Although increased competition was associated with a 17% decline in growth ratio ($p < 0.001$), our model also indicated that the duration of drought had a greater effect on drought resistance than competition (**Table 4**). Year of drought was negatively associated with drought resistance, with an average 27% reduction in growth ratio in 2016 relative to 2012. Despite reductions, trees with the lowest levels of competition still showed 21% higher growth ratio than pre-drought conditions. Conversely, live white fir with the highest levels of competition showed 30% lower growth ratio than pre-drought conditions. Drought resistance also varied by tree size, with our model indicating that growth ratio was negatively associated with DBH ($p = 0.015$).

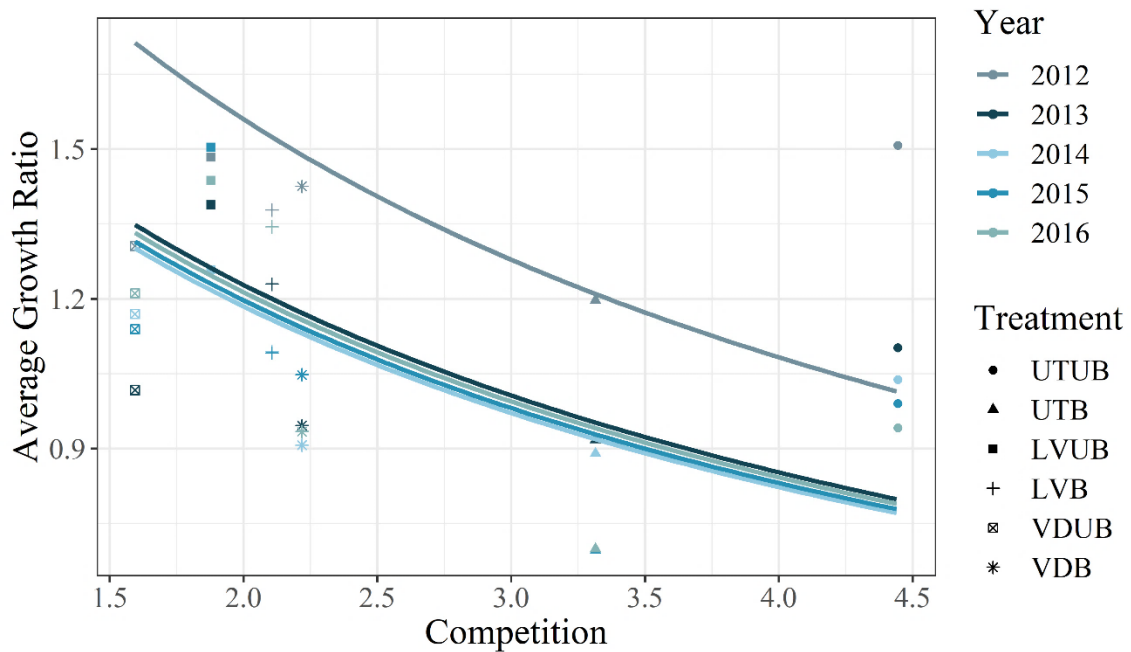


Figure 9 Response curves of model predicting growth ratio of live white fir over the duration of drought, with competition measured using the Hegyi Index. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned.

Table 4 Generalized linear model inputs and outputs predicting average growth ratio of live white fir over the duration of drought. Values in bold indicate significance based on an alpha level of 0.05 and variance inflation factor (VIF) describes multi-collinearity potential of each parameter with values less than 2 indicating low collinearity.

Parameter	Coefficient	Standard error	p-value	VIF
Average competition	0.83	0.05	0.002	1.82
Year 2013	0.78	0.09	0.013	1.00
Year 2014	0.76	0.09	0.005	-
Year 2015	0.77	0.09	0.007	-
Year 2016	0.78	0.09	0.009	-
Average DBH	0.98	0.01	0.015	1.82

DISCUSSION

As managers seek to develop new strategies that accomplish multiple objectives under a changing climate, alternative pathways exist to meet those objectives without compromising tree resistance to disturbances. Our results suggest that trees were able to survive bark beetle outbreak when growth was maintained during drought. We found that treatments which reduced competition may have promoted drought resistance in sugar pine and white fir by increasing or maintaining growth despite prolonged drought conditions. Should another drought or bark beetle outbreak occur, residual sugar pine and white fir within thinning treatments appear to have the greatest capacity to resist future disturbances.

To our knowledge, this is one of the first studies attempting to relate drought resistance to bark beetle-associated mortality, where we found that surviving sugar pine and white fir had greater drought resistance than those that died. Resistance is contingent on the ability of an organism to maintain physiological processes during a disturbance. For trees, growth is often a proxy of tree health, with declines in growth indicating that a tree is unable to maintain physiological processes due to some form of stress (Dobbertin 2005, Lloret et al. 2011) and that stress can possibly lead to mortality. Limited resources during drought can lead to declines in tree health (Eamus et al. 2013), possibly predisposing trees to bark beetle selection or inhibit the ability of trees to defend themselves against attack (Raffa et al. 2008). If trees that survived had more resources during drought to resist selection or beetle attack, then patterns of tree vigor may vary

between trees that survived and those that died (Kane and Kolb 2014). Although previous research has shown that treatments can promote drought resistance in live trees (Thomas and Waring 2014), comparing drought resistance between trees that survived bark beetle-associated mortality and those that died provides a better understanding of the physiological mechanisms that may enable trees to resist multiple disturbances. With disturbances expected to increase in frequency and severity with climate change (Seidl et al. 2017), linking relationships between resistance and mortality is critical for developing treatments that aim to reduce tree mortality.

Although bark beetle-associated mortality has been more strongly related to constitutive resin duct properties than growth in other pine species (Kane and Kolb 2010, Ferrenberg et al. 2014), induced resin defenses may explain why we did not find differences in resin duct size between sugar pine that died from bark beetle-associated mortality and those that survived. Sugar pine that died from bark beetle-associated mortality had greater drought stress, as evidenced by their lower growth ratio relative to sugar pine that survived. Accumulation of volatile compounds in stressed hosts may be related to beetle host selection (Kelsey et al. 2014), possibly increasing the vulnerability of these trees to beetle attack. As beetle attacks commenced, trees may have induced defense mechanisms in order to avoid successful colonization. Studies that simulate insect attack via mechanical wounding show increased resin responses (Hood and Sala 2015) and enhanced expression of genes that regulate oleoresin production (McKay et al. 2003). However, lower growth ratio in dead sugar pine may be indicative of their limited photosynthetic capacity. Although induced defenses could have initiated upon beetle

attack, susceptible trees may have had inadequate resources to support a sufficient amount of induced defenses to resist mortality.

Similar to other research, we found that drought resistance was negatively associated with competition (Vernon et al. 2018), suggesting that thinning could be a viable management method for mitigating tree mortality from bark beetles (Mitchel et al. 1983, Hood et al. 2016). Tree vigor is negatively associated with tree density (Larsson et al. 1983), possibly due to the greater water stress observed with higher levels of competition (Zausen et al. 2005). Increases in soil water content and water uptake have been found following thinning treatments alone and in combination with prescribed fire (Feeney et al. 1998, Wallin et al. 2004), suggesting that reduced competition may increase the amount of resources available for trees to avoid beetle attack. Although metrics associated with resistance to bark beetles, such as growth and resin ducts, can increase following thinning treatments (Hood et al. 2016), we did not find an association between competition and average duct size. However, resin ducts are genetically-associated traits (Rosner and Hannrup 2004) that can also vary with age (Westbrook et al. 2014). These factors were not taken into consideration in our experimental design, possibly obscuring any effects of competition on average duct size.

While reductions in competition can increase resources, such as light and water (Aussenac 2000), mechanisms underlying increased drought resistance may vary by how species respond to variation in post-thinning structure and composition. Since sugar pine is relatively shade-intolerant, higher light resource availability in gaps (York et al. 2003, York et al. 2011) may have promoted the greater growth we observed despite drought

conditions. However, white fir can have lower stomatal control than pines (Barker et al. 1973), possibly rendering them more sensitive to transpirational water loss if left in gaps or overly-exposed sites. If thinning can also increase soil temperature (Covington et al. 1997), then shade may become an important determinant of white fir growth when soil moisture is low (Conrad and Radosevich 1982) and possibly offset the effects of low stomatal control. A higher frequency of 30 to 70% canopy cover in low variability thinning treatments (Knapp et al. 2017) may have led to the greater drought resistance we observed in white fir even during the latter years of drought. Although our sample size precluded direct comparison of drought resistance amongst treatments, trends in species-dependent responses warrant further investigation regarding the effects of the spatial variability of thinning on drought and bark beetle-resistance.

Although drought resistance was higher in lower competitive environments, more open growing white fir may be more vulnerable to future drought events than open grown sugar pine. We found that there was a stronger negative association amongst all years of drought and white fir drought resistance than competition. The importance of competition can decrease with increasing abiotic stress, varying by the shade tolerance of a species (Kunstler et al. 2011). Leaf areas exhibited by shade-tolerant species (Lusk 2002) may increase photosynthetic rates, but at the cost of transpirational water loss (Carter and Smith 1988). Although reductions in competition could improve growth of residual white fir initially, the respirational requirements of larger crowns may offset these benefits during periods of severe drought stress. These additional respirational requirements may also be why we found a negative relationship between tree size and drought resistance in

white fir, although the effect size (2%) is fairly negligible compared to year of drought and competition. Pines can have greater water-use efficiency than firs (Carter and Smith 1988), possibly maintaining growth even under drier conditions. Although we observed reductions in sugar pine growth ratio as the drought progressed, only 2014 showed significantly lower drought resistance relative to 2012. It is possible that sugar pine responded to the thinning treatments by expanding their crowns initially, leading to higher transpiration costs during the first years of drought. However, pines may have greater plasticity in leaf retention than firs, which could lead to decreased allocation of above-ground biomass to foliage (Lusk 2002) under severe drought stress. In combination with greater stomatal control (Barker et al. 1973), this could have facilitated the recovery of sugar pine growth we observed in the latter years of drought.

Results from our study indicate that thinning may be a viable treatment for promoting resistance to drought and bark beetle-associated mortality. While our findings suggest that thinning in general is beneficial across different species, sugar pine and white fir may have different responses to the spatial variability of thinning. Although we did not explicitly compare the effects amongst thinning treatments, sugar pine appears to respond more positively to variable density thinning while white fir shows a greater response to low variability thinning. We suggest tailoring prescriptions for species-specific responses to treatments, prioritizing reductions in stand density and strategically placing residual trees based on shade-tolerance and microsite conditions. If managers seek to increase forest heterogeneity by applying variable density thinning treatments, we found no evidence to suggest that doing so would compromise tree vigor.

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, N., McDowell, M., Vennetier, T., Rigling, A., Breshers, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J., Allard, G., Running, S.W., Semerci, A., and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forest. *Forest Ecology and Management* 259:660-684.
- Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science* 57:287-301.
- Barker, J.E. 1973. Diurnal patterns of water potential in *Abies concolor* and *Pinus ponderosa*. *Canadian Journal of Forest Research* 3:556-564.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and S.J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602-613.
- Biging, G.S and M. Dobbertin. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science* 38:695-720.

Breece, C.R., Kolb, T.E., Dickson, B.G., McMillin, J.D., and K.M. Clancy. 2008.

Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. *Forest Ecology and Management* 255:119-128.

Burnham, K.P. and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer: New York, NY.

Busse, M.D., Simon, S.A., and G.M. Riegel. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of Central Oregon. *Forest Science* 46:258-268.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Cada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gilner, S., Haavik, L.J., Hartmann, H., Heres, A., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Mayr, S., Meszaros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petrita, A.M., Rohner, B., Sanguesa-Barreda, G., Sarris, D., Smith, J.M., Stand, A.B., Sterck, F., Stojanovic, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., and J. Martinez-Vilalta. 2016. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* 23:1675-1690.

Canty, A. and B. Ripley. 2007. boot: Bootstrap R (S-Plus) functions. R package version 1.3-20.

- Carter, G.A. and W.K. Smith. 1988. Microhabitat comparisons of transpiration and photosynthesis in three subalpine conifers. *Canadian Journal of Botany* 66:963-969.
- Cayan, D.R., Maurer, E.P., Dettinger, M.D., Tyree, M., and K. Hayhoe. 2008. Climate change scenarios for the California region. *Climate Change* 87:S21-S42.
- Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, M.C., Hessburg, P.F., and J.A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management* 291:442-457.
- Collins, B.M., Das, A.J., Battles, J.J., Fry, D.L., Krasnow, K.D., and S.L. Stephens. 2014. Beyond reducing fire hazard: fuel treatment impacts on overstory tree survival. *Ecological Applications* 24:1879-1886.
- Conrad, S.G. and S.R. Radosevich. 1982. Growth responses of white fir to decreased shading and root competition by montane chaparral shrubs. *Forest Science* 28:309-320.
- Contreras, M.A., Affleck, D., and W. Chung. 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *Forest Ecology and Management* 262:1939-1949.
- Coops, N.C., Waring, R.H., Wulder, M.A., and J.C. White. 2009. Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *Remote Sensing of Environment* 113:1058-1066.
- Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sacket,

- S.S., and M.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forest of the Southwest. *Journal of Forestry* 95:23-29.
- Dobbertin, M. 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Forest Research* 124:319-333.
- Eamus, D., Boulain, N., Cleverly, J., and D.D. Breshears. 2013. Global change-type drought-induced tree mortality: vapor pressure deficit is more important than temperature per se in causing decline in tree health. *Ecology and Evolution* 3:2711-2729.
- Feeney, S.R., Kolb, T.E., Covington, W.W., and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. *Canadian Journal of Forest Research* 28:1295-1306.
- Ferrenberg, S., Kane, J.M., and J.B. Mitton. 2014. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* 174:1283-1292.
- Fettig, C.J. 2012. Forest health and bark beetles. In: North, M., (Ed.), *Managing Sierra Nevada forests*. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report 237, Albany, CA.
- Franceschi, V.R., Krokene, P., Christiansen, E., and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167:353-376.

- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399-423.
- Franklin, J.F., Mitchell, R.J., and B.J. Palik. 2007. Natural disturbance and stand development principles for ecological forestry. United States Department of Agriculture, Forest Service, Northern Research Stations, General Technical Report NRS – 19.
- Griffin, D. and K.J. Anchukaitis. 2014. How unusual is the 2012-2014 California drought? *Geophysical Research Letters* 41:9017-9023.
- Grissino-Mayer. 2001. Evaluating cross-dating accuracy: A manual and tutorial for the computer program COFECHA. *Tree Ring Society* 57:205-221.
- Hegyi, F. 1974. A simulation model for managing jack pine stands. In: Fries, J. (Ed.), *Growth Models for Tree and Stand Simulation*. In: International Union of Forestry Research Organizations working party S4.01-4: proceedings of meetings in 1973 Royal College of Forestry. Stockholm, Sweden. 74-90.
- Hood, S. and A. Sala. 2015. Ponderosa pine resin defenses and growth: metrics matter. *Tree Physiology* 35:1223-1235.
- Hood, S., Sala, A., Heyerdahl, E.K., and M. Boutin. 2015. Low-severity fire increases tree defense against bark beetles. *Ecology* 96:1846-1855.

- Hood, S., Baker, S., and A. Sala. 2016. Fortifying the forest: thinning and burning increase resistance to bark beetle outbreak and promote forest resilience. *Ecological Applications* 26: 1984-2000.
- Kane, J.M. and T.E. Kolb. 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia* 164:601-609.
- Kane, J.M. and T.E. Kolb. 2014. Short- and long-term growth characteristics associated with tree mortality in southwestern mixed-conifer forests. *Canadian Journal of Forest Research* 55:1227-1235.
- Kautz, M., Imron, M.A., Dworschak, K., and R. Schopf. 2016. Dispersal variability and associated population-level consequences in tree-killing bark beetles. *Movement Ecology* 4:1-12.
- Kelsey, R.G., Gallego, D., Sanchez-Garcia, F.J., and J.A. Pajares. 2014. Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. *Canadian Journal of Forest Research* 44:554-561.
- Knapp, E.E., Skinner, C.N., North, M.P., and B.L. Estes. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 310:903-914.
- Knapp, E. E., Lydersen, J.M., North, M.P., and B.M. Collins. 2017. Efficacy of variable density thinning and prescribed fire for restoring heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *Forest Ecology and Management* 406:228-241.

- Kunstler, G., Albert, C.H., Courbaud, B., Lavergne, S., Thuiller, W., Vieilledent, G., Zimmermann, N.E., and D.A. Coomes. 2011. Effects of competition on tree radial-growth vary in importance but not intensity along climatic gradients. *Journal of Ecology* 99:300-312.
- Larson, A.J. and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *Forest Ecology and Management* 267:74-92.
- Larsson, S., Oren, R., Waring, R.H., and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science* 29:395-402.
- Lloret, F., Keeling, E.G., and A. Sala. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 102:1909-1920.
- Lombardero, M.J., Ayres, M.P., Lorio P.L., and J.J. Ruel. 2000. Environmental effects of constitutive and inducible resin defences of *Pinus taeda*. *Ecology Letter* 3:329-339.
- Lusk, C.H. 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. *Ecophysiology* 132:188-196.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26:523-532.

- McKay, S.A.B., Hunter, W.L., Godard, K., Wang, S.X., Martin, D.M., Bohlmann, J., and A.L. Plant. 2003. Insect attack and wounding induce traumatic resin duct development and gene expression of (-)-pinene synthase in Sitka spruce. *Plant Physiology* 133:368-378.
- Mitchell, R.G., Waring, R.H., and G.B. Pittman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* 29:204-211.
- Moreira, X., Zas, R., Solla, A., and L. Sampedro. 2015. Differentiation of persistent anatomical defensive structures is costly and determined by nutrient availability and genetic growth-defence constraints. *Tree Physiology* 35:112-123.
- North, M., Stine, P., O'Hara, K., Zielinski, W., and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report 220, Albany, CA.
- Paine, T.D., Raffa, K.F., and T.C. Harrington. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host confers. *Annual Review of Entomology* 42:179-206.
- Perrakis, D.D.B. and J.K. Agee. 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. *Canadian Journal of Forest Research* 36:238-254.
- Perrakis, D.D.B., Agee, J.K., and A. Eglitis. 2011. Effects of prescribed burning on mortality and resin defenses in old growth ponderosa pine (Crater Lake, Oregon): four years of post-fire monitoring. *Natural Areas Journal* 31:14-25.

- Perry, D.A. and M.P. Amaranthus. 1997. Disturbance, recovery, and stability. P. 31-56 in *Creating a Forestry for the Twenty-First Century: The Science of Ecosystem Management*, Kohm, K.A., and J.F. Franklin (eds.). Island Press: Washington, D.C.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created on March, 2019.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and W.H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58:501-517.
- Raphael, M.G. and M.L. Morrison. 1987. Notes: decay and dynamics of snags in the Sierra Nevada, California. *Forest Science* 33:774-783.
- Rosner, S. and B. Hannrup. 2004. Resin canal traits relevant for constitutive resistance of Norway spruce against bark beetles: environmental and genetic variability. *Forest Ecology and Management* 200:77-87.
- Schneider, C.A., Rasband, W.S., and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671-675.
- Seidl, R., Donato, D.C., Raffa, K.F., and M.G. Turner. 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. *Proceedings of the National Academy of Sciences* 113:13075-13080.

- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Svoboda, M., Fabrika, M., Nagel, T.A., and C.P.O. Reyer. 2017. Forest disturbances under climate change. *Nature Climate Change* 7:395-402.
- Stark, D.T., Wood, D.L., Storer, A.J., and S.L. Stephens. 2013. Prescribed fire and mechanical thinning effects on bark beetle caused tree mortality in a mid-elevation Sierran mixed-conifer forest. *Forest Ecology and Management* 306:61-67.
- Thomas, Z. and K.M. Waring. 2014. Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in Northern New Mexico, USA. *Forest Science* 61:93-104.
- Turner, M.G., Gardern, R.H., Dale, V.H., and R.V. O'Neill. 1989. Predicting the spread of disturbances across heterogeneous landscapes. *Oikos* 55:121-129.
- United States Department of Agriculture. NAIP 2012 aerial imagery, 1-meter resolution, in natural color [imagery]. Obtained from California Department of Fish and Wildlife, February 9, 2019.
- van Mantgem, P.J. and N.L. Stephenson. 2007. Apparently climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* 10:909-916.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and T.T. Veblen. 2009. Widespread increase of tree mortality rates in the Western United States. *Science* 323:521-524.

- Vernon, M.J., Sherriff, R.L., van Mantgem P., and J.M. Kane. 2018. Thinning, tree-growth, and resistance to multi-year drought in a mixed-conifer forest of northern California. *Forest Ecology and Management* 422:190-198.
- Waring, R.H., Thies, W.G., and D. Muscato. 1980. Stem growth per unit leaf area: a measure of tree vigor. *Forest Science* 26:112-117.
- Westbrook, J.W., Walker, A.R., Neves, L.G., Munoz, P., Resende Jr., M.F.R., Neale, D.B., Wegryzn, J.L., Huber, D.A., Kirst, M., Davis, J.M., and G.F. Peter. 2014. Discovering candidate genes that regulate resin canal number in *Pinus taeda* stems by integrating genetic analysis across environments, ages, and populations. *New Phytologist* 205:627-641.
- York, R.A., Battles, J.J., and R.C. Heald. 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. *Forest Ecology and Management* 179:107-121.
- York, R.A., Battles, J.J., Wenk, R.C., and D. Saah. 2011. A gap-based approach for regenerating pine species and reducing surface fuels in multi-aged mixed conifer stands in the Sierra Nevada, California. *Forestry* 85:203-213.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., and A.M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20:78-86.
- Zausen, G.L., Kolb, T.E., Bailey, J.D., and M.R. Wagner. 2005. Long-term impacts and stand management on ponderosa pine physiology and bark beetle abundance in

northern Arizona: A replicated landscape study. *Forest Ecology and Management* 218:291-305.

CHAPTER 2: MECHANISMS AND SPATIAL PATTERNS OF BARK BEETLE-
ASSOCIATED MORTALITY FOLLOWING VARIABLE DENSITY THINNING
TREATMENTS IN A SIERRA MIXED CONIFER FOREST

ABSTRACT

Over recent decades, increases in substantial tree mortality events have coincided with severe drought and bark beetle outbreak. This has prompted forest managers to find treatments that enhance resistance to disturbances. Variable density thinning is an alternative management method intended to increase spatial heterogeneity, with the potential to influence levels of bark beetle-associated mortality. However, there is limited research on the ecological consequences related to the structures that characterize variable density thinning. This study evaluated how structures within variable density thinning affect resistance to bark beetle outbreak, whether the influence of these structures change with scale, and what spatial patterns of bark beetle-associated mortality arise in variable density thinning treatments following a drought. We conducted stand inventories of eight variable density thinning units (4 ha each) within the Stanislaus-Tuolumne Experimental Forest. We collected data on all trees ≥ 25 cm diameter at breast height and recorded species, diameter at breast height, and whether trees died from bark beetle-associated mortality. We used this data to conduct spatial analysis evaluating the effects of total basal area, intraspecific host proportion, intraspecific host gaps, quadratic mean diameter, and canopy cover on tree mortality at different scales. Our results showed

that bark beetle-associated mortality was relatively low in sugar pine (14 %) and equivalent to other levels of reported mortality amongst white fir (24 %) during this most recent drought and insect outbreak in the Sierra Nevada. We found that the proportion of intraspecific hosts was positively associated with white fir mortality at small scales (10 to 20 m), while quadratic mean diameter was negatively associated with mortality at larger scales (30 to 50 m). Increased canopy cover was positively related to bark beetle-associated mortality in sugar pine at 10 m, while proportion of intraspecific hosts had a stronger positive association with mortality at larger scales (20 to 50 m). Despite structural characteristics influencing proportion of bark beetle-associated mortality, spatial analyses revealed that white fir and sugar pine mortality was limited across space, with clustering of mortality occurring at scales less than 14 m. These results suggest that treatments intended to increase spatial heterogeneity may have the added benefit of mitigating the levels and spatial patterns of bark beetle-associated mortality if proportion of hosts, average host size, and canopy cover are taken into consideration when designing prescriptions.

INTRODUCTION

Although drought is a common occurrence across the world, climate change can cause substantial tree mortality by increasing the frequency and intensity of regional droughts (Allen et al. 2015). Long-term tree mortality trends have increased over the last several decades, coinciding with above-average temperatures, high climatic water deficits, and bark beetle outbreak (van Mantgem et al. 2009, Meddens et al. 2012, Young et al. 2017). Changes in the frequency and intensity of disturbances predicted under climate change may increase the vulnerability of forest ecosystems (Allen et al. 2010), potentially altering the trajectory of forest ecosystems in unanticipated directions. Uncertainty in how forests will respond to disturbances under climate change necessitates creative ways to manage forests.

Thinning and prescribed fire are commonly used methods to reduce competition, which can potentially mitigate tree mortality to drought and bark beetles. These treatments mainly focus on reducing stand density to create sufficient resources to resist bark beetles (Coops et al. 2009, Fettig et al. 2012, Stark et al. 2013). Despite the efficacy of these treatments for enhancing tree survival during drought (van Mantgem et al. 2016) and bark beetle attack (Hood et al. 2015, Hood et al. 2016), they may lack spatial complexity that promotes forest resistance (North et al. 2009, Fettig et al. 2012) and lack other important stand structures valued by wildlife species (Carey 2003).

The effects of spatial heterogeneity on bark beetle-associated mortality can vary based on the resultant structural characteristics within a stand. Highly competitive

environments can be significant drivers of tree mortality (Das et al. 2011), possibly increasing bark beetle-associated mortality if areas of greater competition increase tree stress. Bark beetles are host specific, often attacking trees of a particular genus. Facilitation of bark beetle dispersal and colonization may occur if part of a stand contains a greater density of conspecific hosts or hosts within close proximity to each other, increasing the vulnerability of trees to mortality (Raffa and Berryman 1975). Larger trees may also be more susceptible to bark beetle-caused mortality because they tend to be more drought-stressed (Bennett et al. 2015) and are often the preferred host size of bark beetles (Raffa et al. 2008). Therefore, the size of hosts across space may also affect tree mortality. If openings increase light availability and enhance tree vigor (York et al. 2003, York et al. 2011), then decreases in canopy cover may mitigate bark beetle-associated mortality.

Spatial patterns of tree mortality may also indicate whether spatial heterogeneity can confer resistance to bark beetle-associated mortality. Because beetle dispersal is constrained by host proximity and host selection (Kautz et al. 2011, Kautz et al. 2016), movement across structures may depend on the amount of susceptible hosts. Tree mortality often occurs in clustered spatial patterns from tree to stand scales (Smith et al. 2005), possibly due to high host susceptibility within forest structures (Raffa and Berryman 1975). If greater host stocking leads to higher probability of beetle infestation (Negron and Popp 2004), then spatial variability may disrupt the continuity of available hosts and limit bark beetle-associated mortality across space (Seidl et al. 2016).

Variable density thinning (VDT) is an alternative management method that can reduce stand density, with the additional benefit of promoting spatial heterogeneity. VDT enhances forest heterogeneity by increasing variation in tree density, species composition, and size classes (Knapp et al. 2017). By mimicking the individual trees, clumps of trees, and openings that were present historically, VDT incorporates structural legacies that once helped forests evade, resist, or recover from disturbances prior to logging and fire exclusion (Perry and Amaranthus 1997). However, there is limited research on how the residual structures in VDT affect the levels and spatial patterns of bark beetle-associated mortality.

The overall objective of our study was to discern how structural characteristics within VDT affect resistance to disturbance. To meet this objective, we addressed the following questions 1) how do structural characteristics influence resistance to bark beetle-associated mortality, 2) at which scales do these structures have the greatest influence on tree mortality, and 3) what are the spatial patterns of bark beetle-associated mortality within stands treated with VDT? Although managers tailor plans to meet landowner objectives, increasing frequency and intensity of disturbances may prevent managers from achieving those objectives. Findings from our research can provide insight on how managers can effectively manipulate structural elements to create resistant forests in the face of climate change.

MATERIALS AND METHODS

Study Site

Our study site consists of a 100 ha mixed-conifer forest located within the Stanislaus-Tuolumne Experimental Forest in the central Sierra Nevada of California (**Figure 10**). At an elevation of 1740 m to 1900 m, stands at this site are composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and incense-cedar (*Calocedrus decurrens*). Four years prior to the onset of drought (2008 – 2011), average temperature ranged from 8.7 °C to 9.9 °C and precipitation ranged from 90.6 cm – 160.4 cm (PRISM, 2019). During the extended drought from 2012 to 2015, average temperature was 15 % higher than average (range = 10.6 – 11.4 °C) and precipitation was 44 % lower than average (range = 36.6 – 115.6 cm).

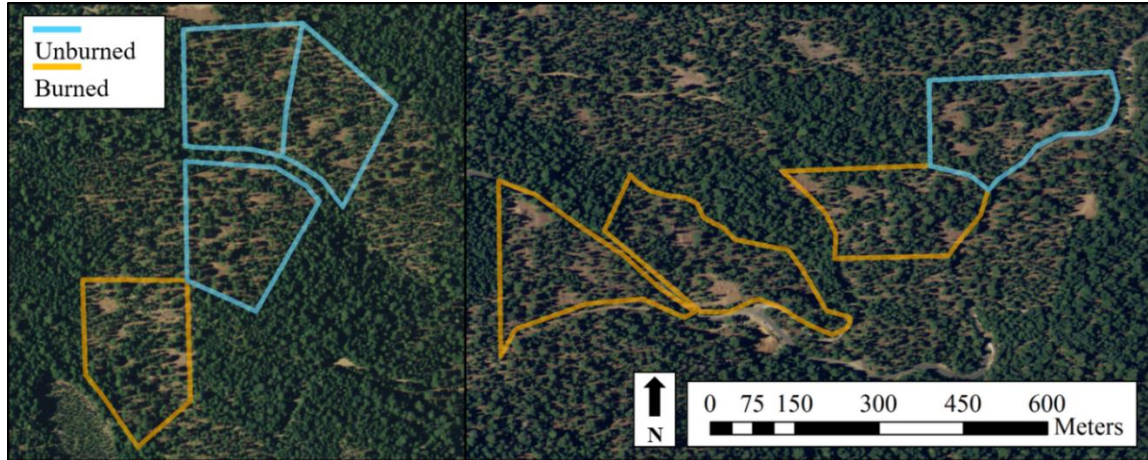


Figure 10 Locations of variable density thinning units within the Stanislaus-Tuolumne Experimental Forest. Unit boundaries superimposed on aerial photos provided by the United States Department of Agriculture National Agriculture Imagery Program, 2012.

A combination of logging practices from the 1920s and fire exclusion increased tree densities within the Stanislaus-Tuolumne Experimental Forest and shifted dominance towards shade-tolerant species and trees of smaller-sized diameter classes (Knapp et al. 2013). In 2011, the United States Department of Agriculture Forest Service implemented a variable density thinning experiment, where eight units (4 ha each) were thinned to generate high variability stand structures similar to conditions pre-logging and fire suppression (Knapp et al. 2017). In each VDT unit, five gaps were created ranging from 0.04 – 0.2 ha within areas dominated by shade-tolerant species or with root disease present. The remainder of each VDT unit was divided into groups of similar-sized trees, with each group thinned either to a low ($27.5 \text{ m}^2 \text{ ha}^{-1}$), medium ($50.5 \text{ m}^2 \text{ ha}^{-1}$), or high ($73.5 \text{ m}^2 \text{ ha}^{-1}$) basal area target. A prescribed fire was applied to half of the units,

generating two different treatments, a variable density thin and burned treatment and a variable density thin and unburned treatment.

Stand Maps

To create maps of current stand structures, we utilized light detection and ranging (LiDAR) data collected by Quantum Spatial in 2014. This dataset included each treated unit, showing a range of point densities from 14 to 20 points m^{-2} . Using this LiDAR dataset, we detected treetops with the *lidR* package (Roussel and Auty 2018) in R (R Core Team 2018). This package contains a function that uses local maxima filters to estimate the location of individual trees. From these estimates, we created digitized maps of tree locations for each unit that we subsequently used in the field to conduct stand inventories. The spatial reference system for all datasets used in our analyses was North American Datum 1983, Universal Transverse Mercator Zone 10 North.

Data Collection

With our digitized maps, we confirmed the location of all trees ≥ 25 cm diameter at breast height (DBH). In the field, we found that our LiDAR-generated maps did not always distinguish tree locations in areas with high canopy cover, resulting in an underestimation of trees (**Figure 11**). We added these locations to our dataset by estimating distance and bearing from the closest tree of known location. In some cases, the irregular crown structure of a single tree showed multiple tree-tops in our LiDAR-generated maps. To determine the most accurate location, we measured the distance (m)

and bearing (°) from each predicted location to a tree of known location and chose the predicted point with the closest estimates. During instances where predicted points poorly reflected the actual tree location, we added new coordinates based on the distance and bearing from a tree of known location. Once a tree's location was confirmed, we recorded species, status (live or dead), and diameter at breast height (DBH, cm). If a tree was dead, we removed the bark to confirm bark beetle activity by identifying larval galleries of fir engraver (*Scolytus ventralis*) on white fir and mountain pine beetle (*Dendroctonus ponderosae*) on sugar pine.

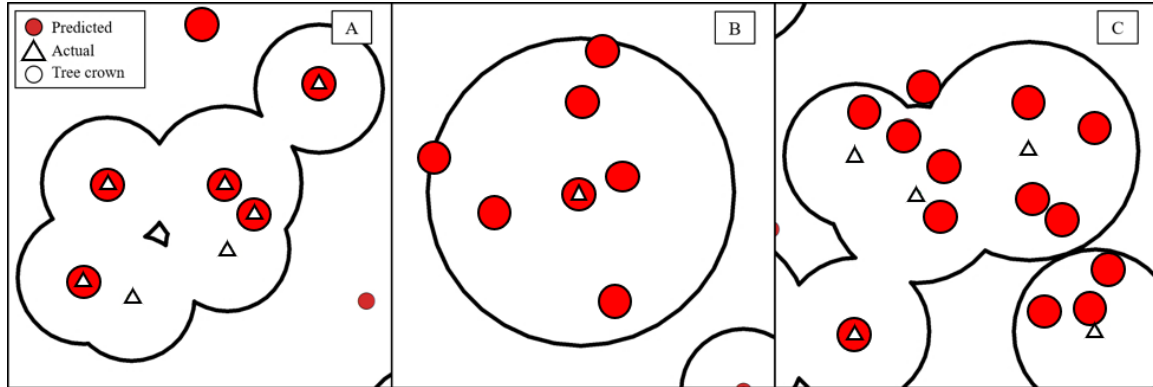


Figure 11 Map of predicted tree locations from LiDAR data and actual locations of trees. Panel A depicts underestimation of tree counts, panel B depicts overestimation of tree counts, and panel C depicts poor estimations of tree locations.

Stand Structures

Once all units were inventoried, we transferred each tree's information to the existing shapefile of tree locations using ArcMap 10.5.1 (ESRI, Redlands, CA). Our digitized maps with all tree locations also included point locations of a previously established 30 m systematic grid, which we used as plot centers to quantify proportion of tree mortality associated with fir engraver and mountain pine beetle. Using the *sf* package (Pebesma 2018) in R (R Core Team 2018), we delineated multi-ring buffers in intervals of 10 m, ranging from 10 to 50 m from each plot center to determine if the influence of structures change with scale. If a point had a buffer that was located outside of a unit boundary or if a plot did not contain any sugar pine or white fir, we excluded that point from further analysis. Although exclusion resulted in a reduced sample size (**Appendix H**), this was a conservative approach to reduce bias in our analyses (Pommerening and Stoyan 2006). Within each buffer, we quantified structural characteristics including

competition from all trees (total basal area, $\text{m}^2 \text{ha}^{-1}$), intraspecific host proportion (number of potential beetle hosts/total number of trees), host gap (area unoccupied by potential beetle hosts, ha), and quadratic mean diameter of potential hosts (cm). Based on allometric equations derived from Gill et al. (2000), we estimated crown radius (m) for each tree based on DBH and used these radii to estimate canopy cover (%).

Data Analysis

We created separate logistic regression models to predict the proportion of white fir and sugar pine mortality across different scales. Using structural characteristics as explanatory variables, we evaluated the effect of each metric independently at a given distance from plot center. Preliminary analysis using likelihood ratio tests showed that the addition of prescribed fire as a covariate did not improve model performance. Therefore, we included all eight variable density units but excluded prescribed fire as a parameter in further analyses. We repeated these models for all distances, totaling five models for each distance and 25 models in total. We reported all models and determined the top model predicting the proportion of white fir or sugar pine mortality based on the lowest Akaike Information Criterion (AIC) values. We also assigned Akaike weights with the following formula to determine the probability that a given model was the best (Wagenmakers and Farrell 2004):

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}$$

The numerator represents the relative likelihood of model i , where Δ_i is the difference in AIC values between model i and the best model. The denominator represents the sum of relative likelihoods from all models being compared.

Spatial patterns of mortality

In the *spatstat* (Baddeley et al. 2015) package in R, we discerned the spatial patterns of bark beetle-associated mortality by employing the pair correlation function, which is a derivative of the Ripley's K function and is defined as:

$$g(r) = \frac{K'(r)}{2\pi r}$$

Where $g(r)$ represents the probability of observing a pair of points at an interpoint distance of r (Baddeley et al. 2015). We used the univariate form of $g(r)$ to calculate distances between trees that died from bark beetle-associated mortality, $g_{d,d}(r)$, and the bivariate form to calculate distances from trees that died from bark beetle-associated mortality and those that survived, $g_{d,l}(r)$. Within multiple distances of a dead tree, the number of neighboring dead trees and the number of trees that survived were counted. Similar to Larson et al. (2015), we generated 999 simulations of random point patterns for each distance to generate a random distribution envelope that compares the number of observed point patterns with a random distribution of trees. We pooled these Monte Carlo simulations across all individual units to assess deviations from random distributions. We then evaluated the extent of bark beetle-associated mortality by using $g_{d,d}(r) - g_{d,l}(r)$, which compares the probability of dead trees surrounding other dead trees with the

probability of live trees surrounding dead trees. Positive values ($g_{d,d}(r) > g_{d,l}(r)$) indicate that dead trees were clustered amongst other trees that died from bark beetle-associated mortality, while negative values ($g_{d,d}(r) < g_{d,l}(r)$) indicated that dead trees were dispersed amongst live trees.

RESULTS

At our study site, 15 % of all trees died between 2012 and 2018. Although bark beetle galleries were present on 77 % of the white fir and 95 % of the sugar pine that died, bark beetle-associated mortality affected only 24 % of all white fir and 14 % of all sugar pine. At the plot level, white fir mortality was on average 63 to 75 % higher than sugar pine mortality across all distances.

White fir mortality

Our top models predicting proportion of white fir mortality included intraspecific host proportion and quadratic mean diameter (**Table 5**). At smaller scales (10 and 20 m), proportion of intraspecific hosts was positively related to proportion of white fir mortality ($p = 0.018$ and $p < 0.001$, respectively), with plots entirely composed of white fir having 20 % mortality (**Figure 12**). At larger scales (30 to 50 m), quadratic mean diameter was negatively associated with fir mortality ($p < 0.001$, **Appendix I**), with plots having 15% mortality when quadratic mean diameter of white fir was less than 40 cm. While our other models also included total basal area, canopy cover, and host gap area, these models were greater than 2 AIC points from the top models for each distance, suggesting that the quality of these models were lower relative to the top models.

Table 5 Summary of model inputs predicting the proportion of white fir mortality and model performance metrics. K indicates the number of parameters in the model. Δ AIC indicates the difference between AIC values from a given model and the top-rated model. AIC weight suggests the probability that a given model is the best model in comparison to all model being evaluated. Log likelihood describes the fit of estimated coefficients to observed data, with higher values suggesting a better fit.

Model inputs	K	Δ AIC	AIC weight	Log likelihood
<i>10 meter buffers</i>				
Host proportion	1	0.00	0.60	-104.91
Host gap	1	2.22	0.20	-106.02
Quadratic mean diameter	1	3.28	0.14	-105.51
Total BA	1	5.26	0.05	-107.54
Canopy cover	1	5.57	0.04	-107.69
<i>20 meter buffers</i>				
Host proportion	1	0.00	0.97	-193.89
Quadratic mean diameter	1	7.30	0.03	-192.04
Host gap	1	26.72	<0.01	-207.25
Canopy cover	1	36.36	<0.01	-212.07
Total BA	1	39.22	<0.01	-213.50
<i>30 meter buffers</i>				
Quadratic mean diameter	1	0.00	0.99	-178.03
Host proportion	1	25.97	<0.01	-190.51
Host gap	1	31.43	<0.01	-193.24
Canopy cover	1	31.93	<0.01	-193.49
Total BA	1	32.07	<0.01	-193.56
<i>40 meter buffers</i>				
Quadratic mean diameter	1	0.00	0.99	-98.42
Total BA	1	25.24	<0.01	-110.94
Host gap	1	25.48	<0.01	-111.06
Canopy cover	1	26.84	<0.01	-111.74
Host proportion	1	26.95	<0.01	-111.79
<i>50 meter buffers</i>				
Quadratic mean diameter	1	0.00	0.98	-61.70
Host proportion	1	9.05	0.01	-66.22
Host gap	1	10.11	<0.01	-66.75
Total BA	1	17.17	<0.01	-70.29
Canopy cover	1	20.79	<0.01	-72.10

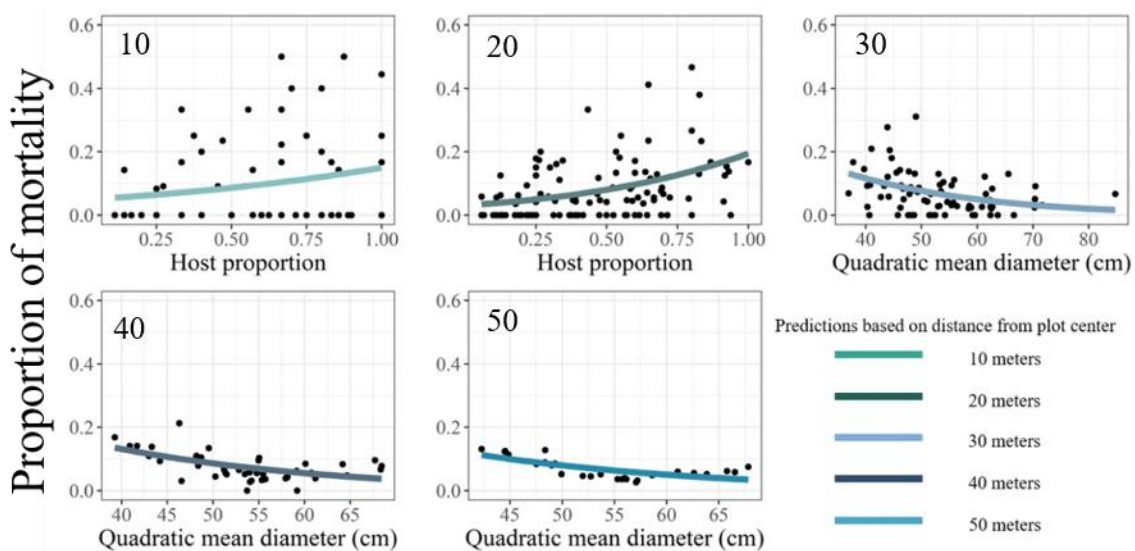


Figure 12 Response curves from top logistic regression models predicting the proportion of white fir mortality across different scales, with black dots representing observed values. Numbers in top left corner indicate distance (m) from plot center.

Sugar pine mortality

Our top models predicting the proportion of sugar pine mortality included canopy cover and intraspecific host proportion (

Table 6). Canopy cover at smaller scales (10 m) had a positive association with sugar pine mortality ($p = 0.026$, **Appendix J**), with plots containing less than 40 % canopy cover exhibiting no sugar pine mortality (**Figure 13**). At larger scales (20 to 50 m), intraspecific host proportion was positively associated with sugar pine mortality ($p < 0.001$), with plots composed entirely of sugar pine increasing mortality up to 10 %. While our other models also included total basal area, quadratic mean diameter, and host gap area, these models were greater than 2 AIC points from the top models for each distance, suggesting that the quality of these models were lower relative to the top models.

Table 6 Summary of model inputs predicting the proportion of sugar pine mortality and model performance metrics. K indicates the number of parameters in the model. Δ AIC indicates the difference between AIC values from a given model and the top-rated model. AIC weight suggests the probability that a given model is the best model in comparison to all model models evaluated. Log likelihood describes the fit of estimated coefficients to observed data, with higher values suggesting a better fit.

Model inputs	K	Δ AIC	AIC weight	Log likelihood
<i>10 meter buffers</i>				
Canopy cover	1	0.00	0.75	-25.78
Host proportion	1	4.71	0.07	-28.13
Host gap	1	4.95	0.06	-28.25
Total BA	1	5.10	0.06	-28.33
Quadratic mean diameter	1	5.26	0.05	-28.41
<i>20 meter buffers</i>				
Host proportion	1	0.00	0.96	-81.88
Host gap	1	6.90	0.03	-85.34
Total BA	1	11.30	<0.01	-87.53
Quadratic mean diameter	1	11.55	<0.01	-87.66
Canopy cover	1	11.86	<0.01	-87.81
<i>30 meter buffers</i>				
Host proportion	1	0.00	0.99	-90.05
Host gap	1	8.66	0.01	-94.38
Canopy cover	1	20.41	<0.01	-100.25
Total BA	1	20.78	<0.01	-100.44
Quadratic mean diameter	1	22.66	<0.01	-101.38
<i>40 meter buffers</i>				
Host proportion	1	0.00	0.96	-64.65
Quadratic mean diameter	1	6.57	0.04	-67.94
Host gap	1	11.36	<0.01	-70.32
Canopy cover	1	13.93	<0.01	-71.62
Total BA	1	14.08	<0.01	-71.70
<i>50 meter buffers</i>				
Host proportion	1	0.00	0.99	-45.69
Quadratic mean diameter	1	17.78	<0.01	-49.57
Host gap	1	18.22	<0.01	-49.80
Total BA	1	21.40	<0.01	-51.38
Canopy cover	1	21.49	<0.01	-51.43

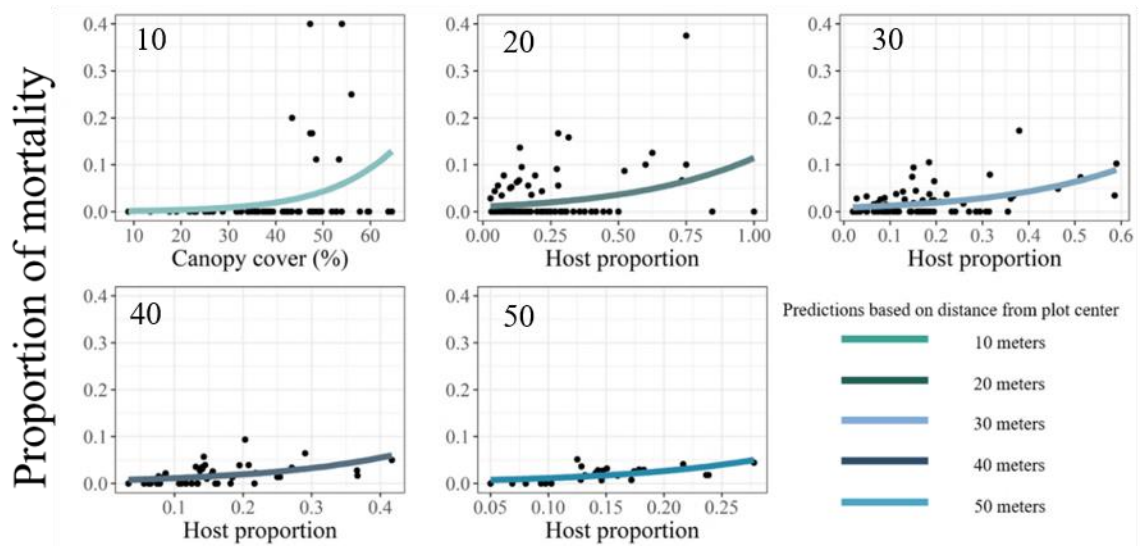


Figure 13 Response curves from top logistic regression models predicting the proportion of sugar pine mortality across different scales, with black dots representing observed values. Numbers in top left corner indicate distance (m) from plot center.

Spatial patterns of mortality

Our spatial analysis suggested that patterns of bark beetle-associated mortality were similar for white fir and sugar pine. While individual units showed clustered patterns of white fir mortality across varying distances (**Appendix K**), pooled estimates indicated a clustered mortality pattern at scales less than 12 m (**Figure 14**). At scales greater than 12 m, observed patterns of white fir mortality did not deviate from mortality patterns generated by complete spatial randomness, suggesting that mortality was randomly distributed at these larger scales. Due to a small sample size of sugar pine that

died from bark beetle-associated mortality within individual units, we were unable to generate $g(r)$ estimates of random patterns of mortality for all units. Therefore, we excluded six units from further analysis (**Appendix L**). However, pooled estimates of the patterns across two units with sufficient sample size showed observations of sugar pine mortality clustered at scales less than 14 m (**Figure 15**). At scales greater than 14 m, patterns of sugar pine mortality did not deviate from mortality patterns generated by complete spatial randomness, suggesting that mortality was also randomly distributed at larger scales.

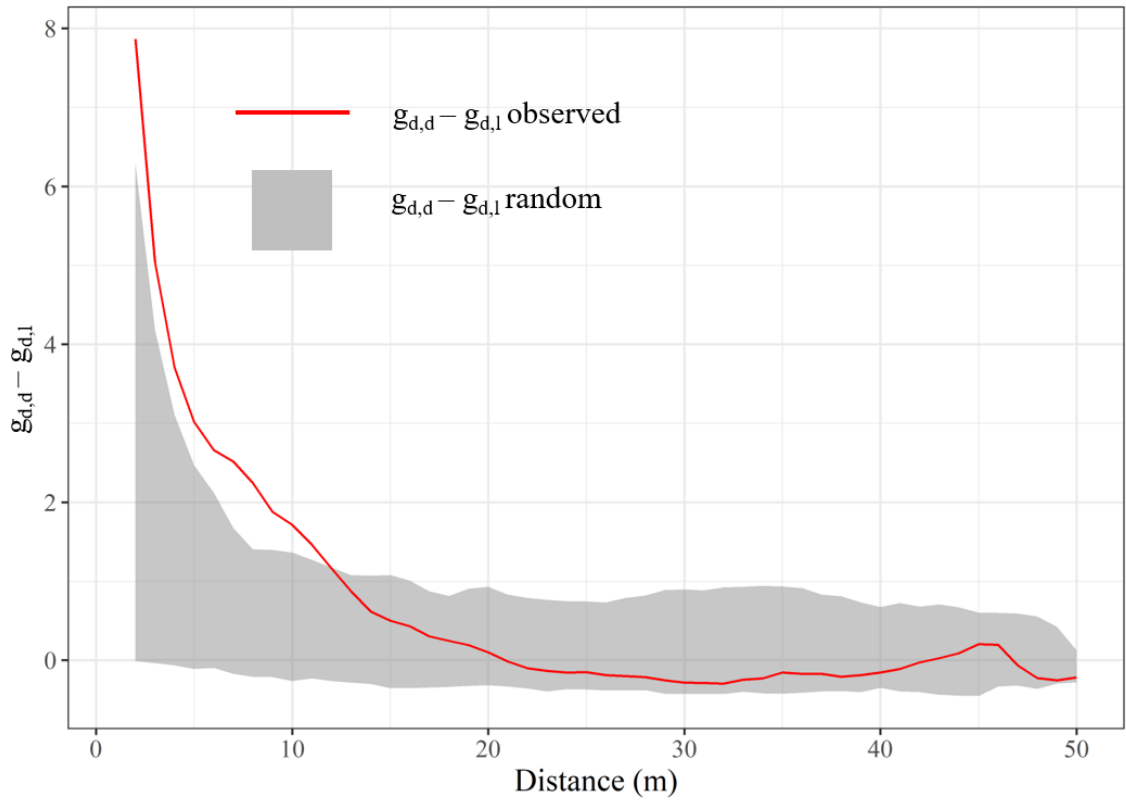


Figure 14 Pooled estimates of spatial patterns of bark beetle-associated mortality between observed dead white fir (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,d} - g_{d,l,observed} > g_{d,d} - g_{d,l,random}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality.

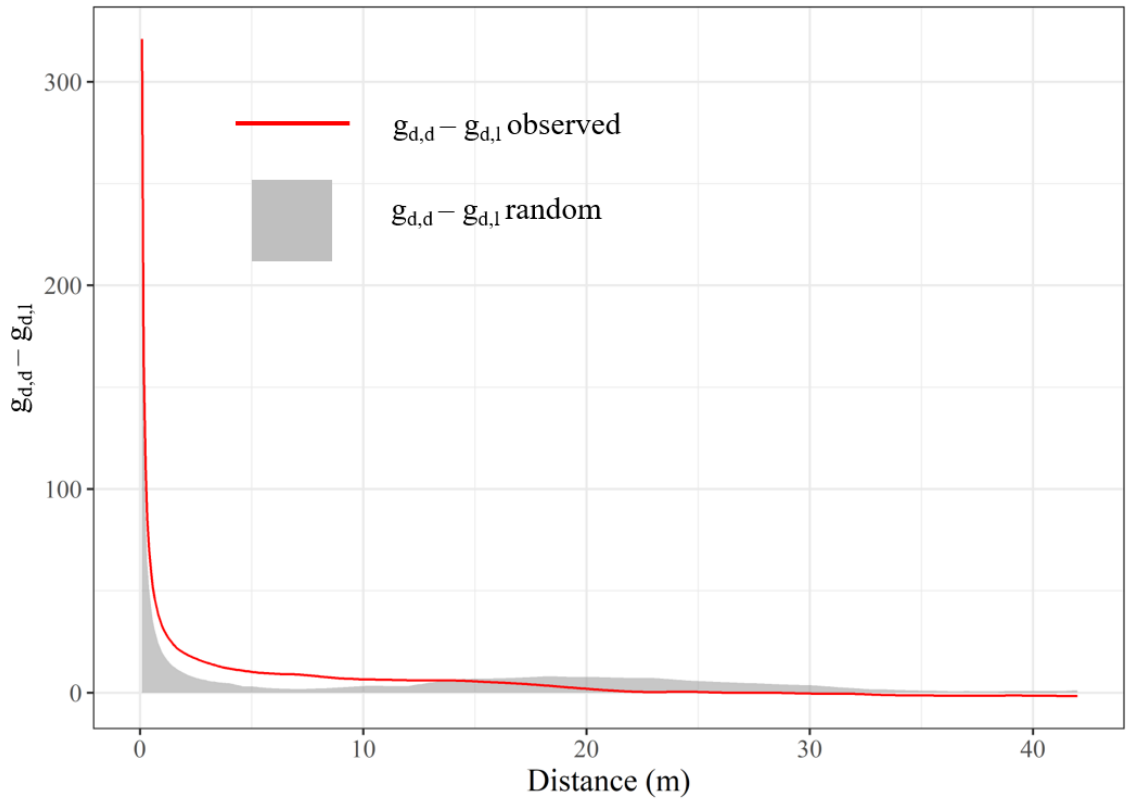


Figure 15 Pooled estimates of spatial patterns of bark beetle-associated mortality between observed dead sugar pine (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,d} - g_{d,l_{observed}} > g_{d,d} - g_{d,l_{random}}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality.

DISCUSSION

While VDT is a management method that increases spatial heterogeneity (Knapp et al. 2017), there is limited research on how residual structures influence mortality during drought and bark beetle outbreak. By observing patterns of bark beetle-associated mortality during an unprecedented drought (Griffin and Anchukaitis 2014), we found higher levels of mortality for both sugar pine and white fir than the 2 % annual rate of tree mortality generally caused by bark beetles under endemic levels (Samman and Logan 2000). Despite increased mortality, our observations of sugar pine mortality were less than the 48 % mortality levels reported in untreated stands within the same region (Fettig et al. 2019). However, our observations of white fir mortality were equivalent to the 26 % also reported in untreated stands within the Sierra Nevada (Fettig et al. 2019). Although we found elevated levels of bark beetle-associated mortality, the spatial patterning of dead sugar pine and white fir was randomly distributed at scales greater than 14 m, suggesting that structures within variable density thinning treatments may be manipulated to limit tree mortality across space.

Our results indicate that the proportion of intraspecific hosts was the primary driver of fir mortality. Bark beetle attack and white fir basal area have been positively related to tree mortality in mixed conifer forests of Arizona, with substantial tree mortality (>30 %) during extended drought conditions (Kane et al. 2014). Percentage of white fir mortality may be directly proportional to the density of available hosts (Egan et al. 2010), with our findings showing greater mortality of white fir at smaller scales (10 to

20 m) when white fir were the only species present. Density-dependent mortality is influenced by the increased presence of conspecific neighbors (Fangliang and Duncan 2000), possibly increasing mortality risk due to competition for similar niches when resources are limited (Duncan 1991) during the drought. However, the importance of conspecific density at these localized scales may also arise from interactions between host selection and host abundance. Fir engraver shows strong host selection for trees infected with root rot (Hertert et al. 1975, Macias-Samano et al. 1998), with root pathogens concentrating in clustered disease centers (Hansen and Goheen 2000). Therefore, mortality attributed to fir engraver may be associated with the abundance of stressed hosts within close proximity to each other. VDT may have created dispersed clumps of infected hosts across space, possibly diminishing the importance of conspecific density at larger scales.

We also found that white fir mortality was negatively associated with tree size at larger scales (30 to 50 m), with other studies finding an inverse relationship between tree size and the probability of bark beetle-associated mortality during drought conditions (Negron et al. 2009). Evidence suggests that larger trees tend to be more drought-stressed (Bennet et al. 2015), possibly due to the greater radiation exposure and evaporative demand or larger crowns (Roberts et al. 1990). However, physiological performance can be related to suitable microsite conditions (Carter and Smith 1988). White fir establish in sites with greater soil moisture, with basal area positively associated with soil thickness (Meyer et al. 2007). It is possible that larger white fir already existed in suitable sites with greater water resources, rendering them more vigorous and less susceptible to bark

beetle-associated mortality. Other studies have found that white fir that died from bark beetle-associated mortality had shorter crowns and lower tree vigor than trees that survived (Ferrell et al. 1994). Because prescriptions for VDT preferentially chose large and vigorous trees (Knapp et al. 2017), smaller trees with high vigor may have been less prominent across these treatments and limited host availability at larger scales.

While sugar pine mortality was also primarily driven by the proportion of conspecific hosts, this effect was stronger at larger scales (20 to 50 m). While disrupting the continuity of hosts prevents bark beetle-associated mortality from clustering at smaller scales (Smith et al. 2005), mortality at larger scales may still occur if susceptible hosts remain on the landscape. Because sugar pine are relatively shade intolerant (Franklin and Dyrness 1973), increases in canopy cover may decrease light availability and tree vigor (York et al. 2003). If sugar pine were further away from other hosts, mountain pine beetle would need to be more efficient at host detection to make long-range dispersal less risky (Kautz et al. 2016). Therefore, the negative effects of host proportion at larger scales may be a combination of lower tree vigor and more efficient host detection by bark beetles.

Contrary to expectations, total competition alone was not the predominant factor explaining the variation in proportion of sugar pine and white fir mortality at any of the scales we investigated. Competition may be a significant driver of tree mortality (Das et al. 2011, Ruiz-Benito et al. 2013), especially under severe drought conditions (Young et al. 2017). However, other studies have found that mortality rates are not always attributed to competition (van Mantgem et al. 2009), possibly due to the effect of climatic stress

superseding the effects of competitive stress under prolonged drought (Floyd et al. 2009). Although trees avoid drought-induced mortality by restricting transpiration, doing so weakens host defenses (McDowell et al. 2011) and creates opportunities for bark beetles to colonize and kill host trees (Bentz et al. 2010). If severe drought leads to insufficient resources for all trees, then increased stomatal control during drought may have predisposed trees to bark beetle-associated mortality (Plaut et al. 2012) regardless of competition. If all preferred beetle hosts are susceptible to attack due to severe climatic stress, then mortality may be more influenced by the number of available hosts that can facilitate beetle dispersal rather than the influence of stand density on tree vigor.

Although rates of bark beetle-associated mortality can increase following drought (Dobbertin et al. 2007), our results indicate mortality was limited across VDT treatments. Bark beetle dispersal distances can range from 30 to 50 m, suggesting that infestations stay relatively localized during the initial stages of an outbreak (Robertson et al. 2007). As outbreak conditions progress, mortality generally occurs in clustered patterns (Grodzki et al. 2003, Robertson et al. 2007) and radiates outwards from multiple epicenters of beetle activity until clusters coalesce across larger landscapes (Chapman et al. 2012). Generally, our findings show that spatial patterns of bark beetle-associated mortality in VDT were apparent at scales less than 14 m, but were not different than mortality patterns generated by complete spatial randomness at larger scales. Beetles are host-specific and often attack trees with weakened defense systems (Raffa et al. 2008), suggesting that structural characteristics created by VDT may have inhibited beetle

detection or dispersal by limiting host availability through variable species composition or increasing the amount of resistant hosts.

Our results show that structural elements within treatments intended to increase spatial heterogeneity may influence bark beetle-associated mortality during unprecedented drought conditions. Although treatments that increase spatial complexity have been proposed as a way to enhance forest resistance (North et al. 2009), valid concerns exist about using the historical range of variation to guide treatments for future disturbances. Historical disturbance regimes may not serve as an appropriate analogue for due to on-going and projected increases in the frequency and intensity of many disturbances (O'Hara 2016). In anticipation of novel ecosystems under climate change, some argue for more proactive approaches that focus less on returning to past conditions and focus more on creating desirable states for the future (Seastedt et al. 2008). Although our results found that bark beetle-associated mortality can be influenced by structural elements indicative of historical reference conditions, mortality patterns did not coalesce into larger patches of tree mortality indicative of outbreak conditions. Our findings also suggest that prescriptions designed to increase species diversity and increase variation in tree size may complement reductions in competition when climatic water stress overrides competitive stress. While these findings do not imply that recreating historical structures is optimal relative to other thinning methods, it does suggest treatments intended to increase spatial heterogeneity on the scale that was present historically may have the added benefit of mitigating tree mortality to disturbances.

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., and N. Cobb. 2010. A global overview of drought and heat-induced treemortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660-684.
- Allen, C.D., Breshears, D.D., and N.G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:1-55.
- Baddeley, A., Rubak, E., and R. Turner. 2015 *Spatial Point Patterns: Methodology and Applications with R*. CRC Press: Boca Raton, FL.
- Bennett, A.C., McDowell, N.G., Allen, C.D., and K.J. Anderson-Teixeira. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* 15139.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and S.J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602-613.
- Carey, A.B. 2003. Bioclomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. *Forestry* 76:127-136.

- Carter, G.A. and W.K. Smith. 1988. Microhabitat comparisons of transpiration and photosynthesis in three subalpine conifers. *Canadian Journal of Botany* 66:963-969.
- Chapman, T.B., Veblen, T.T., and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93:2175-2185.
- Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, M.C., Hessburg, P.F., and J.A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management* 291:442-457.
- Coops, N.C., Waring, R.H., Wulder, M.A., and J.C. White. 2009. Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *Remote Sensing of Environment* 113:1058-1066.
- Das, A., Battles, J., Stephenson, N.L., and P.J. van Mantgem. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. *Forest Ecology and Management* 261:1203-1213.
- Dobbertin, M., Wemelin, B., Bigler, C., Burgi, M., Carron, M., Forster, B., Gimmi, U., and A. Rigling. 2007. Linking increasing drought stress to Scots pine mortality and bark beetle infestations. *The Scientific World Journal* 7:231-239.
- Duncan, R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. *Journal of Ecology* 79:1073-1084.

- Egan, J.M., Jacobi, W.R., Negrón, J.F., Smith, S.L., and D.R. Cluck. 2010. Forest thinning and subsequent bark beetle-caused mortality in Northeastern California. *Forest Ecology and Management* 260:1832-1842.
- Fangliang, H. and R.P. Duncan. 2000. Density-dependent effects on tree survival in an old-growth Douglas-fir forest. *Journal of Ecology* 88:676-688.
- Ferrell, G.T., Otrosina, W.J., and C.J. Demars Jr. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. *Canadian Journal of Forest Research* 24:302-305.
- Fettig, C.J., Hayes, C.J., Jones, K.J., Mckelvey S.R., Mori S.L., and S.L. Smith. 2012. Thinning Jeffrey pine stands to reduce susceptibility to bark beetle infestation in California, U.S.A. *Agricultural and Forest Entomology* 14:111-117.
- Fettig, C.J., Mortense, L.A., Bulaon, B.M., and P.B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *Forest Ecology and Management* 432:164-178.
- Floyd, M.L., Clifford, M., Cobb, N.S., Hanna, D., Delph, R., Ford, P., and D. Turner. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern pinyon-juniper woodlands. *Ecological Applications* 19:1223-1230.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. United States Department of Agriculture Forest Service. GTR PNW-8. Pacific Northwest Forest and Range Experiment station: Portland, Oregon.
- Gill, S.J., Biging, G.S., and E.C. Murphy. 2000. Modeling conifer tree crown radius and estimating canopy cover. *Forest Ecology and Management* 126:405-416.

- Griffin, D. and K.J. Anchukaitis. 2014. How unusual is the 2012-2014 California drought? *Geophysical Research Letters* 41:9017-9023.
- Grodzki, W. Jakus, R. and M. Gazda. 2003. Patterns of bark beetle occurrence in Norway spruce stands of national parks in Tatra Mountains in Poland and Slovakia. *Journal of Pest Science* 76:78-82.
- Hansen, E.M. and E.M. Goheen. 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in Western North America. *Annual Review of Phytopathology* 38:515-539.
- Hertert, H.D., Miller, D.L., and A.D. Partridge. 1975. Interaction of bark beetles (Coleoptera: Scolytidae) and root-rot pathogens in grand fir in northern Idaho. *Canadian Entomology* 107:829-904.
- Hood, S., Sala, A., Heyerdahl, E.K., and M. Boutin. 2015. Low-severity fire increases tree defense against bark beetles. *Ecology* 96:1846-1855.
- Hood, S., Baker, S., and A. Sala. 2016. Fortifying the forest: thinning and burning increase resistance to bark beetle outbreak and promote forest resilience. *Ecological Applications* 26:1984-2000.
- Kane, J.M., Kolb, T.E., and J.D. McMillin. 2014. Stand-scale tree mortality factors differ by site and species following drought in southwestern mixed conifer forests. *Forest Ecology and Management* 330:171-182.
- Kautz, M., Dworschak, K., Gruppe, A., and R. Schopf. 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. *Forest Ecology and Management* 262:598-608.

- Kautz, M., Imron, M.A., Dworschak, K., and R. Schopf. 2016. Dispersal variability and associated population-level consequences in tree-killing bark beetles. *Movement Ecology* 4:1-12.
- Knapp, E.E., Skinner, C.N., North, M.P., and B.L. Estes. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 310:903-914.
- Knapp, E. E., Lydersen, J.M., North, M.P., and B.M. Collins. 2017. Efficacy of variable density thinning and prescribed fire for restoring heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *Forest Ecology and Management* 406:228-241.
- Larson, A.J. and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *Forest Ecology and Management* 267:74-92.
- Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A. Swanson, M.E., HilleRisLambers, J., Sprugel D.G., and J.F. Franklin. 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology* 96:2855-2861.
- Macias-Samano, J.E., Borden, J.H., Gries, R., Pierce, H.D., Gries, G., and G.G.S. King. 1998. Primary attraction of the fir engraver, *Scolytus ventralis*. *Journal of Chemical Ecology* 25:1049-1075.

- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26:523-532.
- Meddens, A.J., Hicke, J.A., and C.A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-cause tree mortality in British Columbia and the western United States. *Ecological Applications* 22:1876-1891.
- Meyer, M.D., North, M.P., Gray, A.N., and H.S.J. Zald. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. *Plant and Soil* 294:113-123.
- Negron, J.F. and J.B. Popp. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. *Forest Ecology and Management* 191:17-27.
- Negron, J.F., McMillin, J.D., Anhold, J.A., and D. Coulson. 2009. Bark beetle-caused mortality in drought-affected ponderosa pine landscape in Arizona, USA. *Forest Ecology & Management* 257:1353-1362.
- North, M., Stine, P., O'Hara, K., Zielinski, W., and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report 220.
- O'Hara, K.L. 2016. What is close-to-nature silviculture in a changing world? *Forestry* 89:1-6.

- Pebesma, E. 2018. Simple features for R: Standardized support for spatial vector data. *The R Journal* 10:439-446.
- Perry, D.A. and M.P. Amaranthus. 1997. Disturbance, recovery, and stability. P. 31-56 in *Creating a forestry for the twenty-first century: The science of ecosystem management*, Kohm, K.A., and J.F. Franklin (eds.). Island Press: Washington, D.C.
- Plaut, J.A., Yepez, E.A., Hill, J., Pangle, R., Sperry, J.S., Pockman, W.T., and N.G. McDowell. 2012. Hydraulic limits preceding mortality in a piñon-juniper woodland under experimental drought. *Plant, Cell, and Environment* 35:1601-1617.
- Pommerening A. and D. Stoyan. 2006. Edge-correction needs in estimating indices of spatial forest structure. *Canadian Journal of Forest Research* 36:1723-1739.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created on March, 2019.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raffa, K.F. and A.A. Berryman. 1975. Flight responses and host selection by bark beetles. In: *Dispersal of forest insects: Evaluation, theory and management implications* (A.A. Berryman and L. Safranyik, eds.). Proceedings of the second IUFRO Conference. Canadian and United States Department of Agriculture Forest Service, Washington State University.

- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and W.H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58:501-517.
- Roberts, J., Cabra, O.M.R., and L. Ferreira de Aguiar. 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. *Journal of Applied Ecology* 27:336-353.
- Robertson, C., Nelson, T.A., and B. Boots. 2007. Mountain pine beetle dispersal: The spatial-temporal interaction of infestation. *Forest Science* 53:395-405.
- Roussel, J. and D. Auty. 2018. lidR: airborne LiDAR data manipulation and visualization for forestry applications. R package version 1.4.2.
- Ruiz-Benito, P., Lines, E.R., Gomez-Aparicio, L., Zavala, M.A., and D.A. Coomes. 2013. Patterns and drivers of tree mortality in Iberian forests: Climatic effects are modified by competition. *PLoS ONE* 8:e56843.
- Samman, S. and J. Logan (eds.). 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. Report to Congress from Forest Health Protection, Washington Office. United States Department of Agriculture Forest Service, Rocky Mountain Research Station. RMRS-GTR-62, Fort Collins, Colorado.
- Seastedt, T.R., Hobbs, J.R., and K.N. Suding. 2008. Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment* 6:547-553.

- Seidl, R., Donato, D.C., Raffa, K.F., and M.G. Turner. 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. *Proceedings of the National Academy of Sciences* 113:13075-13080.
- Smith, T.F., Rizzo, D.M., and M. North. 2005. Patterns of mortality in an old-growth mixed-conifer forest of the Southern Sierra Nevada, California. *Forest Science* 51:266-275.
- Stark, D.T., Wood, D.L., Storer, A.J., and S.L. Stephens. 2013. Prescribed fire and mechanical thinning effects on bark beetle caused tree mortality in a mid-elevation Sierran mixed-conifer forest. *Forest Ecology and Management* 306:61-67.
- Turner, M.G., Gardern, R.H., Dale, V.H., and R.V. O'Neill. 1989. Predicting the spread of disturbances across heterogeneous landscapes. *Oikos* 55:121-129.
- United States Department of Agriculture. NAIP 2012 aerial imagery, 1-meter resolution, in natural color [imagery]. Obtained from California Department of Fish and Wildlife, February 9, 2019.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and T.T. Veblen. 2009. Widespread increase of tree mortality rates in the Western United States. *Science* 323: 521-524.
- van Mantgem, P.J., Caprio, A.C., Stephenson, N.L., and A.J. Das. 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? *Fire Ecology* 12:13-24.

- Wagenmakers, E. and S. Farrell. Notes and comment: AIC model selection using Akaike weights. *Psychonomic Bulletin & Review* 11:192-196.
- York, R.A., Battles, J.J., and R.C. Heald. 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. *Forest Ecology and Management* 179:107-121.
- York, R.A., Battles, J.J., Wenk, R.C., and D. Saah. 2011. A gap-based approach for regenerating pine species and reducing surface fuels in multi-aged mixed conifer stands in the Sierra Nevada, California. *Forestry* 85:203-213.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., and A.M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20:78-86.

CONCLUSION

The results from our study provides valuable information regarding the mechanisms underlying bark beetle-associated mortality during severe drought conditions. In the first chapter, we found a relationship between drought resistance and bark beetle-associated mortality, suggesting that treatments which increase drought resistance may also mitigate tree mortality to bark beetles. Although competition was negatively associated with drought resistance, our second chapter results suggested that competition was not the predominant driver of bark beetle-associated mortality. While greater competition may increase individual tree stress, bark beetle-associated mortality may ultimately arise as a function of host availability. More contiguous areas of drought stressed trees may be the most vulnerable to mortality, suggesting prescriptions that focus on reducing competition should also take into account the mixture of residual species, size variation, and species response to microhabitat conditions.

Although this study provides a better understanding of the mechanisms that drive bark beetle-associated mortality, we were unable to directly compare the effects of variable density thinning with other thinning methods. Future research could focus on the mechanisms of mortality across a gradient of spatial variability of competition and not just absolute measures of competition alone. The use of drought resistance as a metric of tree vigor should also be investigated further, with trees subjected to multiple droughts evaluated to determine the longevity of treatment effects on resistance to bark beetles. Furthermore, all of our analyses were confined to either the individual tree or stand scale.

Because bark beetle outbreaks can manifest at broader scales, expanding this research beyond the stand level would provide a better understanding of how smaller scale effects may translate to landscape resistance to disturbances.

APPENDICES CHAPTER 1

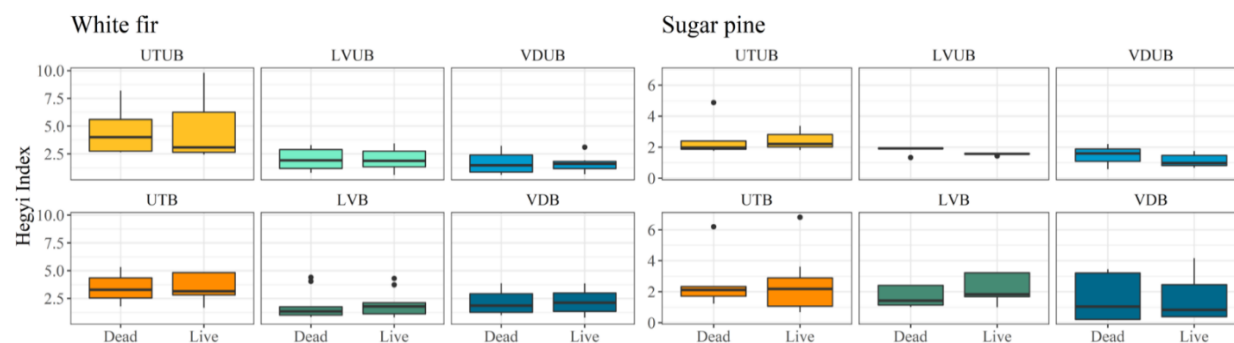
Appendix A Summary of paired white fir samples found for analysis.

White fir	Sample pairs	Average live DBH (range)	Average dead DBH (range)
UTUB (unthinned unburned)	8	32.7 (13.3-61.3)	33.2 (14.4-57.5)
UTB (unthinned burned)	8	38.7 (22.7-57.4)	39.0 (23.7-56.7)
LVUB (low variability unburned)	8	41.3 (25.6-88.7)	40.6 (23.4-86.6)
LVB (low variability burned)	8	47.7 (29.3-70.6)	48.7 (30.7-66.4)
VDUB (VDT unburned)	8	55.0 (33.0-78.5)	54.5 (33.8-75.2)
VDB (VDT burned)	8	53.1 (30.3-72.4)	52.8 (29.6-71.9)

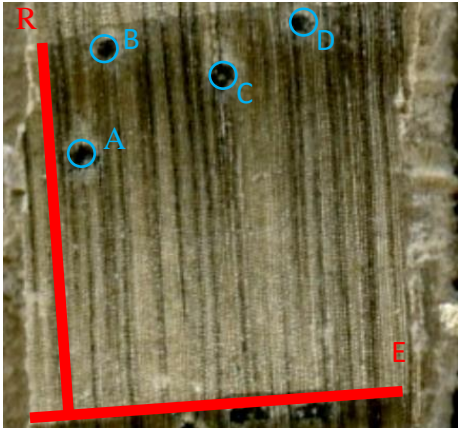
Appendix B Summary of paired sugar pine samples found for analysis.

Sugar pine	Sample pairs	Average live DBH (range)	Average dead DBH (range)
UTUB (unthinned unburned)	8	49.2 (25.2-90.6)	49.9 (25.9-94.1)
UTB (unthinned burned)	8	63.28 (26.4-99.6)	62.23 (28.9-96.9)
LVUB (low variability unburned)	2	40.46 (39.9-41.0)	41.1 (38.0-44.2)
LVB (low variability burned)	7	60.6 (43.1-75.3)	60.3 (42.8-81.4)
VDUB (VDT unburned)	7	67.66 (25.0-101.0)	66.6 (25.0-102.3)
VDB (VDT burned)	7	52.3 (38.2-72.2)	51.3 (37.2-72.5)

Appendix C Competition for live and dead trees across treatments. UTUB is unthinned-unburned, UTB is unthinned-burned, LVUB is low variability thin-unburned, LVB is low variability thin-burned, VDUB is variable density thin-unburned, and VDB is variable density thin-burned.



Appendix D A description of resin duct variables measured from sugar pine tree cores.

<div style="display: flex; align-items: center;">  <div style="margin-left: 20px;"> <p>A = Ring area of duct A (mm²)</p> <p>B = Ring area of duct B (mm²)</p> <p>C = Ring area of duct C (mm²)</p> <p>D = Ring area of duct D (mm²)</p> <p>R = Ring width (mm)</p> <p>E = Core diameter (mm)</p> </div> </div>			
Variable	Description	Formula	Example
Average duct size (mm ²)	Average area of individual resin ducts/year	$\sum \text{resin duct area} / \# \text{ resin ducts}$	$\frac{A + B + C + D}{4}$
Duct production (no. year ⁻¹)	Total number of individual resin ducts/year	$\sum \text{of resin ducts}$	$1 + 1 + 1 + 1 = 4$
Total duct area (mm ⁻² year ⁻¹)	Sum of resin duct area/year	$\sum \text{resin duct area}$	$A + B + C + D$
Duct density (no. mm ⁻² year ⁻¹)	Total number of individual resin ducts /year divided by ring area	$\sum \text{of resin ducts} / \text{ring area}$	$\frac{1 + 1 + 1 + 1}{R \times E}$
Relative duct area (% annual ring)	Total resin duct area divided by ring area x 100	$(\sum \text{resin duct area} / \text{ring area}) \times 100$	$\left(\frac{A + B + C + D}{R \times E} \right) \times 100$

Appendix E Spearman's rank correlation coefficient matrix. Values in bold indicate p-value < 0.05.

	Duct size	Duct production	Total duct area	Duct density	Relative duct area
Duct size	-	-0.19	0.31	-0.26	0.29
Duct production	-0.19	-	0.79	0.94	0.80
Total duct area	0.31	0.79	-	0.65	0.92
Duct density	-0.26	0.94	0.65	-	0.81
Relative duct area	0.29	0.80	0.92	0.81	-

Appendix F Average sugar pine growth and resin duct size ratio ($\pm 2\text{SE}$) for live and dead white fir during the year preceding mortality of dead counterparts.

Live growth	Dead growth	Live duct size	Dead duct size
1.23 (0.18)	0.82 (0.24)	1.10 (0.11)	1.14 (0.14)

Appendix G Summary of average growth ratio (± 2 SE) for live and dead white fir during the year preceding mortality of dead counterparts.

Live	Dead
1.12 (0.13)	0.88 (0.14)

APPENDICES CHAPTER 2

Appendix H Number of plots containing bark beetle-associated mortality of white fir or sugar pine.

	10 m	20 m	30 m	40 m	50
White fir	120	120	81	45	28
Sugar pine	72	106	78	45	28

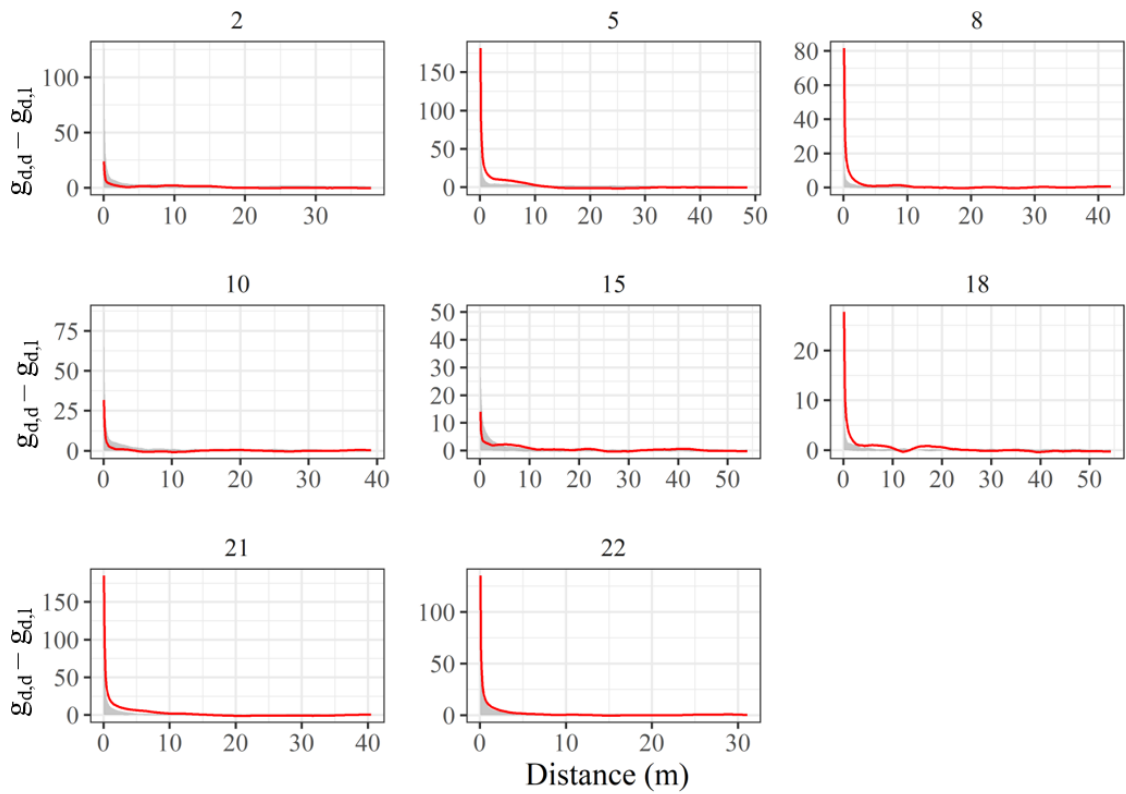
Appendix I Summary of effect size for top logistic regression models predicting proportion of white fir mortality across different scales.

Model inputs	Coefficient estimate (β)	Standard error	p-value
<i>10 meters</i>			
Intercept	0.08	0.54	<0.001
Conspecific density	1.00	0.98	0.018
<i>20 meters</i>			
Intercept	0.07	0.52	<0.001
Conspecific density	1.00	0.92	<0.001
<i>30 meters</i>			
Intercept	0.01	0.52	<0.001
Quadratic mean diameter	0.50	0.50	<0.001
<i>40 meters</i>			
Intercept	0.01	0.52	<0.001
Quadratic mean diameter	0.50	0.50	<0.001
<i>50 meters</i>			
Intercept	0.01	0.52	<0.001
Quadratic mean diameter	0.50	0.50	<0.001

Appendix J Summary of effect size for top logistic regression models predicting proportion of sugar pine mortality across different scales.

Model inputs	Coefficient estimate (β)	Standard error	p-value
<i>10 meters</i>			
Intercept	1.00	1.00	0.028
Canopy cover	0.54	0.52	0.026
<i>20 meters</i>			
Intercept	0.55	0.55	<0.001
Conspecific density	1.00	1.00	<0.001
<i>30 meters</i>			
Intercept	0.02	0.54	<0.001
Conspecific density	1.00	1.00	<0.001
<i>40 meters</i>			
Intercept	0.02	0.54	<0.001
Conspecific density	1.00	1.00	<0.001
<i>50 meters</i>			
Intercept	0.02	0.53	<0.001
Conspecific density	1.00	1.00	<0.001

Appendix K Individual unit estimates of spatial patterns of bark beetle-associated mortality between observed dead white fir (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,d} - g_{d,l_{observed}} > g_{d,d} - g_{d,l_{random}}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. Plots without patterns of random mortality did not contain an adequate sample of dead trees to generate simulation envelopes and were removed from the pooled estimate of $g(r)$.



Appendix L Individual unit estimates of spatial patterns of bark beetle-associated mortality between observed dead sugar pine (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,d} - g_{d,l_{observed}} > g_{d,d} - g_{d,l_{random}}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. Plots without patterns of random mortality did not contain an adequate sample of dead trees to generate simulation envelopes and were removed from the pooled estimate of $g(r)$.

