The Relationship Between Forest Structure, Composition, and Landscape on Bark Beetle Related Tree Mortality in Sequoia and Kings Canyon National Parks, California

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Citation	Lyons, Cailin M. 2019. The Relationship Between Forest Structure, Composition, and Landscape on Bark Beetle Related Tree Mortality in Sequoia and Kings Canyon National Parks, California. Master's thesis, Harvard Extension School.
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The Relationship Between Forest Structure, Composition, and Landscape on Bark Beetle Related

Tree Mortality in Sequoia and Kings Canyon National Parks, California

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A Thesis in the Field of Sustainability and Environmental Management

for the Degree of Master of Liberal Arts in Extension Studies

Harvard University

May 2019

Abstract

Outbreaks of bark beetles (*Dendroctonus* spp., *Ips* spp., *Scolytus* spp.) have

resulted in widespread tree mortality throughout the western United States, with the area

of forest die-off in California quadrupling to over 4 million acres between 2014 and 2016

during a period of intense drought (California Forest Pest Council, 2016). Scientists are

concerned that the rate of tree mortality is exceeding the rate at which forests can

regenerate, which could result in landscape level changes and have long-term

implications for species, climate, and water supply (Bentz et al., 2009). While research

indicates that prolonged drought and crowded, homogeneous tree stands have made

forests susceptible to bark beetle attacks, very few studies have looked comprehensively

at what specific tree characteristics, stand conditions, and landscape factors are most

significant in mediating these outbreaks.

To better understand the key factors influencing the bark beetle outbreak in the

Sierra Nevada, my research focused on two heavily impacted tree species in Sequoia and

Kings Canyon National Parks, white fir and sugar pine. The primary research question

addressed in this study was: What are the main ecological drivers mediating bark beetle

infestations in white fir and sugar pine? I hypothesized that DBH, slope, and time since

last fire would have a positive correlation and aspect, elevation, species diversity, and

stand density would have a negative correlation with bark beetle related tree mortality in

both white firs and sugar pines.

To test these hypotheses, I surveyed 72 red fir-white fir forest plots in Sequoia

and Kings Canyon National Parks in 2018. Within each plot, trees were evaluated to

determine species, size, and individual mortality factors. These data were then used to calculate stand characteristics such as stand density and species diversity within each plot. Time since last fire and other landscape factors, such as elevation, slope, and aspect, were evaluated at the plot level based on field measurements and existing Geographic Information Systems data. In addition, mortality data collected by U.S. Geological Survey in 2016 and 2018 from mixed conifer forests were also analyzed for this study.

Mixed effects logistic regression models were then run for each individual dataset as well as in a combined model to determine which factors were correlated with bark beetle related mortality in white fir and sugar pine. The results indicate that bark beetle related mortality was positively correlated with DBH and negatively correlated with slope in sugar pine. In white fir, the results indicate that bark beetle related mortality had a negative correlation with DBH and elevation and a positive correlation with time since last fire. I concluded that these differences in mortality factors could be attributed to differences in host preferences for the main pests found in each tree species, including fir engraver (*Scolytus ventralis), Scolytus subscaber,* and *Scolytus praeceps* for white fir and mountain pine beetle (*Dendroctonus ponderosae*) for sugar pine.

While this analysis is limited to white fir and sugar pine in Sequoia and Kings Canyon National Parks, the results further our understanding of bark beetle epidemiology and tree mortality factors in the southern Sierra Nevada mountain range of California. Understanding these drivers are key not only to identify which forest stands are most susceptible to future bark beetle attacks, but also to determine if any conditions can be managed to reduce the risk of tree mortality. The results suggest that management measures such as prescribed fire may be more effective in lower elevational forests

comprised of trees targeted by "secondary" pests, which generally attack stands stressed

by a wider range of stand characteristics and landscape factors.

Acknowledgments

There are many people without whom this project would not have been possible. Thank you to my Research Advisor, Dr. Mark Leighton, for providing direction and encouragement during the proposal and planning phases of this project and for being a continued source of inspiration throughout my time as a graduate student. Special thanks to my Thesis Director, Dr. Adrian Das, for providing a tremendous amount of guidance and resources during implementation of this project. This research truly would not have been possible without your expertise and guidance. I would also like to thank the many students of the Harvard Sustainability program for providing that great back and forth that leads to sound science and academic discovery, with special gratitude to Mel Wilson and Brigitte Boeck-Chenevier for their insights on the draft proposal and comradery.

Thanks are also in order to the many other researchers and scientists in the Sierra Nevada that provided their knowledge and resources in support of this project: Beverly Bulaon (U.S. Forest Service), Nate Stephenson (U.S. Geological Survey), Annie Esperanza (National Park Service), Nate Moore (National Park Service), and Anne Kelly (Sierra Nevada Research Institute). Special thanks to RECON Environmental and Frank McDermott for providing Geographic Information Systems (GIS) services for this project, as well as to my research assistant Rachel Hunter for providing field support.

These acknowledgements would also not be complete without expressing my gratitude to my family and husband, Steven Lyons, for providing continued support and encouragement throughout the duration of this project and my time as a graduate student.

Table of Contents

List of Tables

List of Figures

Chapter I

Introduction

Large expanses of forest are dying at a precipitous rate throughout the western

United States, primarily due to outbreaks of bark beetles (*Dendroctonus* spp., *Ips* spp.,

Scolytus spp.). During a period of severe drought in California, the area of forest die-off

more than quadrupled over the span of two years, increasing from an estimated 820,000

acres in 2014 to a peak of over 4 million acres in 2016 (California Forest Pest Council,

2016). The central and southern Sierra Nevada mountain range has been the most heavily

impacted area in California, with some areas experiencing greater than 90% tree

mortality (U.S. Department of Agriculture [USDA], 2017a; Stephens et al., 2018). Figure

1 shows the progress of tree mortality in the Sierra Nevada as bark beetle outbreaks

developed under drought conditions, starting in 2015. Within this region, widespread

mortality of pines and conifers has resulted from increased pressure from bark beetles,

with extensive mortality of Ponderosa pine (*Pinus ponderosa*), red fir (*Abies magnifica*),

and white fir (*Abies concolor*) in Sequoia and Kings Canyon National Parks (California

Forest Pest Council, 2016). Elevated levels of mortality have also been noted in sugar

pine (*Pinus lambertiana*), Jeffrey pine (*Pinus jeffreyi*), and incense cedar (*Calocedrus*

decurrens) in the southern Sierra Nevada (California Forest Pest Council, 2016;

Mortensen, Fettig, Bulaon, & Foulk, 2018).

While bark beetles naturally regulate forest stands by causing low levels of

mortality, current mortality levels may be exceeding the ability of forests to naturally

regenerate and result in landscape-level changes, which could have cascading environmental consequences (Bentz et al., 2009; Edburg et al., 2012). One alarming consequence from this widespread tree mortality is the large-scale reduction of carbon storage provided by these forests as well as the simultaneous release of carbon into the atmosphere, which may have consequences on climate systems at both the regional and global scale (Swann et al., 2018). In addition, large-scale tree mortality is expected to increase the frequency and severity of catastrophic fires and reduce water quantity, further compounding the effects of drought and climate change (Jenkins, Hebertson, Page, & Jorgensen, 2008; Edburg et al., 2012). The bark beetle outbreak may also threaten sensitive species such as whitebark pine (*Pinus albicaulis*), which is currently proposed for listing under the Endangered Species Act (Meyer, Bulaon, MacKenzie, & Safford, 2016). In Sequoia and Kings Canyon National Parks, the bark beetle outbreak also presents a unique set of management challenges due to visitation and recreation within the parks. Tree mortality adjacent to roads, campgrounds, and buildings threatens visitor safety as well as critical infrastructure, requiring tree removal efforts (A. Esperanza, personal communication, July 24, 2018).

Current research indicates that prolonged drought combined with forest overcrowding has provided optimal conditions for these beetles to proliferate, causing mass mortality throughout forests in the west (Bentz et al., 2009; Jenkins et al., 2008). However, few studies have looked comprehensively at what specific tree characteristics, stand conditions, and landscape factors make trees most susceptible to these infestations, particularly in the Sierra Nevada mountain range of California. Understanding the drivers
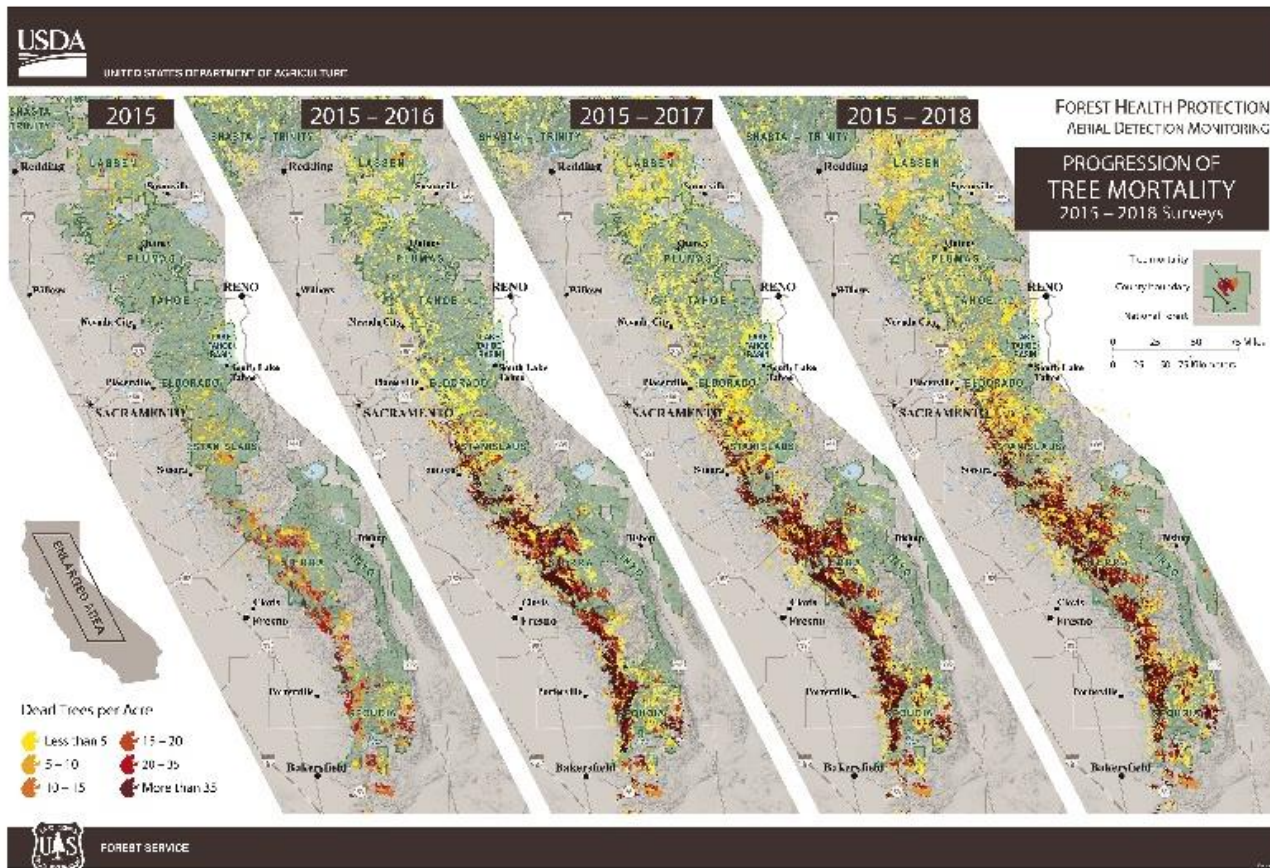
Figure 1. Progression of tree mortality in California from 2014 to 2018 (USDA, 2017b).

Elevated levels of tree mortality are shown as prolonged drought and bark beetle outbreak conditions develop primarily in the southern Sierra Nevada between 2015 and 2018.

behind this ecological change is necessary to inform forest management decisions and improve the resiliency of forests over the long-term.

Research Significance and Objectives

This research will identify key factors that are associated with bark beetle related tree mortality in white fir and sugar pine in Sequoia and Kings Canyon National Parks. Understanding these drivers is important not only to identify which trees are most susceptible to bark beetle attacks, but also to determine if any conditions can be effectively managed to reduce the risk of widespread tree mortality over the long-term. While this analysis is limited to white fir and sugar pine in Sequoia and Kings Canyon National Parks, the results will further our understanding of bark beetle epidemiology and tree mortality factors in the southern Sierra Nevada mountain range of California and may be applicable to other species and regions. The research objectives for this study include:

- To evaluate which tree characteristics, stand conditions, and landscape factors mediate bark beetle-related mortality in white fir and sugar pine in the southern Sierra Nevada.
- To determine if fire history has a significant effect on bark beetle related mortality in white fir and sugar pine.
- To lead to more informed decision-making regarding how white fir and sugar pine stands can be managed to improve the resiliency of forests to bark beetle infestation.

Background

Bark beetles are native residents of forest ecosystems in North America and play an important role in the regeneration of forests, typically by killing old or compromised trees which provides additional light and resources for newer trees to mature (Bentz et al., 2009). Under background conditions, tree mortality in forests typically varies between 0.5 to 2% annually, with bark beetles as the primary mortality agent for approximately 40% of that number (Das, Stephenson, & Davis, 2016). However, bark beetle populations are known to undergo periodic outbreaks and cause mass mortality events that exceed background tree mortality levels (Bentz et al., 2009; USDA, 2012a). These periodic outbreaks are typically tied to climatic conditions such as elevated temperatures and prolonged drought (Bentz et al., 2009; USDA, 2012a). Bark beetle outbreaks are known from North American conifer forests throughout history based on records dating back to the 1700's; however, recent outbreaks are believed to differ from historic outbreaks due to their intensity, synchroneity, and extent (Bentz et al., 2009). Recent outbreaks are believed to have killed a larger number of trees at a faster pace over a longer duration, with mass mortality events occurring simultaneously at multiple locations throughout western North America (Bentz at al., 2009). In addition, outbreaks of beetles have been observed in areas such as British Columbia, Alaska, and northern Mexico, where large-scale infestations have not previously been recorded and reflect range expansions for some beetle species (Bentz et al., 2009).

Bark Beetle Life History

Several bark beetle species are associated with tree mortality in the Sierra Nevada mountain range, including mountain pine beetle (*Dendroctonus ponderosae*), western pine beetle (*Dendroctonus brevicomis*), Jeffrey pine beetle (*Dendroctonus jeffreyi*), fir engraver (*Scolytus ventralis*), pine engraver (*Ips pini*), piñon ips (*Ips confusus*), and California fivespined ips (*Ips paraconfusus*) (Bentz et al., 2009; USDA, 2012a; California Forest Pest Council, 2016). Species in the *Dendroctonus* genus are generally considered "primary" bark beetles due to their capability of attacking healthy, vigorous trees (Gaylord, 2014). Species in the *Ips* and *Scolytus* genera are generally considered "secondary" bark beetles, as they typically attack compromised trees (Gaylord, 2014). Both primary and secondary bark beetle species have a similar life history and effect on their respective tree hosts. Understanding the life history of these species is integral in understanding the outbreak conditions that have resulted in widespread tree mortality in the Sierra Nevada.

Bark beetles will use an array of sensory modalities, including visual, olfactory, gustatory, and tactile signals, during host selection when initiating an attack (Raffa, Andersson, & Schlyter, 2016; Stephenson et al., 2019). After a host has been selected, adult beetles will attempt to bore through a tree's bark directly into the cambium for feeding and reproduction (USDA, 2012b). Trees may resist these attacks through the release of oleoresin, which serves as a physical barrier to bark beetles by flushing and sealing wounds and also may excrete defensive chemicals with insecticidal and antifungal properties (West, Bernklau, Bjostad, & Jacobi, 2016). Therefore, bark beetles must typically attract a critical minimum number of beetles to overcome the tree's

defenses (Bentz et al., 2009; USDA, 2012a). Primary beetle species such as mountain pine beetle will utilize a tree's semiochemicals to produce conspecific attraction or aggregation pheromones to induce a mass attack, and thus are able to successfully colonize even healthy trees (West et al., 2016; Gaylord, 2014; Bentz et al., 2009). The beetles will then create galleries and lay eggs in the cambium of successfully colonized trees, which allow for larvae to feed on the tree's phloem before pupating and exiting the tree to find another host (USDA, 2012b). Oftentimes these beetles will also inoculate the trees with fungi that inhibit water transport, further reducing the tree's defenses (Smith, 2007). Over time, the combination of boring and gallery construction, feeding, and fungi result in tree mortality (Smith, 2007; USDA, 2012b).

Generational times vary among bark beetle species, with species such as western pine beetle and piñon ips producing more than one generation per year (Bentz et al., 2010). Other species such as mountain pine beetle can take between one and three years to produce a single generation depending upon climatic conditions (Bentz et al., 2010). However, changes in climate and temperature may affect the developmental timing, life history, and fitness of bark beetle species (Bentz et al., 2010). Rises in temperature may alter the life cycles of these species, increasing developmental and reproductive rates and allowing for some beetle species to increase the number of generations produced per year (Bentz, 2009; Bentz et al., 2010). In a study of climatic influences on mountain pine beetle, models suggested that recent rises in temperatures may be inhibiting cold-induced mortality of beetles in northern eco-regions, resulting in increased longevity of beetles and permitting outbreak conditions to occur (Weed, Bentz, Ayres, & Holmes, 2015). Winter warming in these regions have also allowed some beetle species to expand to

higher altitudes and latitudes, resulting in range expansions (Weed et al., 2014; Bentz et al. 2009). However, in coastal and southern eco-regions such as the Sierra Nevada, historical temperatures typically don't drop below the predicted lower lethal temperatures for mountain pine beetle, suggesting that warming temperatures have not significantly altered beetle longevity or distribution in these regions (Weed et al., 2014).

Sierra Nevada Forests Impacted by Bark Beetles

Elevated levels of tree mortality within the Sierra Nevada were recorded starting in 2010, with an estimated 129 million trees dead recorded by 2017 (USFS, 2017c). During this time, a five-year drought spanning from 2012 to 2017 occurred in California, which included some of the hottest and driest years on record (Mortensen et al., 2018; Stephenson et al., 2019). Data from tree ring analysis further suggests that this drought was the most severe drought event within a 1,200-year chronology (Mortensen et al., 2018). While this landscape-level data is based on an aerial survey that did not directly attribute mortality to any specific agent, emerging data suggests that a majority of tree mortality in this region can be attributed to bark beetles (Stephenson et al., 2019; Mortensen et al., 2018). In a study of tree mortality within Sequoia and Kings Canyon National Park, it was found that 73.5% of trees that died between 2014 and 2017 could be attributed to bark beetles (Stephenson et al., 2019).

The intensity and extent of bark beetle related tree mortality during this drought event has also varied temporally and spatially by species. In 2016, mortality of white fir and red fir attributed to fir engravers was estimated at a peak of 2.65 million acres state-wide, an increase from 460,000 acres in 2014 (California Forest Pest Council, 2016). Similarly, pine mortality (primarily Ponderosa pine) from mountain pine beetle was

estimated at a peak of 2 million acres in 2016 (California Forest Pest Council, 2016). One study found 89.6% mortality of Ponderosa pine and 48.1% mortality of sugar pine in study plots attributed to mountain pine beetle in the southern and central Sierra Nevada in 2017 (Mortensen et al., 2018).

At the regional level within California, the southern Sierra Nevada mountain range has been the most affected by both drought and tree mortality, with Sequoia and Kings Canyon National Parks containing some of the highest recorded mortality levels particularly for white fir, red fir, and Ponderosa pine (USDA, 2017a; Stephens et al., 2018; California Forest Pest Council, 2016). Other species, such as sugar pine, Jeffrey pine, and incense cedar, have also exhibited elevated levels of mortality throughout the southern Sierra Nevada (California Forest Pest Council, 2016; Mortensen et al., 2018). Tree mortality in this region was initially reported at lower elevations based on aerial survey results; however, significant mortality of trees was reported at higher elevations as early as 2016 (Moore, 2017; California Forest Pest Council, 2016). In addition, mortality was also reported to be increasing in more northern regions in 2016 (California Forest Pest Council, 2016).

Potential Factors Contributing to Host Susceptibility

Under background conditions, native bark beetles typically colonize trees that are compromised by disease, injury, and other factors, resulting in low levels of mortality (Smith, 2007; Das et al., 2016). However, environmental conditions such as elevated temperatures and drought combined with stand conditions are believed to have promoted outbreak conditions, causing mass mortality events throughout the west. While outbreak conditions have been known to occur periodically throughout history, the intensity,

synchroneity, and extent of recent outbreaks are believed to exceed previous outbreaks in recorded history (Bentz et al., 2009). Scientists believe that a combination of biotic and abiotic factors have increased the susceptibility of host trees to bark beetle attack and thereby promoting outbreaks (Bentz et al., 2009; Jenkins et al., 2008). These factors include a number of tree characteristics, stand conditions, and landscape factors that influence forest structure and composition, tree health, and moisture availability and are influenced by dynamic ecological processes such as fire and drought.

Tree Characteristics and Stand Conditions

Although many factors such as environmental conditions, host availability, and predator-prey relationships contribute to the level of bark beetle activity, it is believed that stand conditions play a large role in the development of outbreak conditions (Bentz et al., 2009; Jenkins et al., 2008). Decades of management practices such as fire suppression, logging, and grazing have altered forest composition and structure, resulting in denser, more homogenous tree stands dominated by old, large diameter, and less vigorous trees that are more susceptible to bark beetle infestation (Bentz et al., 2009; Fettig et al., 2007; Jenkins et al., 2008). The influence of tree characteristics and stand conditions may differ between forest types due to differences in species-host interactions; however, stand density, tree size, and lack of heterogeneity are commonly cited as potential factors influencing outbreak conditions and bark beetle-related tree mortality (Bentz et al., 2009; Fettig et al., 2007; Jenkins et al., 2008).

Stand density. Numerous studies have demonstrated a positive correlation between bark beetle related tree mortality and stand densities (Hayes, Fettig, & Merrill, 2009; Negron

& Popp, 2009; Negron, Allen, Cook, & Winthrow, 2007; Negron et al., 2017). This relationship is generally attributed to increased competition between trees for resources such as water, light, and nutrients in crowded stands, which reduces the tree's defensive capacity and resiliency to bark beetle attack (USDA, 2012a; USDA, 2012b). Bark beetle pheromone plumes have also been shown to be more concentrated and continuous in forest stands with higher densities, likely helping to facilitate mass attacks (Thistle et al., 2005). In a study of five national forests infested with western pine beetle in northern California, stand density was found to be the most important predictor of western pine beetle related tree mortality (Hayes et al., 2009). Similar results have been shown in studies of mountain pine beetle in Ponderosa pine stands, which have indicated a positive correlation between mountain pine beetle attack and stand density index, as well as increased mountain pine beetle-related tree mortality in un-thinned stands with higher stand densities (Negron et al., 2007; Negron & Popp, 2009; Negron et al., 2017).

Tree size. Bark beetles may also preferentially select for different size classes of trees, depending on the species-host interaction. Some bark beetle species may preferentially select for larger diameter trees as they provide a greater visual target and may also allow for female beetles to produce more offspring due to increased phloem (Bentz et al., 2009). The primary pests of sugar pine and white fir in the southern Sierra Nevada, mountain pine beetle and fir engraver, are both believed to prefer medium to large diameter trees (Negron et al., 2008; Negron & Popp, 2003; Walker et al., 2015). In stands of Ponderosa pines in South Dakota and Wyoming, it was demonstrated probability of mountain pine beetle attack increased in trees greater than 24.5 cm DBH

(Negron et al., 2008). In mixed conifer forests in the Sierra Nevada, the fir engraver appeared to preferentially attack white fir in size classes between 20.3 and 50.5 cm DBH (Walker et al., 2015). However, it should be noted that both studies were conducted under background conditions of low mortality, and bark beetles can exhibit behavioral plasticity that may affect host selection under outbreak conditions (Boone et al., 2011). In a study of mountain pine beetle behavior in lodgepole pines, it was observed that bark beetles typically attacked weakened trees and were less likely to attack well-defended, larger-diameter trees with high terpene concentrations under background conditions (Boone et al., 2011). However, as mountain pine beetle populations increased at the stand-level, mountain pine beetles increasingly attacked larger-diameter, more heavily defended trees (Boone et al., 2011). Thus, size class preferences exhibited by bark beetles under background conditions may differ from those exhibited during outbreak conditions where bark beetles can more easily obtain critical mass.

Heterogeneity. Lack of heterogeneity is also commonly cited as a factor that increases susceptibility to bark beetle attack and can be measured through a variety of factors, including species diversity and age or size class structure (USDA, 2012a; Bentz et al., 2009; Jenkins et al., 2008). In general, homogeneous stands dominated by a single species where a majority of the trees are older and larger diameter are considered to be more susceptible to bark beetle outbreaks than heterogeneous stands comprised of trees of many ages, size classes, and species (Bentz et al., 2009; Fettig et al., 2007; Jenkins et al., 2008). In a study of bark beetle preferences in mixed conifer forests in the Sierra Nevada, species diversity was negatively correlated with tree pitch tubes (Walker et al.,

2015). White fir prevalence was also positively correlated with pitch tube count and white fir mortality (Walker et al., 2015). Based on these results, the study concluded that low species diversity and prevalence of hosts may be correlated with bark beetle attacks (Walker et al., 2015). However, while pitch tubes can be used as an indicator of bark beetle attack, pitch tubes may not be produced by stressed trees that have been successfully colonized by bark beetles (Adrian Das, personal communication, August 21, 2018). Further study is needed to determine the role of species diversity in mixed conifer forests.

Landscape Factors

Host susceptibility to bark beetle attack is also attributed to prolonged drought in the Sierra Nevada mountain range. During drought, plant stomates will close to restrict transpiration, which has a secondary effect of limiting carbon assimilation (Bentz et al., 2010). Changes in carbon assimilation alter the allocation of carbohydrates within the plant for growth, defense, and tissue repair, thereby limiting the plant's defensive capacity and reducing the number of beetles needed for a successful mass attack (Bentz et al., 2010). It is also well documented that decline in tree health due to moisture deficiencies is correlated with insect outbreaks, with short-term moisture deficiencies resulting in small-scale, recurrent outbreaks and long-term deficiencies resulting in large-scale outbreaks (Fettig et al., 2007). Thus, landscape factors that influence moisture availability may further compound the effects of drought and thus have the potential to influence bark beetle related tree mortality.

Potential landscape factors that may influence moisture availability include slope aspect, slope gradient, and elevation. Slope aspect influences the amount of solar

radiation and evapotranspiration received by a slope (Guarin & Taylor, 2005). South-facing slopes in the northern hemisphere receive more solar radiation and evapotranspiration than north-facing slopes, and thus are typically hotter and drier with less plant available water (Guarin & Taylor, 2005). Slope gradient also influences soil moisture through water run-off rates, with steeper slopes associated with high run-off rates and shallower slopes associated with slower run-off (Paz-Kagan et al., 2017). Elevation also plays a key role in influencing microclimate. Temperature, snowfall versus rainfall apportionment, and snowmelt timing vary with elevation, with lower elevations typically having higher temperatures, higher evaporative demand, reduced snowpack, and earlier snowmelt (Trujillo et al., 2012; Stephenson et al., 2018).

Several studies have looked at the influence of landscape characteristics on tree mortality during drought in the Sierra Nevada mountain range. In a study of forest mortality in Sequoia National Park, elevation was found to have the highest relative importance in predicting forest dieback from drought stress and insect outbreaks, with higher levels of mortality at lower elevations (Paz-Kagan et al., 2017). In addition, southwestern and western exposures and shallower slopes were found to be correlated with higher levels of tree mortality (Paz-Kagan et al., 2017). Conversely, in a study of drought-mediated tree mortality in mixed conifer forests dominated by Ponderosa pine, incense cedar, and white fir in Yosemite National Park, there was no significant difference in temporal patterns of tree death due to slope aspect (Guarin & Taylor, 2005). However, the density of dead trees was higher on north-facing slopes indicating that stand characteristics such as stand density may have outweighed any potential buffering effects from landscape factors in mediating tree mortality (Guarin & Taylor, 2005).

While these results likely have implications for bark beetle-related tree mortality, it should be noted that both studies did not specifically target tree mortality from bark beetles and included trees that died from pathogens, drought stress, and other factors.

The role of these landscape factors may also be further amplified as tree mortality occurs. As branch die-back creates more openings in the crown canopy, solar radiation and evaporative demand may increase (Trujillo et al., 2012; Edburg et al., 2012). Thus, landscape factors such as aspect, slope, and elevation may play an even more significant role under outbreak conditions where large-scale mortality events cause changes in the canopy structure.

Fire History

Prior to European settlement, mixed conifer forests of the Sierra Nevada were generally subject to frequent, low to moderate intensity, stand-modifying fires (Caprio & Lineback, 1997; van Wagtendonk et al., 2001). These fires were a result of both natural fire sources (e.g. lightning) and anthropogenic fire sources (e.g. Native Americans) (Caprio & Lineback, 1997). More frequent fires combined with intensive grazing implemented by Native Americans are believed to have maintained more open canopies and reduced fuels historically within forests in the Sierra Nevada (Caprio & Lineback, 1997). However, current fire regimes in the Sierra Nevada have departed from historic fire regimes, primarily due to fire suppression policies implemented by the U.S. government in the 20th century (Caprio & Lineback, 1997; Bentz et al., 2009). Historic fire suppression is believed to have resulted in changes in forest composition and structure, such as higher stand densities, increased fuels, and more homogeneous stand composition, with stands comprised of larger, older trees (Caprio & Lineback, 1997;

Bentz et al., 2009). In addition, these changes in stand structure have led to an increase in large-scale, stand-replacing, catastrophic fire events (Caprio & Lineback, 1997; Bentz et al., 2009).

A majority of the research exploring the relationship between fire and bark beetle attacks focuses on the short-term effects of fire and shows both positive and negative correlations. Some studies have shown that conifers in burned stands produce higher oleoresin than trees in unburned stands for up to seven years post-fire, which may increase resilience to bark beetle infestations (Gaylord, 2014). However, other studies have shown that fire damage sustained to the tree crown reduces the flow of oleoresin and increases the likelihood of bark beetle attacks (Gaylord, 2014). This indicates that the benefits of fire may be limited to areas subject to frequent, low intensity fires as opposed to areas with infrequent, high intensity fires.

Very little research focuses on the long-term effects of fire, particularly fire history, with regards to bark beetle outbreaks. One study in Sequoia National Park explored the relationship between time since last fire and tree mortality from drought and bark beetle attack but found no significant relationship (Paz-Kagan et al., 2017). In addition, a study of tree mortality in the western United States concluded that increased tree mortality rates could not be explained by fire suppression, as tree mortality rates were elevated in forests of all fire regime classes (van Mantgem et al., 2009). This was based on the assumption that forests with short fire return intervals (<25 years) which have experienced substantial changes in fire regime would have greater mortality rates than forests with long fire return intervals (>250 years), which have experienced little to no change in fire regime (van Mantgem et al., 2009). However, anecdotally, extensive

white fir mortality has been observed in Modoc National Forest in stands exhibiting high stand densities that have not burned in over 100 years (California Forest Pest Council, 2016). This observation indicates that the influence of fire on stand dynamics may play a role in bark beetle related tree mortality, particularly in white firs.

Knowledge Gaps

Bark beetle related tree mortality is likely influenced by a complex set of factors, based on tree characteristics, stand conditions, landscape factors, and ecological processes such as fire and drought. Though research has focused on many of these factors separately, a comprehensive study is needed to determine their combined significance in mediating bark beetle-related mortality. Limited data is also available regarding mortality trends in white firs and sugar pines, particularly under outbreak conditions, and thus presents a unique opportunity to evaluate these factors. Furthermore, though landscape factors such as elevation, slope, and aspect are typically evaluated in relation to drought-mediated tree mortality, these landscape factors are not commonly studied specific to bark beetle related tree mortality despite the interconnected nature between bark beetle outbreaks and drought. In addition, host selection preferences exhibited by bark beetles may differ under outbreak conditions due to behavioral plasticity (Boone et al., 2011). Thus, mortality patterns demonstrated by studies conducted under background conditions may not be applicable to the current outbreak conditions in the Sierra Nevada. Further research is needed to better understand the role of these abiotic and biotic factors in mediating bark beetle-related tree mortality in these species under extended drought and outbreak conditions.

Research Question, Hypotheses and Specific Aims

The primary research question addressed in this study was: What are the main ecological drivers mediating recent bark beetle-related tree mortality in white firs and sugar pines in the southern Sierra Nevada? The primary hypotheses I examined through this research include:

1. Stand density, DBH, slope, and time since last fire will have a positive correlation with bark beetle related mortality in both white fir and sugar pine.

2. Species diversity, elevation, and aspect will have a negative correlation with bark beetle related mortality in both white fir and sugar pine.

3. Stand density will have the greatest correlation of all factors with bark beetle mortality in both white fir and sugar pine.

I hypothesized that as stand density, DBH, slope, and time since last fire increase, bark beetle mortality will increase. Numerous studies have supported a correlation between stand density and bark beetle related tree mortality (Hayes et al., 2009; Negron & Popp, 2009; Negron et al., 2007; Negron et al., 2017), supporting the theory that the effects of fire suppression on stand structure have facilitated the bark beetle outbreak to occur (Caprio & Lineback, 1997; Bentz et al., 2009). In addition, several studies have shown that mountain pine beetle and fir engraver, the primary pests of sugar pine and white fir, preferentially select for larger diameter trees (greater than 24.5 cm DBH for mountain pine beetle and between 20.3 and 50.5 cm for fir engraver (Negron et al., 2008; Walker et al., 2015). Though one study of the Sierra Nevada indicated a negative correlation between slope and tree mortality from multiple factors (Paz-Kagan et al.,

2017), I predicted that tree mortality is higher on steeper slopes due to the effects of slope on soil moisture availability.

I also hypothesized that as species diversity, aspect (as defined by northness), and elevation decrease, bark beetle mortality will increase. I predicted that species diversity will have a negative correlation with tree mortality as it is frequently cited that homogeneous tree stands are more susceptible to bark beetle attack (Bentz et al., 2009; Fettig et al., 2007; Jenkins et al., 2008). I also hypothesized that bark beetle related tree mortality will increase as elevation decreases and on southerly exposures due to their effects on microclimate and moisture availability (Trujillo et al., 2012; Stephenson et al., 2018; Guarin & Taylor, 2005).

Lastly, I hypothesized that stand density will be the most significant predictor of bark beetle related tree mortality, due to the numerous studies that have indicated a strong correlation between these two variables (Hayes et al., 2009; Negron & Popp, 2009; Negron et al., 2007; Negron et al., 2017).

Specific Aims

To test these hypotheses, the specific aims of this research project were to:

1. Collect field data to determine tree characteristics (e.g. DBH, mortality factors) and stand conditions within red fir-white fir forest stands in Sequoia and Kings Canyon National Parks.

2. Calculate stand conditions such as stand density and species diversity from Lyons 2018 red fir-white fir forest data, as well as 2016 and 2018 mixed conifer forest data provided by the U.S. Geological Survey (USGS).

3. Derive different landscape factors and fire history metrics such as elevation, slope, aspect, and Time Since Last Fire from geospatial data using existing park GIS layers or from field data.

4. Incorporate data into multiple mixed effects logistic regression models to analyze the correlation between bark beetle related mortality in white fir and sugar pine individuals and different tree characteristics, stand conditions, landscape factors, and fire history.

Chapter II

Methods

This study evaluated tree mortality data collected in Sequoia and Kings Canyon National Parks in 2016 and 2018 to determine if there was a correlation between recent bark beetle related mortality in white firs and sugar pines and specific tree characteristics, stand conditions, landscape factors, and fire history metrics. The field survey portion of the study included tree surveys within red fir-white fir forest plots randomly selected throughout both parks. Tree survey data collected by USGS in 2016 and 2018 within mixed conifer forest plots were also incorporated into the study to expand the dataset for this project. Figure 2 shows the locations of the study plots from the three different datasets. Tree characteristics, stand conditions, landscape factors, and fire history metrics were derived from the field data and/or using GIS. Mixed effects logistic regression models were fit using the lme4 package in the statistical software program R to determine what factors have a significant relationship with bark beetle related mortality in white firs and sugar pines (R Core Team, 2015).

Field Surveys

Field surveys were conducted to gather data on tree mortality in red fir-white fir forest in Sequoia and Kings Canyon National Parks in August and September of 2018. I was assisted in the field research by Rachel Hunter (California Polytechnic University, San Luis Obispo). Training in bark beetle identification and forest mensuration
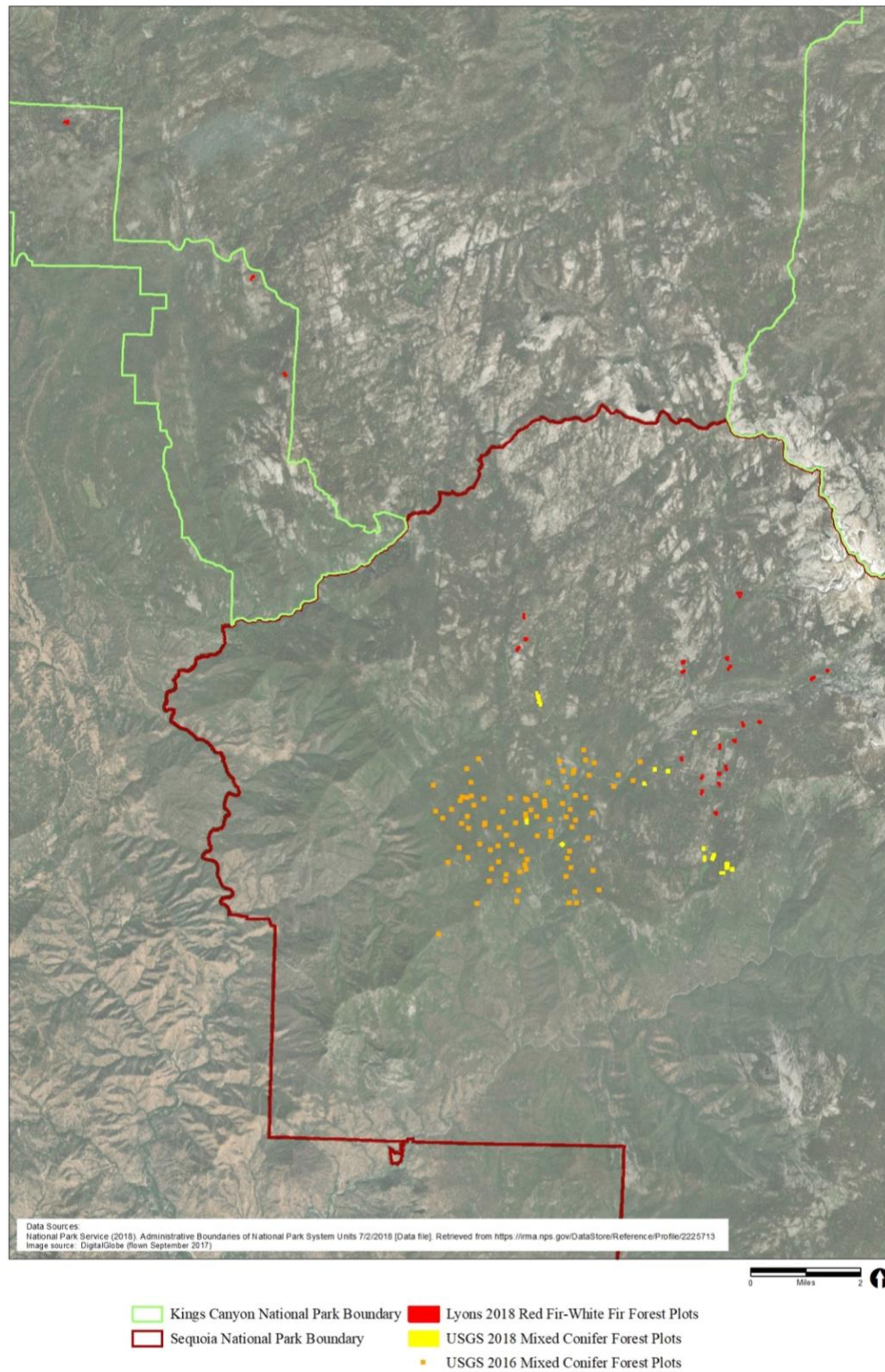
Figure 2. Locations of the study plots.

techniques were provided by Dr. Adrian Das (USGS) and Dr. Beverly Bulaon (U.S. Forest Service) prior to conducting surveys.

Study Area

To determine the study area for the field surveys, a preliminary analysis was conducted using GIS to evaluate the locations and accessibility of red fir-white fir forest within Sequoia and Kings Canyon National Parks. Red fir-white fir forest stands were located using the geospatial data for the Vegetation Mapping Inventory Project of Sequoia and Kings Canyon National Parks conducted by the National Park Service in 2014 (NPS, 2014b). Geospatial data containing roads, trails, and parking lots were then overlaid onto the red fir-white fir forest in GIS (Folger, 2018a; Folger, 2018b). To ensure sampling locations could be accessed by trail within a single day, only red fir-white fir forest stands located within 150 m of a designated trail and a 5 km radius of a designated parking lot were included within the study area for the project (Figure 2).

Sampling Design

A nested sampling design was used in which randomized plots were selected from within different forest blocks to calculate the mean values for stand characteristics, landscape factors, and fire history. The goal of sampling multiple areas within an individual forest block is to account for variation within the stand and therefore be more representative of the overall stand conditions. To determine the forest blocks to be sampled, the study area was overlaid with a numbered grid comprised of 150 m by 150 m cells in GIS. A total of 24 blocks were randomly selected for sampling from the numbered grid using a random number generator. Each forest block selected was then

sub-divided into 30 m by 30 m cells to determine the plot locations to be sampled. The center points of the cells were delineated in GIS to form the basis for the plots, which consisted of a 10 m radius circular sample plot from the center of the cell. Basing the plot locations on a 30 m by 30 m ensured that plots would be offset a minimum of 10 m to be stratified within each forest block.

A total of three plots were randomly selected from each block using a number generator in GIS. To reduce the potential for edge effects and confounding factors, plots located within 50 m of a road or parking lot or intersecting a trail were discarded based on GIS analysis. Plots were then field verified to ensure that transects were offset a minimum of 10 meters from trails to reduce the potential for edge effects. Additional plots were pre-selected in GIS to ensure that plots could be discarded during field verification in the event that confounding factors were observed.

Survey Methods

A total of 72 plots were surveyed within the red fir-white fir forest in Sequoia and Kings Canyon National Park at elevations ranging from 2,075 m to 2,476 m (6,808 and 8,123 ft) (Figure 2). Plots were located in the field using GPS and then delineated using two transect tapes running 10 m perpendicularly from the center point along the slope and cross-slope. For every plot, aspect was determined using a compass sighted from the center point of the transect. Percent slope was also determined using a clinometer sighted from the center point of the transect to both ends of the tape. All trees and shrubs within the plot were evaluated. Only trees retaining foliage were recorded in an effort to capture recently dead trees from the current mortality event. Trees and shrubs located on the edge of the plot were recorded if 50% or more of the bole was located within the 10 m radius

plot. Dead trees that did not retain any foliage, were leaning more than 45 degrees, or were less than 1.37 m in height were not recorded.

The following variables were collected for all sampled trees and shrubs within each plot: tree condition, species, and DBH (Table 1). To determine the tree condition, a visual inspection was conducted of each tree for crown die-off evidenced by color change. Each tree was assigned one of the following tree condition classifications: Live; Dead – successful bark beetle attack; or Dead – no evidence of successful bark beetle attack. Dead trees were also assigned a foliage condition (F1-F3) based on methodologies developed by the USGS Western Ecological Research Center (Table 1; Adrian Das, personal communication, August 21, 2018). For all dead trees retaining foliage, a minor amount of bark was removed from the trunk to determine if bark beetle galleries were present in the cambium, indicating successful bark beetle attack. Secondary indicators such as entry/exit holes, pitch tubes, veiled polypore (*Cryptoporus volvatus*), and frass were also noted but not considered evidence of successful attack. Species that could not be readily identified were determined using the Jepson Manual, a taxonomic key. DBH was measured at 1.37 m above-ground along the side slope to ensure consistency. Trees with multiple boles at breast height (1.37 m) were counted as separate trees. For deciduous trees and shrubs, only stems with greater than 2 cm DBH were recorded.

To distinguish this set of samples from the two additional datasets I describe below, I will refer to these as the Lyons 2018 red fir-white fir forest plots.

Additional Data Sources

Additional tree mortality data were provided by the Sequoia and Kings Canyon Field Station of the USGS Western Ecological Research Center and incorporated

Table 1. Tree and foliage condition classifications.

Classification	Definition
Tree Condition	
Live	Tree retains any green foliage
Dead – evidence of successful bark beetle attack	Tree retains no green foliage with visible evidence of galleries on the bole
Dead – no evidence of successful bark beetle attack	Tree retains no green foliage with no visible evidence of galleries on the bole
Foliage Condition	
F1	Foliage (e.g. needles or leaves) on less than 1/3rd of the tree
F2	Foliage on more than 1/3rd but less than 2/3rd of the tree
F3	Foliage more than 2/3rd of the tree

study. Data provided by USGS included tree mortality data collected in 2016 in an area

of Sequoia National Park with elevated levels of bark-beetle related tree mortality

(henceforth referred to as USGS 2016 mixed conifer plots; Stephenson et al., 2019). In

addition, data from a sub-set of mixed conifer plots from the Sierra Nevada Forest

Dynamics Plot Network were provided (henceforth referred to as USGS 2018 mixed

conifer plots; Stephenson et al., 2019). These datasets expand upon the red fir-white fir

forest data collected by this study to provide a more complete picture of mortality across

the lower montane forest in Sequoia and Kings Canyon National Parks.

USGS 2016 Mixed Conifer Plots

The USGS 2016 mixed conifer plots total 89 plots located throughout an area of

mixed conifer forest with high levels of bark-beetle related tree mortality along Crystal

Cave Road between 1,535 m and 1,826 m (5,000 and 6,000 ft) elevation (Figure 2). The

plots consisted of 0.10 ha circular sampling plots (17.84 m radius) and were randomly

selected using Generalized Random Tessellation Stratified sampling, which ensures plots

are spatially balanced within the survey area. Within the plots, every standing tree greater

than 1.37 m in height was identified to species and assigned a 5 cm DBH class and

condition (live or dead). Dead trees were also assigned a foliage condition classification

(see Table 1). Trees that were leaning more than 45 degrees or broken below 1.37 m were

considered fallen and were not recorded. In addition, only stems greater than 5 cm in size

were measured for deciduous trees. Plot attributes such as slope and aspect were also

measured in the field.

The field methods did not include as assessment of mortality factors for each tree.

However, for the purposes of this study, all dead trees were assumed to have successful

bark beetle attack due to the high levels of bark beetle related tree mortality documented in this area. In addition, trees that did not retain any foliage (e.g., foliage classification of T1, T2, and T3) were removed from the dataset to be consistent with the field methods used for the Lyons 2018 red fir-white fir forest plots. A small number of trees that were missing data (e.g. foliage classification or DBH) were also removed from the dataset.

USGS 2018 Mixed Conifer Plots

The fifteen USGS 2018 mixed conifer plots analyzed in this study were a sub-set of plots from the Sierra Nevada Forest Dynamics Plot Network, a system of 30 permanent, long-term research plots that are monitored annually to detect changes within different forest communities in Sequoia and Yosemite national parks (Figure 2). The USGS 2018 mixed conifer plots selected for the study were comprised of Ponderosa pine-mixed conifer, white fir-mixed conifer, and giant sequoia (*Sequoiadendron giganteum*)-mixed conifer forest stands in Sequoia National Park. Plots were located between 1,618 m and 2,210 m (5,308 and 7,251 ft) elevation and ranged in size from 0.86 ha to 2.46 ha.

Within the plots, all trees have been mapped, measured, and identified to species, with new in-growths and dead trees recorded on an annual basis. All standing dead trees greater than 1.37 m in height were visually inspected for mortality factors and assigned a foliage condition classification, with the most recent evaluation occurring in 2018 (see Table 1). Mortality factors were determined through visual inspections of dead trees, which included the removal of bark to locate bark beetle galleries. It should be noted that DBH is recorded for trees on 5-year intervals, and therefore was not recorded for all trees in 2018. To be consistent with the field methods used for the Lyons 2018 red fir-white fir

plots, all dead trees that did not retain any foliage (e.g., foliage classification of T1, T2, and T3) and deciduous trees less than 2 cm DBH were removed from the dataset. In addition, a minor number of trees that were missing data (e.g. foliage classification or DBH) were removed from the dataset.

Data Analysis

Tree characteristics related to tree mortality and DBH were derived from the field data for the USGS 2016 mixed conifer, USGS 2018 mixed conifer, and Lyons 2018 red fir-white fir datasets. Mortality classes were assigned to trees based on the field results. Dead trees with evidence of successful bark beetle attack were assigned the integer 1. Live trees and dead trees with no evidence of successful bark beetle attack were assigned the integer 0. For the USGS 2016 mixed conifer dataset, DBH was assigned as the middle of the range from the DBH size classes recorded for each tree (e.g. 2.5 cm for the 0 to 5 cm class, 7.5 cm for the 5 to 10 cm class, etc.).

Quantitative measures of stand conditions such as stand density and species diversity were also derived from the field data. Stand density was calculated using Reineke's stand density index, a standard measure of relative density within a forest stand. To calculate the stand density of the Lyons 2018 red fir-white fir plots, the sample areas were corrected for slope using the mean slope derived from the field data. The USGS 2016 mixed conifer forest plot areas were corrected in the field and the USGS 2018 mixed conifer forest plot areas were derived from GIS and, therefore, did not require slope correction. Simpson's diversity index, a standard measure of proportional abundance, was used to calculate species diversity. In the Lyons 2018 red fir-white fir

dataset, several sub-plots were comprised of 1 individual tree and thus yielded undefined numbers for the diversity index due to having a denominator of 0. These sub-plots were manually assigned a diversity index of 0 to represent no diversity within the sub-plot.

Other metrics related to landscape factors and fire history were calculated from field measurements and GIS using the USGS 30-meter Digital Elevation Model (DEM) and 2017 Fire Return Interval Departure for Sequoia and Kings Canyon National Parks geospatial datasets (Guthrie, 2005; Folger, 2017). The DEM geospatial data were used to determine elevation for all three datasets, as well as aspect and slope for the USGS 2018 mixed conifer dataset and slope for the Lyons 2018 red fir-white fir dataset. Elevation, slope, and aspect were calculated from the center point of each sample area for the smaller USGS 2016 mixed conifer and Lyons 2018 red fir-white fir forest plots, whereas these factors were based on mean values within the larger USGS 2018 mixed conifer forest plots. Aspect was cosine-transformed to determine northing. Time since last fire was calculated by subtracting the last recorded fire year from 2018 for the USGS 2018 mixed conifer plots and Lyons 2018 red fir-white fir plots and from 2016 for the USGS 2016 mixed conifer plots. In some instances, last fire year was assumed to be 1899 where data were missing from the 2017 Fire Return Interval Departure for Sequoia and Kings Canyon National Parks geospatial dataset, consistent with the methods described for determining last fire year in the GIS metadata (Folger, 2017).

Statistical analysis of each dataset was then performed by running mixed effects logistic regression models in the statistical software R, using the glmer function of the lme4 package (R Core Team, 2015). Within the models, mortality of individual trees was the response variable, plot was assigned as a random effect, and the following were

predictor variables: DBH, elevation, aspect, slope, time since last fire, diversity, and

density. The predictor variables were divided by their mean values to put all variables on

a similar scale. The data were then fitted to separate models for white fir and sugar pine.

Models were run on the individual USGS 2016 mixed conifer, USGS 2018 mixed

conifer, and Lyons 2018 red fir-white fir datasets, as well as a combined dataset using all

three sources, to determine if there is a difference in correlations between bark beetle

related mortality and the predictor variables for white fir and sugar pine in each dataset.

Chapter III

Results

Tree mortality factors were evaluated for white fir and sugar pine within the

USGS 2016 mixed conifer, USGS 2018 mixed conifer, and Lyons 2018 red fir-white fir

plots using mixed effects logistic regression models for the combined datasets and each

dataset individually. The USGS 2016 mixed conifer plot dataset consisted of 88 plots,

containing a total of 8,823 trees and encompassing a total of 8.8 ha. The USGS 2018

mixed conifer plot dataset were comprised of 15 plots spanning 21.4 ha with 10,376

trees. The Lyons 2018 red fir-white fir plot dataset contained 72 plots, for a total of 1,211

trees sampled spanning 2.2 ha. Stand characteristics and landscape factors were derived

at the plot-level for individual white fir and sugar pine trees. A summary of the different

variables for the white fir and sugar pine samples are shown in Tables 2 and 3,

respectively, for each dataset.

White Fir Results

A total of 9,013 white fir individuals were sampled across the USGS 2016 mixed

conifer, USGS 2018 mixed conifer, and Lyons 2018 red fir-white fir forest plots. Of the

white firs sampled, a total of 1,266 individuals (14.0%) had mortality attributed to bark

beetles. Individually, mortality levels were highest (22.2%) in the USGS 2016 mixed

conifer plots. Mortality levels in the USGS 2018 mixed conifer plots and Lyons 2018 red

fir-white fir plots ranged respectively from 10.7% to 8.0%. The mixed effects logistic

Table 2. Summary statistics for white fir stand and landscape variables.

Predictor	USGS 2016 Mixed Conifer Plots			USGS 2018 Mixed Conifer Plots			Lyons 2018 Red Fir-White Fir Plots		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
DBH (cm)	2.50	19.42	137.50	0.20	23.04	174.20	0.50	33.65	188.00
Elevation (m)	1,535	1,681	1,826	1,618	2,032	2,210	2,075	2,255	2,476
Aspect (northing)	-0.9998	0.1609	0.9976	-1.0000	-0.6202	0.7915	-1.0000	-0.1772	0.9816
Slope (radians)	0.0873	0.4180	0.7854	0.1334	0.2339	0.3628	0.0381	0.2341	0.4973
Time Since Last Fire (years)	24.00	79.87	117.00	14.00	96.17	119.00	9.00	82.77	119.00
Species Diversity Index	0.2660	0.5599	0.8150	0.0950	0.4539	0.7232	0.0000	0.3458	0.7500
Stand Density Index	167.5	1,322.4	4,422.3	374.7	1,213.8	2,124.1	205.3	1,419.7	3,164.9

The range of the non-adjusted variables analyzed for each dataset in the white fir mixed effects logistic regression models are shown from left to right for the following datasets: USGS 2016 mixed conifer, USGS 2018 mixed conifer, and Lyons 2018 red fir-white fir.

Table 3. Summary statistics for sugar pine stand and landscape variables.

Predictor	USGS 2016 Mixed Conifer Plots			USGS 2018 Mixed Conifer Plots			Lyons 2018 Red Fir-White Fir Plots		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
DBH (cm)	2.50	18.38	172.5	0.30	26.11	171.70	1.00	14.39	54.50
Elevation (m)	1,535	1,703	1,826	1,618	1,889	2,210	2,075	2,153	2,263
Aspect (northing)	-0.99980	-0.06467	0.99760	-1.0000	-0.7364	0.7915	-0.88290	0.08478	0.86600
Slope (radians)	0.0873	0.4724	0.7854	0.1334	0.2271	0.3628	0.0896	0.3294	0.4053
Time Since Last Fire (years)	24.00	79.51	117.00	14.00	91.12	119.00	17.00	47.26	119.00
Species Diversity Index	0.2660	0.6649	0.8150	0.0950	0.5747	0.7232	0.0000	0.1678	0.7500
Stand Density Index	167.5	1,197.2	4,422.3	374.7	1,063.6	2,124.1	38.81	389.03	1,647.17

The range of the non-adjusted variables analyzed for each dataset in the sugar pine mixed effects logistic regression models are shown from left to right for the following datasets: USGS 2016 mixed conifer, USGS 2018 mixed conifer, and Lyons 2018 red fir-white fir.

regression models indicated significant correlations between bark beetle related mortality of white firs and several factors, including DBH, elevation, time since last fire, and species diversity, though results varied between the models for the combined and individual datasets.

In the mixed effects logistic regression model for the combined dataset, bark beetle related white fir mortality showed a negative correlation with DBH and elevation and a positive correlation with time since last fire (Table 4). As shown on Figure 3, the probability of mortality decreased from approximately 20% to almost 0% as elevation increases from 1,600 m 2,400 m on sites with 100 years since the last fire across the full range of DBH. When analyzing the datasets in the separate mixed effects logistic regression models, bark beetle related white fir mortality continued to show a strong negative correlation with DBH throughout all of the datasets (Table 5). A significant positive correlation was also shown between bark beetle related white fir mortality and time since last fire in the USGS 2018 mixed conifer model and Lyons 2018 red fir-white fir model (Table 5). Species diversity also had a negative relationship with bark beetle related white fir mortality in the USGS 2016 mixed conifer model (Table 5). No significant correlation with elevation was found in any of the individual datasets.

It should be noted that the random effects for the USGS 2016 mixed conifer, Lyons 2018 red fir-white fir, and combined datasets had relatively high variance (1.218, 5.184, and 1.622, respectively) and standard deviation (1.104, 2.277, and 1.274, respectively). In comparison, the USGS 2018 mixed conifer data had relatively low variance (0.1717) and standard deviation (0.4143).

Table 4. Mixed effects logistic regression model results for the combined dataset.

Predictor	White Fir – Combined Datasets			Sugar Pine – Combined Datasets		
	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)
Intercept	1.25705	1.69306	0.457802	-2.84056	2.87447	0.32305
DBH	-0.27329	0.03714	1.85e-13***	0.56246	0.06033	< 2e-16***
Elevation	-4.26297	1.28232	0.000886***	-1.02772	2.16624	0.63520
Aspect	-0.01123	0.07755	0.884862	-0.02221	0.13565	0.86995
Slope	0.05869	0.29846	0.844112	1.19632	0.40625	0.00323**
Time Since Last Fire	0.76648	0.28896	0.007988**	-0.12120	0.35862	0.73540
Species Diversity Index	0.03111	0.46085	0.946177	0.46481	0.87922	0.59704
Stand Density Index	0.19713	0.28783	0.493422	0.06109	0.34996	0.86142

Symbols correspond to the following significance levels: *** = $p<0.001$, **=$p<0.01$, *=$p<0.05$, and .=$p<0$.
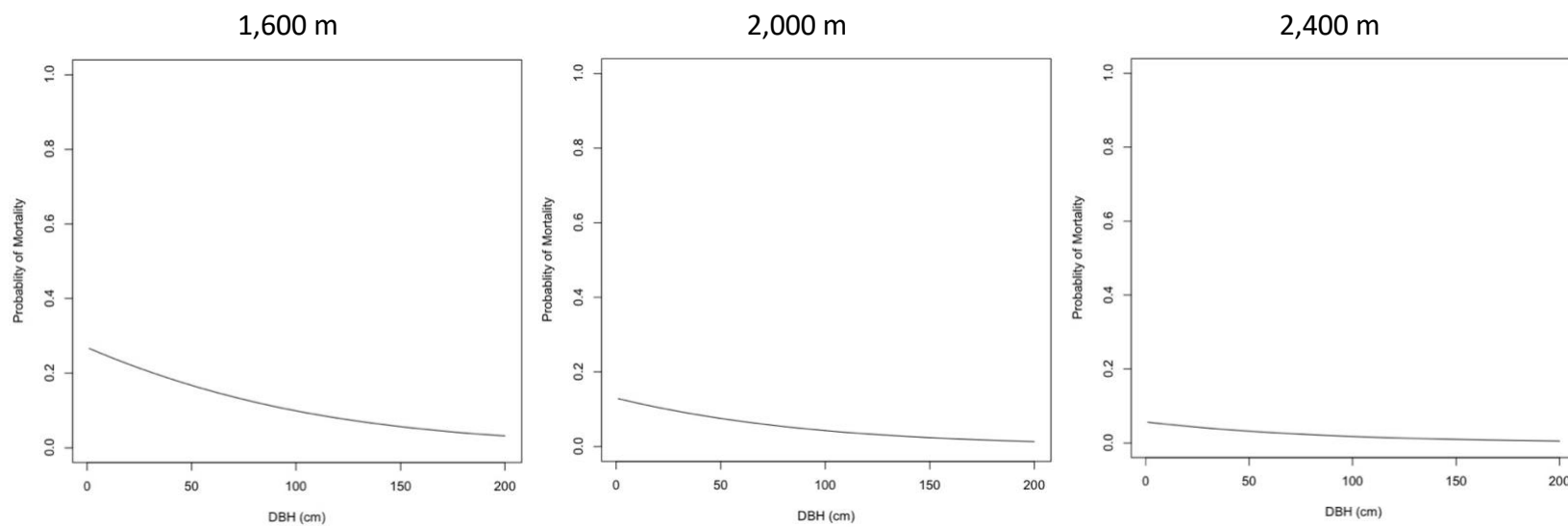
Figure 3. The effect of elevation and DBH on white fir mortality.

Table 5. White fir mixed effects logistic regression model results for the three individual datasets.

Predictor	USGS 2016 Mixed Conifer Plots			USGS 2018 Mixed Conifer Plots			Lyons 2018 Red Fir-White Fir Plots		
	Estimate	Std. Error	Pr(>|z|)	Estimate	Std. Error	Pr(>|z|)	Estimate	Std. Error	Pr(>|z|)
Intercept	4.010459	3.937589	0.30844	-2.98828	3.55311	0.400	-14.647716	10.902589	0.17911
DBH	-0.143384	0.055278	0.00949**	-0.28445	0.04802	3.10e-09***	-1.417857	0.431170	0.00101**
Elevation	-4.851702	3.757868	0.19668	-2.30325	2.39727	0.337	8.237464	10.270503	0.42252
Aspect	-0.005284	0.041556	0.89882	-0.27848	0.21754	0.200	0.003763	0.150130	0.98000
Slope	0.582747	0.476893	0.22172	0.77133	0.66655	0.247	-0.613357	1.430605	0.66811
Time Since Last Fire	-0.041764	0.332806	0.90014	1.81496	0.33496	0.01e-08***	1.969255	0.994920	0.04778*
Species Diversity Index	-1.729213	0.775386	0.02574*	0.89709	0.62368	0.150	1.266183	0.910939	0.16454
Stand Density Index	0.695266	0.395547	0.07879.	0.03263	0.32313	0.920	0.528579	1.000611	0.59732

Symbols correspond to the following significance levels: *** = p<0.001, **=p<0.01, *=p<0.05, and .=p<0.

Sugar Pine

A total of 1,203 sugar pine individuals were sampled across the USGS 2016 mixed conifer, USGS 2018 mixed conifer, and Lyons 2018 red fir-white fir forest plots. Of the sugar pines sampled, a total of 244 individuals (20.3%) had mortality attributed to bark beetles. Mortality was highest (30.8%) in the USGS 2016 mixed conifer plots. Elevated mortality levels were also exhibited in the USGS 2018 mixed conifer plots and Lyons 2018 red fir-white fir plots, ranging respectively from 13.6% to 15.8%. The mixed effects logistic regression models exhibited significant correlations between bark beetle related mortality of sugar pines and several factors, including DBH and slope, though results varied between the combined and individual models.

In the mixed effects logistic regression model for the combined dataset, bark beetle related sugar pine showed a positive correlation with DBH and slope (Table 4). As shown on Figure 4, the probability of mortality increased approximately 40% for smaller size sugar pines as slope increases from 0.10 to 0.40 to 0.70 radians. That is, the probability of mortality is greatest on steeper slopes, particularly for trees in the smaller size classes. When analyzing the datasets in separate mixed effects logistic regression models, bark beetle related sugar pine mortality continued to show a strong positive correlation with DBH in both the USGS 2016 mixed conifer and USGS 2018 mixed conifer models (Table 6). A positive correlation between bark beetle related mortality in sugar pines and slope was also exhibited in the USGS 2016 mixed conifer model (Table 6). The Lyons 2018 red fir-white fir dataset did not have an adequate number of samples to run an individual model due to the number of predictors being analyzed.
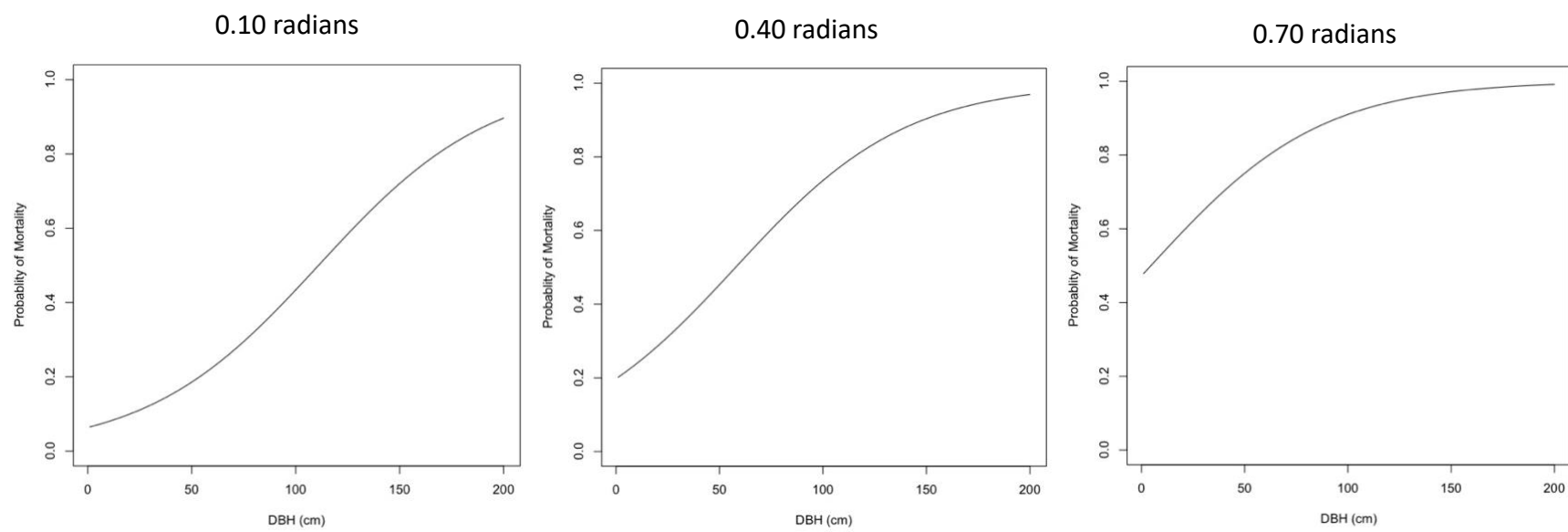
Figure 4. The effect of slope and DBH on sugar pine mortality.

Table 6. Sugar pine mixed effects logistic regression model results for the three individual datasets.

Predictor	USGS 2016 Mixed Conifer Plots			USGS 2018 Mixed Conifer Plots		
	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)
Intercept	2.643382	5.235585	0.61364	-8.36199	7.91668	0.2909
DBH	0.752834	0.117633	1.56e-10***	0.49784	0.07886	2.74e-10***
Elevation	-7.357902	4.981105	0.13963	1.67832	4.98350	0.7363
Aspect	0.003437	0.023382	0.88313	0.04033	0.58675	0.9452
Slope	1.947419	0.748698	0.00929**	2.39753	1.31680	0.0686
Time Since Last Fire	-0.533980	0.455532	0.24111	0.83043	0.67492	0.2185
Species Diversity Index	1.725131	1.435498	0.22945	-0.05336	1.67580	0.9746
Stand Density Index	-0.390050	0.457939	0.39435	0.57933	0.65633	0.3774

Symbols correspond to the following significance levels: *** = $p<0.001$, **=$p<0.01$, *=$p<0.05$, and .=$p<0$.

It should be noted that the random effects for the USGS 2016 mixed conifer and combined datasets had relatively high variance (1.054 and 1.085, respectively) and standard deviation (1.027 and 1.041, respectively). The USGS 2018 mixed conifer data had a relatively lower variance (0.6496) and standard deviation (0.806).

Chapter IV

Discussion

The results suggest a diverse set of factors influenced bark beetle related mortality in sugar pines and white firs in the southern Sierra Nevada. For white firs, the results indicate that beetle related mortality had a higher probability of occurring in smaller diameter trees on lower elevational sites that have experienced longer burn intervals. Species diversity may also play a role in white fir mortality. For sugar pine, the results indicate that bark beetle related mortality had a higher probability in larger diameter trees on sites with steep slopes.

Tree Size

The datasets indicate a strong correlation between DBH and bark beetle related tree mortality in both white fir and sugar pine. In white fir, a negative correlation between DBH and bark beetle related mortality was exhibited across all four datasets analyzed (Tables 4 & 5). However, a positive correlation between bark beetle related mortality and DBH was also exhibited in sugar pines across all three datasets analyzed (Tables 4 & 6). In comparison, the effects of DBH on bark beetle related mortality was markedly stronger in sugar pines than in white fir.

The combined model results indicate an inverse relationship between bark beetle related mortality and tree size in white firs, meaning probability of mortality increased as white fir diameter decreased. While these results suggest that smaller sized white firs are most vulnerable to successful bark beetle attack, only a modest increase was seen in

43

mortality levels in the smaller size classes when compared to the larger size classes. Within all of the white firs, bark beetle related mortality totaled 14.3% in the 0 to 10 cm DBH class, 19.3% in the 10 to 20 cm DBH class, 15.7% in the 20 to 30 cm DBH class, 11.4% in the 30 to 50 cm DBH class, and 7.8% in the greater than 50 cm DBH class. This is likely an effect of mixed responses to three bark beetle species that were noted during surveys: fir engraver*, Scolytus praeceps,* and *Scolytus subscaber.* (Note: *Scolytus pracetus* and *Scolytus subscaber* do not have common names). Fir engraver is known for killing larger, less-vigorous trees, while *Scolytus praeceps* and *Scolytus subscaber* are known for killing smaller, suppressed trees (Stephenson et al., 2019; Estes & Bulaon, 2016). While all three species are considered "secondary" bark beetles that tend to kill suppressed trees, fir engraver is known for undergoing outbreaks during drought and is associated with significant amounts of tree mortality in the Sierra Nevada (Stephenson et al., 2019; USDA, 2012a; California Forest Pest Council, 2017; California Forest Pest Council, 2016). However, the increased probability of mortality in smaller tree sizes may indicate that the less aggressive *Scolytus praeceps* and *Scolytus subscaber* have also undergone outbreak conditions and are playing a more significant role in the current mortality event in the Sierra Nevada.

While *Scolytus praeceps* primarily occurred in smaller size classes in the USGS 2018 mixed conifer plots, *Scolytus praeceps* was also noted in the USGS 2018 mixed conifer plots in medium to large DBH white firs. This is an interesting observation because *Scolytus praeceps* is believed to preferentially select stems less than 4 cm DBH (Estes & Bulaon, 2016). *Scolytus praeceps* was noted occurring singularly as well as co-occurring with fir engraver in numerous white firs between 10 and 30 cm DBH. Several

larger diameter white firs (95.9 cm, 42.1 cm, and 36.4 cm DBH) were also noted as containing both *Scolytus praeceps* and fir engraver. Though few studies examine the behavior of *Scolytus praeceps* during background conditions, the occurrence of *Scolytus praeceps* in these larger size classes may indicate that the species exhibits broader size class preferences under outbreak conditions. In addition, weakened tree defenses from prolonged drought may also allow for *Scolytus praeceps* to successfully colonize size classes that would not be overcome during background conditions.

In contrast to the white fir results, the combined model results for sugar pine indicate a strong positive correlation between bark beetle related mortality and tree size, meaning that probability of mortality increased with increasing tree size. Sugar pines above 20 cm DBH in size had 41.1% mortality overall, with successful attacks occurring in sugar pines of up to 172.5 cm DBH. Sugar pines in smaller size classes had distinctly lower mortality rates, with 22.3% mortality in the 10 and 20 cm DBH size class and 8.7% in the 0 and 10 cm DBH size class. This result is not surprising as mountain pine beetle, which was anecdotally noted in many of the deceased trees and is the primary beetle associated with pine mortality in the southern Sierra Nevada, has been documented to preferentially select for larger size class trees under epidemic conditions (Cole & Amman, 1969). A study of lodgepole pines indicated that larger diameter trees were infested and killed first during a mountain pine beetle epidemic in Wyoming, with 87% mortality in trees greater than 40 cm DBH (Cole & Amman, 1969). However, mountain pine beetle attacks have been noted in medium size classes (e.g. 20 to 30 cm) in other species such as Ponderosa pines and in lodgepole pines to a lesser degree (Gibson, Kegley, and Bentz, 2009; Cole & Amman, 1969). Limited data exists regarding mountain

pine beetle's interaction with sugar pines; however, the data suggests that the mountain pine beetle's size class preferences in sugar pines may be similar to those exhibited in Ponderosa and lodgepole pine. Notably, red turpentine beetle (*Dendroctonus valens*) was also indicated anecdotally as co-occurring with mountain pine beetle in many of the deceased sugar pines; however, this pest is generally not considered to be an aggressive bark beetle species and therefore is not typically considered a direct cause of mortality.

Furthermore, it should also be noted that bark beetle related tree mortality may be underestimated in the USGS 2018 mixed conifer and Lyons 2018 red fir-white fir models. While the upper portions of trees were inspected for galleries, pitch tubes, and other bark beetle signs using binoculars, bark removal to confirm the presence of beetle galleries could only occur at heights of approximately 6 feet or lower. Resource partitioning amongst bark beetle species and pests such as wood borers could limit detection of some beetle species on the bole (Estes & Bulaon, 2016; Paine, Birch, and Svihra, 1981; Beverly Bulaon, personal communication, August 23, 2018). In addition, some bark beetle species in the Sierra Nevada such as *Scolytus subscaber, Scolytus praeceps,* pine engraver, and California five-spined ips are known to attack the tops of firs and pines and thus may not have been detected in larger, taller trees (Estes & Bulaon, 2016; Schultz & Bedard, 1987; Kegley, Livingston, & Gibson, 1997). While fir engravers can attack firs in their entirety, they are also known to only attack the tree crown in some instances, resulting in top-kill (Randall, 2006). Mountain pine beetles generally infest the lower 15 feet of trees initially; however, this species has also been documented attacking the crowns of larger sugar pines in the initial stage of attacks (Gibson et al., 2009). Thus,

bark beetle related tree mortality may be under-estimated in the USGS 2018 mixed

conifer and Lyons 2018 red fir-white fir datasets, particularly in larger, taller trees.

Elevation

The combined results indicate that white firs are also more vulnerable to bark

beetle related mortality on lower elevational sites. High levels of white fir mortality were

noted at lower elevations, with 26.5% of the white firs under 1,600 m elevation

experiencing beetle related mortality. Similar results were shown from 1,600 to 1,800 m

and 1,800 m to 2,000 m with 20.0% and 21.3% white fir mortality, respectively.

However, mortality levelled off at higher elevations with 8.0% white fir mortality

between 2,000 and 2,200 m and 11.3% mortality above 2,200 m. Tree mortality at lower

elevations in the Sierra Nevada has been well-documented via studies relying on aerial

imagery. An aerial survey of the Sierra Nevada showed that over half of the total

mortality occurred in the mid-elevation zone between 1,000 and 2,000 meters (Potter,

2017). Similarly, a study of the Sequoia National Park showed that elevation had the

highest relative importance in predicting tree mortality (Paz-Kagan et al., 2017).

However, these studies did not distinguish between mortality related to bark beetles and

other factors such as drought stress, mistletoe infestation, and fire, and also did not

account for spatial variability in density between elevations. However, the results of this

study indicate that elevation similarly plays a role in bark beetle related mortality in white

firs, given the prevalence of bark beetle related mortality throughout the lower elevations.

This is likely due to lower elevations being associated with higher temperatures, higher

evaporative demand, reduced snowpack, and earlier snowmelt, further compounding the

effects of prolonged drought in trees and resulting in a reduced resiliency to bark beetle attack (Trujillo et al., 2012; Stephenson et al., 2018).

However, it is notable that the correlation between bark beetle related mortality in white firs and elevation only occurs in the combined model and does not appear in any of the individual models. Elevations ranged between the datasets, with elevations of less than 1,600 m occurring only in the USGS 2016 mixed conifer dataset and elevations greater than 2,200 m occurring only in the Lyons 2018 red fir-white fir dataset. Thus, it is possible that the entire landscape of the lower montane zone must be looked at to see a significant elevational pattern in bark beetle related mortality. However, this interpretation is given with caution, as it is possible that this may also be an effect of combining different size plots with varying sample sizes.

While elevation had a significant correlation with bark beetle related tree mortality in white firs, this correlation was not noted in sugar pine. It is possible that the effects of landscape characteristics may be different between these tree species due to differences in host preferences exhibited by fir engraver, *Scolytus subscaber*, and *Scolytus praeceps* in white fir and mountain pine beetle in sugar pine. Fir engraver*, Scolytus praeceps,* and *Scolytus subscaber* are "secondary" pests that are known to attack firs that have been compromised (Stephenson et al., 2019; Estes & Bulaon, 2016). However, mountain pine beetle is considered a "primary" pest due to its ability to overcome trees through pheromone-mediated mass attacks and is known to attack healthy trees, particularly under outbreak conditions (Gaylord, 2014). Thus, this ability of primary pests to attack healthy stands may dampen any elevational effect. However, the results suggest that the effects of landscape characteristics may play a stronger role in

host selection for secondary pests such as fir engraver, *Scolytus subscaber,* and *Scolytus praeceps.*

Time Since Last Fire

Time since last fire had a negative correlation with white fir, meaning the probability of white fir mortality was lower on sites that had burned recently. Only 1.9% of white firs on sites that had burned in the previous 25 years experienced bark beetle related tree mortality. In stands that hadn't burned in over 25 years, bark beetle related mortality increased to 16.2%. Correlations between white fir mortality and time since last fire were noted in the mixed effects regression models for the combined dataset, as well as the USGS 2018 mixed conifer and Lyons 2018 red fir-white fir datasets. A correlation was not noted the USGS 2016 mixed conifer model, which can be attributed to a lack of sites with recent burn history (less than 25 years).

Frequent low-intensity, stand modifying fires are commonly cited as improving resiliency of trees to bark beetle attack by reducing stand densities (Bentz et al., 2009; Gaylord, 2014; Fettig et al., 2007). However, in this study, stand density was not significantly related to bark beetle related tree mortality in any of the models. It is possible that the beneficial effect of fire shown in the white fir models could be related to other mechanisms, such as stand health and oleoresin production. It is probable that recent fire events would result in the mortality of more chronically stressed trees, leaving a more healthy, resilient population. In addition, increased oleoresin production has been noted in Ponderosa pine stands that have undergone burn treatments for up to seven years (Gaylord, 2017), and could potentially have a longer lasting effect in firs.

A correlation between time since last fire and bark beetle related mortality in sugar pine was not noted in any of the models, despite the beneficial effects of fire in oleoresin production in pines. Again, this discrepancy could potentially be a function of primary and secondary pest host preferences. Potential beneficial effects of fire related to stand health and oleoresin production may have a greater role in deterring secondary pests such as fir engraver, *Scolytus praeceps,* and *Scolytus subscaber* than primary pests that are able to overcome healthy trees such as mountain pine beetle. However, caution should be used in interpreting these results due to potential inaccuracies in the GIS data. The time since last fire dataset is based on historic fire records and fire history reconstructions, and thus may not be accurate at the plot level (Folger, 2017).

Slope

For sugar pine, there was also a positive correlation between slope and bark beetle related tree mortality in both the combined and USGS 2016 mixed conifer models, indicating that probability of mortality increased as slope increased. This could be due to the relationship of slope with water availability, with shallower slopes having higher water retention and subsurface flows and steeper slopes being subject to more runoff and having less available water (Stephenson et al., 2018; Paz-Kagan et al., 2017). This interpretation is also consistent with existing research related to giant sequoia dieback in Sequoia and Kings Canyon National Parks, which was positively correlated with slope steepness during the 2014 drought year (Stephenson et al., 2018).

However, as shown on Figure 4, the effect of slope appears to occur primarily in smaller sugar pines. It is possible that the effect of landscape factors such as slope may be more significant in mediating mortality in smaller sugar pines. The absence of the slope

correlation from the USGS 2018 mixed conifer dataset could indicate that slope played a

larger role at earlier stages in the outbreak (e.g. 2016), when mountain pine beetle would

have been more likely to attack smaller, stressed trees. However, mortality factors were

assumed for the USGS 2016 mixed conifer dataset, so it is also possible that a different

agent is responsible for mortality within this subset of trees, such as weevil (*Pissodes*

schwarzii) which was known to be attacking and killing small, drought stressed sugar

pines in the region (A. Das, personal communication, February 19, 2019).

Furthermore, no significant correlation between slope and bark beetle related tree

mortality was exhibited in white firs in any of the datasets. It seems likely that the effects

of elevation on water availability plays the most significant role in mediating drought

stress in white firs. In a study of overall tree mortality in Sequoia National Park, it was

found that elevation and distance to water were the most significant factors in predicting

tree mortality (Paz-Kagan et al., 2017). It was also found that slope had a modest inverse

effect on overall tree mortality, meaning probability of mortality was higher on flatter

slopes, though to a much lesser degree (Paz-Kagan et al., 2017). These results suggest

that soil water availability is a key determinant in tree mortality, and that elevation plays

a greater role than slope in mediating mortality during drought.

Species Diversity

Species diversity had a significant negative correlation with bark beetle related

white fir mortality in the USGS 2016 mixed conifer dataset but was not a significant

predictor in any of the other datasets for white fir or sugar pine. The results support a

previous study of bark beetle demography in the Sierra Nevada, which showed that low

species diversity and prevalence of hosts were correlated with bark beetle attacks in white

fir (Walker et al., 2015) It is possible that the role of species diversity, as well as host prevalence, may be particularly important in facilitating secondary pests such as fir engraver, *Scolytus subscaber,* and *Scolytus praeceps* in locating and attacking firs, particularly since no chemical attractants such as pheromones are known to assist with mass attacks in this genus. Conversely, in primary pests such as mountain pine beetle, it is possible that species diversity plays a more limited role in facilitating bark beetle attacks as these species are able to produce aggregation pheromones. However, sugar pines were a less dominant component of the forest types sampled than white fir, so it is also possible that the study didn't have a wide enough range of pine abundance to show an effect of species diversity on sugar pine mortality,

In addition, variability amongst the white fir models may be attributed to the different scales used when calculating species diversity in the different datasets. Species diversity was calculated at the plot-level, which ranged in size from 0.10 ha in the USGS 2016 mixed conifer plots, between 0.86 and 2.46 ha for the USGS 2018 mixed conifer plots, and 0.03 ha for the Lyons 2018 red fir-white fir plots. Though 0.10 ha may indicate a scale at which species diversity plays a role in host susceptibility to species in the *Scolytus* genus, these results must be interpreted with caution at the landscape level.

Random Effects

For both white fir and sugar pine, all of the models except for the USGS 2018 mixed conifer model had relatively high variance and standard deviation for the random effects, meaning that much of the variability in the data unexplained by the predictor variables may be attributed to plot location. That is, there is spatial variability in mortality that is driven by factors not incorporated into the model. This may be driven by bark

beetle population dynamics outside the effect of host trees. In addition, other stand characteristics or landscape factors could explain some of the variability in the data, including metrics related to competitive pressure and/or soil type, which influences moisture availability.

<center>Predictors Found Not to be Significant</center>

Two predictors were not found to be significant in any of the models: stand density and aspect. In sugar pines, the study results show that tree size is the greatest predictor for mortality and that slope may also be a predictor for smaller trees. Based on these results, it appears that factors which influence competition and tree health may be less important for sugar pine mortality, which is plausible as mountain pine beetle is able to kill healthy trees during an outbreak. However, for white firs, the study results suggest that competition and tree health does play a role in bark beetle related tree mortality, which is supported by evidence that species in the genus *Scolytus* favor compromised trees. The study results also show a strong correlation with tree size, as well as other factors that influence tree health and heterogeneity such as time since last fire, elevation, and species diversity. It is possible that these factors are more important in mediating bark beetle related tree mortality than stand density and aspect, particularly during outbreak conditions.

The lack of effect from stand density is particularly surprising, due to an extensive number of studies citing stand density as having a positive correlation with mountain pine beetle related tree mortality in Ponderosa pines at both the tree and stand-level (Hayes et al., 2009; Negron & Popp, 2009; Negron et al., 2007; Negron et al., 2017). However, Negron et al. (2017) noted extensive mortality (61%) of Ponderosa pine in a 130-acre

stand that had undergone thinning treatments to reduce stand density. The study indicated

that with sufficient beetle pressure, thinning treatments may be ineffective for bark beetle

management (Negron et al., 2017). Thus, it is possible that outbreak conditions in the

Sierra Nevada have resulted in sufficient pressure to dampen the effect of stand density.

However, to evaluate the effects of stand density on bark beetle related tree

mortality, this study used Reineke's stand density index, which is a standard forestry

measure of relative density within a forest stand. Other measures related to individual

competition pressure may better capture the effects of stand density on bark beetle related

mortality at the tree level. In addition, different scales were used when calculating stand

density due to inherent differences in the datasets from the data collection methods (e.g.

plot size), which may have affected the outcome. Given the strong evidence that stand

density correlates with bark beetle related tree mortality, further research is recommended

to evaluate the effects of stand density on bark beetle related tree mortality in white fir

and sugar pine in the Sierra Nevada.

Research Limitations

While combining the data from USGS 2016 mixed conifer, 2016 USGS mixed

conifer, and Lyons 2018 red fir-white fir plots broadens the scope of this research and

increases the overall sample size, there are research limitations related to this approach.

While each dataset utilized similar data collection methods, the field methods used to

quantify bark beetle related mortality varied between the 2016 and 2018 datasets. Field

methods to identify bark beetle related mortality were limited to observation of visual

signs of infestation (e.g. galleries) in both the USGS 2018 mixed conifer and Lyons 2018

red fir-white fir plots, which may result in underestimates for trees with bark beetle

attacks higher on the crown due to species preferences or resource partitioning. Conversely, this study assumes bark beetles as a mortality factor for all dead trees within the 2016 mixed conifer plots due to the high levels on bark beetle infestation recorded, which may result in an overestimate. In addition, the number of samples and plot sizes varied between each dataset, which may result in high variance when combining the datasets. To rectify these inconsistencies, this study ran mixed effect models for both the combined and individual datasets and noted any differences between them.

It should also be noted that while the USGS 2016 mixed conifer and Lyons 2018 red fir-white fir plots utilized randomized sampling approaches appropriate for making inferences at the landscape-level, the USGS 2018 mixed conifer plots were not randomly selected. The USGS 2018 mixed conifer plots are from the Sierra Nevada Forest Dynamics Plot Network, which is a compilation of long-term monitoring plots that were chosen decades earlier for accessibility and species composition (Stephenson et al., 2019). Though randomized, the Lyons 2018 red fir-white fir plots were also selected from a restricted area to ensure accessibility, which may have had an effect on sampling. Though the combined datasets were generally stratified throughout the forest types analyzed, caution should be used in making landscape-level inferences due to the sampling approaches.

Research limitations may additionally result from the data sources utilized for landscape factors. This study relies on existing GIS data for slope, aspect, elevation, and time since last fire in some instances, which may vary in the level of precision. Slope, elevation, and aspect are based on 10-meter digital elevation models which are considered relatively precise but may result in minor errors at the plot level. In addition,

the time since last fire data were derived from the NPS Fire Return Interval geospatial dataset, which is based on fire history records and reconstructions for different vegetation communities (Folger, 2017). Thus, the fire history may have some inaccuracies, particularly along vegetation community edges. In addition, 1899 was used as the last burn date in the instance where the fire history is unknown and may not account for smaller fires (Folger, 2017). In addition, stand conditions such as species diversity and stand density index were calculated at different scales between the three datasets due to differences in plot size, which may have affected the outcomes for these predictors.

Questions for Future Research

While this study sought to explore the relationship of a broad array of tree characteristics, stand conditions, and landscape factors with bark beetle related tree mortality, forests are complex ecological systems and there may be other dynamics that influence bark beetle outbreaks outside the scope of this study. Many opportunities exist for future research related to other factors potentially influencing tree mortality related to bark beetles, as well as more comprehensive datasets of the predictors analyzed in this study.

Soils may be an additional landscape factor that have potential to influence drought stress and, thus, bark beetle related mortality in trees. In a study of drought-related tree mortality (including bark beetle related tree mortality) in the Sierra Nevada, it was found that probability of mortality increased with rock cover, which was used as a proxy for soil depth (Paz-Kagan et al., 2017). Soils are also characterized by available water capacity, which is a measurement indicating the maximum amount of water a soil can make available to plants and is based on soil texture, amount of rock fragments, and

soil depth and layers (USDA, 2008). In general, finer textured soils with low rock fragments and deeper soils have higher field capacities and hold more water (USDA, 2008). Soils with low available water capacity may further compound the effects of drought and thus may have the potential to influence bark beetle related tree mortality. At the time of the study, comprehensive soils mapping for Sequoia and Kings Canyon National Park was in process by the National Park Service but had not been completed, thus this factor was not included in the models for this study.

Time since last fire yielded a positive correlation with bark beetle associated white fir mortality in some of the models; however, this metric doesn't distinguish the intensity of the previous fire. Fire damage sustained to the tree crown can reduce the flow of oleoresin and may increase the likelihood of bark beetle attacks, whereas low intensity fires may improve oleoresin production and reduce susceptibility to bark beetle attacks (Gaylord, 2014). Further study related to fire intensity in recent fires may provide additional information regarding the relationship of bark beetle related tree mortality and fire in the Sierra Nevada.

Competition is known to play a substantial role in Sierra Nevada forest dynamics, with a complex relationship between effective neighborhood size, tree size, neighbor distance and size, and the competitive interaction between species (Das, 2012). Metrics that capture individual competition pressure may better represent the effects of stand density on bark beetle related tree mortality at the tree level such as the Hegyi Index or Crown Position Index. The Hegyi Index is an index of competition based on DBH and distance between trees (O'Neal, Houston, Buckner, & Meadows, n.d.). The Crown Position Index is an index of competition based on mean crown radius, height, and

distance between trees (O'Neal at al., n.d.). Not only would these indices represent competition at the individual tree level, they may also capture spatial dynamics related to bark beetles. Distance between trees may affect bark beetles' ability to locate suitable hosts and, in the case of primary beetle species, attract other beetles for mass attacks using pheromones. In addition, bark beetle species such as mountain pine beetle are known to result in group kills, killing multiple trees in close proximity to each other (USDA, 2012b). Further research regarding competition and spatial dynamics may be key to understanding bark beetle behavior and host susceptibility.

Conclusions

While this analysis is limited to white fir and sugar pine in Sequoia and Kings Canyon National Parks, the results further our understanding of bark beetle epidemiology and tree mortality factors in the southern Sierra Nevada mountain range of California. Understanding these drivers are key not only to identify which forest stands are most susceptible to future bark beetle attacks, but also to determine if any conditions can be managed to reduce the risk of tree mortality. The results suggest that bark beetle related mortality in white firs may be associated with a broad range of tree characteristics, stand conditions, and landscape factors that influence tree health and resiliency to attack; whereas mortality in sugar pine is more narrowly related to host preferences (e.g. tree size) with only a marginal effect from landscape characteristics. Based on these results, it appears that current management recommendations to improve forest health and resiliency to bark beetle attacks through prescribed fire and mechanical thinning may be most effective in stands of trees dominated by species such as white firs that are targeted by "secondary" pests, which generally attack stressed trees. However, given the strong

evidence from other studies which indicate that mountain pine beetle attacks correlate

with stand density, further research is needed regarding the efficacy of these management

methods in bark beetle management and prevention for both white fir and sugar pine.

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