Big Fires, Big Trees, and Big Plots: Enhancing our Ecological Understanding of Fire With Unprecedented Field Data

Tucker J. Furniss
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BIG FIRES, BIG TREES, AND BIG PLOTS: ENHANCING OUR ECOLOGICAL UNDERSTANDING OF FIRE WITH UNPRECEDENTED FIELD DATA

by

Tucker J. Furniss

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

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2021
ABSTRACT

Big Fires, Big Trees, and Big Plots: Enhancing our Ecological Understanding of Fire with Unprecedented Field Data

by

Tucker J. Furniss, Doctor of Philosophy

Utah State University, 2021

Major Professor: Dr. James A. Lutz
Department: Wildland Resources

Fire is foundational to western forest ecosystems, and managers are increasingly relying on wildfire to restore resilience to fire-prone forests. In this dissertation, I produced research that will help guide difficult management decisions, facilitate the use of wildfire as a restoration tool, and support science-based wildland fire policy.

In Chapter II, I evaluate the performance of post-fire tree mortality models, a vital tool used by land managers to predict mortality and model fire effects. I employed a dataset comprising 34,174 individual trees, the most comprehensive model validation yet conducted with a consistent dataset. Mortality was under-predicted for conifers, especially for large-diameter trees. I demonstrate ways to enhance the accuracy of mortality models and to reduce spatially autocorrelated error.

In Chapter III, I evaluate satellite-derived severity indices, a ubiquitous method of quantifying broad scale patterns in fire severity. Using individual-tree-level mortality measurements, I found that there was a great deal of unexplained variance contained within severity maps, especially at intermediate severity levels. I suggest ways to account
for uncertainty that facilitate a more ecologically accurate interpretation of severity maps.

In Chapter IV, I explore the spatial elements of fire and background mortality. I reviewed the literature regarding the spatial structuring of tree mortality, and developed a conceptual framework describing the spatio-temporal scales of tree mortality. I then characterized the rates, causes, and spatial pattern of mortality annually before, immediately after, and for five years following fire. Direct fire damage caused the greatest number of mortalities, but the more enduring effects of fire on large-diameter trees emerged over the years following fire.

In Chapter V, I combined two longitudinal datasets in a post-hoc factorial design to disentangle the complex interactions between fire, bark beetles, climate, and crowding. I found that climate was an important determinant of fire severity, but local tree neighborhood was a more important factor. Fire reduced drought-related mortality, but only for a brief window 7-15 years post-fire. This study provides a more mechanistic understanding of the interactions between forest disturbances, and it reveals ways to bolster resilience to fire, insects, and climate change.

This dissertation represents the first collection of fire ecology research to emerge from a single, exhaustively sampled, longitudinal monitoring plot. The unique perspectives conferred by this dataset exposed many insightful contrasts with previous research, demonstrating great potential for large-scale observational science to make important contributions to the fields of fire science and forest ecology.

(293 pages)
PUBLIC ABSTRACT

Big fires, big trees, and big plots: Enhancing our ecological understanding of fire with unprecedented field data

Tucker J. Furniss

Wildfire is an inexorable process in western landscapes, posing a major challenge to land managers: how can we use fire to restore healthy forests without jeopardizing human communities? The purpose of this dissertation is to produce research that will help guide management and support effective wildland fire use in fire-prone forests.

I utilized a longitudinal dataset from a single, large forest plot that burned under serendipitous circumstances during the 2013 Rim Fire. My research revealed that post-fire mortality models under-predict mortality of large trees, and may need to be re-calibrated to perform well under future climates. I used satellite-derived data to estimate fire severity, and found that while severity maps may be accurate at broad scales, they failed to capture fine-scale patterns in fire effects. I examined the spatial elements of fire-related mortality, and demonstrate that beetles, pathogens, and inter-tree competition mediated fire effects and provoked complex, spatially structured mortality for years following fire. Finally, I disentangled the interactive effects of fire, beetles, and drought to provide a more mechanistic understanding of compound disturbance dynamics.

This represents the first collection of fire ecology research to emerge from a single, exhaustively sampled, longitudinal monitoring plot. This dissertation not only enhances our ecological understanding of fire, it demonstrates the profound potential for large-scale observational research to contribute novel perspectives to the field of fire science.
For the big trees – our Old Ones
   May they endure us.

   And for those willing
   to listen to their silence.
ACKNOWLEDGMENTS

I sincerely thank those who advocate for the conservation of old-growth forests in the Sierra Nevada, Yosemite resource managers for stewarding our public lands and restoring fire to the park, and the Rockefellers who protected the forest surrounding the YFDP from being logged in the 1930s. This research would not have been possible without their efforts to conserve these magnificent forests. Nor would it have been possible without financial support provided by the Joint Fire Science Program, National Park Service, USU Ecology Center, and the Utah Agricultural Extension Station.

The establishment and maintenance of permanent plots requires an immense amount of effort, and I am grateful to all those who have contributed their time, effort, and expertise to the Yosemite Forest Dynamics Plot. In particular, I thank Jim Lutz, Mark Swanson, and Andrew Larson for their foresight in establishing the YFDP, their enduring commitment to the plot, and for everything that they taught me in the field. I am also grateful to those who have worked in the YFDP for many years including Kendall Becker, Sara Germain, Erika Blomdahl, Alina Cansler, Sean Jeronimo, and Jan Ng, and to Caroline Kittle and Soren Struckman who will carry the torch for the next few years. I thank Jerry Franklin for being an early advocate of permanent plot research, and Nate Stephenson and Joe Meyer for their support of our research in Yosemite.

I am deeply grateful to my advisor, Jim Lutz, for his guidance, mentorship, insights, and friendship over the past decade. Thank you, Jim, for everything; what a journey it has been! I am also very grateful to Andrew Larson, who in addition to serving on my Masters and PhD committees, has been a profoundly important mentor to me. I also thank my committee members Larissa Yocom, Mark Brunson, and Doug Ramsey, for their
valuable comments on my dissertation and their advice throughout my time at USU.

I thank all of the many close friends that have made my time in Logan a delight, and friends from afar who have put in the time and effort to stay close. I am so lucky to have all of you in my life. Finally, I am forever grateful for the infinite love and support of my family, Phil, Bev, and Kinsey, and my wife Sara, whom I fell in love with in the YFDP.

Tucker J. Furniss
This dissertation represents something much more personal than the research that it comprises. It was on little more than a whim that I got involved in the establishment of the Yosemite Forest Dynamics Plot (YFDP) as an undergraduate student over a decade ago. It did not take long for me to become enamored with the enormous sugar pines, the immersive ecology, and the allure of Big Plot research. It has been my pleasure, and my privilege, to lead and collaborate on research in YFDP for the past decade; it has been a profoundly formative experience. It was a childhood dream of mine to find a place in the woods somewhere, become intimately familiar with it, and to spend years watching it change. How lucky I am to have had this opportunity to live that dream, and to produce this dissertation in the process. I am deeply grateful for the days, seasons, and years that I have spent in the YFDP. I will never truly know how much that forest taught me.
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CHAPTER I

INTRODUCTION

Fire is a keystone process in western forest ecosystems (Agee 1998, Schoennagel et al. 2017, van Wagtendonk et al. 2020). The west has burned for millennia (Gavin et al. 2007, Pechony and Shindell 2010), and it will continue to burn no matter the resources we pour into suppression efforts (Koch 1935, Franklin and Agee 2003, Stephens and Ruth 2005). Fire frequency, size, and severity will increase in the coming decades (Westerling et al. 2006, Littell et al. 2009, van Mantgem et al. 2013), and there is growing awareness that universal fire suppression policies were more plague than a panacea (Weaver 1943, Kauffman 2004, van Wagtendonk 2007, North et al. 2015).

The science is clear: we must adapt our socio-pyro paradigm—everything from land management policy to landscape design and residential development—to a future in which we coexist with fire (Moritz et al. 2014, Schoennagel et al. 2017, Kolden 2018). There is no alternative; fire is an inexorable feature of dry ecosystems (North et al. 2015). Continuing to preclude fire from western forests, and the communities that we have built in these fire-prone places, is a delusion of grandeur.

Prescribed fire and mechanical thinning may be used to reduce fuel loads in targeted areas, but high per-acre cost (North et al. 2012) renders these treatments insufficient to restore vast landscapes (Franklin and Agee 2003). The only way for land managers to cultivate resistance to megafires is to use wildfire itself to “treat” large areas when burning conditions are amenable (van Wagtendonk 2007, North et al. 2015), eventually restoring the landscape heterogeneity that allows fire to be a self-regulating ecological
process (Miller 2003, Hessburg et al. 2005, 2015, Parks et al. 2015). Returning wildfire to western landscapes will have the concomitant benefit of reducing tree density and restoring spatial complexity, and this will foster resilience to future climates, insects, and novel disturbance regimes as well (Millar and Stephenson 2015, Seidl et al. 2016).

This poses a great challenge to land managers: how do we use fire to restore and maintain healthy forest ecosystems without jeopardizing nearby human communities or causing undesirable ecological consequences? Managing fire is expensive and inherently risky; there is a great deal of public distress over air quality and risk to human and natural resources, and the decision to let a fire burn can be a major political and legal liability (North et al. 2012, 2015). Despite the challenges, land managers throughout the west are increasingly relying on managed wildfire to restore heterogeneity and resilience to western landscapes (van Wagtendonk 2007). The purpose of this dissertation is to aide their efforts. It is my sincere hope that this research will help guide difficult management decisions, facilitate the use of wildfire as a restoration tool, and support science-based wildland fire policy in frequent-fire forest ecosystems.

This dissertation was guided by dual motives: 1) evaluate and refine the analytical tools used to measure, model, and predict fire effects, and 2) enhance our fundamental understanding of fire as an ecological process. The research contained in this dissertation may be grouped according to these two general themes. Chapters II and III address the applied science of mortality models and remote sensing, two primary tools used to guide fire-related management decisions. Chapters IV and V address more theoretical aspects of fire ecology: the reciprocal dynamics of fire and tree spatial patterns, and the three-way interactions between fire, drought, and bark beetles.
THE YOSEMITE FOREST DYNAMICS PLOT

This dissertation is rooted in an approach uncommon among previous fire science research (Lutz et al. 2018): the longitudinal monitoring of tens of thousands of individual trees contained in a single, large, exhaustively measured forest plot. The Yosemite Forest Dynamics Plot (YFDP) was established in 2010 in an old-growth white fir–sugar pine forest in the lower montane mixed-conifer zone of Yosemite National Park (Fig. 1.1) with the broad objective of studying tree mortality, forest dynamics, and climate-driven forest change. The YFDP was burned in the Rim Fire in 2013, providing a serendipitous opportunity to study the effects of reintroduced fire following over a century of fire suppression. Three years of pre-fire mortality and recruitment surveys provided a foundational understanding of this forest before the fire, making the YFDP a particularly unique lens through which to study a broad range of fire-related research topics.

The plot burned amid the most severe drought that California has experienced in at least 500 years (Belmecheri et al. 2016), and the compound effects of fire and drought provoked extensive mortality among large, old-growth sugar pines 2-3 years after the fire. While these climatic conditions were historically unprecedented, drought and fire are expected to co-occur with increasing frequency in the coming decades (Allen et al. 2015, Berner et al. 2017). The research contained in this dissertation may therefore provide prescient insights regarding tree mortality and fire effects under novel climate regimes.

In the following section I provide a brief context for the research contained in each of the next four chapters, and I highlight characteristics of the YFDP dataset (e.g., Lutz 2015) that may yield insightful contrasts with previous fire research.
In Chapter II, I examine post-fire tree mortality models and evaluate their accuracy in a variety of ecological contexts. Post-fire mortality models use tree-level measurements of fire damage (i.e., crown scorch) to predict the probability of post-fire mortality at either individual-tree or stand-level scales. I focus on the most widely used mortality models, those contained within the First Order Fire Effects Model (FOFEM), BehavePlus, and the Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS). These software packages are developed and distributed by the US Forest Service, and they are used widely to predict fire effects, estimate mortality following fire, and to inform post-fire management decisions related to salvage logging and hazard tree removal (Hood and Lutes 2017).

Mortality models have been a foundational tool for fire scientists for decades (Ryan and Amman 1994), but the YFDP dataset permitted a few key contrasts with previous mortality model studies. First, the large number trees in the YFDP (Fig. 1.1 E) is far greater than the sample size used to parameterize these models (Hood and Lutes 2017), and validations with independent datasets are rare (e.g., Grayson et al. 2017 and Kane et al. 2017). The sample size within the YFDP facilitated the explicit consideration of large-diameter trees, a critical yet threatened component of old-growth forests (Lutz et al. 2009). The low abundance of the largest trees renders their sample size insufficient among most validation datasets, but there are important differences in how big trees respond to fire (Kolb et al. 2007, Hood et al. 2018) that may be detected with the ample sample size of large-diameter trees within the YFDP. Second, the spatially explicit nature of the YFDP enabled an examination of model performance at a range of spatial scales,
and an assessment of spatially autocorrelated prediction error. Finally, the timing of the fire during a severe drought provided the first opportunity that I am aware of to evaluate these widely used mortality models under climatic conditions representative of warmer future climates. As the FOFEM mortality models were parameterized with data collected in previous decades, it remains unknown to what extent these models will remain relevant to predict tree mortality under future climates.

In Chapter III I examine perhaps the most ubiquitous method used to quantify fire severity: satellite-derived fire severity maps. These maps provide critical information about fire severity and are relied upon heavily to guide post-fire management (Eidenshink et al. 2007). Previous studies have demonstrated that satellite derived severity indices are closely correlated with field-based measures of severity (Key and Benson 2006, Miller and Thode 2007), but relatively little consideration has been given to the range in fire effects that are indistinguishable from space.

The 30-m resolution of Landsat pixels poses a fundamental limitation to the ecological accuracy severity maps because pixel values represent an “average” spectral response based on a range of spectral changes occurring at the sub-pixel scale. The problem this creates is that the mortality of many small trees may elicit the same spectral response as the mortality of one large tree, yet the ecological implications of these two scenarios are vastly different. This variability will average out at large scales, but it also represents tangible heterogeneity in fire effects that is of considerable ecological importance (Meddens et al. 2018, Blomdahl et al. 2019).

I use the map of stems in the YFDP to isolate the trees contained within each pixel, then I evaluate satellite-derived severity metrics with tree-based measures of fire severity.
This allowed me to examine uncertainty in ecologically meaningful terms (e.g., range in percent tree mortality) without relying on semi-quantitative measures of severity (Composite Burn Index, Key and Benson 2006) that are common among previous studies that have calibrated severity indices with field data (Miller et al. 2009, Parks et al. 2014). Another distinguishing characteristic of this study is that it was conducted in a single, large fire (Fig. 1.1 D), enabling me to isolate uncertainty due to intrinsic factors from the variance in spectral response due to fires that burn in different regions or in different forest types (Harvey et al. 2019). This permitted a detailed evaluation of the maximum accuracy that may be attained with Landsat-derived spectral indices for any given fire, and provides an estimate of the fundamental accuracy limitations due to the spatial and spectral resolution of the Landsat 8 OLI sensor.

The scope of study changes with Chapter IV as I examine how fire, drought, and background mortality agents regulate tree mortality and drive spatial pattern dynamics of trees within a forest. This chapter begins with a literature review and conceptual synthesis of the spatial elements of background tree mortality processes. I then partition the past decade of mortality observed in the YFDP into three distinct mortality regimes (background mortality, direct fire mortality, and post-fire mortality), and I characterize each regime in terms of the rates, causes, and spatial structure of mortality. Although previous studies have examined these distinct forms of tree mortality independently (e.g., Das et al. 2016, van Mantgem et al. 2011), the longitudinal nature of the YFDP allowed this to be done in the same forest. To my knowledge, this study is the first that has been able to do this. This chapter examines the spatial structuring of mortality, including both spatially non-random patterns in mortality and the influence of local neighborhood on
mortality risk. Disentangling the relationship between pattern and process is a long-standing challenge in ecology (Cale et al. 1989, McIntire and Fajardo 2009), one that the YFDP is uniquely suited to handle. This chapter employs two of the most distinct attributes of the YFDP dataset—annual mortality surveys and a large pre-fire stem map—and exposes the unique potential of longitudinal observational ecology.

In Chapter V, I continue to examine the more basic, ecological aspects of fire. Patterns in disturbance severity are governed by complex, cross-scale interactions (Peters et al. 2004, Raffa et al. 2008, Miller et al. 2012), but our understanding of the ecological characteristics that make ecosystems resilient is primarily based on large-scale studies that focus on landscape resilience (e.g., Hessburg et al. 2015). Both broad- and fine-scale patterns in vegetation structure are crucial to the overall resilience of forested landscapes, but we lack a generalizable understanding of how fine-scale forest structure confers resilience to fire, bark beetles, and drought. This limits our ability to develop within-stand level silvicultural prescriptions to adaptively manage forests amidst novel climates and disturbance regimes. In this chapter I combine the YFDP dataset with another annual mortality dataset from the Sierra Nevada (Fig. 1.1C) containing 18, 1-ha plots, that burned under a range of climatic conditions. This multi-plot, longitudinal dataset enabled me to create a post-hoc factorial design through which I explicitly examine how climate and tree neighborhoods mediate fire severity and beetle risk post-fire to provide a foundational understanding of how forest structure and spatial pattern regulate the severity of, and interactions between, compound disturbance events.
SCOPE OF INFERENCE

The YFDP was established in a forest with vegetation structure and composition characteristic of the lower montane mixed-conifer zone of the Sierra Nevada (Lutz et al. 2010, 2012, Keeler-Wolf et al. 2012, van Wagendonk et al. 2020), a location selected to serve as an archetypal example of long-unburned, fire-adapted, mixed-conifer forest ecosystems. These forests are widespread throughout the Sierra Nevada, where the specifics findings of this dissertation will maintain strong relevance.

The purpose of this dissertation, however, is not only to contribute to a better understanding of the forests the Sierra Nevada; it is to enhance our understanding of fire as an ecological process and to refine the analytical tools used to study it. In each of the chapters, whether applied or basic, I emphasize the aspects of this research that are broadly generalizable. Although the specific values reported in each chapter may pertain primarily to the Sierra Nevada, the overall conclusions bear considerable relevance to fire-prone forested ecosystems around the globe (Fig. 1.1 A). This includes temperate, Mediterranean, boreal, and subtropical forests that experience non-stand-replacing fire. This research may be most pertinent to conifer-dominated forests, as fire-adapted life history traits (Bond and Keeley 2005) of many conifer species confers a greater ability to tolerate fire compared with many hardwood species, but my research will likely maintain relevance among fire-adapted hardwood forests as well (e.g., Eucalyptus forests). The central themes that emerge in this dissertation deepen our knowledge of tree mortality, fire, and forest spatial patterns, and in doing so they improve our understanding of forest dynamics and contribute to the science of ecology as a whole.
LITERATURE CITED


Miller, C. 2003. Wildland fire use: a wilderness perspective on fuel management. Page USDA Forest Service Proceedings RMRS-P-29. USDA Forest Service Rocky Mountain Research Station, 2150 Centre Avenue Fort Collins CO 80526 USA.


Fig. 1.1. Global distribution of conifer-dominated, fire-prone forest ecoregions (A) in temperate, mediterranean, boreal, and subtropical climate zones (data source: Olson et al. 2001). This dissertation was conducted in forests of the Sierra Nevada (B); Chapter V utilizes the Sierra Nevada Forest Dynamics Plots (SNFDP), a network of stem-mapped 1-ha forest demography plots, and Chapter III utilizes 54 plots (JFSP plots) distributed throughout the 2013 Rim Fire footprint within Yosemite National Park (D). The Yosemite Forest Dynamics Plot (YFDP; E) is a longitudinal forest monitoring plot (C & D), and is central to all chapters contained in this dissertation.
CHAPTER II

MULTI-SCALE ASSESSMENT OF POST-FIRE TREE MORTALITY MODELS

Abstract

Post-fire tree mortality models are vital tools used by forest land managers to predict fire effects, estimate delayed mortality, and develop management prescriptions. We evaluated the performance of mortality models within the First Order Fire Effects Model (FOFEM) software, and compared their performance to locally-parameterized models based on five different forms. We evaluated all models at the individual tree and stand levels with a dataset comprising 34,174 trees from a mixed-conifer forest in the Sierra Nevada, California that burned in the 2013 Rim Fire. We compared stand-level accuracy across a range of spatial scales, and we used point pattern analysis to test the accuracy with which mortality models predict post-fire tree spatial pattern.

The FOFEM models under-predicted mortality for conifers, possibly because the Rim Fire burned during a severe drought. Locally-parameterized models based on crown scorch were most accurate in predicting individual tree mortality, but diameter-based models were more accurate at the stand level for *Abies concolor* and large-diameter *Pinus lambertiana*, the most abundant trees in this forest. Stand-level accuracy was reduced by spatially correlated error at small spatial scales, but stabilized at scales ≥1 ha. Mortality models generated inaccurate predictions of post-fire spatial pattern at small scales, but this error could be reduced by improving FOFEM model accuracy for small trees.

Introduction

First-order fire effects models are essential tools used by land managers in fire-prone forest ecosystems. These models are used to estimate the direct effects of fire including tree mortality, soil heating, fuel consumption, and smoke production (Reinhardt and Dickinson 2010). Of particular interest to forest land managers are tree mortality models which are used to estimate the probability of mortality for individual trees or proportion of mortality for stands (Woolley et al. 2012). These tree mortality models are used in post-fire landscapes to estimate fire severity and assess changes to stand structure, and to develop salvage marking and hazard tree guidelines (Hood et al. 2007). Mortality models are also used by managers in pre-fire applications to predict fire effects, conduct landscape-scale risk assessments, and to develop silvicultural prescriptions and prescribed fire treatments (Reinhardt and Dickinson 2010).

There are two main types of first-order tree mortality models: process-based models that use a mechanistic approach to simulate the processes involved in fire spread, heat-caused injury, and subsequent tree mortality (e.g., Michaletz and Johnson 2006), and empirical logistic regression models that use individual tree level explanatory variables (e.g., bark thickness, crown base height, crown volume scorched [CVS]) to predict probability of mortality (e.g., Ryan and Reinhardt 1988). While process-based approaches have a strong theoretical basis and contribute to our understanding of exactly how a tree is killed by fire, the complexity of these models has precluded their widespread use among managers (Woolley et al. 2012), and their focus on direct fire damage fails to capture the suite of biological and ecological processes that contribute to delayed mortality 1 to 5 years post fire (e.g., bark beetles and structural failure, Ryan and Amman 1994). Though empirical logistic regression models lack a mechanistic
representation of tree mortality, their simplicity and implicit integration of both immediate and delayed mortality processes (mortality is typically assessed 3 years post-fire) have made them the most practical and widely accessible tool for modeling fire-related tree mortality among both researchers and land managers (e.g., Ryan and Amman 1994; Reinhardt and Crookston 2003; Sieg et al. 2006; Hood et al. 2007; Lutes et al. 2016; Grayson et al. 2017).

Empirical logistic regression models are the foundation for the tree mortality models within widely used fire effects modeling software packages including the First Order Fire Effects Model (FOFEM), BehavePlus, and the Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS). Though over 100 logistic regression models for western North American conifer species have been developed (Woolley et al. 2012), the tree mortality models incorporated within these software packages are based on a single logistic regression model known as the Ryan and Amman (R-A) model. The R-A model was originally developed in the late 1980’s by Ryan and Reinhardt (1988), refined by Ryan and Amman (1994), and most recently updated by Hood and Lutes (2017) who parameterized a set of 12 species-specific models that have been incorporated into FOFEM since version 5.7.

The R-A model (hereafter FOFEMRA) is perhaps the single most widely used tree mortality model (Hood et al. 2007; Reinhardt and Dickinson 2010), but it is based on a relatively small sample of trees ($n = 2,356;$ Ryan and Reinhardt 1988) and is infrequently validated with independent data (but see Hood et al. 2007; Kane et al. 2017 for validations with many species, and see Ganio et al. 2015; Ganio and Progar 2017 for validations for *Pinus ponderosa* and *Pseudotsuga menziesii*). The recent development of
species-specific versions of this model (hereafter FOFEM$_{SP}$) improved model performance and increased sample sizes for certain species (average $n$ per species = 1,403 trees, Hood and Lutes 2017), but validation of these species-specific models with independent data is still rare (but see Grayson et al. 2017 for a recent validation of FOFEM$_{SP}$).

Additionally, the mortality predictions made with these empirical models are inherently reflective of the climatic conditions during which the parameterization data were collected. As climate influences the susceptibility of trees to fire-related mortality (van Mantgem et al. 2013; Stephens et al. 2018), empirical models developed under past climates may under-predict mortality from fires that burn under hotter and drier conditions.

The FOFEM$_{RA}$ and FOFEM$_{SP}$ models were not parameterized with small-diameter stems (<10 cm diameter at breast height [DBH]; there are two exceptions – the lower diameter limit was 8 cm for *Pseudotsuga menziesii* [Ryan and Reinhardt 1988] and 6 cm for “yellow pine” [Hood et al. 2017]), and validation of these models with small stems is rare (but see Engber and Varner 2012 and Kane et al. 2017). Some studies have developed logistic mortality models specifically for small-diameter stems (e.g., Battaglia et al. 2009), but these studies did not conduct a validation of the exact FOFEM models. Trees <10 cm DBH are more abundant than stems ≥10 cm DBH in many forests, especially if fire has been suppressed for many decades. They influence future fire behavior and act as ladder fuels, and they are ecologically important as components of the understory (re-sprouters) or advanced regeneration (surviving conifers). Previous studies have found that crown scorch influences mortality differently for small-diameter
stems compared to mature trees (Engber and Varner 2012), and this interaction may compromise the accuracy with which FOFEM predicts mortality for small-diameter trees.

Previous validations of the FOFEM\textsubscript{RA} and FOFEM\textsubscript{SP} models have also not assessed how stand-level accuracy may vary across a range of spatial scales. Stand-level accuracy is typically assessed by grouping trees according to their probability of mortality, then calculating the proportion of observed mortality within each group (\textit{sensu} Hood \textit{et al.} 2007). While this approach may be used to estimate stand-level accuracy without requiring a spatially-explicit (i.e., stem-mapped; Lutz \textit{et al.} 2018b) dataset, it implicitly assumes that fire-related mortality is a spatially homogeneous process. As mechanisms of delayed fire mortality can be spatially auto-correlated (e.g., bark beetle activity is patchy, and trees may survive higher levels of fire damage if they are in a more mesic area), stand-level model accuracy may therefore be modified by the presence or absence of these neighborhood-level variables. The positive and negative effects associated with spatially correlated mechanisms of delayed mortality may equalize if stand-level accuracy is assessed at a large enough scale, but the scale at which this happens remains unknown. A multi-scale assessment of stand-level accuracy would provide a more robust estimate of model performance, and would enable us to quantify the scale at which spatially local neighborhoods may mediate delayed mortality.

Mortality models are often used in a pre-fire context to assess potential fire effects and plan restoration activity, but a challenge to using the FOFEM models in a pre-fire context is that they require metrics of fire injury as predictor variables. Out of over 100 models that have been developed (Woolley \textit{et al.} 2012), we found no model that relies exclusively on pre-fire tree attributes to predict mortality. The reason for this is obvious –
fire damage is an important determinant of fire-related mortality. However, this limits the utility of these models in pre-fire planning applications because fire-damage attributes must be estimated, and this introduces an additional layer of uncertainty when interpreting the model results and evaluating their predictive accuracy. Metrics of fire damage have been considered necessary to create acceptably accurate mortality models, but these metrics are often tightly correlated with tree attributes that may be measured pre-fire, such as diameter at breast height (Fig. A.1). Given this correlation, a pre-fire model based on diameter, species, and surface fuel loads may predict mortality with an acceptable level of accuracy, and this may be useful to managers seeking to model mortality in a pre-fire context.

A final area for improvement in empirical mortality modeling is to consider the accuracy of mortality models in predicting post-fire tree spatial patterns. Fire is a spatially explicit disturbance process (Meddens et al. 2018) and is an important driver of spatially structured stand dynamics in fire-adapted forests (Larson and Churchill 2012). Spatial pattern is a key element of forest structure (Lutz et al. 2013), and it has an important influence on forest heterogeneity, resilience, and future disturbance dynamics (Stephens et al. 2008). Restoring spatial patterns and heterogeneity characteristic of fire-prone forests has become a central aim of many forest restoration efforts throughout the western United States (e.g., Allen et al. 2002; North et al. 2007, 2009; Churchill et al. 2013), but to our knowledge the accuracy with which logistic mortality models scale-up to predict post-fire tree spatial patterns has not been assessed.

Our objective was to advance the science of empirical fire mortality modeling in three ways. First, we conducted a validation of the widely used FOFEM tree mortality models
with a sample size of 34,174 stems ranging from 1.0 cm to 200.7 cm DBH, and we assessed both the individual tree- and stand-level accuracy of these models. Second, we developed locally-parameterized logistic regression models based on CVS and DBH to estimate of the maximum accuracy these models may attain, and to compare how different model forms influence model performance across different diameter classes. Third, we developed methods for quantifying model accuracy at a range of spatial scales and assessing the accuracy with which mortality models predict fire-induced change in tree spatial patterns.

This study is unique among existing mortality modeling literature in that the dataset we used is a census rather than a sample. Previous mortality modeling studies generally sample post-fire forests across multiple regions and fire events, selecting a subset of trees to create a relatively balanced sample across diameter and CVS classes. This approach is well-suited to developing mortality models with broad applicability, but it is less optimal for validating those models because the dataset is balanced, but not representative. An optimal validation dataset includes a large number of stems, representing a wide range of diameters, in proportion to their abundance in a specific forest type. A validation with this type of dataset permits mortality models to be tested in a context similar to how they are used by managers - to predict structural and compositional changes to a specific forest following fire. Model accuracy may then be assessed in terms of “percent error” by diameter class, a metric with very tangible implications for managers using mortality models to estimate fire effects at the stand scale. In this study, we conduct the first validation of FOFEM using a complete census of trees ≥1 cm DBH from a large-scale permanent forest plot.
Methods

Study area

We conducted this study in the lower montane, mixed-conifer zone of the Sierra Nevada, California, USA (Fig. 2.1A). We used data from the Yosemite Forest Dynamics Plot (YFDP; Lutz et al. 2012, 2014b), a 25.6-ha plot affiliated with the Smithsonian ForestGEO network (Anderson-Teixeira et al. 2015; Lutz 2015). The YFDP is located in an old-growth (oldest trees >500 years old) Abies concolor – Pinus lambertiana (white fir – sugar pine) forest between 1774 m and 1911 m elevation (Fig. 2.1B, C) with species composition representative of the Sierra Nevada white fir superassociation (Keeler-Wolf et al. 2012). Within the YFDP, all tree stems ≥1 cm DBH were tagged, identified, mapped in 2009 and 2010 (n = 34,458 live stems; Lutz et al. 2012), and tree status was updated in June 2013, two months before the YFDP burned. We considered the five most abundant species within the YFDP: white fir (Abies concolor [Gordon] Lindl. ex Hildebr.; 939 stems ha⁻¹), sugar pine (Pinus lambertiana Douglas; 180 stems ha⁻¹), Pacific dogwood (Cornus nuttallii Audobon; 106 stems ha⁻¹), incense cedar (Calocedrus decurrens [Torr.] Florin; 64 stems ha⁻¹), and California black oak (Quercus kelloggii Newb.; 46 stems ha⁻¹). Though A. concolor was the most abundant species, P. lambertiana had roughly the same pre-fire live basal area (30.6 m² ha⁻¹ and 28.8 m² ha⁻¹, respectively) and was the most abundant large-diameter (≥100 cm DBH) stem (n = 343 stems, Table 2.1).

The historical (pre-suppression) fire regime in lower mixed-conifer forests of the Sierra Nevada was characterized by frequent (fire-return intervals ranging from 5 to 32 years, Caprio and Swetnam 1995), relatively small (median area = 115 ha, Scholl and Taylor 2010), low- to moderate-severity fires (van Wagendonk and Fites-Kaufman...
In the modern post-suppression era, fires in Sierra Nevada forests have become larger in overall size and have greater proportions of moderate- and high-severity (van Wagtendonk and Lutz 2007), and this trend is predicted to continue as winter snowpack declines (Lutz et al. 2009). Prior to 1900, the mean fire return interval in the YFDP was 29.5 years, with the last widespread fire occurring in 1900 (Barth et al. 2015).

The YFDP was burned on September 1st and 2nd, 2013 in a management-ignited fire set to control the spread of the Rim fire, a large wildfire that burned 104,131 ha of Stanislaus National Forest and Yosemite National Park (Fig. 2.1B; Lydersen et al. 2014). The ignition occurred in the afternoon in a mixed forest-chaparral vegetation type atop the Crane Flat lookout about 1 km from the plot, and no management action was taken within the YFDP before or after ignition. The fire backed downslope through the western portion of the plot during the night of September 1st, and burned upslope through the remaining eastern portion the following day (Larson et al. 2016). The fire was active within the YFDP for approximately 30 hours, though smoldering continued in some large coarse woody debris through November, 2013 (T. Furniss and J. Lutz, pers. obs.). Fire intensity ranged from low intensity to high intensity surface fire with some crown torching (based on Fire Behavior Assessment Team cameras and thermocouples, (Lutz et al. 2017a); Fig. 2.1C). Surface fuel consumption was 95% for litter, 93% for duff, 90% for 1 hour fuels, 86% for 10 hour fuels, 96% for 100 hour fuels, and 61% for ≥1000 hour fuels (Larson et al. 2016; Cansler et al. 2019). Though the fire was management ignited, satellite-derived fire severity (Fig. 2.1C) was consistent with recent fires in the mixed-conifer zone of the Sierra Nevada (van Wagtendonk 2007; Lutz et al. 2009), and the area that was management ignited was found to be indistinguishable from the wildfire-ignited
area within the fire footprint (except for that portion that was plume-dominated) using a wide range of remote sensing techniques (Kane et al. 2015).

In May 2014, we revisited every stem in the YFDP and measured CVS, DBH, and live/dead status (hereafter “immediate fire mortality”). We also conducted full mortality censuses in the summers of 2015 and 2016 to measure delayed fire-related mortality (i.e., mortality of trees that survived >1 year post-fire). We considered “mortality” as the above-ground death of individual stems, a method which overestimates mortality of some hardwood species which are fire-adapted to re-sprout post-fire. Considering this, we also recorded whether *C. nuttallii* and *Q. kelloggii* individuals were sprouting post-fire.

**Model parameterization**

For each species, we extracted the corresponding logistic model forms and regression coefficients used in the FOFEM software (Lutes et al. 2016). Species-specific models based on CVS were available for *A. concolor*, *P. lambertiana*, and *C. decurrens* (FOFEMSP; Hood and Lutes 2017). Species-specific models were not available for *Q. kelloggii* and *C. nuttallii*, so we used the default model (FOFEMRA; Ryan and Reinhardt 1988). The FOFEMRA model uses two independent variables, CVS and bark thickness (BT), where BT is calculated according to the function DBH × Vsp, where Vsp is a species-specific coefficient (Table 4.76 in Reinhardt and Crookston 2003).

We created locally-parameterized models based on the same independent variables and general model forms used in FOFEM, but with re-parameterized coefficients. For each species, we created 1st, 2nd, and 3rd order polynomial models with CVS as the single independent variable and 3-year post-fire status as the binomial response variable (as with FOFEMSP), and we chose the model with the minimum AIC as our final “CVS”
model. For *Q. kelloggii* and *C. nuttallii* we created optimized models with both BT and CVS as independent variables, but we eliminated BT from our final models because we attained a better fit using CVS alone. All models we created were generalized linear models with a logit link and the logistic model form:

\[
P_m = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + ... + \beta_t x_t)}}
\]

where \( P_m \) is probability of mortality (within 3 years), \( e \) is the base of the natural logarithm, \( \beta_0 - \beta_t \) are regression coefficients, and \( x_1 - x_t \) are predictor variables (e.g., CVS, CVS^2, etc.). We fit each model using the iteratively reweighted least squares method of maximum likelihood estimation.

Upon preliminary analysis, we found that the third-order polynomial equations typically used in logistic mortality modeling often resulted in non-monotonic fits to our data (i.e., a tree with 25% CVS had a higher modeled probability of mortality \( P_m \) than a tree with 50% CVS; Fig. A.2). This was likely caused by the combination of two factors: tree DBH was negatively related to CVS (Fig. A.1), and large-diameter trees can be more susceptible to fire damage compared to small trees (Kolb et al. 2007). The higher relative proportion of large-diameter trees at low CVS levels may have inflated \( P_m \) (20-30% CVS; Fig. A.2), while the higher proportion of medium-sized trees may have reduced \( P_m \) for intermediate CVS levels (40-60% CVS; Fig. A.2). This suggests that the dip in \( P_m \) is an artifact related to the interaction between CVS and DBH, and may not reflect the true physiological relationship between CVS and \( P_m \) for trees of the same size. Although there are multiple mechanisms through which fire damage may lead to mortality (e.g., reduced photosynthesis [Smith et al. 2016, 2017], increased susceptibility to beetles and pathogens [Parker et al. 2006; Hood and Bentz 2007; Kane et al. 2017]), these
mechanisms are all positively related to fire damage. In other words, a tree with more fire
damage will have greater reduction to photosynthetic ability and be more susceptible to
biotic mortality agents, and both of these indirect fire effects will increase probability of
mortality. We resolved this problem in three different ways: we rarefied our dataset by
CVS, we created additional CVS-based models which were constrained to be monotonic
(i.e., no dip), and we created CVS-based models with a CVS:DBH interaction term.

We rarefied our dataset by 20% CVS bin (10% bins used at high and low limits) by
randomly selecting \( n \) trees from each CVS bin where \( n \) is the minimum number of trees
in any of the bins (\( n \) per species reported in Table 2.1). This rarefaction procedure
reduced the severity of the dip, but it did not remove it entirely (Fig. A.2). To reduce the
dip completely, we developed an alternative CVS-based model form that was constrained
to be monotonically-increasing (slope was not held constant, but was always positive).
This alternative model, “CVS\(_{\text{mono}}\)”, used CVS and CVS\(^2\) terms to fit the lower range of
CVS values, but replaced the CVS\(^3\) term with a higher-order polynomial (e.g., CVS\(^8\)).
Removing the CVS\(^3\) term removed the dip, and the high-order polynomial gave the curve
an inflection point and a steep increase in predicted \( P_m \) values above the inflection. The
power of the polynomial was chosen using an iterative procedure beginning with the
lowest value necessary to obtain a monotonic fit (CVS\(^4\) or CVS\(^5\)) and raising the power
by one until minimum AIC was reached. As we increased the power of the polynomial,
the inflection point moved to the right and the slope of the curve beyond the inflection
point became steeper. We dropped the CVS\(^2\) term if we obtained a better AIC without it.
Though this approach is novel, it was the most tractable way could find to constrain a
logistic model to be monotonically-increasing. Full R code developed for this model
fitting procedure in the Supplementary materials.

The final method we used to address the interaction between CVS and DBH was to develop additional CVS-based models which included both DBH and CVS:DBH interaction terms (one interaction term per CVS polynomial level; CVS:DBH, CVS^2:DBH, and CVS^3:DBH). In previously developed CVS-based mortality models, DBH has often been omitted because CVS and DBH can be co-linear, and dropping the DBH term may actually improve AIC (this was the case with FOFEMSP; Hood and Lutes 2017). However, eliminating the DBH term ignores any possible interactions between CVS and DBH (e.g., Kolb et al. 2007; Engber and Varner 2012), and this may bias CVS-based models to be less accurate for large-diameter trees (which are less abundant).

To facilitate comparisons with previous studies, we created one final CVS model based only on trees ≥10 cm DBH, “CVS_{gt10}”. Lastly, we generated species-specific mortality models using pre-fire DBH as the single predictor. In total, we evaluated and compared six models for each species: FOFEM (FOFEM_{RA} for Q. kelloggii and C. nuttallii and FOFEM_{SP} for all other species), four locally-parameterized CVS-based models (CVS, CVS_{mono}, CVS+DBH, and CVS_{gt10}), and a locally-parameterized DBH model (DBH). All CVS-based models were parameterized using the rarefied dataset.

Model validation

We validated all models using 10-fold cross validation (sensu Regelbrugge and Conard 1993; Hood and Lutes 2017) to minimize the bias associated with parameterizing and validating models using the same dataset (Kohavi 1995). We performed this procedure by first partitioning our data into 10 random groups. We then used nine groups to parameterize each model and generate predictions for the trees in the 10th group. This
process was repeated 10 times, leaving out a different group each time. The resulting model prediction for each tree is therefore based on a model that was parameterized using a different subset of the data. Although models were parameterized using the rarefied dataset, we used the full dataset to validate each model.

We summarized model performance in three ways: individual tree-level accuracy (correctly classifying individual stems), stand-level accuracy (predicting the proportion of mortality per species and diameter class), and accuracy in predicting post-fire tree spatial pattern. A key distinction between these three levels is that individual tree metrics use the model response value, $P_m$, as a binomial classifier thus requiring a cutoff threshold (e.g., trees with $P_m \geq 0.5$ are predicted to die while trees with $P_m < 0.5$ are predicted to survive). Stand-level and spatial pattern accuracy may be summarized by using $P_m$ as continuous probability value (e.g., for trees with $P_m = 0.8$, 80% will be predicted to die).

**Individual tree accuracy**

We assessed individual tree-level model accuracy by calculating sensitivity (correctly identified mortalities), specificity (correctly identified survival), overall accuracy (percent correctly categorized), $\Delta$AIC (AIC for each model minus the lowest AIC value), and area under the Receiver Operating Characteristics (ROC) curve (AUC). We used a threshold $P_m$ value of 0.5 to classify trees as live or dead.

Although individual tree-level metrics are widely used to evaluate mortality model accuracy (e.g., Grayson *et al.* 2017), these metrics may not be simply scaled up to evaluate stand-level performance. In other words, a model may have high individual-tree accuracy while systematically over- or under-predicting mortality at the population or forest stand level. The strength of stand-level model accuracy assessment is that it
permits the evaluation and comparison of mortality models in a way that describes observable changes in forest structure following fire. For example, a model may accurately predict small-diameter mortality while under-predicting large-diameter mortality (due to large-diameter trees having unique vulnerabilities to fire damage [Kolb et al. 2007]). This model would have high individual-level accuracy because small-diameter trees are abundant and individual accuracy metrics weight all trees equally, but it would not be reliable for predicting mortality of large-diameter trees. Large-diameter trees represent an ecologically unique element of forest structure (Lutz et al. 2018a), and accurately predicting their fate following fire is important for improved predictions of aboveground biomass and carbon storage (sensu Lutz et al. 2017b).

**Stand-level accuracy**

We used individual tree model response values to scale up our predictions to the population-level for each species. While this analysis was based on populations (grouped by species), we refer to this scale as “stand-level” to maintain consistency with previous studies (sensu Hood et al. 2007). We assessed model accuracy by grouping trees by species and diameter and calculating percent error as \((N_{\text{model}} - N_{\text{obs}})/ N_{\text{bin}}\), where \(N_{\text{model}}\) is the number of modeled mortalities, \(N_{\text{obs}}\) is the number of observed mortalities, and \(N_{\text{bin}}\) is the number of trees in each diameter class. This approach is similar to the method used by Hood et al. (2007) to assess stand-level accuracy, but we grouped stems by diameter class rather than by \(Pm\) (sensu Kane et al. 2017). This allows us to evaluate model performance across a range of diameter classes rather than across the range of \(Pm\) values. The number of dead trees predicted were identified for each model by assigning a status of either live or dead based on the continuous value of \(Pm\) for that individual stem (e.g., a
stem with a $P_m$ of 0.85 has an 85% chance of being identified as a dead tree), and these dead trees were summed for each bin.

**Multi-scale stand-level accuracy**

We summarized stand-level accuracy across a range of spatial scales by sampling trees within randomly located quadrats within the YFDP ranging in area from 0.04 ha (20 m $\times$ 20 m) to 2.56 ha (160 m $\times$ 160 m). We sampled 10 quadrats of each size without replacement and calculated the stand-level error for all trees within each quadrat. There are two potential sources of this stand-level error: 1) small spatial scales include few trees, and there is more stochastic error because there is higher variability between sample means for smaller samples compared to larger samples, and 2) spatially correlated error due to the spatial autocorrelation of agents of delayed mortality. In other words, trees with the same level of fire damage may die at different rates if they are on a ridge vs. in a drainage, or if they are in a beetle-kill patch vs. a patch with no beetles. As mortality models predict mortality based only on individual tree properties, these neighborhood-level factors affecting mortality contribute to model error.

To differentiate between these two sources of error, we used a null model designed to capture stochastic error (due to small sample size) but not spatially correlated error. We created this model by pairing each spatially explicit sample with a non-spatial sample of the same number of trees, randomly selected from the entire YFDP. This null model may be interpreted as the amount of error due to small sample sizes, and any excess error is attributable to spatially correlated processes that modify the probability of mortality for all trees within a given area.

We note that spatially correlated error is not the same as patchiness in fire effects:
patchy fire behavior is largely captured by tree-level metrics of fire damage such as CVS (resulting in spatially correlated mortality, but not necessarily model error), while spatially correlated error describes model error due primarily to the spatial signature of factors influencing delayed mortality.

**Spatial pattern accuracy**

We further scaled our assessment of model performance to the community level by evaluating spatial patterns for the entire forest community (all species grouped). We assessed post-fire spatial pattern accuracy by quantifying and comparing pre-fire, post-fire, and modeled post-fire spatial patterns of trees within the YFDP. We used two methods: clump size analysis, a method of local pattern analysis often used to characterize spatial patterns in frequent-fire forest ecosystems (Plotkin et al. 2002; Larson and Churchill 2008); and spatial point pattern analysis, a method that has been used to infer ecological process in a variety of contexts (e.g., (Lutz et al. 2014a, Larson et al. 2015; Furniss et al. 2017).

For the clump size analysis, we summarized spatial pattern as the number of clumps of trees as a function of clump sizes (i.e., number of clumps with 2 trees, 3 trees, 4 trees, etc.). We used an inter-tree distance threshold of 6 m to identify distinct clumps (i.e. clumps are groups of trees which are spaced no further apart than 6 m), as this was a found to be an optimal distance by Churchill et al. (2013). We compared each model by generating 99 simulations of mortality (where each tree was assigned a status of live or dead based on P_m) to obtain an estimate of the amount of variability in the modeled spatial pattern for each model.

For the point pattern analysis, we summarized spatial patterns with the pair
correlation function (PCF), $g(r)$, a point pattern summary statistic that describes the second-order characteristics of a spatial pattern across a range of scales (Wiegand and Moloney 2004). The PCF is defined as:

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

where $K'(r)$ is the derivative of Ripley’s K function (Ripley 1976). To summarize observed patterns, we calculated $g_{pre}(r)$ based on the pattern of trees that were alive pre-fire in 2013, and $g_{post}(r)$ based on the pattern of trees that survived for at least three years post-fire (live as of 2016). We quantified model accuracy in predicting post-fire spatial patterns by generating 99 simulations of mortality for each model (where mortality was re-assigned for each simulation, as with the clump analysis), and $g_{model}(r)$ was calculated for the set of “surviving” trees for each of these simulations. We generated simulation envelopes (Baddeley et al. 2014) based on the minimum and maximum values from these simulations, and an estimate of the true value of $g_{model}(r)$ based on the mean value from the simulations. We calculated change in pattern by $g_{post}(r) - g_{pre}(r)$. We compared the observed and modeled patterns to the null model of complete spatial randomness (CSR; Wiegand and Moloney 2004) for the static patterns, $g_{model}(r)$, and the null model of “no change” for the differenced patterns, $g_{post}(r) - g_{pre}(r)$.

For the multi-scale accuracy and spatial pattern analyses, we omitted two of the CVS-based models (CVS, CVSmono, and CVSgt10 all performed similarly; we retained the best one) to maintain interpretability of the figures. Analyses were conducted in R v3.4.1 (R Core Team 2017) using the spatstat package v1.52-1 (Baddeley et al. 2015).
**Results**

Out of 34,174 pre-fire stems (1 cm ≤ DBH < 201 cm), there was immediate mortality of 24,151 stems and delayed mortality of 3,818 stems (Table 2.1). The mean CVS for immediate mortalities was 99.7%, 66% for delayed mortalities, and 23% for surviving trees (Fig. A.3). The mean CVS for trees ≥1 cm DBH was 82%, 19% for trees ≥50 cm DBH, and 12% for trees ≥100 cm DBH. Mortality rates (three-year rates) by diameter class were 82% for trees ≥1 cm DBH, 63% for trees ≥50 cm DBH, and 28% for trees ≥100 cm DBH. Mortality rates for conifers were 84% for *A. concolor*, 77% for *P. lambertiana*, and 71% for *C. decurrens* (Table 2.1). Mortality rates for the hardwoods were 82% for *C. nuttallii* and 69% for *Q. kelloggii*, though 19% of top-killed *C. nuttallii* and 70% of top-killed *Q. kelloggii* were re-sprouting post-fire. The mean (and median) DBH was 7.4 cm (5.2 cm) for immediate mortality, 24.8 cm (18.1 cm) for delayed mortality, and 35.1 cm (25.9 cm) for surviving trees.

**Individual tree accuracy**

The locally parameterized CVS-based models had the best AIC and higher overall accuracy compared to FOFEM and DBH-based models (Table 2.2). Adding a DBH interaction term (CVS+DBH model) improved AIC for *A. concolor*, but did not improve AIC for other species. The monotonic CVS model (CVSmono) improved AIC for all conifers (Table 2.2). Although the AIC of the FOFEM models was worse than the AIC of the locally-parameterized CVS models, overall accuracy (i.e., total percent correct) for FOFEM was similar for all three gymnosperms.

**Stand-level accuracy**

Considering stand-level accuracy, the DBH model was the best model for small to
medium diameter trees (≪20 cm DBH) of most species (Table 2.2). For *A. concolor*, the DBH model was the most accurate for stand-level predictions for all diameter classes. For *P. lambertiana*, the FOFEM$_{sp}$ model was best for stems <10 cm DBH, the CVS models were best for stems 10 ≤ DBH < 100, and the DBH model was most accurate for stems ≥100 cm DBH. Adding the DBH interaction term improved model performance considerably for *A. concolor*, compared to CVS-based models without the interaction term. The DBH interaction term did not improve performance for most size classes of *C. decurrens* and *P. lambertiana*, but the CVS+DBH model did improve accuracy by 2% for large-diameter *C. decurrens* and *P. lambertiana* (>100 cm DBH; Table 2.2). In contrast, the CVS+DBH model decreased model accuracy for the largest stems of both hardwood species. The CVS$_{mono}$ model was more accurate than the non-monotonic CVS model for stems <20 cm among all species, but the two CVS models were generally equivalent for larger diameter classes (Table 2.2; Fig. 2.2). The CVS models based only on stems ≥10 cm (CVS$_{gt10}$) were generally equivalent to the base CVS model for stems ≥20 cm DBH, but accuracy was worse for stems <20 cm DBH and all sizes of *Q. kelloggii*.

Stand-level accuracy of the FOFEM models was within 15% of observed mortality for *A. concolor*, *C. decurrens*, and *P. lambertiana* <40 cm DBH, but mortality was consistently under-predicted (Table 2.2; Fig. 2.2). The FOFEM model under-predicted large-diameter (≥100 cm DBH) *P. lambertiana* mortality by 17%. The FOFEM model over-predicted mortality for *Q. kelloggii* and *C. nuttallii*, especially for stems ≥10 cm DBH (18-32%).

**Multi-scale accuracy**

Stand-level error was negatively related to spatial scale (Fig. 2.3A-D). We observed
this pattern for all models, as well as for each null model. The decreasing error in the null models indicates that some of the error was due to the small number of trees included in the spatial samples at small scales. As spatial scale increased, sample size grew and error in the null model was reduced. However, we also observed additional error in the spatially explicit samples that was greater than the error captured by the null models, indicating that there was spatially correlated error. The CVS-based models were the most accurate at small scales, predicting mortality within 10% of observed levels at all scales $>0.1$ ha. Model error for FOFEM and the DBH model fell within 10% at scales $>1.4$ ha and $>1.2$ ha, respectively, but the DBH model had much greater error at scales $<1$ ha.

**Spatial pattern accuracy**

The fire decreased the number of clumps from 3 ha$^{-1}$ to 1 ha$^{-1}$ for clumps of 5-20 trees, and mean clump size decreased from 10 to 7 trees per clump. All models accurately predicted this change (Fig. 2.3E), though the FOFEM model slightly overestimated the number of clumps at clump sizes ranging from 5 to 26 trees per clump. We were not able to differentiate the CVS- or DBH-based models from the observed pattern using the clump size analysis.

The spatial pattern of live stems within the YFDP became more aggregated after the fire (Fig. 2.3F). Both the CVS$_{mono}$ and CVS+DBH models accurately predicted this change in pattern, although the magnitude of the observed increase in aggregation was greater than the models predicted, especially at small scales (0 to 2 m; Fig. 2.3G). The CVS$_{mono}$ model had the greatest spatial pattern accuracy: the mean value of $g(r)$ from the 99 simulations was the closest to the observed post-fire pattern, and this was the only model for which the observed value of $g_{post}(r) - g_{pre}(r)$ fell within the model’s simulation.
envelope (at \( r > 2 \text{ m} \); Fig. 2.3F, G). In contrast to the observed increase in aggregation post-fire, the DBH and FOFEM models both predicted reduced aggregation at small scales post-fire (Fig. 2.3G). Although the FOFEM model correctly predicted increased aggregation at spatial scales \( >1.5 \text{ m} \), the DBH model predicted increased dispersion at all scales 0 to 10 m.

**Discussion**

*Model validation*

Mortality of individual trees was predicted with a high degree of accuracy by all CVS-based models (CVS, CVSmono, CVSgt10, CVS+DBH, and FOFEM; Table 2.2). Indeed, CVS is a direct measure of physical damage incurred during the fire, and this damage is closely related to tree death (Peterson 1985; Weatherby et al. 1994; Sieg et al. 2006). This result is intuitive and expected, and it supports decades of previous work that have focused on CVS as a key parameter in empirical mortality models (Ryan and Reinhardt 1988; Woolley et al. 2012; Hood and Lutes 2017; Grayson et al. 2017).

Immediate mortality was comprised almost entirely of trees with 100% CVS, while delayed mortality was dominated by trees with lower CVS (Fig. A.3). Mortality models based on three-year mortality (such as FOFEM) are not well calibrated to predict immediate mortality, as they will over-predict mortality for trees with CVS <100%. The FOFEMSP models more closely reflected the observed patterns in delayed mortality for most species, as to be expected because they were parameterized based on three-year mortality. We used three years as the cutoff for delayed mortality to maintain consistency with previous studies, though recent work has suggested that this timespan may not be sufficient to fully capture the all delayed mortality (van Mantgem et al. 2011).
Though the FOFEM<sub>SP</sub> models had high individual tree accuracy, they under-predicted mortality at the stand level for <i>A. concolor</i>, <i>C. decurrens</i>, and <i>P. lambertiana</i> by 2% to 18% (Table 2.2; Fig. 2.2). A possible explanation for this is that the Sierra Nevada experienced a multi-year drought from 2012 to 2015 (Belmecheri <i>et al.</i> 2016), and this may have exaggerated mortality (e.g., Stephens <i>et al.</i> 2018). The extent to which fire-related mortality was affected by the drought is impossible to quantify for the YFDP, and a thorough analysis of the interactive effects between bark beetles, drought, and fire on tree mortality in the Sierra Nevada will require a multi-plot analysis that is beyond the scope of this study. Other studies have found that pre-fire climate appears to have a stronger influence on fire-related mortality than does post-fire climate (van Mantgem <i>et al.</i> 2013), suggesting that the timing of the Rim Fire early in the drought may have reduced the potential confound between drought- and fire-induced mortality.

This reveals an important question: will mortality models developed under non-drought conditions be useful in predicting mortality for fires that occur in a future climate characterized by greater drought stress? Though we cannot quantify the degree to which drought influenced mortality, we found that mortality models parameterized for past climates may under-predict mortality when fire events are coupled with multi-year drought. As climate warms and drought becomes more frequent, mortality models may need to be revised to reflect the modified relationship between fire damage and mortality probability under a drier climate. This may be done through re-parameterizing models using fires that burned during a drought, or by explicitly including climatic variables as independent variables. Addressing this issue is a high priority for management-oriented modeling research, as the suitability of existing mortality models may decline as the co-
occurrence of drought and fire becomes increasingly frequent.

In contrast to the under-prediction of mortality for conifers, the FOFEMRA model greatly over-predicted stand-level mortality of *C. nuttallii* and *Q. kelloggii* by 5% to 32% (Table 2.2). Even for stems with 0% CVS, the FOFEMRA model predicted a 72% chance of mortality for *Q. kelloggii* and 84% chance of mortality for *C. nuttallii*, but observed mortality was <10% for stems with 0% CVS for both species (Fig. 2.2). This is consistent with the findings of Kane *et al.* (2017) who found FOFEM over-predicted mortality for three hardwood species (including *Q. kelloggii*). Our observation that 70% of top-killed *Q. kelloggii* re-sprouted post-fire indicates that above-ground stem death may not be an appropriate measure of mortality for individuals of re-sprouting species. Re-sprouting individuals have an important effect on post-fire regeneration by rapidly sprouting new stems that grow much faster than conifer seedlings post-fire, and these sprouts maintain spatial pattern of the parent trees. Other studies have observed this discrepancy between actual mortality and top-kill (e.g., Catry *et al.* 2013), though most mortality models are primarily focused on top-kill. This result underscores the need to develop more species-specific models for the FOFEM, and the need to consider multiple types of mortality for hardwoods.

*Individual tree vs. stand-level accuracy*

Surprisingly, the high individual tree accuracy did not always translate into high stand-level accuracy, and this discrepancy highlights the importance of multiple tests of model performance. This was especially evident with the FOFEM models which generally performed well at the individual tree level but had high stand-level error for some species and diameter classes. Though this has been considered elsewhere (e.g.,
Hood et al. 2007; Belote et al. 2015), individual tree accuracy dominates the literature as the most widely used method for model parameterization, validation, and comparison (e.g., Hood and Lutes 2017; Grayson et al. 2017). These results support the inclusion of stand-level accuracy metrics in future model development as this permits the explicit consideration of model accuracy for rare but important sub-populations such as large-diameter trees. The disparity between individual and stand-level accuracy should also be considered when using mortality models for stand-level inference and management decisions such as post-fire salvage harvest.

**CVS:DBH interaction**

Pre-fire models based on DBH alone were often more accurate than the CVS-based models at the stand-level, most notably in predicting mortality of *A. concolor* and large-diameter *P. lambertiana* (Table 2.2). While this may be partially explained by the tight correlation between CVS and DBH (Fig. A.1), DBH should not perform better than CVS if it is primarily acting as a proxy for CVS. An alternative explanation is that there could be an interaction between CVS and DBH at large-diameters that is not captured by using CVS alone (McHugh and Kolb 2003; Kolb et al. 2007). In other words, a small-diameter stem with 80% CVS may not have the same $P_m$ as a large-diameter stem with 80% CVS. The presence of a CVS:DBH interaction also explains why stand-level accuracy was generally higher for the CVS+DBH model compared to CVS alone.

Interestingly, despite the improved stand-level performance of the CVS+DBH, AIC was best for CVS alone (all species except *A. concolor*). Standard model selection procedures are generally based only on AIC, and would therefore select the CVS model without a DBH term (sensu Hood and Lutes 2017). Though this maximizes AIC, our
results demonstrate AIC does not necessarily correlate with stand-level accuracy, especially for large-diameter trees. To maximize model accuracy across a broad range of tree diameters, we suggest evaluating models based on stand-level accuracy in addition to AIC, and including a DBH interaction term to account for the known interactive effects between CVS and DBH.

The high accuracy of the DBH model at the stand-level suggests that post-fire data may not be necessary to develop an acceptable stand-level mortality model. However, as DBH does not implicitly capture fire behavior as CVS does, site-specific fuel information (e.g., surface fuel loads) would have to be incorporated to calibrate the model for use in different forests. The resulting model would be similar to a CVS-based model used in a pre-fire context which relies on a separate model to predict scorch height based on fuel levels. This would enable users to assess mortality as a function of DBH rather than CVS, and this may be useful for managers seeking to minimize (or maximize) mortality for specific diameter classes.

A problem we encountered with the DBH models is that standard logistic model forms did not represent the data well. First-, second-, and third-order polynomial models all predicted low $P_m$ values (0 to 0.1%) at the large end of the diameter range for all conifer species, whereas the data show the true proportion of mortality was closer to 50% (Fig. A.4). We expect the true probability of mortality to be minimized for intermediate diameters and to increase for trees at the upper diameter range (e.g., McHugh and Kolb 2003). There are a few possible explanations for this: large-diameter trees often have cavities and scars from previous fires that can serve as an entry point for flames and embers and can lead to mechanical failure (7 out of 20 immediate mortalities >100 cm
DBH were due to mechanical failure at a fire scar; they often have large-duff mounds around the base that can smolder and cause prolonged soil heating at the root crown (Varner et al. 2009), and they may be more susceptible to beetle attack and drought post-fire (Hood and Bentz 2007; Kolb et al. 2007). Alternative approaches such as using linear models to predict the proportion of mortality (based on binned data) offer more control over the shape of the model response curve (compared to logistic regression), and this may result in models that more closely reflect the observed shape of the DBH – mortality response curve.

**Monotonic vs. third-order polynomial models**

The standard third-order polynomial CVS models predicted individual-tree mortality with a high degree of accuracy, but the CVSmono models improved individual and stand-level accuracy for all conifers in this study (Table 2.2). Graphical representations of these models demonstrate differences in the fundamental shape of these two model forms (Fig. 2.2; Fig. A.2). The third-order polynomial models had a dip in $P_m$ values in the middle of CVS range while the CVSmono models had a steady increase (e.g., *P. lambertiana*) or a slight plateau (e.g., *A. concolor*). Though there may be a biological basis for a plateau in $P_m$ at intermediate CVS levels, a negative relationship is biologically implausible. Fitting monotonic models solved this problem while still capturing the subtleties of the underlying data that would have been lost by using a simple linear formula (e.g., low slope at low CVS, steep slope at upper CVS). Though the exact models we generated may not be broadly applicable to other sites as the position of the inflection point (determined by the power of the polynomial and the coefficients) may be highly susceptible to specific sites and fire events, we suggest a monotonic model form as an
alternative if the common third-order polynomial model form results in a non-monotonic fit. Monotonic CVS models were more accurate at all scales, and they bear more relevance to the underlying processes determining mortality.

**Multi-scale accuracy**

Stand-level accuracy was dependent on spatial scale for all models. We were able to partition this error into two categories: error due to small sample size (this error is represented by the null models; grey regions in Fig. 2.3A-D) and spatially correlated error (this error is represented by the colored areas outside of the grey regions in Fig. 2.3A-D). We were not able to identify the mechanisms driving the spatially correlated error, but there are a few plausible explanations based on the spatially explicit nature of ecological processes that mediate delayed mortality. For example, imagine two stands that were burned identically; FOFEM will predict the same probability of mortality for each tree, and the same proportion of mortality at the stand-level. If one of these stands experienced a bark beetle attack immediately post-fire while the other stand did not, the FOFEM mortality prediction will be too low for the stand that was attacked by beetles (and too high for the beetle-free stand), resulting in spatially correlated error. One could imagine a similar scenario based on other mechanisms that mediate delayed mortality such as spatial variability of soil depth or moisture holding capacity, or patchily distributed pathogens. Mortality models do not yet include these mechanisms as input variables, but they implicitly consider them by predicting mortality based on average mortality rates. If a prediction is made for a large-enough area, these spatially autocorrelated factors will be integrated together and the average mortality rates become a reasonable approximation. However, we found spatially correlated error at all spatial
scales up to the maximum scale of our analysis (2.5 ha).

Spatial patterns

Restoring structural heterogeneity and spatial patterns to reflect pre-fire suppression reference conditions is a frequent goal of prescribed fire restoration efforts (North et al. 2009), but the ability of mortality models to accurately predict change in spatial pattern remains unstudied. We found that both point pattern analysis and clump size analysis detected a change in pattern post-fire, but point pattern analysis was more sensitive to differences among modeled post-fire patterns. A likely explanation for this is that our choice of a 6 m threshold for the clump size analysis limits the scale of pattern detection to spatial scales >6 m, and the greatest pattern dynamics we observed using the point pattern analysis were at spatial scales 0 m to 2 m. The clump size analysis may be better suited to larger-scale pattern dynamics, which all mortality models predicted reasonably well.

The point pattern analysis showed that the spatial pattern of live trees became more aggregated post-fire, and the CVS$_{mono}$ model predicted this with the greatest accuracy (Fig. 2.3F, G). The FOFEM model and the DBH model were inaccurate at small spatial scales, predicting increased dispersion rather than increased aggregation post-fire. The FOFEM model accuracy improved at scales >1.5 m, while the DBH model was inaccurate at all scales 0 – 10 m.

The DBH model predicted a more dispersed (i.e., regular) post-fire pattern because the model predicted that large-diameter trees would survive and small-diameter trees would die (Fig. A.4). The resulting spatial pattern is therefore closely based on the pre-fire spatial pattern of large-diameter trees, which was more regular than the pre-fire
pattern of small-diameter trees. The CVS models, in contrast, use CVS which is an indirect measure of fire intensity and it therefore reflects the spatial auto-correlation of fire behavior and subsequent mortality. In other words, small scale patterns in fire intensity is driven by small scale heterogeneity in fuels, stand structure, and wind (Thaxton and Platt 2006; Hiers et al. 2009; Loudermilk et al. 2012), and measurements of CVS implicitly captured this patchiness. The mortality we predicted by the CVS models was therefore spatially structured, resulting in a predicted post-fire spatial pattern that closely reflects the observed post-fire pattern.

The FOFEM models had poor spatial pattern accuracy at small scales even though they are based on CVS. This was because the FOFEMRA model greatly over-predicted mortality of the two hardwood species (15% for *C. nuttallii*, 19% for *Q. kelloggii*), and those species tend to be highly aggregated (Fig. A.5A). This resulted in a modeled post-fire spatial pattern that included very few *C. nuttallii* or *Q. kelloggii* and was therefore much more dispersed (Fig. A.5B). The CVS-based models predicted hardwood survival more accurately, resulting in modeled spatial patterns that more closely reflected the observed post-fire pattern (Fig. 2.3F, G). This finding highlights the need to develop species-specific mortality models for hardwoods which will improve the spatial pattern accuracy of FOFEM.

*Model validation with census vs. sample datasets*

The YFDP dataset is unique among the datasets used in previous mortality model validations, and many of the novel contributions of this study may be attributed to the representative nature of this dataset. As the population of each species and diameter class was a known quantity, we were able to quantify percent error – a metric that easily
translates to population-level predictions for a given forest stand. Though the data were numerically dominated by small- and medium-diameter trees, we were able to quantify percent error across the full range of diameter classes, and this demonstrated the importance of using stand-level metrics in addition to individual-tree accuracy when comparing models. The spatial nature of the dataset allowed us to determine the scales at which there was spatially-correlated error in model predictions, and to differentiate this from error due to small sample sizes. We were also able to use mortality models to predict change in spatial patterns, and we demonstrated how this can be used to compare models.

Conclusions

The large sample size in this study allowed us to conduct a detailed validation of the FOFEM models for five species, and to evaluate logistic mortality models in a few novel ways. The FOFEM SP models had high individual tree accuracy, but they systematically under-predicted mortality at the stand level. Some of this error is likely due to the timing of the Rim Fire in the middle of a severe, multi-year drought. We showed that existing mortality models may not be sufficient to accurately predict mortality under future climates, and this may require re-parameterizing mortality models to capture the modified relationship between CVS and mortality under droughty conditions. The models we developed in this study accomplish this for five species, though we recommend validating these models with independent data before they are applied in a management context. The FOFEM RA model was inadequate for *C. nuttallii* and *Q. kelloggii*, and accuracy may be improved by 15% to 21% (individual accuracy, Table 2.2) by using the CVS models we created. Incorporating these species-specific models into FOFEM will
also improve community-level spatial pattern predictions.

We compared five different locally-parameterized models and found that there was no clear winner. Though CVS models had high individual tree accuracy, DBH models were often more accurate at the stand level. Incorporating a DBH interaction term into CVS-based models improved stand-level performance, but the interaction term also introduced a considerable decline in accuracy for stems at the upper limit of the DBH range (e.g., *A. concolor* >100 cm DBH, *Q. kelloggii* >20 cm DBH, *C. nuttallii* >5 cm DBH). The CVS_{mono} models were generally the most accurate according to both AIC and stand-level metrics, but the monotonic model fitting procedure we developed created models with inflection points that may be less accurate when validated with independent data. These results emphasize the need to develop a stronger theoretical foundation for model forms; model parameters should be chosen based on known processes and interactions, and model forms should be constrained to biologically plausible relationships.

We found that stand-level accuracy improved with increasing spatial scale, though 2.5 ha was not large enough to eliminate spatially correlated error entirely. The spatial analysis revealed the importance of spatial processes to fire-related mortality, and it demonstrated that CVS captures some of this spatial variability. This study not only provides robust estimates of multi-scale mortality model accuracy for five species – it offers a re-evaluation of the fundamental approach (i.e., individual-level accuracy metrics and third-order polynomial model forms) that have dominated empirical mortality modeling for 30 years, and it reveals that existing models may be inadequate for fires that occur during drought. Logistic mortality models are well suited to individual tree
predictions, but evaluating accuracy with multi-scale performance metrics and exploring alternative modeling approaches will advance our ability to model population and community level fire effects.

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Tables

Table 2.1. Number of pre-fire live stems of the five most common species within the Yosemite Forest Dynamics Plot (YFDP). Immediate mortalities are those stems identified as dead in May 2014, eight months after the California Rim fire. Delayed mortalities are stems that survived through May 2014, but died within the following two years. Total fire-related mortalities includes all stems that died within three years of the fire. Rarefied \( N \) is the number of stems retained after the dataset was rarefied by 20% CVS bins. Crown volume scorched (CVS) and diameter at breast height (1.37 m, DBH) metrics indicate mean values for the stems used in all analyses. Minimum DBH for all species was 1 cm. The range of CVS values was 0 to 100 %, and median CVS was 100% for all species. The “95th” column represents the 95th percentile threshold diameter.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rarefied ( N )</th>
<th>Number of stems</th>
<th>CVS (%)</th>
<th>DBH (cm)</th>
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<td>Live pre-fire</td>
<td>Fire-related mortality</td>
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<td>Mean</td>
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<td>≥50 cm</td>
<td>≥100 cm</td>
<td>Immediate</td>
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Table 2.2. Comparison of individual and stand level model performance for six different species-specific mortality models in predicting fire-related mortality. The six models include a diameter at breast height (DBH) model, three crown volume scorch models (3rd order polynomial [CVS], monotonic polynomial [CVSmono], and based on trees ≥10 cm [CVSgt10]), one CVS model with a DBH interaction (CVS+DBH), and the models used in the First Order Fire Effects Models (FOFEM) software version 5.7+. We quantified model performance for individual trees with mortality percent correct (Mort.; true positive rate, TPR), survival percent correct (Surv.; true negative rate, TNR), overall accuracy (Acc.), Akaike information criterion (ΔAIC), and area under ROC curve (AUC). We quantified stand-level model performance using percent error by diameter class (positive % error indicates over prediction of mortality, negative indicates under prediction). The Top 5% includes the largest 5% of stems for each species (diameter thresholds for the top 5% may be found in Table 2.1).

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Fig. 2.1. Location of the Yosemite Forest Dynamics Plot (YFDP) on the western slope of the Sierra Nevada, California, USA (A). The YFDP was burned in a backfire set in the path of the California Rim fire in September of 2013 (B). Burn severity classifications based on differenced Normalized Burn Ratio (Miller and Thode 2007). The dimensions of the YFDP are 800 m east-west by 320 m north-south, elevations range from 1774 m to 1911 m (C); dots represent 34,458 trees sized by diameter at breast height (DBH; cm) and colored by crown volume scorched (CVS; %). Background: Landsat 8, natural color image, August 10, 2017.
Fig. 2.2. Probability of mortality ($P_m$) as a function of crown volume scorched (CVS). Dots represent observed proportion of stems that were killed in each CVS category (10% bins plus 0% and 100% bins), and lines represent species-specific logistic regression models using CVS as the independent variable and binary mortality status as the response. The dots are for visualization purposes only; the models were parameterized on rarefied, un-binned data. For the CVS+DBH and FOFEM$_{RA}$ models, shaded areas represent the full range of modeled $P_m$ values (CVS+DBH colored, FOFE$_{MRA}$ in grey), while the dotted lines represent $P_m$ while DBH was held constant (using average DBH).
Fig. 2.3. Stand-level accuracy as a function of spatial scale (A-D), and spatial pattern accuracy of mortality models (E-G). Colored lines and shading represent model predictions for four different mortality models. The y-axis in A-D represents the min and max values of stand-level error from 10 spatially explicit sub-samples within the YFDP. Grey envelopes in A-D represent spatially random null models based on the same number of trees. The lines in E-G represent the pre- (grey) and post-fire (black) live spatial pattern, and modeled post-fire spatial patterns (colors). The y-axis in E represents the number of clumps as a function of clump size. The y-axis in F is the value of the pair-correlation function, \( g(r) \), while the y-axis in G represents change in spatial pattern after the fire. Shaded areas represent a 95% confidence envelope generated by 99 simulations of mortality. The grey dotted lines represent the expected value of \( g(r) \) under the null model of complete spatial randomness (F), or “no change” (G). Shaded regions represent variation expected under the null model. Values above the line indicate aggregation, while values below indicate hyper-dispersion.
CHAPTER III

DETECTING TREE MORTALITY WITH LANDSAT-DERIVED SPECTRAL INDICES: IMPROVING ECOLOGICAL ACCURACY BY EXAMINING UNCERTAINTY

Abstract

Satellite-derived fire severity metrics are a foundational tool used to estimate fire effects at the landscape scale. Changes in surface characteristics permit reasonably accurate delineation between burned and unburned areas, but variability in severity is much more challenging to detect. Previous studies have relied primarily on categorical data to calibrate severity indices in terms of classification accuracy, but this approach does not readily translate into an expected amount of error in terms of actual tree mortality. We addressed this issue by examining a dataset of 40,370 geolocated trees that burned in the 2013 California Rim Fire using 36 Landsat-derived spectral indices.

The differenced Normalized Burn Ratio (dNBR) performed reliably well, but the differenced SWIR1:NIR ratio most accurately predicted percent basal area mortality and the differenced normalized vegetation index (dNDVI) most accurately predicted percent mortality of stems ≥10 cm diameter at breast height. Relativized versions of dNBR did not consistently improve accuracy; the relativized burn ratio (RBR) was generally equivalent to dNBR while the Relative dNBR (RdNBR) had consistently lower accuracy.

There was a high degree of variability in observed tree mortality, especially at

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intermediate spectral index values. This translated into a considerable amount of uncertainty at the landscape scale, with an expected range in estimated percent basal area mortality greater than 37% for half of the area burned (>50,000 ha). In other words, a 37% range in predicted mortality rate was insufficient to capture the observed mortality rate for half of the area burned. Uncertainty was even greater for percent stem mortality, with half of the area burned exceeding a 46% range in predicted mortality rate. The high degree of uncertainty in tree mortality that we observed challenges the confidence with which Landsat-derived spectral indices have been used to measure fire effects, and this has broad implications for research and management related to post-fire landscape complexity, distribution of seed sources, or persistence of fire refugia. We suggest ways to account for uncertainty that will facilitate a more nuanced and ecologically-accurate interpretation of fire effects.

This study makes three key contributions to the field of remote sensing of fire effects. First, we conducted the most comprehensive comparison to date of all previously published severity indices using the largest contiguous set of georeferenced tree mortality field data, revealing that the accuracy of both absolute and relative spectral indices depends on the tree mortality metric of interest. Second, we conducted this study in a single, large fire that enabled us to isolate variability due to intrinsic, within-landscape factors without the additional variance due to extrinsic factors associated with different biogeographies or climatic conditions. We show that uncertainty is related to fire severity and is greatest at intermediate severity levels. Finally, we identified the range in tree mortality that may be indistinguishable based on spectral indices derived from Landsat satellites, and we demonstrated how this variability translates into a considerable amount
of uncertainty in fire effects at the landscape scale.

1. Introduction

The ecological effects of fire (hereafter “burn severity” sensu Morgan et al., 2014) are highly variable in both space and time, posing a challenge to managers and scientists who seek to quantify patterns in fire effects across large landscapes. For all but the smallest fires, satellite imagery is the only feasible way to accomplish this. Satellite-derived spectral indices can provide reasonably accurate estimates of burn severity over large landscapes (Miller et al., 2009), and they are relied upon heavily by land managers and fire scientists alike (Eidenshink et al., 2007). Since the formalized development of dNBR as a tool to detect burn severity in the early 2000’s (Miller and Yool, 2002; Key and Benson, 2006) researchers have continued to develop and refine alternative indices (e.g., RdNBR, RBR, MIRBI), striving to improve accuracy and consistency among fires and across regions (Trigg and Flasse, 2001; Roy et al., 2006; Miller and Thode, 2007; Parks et al., 2014; McCarley et al., 2018). As numerous indices have been developed, there is a pressing need to compare the growing collection of spectral indices with a consistent dataset to determine which estimate tree mortality with the greatest accuracy, and to characterize the uncertainty that should be expected across the range of satellite-derived spectral index values.

A few studies have conducted such comparisons, but the emphasis has been on classification accuracy regarding categorical severity classes (burned vs. unburned areas [Brewer et al., 2005; Meddens et al., 2016]; or low, medium, and high severity [Epting et al., 2005; Miller and Thode, 2007; Cansler and McKenzie, 2012]). These approaches can determine overall classification accuracy, but they do not permit error to be quantified
and assessed as a continuous variable. Recent studies have begun to address this research gap by calibrating spectral indices using continuous, field-based measures of burn severity (Miller et al., 2009; Whitman et al., 2018; Harvey et al., 2019), but these studies have utilized model performance metrics such as $R^2$, AUC, AIC, and Kappa – strong in a statistical sense but quite limited in their ability to describe uncertainty in tangible, ecological terms (e.g., range of fire effects that should be expected). To our knowledge no study to date has quantified the range in tree mortality that should be expected at any given value of a spectral index (but see Harvey et al., 2019 for a closely related example).

The 30-m resolution of Landsat pixels poses a challenge to ecological interpretation of reflectance values. There is a fundamental mis-match between the size of 30-m pixels and the crown spread of individual trees; pixel values therefore represent an “average” spectral response based on the wide range of spectral changes occurring among individual trees at the sub-pixel scale. The problem this creates is that the mortality of many smaller trees may elicit the same spectral response as the mortality of one very large tree (Fig. 3.1, 3.6), just as one can achieve the same reduction in canopy cover by removing many small trees or few large trees, yet the ecological implications of these two scenarios are vastly different. Presently, one may refer to the literature to determine which spectral index has the highest classification accuracy, but until recently there was no way to translate spectral index values into an estimate of actual tree mortality (e.g., percent change in canopy cover, basal area, or number of stems; see Whitman et al., 2018 and Harvey et al., 2019 for two recent examples). A patch of Landsat pixels may appear to have burned with homogeneous severity based on satellite-derived indices, but the actual variability in fire effects (e.g., Fig. 3.1) remains uncharacterized. What is the range
in tree mortality that may appear equivalent using satellite-derived data, and with what resolution can different fire severities reliably be delineated?

Understanding the relationship between Landsat-derived spectral indices and actual tree mortality will better enable both researchers and managers to accurately assess fire effects and their concomitant ramifications for changes to forest structure (Morgan et al., 2014). We evaluated 36 spectral indices using spatially-explicit, georeferenced forest inventory data of 40,370 trees that were alive pre-fire. The purpose of this study was not to identify a single optimal index or to advance a new remote sensing technique. Rather, this study was designed to serve as a guide to enhanced ecological interpretation of Landsat-derived spectral indices. Our objectives were to: 1) quantify the variability in field-measured tree mortality (in terms of number of stems and basal area) that should be expected across different satellite-derived spectral index values; 2) determine which spectral indices have the highest accuracy for those field-based tree mortality metrics (i.e., basal area of mortality, percent change in density, and mortality of large-diameter trees); and 3) examine how variability in satellite-derived estimates of observed mortality may be scaled up to assess uncertainty at the landscape scale (>1,000 km²).

2. Methods

2.1. Study sites

We conducted this study in the lower-montane mixed-coniferous forest zone of the Sierra Nevada Mountains, California, USA (Fig. 3.2). We combined two datasets: a long-term 25.6-ha permanent monitoring plot established in 2010 (the Yosemite Forest Dynamics Plot [YFDP]; Lutz et al., 2012; Lutz, 2015), and a network of 53 0.25-ha plots
established in 2017 (hereafter Joint Fire Science Program [JFSP] plots; Macriss et al. 2019). All study sites were within Yosemite National Park (Yosemite) and were within the footprint of the 2013 California Rim Fire (excluding four unburned JFSP plots).

The YFDP has dimensions of 320 m × 800 m and contains 260 contiguous 30 m × 30 m Landsat pixels (Lutz et al., 2018b; Fig. B.1). It is located at a mean elevation of 1,843 m in an old-growth *Abies concolor – Pinus lambertiana* (white fir – sugar pine) forest on predominantly northerly aspects. In 2009 – 2010, all live trees ≥1 cm and all snags ≥10 cm diameter at breast height (DBH; 1.37 m) were tagged, identified, and mapped (34,458 live trees; 2,697 snags). The plot has been censused every year since establishment; newly recruiting trees have been tagged and newly dead trees have been characterized by the factors contributing to their mortality. In August of 2013, the YFDP was burned for the first time since 1900 (Barth et al., 2015). A full post-fire remeasurement was conducted in May 2014.

The JFSP plots were selected to capture the range of forest types, fire histories, and burn severities within the Yosemite Rim Fire footprint (Figs. 3.2, B.1&B.2). The JFSP plots were square 50 m × 50 m plots established in *Pinus ponderosa – Calocedrus decurrens*, *Pinus jeffreyi*, *Abies magnifica – Abies concolor*, and *Abies concolor – Pinus lambertiana* forest types between 1,431 m and 2,250 m elevation. Plots were installed post-fire based on a randomly chosen locations stratified by severity category (Fig. B.2). Satellite-derived severity was estimated before plot installation using dNBR derived from Landsat 8 images (pre-fire scene July 14, 2013 and post-fire scene July 1, 2014). Plots were placed within patches of uniform severity class at least 3 × 3 pixels (90 m square; 0.81 ha) to buffer against positional error (Fig. B.1). The distance to roads and trails was
>0.1 km and <1.5 km to minimize edge effects while maintaining accessibility. Plots were located in the field using a handheld GPS, after which we collected precise positional data using a survey-grade GNSS receiver (Topcon HiPer SR). We post-processed plot coordinates to sub-meter accuracy with Natural Resources Canada Precise Point Positioning tool (https://webapp.geod.nrcan.gc.ca/geod/tools-ouils/ppp.php). Within each JFSP plot, all trees ≥10 cm DBH were identified, measured, and mapped.

Trees were mapped from permanent grid markers using transect tapes and lasers and are within ±0.25 m to the datum (details in Lutz et al., 2012). Status was recorded as either live, fire-killed, or dead but not due to fire; no trees ≥10 cm DBH were fully consumed. Field personnel used a variety of cues to successfully determine status (see Jeronimo et al., in press for details).

2.2. Rim fire

The Rim Fire began in August 2013 and was active for over two months, burning 104,131 ha of the Stanislaus National Forest and Yosemite National Park. After it finished burning it was the largest fire on record in the Sierra Nevada and the third largest in California, though it has since been surpassed by two similarly large fires in other parts of California (CAL FIRE 2018). The sites used in the present study burned with mixed severity (Figs. 3.2 & B.2; Larson et al., 2016; Cansler et al., 2019; Kane et al., 2015; Furniss et al., 2019), with weather conditions more moderate compared to the low relative humidity and plume-dominated fire that resulted in large, high-severity patches in the Stanislaus NF and some parts of Yosemite (Lydersen et al., 2014; Lutz et al., 2017a, Collins et al., 2019).

Within Yosemite National Park, the Rim Fire burned with a higher proportion of
moderate-severity (25% to 75% mortality by basal area) and high-severity (≥75% mortality by basal area) than was characteristic of the pre-suppression fire regime in lower-montane mixed conifer forests of the Sierra Nevada (based on Landsat-derived severity maps; Lydersen et al., 2014; Harris and Taylor, 2015). However, since the reintroduction of fire to the park in the 1970s, there has been a shift to larger fires with greater areas of moderate- and high-severity (van Wagtendonk and Lutz, 2007; Lutz et al., 2011; Collins et al., 2019), and the severity distribution for the Rim Fire within Yosemite was representative of this contemporary regime (Fig. B.2). Fires in the Sierra Nevada are projected to either sustain or increase in size, frequency, and severity in the coming decades (Lutz et al., 2009), making the Rim Fire an optimal case study generalizable to other large, mixed-severity fires in the region.

2.3. Landsat data

Landsat 8 scenes were chosen to maximize scene clarity while matching pre- and post-fire phenology (sensu Key and Benson, 2006). We conducted both initial (post-fire imagery taken immediately following fire) and extended assessments (post-fire imagery taken approximately one year post-fire). While extended assessments are generally considered to more accurately capture fire effects in forests (Key and Benson, 2006; Miller and Thode, 2007), initial assessment may be important to inform management action within the year following the fire.

Extended assessments were conducted using data from July 14, 2013 (pre-fire) and July 1, 2014 (post-fire). Initial assessments were conducted using data from August 15, 2013 (pre-fire) and September 16, 2013 (post-fire). We were not able to select a more phenologically matched scene pair for the initial assessment (i.e., matching scenes
separated by 12 months) because adequate Landsat imagery was not available the year prior to the fire (2012) – the Landsat 8 satellite was launched in 2013, the striping in Landsat 7 images covers the study area, and the Landsat 5 TM sensor failed in 2011. Though both scenes used in the initial assessment were from the same season, we conducted a phenological offset calibration to minimize the difference in phenology between the two scenes (details below).

Images were terrain corrected and co-registered by the USGS Earth Resources Observation and Science Center (EROS). These orthorectified top-of-atmosphere reflectance images (Level 1T products) were further processed by USGS EROS to remove atmospheric effects (Vermote et al., 2016), resulting in Level-2 surface reflectance (SR) image products that were accessed through the EROS Science Processing Architecture bulk ordering service (https://espa.cr.usgs.gov).

For the bi-temporal indices (i.e., indices based on differencing the pre- and post-fire scenes), we conducted a phenological calibration to minimize phenological mismatch between the two scenes. This was done by selecting a calibration zone adjacent to the fire (and in the same forest type) that did not burn, calculating the mean of the index values from the calibration area of the post-fire image, and subtracting this value from the entire scene (sensu Parks et al., 2014; Meddens et al., 2016). This reduces phenological bias and more clearly isolates fire-induced changes to vegetation.

2.4. Spectral index calculations

We compiled a list of 36 spectral indices that are sensitive changes in vegetation, with an emphasis on indices that have been used to detect fire effects (Table 3.1). We included both “snapshot” indices (based only on post-fire scene; 14 indices) and bi-temporal
indices (difference between pre- and post-fire scenes; 22 indices). Indices were calculated according to published formulas included in Table 3.1. We also included slope, aspect, and landscape position as these topographic variables have been shown to influence fire behavior (Kane et al., 2015; Meddens et al., 2016). Topographic variables were calculated based on a 10-m digital elevation model (USGS 2007) that we resampled to match the resolution and extent of the Landsat images. Slope, aspect, and landscape position were calculated based on eight neighboring cells, and aspect was cosine-transformed.

2.5. Spectral index validation

We treated each of the 260 Landsat pixels within the YFDP as individual sampling units, and we generated separate tree lists based on the trees that fell within each pixel. We calculated all spectral indices for the entire Rim Fire, then we extracted the index values for each individual pixel. We also assigned an area-weighted average index value to each pixel based on adjacent pixels intersected by a 6-m buffer to account for the positional error of the Landsat scenes and canopy overlap of trees rooted in adjacent pixels. For the JFSP plots, we generated individual tree lists associated with each of the 53 plots. Pixel values for the JFSP plots were assigned using an area-weighted average because each of the 0.25-ha plots contained 4 to 6 partial pixels (Fig. B.1). For each tree list, we calculated mortality rate by density and basal area (BA) as the percentage of pre-fire live trees ≥10 cm DBH (% stems ha⁻¹ for density; % m² ha⁻¹ for BA) that were killed within one year of the fire.

2.6. Quantifying error

To quantify the accuracy of each spectral index, we created individual random forest
models for each index with the index value as the predictor variable and observed mortality (% stems ha\(^{-1}\) for density and % m\(^2\) ha\(^{-1}\) for BA) as the response. Correlations were summarized using percent variance explained (%VE), an independent out-of-bag estimate of error generated by the random forest algorithm. We used random forest analysis because it is a non-parametric statistical method that does not require the assumption of normality (Cutler et al., 2007), making it ideal to model fire severity data that may assume different non-linear response curves and contain non-normal residual distributions (Meddens et al., 2016; Whitman et al., 2018; Parks et al., 2018). We created separate models for each spectral index to avoid biased estimates of model performance due to collinearity between indices.

Because the ecological effects of tree death depend on the metric used (Lutz and Halpern, 2006), we partitioned observed mortality in different ways to assess how each index detected the following observed mortality categories: percent basal area mortality (hereafter BA mortality), percent small tree mortality (1 cm ≤ DBH < 10 cm; this was only calculated for pixels within the YFDP), percent stem mortality for trees ≥10 cm DBH (hereafter stem mortality), percent stem mortality for trees ≥50 cm DBH (hereafter stem ≥50 cm DBH mortality), and percent stem mortality for trees ≥100 cm DBH (hereafter stem ≥100 cm DBH mortality). The subset of trees ≥10 cm DBH was used to permit direct comparison with other datasets that do not contain trees smaller than 10 cm DBH (as with many forest inventory datasets). We assessed small-diameter tree mortality separately for the distinct ecological role they play as a regenerating cohort. Our assessment of mortality of medium- and large-diameter (≥50 and ≥100 cm DBH, respectively) trees enabled us to test whether mortality of these less numerous but
disproportionately important (Lutz et al., 2018a) trees may be accurately estimated with Landsat-derived indices.

In addition to the random forest analysis, we assessed accuracy using locally-weighted scatterplot smoothing (LOESS) models, a non-parametric statistical method which fits a regression line based on localized subsets of data points. For this analysis, we summarized observed mortality in two ways: percent BA and percent stem ≥10 cm DBH mortality. We avoided using generalized linear models because there is a weak theoretical basis for the shape of the relationship between spectral indices and tree mortality (e.g., van Wagtendonk et al., 2004; McCarley et al., 2017; Whitman et al., 2018), and this would have biased our results towards indices that happen to conform most closely to an arbitrarily-chosen model form. The LOESS technique performs regression based on the observed shape of the data rather than an a priori functional form, and may be used with non-linear data and non-normal distributions of residuals. We used the loess.sd() function from the msir package version 1.3.1 (Scrucca, 2011) with the “span” parameter set to 0.8 and all other parameters set to their defaults.

We generated LOESS models for each spectral index with observed mortality as the independent variable and normalized index values as the dependent variable, and we extracted the standard deviation of the model as a continuous function of observed mortality values. We multiplied the standard deviation values by ±1.96 to create an error envelope that contained (approximately) 95% of the data points. This error envelope may be interpreted as the amount of variability in the spectral response of each index as a function of observed burn severity. This is intentionally different from a confidence interval based on standard error which would reflect the certainty with which one could
estimate the “true” mean value. To characterize the variability in observed mortality across the range of spectral index values (as opposed to the variability in spectral indices across the range in observe mortality), we created additional LOESS models with raw (non-normalized) index values as the independent variable and observed mortality as the dependent variable (same two variables, but axes were reversed; \textit{sensu} Miller and Thode, 2007; Miller et al., 2009; Parks et al., 2014; Whitman et al., 2018; Harvey et al., 2019). These models may be interpreted as the expected amount of \textit{variability in observed tree mortality as a function of the values of each spectral index.}

We tested whether variability in satellite-derived spectral index values were related to pre-fire forest characteristics by extracting the residuals (predicted minus observed) from the LOESS models. Pre-fire structure for the JFSP plots was reconstructed by considering all fire-killed trees as live pre-fire and adding them to the populations of trees that were alive when the plots were established. We tested for correlations using linear regression between LOESS residuals and pre-fire stand attributes including pre-fire stand structure (density and basal area), LiDAR-derived topographic metrics (topographic position, slope, aspect, solar irradiance), and LiDAR-derived percentage canopy cover for four canopy height strata (>2 m, 2 m – 8 m, 8 m – 16 m, and 16 m – 32 m; details may be found in Kane et al., 2015). We examined spatial auto-correlation with the YFDP by creating semivariograms for basal area mortality and residuals of the LOESS model for dNBR.

2.7. Rarefied spectral index validation

Considering the uneven distribution of severities in the study sites (most pixels were low-severity (≤25% mortality by basal area) to moderate-severity; Fig. B.1&B.2), we
conducted an additional validation based on a subset of the full dataset which was stratified by observed mortality class. The validation based on the full dataset will be most relevant for fires that burn with a similar severity distribution as the data used in this study (primarily low- to moderate-severity, as with many mixed-severity fires in the Sierra Nevada), the rarefied validation dataset will provide a more robust estimate of spectral index accuracy even at severity levels that are under-represented by our dataset (primarily high severity). This validation may therefore be more applicable to areas which burn with larger proportions of high-severity.

To create a rarefied dataset, we classified the full dataset into 10% bins based on observed mortality, and we randomly selected two observations from each of these bin to create a subset of 20 data points. At first we selected observations without replacement, then we selected with replacement once all observations in a given bin had been used. We continued to select unique subsets until each observation was used at least once, then we generated a random forest model for each spectral index based on each rarefied sample. Percent variance explained was averaged among all subsets to create a final rarefied accuracy estimate for each index. We performed this analysis on the five best performing indices as determined by the random forest models created with the full dataset. We calculated standard error and used Tukey’s honest significant difference to identify significant differences between indices at $\alpha = 0.05$.

2.8. Estimating uncertainty at the landscape scale

We scaled the satellite-derived mortality predictions and associated variability to the entire Rim Fire footprint to explore how variability in a satellite-derived spectral index may translate to uncertainty in fire effects at the landscape scale (>1,000 km²). We
performed this analysis with dNBR, as it is perhaps the most ubiquitous severity index (Eidenshink et al., 2007; Meddens et al., 2016; McCarley et al., 2017). We used LOESS models that were created for dNBR to generate a predicted mortality rate (percent of BA and percent of stems ≥10 cm DBH) and associated standard deviation across the full range of dNBR values observed within the Rim Fire. We then assigned the predicted mortality rate and a 95% confidence envelop based on the dNBR value for every Landsat pixel within the fire footprint. We calculated high and low estimates of mortality based on the predicted mortality rate ± 1.96 standard deviations, and generated an uncertainty map based on the difference between the high and low mortality estimates. The range of severities captured by our study sites represented 92% of the area burned by the Rim Fire (dNBR was lower in 5% and higher in 3% of the fire footprint), and we used conservative estimates of uncertainty for those extremities to avoid over-estimating uncertainty (we estimated 20% uncertainty for the lowest severities and 1% for the highest severities; both values were less than the observed level of uncertainty for at similar severity levels). The resulting map of uncertainty may be interpreted as the range in predicted mortality values that is necessary to bracket the true level of mortality 95% of the time. We conducted this analysis for both percent BA and percent stem mortality, and with both 95% and 68% confidence envelopes (±1.96 SD and ±1 SD, respectively).

All analyses were performed in R version 3.5.2 (R Core Team, 2018) using version 1.3.1 of msir (Scrucca, 2011), version 4.6.14 of randomForest (Liaw and Wiener, 2002), and version 2.6.7 of raster (Hijmans, 2016).
3. RESULTS

Stem mortality ≥10 cm DBH one year post-fire ranged from 0% to 100% within the 53 JFSP plots and 0% to 88% within the 260 contiguous Landsat pixels within the YFDP. Basal area mortality ≥10 cm DBH was 0% to 100% within the JFSP plots and 0% to 74% within the YFDP (Fig. 3.3). Average mortality among the 313 plots was 43% of trees ≥10 cm DBH and 21% of BA. Crown torching was minimal within the YFDP, and most fire-killed trees retained red needles >1 yr post-fire. Satellite-derived severity ranged from unburned (no change detected) to high severity (minimum dNBR -11, maximum dNBR 870; Table B.1), spanning a range of dNBR values representative of 92% of the area within the Rim fire footprint (5% of the fire footprint had dNBR values <-11 and 3% had dNBR values >870). Most of the study area was burned at low and moderate severities (Figs. 3.2, B.1, B.2; Table B.1).

3.1 Detecting mortality with spectral indices

The extended assessment was more accurate than the initial assessment, especially for stem mortality (Table 3.2). The extended assessment increased percent variance explained (%VE) from 28% to 49% for percent stem mortality and from 58% to 63% for percent BA mortality. The most accurate indices for the initial assessment were dTC.WET (percent stem mortality only), dNBR (percent BA mortality only), and RBR (both stem and BA mortality). The most accurate indices for the extended assessment were dNDVI (percent stem mortality), dSWIR1.NIR (percent BA mortality), and dNBR (both stem and BA mortality). RBR and dNBR detected basal area mortality with similar accuracy (57.3%VE and 56.7%VE, respectively), but dNBR was more accurate for percent stem mortality (Table 3.2). RBR was more accurate for percent mortality of
stems ≥50 cm DBH, and both indices had low accuracy for percent stem mortality of large-diameter stems (≥100 cm DBH). RdNBR was inferior to both dNBR and RBR in all mortality categories, with the exception of the marginal increase in accuracy for large-diameter stem mortality. The results for dSAVI were functionally equivalent to those of dNDVI for all analyses (their formulae are nearly identical); all discussion of dNDVI henceforth applies to dSAVI as well.

Accuracy was generally higher for percent BA mortality compared to percent stem mortality (stems ≥10 cm DBH), with an increase in %VE of 22% for RBR and 15% for dNBR. dNDVI, in contrast, was more accurate for percent stem mortality (Table 3.2). All spectral indices had very low accuracy in estimating percent mortality of saplings (1 cm ≤ DBH < 10 cm; maximum 8% for NDVI), but there was a steep increase in %VE for small- and intermediate-sized stems (≥10 cm DBH; 49% for dNDVI). Percent stem mortality was estimated most accurately for stems ≥50 cm DBH (57% for dR), then declined for stems ≥100 cm DBH (33% for dSWIR2). Accuracy was higher for the JFSP plots compared to the YFDP, with maximum %VE for BA mortality of 83% and 38%, respectively (dR for JFSP and dNBR for YFDP; Table 3.2).

3.2. Spectral index accuracy at different levels of observed mortality

Visual interpretation of the LOESS regression error envelopes corroborated the random forest results (Figs. 3.3&B.3&B.4). The indices with the highest %VE according to random forest models had the tightest error envelopes, and envelopes grew as %VE decreased. The range in observed mortality (both percent stem and BA morality) was greatest at intermediate spectral index values, but this contained pixels that were burned at both moderate- and high-severity according to the categorical severity classes for
dNBR established by Miller and Thode (2007). The range in percent BA mortality was 18\% for unburned (dNBR < 41), 31\% for low severity (41 \leq dNBR < 176), 47\% for moderate severity (177 \leq dNBR < 366), and 61\% for high severity (dNBR \geq 367). The range in percent stem mortality was 34\% for unburned, 61\% for low severity, 65\% for moderate severity, and 37\% for high severity (Fig. 3.3).

The correspondence between observed mortality and spectral indices assumed a different relationship when the axes were swapped (Fig. 3.4). The relative accuracy of each index remained the same, but the distribution of uncertainty was different. The previous analysis demonstrated that uncertainty in observed mortality was greatest at intermediate spectral index values, while this analysis demonstrated that the range in spectral index values was greatest at the highest levels of observed mortality. In other words, a strong spectral response was associated with a very low range in observed mortality (because mortality was 100\%; Fig. 3.3), but a high level of observed mortality (>95\%) was associated with a wide range of spectral responses (Fig. 3.4). For example, the range in dNBR values for plots that had 100\% mortality was 452 to 870 (Figs. 3.3&3.4); a near doubling of spectral response values without any difference in tree mortality. The range in normalized index values was positively related to both percent stem and percent BA mortality; variability was approximately two standard deviations at low (<25\%) mortality levels, while the range often exceeded 3-4 standard deviations at high (>75\%) mortality levels (Fig. 3.4).

Variability in observed mortality (residuals of the LOESS models) was not correlated with any of the pre-fire metrics examined: pre-fire basal area, pre-fire density, LiDAR-derived topographic variables, or LiDAR-derived canopy metrics. Accuracy for the
YFDP pixels was generally reduced by using an area-weighted average pixel value based on a 6 m buffer around each pixel, though some snapshot indices (derived from the post-fire scene alone) were marginally improved with the buffer (Table B.2).

3.3. Rarefied results

Random forest models based on a rarefied dataset yielded subtly different results compared to the models based on the full dataset (Table B.3). The rarefication procedure enabled us to calculate the standard error of %VE for the random forest models based on different subsets of data and to test for significant differences. As with the full dataset models, dSWIR1.NIR had the highest accuracy for percent BA mortality, while dNDVI had the highest accuracy for percent stem mortality (Table B.3). RdNBR, RBR, and dSWIR1.NIR were most accurate for stem mortality of medium-diameter stems, while RdNBR and RBR were most accurate for large-diameter stems. dNBR was not best in any category, but it was never the least accurate.

3.4. Uncertainty at the landscape scale

Scaling the relationship between dNBR and observed mortality to the entire Rim fire, estimated mortality within the year following the fire was 45% of basal area and 60% of stems ≥10 cm DBH (Figs. 3.5&B.5). At a 95% confidence level, uncertainty in percent BA mortality was less than 10% for only 5% of the fire footprint, <20% for 8% of the footprint, and <40% for 53% of the footprint (Fig. 3.5). Uncertainty was generally higher for percent stem mortality, with less than 10% uncertainty for 11% of the fire footprint, <20% for 20% of the footprint, and <40% for 43% of the footprint (Fig. B.5). Half of the area burned by the Rim Fire (median uncertainty value) had a range in estimated mortality of >37% of pre-fire basal area and >46% of pre-fire stems ≥10 cm DBH.
Mortality estimates were most accurate in the high-severity and unburned patches (severity levels based on dNBR) where uncertainty was within 10%, while uncertainty in moderate-severity areas was as high as 80% for percent BA and 70% for percent stem mortality (Figs. 3.5&B.5).

We observed similar results at the 68% confidence level (Figs. B.6&B.7). Uncertainty was greatest overall for percent stem mortality, but the greatest uncertainty for an individual dNBR severity class was for percent BA mortality in moderate-severity areas where the range in estimated percent BA mortality was 40% (Fig. B.6). In other words, a 40% range in predicted BA mortality rates (e.g., BA mortality predicted to be between 50% and 90%) would only contain the true level of mortality approximately two-thirds of the time. The range in the 68% confidence envelope exceeded 22% for percent BA mortality and 29% for percent stem mortality in half of the Rim Fire footprint (Figs. B.6&B.7).

4. Discussion

4.1. The satellite’s perspective

Spectral indices most accurately detected mortality of stems ≥50 cm DBH, an intuitive result considering that medium-diameter stems are the most prominent component of the upper canopy and therefore dominate the satellite’s view of the forest, simultaneously concealing many of the smaller diameter stems in the understory (see also Jeronimo et al., 2019). We might also expect spectral indices to be highly sensitive to large-diameter (≥100 cm DBH) tree mortality, but the lower relative abundance and reduced susceptibility to immediate fire-induced mortality (Furniss et al., 2019) appears to have reduced their contribution to the overall spectral response. The prominence of
stems ≥50 cm DBH in the satellite view of the canopy also explains the strong correlation between spectral indices and %BA mortality, as trees in this diameter class are primary contributors to overall forest BA in many forests (Lutz et al., 2012, 2013, 2018a).

4.2. Spectral index comparison

No single index estimated all forms of observed mortality most accurately. Perhaps the most commonly used spectral index, dNBR, was among the top three indices for most mortality categories, but it was rarely the most accurate. RdNBR and RBR, two indices introduced to improve upon dNBR (Miller and Thode, 2007; Parks et al., 2014), did not offer consistent improvement. dNBR was more accurate than RdNBR in every category other than stem mortality of trees ≥100 cm DBH, while dNBR and RBR were more similar. dNBR has been recognized as outperforming RdNBR under some conditions (Cansler and McKenzie, 2012; Meddens et al., 2016; McCarley et al., 2017, 2018; Veraverbeke and Hook, 2013), and although relativized versions of dNBR may increase accuracy in some contexts, they were not unconditionally better in this study. The benefits of relativized indices may be less dramatic for individual fires at the stand- to landscape-scale, but they may still enhance accuracy when applied to multiple fires at the regional scale. Other indices that have been developed to detect burn severity were less accurate; dNDMI and CSI had accuracies of 41% and 46% for percent stem and percent BA mortality, respectively, while dMIRBI had 0%VE for both types of mortality (Figs. B.3&B.4, Table B.2).

dNBR is likely the best index for general use as it was within the top three indices for both percent stem and percent BA mortality (Table 3.2), but specific aspects of fire-induced structural changes may be estimated more accurately by using dSWIR1.NIR to
estimate BA mortality and dNDVI to estimate stem mortality. If large-diameter trees are of specific concern, dR or dSWIR2 may be more useful. Compared to dNBR, dR improved accuracy by 15% for stems $\geq 50$ cm DBH, and dSWIR2 improved accuracy by 26% for stems $\geq 100$ cm DBH. This result may be of particular interest to carbon modeling research as large-diameter trees contribute disproportionately to above ground biomass (Lutz et al., 2017b, 2018a) and carbon sequestration (Stephenson et al., 2014). Landsat-derived spectral indices did not accurately detect small-diameter tree mortality in our study sites because the upper canopy obscured the satellite view of the sub-canopy trees. In forests with multi-layered canopies, Landsat-derived spectral indices may be an inadequate tool to assess aspects of burn severity that are related to small-diameter tree mortality (e.g., wildlife habitat, advanced regeneration, biodiversity).

A surprising result was that dNDVI was more accurate than dNBR for detecting percent stem mortality for trees $\geq 10$ cm DBH (48% versus 40% VE). A plausible explanation is that dNBR uses the SWIR2 band which is primarily sensitive to newly exposed ash and mineral soil (Miller and Yool, 2002; van Wagendonk et al., 2004), and a high percent stem mortality can be achieved without actually exposing much forest floor if mortality is comprised mostly of trees <10 cm DBH (Figs. 1&6). High BA mortality will more reliably expose forest floor compared to high stem mortality (because medium- and large-diameter trees occupy more canopy surface area; Fig. 3.6), commanding a tighter relationship between BA mortality and post-fire reflectance in the SWIR2 band (Fig. B.8). Conversely, dNDVI replaces the SWIR2 band with the red band which is more sensitive to the density and health of vegetation (Tucker, 1979). dNDVI may therefore be less sensitive to newly exposed forest floor and more sensitive to the
reduction in canopy density and depth associated with mortality of shrubs and trees <50 cm DBH that are more numerically abundant (Lutz et al., 2014, 2017a) yet contribute little to overall BA. dNDVI may also be more sensitive to the mortality associated with non-crowning fire behavior that leaves many of the needles in the canopy intact, as was the case for the majority of our study area (Figs. 3.2,B.1&B.2). As needles may be killed but not consumed by surface (non-crowning) fire, they continue to obscure the forest floor post-fire which reduces the spectral response of the SWIR2 band while simultaneously inducing a strong response in the red band due to their senescence and loss of chlorophyll.

An additional explanation is that mortality of large trees requires greater fire intensity compared to mortality of smaller trees (due to thicker bark and higher crown base height; Hood et al., 2018), and this higher fire intensity may be associated with more duff consumption and exposed mineral soil post-fire. Both of these explanations are supported by post-hoc analyses demonstrating that the red band was most strongly correlated with percent stem mortality (compared to NIR and SWIR2), while the SWIR2 band was more strongly correlated with percent BA mortality (Fig. B.8). Based on these correlations, one would expect the index containing the Red band (dNDVI) to have a higher sensitivity to stem mortality and the index containing the SWIR2 band (dNBR) to be more sensitive to BA mortality.

The best spectral index may depend on forest type, successional stage, and the history of disturbance. dNDVI had high accuracy in the mixed conifer forests within our study area (density between 42 and 1233 stems ≥10 cm ha⁻¹; Table B.1), but indices that incorporate a SWIR band may be more appropriate in more open forests because of their
sensitivity to ash and mineral soil on the forest floor. RdNBR and RBR were not consistently better than dNBR within our study area, but they may enhance accuracy when applied to broad spatial or temporal scales that contain greater variability in biophysical conditions (e.g., Miller and Thode, 2007; Parks et al., 2014, 2018; Harvey et al., 2019).

4.3. Challenges in detecting tree mortality from space

The 30-m spatial resolution of Landsat pixels imposes some inescapable uncertainties associated with calibrating satellite-derived spectral indices to field-based metrics of burn severity, and this may be especially pronounced in ecosystems with heterogeneous vegetation and fire behavior (Morgan et al., 2014). Landsat pixels are broader than the scale of individual trees; the crown spread of even the largest *P. lambertiana* is <20 m (Van Pelt, 2001), which combined with the dispersed spatial pattern of large-diameter trees (Lutz et al., 2012) represents a maximum of 37% of the area contained within a single pixel. Furthermore, fire behavior in the Sierra Nevada can be heterogeneous at very fine spatial scales (Kolden et al., 2012; Meddens et al., 2018a, Blomdahl et al., 2019; Furniss et al., 2019). Spectral reflectance for each pixel in a low- to moderate-severity fire therefore represents a mixture of patches experiencing different levels of mortality; the mortality of one large-diameter tree may elicit the same spectral response as the mortality of many smaller trees (Fig. 3.6).

Consider a pair of pixels chosen to illustrate how these ecologically disparate scenarios that can appear spectrally identical (Fig. 3.1). These two pixels experienced basal area mortality rates of 16% and 96%, but dNBR was the same (dNBR ~ 323; Fig. 3.1, top row). The plot with the low mortality rate had a high pre-fire density (644 stems
ha\(^{-1}\)), and mortality was entirely stems <41 cm DBH. Conversely, the plot with a high basal area mortality rate had a lower absolute mortality rate (299 vs 411 mortalities ≥10 cm DBH ha\(^{-1}\)), but a much higher mortality rate of stems ≥50 cm DBH (109 vs 0 mortalities ≥10 cm DBH ha\(^{-1}\)). Relativized indices such as RdNBR or RBR may reduce this variability, but neither can entirely eliminate this problem of scale. Both RdNBR and RBR were more closely related to observed percent BA mortality compared to dNBR for the present pair of plots (RdNBR = 405 vs. RdNBR = 905; Fig. 3.1, top row), but this relationship was not consistent. Consider another pair of plots with similar dNBR values (dNBR ~ 155; Fig. 3.1, bottom row); the plot with high pre-fire density (505 stems >10 cm ha\(^{-1}\)) experienced 39% BA mortality with RdNBR = 186 and RBR = 91, while the plot with low pre-fire density (42 stems >10 cm ha\(^{-1}\)) experienced only 4% BA mortality with RdNBR = 733 and RBR = 148. In the high-density plot the surviving overstory trees obscured the satellite’s view of actual mortality and resulted in an under-estimate of severity (i.e., low index values), while shrub mortality and soil scorching in the low-density plot elicited a strong spectral response and an over-estimate of severity (Fig. 3.1). Both RdNBR and RBR inflated the satellite-derived index value for the low-density plots, but this did not consistently improve their correspondence to field-based measurements of severity. These case studies were not chosen to be representative of average conditions; rather, they were selected to reveal some of the confounding factors that can compromise the accuracy of satellite-derived spectral indices in heterogeneous environments. If one is interested in average conditions, much of the uncertainty illustrated by this case study will average out. If one is interested in heterogeneity, however, these plots serve as a useful example of the range in fire effects that can be
indistinguishable with 30-m Landsat pixels.

Higher-resolution imagery can be used to reduce uncertainty associated with the 30-m pixel scale (e.g., Meng et al., 2017), but the temporal resolution of the Landsat and Sentinel satellites remains unmatched by sources of satellite imagery with finer spatial resolutions. The high temporal resolution (16 days for Landsat-8 and 10 days for Sentinel-2) and 35-year legacy of the Landsat program have made Landsat imagery indispensable for the remote detection of fire severity, rendering the uncertainty associated with a 30-m pixel scale a persistent feature of most fire severity maps. Analytical techniques such as spectral mixture analysis (e.g., Quintano et al., 2013) may be used to reduce this uncertainty without relying on higher resolution imagery, but there remains a need for more validations of novel analytical approaches with field-based data.

The large range in spectral index values at high levels of observed mortality (Fig. 3.4) was likely due to the fact that 100% mortality is the maxima for tree-based metrics of severity, but it does not necessarily represent an endpoint of potential fire effects (e.g., soil scorching, shrub and herb mortality). All trees may be killed without incinerating everything else within pixel (i.e., shrubs, grasses, and organic soil), resulting in a lower spectral index value compared to a pixel in which more of the understory, surface fuels, and organic material in the soil are consumed.

4.4. Accounting for uncertainty

This study exposed the high amount of variability in observed mortality levels associated with all spectral indices, especially at intermediate burn severity levels (Fig. 3.3). Although this variability may appear inconsistent with previous studies that have reported strong correlations between spectral indices and field-based measures of severity
(e.g., Miller and Thode, 2007; Parks et al., 2014; Meddens et al., 2016; Veraverbeke and Hook, 2013), it is critical to differentiate between classification accuracy derived using categorical severity classes (unburned vs. burned; low vs. moderate vs. high) and accuracy metrics based on continuous data. The variability we observed is consistent with other spectral index calibrations based on continuous, field-based measures of burn severity (e.g., Miller et al., 2009; Whitman et al., 2018; Harvey et al., 2019), and it emphasizes the persistent need for more quantitative, field-based evaluations of satellite-derived severity products that has existed for over a decade (Lentile et al., 2006).

We suggest a few ways for users of satellite-derived severity products to cope with this uncertainty: 1) use continuous estimates of severity and associated variance (e.g., tree mortality is predicted to be between 50% and 75%), 2) associate a probability level to categorical severity classes (e.g., a moderate-severity pixel may have a 75% chance of being correctly classified), and 3) supplement satellite-derived estimates of burn severity with field-based observations. These approaches will facilitate a more nuanced and ecologically-relevant interpretation of satellite-derived severity metrics. Variability that is not detected by satellite-derived spectral indices represents actual heterogeneity in fire effects that can be of great ecological significance (Kolden et al., 2015; Cansler et al., 2018; Meddens et al., 2018b, Blomdahl et al., 2019), and this could have broad implications for applications ranging from quantifying spatial patterns in burn severity to planning post-fire management actions.

Accounting for uncertainty is particularly important in areas that burn at intermediate severities, particularly when burn severity indices are used to parameterize further calculations (e.g., carbon emissions; Stenzel et al., 2019), examine spatial patterns in burn
severity (e.g., Meddens et al., 2018a; Collins et al., 2019), evaluate landscape change and restoration strategies (e.g., Kane et al., 2014; Becker and Lutz, 2016; Blomdahl et al., 2019), or to examine future fire vulnerability (e.g., Smith et al., 2014). These areas can represent large proportions of the area within a fire footprint (Figs. 3.5&B.2). In the case of the Rim Fire, half of the fire footprint (>50,000 ha) had an uncertainty in predicted mortality of over 37% (±19%) for percent BA mortality and over 46% (±23%) for percent stem mortality (Figs. 3.5&B.5). This is consistent with other studies that have shown uncertainty can severely compromise the accuracy of ecological models when they are applied across heterogeneous landscapes (Hunsaker et al., 2013; Wu et al., 2006; Harmon et al., 2015; Lutz et al., 2017b, Furniss et al., 2017; 2019), and this can limit their utility to resource managers and policy makers (Funtowicz and Ravetz, 1990).

Some of this uncertainty will average out when fire effects are assessed at a large enough scale, potentially yielding estimates of mortality that accurately capture average conditions. The higher accuracy we observed for the JFSP plots compared to the YFDP (Table 3.2) supports this point; we calculated area-weighted averages for the 50 × 50 m JFSP plots which contained 4 to 9 partial pixels (Fig. B.1), and this reduced the potential range of variability in observed mortality compared to the YFDP pixels which were assessed at a 30 × 30 m scale. We conducted a post-hoc test of this hypothesis by aggregating the YFDP pixels into groups of 4 (2 × 2 pixels), 9 (3 × 3 pixels), and 16 (4 × 4 pixels) and assessing %VE with random forest. We found that accuracy increased as we aggregated pixels up to the 3 × 3 pixel scale (67% compared to 38% variance explained at the individual-pixel scale), but accuracy declined as we continued to aggregate (50% at the 4 × 4 pixel scale).
If the metric of interest is simply the amount of area burned at a given severity, and if the scope of inference is broad enough, then the uncertainty that this study exposed may be of little importance. However, for applications that rely on burn areas that have been characterized as homogeneous (e.g., patch metrics *sensu* Keane et al., [2008], distance to seed source, etc.), uncertainty in fire effects should be carefully considered. *While error will average out at large scales, the heterogeneity that this uncertainty represents does not disappear.* In other words, a 46% range in mortality does not mean that mortality predictions will be off by 46%; it means that an area that appears homogeneous based on Landsat-derived spectral indices may actually contain pixels in which mortality was 23% higher or lower than the average conditions.

4.5. The single-fire approach

With a single-fire study there is always the question about generalizability to other fires and biogeographical regions, but the single-fire approach can provide a unique perspective that is more akin to how managers use satellite-derived severity maps to guide post-fire management and restoration. This approach allowed us to isolate variability due to intrinsic, within-landscape factors without the additional variance due to extrinsic factors associated with fires that burn in different biogeographical regions and under different climates (e.g., Harvey et al., 2019).

We note that neither approach is inherently better; the most optimal approach will depend on the nature of the desired inferences. Multiple-fire studies offer greater capacity to parameterize models and generalize across broad regions, while single-fire studies permit a more precise evaluation of the maximum accuracy that may be attained with a Landsat-derived severity map for any given fire. By choosing a fire characteristic of the
new fire regime in the Sierra Nevada (van Wagtendonk and Lutz, 2007; Lutz et al., 2009; Lydersen et al., 2014) and establishing a large calibration dataset with a wide range of severities (Fig. B.2), we were able to consistently evaluate the relationship between spectral indices, tree-based mortality, and the uncertainty of the estimates. This provides a rigorous estimate of maximal severity index accuracy for Sierra Nevada mixed-conifer forests.

This study is also unique in that we relied heavily on tree mortality data from a single large study plot that contained many contiguous Landsat pixels; this is distinctly different from the 30-m Composite Burn Index (CBI) plots that have been widely used to calibrate spectral indices for over a decade (Key and Benson, 2006; Eidenshink et al., 2007; Miller and Thode, 2007; Parks et al., 2014, 2018). CBI calibration plots are typically located in patches of homogeneous fire severity to minimize uncertainty due to co-registration error between the field plots and Landsat pixels, and spectral response values are calculated based on an area-weighted average of up to four different Landsat pixels. Two key problems with the CBI approach are that it may artificially inflate perceived accuracy by aggregating pixel values (i.e., the aggregation problem, Marceau et al., 1994), and it precludes the comparison of field measured severity between adjacent pixels (because field plots are not contiguous). We chose to evaluate spectral index accuracy using a large, fully censused forest plot because it enabled us to minimize potential bias associated with pixel aggregation and to quantify the correlation between field-based measures of fire effects and the spectral response of individual Landsat pixels. There are indeed both benefits and limitations to our ‘big plot’ design (Lutz, 2015), but it provides a valuable contrast with the existing remote detection of fire severity literature.
Another consideration with our study design potential for spatial auto-correlation due to patchy fire behavior within the YFDP (e.g., Fig. B.1). Semivariograms revealed that while mortality was spatially auto-correlated at spatial scales <100 m, uncertainty was spatially random (Fig. B.9). In other words, the difference between predicted mortality rate and observed mortality rate for any given pixel was independent of surrounding pixels. We did not explicitly control for the autocorrelation in mortality because we were primarily interested in the variance between observed mortality and spectral response (which was not autocorrelated), and previous research has shown that the spatial autocorrelation of fire has a negligible influence on assessment of fire effects in the Sierra Nevada (van Mantgem and Schwik, 2009).

The results of the rarefied spectral index validation provide further evidence that spatially auto-correlated fire behavior did not compromise our results. The rarefied sampling procedure greatly reduced spatial auto-correlation by sampling 20 plots at a time; greatly reducing the chance that neighboring pixels would be sampled. The average distance between any two YFDP pixels was 296 m, far greater than the 100 m scale at which mortality was auto-correlated.

4.6. Advancing the ecological relevance of future spectral index calibrations

Continuing to perform calibrations with continuous, field-based metrics of severity will enhance the ecological interpretation of satellite-derived severity maps (e.g., Whitman et al., 2018; Harvey et al., 2019). Tree-based metrics such as percent stem mortality, change in canopy cover, and basal area mortality can provide more well-defined indicators burn severity (Morgan et al., 2014); they are preferable to semi-quantitative metrics such as the Composite Burn Index (Key and Benson, 2006) because
they are more directly applicable to post-fire management (Kolden et al., 2015), and they allow uncertainty to be assessed independently for different elements of forest ecosystems (i.e., soil, shrubs, large trees, etc.).

Traditional accuracy metrics such as $R^2$ and AIC will continue to be useful ways to compare indices (e.g., Miller et al., 2009; Whitman et al., 2018; Parks et al., 2018), but we suggest continuing to explore novel ways of quantifying accuracy that reveal error in ecologically-relevant terms (e.g., Figs. 2 – 4; Harvey et al., 2019) such as the range in tree mortality that should be expected based on spectral index values. The development of region-specific variance models (e.g., Figs. 3.4, B.5 – B.7) may be used to create uncertainty maps which will permit more ecologically accurate interpretation of satellite-derived severity; the variance model we developed in this study may be adequate for Sierra Nevada mixed-conifer forests, but additional models would improve performance for other forest types.

Finally, there is a general need to enhance the theoretical foundation from which we develop, calibrate, and compare spectral indices. Improving our understanding of how various ecosystem attributes influence spectral reflectance will facilitate a more cohesive synthesis of the inconsistencies in the literature regarding which spectral index is best (e.g., Roy et al., 2006; Miller and Thode, 2007; Cansler and McKenzie, 2012; Parks et al., 2014; McCarley et al., 2018).

5. Conclusions

This study makes three key contributions to the field of remote sensing of fire effects. First, we conducted a comprehensive comparison of previously published severity indices using the largest set of contiguous, field-based, georeferenced individual-tree level
mortality data to date. This revealed that both absolute and relative spectral index accuracy depends on the tree mortality metric of interest, and different indices may be optimal for different ecological objectives. Second, we conducted this study in a single, large fire that enabled us to isolate variability due to intrinsic, within-landscape factors without the additional variance due to extrinsic factors associated different biogeographies or climatic conditions. This permitted a detailed evaluation of the maximum accuracy that may be attained with Landsat-derived spectral indices for any given fire, and this revealed a great deal of persistent uncertainty that may reflect a fundamental accuracy limit due to the spatial and spectral resolution of the Landsat 8 OLI sensor. Finally, we identified the range in tree mortality that may be indistinguishable based on spectral indices derived from Landsat satellites, and we demonstrated how this variability translates into uncertainty in fire effects and patterns in burn severity at the landscape scale.

The range in observed tree mortality was highest at intermediate spectral index values, with a range in expected mortality as high as 70% (±35%) of stems and 80% (±40%) of basal area (Figs. 3.5&B.5). This uncertainty in observed tree mortality reveals that apparently homogeneous patches may actually contain a considerable amount of variability in fire effects and post-fire dynamics. This may be dealt with by estimating severity with tree-based metrics of fire effects (sensu Kolden et al., 2015; Harvey et al., 2019) and associated estimates of variance, calculating the probability that a pixel is classified in the correct categorical severity class, or supplementing remotely-sensed data with field-based observations.

Explicitly accounting for uncertainty in satellite-derived estimates of burn severity
will facilitate a more ecologically-nuanced and accurate interpretation of fire effects. The high degree of uncertainty in actual tree mortality that we observed challenges the confidence with which Landsat-derived spectral indices have been used to measure fire effects, and this has broad implications for any studies or management actions that rely on accurate assessments of patterns in fire severity, distribution of seed sources, persistence of fire refugia, or post-fire landscape complexity.

References


CAL FIRE. 2018. Top 20 largest California wildfires.


Whitman, E., M.-A. Parisien, D. K. Thompson, R. J. Hall, R. S. Skakun, and M. D.


Table 3.1. Formulation of satellite-derived spectral indices and topographic variables. Subscripts ‘pre’ and ‘post’ indicate pre-fire and post-fire; L8 stands for Landsat 8; ‘R’ stands for spectral wavelengths within the red band, ‘G’ for the green band, ‘B’ for the blue band, ‘NIR’ for the near-infrared band, ‘SWIR1’ for the shortwave infrared band centered at 1.6 μm, and ‘SWIR2’ for the shortwave infrared band centered at 2.2 μm. Wavelength thresholds for each band may be found in the Landsat 8 handbook (USGS 2016). Coefficients for the tassled-cap transformation for L8 from in Baig et al. (2014).

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<th>Index</th>
<th>Code</th>
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<td>Normalized differenced vegetation index</td>
<td>NDVI</td>
<td>(NIR - Red) / (NIR + Red)</td>
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<td>(NIR - SWIR2) / (NIR + SWIR2)*1000</td>
<td>Key and Benson 2006</td>
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<td>CSI</td>
<td>NIR / SWIR1</td>
<td>Smith et al. 2007</td>
</tr>
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<td>(NIR - SWIR2) / (NIR + SWIR2)*1000</td>
<td>Key and Benson 2006</td>
</tr>
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<td>SWIR1 / NIR</td>
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Table 3.2. Correlations between spectral indices and observed mortality. Values represent the percent variance explained determined with individual random forest models. Spectral index values and observed mortality were calculated for each Landsat pixel without a buffer (results based on buffered pixels may be found in Table B.2). Observed mortality was quantified as percent of pre-fire live stems (or basal area [BA]) that was killed by fire. “Initial” columns represent correlations based on a post-fire Landsat scene from immediately after the fire (September 16, 2013), while “extended” columns use a post-fire scene taken one year following the fire (July 1, 2014). Column titles indicate which structural subsets were used to calculate observed mortality. The data were also subset by plot to compare accuracy between the two datasets. Bold indicates the best three spectral indices for each category of observed mortality. This table includes the best five indices for each category of observed mortality; see Table B.2 for results for all indices.

<table>
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<td>JFSP</td>
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Fig. 3.1. Images depicting the range in variability in actual fire effects compared to Landsat-derived spectral indices. Plots were selected to demonstrate how variability in biophysical conditions can elicit a wide range of spectral responses, and this is a source of considerable uncertainty in satellite-derived estimates of fire severity. The images represent two pairs of plots with approximately equivalent dNBR (320 – 322 for the top two images, 150 – 158 for the bottom two images). Images were taken in 2017, four years after the plots burned in the Rim Fire. The images are from four different sampling plots (of 313 total) and are intended to be representative of the overall fire effects. The plots include pixel 85 with the Yosemite Forest Dynamics Plot (top left) and three Joint Fire Science Program plots (G7-P3, top right; G5-P7, bottom left; G7-P4, bottom right). Plot names correspond to plot maps in Fig. B.1.
Fig. 3.2. Location of study sites on the western slope of the Sierra Nevada (A) within the lower-montane mixed-conifer zone of Yosemite National Park (B,C). Study sites were burned in the 2013 California Rim Fire and were selected to represent a broad range in fire severity (B). Burn severity classifications based on differenced Normalized Burn Ratio (dNBR) derived using Landsat 8 images (pre-fire scene July 14, 2013 and post-fire scene July 1, 2014). The study sites include 53 0.25-ha stem-mapped plots (colored according to dNBR severity classification) and the 25.6-ha Yosemite Forest Dynamics Plot (blue rectangle).
Fig. 3.3. Relationship between satellite-derived spectral indices and observed mortality of trees ≥10 cm diameter at breast height (1.37 m). Points represent 53 individual plots (JFSP) and 260 Landsat pixels within the Yosemite Forest Dynamics Plot (YFDP). Shaded envelopes represent the variability in observed mortality as a function of each spectral index. Envelopes were derived from continuous estimates of the mean and standard deviation of the data generated with locally-weighted scatterplot smoothing (LOESS) regression models and scaled to capture 95% of the variability in observations. The %VE indicates the percent variance explained using random forest models (Table 3.2, B.2). See Figs. B.3&B.4 for results for all 36 indices.
Fig. 3.4. Variance in satellite-derived spectral indices as a function of observed mortality of trees ≥10 cm diameter at breast height (1.37 m). Points represent 53 individual plots (JFSP) and 260 Landsat pixels with in the Yosemite Forest Dynamics Plot (YFDP). Shaded envelopes represent the variability in observed mortality as a function of each spectral index. Envelopes were derived from continuous estimates of the mean and standard deviation of the data generated with locally-weighted scatterplot smoothing (LOESS) regression models and scaled to capture 95% of the variability in observations. Spectral index units were normalized to enable comparison between different spectral index values.
Fig. 3.5. Satellite-derived burn severity (dNBR) of the California Rim Fire. The scatterplot displays the relationship between dNBR and observed percent basal area mortality (red line is predicted mortality rate of LOESS model; shaded region is 95% confidence envelope). The histogram shows proportion of area within the Rim Fire at various levels of uncertainty. Maps show mean, low, and high estimates of percent basal area mortality. The uncertainty map displays the range in predicted percent basal area mortality necessary to capture the true mortality rate, 95% of the time (i.e., a 40% uncertainty level indicates a ±20% range in expected mortality levels). Iterations of this figure depicting 95% confidence envelopes around percent stem mortality and 68% confidence envelopes around basal area and stem mortality may be found in the supplemental information (Fig. B.5&B.6&B.7).
Fig. 3.6. Inherent uncertainties in interpreting tree mortality from Landsat-derived data. Changes in canopy cover associated with fire-induced mortality are shown as a percentage of pre-fire stem density (top panels) and basal area (bottom panels) mortality. The points represent the location of individual trees contained within a single Landsat pixel within the Yosemite Forest Dynamics Plot (pixel 120 in Fig. B.1). The ecological effect of mortality depends on both the number and size of trees killed, but different combinations of mortality can elicit the same spectral response when averaged over a 30-m Landsat pixel. Mortality was simulated by identifying either the smallest trees (top panels) or a stratified selection from the full range of diameters (bottom panels). The left panels show changes in canopy cover associated with low-severity fire, while the right panels show changes associated with moderate- to high-severity fire. Green circles represent the two-dimensional crown footprint of surviving trees, red circles represent fire-killed trees. Canopy diameters were scaled according to the diameter at breast height (1.37 m) for each tree.
CHAPTER IV

WILDFIRE AND DROUGHT MODERATE THE SPATIAL ELEMENTS OF TREE MORTALITY

ABSTRACT

Background tree mortality is a complex process that requires large sample sizes and long time scales to disentangle the suite of ecological factors that collectively contribute to tree stress, decline, and eventual mortality. Tree mortality associated with acute disturbance events, in contrast, is conspicuous and frequently studied, but there remains a lack of research regarding the role of background mortality processes in mediating the severity and delayed effects of disturbance. We conducted an empirical study by measuring the rates, causes, and spatial pattern of mortality annually among 32,989 individual trees within a large forest demography plot in the Sierra Nevada. We characterized the relationships between background mortality, compound disturbances (fire and drought), and forest spatial structure, and we integrated our findings with a synthesis of the existing literature from around the world to develop a conceptual framework describing the spatio-temporal signatures of background and disturbance-related tree mortality.

The interactive effects of fire, drought, and background mortality processes altered the rate, spatial structuring, and ecological consequences of mortality. Before fire, spatially non-random mortality was only evident among small (1<cm DBH≤10) and

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3 This chapter was published in Ecosphere on August 6, 2020, and should be cited as: Furniss, T. J., A. J. Larson, V. R. Kane, and J. A. Lutz. 2020. Wildfire and drought moderate the spatial elements of tree mortality. Ecosphere 11(8):e03214 https://doi.org/10.1002/ecs2.3214
medium (10<cm DBH≤60) diameter classes; mortality rates were low (1.7% yr⁻¹), and mortality was density-dependent among small-diameter trees. Direct fire damage caused the greatest number of mortalities (70% of stems ≥1 cm DBH), but the more enduring effects of this disturbance on the demography and spatial pattern of large-diameter trees occurred during the post-fire mortality regime. The combined effects of disturbance and biotic mortality agents provoked density-dependent mortality among large-diameter (≥60 cm DBH) trees, eliciting a distinct post-disturbance mortality regime that did not resemble the pattern of either pre-fire mortality or direct fire effects. The disproportionate ecological significance of the largest trees renders this mortality regime acutely consequential to the long-term structure and function of forests.

**INTRODUCTION**

Tree mortality is regulated by complex interactions among many physical, biological, and ecological stressors (e.g., competition; Franklin et al. 1987). These stressors operate across a wide range of temporal and spatial scales (<0.1 ha to >1000 ha; Das et al. 2008, van Mantgem et al. 2009, Birch et al. 2019a) to determine the rates and causes of “background” mortality (Das et al. 2016). Acute disturbances (e.g., wildfire), in comparison, result in rapid and conspicuous mortality events that can affect entire stands, landscapes, or regions (Turner et al. 1997, Meddens et al. 2012, 2018a). Disturbances are often studied in isolation from background mortality processes, but recent research indicates that these omnipresent ecological processes can alter disturbance severity and mediate delayed mortality (van Mantgem et al. 2018, Hood et al. 2018). Here, we synthesize previous research with an empirical study to develop a conceptual framework
describing how background mortality processes and acute disturbance events collectively regulate tree mortality.

We first discuss the relevant literature and ecological basis regarding the spatial elements of background mortality, spatial elements of fire-related mortality, and interactions between these processes. Rather than a systematic literature review, we incorporated representative studies that serve to frame our understanding of the scales at which various ecological processes elicit spatially non-random patterns in mortality. To do this, we considered research that has explicitly addressed spatial scale, and we developed a conceptual framework describing the spatio-temporal scales at which each mortality process is most evident. We emphasized research from temperate forests of western North America to maintain relevance to the forest in which this study was conducted, but we also incorporated research from around the world to demonstrate the potential for this conceptual framework to have a broad biogeographic scope. In addition to eight studies spanning western North America and two based on global datasets, this synthesis was based on studies from the Sierra Nevada (5), Pacific Northwest (10), Northeast US and Canada (4), Southwest US (4), Southeast US (2), Rocky Mountains (2), Europe (4), Northeast China (2), Northern Africa (1), and Patagonia (1).

We then conduct an empirical assessment of the spatial elements of tree mortality using nine years of annual mortality among 32,989 individual trees within a large (25.6-ha), stem-mapped forest demography plot that was exposed to both fire and severe drought part way through the study period. The temporal and spatial scope of this study, combined with process-based measurements of tree mortality, renders our dataset uniquely poised to quantify the relationship between background mortality processes,
disturbance-related mortality, and forest spatial structure. Focusing on the spatial aspects of mortality and the reciprocal nature of various mortality processes (i.e., mortality refines spatial patterns, and spatial patterns regulate mortality risk), we used multiple analytical methods to empirically evaluate the annual rates, causes, and spatial elements of tree mortality during three distinct mortality regimes: 

- **a)** background (i.e., pre-fire) mortality,
- **b)** immediate fire-induced mortality (due to direct fire damage), and
- **c)** post-disturbance mortality (determined by the additive and interactive effects of background mortality agents, fire, and severe drought).

**The spatio-temporal signature of tree mortality processes**

Tree mortality processes can be described in terms of the agents of mortality, spatial scale, and temporal scale (Fig. 4.1A). Many mortality processes have been well-studied and quantitatively described at a range of spatial scales including insect epidemics, drought, and storm events (e.g., windthrow, ice storms). The time-scale of these conspicuous mortality agents can be extremely acute (e.g., storms) or span multiple years (e.g., beetle epidemic, multi-year drought), and they create patterns in mortality that are evident at both intermediate and broad spatial scales (10–10,000 ha; Raffa et al. 2008, Allen et al. 2010, Meddens et al. 2012, 2018a, Baguskas et al. 2014). Conversely, slower-acting “background” mortality processes, including competition, endemic bark beetle activity, and pathogens, are more evident at finer spatial scales (<1 ha) and longer temporal scales (>3 years; Fig. 4.1A). The slower dynamics of these processes makes them challenging to study, often requiring long observation periods and large plots for patterns in mortality to emerge (Clark and Clark 1996, Lutz and Halpern 2006, McMahon et al. 2019). Although subtle, background mortality processes regulate forest turnover
rates in the absence of severe disturbance (van Mantgem et al. 2009), and they are important determinants of fine-scale spatial dynamics within stands (Das et al. 2008, Larson et al. 2015).

**Mechanisms of spatial structuring**

The ecological mechanisms that give rise to spatio-temporal patterns in tree mortality may be broadly grouped into three categories: density dependence, distance dependence, and environmental heterogeneity. Density-dependent mortality emerges when tree neighborhoods mediate mortality risk (Kenkel 1988, Larson et al. 2015), and is evident as elevated susceptibility to competition (Gray and He 2009, Das et al. 2011), biotic mortality agents (Janzen 1970, Packer and Clay 2000, Johnson et al. 2014), and abiotic mechanisms (King 1986, Das et al. 2008, Yu et al. 2009, Schaedel et al. 2017) in dense tree neighborhoods. Distance dependence, in contrast, refers to the elevated risk of mortality for trees close to an affected individual, a characteristic associated with many mortality agents including pathogens, insects, and crushing (i.e., contagion; Goheen and Hansen 1993, Raffa et al. 2008, Das et al. 2008). Finally, environmental heterogeneity contributes to non-random patterns in tree mortality by introducing variability in light, water, soil resources, and habitat suitability which influence growth rate, vigor, and concomitant mortality risk (Greenwood and Weisberg 2008, Linares et al. 2011, Furniss et al. 2017). These mechanisms function simultaneously, and the spatio-temporal patterns of mortality are generally determined by a combination of all three mechanisms.

While “density dependence” has been used to describe patterns of both distance- and density-dependent mortality associated with competition and biotic mortality agents (e.g., insects, pathogens), we define these terms separately to decouple the distinct
relationships between each mechanism and forest spatial structure. Forest spatial structure regulates density-dependent mortality directly through resource competition (Kenkel 1988), morphological constrains (King 1986), accumulation of host-specific plant enemies (Janzen 1970, Connell 1971), and by moderating trees’ ability to invest in defense mechanisms (Lorio 1986, Herms and Mattson 1992, Kolb et al. 1998, Fettig et al. 2007, Hood et al. 2016, Stephenson et al. 2019). Conversely, forest spatial structure does not directly regulate distance-dependent mortality. Rather, distance-dependent mortality processes are spatially autocorrelated due simply to the contagious nature of certain mortality agents (e.g., pathogen spread, beetles dispersing from a recently-killed tree).

While many mortality processes are both distance- and density-dependent, differentiating these terms is critical to understanding the ecological nuances of spatially non-random mortality processes. Distance-dependent mortality may be density-independent (i.e., mortality may be spatially autocorrelated but independent of local density), and conversely, density-dependent mortality may be distance-independent (i.e., mortality may not be spatially autocorrelated despite mortality risk being elevated in dense neighborhoods). In other words, density-dependent mortality is a pattern that emerges when forest spatial structure mediates mortality risk, while distance-dependent mortality is the consequence of autocorrelated mortality processes. This distinction may be conceptualized as opposing directions of the relationship between forest spatial structure and mortality risk: density dependence represents the effect of forest spatial pattern on mortality risk, while distance dependence represents the effect of mortality processes on forest spatial pattern.
Spatial elements of background mortality

Perhaps the most widely recognized example of spatially structured tree mortality is competition-dominated density dependence that defines the competitive exclusion phase of forest succession models (Yoda 1963, Peet and Christensen 1987, Franklin et al. 2002). This form of density dependence is most often observed in young and even-aged forests (Kenkel 1988, Larson et al. 2015, Birch et al. 2019b), but asymmetric competition can continue to cause density-dependent mortality in mature and old-growth forests as well (Lutz et al. 2014, Zhu et al. 2017, Furniss et al. 2017). In these more structurally complex forests (Lutz et al. 2018, Jeronimo et al. 2019), mortality agents including bark beetles, pathogens, and physical damage (Franklin et al. 1987, Larson and Franklin 2010, Das et al. 2016) become increasingly important determinants of mortality, and patterns in background mortality are structured by a complex mix of both distance- and density-dependent mechanisms (Das et al. 2008, 2011, 2016, Silver et al. 2013, Lintz et al. 2016, Gendreau-Berthiaume et al. 2016).

Individual mortality agents may be both distance- and density-dependent. Bark beetles, for example, create contagious patches of mortality (i.e., distance-dependence) by releasing aggregation pheromones that attract nearby beetles to a single individual and overwhelm the tree’s defenses (Raffa and Berryman 1983), and successful mass-attacks result in a concentrated point-source of beetles that disperse to nearby trees (Raffa et al. 2008). Density dependence further contributes to spatial patterns of beetle-related mortality as local forest structure determines the intensity of competition and thus the availability of resources necessary for trees’ to invest in defense chemicals and resist beetle attacks (Lorio 1986, Herms and Mattson 1992, Fettig et al. 2007, Hood et al. 2016). Density dependence is also evident at broad scales as forest composition and host
tree density regulate background beetle population levels which determines success rate of mass attacks, and neighborhoods with high host tree density may be preferentially selected by dispersing beetles (Raffa and Berryman 1983, Kolb et al. 2007, Raffa et al. 2008). Patterns in bark beetle mortality can also be driven by variability in drought intensity across a landscape (Baguskas et al. 2014), as susceptibility to beetle attack is closely related to drought severity (Anderegg et al. 2015, McDowell et al. 2008).

Pathogen-related mortality is determined by a similarly complex mix of spatially structured processes. For example, the widely cited pattern of conspecific negative density dependence (CNDD; Hille Ris Lambers et al. 2002, Comita et al. 2010, LaManna et al. 2017) is often attributed to host-specific pathogen accumulation (Janzen-Connell hypothesis), but this distance-dependent contagion is reinforced by the elevated intensity of intraspecific competition (Adler et al. 2018; but also see Detto et al. 2019) near conspecific host trees (i.e., conspecific density dependence). The below-ground growth form and slow spread rate of pathogens makes their contagion detectable as patches or rings of mortality that manifest at intermediate to large (1 ha – 100 ha) spatial scales (e.g., Lung-Escarmant and Guyon 2004, Schmitt and Tatum 2008), but this is generally only evident over long timescales (decades to centuries, Fig. 4.1A; Waring et al. 1987). The spatial elements of insect activity may also contribute to the spatial structuring of pathogens as fungal spores can be transported to new host trees by the insects themselves (Goheen and Hansen 1993, Paine et al. 1997, Safranyik and Carroll 2006).

Finally, physical mortality agents including crushing and some forms of wind-related mortality (e.g., wind waves) may be regarded as distance-dependent as probability of mortality is positively related to the proximity to a falling tree (Das et al. 2008) or the
edge of a gap (Taylor 1990). Patches of wind-related mortality are often associated with root- and stem-rot (Sprugel 1976), and their spatial structure is therefore additionally influenced by the distribution and spread of saprophytic decay fungi. Physical mortality agents that operate at broader spatial scales such as wind, ice, and snow storms, are most strongly determined by environmental heterogeneity (Rebertus et al. 1997) and the spatial variability in the intensity of the weather event (Pasher and King 2006). The density dependence of physical mortality agents is perhaps most apparent in single-age stands where density directly influences tree morphology (i.e., diameter to height ratio) and thus resistance of trees to strong wind (King 1986). Physical mortality agents may be both positively and negatively density-dependent. Stand density can influence tree morphology (i.e., diameter to height ratio) and thus be positively related to susceptibility of trees to strong wind (King 1986), while high density stands can also ameliorate the localized intensity of wind and ice storms and thus reduce mortality risk (Bragg et al. 2003).

**Spatial elements of direct fire mortality**

Fire is an intrinsically spatial process, causing patterns in mortality that are both distance- (proximity to flames) and density-dependent (density alters fire behavior). Heterogeneity in fire effects introduces complex patterns across a wide range of spatial scales from <0.01 ha (Blomdahl et al. 2019) to >10,000 ha (Turner et al. 1997, Whitman et al. 2018, Meddens et al. 2018a; Fig. 4.1B). Fire behavior is spatially auto-correlated due to heat transfer from burning fuels to adjacent vegetation (Michaletz and Johnson 2006, 2008, Smith et al. 2016, 2017) that creates patchiness in patterns of cambial heating, crown scorch, and concomitant tree mortality (Loudermilk et al. 2012, Hood et
al. 2018, Furniss et al. 2019). During surface fire, tree crowns are damaged primarily by convective heat transfer from plumes of heated air that quickly kill foliage, buds, and vascular tissue, while tree boles are more susceptible to conductive and radiative heat transfer from combustion of surface fuels (Hood et al. 2018). The thick bark of fire-adapted species and large-diameter trees can protect from this radiative heat to some extent (van Wagendonk and Fites-Kaufman 2006, Belote et al. 2015), but the long residence time of heat released from smoldering duff and slow burning fuels (e.g., large woody debris) can penetrate this thick bark and warm the cambium enough to cause tissue death (≥60°C; Hood et al. 2018). By driving both fire temperature and residence time, the size and arrangement of fuels (e.g., Hiers et al. 2009, Loudermilk et al. 2012) influences both the intensity (energy release) and severity (ecological consequences) of fire (Jeronimo et al. 2020).

Weather, topography, and environmental heterogeneity can also create spatial patterns in fire effects. Areas that burn under moderate weather conditions generally burn with lower intensity compared to areas that burn under more extreme fire weather conditions (e.g., strong winds, low relative humidity; Lydersen et al. 2014). This is particularly evident during extreme weather conditions when positive feedback cycles between fire and the atmosphere create self-sustaining, plume-dominated fire behavior that results in large patches of high severity fire effects across vast portions of a landscape (Allen 2007, Lydersen et al. 2014). Topography contributes to spatial autocorrelated fire behavior both directly through regulating fire intensity (e.g., higher intensity toward ridge tops; Turner and Romme 1994, Kane et al. 2015) and indirectly through feedbacks with forest structure (Jeronimo et al. 2020).
Forest structure regulates fire behavior at both fine (Thaxton and Platt 2006, Hiers et al. 2009, Loudermilk et al. 2012) and broad scales (Rothermel 1972, Miller and Urban 1999a, 1999b, 2000a, Harris and Taylor 2015), and it contributes to temporal patterns by moderating fuel connectivity and regulating spread rate (Caprio and Swetnam 1995, Miller and Urban 2000b, Taylor and Skinner 2003). Conversely, repeated fire events influence the spatial pattern dynamics of trees and fuels within stands (scales <10 ha; Youngblood et al. 2004, North et al. 2007, Larson and Churchill 2012), and broad-scale patterns in fire behavior (>10 ha) create, rearrange, and refine patches of forest, unburned islands, and early-seral habitat among stands and across broad landscapes (>1000 ha; Turner et al. 1997, Hessburg et al. 1999, Taylor and Skinner 2003, Kane et al. 2014, Meddens et al. 2018a, 2018b, Jeronimo et al. 2019). In short, heterogeneity in forest spatial structure contributes to variability in fire intensity, and variability in fire intensity perpetuates heterogeneity in forest structure. This reciprocal relationship between fire, fuels, and forest spatial structure mediates the severity of future fires, and this self-regulation renders fire foundational to the structure and function of many forest ecosystems (van Wagtendonk and Fites-Kaufman 2006, Scholl and Taylor 2010, Larson et al. 2013).

Larson and Churchill (2012) reviewed the literature regarding spatial pattern dynamics in frequent fire forests, and they characterized spatial patterns in these forest types as a shifting mosaic of individuals, clumps, and openings. They described the iterative nature of fire-spatial pattern interactions including mechanisms of pattern formation and maintenance, and this model has become an archetype for spatial pattern dynamics in frequent fire forests (Franklin and Johnson 2012, Hessburg et al. 2015, North
et al. 2019). While this model may be sufficient to describe the feedbacks between fire and forest spatial structure, there is limited consideration of how background mortality processes interact with fire to mediate the spatial pattern dynamics in post-fire forests and to moderate mortality in between fire events.

There is extensive overlap between the spatio-temporal signature of fire and background mortality agents (Fig. 4.1B), and this suggests that background mortality processes may be important contributors to patterns observed in post-fire mortality. There are indeed many studies of interactions between background mortality processes and fire in the literature (e.g., Hood and Bentz 2007, Youngblood et al. 2009, van Mantgem et al. 2013, 2018, Kane et al. 2017b, Hood et al. 2018, Stephens et al. 2018), but these studies are focused primarily on the nature of the interaction (i.e., amplified or inhibited; Kane et al. 2017b) rather than the interactive effects of these processes on patterns in mortality.

**Spatial elements of post-fire mortality**

Among the most widely studied mortality process in post-fire forests is competition for water and soil resources. Stand structure mediates the intensity of inter-tree competition and creates heterogeneity in the severity of drought- and competition-related stress (Fensham and Holman 1999, Guarín and Taylor 2005, Allen et al. 2010, van Mantgem et al. 2016), and this modifies the susceptibility of trees to both direct (van Mantgem et al. 2013, Furniss et al. 2019) and indirect fire-related mortality (van Mantgem et al. 2016, 2018, Hood et al. 2018). While inter-tree competition in unburned forests is often considered to primarily inhibit seedlings and small diameter trees, recent studies suggest that competition in post-fire forests can be an important determinant of mortality for larger trees as well (Yu et al. 2009, van Mantgem et al. 2018). The nature of
drought-fire interactions is also dependent on the timing of events: fire reduces stand density and this can make surviving trees less susceptible to competition- and drought-related mortality post-fire (van Mantgem et al. 2011, 2016), but pre-fire drought can hinder trees’ ability to tolerate fire damage and can increase probability of immediate fire-related mortality (van Mantgem et al. 2013, 2018).

Bark beetles have been long considered as an important factor in mediating post-fire mortality (Ryan and Amman 1996, Scott et al. 2002, Sieg et al. 2006, Hood and Bentz 2007), but the effects of local tree neighborhood on susceptibility to bark beetles is complex and dependent on a variety of post-fire factors (Kolb et al. 2007). As with beetle-related mortality in a pre-fire mortality regime, local neighborhood structure and composition influence the availability of resources necessary for trees to invest in defense infrastructure (i.e., resin and resin ducts; Hood and Sala 2015), and this directly contributes to resistance against bark beetle attack (Raffa 2014). As fire decreases density and competition for resources, we might expect fire to enhance resistance to bark beetle attack by increasing resource availability and thus the capacity of trees to invest in resin defenses. However, surviving trees may be temporarily weakened due to direct fire injury to their foliage, cambial tissue, and surface roots, and this may limit their capacity to defend against beetle attack immediately after fire (Kolb et al. 2007, McHugh and Kolb 2003). Fire may further intensify bark beetle pressure by creating an abundance of weakened host trees across the landscape that are susceptible to beetle attack and thus enabling beetle populations to proliferate. This increase in beetle abundance may facilitate more successful mass-attacks, and can catalyze a transition from endemic to epidemic beetle population dynamics (Raffa et al. 2008). Empirical studies have found
evidence for both facilitated and impeded bark beetle mortality post-fire (e.g., Youngblood et al. 2009, Hood et al. 2016): fire may initially increase susceptibility to bark beetles by weakening trees and reducing their ability to defend (McHugh and Kolb 2003, Hood and Bentz 2007, Kolb et al. 2007, Youngblood et al. 2009), but fire is also thought to increase resistance to bark beetles over longer time scales by reducing stand density, increasing the distances between conspecifics, and stimulating the production of resin (Fettig et al. 2007, Hood et al. 2015, 2016).

Pathogens also interact with fire-damage to mediate post-fire mortality (Parker et al. 2006, Kane et al. 2017b), and local tree neighborhoods may affect susceptibility to pathogens post-fire through altering resource availability, overall vigor, and capacity to defend against pathogens. As with bark beetles, it is not clear whether fire will enhance or reduce the prominence of pathogen-related mortality (Kane et al. 2017b). Fire may facilitate the apparent virulence of pathogens by weakening trees (e.g., Parker et al. 2006), but it may also impede pathogens (e.g., Grelen 1983, Beh et al. 2012) by scorching the soil, reducing the number of live trees, and increasing distance between suitable host trees. Three-way interactions between pathogens, bark beetles, drought on fire-weakened trees may further complicate the detection of pathogen-caused mortality in post-fire forests.

**Applications for post-fire mortality models**

There is a growing body of evidence (Youngblood et al. 2009, Hood et al. 2018, van Mantgem et al. 2018, Furniss et al. 2019) that suggests that these background mortality processes play a key role in shaping post-fire mortality, but they are absent from the most widely-used post-fire tree mortality models. A recent update of the First Order Fire
Effects Model (FOFEM; Hood and Lutes 2017) has improved model accuracy by incorporating bark beetle presence/absence as a predictor variable for four species-specific models (Hood and Lutes 2017), but this binary approach is not optimally suited to capture the complex nature of bark beetle population dynamics (e.g., Raffa et al. 2008). Furniss et al. (2019) found that mortality model prediction error was spatially auto-correlated, indicating that spatially structured mortality processes not only mediate patterns in post-fire mortality, they comprise some of the unexplained prediction error within fire effects models. This is supported by recent efforts to integrate background mortality agents including bark beetles, pathogens, and competition into theoretical frameworks describing the mechanisms of post-fire tree mortality at scales ranging from individual trees (Hood et al. 2018) to broad landscapes (Kane et al. 2017b).

**Objectives**

The considerable volume of background tree mortality literature demonstrates a variety of mechanisms by which biotic and abiotic mortality agents evoke spatial patterns in tree mortality (Fig. 4.1). Yet, there is not currently a cohesive framework for assessing how fire and other acute disturbance events may modify the relative importance and spatio-temporal structure of background mortality processes. We addressed this by quantifying the spatial elements of pre-fire, direct fire, and post-fire tree mortality, then developing an empirically informed framework describing how fire and background mortality processes interactively mediate mortality and collectively determine forest spatial pattern dynamics. For each mortality regime (pre-fire, direct fire, and post-fire), we examined the spatial structure of distance-dependent mortality processes using point pattern analysis, and we evaluated the intensity and spatial extent of density dependence.
using generalized linear models.

We tested the null hypothesis that fire and background mortality processes do not interact, resulting in a post-fire mortality regime that may be characterized simply by the additive effects of direct fire damage and background mortality processes. Alternatively, we hypothesized that fire may override and obscure background mortality processes, impeding the spatial elements of background mortality and imposing patterns in post-fire mortality that reflect only the heterogeneity in direct fire damage. In this case, we would expect the spatial patterns associated with background mortality agents (e.g., bark beetles, pathogens) to become spatially random, or to resemble the spatial pattern of direct fire damage (e.g., crown scorch). A second alternative hypothesis is that fire may interact with background mortality processes, creating patterns in post-fire mortality that do not resemble the patterns of either pre-fire or direct fire mortality alone. Finally, we hypothesized that mortality would become less density-dependent post-fire because reduced stand density may have increased above- and below-ground resource availability, thus reducing the sensitivity of surviving trees to competitive stress and contagious mortality agents within their local neighborhoods.

METHODS

Study area

We conducted this study in an old-growth *Abies concolor* – *Pinus lambertiana* (white fir – sugar pine) forest in the lower-montane, mixed-conifer forest zone of the Sierra Nevada, CA, USA. We used data from the Yosemite Forest Dynamics Plot (YFDP; Lutz et al. 2012, Lutz 2015), a 25.6-ha stem-mapped forest monitoring plot located between
1774 and 1911 m elevation in Yosemite National Park, with species composition and structure representative of the Sierra Nevada white fir superassociation (Keeler-Wolf et al. 2012). The YFDP was established in 2009 and 2010 when we tagged, identified, and mapped all tree stems ≥1 cm diameter at breast height (DBH; 1.37 m) within the plot (n = 34,458 live stems; Lutz et al. 2012). We considered four tree species comprising 32,989 stems ≥1 cm DBH within the YFDP: *Abies concolor* [Gordon] Lindl. ex Hildebr. (white fir; 939 stems ha⁻¹), *Pinus lambertiana* Dougl. (sugar pine; 180 stems ha⁻¹), *Calocedrus decurrens* [Torr.] Florin (incense cedar; 64 stems ha⁻¹), and *Quercus kelloggii* Newb. (California black oak; 46 stems ha⁻¹).

**Fire in the YFDP**

The YFDP has been relatively unaffected by timber harvest and grazing, but a century of effective fire suppression had a profound impact on the pre-fire structure and composition of this forest. The lack of fire resulted in an abundance of surface and ladder fuels, uncharacteristically high stem density, and a compositional shift towards shade-tolerant species (Caprio and Swetnam 1995, Scholl and Taylor 2010, North et al. 2019). The high fuel loads associated with these stands can make the reintroduction of fire challenging (Lydersen et al. 2014), often requiring mechanical fuel reduction and prescribed fire treatments to develop historical structure, composition, and spatial pattern that confer resilience to wildfire, drought, and biotic disturbance (North et al. 2007, Stephens et al. 2018).

The YFDP was burned for the first time in 113 years (Barth et al. 2015) as part of a management-ignited fire set to control the spread of the Rim Fire, a 104,131-ha wildfire that burned in August and September of 2013. The fire was ignited ~1 km from the
YFDP on August 31, 2013, and no management action was taken within the YFDP before or after ignition. Fire intensity ranged from low- to high-intensity surface fire with patches of unburned surface fuels (primarily in draws; Lutz et al. 2017a, Blomdahl et al. 2019) and occasional crown torching (Fig. 4.2). Surface fuel consumption was >90% for litter, duff, and small fuels (<1000-h), and 61% for coarse woody debris (Larson et al. 2016, Cansler et al. 2019). Fire effects were heterogeneous with patches of low, moderate, and high tree mortality (Furniss et al. 2020).

Pre-fire mortality was measured through annual mortality surveys in 2011, 2012, and 2013. Each year, we re-visited every tree that was alive in the previous year and we identified new mortalities (no live foliage above DBH). We conducted pathology exams (including removing bark to inspect the cambium) on each newly dead tree and recorded the multiple factors associated with death (e.g., beetle galleries, pathogens, ruptured stem, crushing). We also recorded notes about each live tree pertaining to unique characteristics such as old fire scars. Eight months after the fire we conducted a mortality survey to identify newly dead trees (hereafter “immediate mortality”; trees newly dead between June 2013 and May 2014). In addition to the standard pathology procedure, we also recorded fire damage (bole scorch height and percent crown volume scorched (CVS)) for all live and newly dead trees. Post-fire mortality was measured through annual mortality surveys for five years following the fire (hereafter “post-fire mortality”; trees that survived ≥1 year post-fire but died in 2015 – 2018). Pathology exams were conducted by well-trained, inter-calibrated field crews under the direct supervision of the principal investigators and experienced crew leads, with four personnel present during all ten years of measurement for continuity.
Drought during the study period

California experienced a severe drought from 2012 to 2016 (Belmecheri et al. 2016), coinciding with two years of our pre-fire mortality surveys (2012-2013) and three years of post-fire surveys (2014-2016). We did not detect elevated mortality in the YFDP during the first two years of the drought; this is corroborated by other studies of mortality in the Sierra Nevada during these years (Byer and Jin 2017, Young et al. 2017), and it is consistent with the expectation that may trees are able to persist through the beginning of multi-year droughts (Guarín and Taylor 2005, McDowell et al. 2008). As the drought progressed it began to cause extensive tree mortality throughout the Sierra Nevada (Young et al. 2017), peaking in severity in 2016 (Byer and Jin 2017) before subsiding following the wet winter of 2016-2017.

The timing and severity of drought-induced mortality in the Sierra Nevada is conflated with our measurements of immediate and delayed fire-related mortality. This reveals a persistent challenge regarding natural experiments in long-term monitoring plots: there is no factorial design through which treatment effects may be decoupled. Disentangling the relative contributions of drought and fire to patterns in delayed mortality is not possible with the YFDP dataset alone, and differences in sampling protocols and stand characteristics make comparisons with auxiliary datasets difficult. We note, however, that while the climatic conditions during this study were historically unprecedented (Belmecheri et al. 2016), drought and fire are expected to co-occur with increasing frequency in the coming decades (Allen et al. 2015, Berner et al. 2017); this case study may therefore provide prescient insights regarding mortality patterns following future wildfires.
Analyses

As spatially-explicit mortality processes may differ among species and size classes (Das et al. 2008, Wang et al. 2012), we analyzed each species independently and grouped trees into three size classes chosen to reflect the distinct ecological roles of small (1-10 cm DBH), medium (10-60 cm DBH), and large (≥60 cm DBH) diameter trees (sensu Lutz et al. 2018) while maintaining a robust sample of trees in each diameter class. We restricted all point pattern analyses to species-size classes that contained >100 individuals to minimize exposure to type II error (failure to reject the null when it is false; Rajala et al. 2018).

We grouped mortality into three regimes: pre-fire (background) mortality, direct fire-related mortality, and post-fire mortality. For each mortality regime we assessed both the spatial structure of background mortality processes as well as the effects of local neighborhood structure on mortality risk. To characterize the spatial structure of mortality we used two forms of point pattern analysis: the pair-correlation function to quantitatively compare patterns, and maps of point pattern intensity to qualitatively describe, visualize, and compare patterns. To assess the effects of forest spatial pattern on mortality risk we used generalized linear models based on the local neighborhood spatial structure around each tree. We implemented both types of analysis for each species, size class, and mortality regime.

Point pattern analyses: pair-correlation function

We used point pattern statistics and random labelling null models (sensu Goreaud and Pélissier 2003, Wiegand and Moloney 2004) to test whether mortality was spatially random while controlling for the underlying non-random spatial pattern of the stems
within the YFDP. We summarized the observed spatial pattern of pre-fire, immediate, and post-fire mortality using the univariate form of the inhomogeneous pair correlation function (PCF), \( g(r) \), to control for underlying environmental heterogeneity and variability in first-order intensity (Wiegand and Moloney 2004). This spatial summary statistic, \( g(r) \), quantifies second-order correlations between points, and this can be used to infer biological interaction between trees (Wiegand and Moloney 2004).

We compared \( g(r) \) calculated for the observed pattern of mortalities to the null model of random mortality; a null model that allows one to test whether the process determining mortality is random while controlling for the underlying heterogeneous pattern of trees (Goreaud and Pélissier 2003, Wiegand and Moloney 2004). Simulations of the null model were generated by holding the observed pattern of trees constant while randomly labelling trees as mortalities in proportion to the number of actual mortalities. We selected the 25th largest and smallest values from 999 simulations to create Monte Carlo simulation envelopes around the null model with an \( \alpha \sim 0.05 \) \((sensu \ Grabernik \ et\ al. \ 2011, \ Baddeley \ et \ al. \ 2014)\). This envelope may be interpreted as the amount of variation expected if the process determining the pattern of mortality was spatially random, and deviations from the envelope indicate distances at which mortality was non-random.

We conducted a similar analysis considering only mortalities killed by bark beetles, pathogens, and physical factors (mechanical failure, crushing). Trees were grouped according to factors associated with death as recorded in the year they died (details in \textit{Study site}). Trees that had multiple factors associated with death (e.g., both bark beetles and mechanical failure) were included in multiple groups. We distinguished between fungal pathogens and saprophytes, and our analysis of pathogen-related mortality did not
include trees that died when the stem ruptured due to saprophytic decay in the fire-killed part of the bole (these were considered mechanical mortalities). Simulations were generated by randomly selecting \( n \) trees from the superset of trees within the focal species-size class, where \( n \) is the number of mortalities associated with the focal mortality agent. We performed this analysis on pre-fire and post-fire mortality, as mortality in the year of the fire was dominated by direct fire damage.

For each mortality regime, we analyzed the trees that survived through the previous time period (i.e., direct fire mortality was assessed based on trees that were alive the year before the fire, and post-fire mortality was assessed based on trees that survived \( \geq 1 \) yr post-fire). We conducted each analysis for all species and size classes grouped, as well as for each species-size class independently. We analyzed spatial patterns at scales ranging from 0 m to 30 m because we sought to not only capture plant-plant interactions that operate at small scales (<9 m, Das et al. 2011; <10 m, Furniss et al. 2017; <26.6 m, Wiegand et al. 2007), but to also capture the spatial structure of mortality associated with heterogeneous fire intensity that can occur at larger scales (Larson and Churchill 2012, Kolden et al. 2012, Yocom-Kent et al. 2015). We implemented all point pattern analyses in R v.3.5.2 (R Core Team 2018) using the package spatstat v.1.59-0 (Baddeley et al. 2015).

**Point pattern analyses: maps of pattern intensity**

We created maps of mortality using the density.ppp function from the spatstat package (Baddeley et al. 2015) to estimate point pattern intensity, \( \lambda \), following the methods of Diggle (1985) based on an isotropic Gaussian smoothing kernel. This spatially heterogeneous estimate of intensity provides the basis for the inhomogeneous
pair-correlation function (details above), but the map of point pattern intensity itself can be used to visualize the broad-scale variability in the strength of a process (compared to the pair-correlation function which is used to assess second-order interactions at fine spatial scales [\(<20\ m\)]. We repeated the random labelling procedure (details above) to create a set of simulated realizations of mortality based on random selections of stems that were alive at the beginning of each mortality regime (i.e., simulations for post-fire mortality only included stems that survived \(\geq\)1 year post-fire). For each of the 999 simulations we created a map of point pattern intensity, and we identified the minimum and maximum expected intensity values for each \(1 \times 1\ m\) pixel. We compared the maps of observed intensity to the range of expected values from the simulations and we masked out areas in these observed mortality maps that were within this range. The resulting maps display heterogeneity in the intensity of mortality processes that exceeds the amount of variability that would be expected by chance.

*Generalized linear models*

We summarized the structural attributes of the local neighborhood around each tree and used generalized linear models to quantify the degree to which these structural variables improved prediction accuracy compared to non-spatial null models (*sensu* Das et al. 2008). We quantified the importance of each structural variable by adding it as an additional independent parameter to base models which related probability of mortality to tree DBH (separate models for each structural variable). Structural variables were formulated to reflect different physical and biotic processes that may mediate fire-related mortality including competition, susceptibility to bark beetles, and pathogen activity. We calculated all structural variables for each individual tree within circular neighborhoods.
based on radii of 5, 10, 15, 20, and 30 m. Variables included local neighborhood basal area, density of stems of each size class, nearest neighbor, and the Hegyi index (Hegyi 1974), a distance- and size-weighted competition index designed to reflect competitive inequalities related to tree size and inter-tree distance (Biging and Dobbertin 1992). We also calculated landscape position based on a 1-m LiDAR-derived digital elevation model using the methods of Wilson et al. (2007) at a scale of 53 m (scale chosen to approximate the area of a 30-m radius circle). Finally, we noted the presence of a previous fire scar by querying the field notes associated with each tree for the phrases including “scar”, “fire scar”, and “cat face”. For all neighborhood calculations, we corrected for edge effects by mirroring trees within 30 m of the edge of the YFDP to create a simulated stem map buffer around the entire study area. The complete list of variables, and rationale for the formulation of each variable, may be found in Table C.1.

We generated separate base models for pre-fire, direct fire, and post-fire mortality. For the immediate fire mortality models, we generated two base models: one to capture the direct effects of structural variables on mortality by altering local fire intensity ($P_{fire} \sim DBH$), and one to capture the indirect effects of structural variables on immediate mortality by mediating a tree’s ability to withstand fire damage. We isolated these indirect effects by including crown scorch (CVS) as an independent variable to control for the direct effects of local neighborhood on fire intensity ($P_{fire} \sim DBH * CVS$). For the post-fire models, we included both DBH and CVS as independent variables to control for tree size and extent of fire damage ($P_{post} \sim DBH * CVS$). Models were created using the logistic model form:

$$P = \frac{1}{1+e^{-(\beta_0 + \beta_1 X_1 + \cdots + \beta_t X_t)}}$$
where $P$ is the probability of mortality ($P_{pre}$ for pre-fire mortality, $P_{fire}$ for direct fire mortality, and $P_{post}$ for delayed), $\beta_0 - \beta_t$ are regression coefficients, and $X_1 - X_t$ are predictor variables (DBH, CVS, and each structural variable). We used CVS as a proxy for fire intensity because it is a tree-centric metric of fire intensity that captures the aspects of fire behavior that are most important in determining tree mortality (Sieg et al. 2006, Woolley et al. 2012, Hood and Lutes 2017). For the models that incorporated both CVS and DBH terms, we included a CVS:DBH interaction term to account for the non-linear relationship between DBH and susceptibility to CVS (Kolb et al. 2007, Furniss et al. 2019). For the delayed mortality model, we only considered trees that survived $\geq 1$ yr post-fire. We compared model accuracy using Akaike’s information criterion (AIC) and considered differences in AIC $>7$ as support for a significant difference in model accuracy (Burnham and Anderson 1998). We did not consider any spatial variables that had a $p$-value $>0.01$. All analyses were performed in R ver. 3.5.2 (R Core Team 2018).

**RESULTS**

Pre-fire background mortality rates ranged from 0.1% to 3.2% yr$^{-1}$, with an overall mortality rate of 1.7% yr$^{-1}$ considering all stems $\geq 1$ cm DBH (Table 4.1). For *Abies* and *Calocedrus* rates were lowest (1.4 and 0.1%, respectively) for medium-diameter trees (10 to 60 cm DBH), while for *Pinus* rates were lowest (0.5%) for large-diameter stems ($\geq 60$ cm DBH). Pre-fire mortality rates were highest for small-diameter (1 to 10 cm DBH) *Abies* and *Pinus* (1.8% and 3.2%, respectively), large-diameter *Calocedrus* (0.6%), and medium-diameter *Quercus* (2.5%).

Immediate fire mortality rates were negatively related to diameter for all species, with
a maximum of 95.4% (small-diameter *Pinus*) and a minimum of 2.3% (large-diameter *Pinus*; all rates may be found in Table 4.1). Immediate mortality was rarely attributed to factors other than fire; most trees were killed by direct fire damage alone.

Post-fire mortality rates were also greatest for small-diameter stems, with the exception of *Pinus* which had the greatest mortality rate in the medium-diameter class. Post-fire mortality rates ranged from 2.7% yr\(^{-1}\) for *Calocedrus* to 22.3% yr\(^{-1}\) for small-diameter *Abies* (Table 4.1).

**Distance-dependent mortality**

*Pre-fire mortality*

Pre-fire mortality was aggregated when all stems were pooled (Fig. 4.3), indicating the presence of distance-dependent mortality processes. Mortality was aggregated at the greatest distance for small-diameter stems (0 to 13 m), and this clustering of mortality was evident despite the initial pre-fire pattern of small-diameter stems also being strongly aggregated (Figs. 4.3, C.1). Pre-fire mortality of medium-diameter stems was similarly aggregated, but the clustering of mortality was more clearly differentiated because the initial pattern of medium-diameter stems was more regular (i.e., less aggregated) compared to the initial pattern of small-diameter stems (Fig. 4.3). The spatial pattern of large-diameter mortalities was generally random, but this randomness may indicate a slightly clustered pattern of mortality because the initial pattern of large-diameter trees was hyper-dispersed (Fig. C.1).

Mortality associated with bark beetles was aggregated for all species-size classes (Fig. 4.4; \(n\) for each indicated by bold in Table 4.1). Beetle-related mortality was aggregated from 0 to 4 m for small-diameter (1-10 cm DBH) *Abies*, from 0 to 6 m for
medium-diameter *Abies*, and from 0 to 10 m for *Pinus* of all sizes (Fig. 4.4). Mechanical mortality was also aggregated for small- and medium-diameter *Abies* from 0 to 6 m and 10 to 22 m, respectively. Pathogen mortality was spatially random for small-diameter *Abies*, the only size class that had sufficient numbers of mortality to test (Fig. 4.4).

**Direct fire mortality**

Immediate fire mortality was strongly aggregated for all stems grouped from 0 to 30 m (Fig. 4.3). Fire-induced mortality of small-diameter stems alone was also aggregated from 0 to 30 m, while mortality of medium-diameter stems was aggregated from 0 to 23 m (Fig. 4.3). Large-diameter mortality appeared random (Fig. 4.3), though the immediate mortality rate of large-diameter stems was very low (Table 4.1).

**Post-fire mortality**

Post-fire mortality of all stems ≥1 cm DBH was aggregated from 0 to 7 m, a finer scale compared to both pre-fire and direct fire mortality (Fig. 4.3). Post-fire mortality of small stems was random, while medium-diameter mortalities were slightly aggregated from 0 to 8 m (Fig. 4.3). Post-fire mortality of large-diameter trees, in contrast, was strongly clustered and at greater scales compared to pre-fire mortality (0 to 17 m; Fig. 4.3). The emergence of strongly clustered large-diameter tree mortality was readily apparent in the field, and is also visually discernable from the stem maps of mortality (Fig. C.1). Considering species individually, post-fire mortality was aggregated from 0 to 4 m for *Abies*, from 0 to 17 m for *Pinus*, and was spatially random for *Calocedrus* and *Quercus* (Fig. 4.3).

Post-fire mortality was mediated by biotic and mechanical mortality processes that were spatially structured for all species and diameter classes that we tested. Bark beetle
mortality was aggregated for medium-diameter *Pinus* from 0 to 12 m, large-diameter *Pinus* from 0 to 18 m, and medium-diameter *Abies* from 1 to 8 m (Fig. 4.5). Mechanical mortality was aggregated for medium-diameter *Abies* from 0 to 5 m and 16 to 19 m. Pathogen mortality was also aggregated for medium-diameter *Abies* from 2 to 3.5 m (Fig. 4.5).

**Geographic patterns in mortality**

*Pre-fire mortality*

Maps of mortality intensity revealed complex patterns of mortality across the YFDP. Pre-fire mortality of small- and medium-diameter stems was characterized by patches of both high and low mortality rates separated by regions of random, “ambient” mortality (Figs. 4.6 & C.1). The spatial distribution of pre-fire large-diameter mortalities, however, was random.

*Direct fire mortality*

Direct fire mortality for all size classes exhibited a stronger spatial structure, with larger patches of both elevated and reduced mortality intensity and more area overall that was characterized as non-random. The patches of non-random pre-fire mortality did not simply expand to accommodate the greater number of direct fire mortalities; the distribution of non-random immediate fire mortality assumed a distinct geography (Fig. 4.6). Many areas that were characterized by random mortality pre-fire assumed a non-random spatial structure due to direct fire mortality (e.g., southeast corner of the YFDP in Fig. 4.6). This pattern likely reflected the spatial heterogeneity in pre-fire fuel loadings that caused variability in first order fire intensity and concomitant mortality across the
YFDP (Blomdahl et al. 2019, Cansler et al. 2019, Furniss et al. 2020). As with the pre-fire regime large-diameter mortality was still mostly random, but the direct fire effects did create two small patches of non-random mortality in this size class.

**Post-fire mortality**

The pattern of post-fire mortality assumed a yet third distinct distribution and did not resemble the patterns of either pre-fire or direct fire mortality (Fig. 4.6 & C.1). For small- and medium-diameter stems the area characterized by random mortality increased slightly compared to direct fire mortality, but for medium-diameter stems the total area of non-random mortality was still greater than during the pre-fire regime. In contrast, post-fire mortality of large-diameter trees developed strong spatial structure that was absent during both pre- and direct-fire mortality regimes. Some of these patches of non-random large-diameter mortality overlapped with areas of non-random medium-diameter mortality, but some patches were unique. For example, we observed elevated large-diameter mortality in the northwest part of the YFDP, but the mortality rate of medium-diameter trees in this same area was lower than would have been expected by chance (Fig. 4.6).

**Density-dependent mortality**

**Pre-fire mortality**

Spatial variables improved predictions of pre-fire mortality for small- and medium-diameter *Abies*, medium-diameter *Pinus*, and *Quercus* ≥10 cm DBH (Tables 4.2, C.2). Density of pole-sized conspecifics was the single most important variable in most cases, while basal area was more important for *Abies*. The direction of the relationship was not
consistent; density increased probability of mortality for small-diameter *Abies*, while density decreased probability of mortality for medium-diameter *Pinus* and *Quercus* (Figs. 4.7, 4.8, C.2). Pre-fire mortality of large-diameter trees was density independent for the three conifer species (Figs. 4.7-9).

**Direct fire mortality**

Structural variables improved mortality model accuracy for both immediate and delayed fire-related mortality for all species (Table 4.2, C.3; Figs. 4.7-9, C.2). Structural variables enhanced the immediate-direct models (did not include CVS) for small- and medium-diameter trees of all species, and structural variables improved the immediate-indirect models (did include CVS) for small *Pinus*, all *Quercus*, and medium *Calocedrus*. Local neighborhood density and basal area (BA) were positively related to both immediate and delayed mortality for most species-size classes (Tables 2 & B.3). Density and BA of conspecifics within 30 m were the most important structural variables for immediate mortality of small- and medium-diameter *Abies*, respectively (Fig. 4.7). Landscape position was the best predictor of immediate mortality for small- and medium-diameter *Calocedrus* (Table 4.2); mortality of small-diameter *Calocedrus* was related to the landscape position variable directly (higher mortality in xeric areas), while mortality of medium-diameter *Calocedrus* was evident in the negative association between mortality risk and conspecific BA (*Calocedrus* BA is higher in mesic areas (negative TPI) in Fig. 4.2D). Immediate mortality of small-diameter *Pinus* was positively related to local neighborhood BA and density, but the presence of a fire scar was the best predictor of immediate mortality for medium- and large-diameter *Pinus*. Direct and indirect immediate mortality of *Quercus* was strongly related to local neighborhood density and
Post-fire mortality

Post-fire mortality models were improved by structural variables, especially for medium- and large-diameter trees (Figs. 4.7-9, Tables 4.2 & C.4). A greater number of structural variables were correlated with post-fire mortality compared to either pre-fire or direct fire mortality for all three conifers (Tables C.2-C.4). For medium- and large-diameter *Abies* and *Pinus*, spatial variables improved model AIC for post-fire models more than they did for either pre- or direct-fire models (Table 4.2). Probability of delayed mortality was positively related to local neighborhood density and BA, with the exception of medium-diameter *Abies* which was negatively related to density of surviving small-diameter stems within 10 m (Fig. 4.7). Species identity of neighboring stems was important for *Calocedrus* and *Pinus*; delayed mortality of both species was positively related to BA of conspecifics (Figs. 4.8-9). The Hegyi competition index was the best local neighborhood variable for delayed mortality of large-diameter *Pinus*, but first-order structural metrics (BA and density) were better predictors for other species-size classes (Table 4.2). Neither density of previous year beetle-related mortality nor density of previous year pathogen-related mortality were significant predictors of delayed mortality for any species.

**DISCUSSION**

Fire is an important driver of spatial pattern dynamics (Larson and Churchill 2012), but ecological factors that mediate delayed mortality including climate, bark beetles, and competition (van Mantgem et al. 2013, 2018, Hood et al. 2018) have distinct spatial
signatures (Fig. 4.1) that may contribute to emergent patterns in mortality. These delayed mortality processes are particularly important for fire-tolerant species and large-diameter trees, as these trees are able to withstand the damage associated with low- and moderate-severity fire alone. This study demonstrates that the interactive effects of compound disturbances (fire and drought) and background mortality processes can transform the spatial elements of mortality by altering the scale of distance-dependent processes, increasing the intensity of density dependence, and provoking spatially non-random mortality among large-diameter trees.

The results of this study support our second alternative hypothesis that background mortality processes interact with acute disturbances to create a novel mortality regime. Before fire, density-dependent mortality was only evident among the smallest trees, but the combined effects of fire, drought, and background mortality processes provoked density-dependent mortality among medium- and large-diameter trees as well. Immediate fire effects extended the spatial scale of distance-dependent mortality, and post-fire mortality of large-diameter trees became strongly aggregated. The intensity of mortality assumed a unique spatial distribution throughout the study site, and patches of elevated mortality emerged where they were not present before. The compound effects of fire, drought, and background mortality processes altered both distance- and density-dependent mortality mechanisms, creating a post-fire mortality regime with a more complex spatial structure compared to either pre-fire mortality or direct fire damage. While immediate fire mortality is highly conspicuous, the majority of mortality was among small-diameter stems and the spatial structure was driven primarily by variation in fire intensity. The more ecologically consequential effects of fire were heavily influenced
by the interactive effects of severe drought and biotic mortality agents (i.e., bark beetles) that mediated a period of spatially complex mortality among large and old trees that will have enduring impact on the spatial pattern of this forest.

**Pre-fire mortality**

The overall pre-fire mortality rate of 1.7% yr\(^{-1}\) was within the range of variability expected based on other long-term forest demography plots in similar forest types within the Sierra Nevada (1.5% yr\(^{-1}\); Stephenson and van Mantgem 2005). Sample size constraints limited our assessment of pre-fire mortality for some agents, underscoring the difficulties associated with detecting slow-acting ecological processes such as tree mortality, even within large forest monitoring plots (Clark and Clark 1996, Lutz 2015, Das et al. 2016, McMahon et al. 2019, Birch et al. 2019a).

Pre-fire mortality was aggregated at fine spatial scales (0 to 13 m considering all stems; Fig. 4.3), a pattern of mortality observed in both young and old forests (Kenkel 1988, Das et al. 2008, Lutz et al. 2014, Larson et al. 2015, Furniss et al. 2017). This scale of interaction is consistent with (although slightly larger than) previous studies that have quantified the scale at which second-order (i.e., plant-plant) interactions can moderate mortality risk (4.5 m in Kenkel 1988, 5 m in He and Duncan 2000, 3 m in Little 2002, 4 m in Yu et al. 2009, 9 m in Das et al. 2011, 9 m in Lutz et al. 2014, 4 m in Larson et al. 2015, 10 m in Punchi-Manage et al. 2015, 6 m in Clyatt et al. 2016, 3 m in Furniss et al. 2017, 5 m in Birch et al. 2019b).

Mortality was clustered for stems of all sizes, but strength and directionality of density dependence varied depending on tree species and size class (Figs. 4.7-9). Pre-fire mortality of small *Abies* stems was positively related to neighborhood density of
conspecifics (i.e., negative density dependence), while mortality risk of medium-diameter *Abies*, *Pinus*, and *Quercus* was negatively related to BA and conspecific density (i.e., positive density dependence; Figs. 4.7, 4.8, C.2). These opposing forms of density-dependence reflect the importance of competition as a primary determinant of mortality for small-diameter trees (Das et al. 2008, 2011, Lutz et al. 2014), and the importance of external factors (i.e., pests, pathogens, and physical damage) that compose the mortality complexes responsible for medium- and large-diameter tree mortality (Franklin et al. 1987, Das et al. 2011, 2016). These results are consistent with the expectation that background mortality transitions from strongly density-dependent within young forests to density-independent among mature trees in old-growth forests (He and Duncan 2000, Gray and He 2009, Yu et al. 2009, Aakala et al. 2012, Hurst et al. 2012, Johnson et al. 2014, Larson et al. 2015), and they provide a more nuanced understanding of this transition by demonstrating that density dependence can continue to regulate mortality among small-diameter stems even within a structurally-complex, old-growth forest.

A likely source of the competitive stress responsible for the density-dependent mortality of small-diameter *Abies* is intraspecific competition from other small-diameter *Abies*. These stems were strongly aggregated (Fig. 4.3; Lutz et al. 2012) and were most abundant in areas with high conspecific density (up to 600 stems ha$^{-1}$; Figs. 4.7 & 4.2), and we may therefore expect mortality in these sites to resemble the self-thinning characteristic of dense, young forests (Kenkel 1988, Gray and He 2009, Larson et al. 2015). Another likely source of competitive stress is strong asymmetric competition from larger trees; the physical dominance of large trees provides them with superior access to both above- and below-ground resources, and this can inhibit survival of smaller trees.
within their local neighborhood (Lutz et al. 2014, Furniss et al. 2017).

There are a few plausible reasons for the positive density dependence we observed among medium-diameter trees (mortality risk decreased with greater basal area and conspecific density; Figs. 4.7, 4.8, C.2). First, the local neighborhoods around medium-diameter trees were characterized by lower densities (up to 200 stems ha\(^{-1}\); Figs. 4.8 & C.2) and more regular spacing (Fig. 4.3, Lutz et al. 2012) compared to small-diameter trees. The reduced crowding in these more open neighborhoods may have reduced overall competitive stress, but this does not fully explain the reversed directionality of density-dependence. Second, this pattern of positive density dependence may be associated with environmental heterogeneity within the YFDP. We would expect medium-diameter trees to be most abundant in high-quality habitats within the YFDP (i.e., environmental filtering; Das et al. 2018), and we might also expect mortality rates to be lowest in these favorable sites; the combination of these two factors could elicit a pattern of positive density dependence. Finally, below-ground fungal symbionts (i.e., ectomycorrhizae; Perry et al. 1989) can confer facilitative effects that may have contributed to this pattern.

These results provide two interesting contrasts with a previous study from similar forests in the Sierra Nevada (Das et al. 2008). First, the authors observed conspecific negative density dependence (i.e., mortality risk increased with higher conspecific density) for *P. lambertiana* \(\geq 12.7\) cm DBH, while we found that mortality risk decreased with increasing conspecific basal area for stems 10-60 cm DBH for that species (Fig. 4.8). Second, they observed a pattern of positive conspecific density dependence for *A. concolor* (of all sizes); our results were consistent with this for medium-diameter stems, but we observed the opposite pattern among small-diameter stems. These contrasts
demonstrate that while local neighborhood structure and composition are important factors determining mortality risk, the nature of neighborhood effects may vary among forest stands. Additionally, grouping trees by diameter may have enabled us to detect neighborhood effects that may be neutralized if all sizes are analyzed together.

Spatial patterns of mortality were also driven by the distance-dependent nature of pests, pathogens, and physical damage, and each of these mortality processes had a distinct spatial structure. Bark-beetle-induced mortality of small- and medium-diameter *Abies* was aggregated at very fine scales (0 to 6 m; Fig. 4.4), while beetle mortality for *Pinus* was aggregated to slightly larger scales (0 to 10 m). Mechanical mortality (i.e., crushing) was aggregated at the greatest scales for small- and medium-diameter *Abies* (0 to 12 m and 0 to 21 m, respectively; Fig. 4.4). This is consistent with our *a priori* conceptualization of these two mortality agents—both bark beetle and mechanical mortality are aggregated at very fine scales (<0.1 ha), but we expected mechanical mortality to remain aggregated at slightly larger scales due to the large height (up to 55 m) and potential propagation of large falling trees (Fig. 4.1A).

We did not detect a spatial structure associated with pathogen-related mortality, perhaps because the slow rate of pathogen spread may necessitate a longer time span for their spatial structure to be detected (Waring et al. 1987, Lung-Escarmant and Guyon 2004). Additionally, our analysis of pre-fire pathogen mortality was limited to small-diameter *Abies* (due to sample size constraints) and competition was a more important driver of mortality for small stems.

Although previous studies have quantified the spatial structure associated with these mortality agents independently (e.g., Safranyik and Carroll 2006, Das et al. 2008, Larson
and Franklin 2010, Bače et al. 2015; Fig. 4.1A), this study is the first that we are aware of that has quantitatively compared the spatially contagious nature of endemic bark beetle mortality, pathogens, and mechanical-related tree mortality within the same study site.

**Direct fire mortality**

Immediate fire mortality was aggregated for small- to medium-diameter stems from 0 to 30 and 0 to 22 m, respectively (Fig. 4.3). This was likely driven primarily by heterogeneity in fuel loadings (Cansler et al. 2019) and topography (Fig. 4.2) that altered fire behavior and resulted in patches of high and low crown scorch across the YFDP (Fig. 4.2). Crown scorch was the strongest predictor of immediate mortality (Furniss et al. 2019), causing the spatial structure of immediate mortality to closely reflect the heterogeneity in fire intensity and flame length (Figs. 4.2 & 4.6). The spatial structure of immediate mortality was clustered at the greatest inter-tree distance of any form of mortality that we assessed (30 m; Fig. 4.3), distinguishing direct fire morality as a key driver of structural heterogeneity and spatial pattern at slightly broader spatial scales (0.1 – 1 ha) compared to background mortality (Figs. 4.1 & 4.2).

Local neighborhood structure was directly related to probability of immediate mortality, presumably because higher stem density was associated with increased fuel loadings (Cansler et al. 2019) that elevated fire intensity (Miller and Urban 1999b, Thaxton and Platt 2006) and induced greater damage to trees. Surprisingly, forest structure was also related to probability of direct fire mortality when we included crown scorch as a predictor variable to control for variability in fire intensity (Table 4.2), suggesting that forest spatial structure also influenced probability of direct mortality by reducing tolerance of individual trees to direct fire damage (perhaps by modifying local
water availability and competitive stress; van Mantgem et al. 2018).

Local neighborhood structure was not of equal importance for all trees; landscape position was more important for immediate morality of small- to medium-diameter *Calocedrus*, and the presence of a previous fire scar the most important factor for immediate mortality of medium- to large-diameter *Pinus*. The importance of fire scars for *Pinus* mortality reflects their tolerance to direct fire damage due to thick bark and high crown base heights, making them less exposed to heat-induced injury (Hood et al. 2018), yet uniquely susceptible to physical failure at scars incurred from past fire events (Kolb et al. 2007, Furniss et al. 2019).

Our findings reveal an important disparity between the scales at which fire operates and the scales at which fire effects are most often monitored. Fire creates ecological mosaics at intermediate and broad scales (>1 ha; Turner et al. 1997, Hessburg et al. 2005, Yocom-Kent et al. 2015, Meddens et al. 2018a), but fine-scale (0.1 – 1 ha) heterogeneity in fire effects performs distinct, and similarly important, ecological functions (Meddens et al. 2018b). Low-, moderate-, and mixed-severity fire introduces spatial pattern complexity (Larson and Churchill 2012, Churchill et al. 2013, Kane et al. 2013, 2014), mitigates susceptibility to drought, competition, and beetle related mortality (van Mantgem et al. 2016, Kolb et al. 2007, Hood et al. 2015, 2016), and confers resilience to future disturbances and climatic variability (Allen et al. 2002, Hessburg et al. 2015, Cansler et al. 2018, Stephens et al. 2018, North et al. 2019). Fine-scale heterogeneity in fire effects is an essential component of these ecological functions, yet a vast amount of fire science is based on remotely-sensed severity products that are limited to the relatively coarse spatial resolution of hyperspectral satellite sensors (e.g., 30 m pixel size
for the Landsat series). Our results demonstrate that traditional satellite-derived data products may not be sufficient to fully capture the fine-scale complexity in fire effects that are central to the ecological function of low, moderate-, and mixed-severity fire (e.g., Furniss et al. 2020).

**Post-fire mortality**

The combination of fire, drought, and background mortality processes enhanced the importance of local stand structure as a mediator of mortality risk and provoked a strong spatial structure among medium- and large-diameter tree mortalities (Fig. 4.10). The post-disturbance mortality regime was not simply an extension of direct fire effects, nor was it a return to the pattern in pre-fire mortality (Figs. 4.3 & 4.6). It was instead a novel regime that emerged from both additive and interactive effects of fire damage, drought, and background mortality agents. Second-order ecological interactions (e.g., bark beetles, mechanical failure, competition) were important determinants of post-fire mortality (Table 4.1, Fig. 4.10), and the contagious nature of these mortality agents became evident at greater distances than pre-fire (Fig. 4.5). Local neighborhood structure assumed a central role in mediating overall mortality risk for all trees, and mortality risk of medium- and large-diameter trees became density-dependent (Figs. 4.7-9).

We speculate a few reasons for the amplified spatial structuring of post-fire mortality. First, contagious mortality processes may have been facilitated by the rapid pulse of fire-weakened trees, causing the pre-fire distribution of biotic mortality agents (bark beetles and pathogens) to become revealed. In other words, the fire may not have changed the spatial structure associated with these contagious agents, it may have simply made their spatial structure more evident. Alternatively, the post-fire proliferation of bark beetles
and pathogens may have enhanced their ability to successfully attack most trees, enabling these mortality agents to kill trees that would have otherwise been resistant. This may have reduced the relative importance of individual tree characteristics (size, vigor, and defenses) and enhanced the importance of proximity to an infected host-tree (i.e., distance dependence). In this case, the contagious nature of these mortality processes may have induced a pattern of aggregated mortality that would not have emerged in the absence of fire, even given enough time.

The elevated intensity of negative density dependence (Figs. 4.7-9) following fire may have also contributed to the increased scale of aggregation among contagious mortality agents. Despite the increased resource availability that would be expected due to direct fire mortality, surviving trees may not have been able to immediately utilize the newly available light, water, and soil resources. It can take years for trees to recover from direct fire damage (van Mantgem et al. 2011, Hood et al. 2018), and during this recuperative period trees may have been particularly sensitive to density-dependent stress that could have increased susceptibility to drought, competition, and insect-related mortality (Kolb et al. 2007, Das et al. 2008, Yu et al. 2009, Anderegg et al. 2015, Clyatt et al. 2016, van Mantgem et al. 2016).

Fire also altered the diameter classes in which spatially structured mortality was most evident (Fig. 4.10). While pre- and direct-fire mortality of small-diameter stems was aggregated, post-fire mortality of these trees became spatially random (Fig. 4.3). Conversely, the post-fire mortality regime induced a strong spatial structure among large-diameter mortalities that was not evident based on pre-fire or direct fire damage alone (Figs. 4.3 & 4.6).
**Distance-dependent post-fire mortality**

Bark beetles have long been a primary agent of large-diameter pine mortality in the Sierra Nevada (Das et al. 2016), and recent fire and drought events have stimulated a widespread increase in beetle-related mortality (van Mantgem et al. 2009, Stephenson et al. 2019). We observed an increase in both the rate and spatial scale of beetle-related mortality for medium- and large-diameter *Abies* and *Pinus* post-fire (Table 4.1, Figs. 4.4 & 4.5). The strong aggregation of large-diameter *Pinus* mortality (Fig. 4.5) is consistent with our expectations based on prior knowledge on beetle life history strategies and dispersal behavior (e.g., Furniss and Carolin 1977, Raffa et al. 2008), and this study offers a novel piece of quantitative evidence regarding the spatial extent of aggregation during a period of virulent beetle activity.

Beetle populations never reached epidemic levels at the YFDP, although they reached an intermediate point along the transition from endemic to epidemic beetle outbreaks known as the “incipient-epidemic” state. This is characterized by a transition of beetle host-selection from weak trees to larger, vigorous, and more well-defended trees (Fig. 4.10; Safranyik and Carroll 2006, de la Mata et al. 2017, Stephenson et al. 2019), and it often spawns epidemic population levels that result in the decimation (>90% mortality) of the host species across broad landscapes (Safranyik and Carroll 2006, Raffa et al. 2008). Despite the increasing frequency of bark beetle epidemics in recent decades (Hicke et al. 2013), the factors governing the transition from endemic to epidemic population levels remain elusive, and beetle epidemics are notoriously difficult to predict (Peters et al. 2004, Raffa et al. 2008).

This study provides a relatively rare example (see Stephenson et al. 2019 for another) of a beetle outbreak that reached incipient-epidemic levels then subsided back to endemic
levels without first erupting into an epidemic. Total post-fire mortality of beetle-killed large-diameter *Pinus* was 36% (Table 4.1), but mortality returned to pre-fire rates as of 2019 (<1% year⁻¹; data not shown). Two key factors likely contributed to the resistance of this forest to high-severity (>90% mortality) beetle outbreak: the high degree of structural and compositional heterogeneity due to centuries of low- to moderate-severity fire, and the wet winter of 2016 – 2017 that provided sudden relief from the extreme 2012 – 2015 drought (NOAA National Climate Data Center, https://www.ncdc.noaa.gov, downloaded June 30, 2019).

Despite the abundance of anecdotal knowledge that bark beetles attack and kill trees in clumps (Safranyik and Carroll 2006, Fettig et al. 2007, Graham et al. 2016; Fig. 4.1), few studies have explicitly quantified the fine-scale (<1 ha) spatial patterns associated with bark beetle activity (due to both the contagious nature of beetle dispersal and density-dependent processes such as tree investment in defenses and beetle neighborhood selection). Most of the quantitative research regarding the spatial structure of bark beetle outbreaks has been conducted at intermediate to large spatial scales (1 – 10,000 ha, Fig. 4.1A; but see Bače et al. 2015 for a retrospective study at fine scales). We found that post-fire bark beetle mortality was aggregated at very fine scales (0 to 18 m) for large-diameter *Pinus*, and at slightly finer scales for medium-diameter *Abies* and *Pinus* (0 to 8 m and 0 to 12 m, respectively; Fig. 4.5). These different scales of aggregation may reflect differences in dispersal and aggregation strategy between the host-specific beetle species (primarily *Scolytus ventralis* LeConte for *Abies*; *Dendroctonus ponderosae* Hopkins and *D. valens* LeConte for *Pinus*), as well as differences in the spatial pattern and neighborhood characteristics around medium- versus large-diameter stems (Figs. 4.2 &
Post-fire mechanical mortality of medium-diameter Abies (Fig. 4.5) was aggregated, a pattern that may have been driven by patches of windthrow in areas exposed to stronger winds (or less stable soil), as well as the crushing of small stems by individual large trees falling. There was a high rate of co-occurrence between saprophytic fungus and mechanical failure (56% of all Abies mechanical mortalities were mediated by wood decay in fire-killed portions of the stem), so the spatial pattern of mechanical mortality may have also been related to the distribution of saprophytic fungi (Fig. 4.10). These results are consistent with previous studies that have identified physical damage as an important mechanism of spatially non-random mortality in unburned, old-growth forests (Das et al. 2008, 2016, Larson and Franklin 2010), and it reveals mechanical mortality as a driver of spatially non-random mortality in post-fire forests as well.

In contrast to the spatial structure of pre-fire pathogen mortality, pathogen-related Abies mortality was slightly aggregated post-fire (Fig. 4.5). The elevated mortality rates post-fire (Table 4.1) may have facilitated the detection of non-random pathogen mortality that was present but undetectable pre-fire, or the fire may have weakened trees and facilitated pathogen-related mortality among trees that would have tolerated pathogen infestation if the fire had not occurred.

**Density-dependent post-fire mortality**

Fire increased the strength of density dependence, particularly for medium- and large-diameter conifers (Figs. 4.7-9, Tables 4.2 & C.4). As the post-fire mortality models controlled for crown volume scorched and DBH, this result does not simply reflect the first-order effects of forest structure on fire intensity (e.g., Fig. 4.2). Rather, delayed
mortality was more likely mediated by density-dependent processes such as competition, drought stress, and susceptibility to biotic mortality agents (Fig. 4.10). While we cannot disentangle the relative influence of each mechanism, the frequency with which basal area was the most important local neighborhood variable (Table 4.2) suggests that asymmetric competition from medium- and large-diameter trees was an important factor governing density-dependent mortality pressure post-fire (*sensu* Lutz et al. 2014, van Mantgem et al. 2018).

For *Abies*, the importance of non-species-specific neighborhood metrics (i.e., density and BA of all species combined, Table 4.1) suggests that density-dependent mortality pressure was conferred by intense competition from both conspecific and heterospecific neighbors. There was a strong positive relationship between large neighbors and mortality risk for *Abies* of all sizes (Fig. 4.7, Table C.4). Surprisingly, we also observed a negative relationship (i.e., positive density dependence—mortality risk decreases with increasing density) between density of surviving stems and mortality risk for medium-diameter *Abies* (Fig. 4.7). This positive density dependence may have emerged because survival of immediate fire effects was highest in mesic areas where fire intensity was lowest (Fig. 4.2), and these sites may have buffered the medium-diameter *Abies* from competition and drought stress post-fire.

For medium- and large-diameter *Pinus*, conversely, neighborhood composition was an important component of post-fire density dependence. The strongest predictor variable for these stems was a conspecific basal area (Tables 4.2 & C.4), a result that reflects the importance of host-specific bark beetles as a primary determinant of post-fire mortality (though see Das et al. 2008 for a similar result from unburned forests). Conspecific
density may have elevated mortality risk by reducing trees’ capacity to invest in resin defenses due to elevated competitive stress associated with strong intraspecific competition (e.g., Kolb et al. 1998, Hood and Sala 2015, de la Mata et al. 2017), and this may have increased susceptibility to bark beetles. Optimal host selection provides an additional explanation for this pattern of strong conspecific negative density dependence (i.e., mortality risk increases with more conspecifics): beetle populations proliferated 2-3 years post-fire (when drought intensity peaked), and this may have enabled beetles to selectively attack larger and more vigorous host trees (Fig. 4.10; Boone et al. 2011, Stephenson et al. 2019). As conspecific basal area is tightly correlated with the abundance of large *Pinus*, neighborhoods with high conspecific basal area would have been preferentially selected by dispersing beetles (Safranyik and Carroll 2006, Barbosa et al. 2009) and this would increase post-fire mortality risk. These results demonstrate that fire and drought may not only make the effects of local neighborhood on bark beetle pressure more pronounced, they may reverse the directionality of density dependence and thus fundamentally alter the consequence of mortality on forest spatial pattern (Fig. 4.8).

**Implications for fire mortality models**

Existing fire mortality models (e.g., FOFEM) predict mortality with a high degree of accuracy (Woolley et al. 2012, Grayson et al. 2017, Hood and Lutes 2017), but performance is inconsistent for large-diameter trees (Hood et al. 2007, Kane et al. 2017a, Furniss et al. 2019). These models perform best when direct fire damage is the primary driver of mortality (i.e., trees with high percent crown scorch), but large-diameter trees are rarely killed by fire damage alone. Our findings concur with the widespread understanding that large-diameter trees are instead more susceptible to the physical and
biotic mortality agents (i.e., drought and bark beetles) that mediate delayed mortality post-fire (Hood et al. 2018), but these background mortality processes are not represented by the independent variables (i.e., crown scorch and DBH) used in most post-fire mortality models (Woolley et al. 2012, Hood and Lutes 2017, Grayson et al. 2017). Spatially structured delayed mortality processes thus contribute to spatially auto-correlated error that manifests as patches of over- or under-predicted mortality within a stand (Furniss et al. 2019). The relative infrequency of large-diameter trees (e.g., ~1% of individuals; Lutz et al. 2018) allows total model accuracy to remain high, despite systematic error that emerges when predictions are aggregated at the stand level (Furniss et al. 2019).

Both types of error may be reduced by incorporating stand structure variables into mortality models to capture the density-dependent processes that regulate delayed mortality (Figs. 4.7-9, Tables 4.2 & C.4). The inclusion of structural variables would particularly enhance the capacity of fire mortality models to predict post-fire spatial pattern: the resulting mortality predictions would not only reflect the variability in first-order fire intensity, they would also capture spatial heterogeneity in mortality risk due to forest composition, structure, and spatial pattern. This would also enhance the utility of mortality models for estimating the effects of fire on carbon stocks, as large-diameter trees contribute disproportionately to forest biomass (Lutz et al. 2018), and accurately modeling their demography will reduce the uncertainty associated with landscape-scale carbon estimates (Lutz et al. 2017b, Stenzel et al. 2019).
CONCLUSIONS

This study is the first quantitative comparison of fine-scale patterns associated with background mortality processes both before and after acute disturbance. Our analysis of pre-fire mortality was consistent with the existing paradigm that density-dependent mortality within late-successional forests is most prominent among the smallest trees, while mortality of larger and older trees is less density-dependent. This lack of strong negative density dependence among large trees, however, should not be conflated with spatially random mortality; contagious mortality processes may provoke distance-dependent mortality (Clyatt et al. 2016), and local neighborhood can still moderate mortality risk (Das et al. 2008). Additionally, disturbance provoked strong density-dependence among large-diameter trees (Fig. 4.10), further contradicting the widespread expectation that large tree mortality in old-growth forests is spatially random (Franklin et al. 2002, Aakala et al. 2012, Lintz et al. 2016).

The mortality regime that emerged post-fire was distinct from either background mortality or direct fire effects (Fig. 4.10). Distance- and density-dependent background mortality processes interacted with fire damage to introduce heterogeneity at finer scales compared fire alone, providing a key insight regarding the formation of the complex, multi-scale spatial structure characteristic of frequent-fire forests (Hessburg et al. 1999, van Wagendonk and Fites-Kaufman 2006). Although the post-fire mortality regime may have been brief relative to the life span of mature trees, the synergistic effects of fire, drought, and background mortality processes will have enduring effects on the spatial pattern of large-diameter trees, and thus the forest as a whole. These findings provide a more mechanistic understanding of temperate forest spatial pattern dynamics, and they
contribute to theoretical models describing disturbances and the maintenance of ecological heterogeneity (e.g., Paine and Levin 1981, Larson and Churchill 2012). The foundational importance of fine-scale heterogeneity (Hessburg et al. 2015, Kelly and Brotons 2017) and the ecological significance of large-diameter trees (Larson et al. 2013, Lutz et al. 2018) renders background mortality processes, and the post-disturbance mortality regime that they moderate, acutely consequential to the structure, function, and spatial pattern of forests.

**Literature Cited**


Stephenson, N. L., and P. J. van Mantgem. 2005. Forest turnover rates follow global and


Table 4.1. Pre-fire mortality, direct fire mortality, and post-fire mortality for trees within the Yosemite Forest Dynamics Plot. Values represent the number of mortalities associated with bark beetles (“Beet.”), pathogens (“Path.”), and mechanical (“Mech.”; e.g., broken stem or crushed) factors associated with death. Individual trees may be associated with multiple factors. Columns reflect the number of mortalities associated with bark beetles, pathogens, and mechanical agents of mortality, while “Rate (% yr⁻¹)” reflects annualized mortality rates. Bold indicates categories with enough stems to be used in spatial analysis (n >100).

<table>
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<th>DBH (cm)</th>
<th>N live at est.</th>
<th>N live at end</th>
<th>Pre-fire</th>
<th>Rate</th>
<th>Direct fire (&lt;1 yr)</th>
<th>Rate</th>
<th>Post-fire</th>
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<td></td>
<td></td>
<td></td>
<td>Pre-fire</td>
<td>Rate</td>
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<td>Rate</td>
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<td>97</td>
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Table 4.2. Mortality rates and spatial metrics that were correlated with mortality. Correlations were identified by pairing each variable with non-spatial “base” models based on DBH and CVS. This table contains the single best structural variable for each species and size class; all significant variables are reported in Tables C.2-C.4. Descriptions of each variable is in Table C.1. The distance values each variable indicate the circular radius at which that structural variable had the most explanatory power. The (+) or (-) next to the structural variable indicates the direction of the relationship (positive indicates greater mortality risk, negative indicates lower mortality risk). Delta Akaike information criterion (dAIC) represents the differential model performance compared to the base (non-spatial) mortality models; more negative numbers indicate greater improvement. Bold indicates that the spatial model was significantly better than the non-spatial base model (|dAIC| > 7).

<table>
<thead>
<tr>
<th>Spp.</th>
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<th>Pre-fire</th>
<th>dAIC</th>
<th>Direct fire</th>
<th>dAIC</th>
<th>Post-fire</th>
<th>dAIC</th>
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<td>Density of conspecifics ≥10 cm DBH (30 m) (+)</td>
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<td>BA (5 m) (+)</td>
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<td>BA of conspecifics (30 m) (+)</td>
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<td>Density of conspecifics ≥10 cm DBH (30 m) (+)</td>
<td>-6.3</td>
<td>Density of stems ≥60 cm DBH (20 m) (+)</td>
<td>-15.2</td>
</tr>
<tr>
<td></td>
<td>1-10</td>
<td>Density of all stems ≥1 cm DBH (20 m) (-)</td>
<td>-5.6</td>
<td>Landscape position (+)</td>
<td>-38.5</td>
<td>BA surviving conspecifics (20 m) (+)</td>
<td>-13.9</td>
</tr>
<tr>
<td></td>
<td>10-60</td>
<td>Density of all stems ≥1 cm DBH (30 m) (-)</td>
<td>-3.0</td>
<td>BA of conspecifics ≥10 cm DBH (30 m) (+)</td>
<td>-12.6</td>
<td>BA surviving conspecifics (5 m) (+)</td>
<td>-7.8</td>
</tr>
<tr>
<td></td>
<td>≥60</td>
<td>Density of stems 10≤ cm DBH&lt;60 (30 m) (+)</td>
<td>-1.9</td>
<td>BA (30 m) (-)</td>
<td>-5.8</td>
<td>BA (30 m) (+)</td>
<td>-2.8</td>
</tr>
<tr>
<td></td>
<td>1-10</td>
<td>Hegyi (+)</td>
<td>-3.9</td>
<td>BA (5 m) (+)</td>
<td>-22.1</td>
<td>BA surviving conspecifics (30 m) (+)</td>
<td>-4.8</td>
</tr>
<tr>
<td></td>
<td>10-60</td>
<td>Density of conspecifics ≥10 cm DBH (20 m) (-)</td>
<td>-9.8</td>
<td>Density of stems ≥1 cm DBH (5 m) (-)</td>
<td>-9.8</td>
<td>BA of conspecifics ≥10 cm DBH (10 m) (+)</td>
<td>-37.2</td>
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<td>Fire scar (+)</td>
<td>-24.0</td>
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<td>-76.8</td>
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<td>Nearest neighbor (+)</td>
<td>-4.6</td>
<td>Density of stems 10≤ cm DBH&lt;60 (15 m) (+)</td>
<td>-41.4</td>
<td>BA (30 m) (+)</td>
<td>-13.7</td>
</tr>
</tbody>
</table>
FIG. 4.1. Spatio-temporal scales of tree mortality processes (A) and fire (B). Letters represent studies that have described each mortality process with explicit consideration of spatial or temporal scale; dark lines indicate the scales at which there is quantitative evidence of each process operating, while dotted lines indicate qualitative descriptions of scale. The two x-axis scales represent area-based scale in hectares (ha) on top with the corresponding linear scale (radii in m) below.
FIG. 4.2. Location of the Yosemite Forest Dynamics Plot (YFDP) within the lower-montane mixed-conifer zone of the Sierra Nevada, CA, USA (A-C). The bottom four panels show stem maps of stems ≥1 cm diameter at breast height (DBH) colored according to (D) landscape position (derived from a LiDAR-measured, 1-m digital elevation model), (E) species (*Abies concolor* (ABCO), *Calocedrus decurrens* (CADE), *Pinus lambertiana* (PILA), and *Quercus kelloggii* (QUKE)), (F) neighborhood density (average density within a 30-m circular radius), and (G) crown volume scorched (CVS).
FIG. 4.3. Spatial pattern of pre-fire mortality, direct fire mortality, and post-fire mortality within the Yosemite Forest Dynamics Plot. The red lines indicate observed patterns, shaded areas represent Monte-Carlo simulation envelopes based on the 2.5th and 97.5th percentiles of 999 simulations generated according to the null hypothesis of random mortality, and dashed lines represent the mean value of simulations. Black dashed lines represent the mean value from the simulations. Vertical dotted lines represent the distance \( r \) at which the observed pattern of mortality became random. Values of \( g(r) \) above the shaded envelope indicate that mortality was aggregated, while values below the envelope indicate hyper-dispersed mortality.
FIG. 4.4. Spatial pattern of agent-specific *pre-fire mortality* within the Yosemite Forest Dynamics Plot. The red lines indicate observed patterns, shaded areas represent Monte-Carlo simulation envelopes based on the 2.5th and 97.5th percentiles of 999 simulations generated according to the null hypothesis of random mortality, and dashed lines represent the mean value of simulations. The vertical dotted lines represent the distance \( r \) at which the observed pattern of mortality became indistinguishable from the null model; values of \( g(r) \) above the shaded envelope indicate clustered mortality while values below indicate hyper-dispersed mortality. Sample size, \( n \), is the number of points in each pattern.
FIG. 4.5. Spatial pattern of agent-specific post-fire mortality within the Yosemite Forest Dynamics Plot. The red lines indicate observed patterns, shaded areas represent Monte-Carlo simulation envelopes based on the 2.5th and 97.5th percentiles of 999 simulations generated according to the null hypothesis of random mortality, and dashed lines represent the mean value of simulations. The vertical dotted lines represent the distance \((r)\) at which the observed pattern of mortality became indistinguishable from the null model; values of \(g(r)\) above the shaded envelope indicate clustered mortality while values below indicate hyper-dispersed mortality. Sample size, \(n\), is the number of points in each pattern.
FIG. 4.6. Maps of mortality intensity (kernel density estimation) of pre-fire, direct fire, and post-fire tree mortality within the Yosemite Forest Dynamics Plot. Colors are relativized per diameter class (i.e., yellow for small-diameter trees represents a higher absolute rate compared to yellow for large-diameter trees; Table 4.1 contains absolute rates). Line color around each polygon indicates whether mortality was higher or lower than would be expected by chance based on the non-random initial pattern of live stems at the beginning of each mortality regime (blue indicates reduced mortality rates, yellow indicates elevated mortality rates). For example, a yellow line around a blue polygon represents a low relative mortality rate (blue fill) that was still higher than would have been expected by chance (yellow border line). The pattern of stems associated with each panel is presented in Fig. C.1.
FIG. 4.7. Relationships between forest spatial structure and *Abies concolor* mortality. Columns represent timing of mortality and rows represent tree diameter classes. Lines show the relationship between forest spatial structure and probability of mortality determined with generalized linear models. Points indicate observed proportion of mortality, and point size reflects relative number of stems in each group. The x-axis for each panel shows the single best structural variable for that mortality regime and size class; all variables may be found in Tables C.2-C.4. dAIC indicates the improvement in model accuracy compared to AIC of the non-spatial base model. Basal area (BA) is reported in m² ha⁻¹, stem categories are in stems ha⁻¹.
FIG. 4.8. Relationships between forest spatial structure and *Pinus lambertiana* mortality. Columns represent timing of mortality and rows represent tree diameter classes. Lines show the relationship between forest spatial structure and probability of mortality determined with generalized linear models. Points indicate observed proportion of mortality, and point size reflects relative number of stems in each group. The x-axis for each panel shows the single best structural variable for that mortality regime and size class; all variables may be found in Tables C.2-C.4. dAIC indicates the improvement in model accuracy compared to AIC of the non-spatial base model. Basal area (BA) is reported in m² ha⁻¹, stem categories are in stems ha⁻¹.
Fig. 4.9. Relationships between forest spatial structure and *Calocedrus decurrens* mortality. Columns represent timing of mortality and rows represent tree diameter classes. Lines show the relationship between forest spatial structure and probability of mortality determined with generalized linear models. Points indicate observed proportion of mortality, and point size reflects relative number of stems in each group. The x-axis for each panel shows the single best structural variable for that mortality regime and size class; all variables may be found in Tables C.2-C.4. dAIC indicates the improvement in model accuracy compared to AIC of the non-spatial base model. Basal area (BA) is reported in m² ha⁻¹, stem categories are in stems ha⁻¹.
FIG. 4.10. Empirically informed conceptual model describing the development of spatially structured mortality processes before, during, and after compound disturbance (fire and drought). Polygons represent different mortality agents (colors match with Fig. 4.1). Position along the y-axis represents the tree diameters (cm DBH) for which each mortality process was spatially structured. The strength of each process (as detected in this study) is also approximately related to polygon size. Superscripts indicate the form of spatial structuring (distance and/or density dependence) that was most evident for each process. Competition among post-fire recruits was not analyzed in this study, but is shown in its hypothesized position.
CHAPTER V

CROWDING, CLIMATE, AND THE CASE FOR SOCIAL DISTANCING AMONG TREES

ABSTRACT

In an emerging era of megadisturbance, bolstering forest resilience to wildfire, insects, and drought is becoming increasingly critical. Climate has received considerable attention as a driver of these disturbances, but few studies have examined the multitudinous and complex climate–vegetation–disturbance interactions. Current strategies for bolstering forest resilience often rely on retrospective approaches, seeking to impart resilience by restoring historical conditions to contemporary landscapes. However, historical conditions are becoming increasingly unattainable amidst modern bioclimatic conditions.

We examined the relationship between forest spatial structure, drought, fire, and bark beetles, and found that while pre-fire drought elevated mortality risk, advantageous local neighborhoods could offset these effects. Surprisingly, mortality risk was higher in crowded local neighborhoods that burned in wet years \( (Pm = 42\%) \) compared with sparse neighborhoods that burned during drought \( (Pm = 30\%) \). Risk of beetle attack was also increased by drought, but lower conspecific crowding impeded the otherwise positive interaction between fire and beetle attack. Antecedent fire increased drought-related mortality over short timespans \( (< 7 \text{ yrs}) \) but reduced mortality over longer intervals. These

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4 This chapter is currently under review at Ecological Applications
results clarify interacting disturbance dynamics and provide a mechanistic underpinning for forest restoration strategies. Importantly, they demonstrate the potential for managed fire and silvicultural strategies to offset climate effects and bolster resilience to fire, beetles, and drought.

**INTRODUCTION**

In forests throughout western North America, ongoing climatic changes are driving increases in wildfire activity (Pechony and Shindell 2010), drought-related tree mortality (Williams et al. 2013), insect outbreaks (Raffa et al. 2008), and background mortality rates (van Mantgem and Stephenson 2007). Together, these stressors pose an existential threat to forest ecosystems (Allen et al. 2015), and maintaining healthy forest ecosystems is becoming increasingly difficult (Millar and Stephenson 2015).

There is a considerable body of literature regarding ecological resilience (Hessburg et al. 2015, North et al. 2019), but most guidelines for forest restoration are rooted in the widespread conception that we can impart resilience by returning forested landscapes to their pre-settlement state. Historical reference conditions are an undeniably valuable benchmark for restoration (Hessburg et al. 2005, North et al. 2007, Keane et al. 2009), but this approach has limitations: historical forests were not universally resilient to disturbance (Veblen et al. 1994), resilience to past disturbance does not necessarily equate to resilience among novel disturbances (Allen et al. 2015, Stephens et al. 2018), and historical conditions may be unattainable amidst contemporary bioclimatic conditions (Keane et al. 2009, Schoennagel et al. 2017, Stephens et al. 2018). The efficacy and adaptability of forest restoration is limited if we do not develop a more...
fundamental understanding of the ecological characteristics that provide the actual mechanisms of resilience.

Recent studies have contributed a more mechanistic understanding of resilience at broad spatial scales (Parks et al. 2015, Kolden et al. 2015, Hessburg et al. 2015), but the factors that confer resilience within a landscape are not equivalent to the ecological attributes that confer resilience within a stand (Falk et al. 2019). A key attribute of resilient landscapes is patchiness: forest mosaics may shift following repeated disturbances, and a resilient landscape comprises many seral stages and patch sizes. Resilience at this scale is an emergent property of large landscapes, and resilient landscapes may therefore be comprised of non-resilient patches. Within-patch resilience is fundamentally different, relying primarily on individual-level resistance and the convergent properties of ecological communities (Falk et al. 2019). A resilient forest is one that recovers—in structure, composition, and function—to its antecedent state (*sensu* Halpern 1988). Resilience at this scale is conferred by the resistance of individual trees, life-history adaptations (e.g., thick bark, serotiny), and fine-grained ecological processes that mediate post-disturbance mortality including inter-tree competition and host-specific insects (Hood et al. 2016, van Mantgem et al. 2018, Furniss et al. 2020b). Some principles of landscape resilience may be relevant across spatial scales (e.g., the physical process of fire spread is regulated by fine-scale surface fuels within a stand as well as the distribution of vegetation across a landscape), but plant-plant interactions (e.g., competition) are fundamentally fine-scale phenomena; there are no clear analogs at the landscape scale.

Patterns in disturbance severity are governed by complex, cross-scale interactions
(Peters et al. 2004, Allen 2007), and this renders both broad- and fine-scale management crucial to the overall resilience of forest landscapes. Active management can mitigate the severity of future disturbances (van Mantgem et al. 2016, Hood et al. 2016, Knapp et al. 2021), but existing research is sparse compared to the multitudinous possible combinations of disturbance events and disparate ecological templates. We currently have an incomplete and sometimes contradictory understanding of disturbance interactions. For example, recent fire has been shown to decrease mortality to drought and insects (van Mantgem et al. 2016, Hood et al. 2016), but recent fire can also increase mortality risk by weakening trees and temporarily increasing susceptibility to drought and post-fire insects (Breece et al. 2008, Furniss et al. 2020b). These divergent outcomes may be determined by the intervals between events, but the complexities of these interactions have not yet been adequately explained.

Despite the increasing frequency of compound disturbances, and growing public concern over widespread forest die-off, very little is known about the fine-scale ecological processes that mediate disturbance interactions. Numerous recent studies have begun to reveal the importance of forest structure in mediating mortality following individual disturbances (Ruiz-Benito et al. 2013, Young et al. 2017, van Mantgem et al. 2018, Restaino et al. 2019, Furniss et al. 2020b, Knapp et al. 2021), but there has been much less attention to the role of forest structure in mediating compound interactions between fire, insects, and climate.

Here we contribute to a foundational understanding of how forest structure and spatial pattern regulate the severity of, and interactions between, disturbance events. We combined two longitudinal datasets from the Sierra Nevada containing annual tree
pathology exams among 50,341 trees within 18 stem mapped forest plots, representing some of the most comprehensive spatially explicit, annual-resolution, tree mortality data in existence (Lutz 2015). Eight of the plots were burned by six different fires over a span of 23 years and under a range of pre- and post-fire climatic conditions, including both wet years and a millennial-scale drought (Belmecheri et al. 2016). This multi-plot, longitudinal dataset enabled us to create a post-hoc factorial design through which we could explicitly examine how climate, tree neighborhoods, and antecedent fire collectively mediate tree mortality, risk of beetle attack, and drought severity.

**METHODS**

*Study area*

We used two longitudinal datasets from the lower montane mixed-conifer zone of the Sierra Nevada: the Sierra Nevada Forest Dynamics Plot Network (SNFDP; van Mantgem and Stephenson 2007) and the Yosemite Forest Dynamics Plot (YFDP; Lutz et al. 2012). The climate in this region is montane mediterranean, with warm, dry summers and cool, wet winters. Pre-suppression fire return intervals were generally <30 years. We used 18 1-ha SNFDP plots (19,562 trees total) from the lower montane mixed-conifer zone of Yosemite and Sequoia & Kings Canyon National Parks (Table D.1), and the YFDP, a single 25.6-ha plot containing 34,458 live trees pre-fire. Seven of the SNFDP plots burned between 1990 and 2009 (Table D.2) under climatic conditions including both wet and dry years (but not during extreme drought), while the YFDP was burned under extreme drought conditions in the 2013 Rim Fire (Lutz et al. 2017). Within each of these study plots, all woody stems ≥1 cm diameter at breast height (DBH; 1.37 m) have been identified, tagged, and mapped. All plots were censused annually for new recruitment and
mortality, and percent crown volume scorched was recorded for each tree within 1 year following fire.

Field Measurements

During the annual mortality surveys, pathology exams were conducted for all newly dead trees. The multiple factors associated with death were identified by trained field technicians who removed bark to reveal evidence of pests and pathogens (details in Das et al. 2016, Furniss et al. 2020b). Bark beetles were identified to species based on the size and shape of galleries, frass color, and actual beetles if present.

We analyzed the five most abundant species: *Abies concolor*, *Calocedrus decurrens*, *Pinus lambertiana*, *Pinus ponderosa*, and *Quercus kelloggii*. We grouped the two *Pinus* species to maintain a robust sample size among all plots as these two species are ecologically similar in their tolerance to fire and their susceptibility to bark beetles of the genus *Dendroctonus*. Results presented in the main text are non-species-specific with species-specific figures are in the SI.

Fire mortality

We used generalized linear mixed models (GLMMs; details below) with a logit link to evaluate the effects of climate and local neighborhood on mortality risk. We used binary classifiers (0, live; 1, dead) to indicate whether trees were killed within 3 years of fire (hereafter “fire-related mortality”), or within 5 years of fire and had bark beetles as a factor associated with death (hereafter “post-fire beetle mortality”). Fire-related mortalities included both direct- and indirect-fire mortalities to minimize potential inconsistencies due to the timing of post-fire mortality surveys. A 3-yr window was used for consistency with previous fire mortality research, while 5 years was used for beetle
mortality to better capture the temporal scale of post-fire insect outbreaks which can last >3 years post-fire.

The relative importance of climate and local tree neighborhood variables (details below) was assessed by comparing individual GLMMs created by combining each climate and local neighborhood variable with a “base” model. Base models included percent crown volume scorched (CVS) and diameter at breast height (DBH) as fixed effects, as well as random effects terms for species and plot to account for species-level differences in sensitivity to fire and background mortality rates (Das et al. 2016) and plot-level differences in background mortality, elevation, and fire characteristics (e.g., Furniss et al. 2020a). The GLMMs estimated probability of mortality ($P_{mij}$) for tree $i$ in plot $j$ as:

$$\text{logit}(P_{m_{ij}}) = \beta_0 + b_{0\text{Plot}} + b_{0\text{Spp}} + (\beta_1 + b_{1\text{Spp}})CVS_{ij} + \beta_2 DBH + \epsilon_{ij}$$

where $\beta_0$ is the intercept, $b_0$ are random intercept terms, $b_{1\text{Spp}}$ is a random slope for each species, and $\beta_{1-2}$ are fitted coefficients for CVS and DBH. The CVS term serves as a proxy for the severity of fire damage, while DBH serves as a proxy for both bark thickness and tree size. Random slope, intercept, and error ($\epsilon_{ij}$) terms were treated as normally distributed random variables. Climate and neighborhood models were created by combining the base model with fixed effect terms, $\beta_C Climate_{ij}$ and $\beta_N Neighborhood_{ij}$, where $\beta_C$ and $\beta_N$ represent fitted coefficients, $Climate_{ij}$ represents a climate parameter for plot $j$ (Table D.3), and $Neighborhood_{ij}$ represents the local neighborhood around tree $i$ in plot $j$ (Table D.1). We created separate GLMMs for each climate variable, each neighborhood variable, and a combined GLMM that included one of each. We included interaction terms between CVS, climate, and neighborhood variables. We did not include a CVS:DBH interaction term so that changes in the $P_m \sim$ CVS relationship could be fully
attributable to interactions climate and neighborhood without being potentially confounded by DBH. We created two complete sets of models for the two response variables: fire-related mortality and post-fire beetle mortality.

We ran preliminary analyses using polynomial CVS terms, but these models produced apparently spurious results when we included interaction terms with climate and neighborhood variables. We opted for more parsimonious models based on a linear CVS term, allowing us to include DBH as well as CVS:climate:neighborhood interaction terms. These non-polynomial models were less sensitive to the uneven distribution of trees among a limited set of plot–fire–climate combinations. The datasets remained somewhat imbalanced, but large, stem-mapped, annually-surveyed forest plots are rare—we believe these to be among the best data available.

For plots that had a high proportion of trees with either 0% or 100% CVS, we rarefied the dataset by reducing the number of trees with 0% or 100% CVS (rarefied N in Table D.1) so that the proportion of trees at maximal CVS values did not exceed 25%, as this can bias model fitting and reduce accuracy at intermediate CVS levels (Furniss et al. 2019). One plot (FFS2BURN) experienced considerable beetle mortality immediately after fire, killing a high proportion of trees that had no crown scorch. For this plot, we considered only trees that had fire as the proximate cause of death for the fire-related mortality model. We repeated all analyses without removing any trees and results were not meaningfully different.

All fixed effect terms were standardized before model fitting. We evaluated model performance using Akaike’s information criterion (AIC) and considered differences in AIC >7 as support for a meaningful difference in model performance (Burnham and
Anderson 1998).

**Drought mortality**

We evaluated the effect of antecedent fire on drought-related mortality by calculating the plot-level mortality rate (Drought mortality, %) during peak years of drought-induced mortality (2015-2016) and regressing mortality rate against number of years since the most recent fire, pre-drought stem density, and elevation. For burned plots we created an additional model for beetle-related Pinus mortality during the drought. We quantified the strength of these relationships using generalized linear models of the form:

\[
Drought mortality (\%) = \beta_0 + \beta_1 x + \beta_2 x^2
\]

where \( x \) is an independent parameter (time-since-fire, density, or elevation) and \( \beta_{0-2} \) are the intercept and fitted coefficients. We used the polynomial form to capture potential threshold effects (e.g., a significant relationship at low elevations, then a plateau in mortality rate above some elevation threshold) and unimodal relationships.

**Local neighborhood variables**

We quantified neighborhood stem density (Density), basal area (BA), and the Hegyi competition index (Biging and Dobbertin 1992) within circular neighborhoods of various sizes around each tree (radii ranged from 3-20 m) to summarize the spatial structure around each tree (considering all neighbors and conspecifics only). We controlled for edge effects by mirroring trees at the edge of each plot so that trees near the edge did not include empty space. Neighborhood metrics for trees near the edge showed no edge effects (Fig. D.1). The full list of neighborhood variables may be found in Table D.1.
Climate data

We summarized pre- and post-fire climate using two ecologically meaningful climate parameters: Climatic Water Deficit (Deficit) and Palmer Drought Severity Index (PDSI). Deficit integrates temperature, precipitation, and soil water storage to approximate water supply and evaporative demand, and it is a key correlate of vegetation patterns (Stephenson 1998, van Wagendonk et al. 2020) and tree mortality (van Mantgem and Stephenson 2007) in the Sierra Nevada. The PDSI employs a similar water-balance-based approach, but it has a longer lag time (~9 months) with antecedent climate. We acquired both climate parameters from TerraClimate, a 4-km gridded dataset of monthly climate and water balance (based on a modified Thorthwaite-Mather water balance model) for global terrestrial surfaces (Abatzoglou et al. 2018). Monthly climate values were averaged over time spans ranging from 5 years pre- to 3 years post-fire (Table D.3), inclusive of the month of the fire. We centered Deficit for each plot (hereafter DΔ) as the difference between the Deficit value for a given timespan month and the 30-yr average (1985-2015). This made Deficit comparable among plots, as a positive DΔ value indicates climatic conditions were droughty compared to normal conditions at that site, regardless of how absolute Deficit compared to other plots. We also calculated mean summer deficit (30-yr average considering only June, July, and August), and peak anomaly (maximum DΔ that occurred within a 3-yr moving window considering 5 yrs pre- and 3 yrs post-fire). Climate data was accessed via Google Earth Engine (https://earthengine.google.com).

All analyses were performed in R v.3.6.3 (R Core Team 2020) using packages lme4 (Bates et al. 2015), pROC (Robin et al. 2011), and plot3D (Soetaert 2019).
RESULTS

Pre-fire drought and crowded local neighborhoods increased probability of fire-related mortality by 22% and 33%, respectively (Fig. 5.1, Table 5.1). Climate effects were most pronounced at low levels of fire damage (CVS ≤25%) where mortality risk was positively related to $D_\Delta$ (Fig. 5.1A). The effects of crowding, conversely, were evident among all levels of CVS, with trees in open neighborhoods (low local BA) having lower modeled mortality risk (~0-80%) compared with trees in denser neighborhoods (~20-90%, Fig. 5.1B). Post-fire $D_\Delta$ and local conspecific BA also increased probability of successful post-fire beetle attack, especially at low levels of crown scorch (Fig. 5.1C&D). Tree diameter was correlated with crown scorch (high CVS categories had smaller average DBH), but was not correlated with neighborhood or climate variables (Fig. 5.1).

Three-way interactions between climate, neighborhood, and fire damage altered the effects of pre-fire $D_\Delta$ and local BA on mortality risk (Fig. 5.2). At low levels of crown scorch (CVS ≤25%), crowding only increased mortality risk if pre-fire climate was droughty. Conversely, for trees with intermediate to high levels of crown scorch (CVS >25%), local BA increased fire-related mortality risk by over 20% among all pre-fire climatic conditions (Fig. 5.2). Climate and crowding also increased risk of post-fire beetle mortality for trees with low amounts of crown scorch as much as 55%, but their effects were not evident at high CVS levels (>75%, Fig. 5.2).

Most climate parameters had significant ($p < 0.05$) interactions with CVS, but only 1-yr pre-fire PDSI and 3-yr pre-fire $D_\Delta$ had significant direct effects for predicting fire-related mortality (Table 5.2). No climate parameters had direct effects for post-fire beetle
mortality, but 1-yr post-fire $D_\Delta$ had a significant interaction with CVS (Appendix II). The optimal neighborhood distance for predicting post-fire mortality was 8 m (Table 5.2, Fig. D.4). Stem density was also positively related to mortality risk, but basal area was a superior metric (Table 5.2). Conspecific basal area within 15 m was best for predicting post-fire beetle mortality, but local basal area of all species was the better metric for overall fire-related mortality (Table 5.1). The Hegyi index performed comparably to basal area (slightly worse AUC, better AIC).

Drought-related mortality in plots unburned for at least 35 years was negatively related to elevation and positively related to stem density (Fig. 5.3). These trends may have been partially confounded by differences in forest productivity and structure, as the plot with the highest mortality rate also had the smallest average tree DBH (Fig. 5.3B), but small trees are not necessarily more susceptible to drought. Drought severity in burned plots was lowest for plots that burned 7-15 years prior (Fig. 5.3D), where mortality rates were comparable with unburned plots. Variation in mortality rate among burned plots, however, could not be explained by stem density and elevation alone ($R^2 \sim 0$, $P > 0.1$; Fig. 5.3C&G). Time since fire was the primary determinant of drought-induced mortality among burned plots; plots that burned <7 years prior to drought experienced higher mortality rates compared with unburned plots at similar elevations and stem densities (28-40% vs. 1-6%; Fig. 5.3A&E). Drought-induced beetle mortality for Pinus followed the same pattern (Fig. 5.3H).

**DISCUSSION**

This study provides an empirical framework for integrating previous research that has
shown interactions between fire and climate (van Mantgem et al. 2013, 2018), local neighborhood (Restaino et al. 2019, Furniss et al. 2020b, Knapp et al. 2021), and bark beetles (Breece et al. 2008, Hood et al. 2016). Crowded tree neighborhoods were the central factor in regulating mortality risk among both burned and unburned forests, and we found that the timing and order of fire and drought can fundamentally alter the nature of their interaction (**sensu** Kane et al. 2017). Climate and local crowding jointly regulated fire-related mortality and risk of post-fire beetle attack, and this relationship was most pronounced at intermediate levels of fire damage.

There is considerable evidence that doughtier climate increases disturbance severity and tree mortality (van Mantgem and Stephenson 2007, Raffa et al. 2008, Flannigan et al. 2009, van Mantgem et al. 2013, Schoennagel et al. 2017, Germain and Lutz 2020), but our results demonstrate that local tree neighborhoods can be equally important countervailing contributors to reducing mortality risk at fine scales. The effects of drought (reduced water supply) are filtered through fine-grained ecological attributes including micro-topography, soil water-holding capacity, and lower forest density (reduced water demand), and these fine-grained ecological variables mediate the realized micro-environment that trees actually experience. Tree neighborhoods capture this net drought effect along with resource competition and spatially non-random mortality processes, all factors that are all inexorably linked to tree-to-tree variance in mortality risk (van Mantgem et al. 2018, Furniss et al. 2020b). Other studies have shown the importance of both climate and forest structure to post-fire mortality risk (Ruiz-Benito et al. 2013, Young et al. 2017, van Mantgem et al. 2018, Restaino et al. 2019), but few studies have directly compared the magnitude of their importance. Our results provide
mechanistic evidence that density management—the primary tool available to land managers—has the potential to compensate for some of the deleterious effects of drought to cultivate persistent resilience to drier futures and novel disturbance regimes.

Higher levels of crowding, drought, and crown scorch increased mortality independently and through positive interactions: crowding caused a greater increase to mortality risk as climate became drier and crown scorch became greater (Fig. 5.2). At intermediate levels of CVS, crowding began to outweigh climate effects. For a tree with 50% CVS, survival was 12% higher in open neighborhoods that burned during drought compared with trees in crowded neighborhoods that burned under wetter conditions (Table 5.1). When drought and fire cooccurred, a 30-cm tree in a dense neighborhood had a probability of mortality twice as high compared to an equivalent tree in an open neighborhood (66% vs 30%, respectively; Table 5.1).

It does not appear that our results were confounded by potential size-dependent differences in sensitivity to fire. Tree DBH was not correlated with local BA or climate variables (Fig. 5.1), and direct effects of tree diameter on mortality risk were assumed by the DBH term in the GLMMs. Size effects are evident, however, in comparing different CVS categories, as CVS was inversely related to tree DBH (Fig. 5.1). This suggests that crowding may alter mortality risk among trees of all diameters, while climate may be primarily important for larger trees (low CVS levels). This may partially explain the diminished importance of climate and crowding for predicting post-fire beetle mortality at high levels of CVS, as post-fire beetle selection pressure on Pinus is typically reduced for small-diameter trees (Stephenson et al. 2019).

Fire can confer either resistance (van Mantgem et al. 2016, Hood et al. 2016) or
increased susceptibility (Breece et al. 2008, Furniss et al. 2020b, Knapp et al. 2021) to drought and bark beetles. Our results may reconcile this apparent contradiction by identifying a time interval at which this relationship appears to invert (~7 years). Multiple physiological mechanisms may be responsible for this temporarily elevated susceptibility to drought, including elevated bark beetle pressure (Breece et al. 2008) and increased risk of cavitation due to fire-induced xylem deformation (Partelli-Feltrin et al. 2020). This ~7-15 year post-fire time period where drought mortality was minimized is consistent with other studies that tracked mortality during the same drought event. Knapp et al. (2021) found elevated mortality rates in plots that burned 2-3 years pre-drought compared to unburned controls, and Steel et al. (2021) found elevated mortality rates in plots that burned in 2001, 14 years prior to the drought. Interestingly, this 7-15 year time span aligns closely with the pre-suppression fire return interval for dry forests in the Sierra Nevada. Although fire can confer resistance to drought, time between events is a critical factor (Fig. 5.3). The limited number of plot × fire × elevation combinations available in this dataset are reason to interpret this result with a degree of caution, as the recently burned plots with high drought mortality rates were at lower elevations compared to most other burned plots. Our results are bounded on both ends by findings from other studies that measured mortality during the 2012-2016 drought (Knapp et al. 2021, Steel et al. 2021), and this study provides observational evidence regarding susceptibility to drought at intermediate time frames. Additional research will be necessary, however, to fully disentangle the confounding effects of elevation, density, and disturbance history on susceptibility to drought.

The pre-fire structure of many of the plots in this study—the YFDP in particular—
was characterized by very high densities (>1000 stems ≥1 cm DBH per ha), dominated by small- and medium-diameter stems of shade-tolerant species that had established during more than a century of fire exclusion (Lutz et al. 2012). In long-unburned forests such as this, reducing forest density in the most crowded neighborhoods (90th percentile for BA ~130 m² ha⁻¹) to plot-level average (63 m² ha⁻¹ in the YFDP) would reduce mortality risk in these areas ~10%. Were a management objective to include maximizing the number of live trees post-fire, this modest increase in survival may not be enough to offset the removal of trees necessary to reduce mortality risk. Density reduction could be an effective strategy, however, if used to mediate which trees were more likely to be killed by fire. By creating advantageous local neighborhoods around specific trees, targeted density reduction could provide a way to minimize mortality risk for trees that are of particular socio-ecological importance. Large-diameter trees, for example, are in decline at regional and global scales (Lutz et al. 2009, Lindenmayer et al. 2014), and are particularly vulnerable to compound disturbance events (Stephenson et al. 2019, Furniss et al. 2020b). These results provide further evidence that targeted silvicultural management could be an effective strategy to mitigate the susceptibility of these long-lived individuals to rapid ecological changes.

Climate and local neighborhood variables offered modest improvements to overall model performance (i.e., AUC, sensitivity, and specificity), but they resulted in meaningful improvements to AIC (Table 5.2). Local neighborhood variables stood out in this regard, with even the weakest local neighborhood metrics producing substantial improvements to model AIC that matched or exceeded the improvements to AIC conferred by any climate parameter. This suggests that model improvements are coming
from enhancing model accuracy among a small number of trees, such as those at the extremities of local neighborhood conditions.

Although climate and crowding are important mediators of post-fire mortality for some trees, the slight difference in overall prediction accuracy underscores the importance of direct fire damage (i.e., CVS) as the primary driver of post-fire mortality risk. Considering model accuracy alone, it may not be worth the added complexity necessary to incorporate climate and crowding as additional terms into management tools such as the First Order Fire Effects Model. As average climate conditions become hotter and drier, however, it will become increasingly important to reparametrize fire effects models with trees that burn under “average” future conditions. The underlying relationship portends a systematic increase in mortality risk as climate becomes more droughty.

These results likely generalize to other dry, frequent-fire forests with mediterranean climates, especially those dominated by Pinus or other genera susceptible to host-specific insect pests. Generalizability may be less among moist, energy-limited forests, as inter-tree competition for water does not bear the same importance as it does in dry, frequent-fire forests. These results are also of limited applicability in forests that burn in crown fires, as trees with high CVS have a high mortality risk no matter the antecedent climate or neighborhood conditions.

**CONCLUSIONS**

Here we show that advantageous local neighborhoods can compensate for adverse climate effects on fire severity by increasing survivorship independent of the degree of
Fire damage a tree receives. Fire and drought increase susceptibility to bark beetles (Breece et al. 2008, Raffa et al. 2008, Stephenson et al. 2019), but lower forest density may subdue these effects by ameliorating water stress (Hood et al. 2016, Sohn et al. 2016, Young et al. 2017, Knapp et al. 2021). The decreased local water demand in sparse neighborhoods counteracts the decreased water supply of drought, mitigating the otherwise positive interactions between drought, fire, and beetles (Fig. D.5).

Lower forest densities are widely acknowledged to decrease tree mortality in severe droughts (Hood et al. 2016, Young et al. 2017, Restaino et al. 2019, Knapp et al. 2021), but we were able to decouple the confounding effects of density, elevation, and time since fire. Recent fire reduced mortality risk, but it took years for this effect to be realized as trees recovered from immediate fire damage. Plots that burned <7 years prior to drought had elevated mortality, despite having lower pre-drought densities compared with unburned counterparts (Fig. 5.3).

These results provide additional evidence for forest restoration treatments that is independent of historical reference conditions. If appropriate historical reference conditions do not exist for a site, or if historical conditions are no longer attainable, these results may provide guidance for silvicultural treatments that is based on a mechanistic understanding of stand-level resistance and resilience to fire, insects, and drought.

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TABLE 5.1. Probability of tree mortality under various climate and neighborhood conditions, corresponding to the three-dimensional surface in Fig. 5.2 (top row, center panel). Values are model predictions from the best fit post-fire model that related probability of mortality, $P_m$, to crown volume scorch (CVS), 3-yr pre-fire Pre-fire $D_\Delta$, and basal area within 8 m. Mortality probabilities are for a tree with DBH = 30 cm, 50% CVS, with neighborhood and climate parameters ±2 standard deviations around the mean.

<table>
<thead>
<tr>
<th>Climate</th>
<th>Neighborhood</th>
<th>Open</th>
<th>Average</th>
<th>Dense</th>
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<tbody>
<tr>
<td>Wet</td>
<td></td>
<td>13.8%</td>
<td>25.2%</td>
<td>41.7%</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>20.7%</td>
<td>35.6%</td>
<td>53.9%</td>
</tr>
<tr>
<td>Dry</td>
<td></td>
<td>29.9%</td>
<td>47.5%</td>
<td>65.7%</td>
</tr>
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</table>
**TABLE 5.2.** Comparison of climate parameters (Climate) and local neighborhood metrics (Spatial) on mortality model performance. Each variable was combined individually with the same base model (top row) that related probability of mortality within 3 years of fire ($P_m$) to percent crown volume scorched (CVS). Climate variables include climatic water deficit (Deficit) anomaly ($D_\Delta$) and the Palmer Drought Severity Index (PDSI). Spatial variables include stem density, conspecific basal area (Consp. BA), and basal area (BA). Model performance was evaluated with Akaike’s Information Criterion (AIC), Area Under the Curve (AUC), True Positive Rate (sensitivity; TPR) and True Negative Rate (specificity; TNR). Delta AIC (dAIC) is relative to the AIC of the base model; lower (i.e., more negative) values indicate better performance, and bold font indicates the best model per section. Differences in $|dAIC| > 7$ indicate a meaningful difference in model support. All models included DBH and interaction terms between CVS, climate, and spatial variables. Parameters that were not significant at alpha < 0.1 were not included. The best models containing both Climate and Spatial variables are reported at the bottom; the model used to generate Figs. 5.1, 5.2, D.1, and D.2 is bolded. Parameter estimates for all models may be found in Appendix II.

<table>
<thead>
<tr>
<th>Response</th>
<th>Climate</th>
<th>Spatial</th>
<th>dAIC</th>
<th>AIC</th>
<th>AUC</th>
<th>TPR</th>
<th>TNR</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mortality within 3 years</td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pre-fire PDSI 1 year</td>
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<td>11956</td>
<td>0.89</td>
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<td>0.80</td>
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<tr>
<td>Pre-fire $D_\Delta$ 3 year</td>
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<td>11643</td>
<td>0.89</td>
<td>0.81</td>
<td>0.82</td>
</tr>
<tr>
<td>-</td>
<td>Density w/in 5 m</td>
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</tr>
<tr>
<td>-</td>
<td>Density w/in 15 m</td>
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<tr>
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<td>0.82</td>
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<td>567</td>
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<td>0.82</td>
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<td>0.80</td>
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<tr>
<td>Pre-fire $D_\Delta$ 3 year</td>
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<td>-593</td>
<td>11362</td>
<td>0.90</td>
<td>0.82</td>
<td>0.82</td>
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<tr>
<td>Beetle-related mortality 2-5 yrs post-fire</td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td></td>
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<td>0.70</td>
<td>0.01</td>
<td>1.00</td>
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<td>-</td>
<td>BA w/in 15 m</td>
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<td>Post-fire $D_\Delta$ 1 year</td>
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<td>0.06</td>
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<td>Post-fire $D_\Delta$ 1 year</td>
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<td>7689</td>
<td>0.72</td>
<td>0.09</td>
<td>0.99</td>
</tr>
</tbody>
</table>
FIG. 5.1. Tree crowding (basal area within 8 m) and drought (3-yr pre-fire $D_A$) moderate probability of mortality (A & B) and beetle-related mortality (C & D) following fire. A & B are considering all species in this study, while C & D are for *Pinus*, a genus that is particularly susceptible to virulent host-specific bark beetles post-fire; species-specific results are in Figs. D.2 & D.3. Units for the x- and y-axes are standard deviations around the mean (specific values may be found in Tables D.1 & D.3). Dotted lines represent “base” models without climate or spatial variables, while solid lines show model predictions considering climate and spatial variables (x-axes). For the model lines DBH was held constant at 30 cm, while the binned data points include all trees. Points show observed proportion of mortality with trees binned according to the x-axis variable. Point size indicates average DBH per group, color indicates average percent CVS.
FIG. 5.2. Net effects of crowding and climate on overall (top) and beetle-related (bottom) post-fire mortality risk. Units for the x- and y-axes are standard deviations around the mean; actual values may be found in Tables D.1 & D.3. Color indicates probability of mortality (same as z-axis values). Crowding variables were basal area within 8 m (top) and conspecific basal area within 15 m (bottom), and climate variables were 3-yr pre-fire $D_\Delta$ (top) and 1-yr post-fire $D_\Delta$ (bottom). A comparison of various climate and crowding parameters may be found in Table 5.2. These surfaces represent predicted response values based on the post-fire mortality model displayed in Fig. 5.1A&B (top row) and the post-fire beetle mortality model in Fig. 5.1C&D (bottom row). The top row is all tree species combined, while the bottom row is for *Pinus*, a genus that is particularly susceptible to virulent host-specific bark beetles post-fire. We modeled these relationships using the average tree DBH (30 cm).
Fig. 5.3. Relationships between drought-related mortality rate and stem density (A, B, C), elevation (E, F, G), and time since last fire (D, H). $R^2$ and p-values indicate the strength of the relationship determined with second-order polynomial linear regression. Drought mortality rates were calculated as the percent of trees that were alive as of 2014 that died during the peak mortality period of the drought (2015-2016), while beetle mortality rate considers only Pinus that were killed by bark beetles. Point size indicates average DBH within each plot, color differentiates burned (red) from unburned (white) plots.
Great advances have been made in the field of fire ecology over the past half-century. Empirical and theoretical work has contributed to a complex understanding of fire as a physical and as an ecological process, and we have developed a veritable collection of tools that are used widely by managers and researchers to understand fire and its effects. Lab experiments have been foundational to this work, allowing researchers to examine the physical process of combustion and fire spread in wind tunnels and fire tables (e.g., Rothermel 1972). This physics-based work has evolved with modern technologies including LiDAR and 3D modeling software (Parsons 2007, Loudermilk et al. 2012, Pimont et al. 2016), yielding a detailed understanding of how fire burns, spreads, and damages vegetation across a broad range of scales (Miller and Urban 1999, Smith et al. 2016, Steady et al. 2019, Hood et al. 2018, Povak et al. 2020). The ongoing proliferation of publicly available, high resolution, satellite-derived imagery (e.g., Landsat program, Sentinel-2) has contributed to a newly realized ability to examine patterns in fire at regional, continental, and global scales (Schultz et al. 2008, Harvey et al. 2019, Coop et al. 2020), fueling the burgeoning body of remote sensing-based fire research.

But fire is a complex, multi-scale, bio-physical phenomenon; one that is not possible to fully grasp by lab experiments, computer modeling, and remote sensing alone. Field-based sampling of fire and fire effects has been the backbone of fire ecology since the very beginning (Weaver 1943), and on-the-ground observations continue to provide critical validation and calibration for every branch of fire science (e.g., Loudermilk et al.)
This dissertation builds upon this previous research, leveraging unique data to provide contrast, examine ecological nuance, and to reveal novel perspectives regarding both applied and basic realms of fire science.

My study of post-fire tree mortality models and satellite-derived severity indices revealed that these tools are reasonably accurate approximations of average fire effects (Hood and Lutes 2017, Miller and Thode 2007), but accurately predicting averages does not adequately capture the heterogeneity in fire effects that is foundational to the ecological function of fire (Agee 1998). Mortality models were accurate for most trees, but not for large-diameter *Pinus*. Although large and old trees are numerically rare, they are keystone structures in resilient forest ecosystems (Franklin and Johnson 2012, Hessburg et al. 2015). Accurately modeling their mortality risk will have only a marginal effect on affect overall model accuracy, but will dramatically improve the ecological relevance of the model. Satellite-derived severity indices were accurate in aggregate, but they were not sufficient to differentiate between the mortality of a single large tree versus many small trees. The spectral signature of these two scenarios is indistinguishable, but the ecological implications are vastly different (e.g., Kolden et al. 2012).

In Chapters IV and V, I focused on fire as an ecological process. I examined the spatial elements of mortality, revealing that background mortality processes mediated both direct and delayed fire effects. I found that the compound effects of fire and drought provoked spatially non-random mortality among large-diameter trees, a result that contrasts with the widespread expectation that large tree mortality in old-growth forests is a spatially random process (Franklin et al. 2002). Although the post-fire mortality regime
may have been brief relative to the life span of these trees, the synergistic effects of fire, drought, and background mortality processes will have enduring impact on the pattern of large-diameter trees, and thus the forest as a whole. In Chapter V, I targeted the interactions between disturbances that were intractable using the Yosemite Forest Dynamics Plot alone. Leveraging two compatible longitudinal datasets enabled me to explicitly examine these interactions, and to demonstrate that climate mediated both fire severity and risk of post-fire beetle attack. The local neighborhood around each tree also mediated mortality risk, potentially outweighing the effects of climate, providing further support for silvicultural strategies as a way to compensate for the deleterious effects of climate change on fire severity (e.g., North et al. 2019). In revealing a better understanding of the interactions between fire, climate, background mortality processes, and forest spatial structure, these chapters enhance the theoretical basis from which the analytical tools used to model fire effects (e.g., Chapters II-III) may be advanced.

In the findings of each of these studies, a few themes emerge. Post-fire mortality is complex, prolonged, and is mediated by climate, local tree neighborhoods, and background mortality processes. Spatially structured ecological processes interact with direct fire effects to moderate both immediate and delayed tree mortality, increasing the degree of spatial pattern complexity compared to direct fire effects alone. Spatial complexity is a key function of fire in many forests, yet satellite-derived severity maps are not currently sufficient to capture this heterogeneity at the finest scales. Although many fire effects are most conspicuous immediately after the smoldering subsides, it can take years until some of the most persistent effects are fully realized. The compound disturbance of fire and drought provoked a pulse in large-diameter tree mortality that
peaked 3-4 years after the fire; a profoundly important event that was not captured by existing fire effects models or detectable with satellite-derived severity maps. The disproportionate ecological significance of the largest trees, and the centuries that it takes for them to grow, die, and disappear, render this drought-fire interaction the single most impactful ecological consequence of the fire. The big tree mortality sustained during this brief window of time will alter the structure and function of this forest for centuries.

These themes may be re-articulated into a few key management-relevant concepts. First, mortality models and satellite-derived severity maps remain foundational tools for evaluating fire effects, but we should not mistake their outputs for reality. The error and uncertainty in their estimation of post-fire landscapes represents unexplained heterogeneity in actual fire effects – heterogeneity that is central to the function of fire as an ecological process. Second, tree neighborhoods are an important mediator of tree mortality risk, in both burned and unburned forests. This knowledge offers a way to optimize scarce funds for restoration by targeted treatments in high-priority stands or around individual trees that are of particular concern. Not only will reducing local neighborhood density lower fire risk by reducing ladder fuels, it will create a more favorable local neighborhood that will improve resistance to drought, beetles, and post-fire mortality. Finally, so many of the findings in this dissertation are simply documentation of the heterogeneity that exists in wildland forest ecosystems, and the key role of fire in creating, modifying, and perpetuating this heterogeneity. As a whole, these studies provide strong support for management actions that foster heterogeneity at scales spanning from trees to landscapes, and for management that facilitates the return of wildfire as a self-regulating process in dry western landscapes.
An overarching theme for this dissertation also emerges: longitudinal, observational datasets offer a unique lens to perceive elusive ecological dynamics, and this can provide insightful contrasts with experimental study designs (Franklin 1989, Franklin et al. 1990, Lutz 2015, Lutz et al. 2018). There are indeed many challenges associated with observational research (Lindenmayer and Likens 2010); there is no balanced factorial design through which interactions may be decoupled, and researchers have very little control over the timing, severity, or application of treatments. These challenges notwithstanding, longitudinal datasets can reveal patterns that are undetectable over short time spans or small spatial scales (e.g., see Fig. 4.1; Levin 1992, Magnuson 1990). The exhaustive censusing of a forest will capture unforeseen events, detect unfamiliar patterns, and monitor rare sub-populations that would be otherwise overlooked by a sampling design optimized for an ecological entity of interest (Davies et al. 2021).

I am far from the first to recognize the immense value of long-term ecological monitoring (Munger 1946, Strayer et al. 1986, Franklin 1989, Lindenmayer et al. 2012). It has been more than three decades since Jerry Franklin wrote: “So, what additional statements are needed regarding the importance of long-term studies in ecological science?” (Franklin 1989). Yet, the struggle to establish and maintain longitudinal datasets is as great as ever. Despite the innumerable impacts of long-term studies to the ecological literature, and their disproportionate contribution to policy making, funding for longitudinal research has declined in recent decades (Hughes et al. 2017).

Some support does exist for existing longitudinal research programs, including the Smithsonian ForestGEO Network (www.forestgeo.si.edu) and the National Science Foundation Long Term Ecological Research Network (www.lternet.edu). But funding
rarely exists for the establishment of new sites, and financial support for existing sites is limited, highly competitive, and subject to renewal. Most long-term research programs must be sustained by cobbling together short-term research grants, occasional institutional support, and the tireless efforts of a few dedicated individuals. It is hard to fathom that we leave such invaluable data streams – irreplaceable records of ecological change and sources of untold potential knowledge – in such a precarious position.

The establishment of the YFDP required over 10,000 volunteered person-hours, two summers of paid field crews, and tens of thousands of dollars in supplies (e.g., tree tags, survey markers, etc.) and field equipment (Lutz, personal communication). More impressively, the YFDP has been surveyed every year for mortality and recruitment, and the plot has been fully re-measured twice. The dataset is exceedingly unique, and it has become quite extensive. The YFDP is now the largest stem-mapped plot in CA (and the second largest in western North America), comprising 12 years of annual mortality surveys spanning the reintroduction of wildfire and a millennial-scale drought. Despite this impressive resumé, there is not currently sufficient funding to support the field work that must begin ten weeks from now. This is not the first time the financial situation has been dire, and it will be this way again. Perhaps the most universal truth of longitudinal research is the struggle to persist through the doldrums between funding cycles. The data always get collected one way or another; I am nothing if not confident in Jim’s abilities to keep the YFDP research going. But what of the YFDP decades from now, and what of other long-term monitoring programs that languish when funding streams dry up? *Is there not compelling reason to support longitudinal datasets today in trust of the insight that they will yield tomorrow?*
There is widespread support in our society to preserve and protect our cherished landscapes, natural resources, cultural sites, and national monuments, held in trust for future generations. Longitudinal ecological datasets represent scientific treasures that warrant protection and preservation as well. These datasets, after all, are a critical source of ecological knowledge; they provide the foundation for effective management of the natural resources that enjoy such forms of publicly funded protection. If we, as a society, are serious about wildland conservation and adaptive management of natural resource, we must dramatically increase the funding and institutional support allocated to longitudinal, observational ecological monitoring. In the face of rapid climatic change, increasing disturbance frequency, and widespread tree mortality, the need to establish and maintain long-term forest dynamics datasets is greater than ever before. As our forests change at an unprecedented rate, it is imperative to record what is here before it is gone (Lindenmayer et al. 2012, Davies et al. 2021).

It is hard to overstate the perpetual value of longitudinal datasets. This dissertation is the culmination of over a decade of research in the YFDP, yet I remain convinced that the most valuable scientific contributions from the YFDP are not contained within this dissertation, nor in any of the dozens of publications that have come out of the YFDP thus far (e.g., Larson et al. 2016, Cansler et al. 2018, 2019, Lutz et al. 2017a, 2017b, 2020, Furniss et al. 2019, 2020a, 2020b, Tamjidi and Lutz 2020a, 2020b). The true value of the YFDP, as with many other longitudinal studies, will mature with time. It will be used decades from now by future scientists who we do not know to answer questions that we cannot conceive of. All we have to do is to keep measuring the trees, keep watching the forest change.
On a personal note, returning to the same site to measure the same individuals, year after year, can cultivate a profound connection with the ecology of a place. It is an intimate familiarity that is difficult to articulate within the bounds of scientific writing. This would be of no surprise to early naturalists, whose observations and experience in a specific place were foundational to the field of ecology (e.g., Thoreau 1854, Muir 1911, Leopold 1949). But slow and steady ecological observation is increasingly overlooked in favor of sophisticated statistics and more efficient sampling strategies. There is much value in efficiency, and many merits of experimental study designs. But so too are there benefits in simplicity, and power in patient observation. The great strength of experimental science is that we may ask a question of nature, apply treatments, and collect data to discern an answer. The great strength of observational ecology is that if we wait in quiet, we may hear when nature speaks its truths. May the studies contained within this dissertation demonstrate the profound potential for observational studies to contribute to the fields of fire science and forest ecology, and may this dissertation as a whole provide evidence for the enduring value of permanent forest dynamics plots.

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APPENDICES
APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER II: MULTI-SCALE ASSESSMENT OF POST-FIRE TREE MORTALITY MODELS
Fig. A.1. The relationship between crown volume scorch and diameter at breast height for five species within the Yosemite Forest Dynamics Plot. Each dot represents a 5 cm diameter class (first dot 1 cm ≤ DBH < 5 cm).
Fig. A.2. Probability of mortality for trees $\geq$1 cm DBH as a function of crown volume scorched (CVS) for different subsets of the data. Dots represent observed proportion of stems that experienced mortality in each CVS category (10% bins; there are 11 dots because there are 0% and 100% bins). Lines represent model predictions of third-order polynomial logistic regression models using subsets of the data (full dataset, removing some trees with 100% CVS, removing all trees with 100% CVS).
Fig. A.3. Probability of immediate and delayed mortality for trees $\geq 1$ cm DBH as a function of crown volume scorched (CVS). Dots represent observed proportion of stems that experienced immediate (black dots) and delayed (grey dots) mortality in each CVS category (10% bins; there are 11 dots because there are 0% and 100% bins). Lines represent model predictions of the logistic mortality models within the First Order Fire Effects Model (FOFEM v6.3).
Fig. A.4. Probability of mortality for trees ≥1 cm DBH as a function of tree diameter (DBH). Dots represent observed proportion of stems that were killed in each DBH category (10 cm bins, first bin 1 cm ≤ DBH < 10 cm), and lines represent species-specific logistic regression models using DBH as the independent variable and binary mortality status as the response. Grey lines represent model forms that we tested but resulted in worse fits. The dots are for graphical purposes only; the models were not parameterized on the binned data used to generate the dots.
Fig. A.5. Pre-fire, post-fire, and modeled post-fire spatial patterns of angiosperms and gymnosperms in the Yosemite Forest Dynamics Plot. The y-axis in A represents the value of the pair-correlation function, \( g(r) \), at a range of inter-tree distances, while the y-axis in B represents change in spatial pattern calculated as \( g_{\text{post}}(r) - g_{\text{pre}}(r) \). The shaded areas represent a 95% confidence envelope around predictions of mortality according to the FOFEM models, generated by 99 simulations of mortality. The grey dotted lines represent the expected value of \( g(r) \) under the null model of complete spatial randomness (A), or “no change” (B). Values above the line indicate aggregation, and values below indicate hyper-dispersion.
APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER III: DETECTING TREE MORTALITY WITH LANDSAT-DERIVED SPECTRAL INDICES:
IMPROVING ECOLOGICAL ACCURACY BY EXAMINING UNCERTAINTY
Table B.1. Stand structure, spectral index values, and topographic variables for the study areas. Values represent individual Landsat pixels (Yosemite Forest Dynamics Plot) or area-weighted average for pixels within 0.25-ha plots (Joint Fire Science Program [JFSP] plots).

<table>
<thead>
<tr>
<th>Code</th>
<th>Yosemite Forest Dynamics Plot</th>
<th>JFSP plots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td>Stems ≥1 cm DBH ha⁻¹</td>
<td>200</td>
<td>3133</td>
</tr>
<tr>
<td>Stems ≥10 cm DBH ha⁻¹</td>
<td>44</td>
<td>1222</td>
</tr>
<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>8.5</td>
<td>129.6</td>
</tr>
<tr>
<td>NDVI</td>
<td>-0.86</td>
<td>-0.45</td>
</tr>
<tr>
<td>MIRBI</td>
<td>-5067</td>
<td>-2153</td>
</tr>
<tr>
<td>NBR</td>
<td>135</td>
<td>664</td>
</tr>
<tr>
<td>CSI</td>
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<td>2.73</td>
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<tr>
<td>SAVI</td>
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<td>1.29</td>
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<tr>
<td>NDMI</td>
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<td>463</td>
</tr>
<tr>
<td>SWIR1:NIR</td>
<td>0.37</td>
<td>1.01</td>
</tr>
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<td>SWIR2:NIR</td>
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<tr>
<td>SWIR2:SWIR1</td>
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<tr>
<td>NIR:G</td>
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<td>NIR:R</td>
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<tr>
<td>TCBRI</td>
<td>1343</td>
<td>2535</td>
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<tr>
<td>TCGRE</td>
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<td>1760</td>
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<tr>
<td>dDB</td>
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<tr>
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<td>dSWIR1</td>
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<tr>
<td>dSWIR2</td>
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<td>24</td>
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<tr>
<td>dNDVI</td>
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<td>dMIRBI</td>
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<td>dNBR</td>
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<td>464</td>
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<td>dSAVI</td>
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<td>dNDMI</td>
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<td>445</td>
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<td>dSWIR1:NIR</td>
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<td>0.01</td>
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<td>dSWIR2:NIR</td>
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<td>dNIR:G</td>
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<td>dTCGRE</td>
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<td>799</td>
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<tr>
<td>dTWET</td>
<td>-20</td>
<td>720</td>
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<td>Slope</td>
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<tr>
<td>Aspect</td>
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<td>TPI</td>
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<td>126.06</td>
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<tr>
<td>Solar irradiance</td>
<td>1.38</td>
<td>1.89</td>
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Table B.2. Correlations between spectral indices and observed mortality of trees ≥10 cm diameter at breast height (1.37 m) determined with individual random forest models and summarized using percent variance explained. Values represent “percent variance explained” determined with individual random forest models. Observed mortality was quantified as percent of pre-fire live stems (or basal area [BA]) that was killed by fire. “Initial” columns represent correlations based on a post-fire Landsat scene from immediately after the fire (September 16, 2013), while “extended” columns use a post-fire scene taken one year following the fire (July 1, 2014). Column titles indicate which structural subsets were used to calculate observed mortality. The data were also subset by plot to compare accuracy between the two datasets.

<table>
<thead>
<tr>
<th>Index</th>
<th>Initial</th>
<th>Extended</th>
<th>% BA</th>
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<tr>
<td></td>
<td>Stems ≥10 cm</td>
<td>Basal area</td>
<td>Stems 1-10 cm</td>
</tr>
<tr>
<td></td>
<td>Basal area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NDVI</td>
<td>3.4</td>
<td>32.7</td>
<td>43.4</td>
</tr>
<tr>
<td>dNDVI</td>
<td>26.3</td>
<td>54.8</td>
<td>42.8</td>
</tr>
<tr>
<td>MIRI</td>
<td>-</td>
<td>9.4</td>
<td>-</td>
</tr>
<tr>
<td>dB</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>TC.WET</td>
<td>-</td>
<td>39.6</td>
<td>27.1</td>
</tr>
<tr>
<td>TWI</td>
<td>-</td>
<td>12.9</td>
<td>48.4</td>
</tr>
<tr>
<td>dB</td>
<td>-</td>
<td>44.4</td>
<td>49.5</td>
</tr>
<tr>
<td>dNIR</td>
<td>3.1</td>
<td>45.1</td>
<td>54.9</td>
</tr>
<tr>
<td>dNIR</td>
<td>-</td>
<td>3.0</td>
<td>-</td>
</tr>
<tr>
<td>dSWIR2</td>
<td>4.1</td>
<td>47.2</td>
<td>56.6</td>
</tr>
</tbody>
</table>

Table B.2. Correlations between spectral indices and observed mortality of trees ≥10 cm diameter at breast height (1.37 m) determined with individual random forest models and summarized using percent variance explained. Values represent “percent variance explained” determined with individual random forest models. Observed mortality was quantified as percent of pre-fire live stems (or basal area [BA]) that was killed by fire. “Initial” columns represent correlations based on a post-fire Landsat scene from immediately after the fire (September 16, 2013), while “extended” columns use a post-fire scene taken one year following the fire (July 1, 2014). Column titles indicate which structural subsets were used to calculate observed mortality. The data were also subset by plot to compare accuracy between the two datasets.
Table B.3. Correlations between spectral indices and observed mortality of trees ≥10 cm diameter at breast height (1.37 m) based on a rarefied dataset. Observed mortality was quantified as percent of pre-fire live stems (or basal area [BA]) that was killed by fire. Values represent percent variance explained (%VE) determined with random forest models, averaged among all rarefied datasets. Values in parentheses indicate standard deviation of %VE among rarefied datasets. Column titles indicate which structural subsets were used to calculate observed mortality. Superscripts indicate significant differences between indices as determined with Tukey’s HSD test. The columns for YFDP (Yosemite Forest Dynamics Plot) and JFSP (Joint Fire Science Program plots) represent percent BA mortality.

<table>
<thead>
<tr>
<th>Index</th>
<th>Basal area</th>
<th>Stems ≥10 cm</th>
<th>Stems ≥50 cm</th>
<th>Stems ≥100 cm</th>
<th>YFDP</th>
<th>JFSP</th>
</tr>
</thead>
<tbody>
<tr>
<td>dNBR</td>
<td>52.4 (2.4)</td>
<td>46.5 (2.4)</td>
<td>38.3 (3.0)</td>
<td>5.6 (4.3)</td>
<td>14.6 (5.6)</td>
<td>34.7 (4.1)</td>
</tr>
<tr>
<td>dNDVI</td>
<td>50.7&lt;sup&gt;a&lt;/sup&gt; (2.3)</td>
<td>52.9&lt;sup&gt;a&lt;/sup&gt; (2.7)</td>
<td>28.7&lt;sup&gt;a&lt;/sup&gt; (3.6)</td>
<td>0&lt;sup&gt;a&lt;/sup&gt; (4.6)</td>
<td>10.8 (4.1)</td>
<td>32.3 (4.0)</td>
</tr>
<tr>
<td>RdNBR</td>
<td>56.9 (2.3)</td>
<td>42.6&lt;sup&gt;b&lt;/sup&gt; (2.7)</td>
<td>47.3&lt;sup&gt;b&lt;/sup&gt; (3.3)</td>
<td>18.8&lt;sup&gt;b&lt;/sup&gt; (4.5)</td>
<td>11.6 (5.6)</td>
<td>32.4 (4.3)</td>
</tr>
<tr>
<td>RBR</td>
<td>58.2 (1.8)</td>
<td>44.6 (2.4)</td>
<td>47.6&lt;sup&gt;b&lt;/sup&gt; (3.0)</td>
<td>18.4&lt;sup&gt;b&lt;/sup&gt; (4.4)</td>
<td>11.6 (5.7)</td>
<td>41.2 (2.9)</td>
</tr>
<tr>
<td>dSWIR1.NIR</td>
<td>59.8&lt;sup&gt;b&lt;/sup&gt; (2.0)</td>
<td>48.1 (2.3)</td>
<td>44.4&lt;sup&gt;b&lt;/sup&gt; (2.8)</td>
<td>8.2 (4.4)</td>
<td>19.0 (4.9)</td>
<td>36.4 (4.2)</td>
</tr>
</tbody>
</table>
Fig. B.1. Landsat pixels within the Yosemite Forest Dynamics Plot (top panel) and Joint Fire Science Plots (Gx-Px titles, bottom panel). Points in the bottom panels represent surviving (white) and fire-killed (black) trees that were live pre-fire.
Fig. B.2. Distribution of fire severity (differenced Normalized Burn Ratio [dNBR]) values within the Joint Fire Science Program plots, Yosemite Forest Dynamics Plot, Rim Fire within Yosemite National Park, and within the entire Rim Fire.
Fig. B.3. Relationship between satellite-derived spectral indices and observed mortality quantified as percent of pre-fire basal area of trees $\geq 10$ cm diameter at breast height (1.37 m) that was killed within one year of the fire. Points represent 53 individual plots (JFSP) and 260 Landsat pixels within the Yosemite Forest Dynamics Plot (YFDP). Shaded envelopes represent the variability in observed mortality as a function of each spectral index. Envelopes were derived from continuous estimates of the mean and standard deviation of the data generated with locally-weighted scatterplot smoothing (LOESS) regression models and scaled to capture 95% of the variability in observations. The %VE indicates the percent variance explained using random forest models (Tables 3.2, B.2).
Fig. B.4. Relationship between satellite-derived spectral indices and observed mortality quantified as percent of pre-fire density of trees ≥10 cm diameter at breast height (1.37 m) that was killed within one year of the fire. Points represent 53 individual plots (JFSP) and 260 Landsat pixels with in the Yosemite Forest Dynamics Plot (YFDP). Shaded envelopes represent the variability in observed mortality as a function of each spectral index. Envelopes were derived from continuous estimates of the mean and standard deviation of the data generated with locally-weighted scatterplot smoothing (LOESS) regression models and scaled to capture 95% of observed variability. The %VE indicates percent variance explained with random forest models (Tables 3.2 & B.2).
Fig. B.5. Same as Fig. 3.5, but observed mortality is quantified as percent stem mortality. Satellite-derived burn severity (dNBR) of the California Rim Fire. The scatterplot displays the relationship between dNBR and observed percent mortality of trees $\geq 10$ cm diameter at breast height (red line is predicted mortality rate of LOESS model; shaded region is 95% confidence envelope). The histogram shows proportion of area within the Rim Fire at various levels of uncertainty. Maps show mean, low, and high estimates of percent stem mortality. The uncertainty map displays the range in predicted percent stem mortality necessary to capture the true mortality rate, 95% of the time (i.e., a 40% uncertainty level indicates a $\pm 20\%$ range in expected mortality levels).
Fig. B.6. Same as Fig. 3.5, but the range in mortality is based on a 68% confidence level. Satellite-derived burn severity (dNBR) of the California Rim Fire. The scatterplot displays the relationship between dNBR and observed percent basal area mortality of trees ≥10 cm diameter at breast height (red line is predicted mortality rate of LOESS model; shaded region is 68% confidence envelope). The histogram shows proportion of area within the Rim Fire at various levels of uncertainty. Maps show mean, low, and high estimates of percent basal area mortality. The uncertainty map displays the range in predicted percent basal area mortality necessary to capture the true mortality rate, 68% of the time (i.e., a 20% uncertainty level indicates a 10% range in expected mortality levels).
Fig. B.7. Same as Fig. B.6, but observed mortality is quantified as percent stem mortality. Satellite-derived burn severity (dNBR) of the California Rim Fire. The scatterplot displays the relationship between dNBR and observed percent stem mortality of trees ≥10 cm diameter at breast height (red line is predicted mortality rate of LOESS model; shaded region is 68% confidence envelope). The histogram shows proportion of area within the Rim Fire at various levels of uncertainty. Maps show mean, low, and high estimates of percent stem mortality. The uncertainty map displays the range in predicted percent stem mortality necessary to capture the true mortality rate, 68% of the time (i.e., a 20% uncertainty level indicates a 10% range in expected mortality levels).
Fig. B.8. Scatterplots of differenced band reflectance values versus mortality of trees \( \geq 10 \) cm DBH. Each row represents a different band (red band is the top row, near-infrared is the middle row, and short-wave infra-red is the bottom row). The left column contains observed mortality measured as percent mortality of stems \( \geq 10 \) cm DBH while the right column contains observed mortality measured as percent of pre-fire basal area.
Fig. B.9. Semivariograms depicting spatial autocorrelation of basal area mortality ($a$) and residuals (predicted minus observed) of the LOESS model (details in Methods) for dNBR ($b$). The top panel reveals that mortality was spatially auto-correlated at spatial scales <100 m, while error in Landsat-derived severity indices was spatially random (i.e., the difference between predicted and observed mortality for any given pixel was independent of surrounding pixels).
APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER IV: WILDFIRE AND DROUGHT MODERATE THE SPATIAL ELEMENTS OF TREE MORTALITY
Table C.1. Possible mechanisms of fire-related mortality. “Timing” indicates whether the mechanism of mortality is thought to be prevalent within 1 year of a fire (fire-related) or is a background mortality process that may be interact with fire to mediate post-fire mortality. “Susceptible stems” indicates the structural classes that are most susceptible to this form of mortality following low- to moderate-severity (i.e., non-crowning) fire; stems of other sizes may also be susceptible, just to a lesser degree. Relevant citations include studies which relate to each category of fire-related mortality; for a more extensive review of fire as a direct and indirect agent of tree mortality, see the recent review by Hood et al. (2018). Full citations are in Appendix C. For delayed mortality, we include relevant studies of tree mortality in the absence of fire as these ecological processes are also relevant in post-fire forests. The “Spatial metrics” columns represent the categories of local neighborhood variables which we hypothesize to be related to each mechanism of mortality, the associated variables that were calculated to reflect potential mortality mechanisms, and the codes representing each variable (codes relate to the results in Table C.2). We calculated each structural variable for each tree within circular local neighborhoods with radii of 5, 10, 15, 20, and 30 m. In codes, “small” indicates stems 1–10 cm DBH, “med” indicates stems 10–60 cm DBH, “big” indicates stems ≥60 cm DBH, and “pole” indicates stems ≥10 cm DBH.

<table>
<thead>
<tr>
<th>Mechanism of mortality</th>
<th>Susceptible stems</th>
<th>Relevant citations</th>
<th>Spatial metrics</th>
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<td></td>
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<td></td>
<td>Den.small.neighbors; Den.med.neighbors; Den.big.neighbors; Den.neighbors;</td>
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<tr>
<td><strong>Indirect; reduced resistance to fire damage</strong></td>
<td>Small and medium stems</td>
<td>van Mantgem et al. 2013, Furniss et al. 2019</td>
<td>Density and basal area of local neighborhood. Competition indices. Nearest neighbor. Landscape position.</td>
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<td></td>
<td></td>
<td></td>
<td>BA; BA.conspecifics; Den.small.neighbors; Den.med.neighbors; Den.big.neighbors; Den.neighbors; HEGYI; INFLUENCE; Nearest.neighbor; LAND_POS;</td>
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<tr>
<td><strong>Indirect; fire-related mechanical failure</strong></td>
<td>Large stems (60+)</td>
<td>This study</td>
<td>Presence of fire scar (binary)</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td><strong>Bark-beetles</strong></td>
<td>Medium and large stems (i.e., “pole-sized”)</td>
<td>Ryan and Amman 1996, Hood and Bentz 2007, Hood et al. 2015, Kolb et al. 2007, Youngblood et al. 2009</td>
<td>Density and basal area of surviving pole-sized and large conspecifics. Density of previous year beetle mortality</td>
</tr>
<tr>
<td></td>
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<td>BA.surv.comspecifics; BA.surv.pole.com; BA.surv;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Den.surv.comspecifics; Den.surv.pole.com; BA.prev.yr.beetle.mort; Den.prev.yr.beetle.mort;</td>
</tr>
<tr>
<td><strong>Pathogens</strong></td>
<td>All</td>
<td>Parker et al. 2006, Das et al. 2016</td>
<td>Density and basal area of surviving trees. Competition indices for surviving trees.</td>
</tr>
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<td>BA.surv; Den.surv.small.neighbors; Den.surv.med.neighbors; Den.surv.big.neighbors; Den.surv.neighbors;HEGYI.surv; Nearest.surv.neighbors;</td>
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<td>BA.prev.yr.fungal.mort; Den.prev.yr.fungal.mort;</td>
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<tr>
<td><strong>Mechanical</strong></td>
<td>Medium and large stems</td>
<td>Das et al. 2016</td>
<td>Density of previous year pathogen mortality. Presence of fire scar.</td>
</tr>
<tr>
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<td></td>
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<tr>
<td></td>
<td></td>
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<td>Landscape position.</td>
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<td></td>
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<td>LAND_POS;</td>
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</table>
Table C.2. Spatially-explicit forest structural attributes that were correlated with pre-fire mortality at α = 0.05. Significant correlations were identified by pairing each variable with a non-spatial, species-specific “base” model based on DBH. The following structural variables were significant at α = 0.05 and improved AIC of the base model by >7 (delta AIC, “dAIC”, is reported for each structural variable). Grey text is used for the single best structural variable for mortality models that were not significantly enhanced by structural variables (|dAIC| < 7).

Structural variables were summarized for each focal tree considering local neighborhood within 5, 10, 15, 20, and 30 m radii (all significant distances reported for each variable). Descriptions of the codes may be found in Table C.1.

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<th>Abies concolor</th>
</tr>
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<tbody>
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<td></td>
</tr>
<tr>
<td>10-60</td>
<td>Den.med.neighbors.05,10,15,20,30m(+);dAIC=-14.1; Den.neighbor.30m(+);dAIC=-17.1; Den.med.neighbors.10m(+);dAIC=-1.9</td>
<td></td>
</tr>
<tr>
<td>≥60</td>
<td>Den.med.neighbors.10m(+);dAIC=-5.4</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Size</th>
<th>Pre-fire</th>
<th>Calocedrus decurrens</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-10</td>
<td>Den.neighbor.20m(+);dAIC=-5.6</td>
<td></td>
</tr>
<tr>
<td>10-60</td>
<td>Den.neighbor.30m(+);dAIC=-3</td>
<td></td>
</tr>
<tr>
<td>≥60</td>
<td>Den.med.neighbors.30m(+);dAIC=-1.9</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Size</th>
<th>Pre-fire</th>
<th>Pinus lambertiana</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-10</td>
<td>HEGYI (+);dAIC=-3.9</td>
<td></td>
</tr>
<tr>
<td>10-60</td>
<td>Den.pole.con.20,15,30,10m(+);dAIC=-9.8</td>
<td></td>
</tr>
<tr>
<td>≥60</td>
<td>BA.pole.con.10m(+);dAIC=-6.2</td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Size</th>
<th>Pre-fire</th>
<th>Quercus kelloggii</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-10</td>
<td>Nearest.neighbor (+);dAIC=-4.6</td>
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</tr>
<tr>
<td>10-60</td>
<td>BA.30m(+);dAIC=-15.1; BA.conspecifics.05,10,15,20,30m(+);dAIC=-15.1; BA.pole.con.05,10,15,20m(+);dAIC=-12.1;</td>
<td></td>
</tr>
<tr>
<td>≥10</td>
<td>Den.big.neighbors.30m(+);dAIC=-8.3; Den.pole.con.10,20,15,30,05m(+);dAIC=-22.9</td>
<td></td>
</tr>
</tbody>
</table>
Table C.3. Spatially-explicit forest structural attributes that were correlated with direct and indirect immediate fire mortality at $\alpha = 0.05$. Significant correlations were identified by pairing each variable with non-spatial “base” models: “Direct fire” was based only on tree diameter (DBH), while “Indirect fire” was based on both DBH and crown volume scorched (CVS). The following structural variables were significant at $\alpha = 0.05$ and improved AIC of the base model by $>7$ (delta AIC, “dAIC”, is reported for each structural variable). Structural variables were summarized for each focal tree considering local neighborhood within 5, 10, 15, 20, and 30 m radii (all significant distances reported for each variable). Descriptions of the codes may be found in Table C.1.

<table>
<thead>
<tr>
<th>Size</th>
<th>Direct fire</th>
<th>Indirect fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>Den.med.neighbors.30m;(-);dAIC=-7.8</td>
<td>Den.neighborhoods.30m;(+);dAIC=14.4</td>
<td></td>
</tr>
<tr>
<td>Den.med.neighbors.30m;(+);dAIC=14.1</td>
<td>Den.med.neighbors.30m;(+);dAIC=14.4</td>
<td></td>
</tr>
<tr>
<td>BA.20,15,30m;(-);dAIC=-12.8</td>
<td>Den.neighborhoods.30m;(-);dAIC=-7.5</td>
<td></td>
</tr>
<tr>
<td>BA.20,15,30m;(+);dAIC=19.4</td>
<td>Den.neighborhoods.30m;(+);dAIC=19.4</td>
<td></td>
</tr>
<tr>
<td>BA.20,15,30m;(-);dAIC=-27.1</td>
<td>Den.neighborhoods.30m;(-);dAIC=-27.1</td>
<td></td>
</tr>
<tr>
<td>BA.20,15,30m;(+);dAIC=20.1</td>
<td>Den.neighborhoods.30m;(+);dAIC=20.1</td>
<td></td>
</tr>
</tbody>
</table>
Table C.4. Spatially-explicit forest structural attributes that were correlated with post-fire mortality at \( \alpha = 0.05 \). Significant correlations were identified by pairing each variable with a non-spatial “base” model based on both DBH and crown volume scorched (CVS). The following structural variables were significant at \( \alpha = 0.05 \) and improved AIC of the base model by >7 (delta AIC, “dAIC”, is reported for each structural variable). Structural variables were summarized for each focal tree considering local neighborhood within 5, 10, 15, 20, and 30 m radii (all significant distances reported for each variable). Descriptions of the codes may be found in Table C.1.

<table>
<thead>
<tr>
<th>Size</th>
<th>Post-fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA.05,10,20m; (+); dAIC = -13.9</td>
<td>BA.surv.conspec.05m; (+); dAIC = -16.8</td>
</tr>
<tr>
<td>BA.mort.pole.con.20m; (+); dAIC = -8.9</td>
<td>Den.big.neighbors.05m; (+); dAIC = -16.9</td>
</tr>
<tr>
<td>BA.pole.con.05m; (+); dAIC = -17.7</td>
<td>Den.med.neighbors.05,10,15m; (+); dAIC = -22.8</td>
</tr>
<tr>
<td>BA.surv.05,10,20m; (+); dAIC = -45.8</td>
<td>Den.pole.con.05,10,20m; (+); dAIC = -29</td>
</tr>
<tr>
<td>BA.surv.5-30m; (+); dAIC = -117.1</td>
<td>Den.big.neighbors.05,10,15m; (+); dAIC = -26.5</td>
</tr>
<tr>
<td>BA.05,10,15,20m; (+); dAIC = -63.2</td>
<td>BA.mort.pole.con.5-30m; (+); dAIC = -54.4</td>
</tr>
<tr>
<td>BA.pole.con.5-30m; (+); dAIC = -115.4</td>
<td>BA.surv.conspec.5-30m; (+); dAIC = -80.3</td>
</tr>
<tr>
<td>BA.surv.conspec.5-30m; (+); dAIC = -82.1</td>
<td>Den.med.neighbors.5-30m; (+); dAIC = -30.4</td>
</tr>
<tr>
<td>BA.surv.5-30m; (+); dAIC = -82.1</td>
<td>Den.med.neighbors.5-30m; (+); dAIC = -30.4</td>
</tr>
<tr>
<td>BA.30,20m; (+); dAIC = -12.4</td>
<td>BA.surv.conspec.15m; (+); dAIC = -8.8</td>
</tr>
<tr>
<td>BA.pole.con.15,10m; (+); dAIC = -9.5</td>
<td>Den.big.neighbors.20,30,15,10m; (+); dAIC = -15.2</td>
</tr>
<tr>
<td>BA.surv.20,30m; (+); dAIC = -8.8</td>
<td>Den.big.neighbors.10-30m; (+); dAIC = -12.9</td>
</tr>
<tr>
<td>BA.20m; (+); dAIC = -13.9</td>
<td>BA.surv.20,15m; (+); dAIC = -13.6</td>
</tr>
<tr>
<td>BA.conspec.20,15m; (+); dAIC = -13.9</td>
<td>BA.surv.20,15m; (+); dAIC = -13.6</td>
</tr>
<tr>
<td>BA.pole.con.20,15m; (+); dAIC = -13.8</td>
<td>BA.surv.20,15m; (+); dAIC = -13.6</td>
</tr>
<tr>
<td>BA.surv.20,15m; (+); dAIC = -13.8</td>
<td>BA.surv.20,15m; (+); dAIC = -13.6</td>
</tr>
<tr>
<td>BA.surv.05,10m; (+); dAIC = -6.7</td>
<td>BA.surv.conspec.05m; (+); dAIC = -7.7</td>
</tr>
<tr>
<td>BA.pole.con.05m; (+); dAIC = -7</td>
<td>BA.surv.conspec.05m; (+); dAIC = -7.7</td>
</tr>
<tr>
<td>BA.surv.05m; (+); dAIC = -7</td>
<td>BA.surv.conspec.05m; (+); dAIC = -7.7</td>
</tr>
<tr>
<td>BA.surv.30m; (+); dAIC = -4.8</td>
<td>BA.surv.conspec.30m; (+); dAIC = -4.8</td>
</tr>
<tr>
<td>BA.05,10,20m; (+); dAIC = -37.2</td>
<td>Den.big.neighbors.05m; (+); dAIC = -21.5</td>
</tr>
<tr>
<td>BA.conspec.5-30m; (+); dAIC = -37.1</td>
<td>Den.neighbors.20,30,15m; (+); dAIC = -10.3</td>
</tr>
<tr>
<td>BA.pole.con.5-30m; (+); dAIC = -37.2</td>
<td>Den.big.neighbors.5m; (+); dAIC = -20.4</td>
</tr>
<tr>
<td>BA.surv.05,10,20m; (+); dAIC = -34.5</td>
<td>Den.pole.con.30,20,15m; (+); dAIC = -19.4</td>
</tr>
<tr>
<td>Hegyi; (+); dAIC = -76.8</td>
<td>BA.surv.pole.con.5-30m; (+); dAIC = -64.2</td>
</tr>
<tr>
<td>BA.5-30m; (+); dAIC = -64.2</td>
<td>BA.surv.pole.con.5-30m; (+); dAIC = -64.2</td>
</tr>
<tr>
<td>BA.conspec.5-30m; (+); dAIC = -63.1</td>
<td>Den.big.neighbors.5-20m; (+); dAIC = -26.6</td>
</tr>
<tr>
<td>BA.pole.con.5-30m; (+); dAIC = -63.3</td>
<td>Den.med.neighbors.10-30m; (+); dAIC = -16.7</td>
</tr>
<tr>
<td>BA.surv.5-30m; (+); dAIC = -64.2</td>
<td>Den.neighbors.5-30m; (+); dAIC = -65.4</td>
</tr>
<tr>
<td>BA.surv.conspec.5-30m; (+); dAIC = -64.2</td>
<td>Den.pole.con.5-30m; (+); dAIC = -44.6</td>
</tr>
<tr>
<td>BA.05,10,20,30m; (+); dAIC = -37.2</td>
<td>BA.surv.conspec.5,10,20,30m; (+); dAIC = -34.3</td>
</tr>
<tr>
<td>BA.pole.con.5-30m; (+); dAIC = -37.1</td>
<td>BA.surv.conspec.5,10,20,30m; (+); dAIC = -34.5</td>
</tr>
<tr>
<td>BA.surv.05,10,20m; (+); dAIC = -34.5</td>
<td>BA.surv.conspec.5,10,20,30m; (+); dAIC = -34.5</td>
</tr>
<tr>
<td>Hegyi; (+); dAIC = -76.8</td>
<td>BA.surv.pole.con.5-30m; (+); dAIC = -64.2</td>
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<tr>
<td>BA.5-30m; (+); dAIC = -64.2</td>
<td>BA.surv.pole.con.5-30m; (+); dAIC = -64.2</td>
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<tr>
<td>BA.conspec.5-30m; (+); dAIC = -63.1</td>
<td>Den.big.neighbors.5-20m; (+); dAIC = -26.6</td>
</tr>
<tr>
<td>BA.pole.con.5-30m; (+); dAIC = -63.3</td>
<td>Den.med.neighbors.10-30m; (+); dAIC = -16.7</td>
</tr>
<tr>
<td>BA.surv.5-30m; (+); dAIC = -64.2</td>
<td>Den.neighbors.5-30m; (+); dAIC = -65.4</td>
</tr>
<tr>
<td>BA.surv.conspec.5-30m; (+); dAIC = -64.2</td>
<td>Den.pole.con.5-30m; (+); dAIC = -44.6</td>
</tr>
<tr>
<td>BA.30,20m; (+); dAIC = -13.7</td>
<td>BA.surv.30m; (+); dAIC = -12</td>
</tr>
<tr>
<td>BA.pole.con.30m; (+); dAIC = -12</td>
<td>BA.surv.30m; (+); dAIC = -12</td>
</tr>
<tr>
<td>BA.surv.30m; (+); dAIC = -12</td>
<td>BA.surv.30m; (+); dAIC = -12</td>
</tr>
</tbody>
</table>
Fig. C.1. Stem maps of pre-fire, direct fire, and post-fire surviving stems (grey dots) and mortalities (red dots) within the Yosemite Forest Dynamics Plot. Maps correspond to the spatial pattern analysis presented in Fig. 6.
Fig. C.2. Relationships between forest spatial structure and *Quercus kelloggii* mortality. Columns represent timing of mortality and rows represent tree diameter classes. Lines show the relationship between forest spatial structure and probability of mortality determined with generalized linear models. Points indicate observed proportion of mortality, and point size reflects relative number of stems in each group. The x-axis for each panel shows the single best structural variable for that mortality regime and size class; all variables may be found in Tables C.2-C.4. \( \Delta \text{AIC} \) indicates the improvement in model accuracy compared to AIC of the non-spatial base model. Basal area (BA) is reported in \( \text{m}^2\ \text{ha}^{-1} \), stem categories are in stems \( \text{ha}^{-1} \).
APPENDIX D

SUPPLEMENTARY MATERIAL FOR CHAPTER V: CROWDING, CLIMATE, AND THE CASE FOR SOCIAL DISTANCING AMONG TREES
TABLE D.1. Plot information and sample size used in this study. \(N\) live indicates the number of stems that were alive pre-fire for burned plots) or at plot establishment for unburned plots. \(N\) (rarefied) indicates the sample size following rarefication to reduce imbalance caused by high numbers of trees with 0% and 100% CVS. Diameter at breast height (DBH; 1.37 m) for each plot is calculated considering only the species used in this study. Density and basal area columns indicate mean (standard deviation) values averaged among all stems in each plot (or by species, below). Headers indicate the size of the circular radii around each tree used to calculate local density and basal area. Local neighborhood variables were not used in any analysis of unburned plots.

<table>
<thead>
<tr>
<th>Plots, spp.</th>
<th>Elev. (m)</th>
<th>(N) live stems</th>
<th>(N) (rarefied)</th>
<th>Stand attributes</th>
<th>Density (stems ha(^{-1}))</th>
<th>Basal area (BA; m(^2) ha(^{-1}))</th>
<th>Conspecific BA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(5) m</td>
<td>(15) m</td>
<td>(3) m</td>
<td>(8) m</td>
</tr>
<tr>
<td>Burned plots</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>YFDP</td>
<td>1857</td>
<td>31054</td>
<td>11536</td>
<td>0.5</td>
<td>15.3</td>
<td>201</td>
<td>1821.1 (1167.5)</td>
</tr>
<tr>
<td>CRCRPIPO</td>
<td>1637</td>
<td>1476</td>
<td>132</td>
<td>0.3</td>
<td>17.1</td>
<td>133</td>
<td>2075.2 (1661.9)</td>
</tr>
<tr>
<td>FFS2BURN</td>
<td>2128</td>
<td>486</td>
<td>211</td>
<td>0.3</td>
<td>26.7</td>
<td>195</td>
<td>944.5 (601.0)</td>
</tr>
<tr>
<td>FFS5BURN</td>
<td>2030</td>
<td>390</td>
<td>166</td>
<td>0.2</td>
<td>35.4</td>
<td>206</td>
<td>533.4 (450.4)</td>
</tr>
<tr>
<td>FFS6BURN</td>
<td>2018</td>
<td>327</td>
<td>226</td>
<td>0.2</td>
<td>33.5</td>
<td>156</td>
<td>610.1 (447.3)</td>
</tr>
<tr>
<td>LOTHAR</td>
<td>2167</td>
<td>492</td>
<td>426</td>
<td>0.7</td>
<td>40.0</td>
<td>197</td>
<td>869.6 (543.5)</td>
</tr>
<tr>
<td>UPTHAR</td>
<td>2202</td>
<td>343</td>
<td>226</td>
<td>0.3</td>
<td>49.9</td>
<td>159</td>
<td>579.9 (407.5)</td>
</tr>
<tr>
<td>YOHOPINO</td>
<td>1500</td>
<td>2651</td>
<td>889</td>
<td>0.1</td>
<td>9.9</td>
<td>200</td>
<td>3784.6 (1670.4)</td>
</tr>
<tr>
<td>Unburned plots</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BBBPIPO</td>
<td>1609</td>
<td>1272</td>
<td></td>
<td>0.2</td>
<td>19.7</td>
<td>181</td>
<td></td>
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<tr>
<td>CCRPIPO</td>
<td>1622</td>
<td>2103</td>
<td></td>
<td>0.1</td>
<td>9.0</td>
<td>170</td>
<td></td>
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<tr>
<td>FFS7CONT</td>
<td>1941</td>
<td>657</td>
<td></td>
<td>0.3</td>
<td>24.4</td>
<td>177</td>
<td></td>
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<tr>
<td>SUABCO</td>
<td>2035</td>
<td>680</td>
<td></td>
<td>0.1</td>
<td>23.5</td>
<td>154</td>
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<tr>
<td>SUPILA</td>
<td>2059</td>
<td>485</td>
<td></td>
<td>0.1</td>
<td>19.5</td>
<td>163</td>
<td></td>
</tr>
<tr>
<td>SURIP</td>
<td>2033</td>
<td>885</td>
<td></td>
<td>0.2</td>
<td>20.8</td>
<td>189</td>
<td></td>
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<tr>
<td>ULOG</td>
<td>2210</td>
<td>434</td>
<td></td>
<td>0.3</td>
<td>27.4</td>
<td>167</td>
<td></td>
</tr>
<tr>
<td>LMCC</td>
<td>2128</td>
<td>672</td>
<td></td>
<td>0.1</td>
<td>24.6</td>
<td>193</td>
<td></td>
</tr>
<tr>
<td>LOGSEGI</td>
<td>2170</td>
<td>1056</td>
<td></td>
<td>0.3</td>
<td>25.0</td>
<td>204</td>
<td></td>
</tr>
<tr>
<td>LOGLOG</td>
<td>2207</td>
<td>140</td>
<td></td>
<td>0.1</td>
<td>27.7</td>
<td>169</td>
<td></td>
</tr>
</tbody>
</table>

\(A.\) concolor | 27454 | 0.2 | 14.5 | 1942.4 (1339.6) | 1592.4 (789.8) | 67.9 (121.0) | 67.8 (50.6) | 68.7 (30.6) | 69.0 (25.7) | 33.8 (42.7) | 33.7 (24) |
\(C.\) decurrens | 3108 | 0.1 | 14.9 | 2040.6 (1631.1) | 1754.0 (1140.3) | 71.2 (115.1) | 71.9 (48.0) | 74.5 (31.0) | 74.0 (24.5) | 10.6 (26.7) | 14.3 (15) |
\(Pinus\) spp. | 5682 | 0.1 | 26.0 | 1712 (1195.3) | 1528.2 (799.5) | 68.5 (124.8) | 64.1 (49.0) | 66.2 (29.5) | 67.0 (24.1) | 27.6 (59.2) | 26.9 (23.4) |
\(Q.\) kelloggii | 1084 | 0.6 | 15.4 | 1674.9 (1007.8) | 1503.3 (567.3) | 36.1 (71.0) | 47.5 (34.6) | 51.1 (21.5) | 52.9 (18.4) | 7.0 (9.2) | 5.3 (5.0) |
Table D.2. Fire attributes, mean crown volume scorch (CVS), and mortality for each plot. These dates reflect first-entry fires; reburns were dropped from the analysis. The pre-fire climate column indicates whether climatic conditions preceding the fire could be classified as dry or wet, while the dagger indicates an intermediate pre-fire climate; full climate values may be found in Table D.3.

<table>
<thead>
<tr>
<th>Plots, spp.</th>
<th>Date (yyyy-mm)</th>
<th>Season</th>
<th>Ignition</th>
<th>Pre-fire climate</th>
<th>Mean CVS (%)</th>
<th>Imm. (&lt;1 yr)</th>
<th>Del. (2-3 yrs)</th>
<th>Beetle-related (2-5 yr)</th>
<th>Total (&lt;5 yr)</th>
<th>Trees w/ CVS 35-65%</th>
</tr>
</thead>
<tbody>
<tr>
<td>YFDP</td>
<td>2013-09</td>
<td>Summer</td>
<td>Wildfire</td>
<td>Dry</td>
<td>82.0</td>
<td>70.3</td>
<td>39.4</td>
<td>16.0</td>
<td>85.0</td>
<td>34.8</td>
</tr>
<tr>
<td>CRCRIPO</td>
<td>2009-09</td>
<td>Summer</td>
<td>Wildfire</td>
<td>Dry</td>
<td>97.8</td>
<td>92.8</td>
<td>48.6</td>
<td>21.5</td>
<td>96.5</td>
<td>22.2</td>
</tr>
<tr>
<td>FFS2BURN</td>
<td>2001-09</td>
<td>Fall</td>
<td>Prescribed</td>
<td>†</td>
<td>36.0</td>
<td>32.3</td>
<td>32.5</td>
<td>23.4</td>
<td>56.2</td>
<td>75.6</td>
</tr>
<tr>
<td>FFS5BURN</td>
<td>2001-10</td>
<td>Fall</td>
<td>Prescribed</td>
<td>Wet</td>
<td>81.8</td>
<td>66.2</td>
<td>25.0</td>
<td>13.6</td>
<td>78.2</td>
<td>27.6</td>
</tr>
<tr>
<td>FFS6BURN</td>
<td>2001-10</td>
<td>Fall</td>
<td>Prescribed</td>
<td>Wet</td>
<td>65.0</td>
<td>44.0</td>
<td>31.1</td>
<td>16.4</td>
<td>63.3</td>
<td>22.9</td>
</tr>
<tr>
<td>LOTHAR</td>
<td>1990-10</td>
<td>Fall</td>
<td>Prescribed</td>
<td>Dry</td>
<td>52.5</td>
<td>35.4</td>
<td>36.2</td>
<td>24.5</td>
<td>62.0</td>
<td>36.8</td>
</tr>
<tr>
<td>YOHOPIPO</td>
<td>2007-06</td>
<td>Spring</td>
<td>Prescribed</td>
<td>†</td>
<td>82.2</td>
<td>51.1</td>
<td>61.1</td>
<td>17.7</td>
<td>81.8</td>
<td>22.8</td>
</tr>
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</table>
Table D.3. Pre- and post-fire climate for each burned plot. Timespans are relative to the month each fire burned in (see Table D.2). Climate parameters include the Palmer Drought Severity Index (PDSI) and Deficit*, calculated as the difference between the Climatic Water Deficit value for the given time range and the 30-yr average (mean monthly value for 1985 – 2015, left column) for each plot. Climate values were derived from TerraClimate (Abatzoglou et al. 2018), accessed via Google Earth Engine (https://earthengine.google.com). Numbers in the column headers indicate the number of additional months before or after the fire over which climate values were averaged. The fire month is indicated by zero, the fire month and one extra month is indicated by “1”, etc. Mean 30-yr Deficit is reported as average monthly Deficit values, and mean summer Deficit is mean monthly values considering only June, July, and August. Values are occasionally repeated for plots that were within the same 4-km climate grid and burned on the same day.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Mean monthly Deficit (1985-2015)</th>
<th>Mean monthly Deficit (Jun – Aug)</th>
<th>PDSI (fire month)</th>
<th>Pre-fire</th>
<th>Deficit* (averaged over this many months before or after fire month)</th>
<th>Post-fire</th>
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</thead>
<tbody>
<tr>
<td>YFDP</td>
<td>548</td>
<td>1383</td>
<td>18</td>
<td>36</td>
<td>24</td>
<td>6</td>
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<tr>
<td>CRCRPIPO</td>
<td>594</td>
<td>1495</td>
<td>24</td>
<td>94</td>
<td>72</td>
<td>94</td>
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<tr>
<td>FFS2BURN</td>
<td>465</td>
<td>1161</td>
<td>-6</td>
<td>170</td>
<td>646</td>
<td>964</td>
</tr>
<tr>
<td>FFS5BURN</td>
<td>465</td>
<td>1161</td>
<td>-3</td>
<td>284</td>
<td>693</td>
<td>560</td>
</tr>
<tr>
<td>FFS6BURN</td>
<td>509</td>
<td>1259</td>
<td>-1</td>
<td>365</td>
<td>744</td>
<td>543</td>
</tr>
<tr>
<td>LOTHAR</td>
<td>603</td>
<td>1465</td>
<td>-3</td>
<td>550</td>
<td>845</td>
<td>535</td>
</tr>
<tr>
<td>UPTHAR</td>
<td>603</td>
<td>1465</td>
<td>-3</td>
<td>550</td>
<td>845</td>
<td>535</td>
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<tr>
<td>YOHOPISO</td>
<td>598</td>
<td>1526</td>
<td>-4</td>
<td>120</td>
<td>627</td>
<td>1026</td>
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</table>
FIG. D.1. Pre-fire stem maps of burned plots showing tree locations, size, and local basal area within 8 m. Plot names above each panel correspond to Tables D.1- D.3. Trees near the edge were mirrored to create a buffer around each plot to eliminate edge effects associated with partially empty local neighborhoods. Point size represents tree diameter (DBH).
FIG. D.2. The effect of climate (3-yr pre-fire Δ) on post-fire mortality risk within 3 years of fire. Units for the x-axis are standard deviations around the mean (values may be found in Table D.1). Point size reflects average DBH per group, color indicates average percent CVS.
FIG. D.3. The effect of crowding (basal area within 8 m) on post-fire mortality risk within 3 years of fire. Units for the x-axis are standard deviations around the mean (values may be found in Table D.1). Point size reflects average DBH per group, color indicates average percent CVS.
FIG. D.4. The effect of neighborhood size (x-axis) on post-fire mortality model fit (y-axis). The neighborhood metric was basal area within a circle of the given radius, calculated for each individual tree. More negative AIC values indicate better fit.
**FIG. D.5.** Forest spatial structure governs complex interactions between fire, drought, bark beetles, and tree mortality. Arrows indicate direct effects and interactive relationships ultimately affecting tree mortality; red arrows indicate positive relationships and amplified interactions, while blue arrows indicate negative effects and impeded interactions. Reduced forest density and more frequent fire may mediate severity of individual disturbances and impede disturbance interactions.
APPENDIX E

PERMISSION-TO-REPRINT AND PERMISSION-TO-USE LETTERS

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CURRICULUM VITAE

Tucker J Furniss
PhD candidate, Utah State University
Email: tucker.furniss@gmail.com • Web: www.tuckerfurniss.com

Education

<table>
<thead>
<tr>
<th>Degree</th>
<th>Institution</th>
<th>Field of Study</th>
<th>Advisor</th>
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<tr>
<td>PhD</td>
<td>Utah State University</td>
<td>Fire Ecology</td>
<td>Dr. James A. Lutz</td>
<td>2021</td>
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<tr>
<td>MS</td>
<td>Utah State University</td>
<td>Ecology</td>
<td>Dr. James A. Lutz</td>
<td>2016</td>
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<tr>
<td>BS</td>
<td>University of Washington</td>
<td>Envir. Science and Resrc. Mgmt</td>
<td>GPA 3.63</td>
<td>2011</td>
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</table>

Professional Experience

**ORISE Research Fellow.** Forest Service PNW Research Station. 2020–present
Supervisor: Dr. Paul F. Hessburg.

**Graduate Research Assistant.** Utah State University. Advisor: Dr. James Lutz. 2017–2020
Dissertation: Big fires, big trees, and big plots: Enhancing our ecological understanding of fire with unprecedented field data

**Field technician.** University of Montana. Supervisor: Dr. Andrew Larson. 2016–2017
Post-fire sampling in the Bob Marshall Wilderness, MT. Two weeks each summer.

**Graduate Research Assistant.** Utah State University. Advisor: Dr. James Lutz. 2014–2016
Thesis: The Utah Forest Dynamics Plot: long-term ecological monitoring and theoretical ecology in a high-elevation subalpine environment

**Crew Lead & Research Assistant,** Utah State University. Supervisor: Dr. Jim Lutz 2013–2014


Peer-Reviewed Publications (†co-lead author)

Google scholar stats (4/27/2021): Citations = 653; H-index = 11


**Outreach and Management Publications**


**Accessioned Datasets**


**Theses and Dissertations**


**Awards and Grants**

- Interactive effects of drought, fire, and bark beetles on tree mortality in the Sierra Nevada, California. *Joint Fire Science Graduate Research Innovation* (award #19-1-01-10). 2019. ($24,774)

- Travel Award. *USU Ecology Center*. 2019. ($600)

- Travel Award. *USU Office of Research and Graduate Studies*. 2019. ($200)

- Spatial Dynamics of Surface Fuels Following Reintroduced Fire. *USU Ecology Center Graduate Research Award*. 2018-2019. ($4928)

**Invited Presentations** (first author was presenter)


**Contributed Presentations** (first author was presenter)

**Furniss, T. J.** and J. A. Lutz. 2020. Big plots, big trees, and big fires: Enhancing our ecological understanding of fire effects with unprecedented field data. Ecological Society of America Annual Meeting. Salt Lake City, UT. August 5. [Video link](#).


Teaching Experience

Instructor:

**WILD 6900** – Spatial analysis of sessile organisms. Utah State University. *Fall 2019.*

**EarthWatch** “The fall of giants: Old-growth trees in the American West”. Field Team Leader (*Summer 2018*)

Guest lecture/teaching assistant:


**WILD 5710** – Forest Vegetation Disturbance Ecology and Management (graduate level). Guest lecture: “Field methods and long-term forest dynamics plots”. Utah State University. Fall 2014.


Service, Skills, Certifications


**Professional Affiliations:** Ecological Society of America, Xi Sigma Pi, Society of American
Foresters, International Association for Landscape Ecology

Symposia:

Service:
- Science fair judge – Hillcrest Elementary Annual Science Fair 2018-2019
- USU Ecology Center Seminar Selection Committee 2018-2019
- Restoring the West Conference Speaker Selection Committee 2018

Statistical expertise (from research published as lead author):
- Generalized linear mixed models
- Ordination (NMDS and PCA)
- Point pattern analysis (e.g., pair-correlation function, Ripley’s K, random labelling analysis)
- Random forest
- Cluster analysis (e.g., ICO sensu Churchill et al. 2013)

Skills:
- Software expertise: R; Google Earth Engine; ArcGIS; MySQL; Adobe CC.
- Land survey: designing surveys, establishing control loops, and installing permanent survey markers using Total Stations and survey-grade GNSS receivers
- Arc, MIG, and TIG welding
- Fifteen+ years of backcountry experience (backpacking, pack rafting, backcountry skiing, climbing, canyoneering, and Leave No Trace ethics and practices)
- Ten years of experience coordinating camp logistics for 25-35 people during research pulses