FINAL REPORT

Title: Interactive effects of drought, fire, and bark beetles on tree mortality in the Sierra Nevada, California

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Tucker J. Furniss
Utah State University

James A. Lutz
Utah State University

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List of Abbreviations

BA – Basal Area
CVS – Crown Volume Scorched (%)
D_{Δ} – differenced Climatic Water Deficit
DBH – Diameter at Breast Height (1.37 m)
FOFEM – First Order Fire Effects Model
SNFDPN – Sierra Nevada Forest Dynamics Plot Network
YFDP – Yosemite Forest Dynamics Plot

Keywords

Bark beetles, climate change, drought, fire, ForestGEO, spatial patterns, temperate forests

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Abstract

In an emerging era of megadisturbance, bolstering forest resilience to wildfire, insects, and drought has become a central objective in many western forests. Climate has received considerable attention as a driver of these disturbances, but few studies have examined the complexities of climate–vegetation–disturbance interactions. Current strategies for creating resilient forests often rely on retrospective approaches, seeking to impart resilience by restoring historical conditions to contemporary landscapes, but historical conditions are becoming increasingly unattainable amidst modern bioclimatic conditions. What becomes an appropriate benchmark for resilience when we have novel forests, rapidly changing climate, and unprecedented disturbance regimes? We combined two longitudinal datasets—each representing some of the most comprehensive spatially explicit, annual tree mortality data in existence—in a post-hoc factorial design to examine the non-linear relationships between fire, climate, forest spatial structure, and bark beetles. We found that while pre-fire drought elevated mortality risk, advantageous local neighborhoods could offset these effects. Surprisingly, mortality risk (Pm) 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 yrs) but reduced mortality over longer intervals. These results clarify interacting disturbance dynamics, provide a mechanistic underpinning for forest restoration strategies, and may be used to adapt post-fire mortality models to novel climatic conditions.

Key publication: Furniss, T. J., A. J. Das, P. J. van Mantgem, N. L. Stephenson, and J. A. Lutz. In Press. Crowding, climate, and the case for social distancing among trees. Ecological Applications. https://doi.org/10.1002/eap.2507

Objectives

1) Quantify the interactions between climate, local neighborhoods, and fire. We hypothesized that trees burned during drought would have a lower tolerance for fire damage, and existing mortality models will therefore under-predict mortality for fires that occur during drought. We further hypothesized that the local neighborhood around each tree effects its ability to tolerate fire damage, and tree neighborhoods may therefore mediate post-fire mortality. Our objective was to quantify and compare the effects of climate and local tree neighborhoods on post-fire mortality and expressed fire severity.

2) Investigate the interactive effects of fire and drought on susceptibility to drought mortality and bark beetle attack. We hypothesized that if fire and drought co-occur, fire- and beetle-induced mortality would be amplified, but if fire occurred before drought, this interaction may be impeded. Our objective was to characterize drought – fire – beetle interactions to determine how the order of disturbance events affects the nature of the interaction.

Background

Recent increases in wildfire activity, bark beetle outbreaks, and severe drought have led to widespread episodes of forest die-off (Breshears et al. 2005, Allen et al. 2010) and an overall increase in tree mortality across the western US (van Mantgem et al. 2009). There has been considerable research on the effects of climate on fire size and frequency (e.g., Westerling et al. 2006, Littell et al. 2009), but relatively little work has addressed the more proximate effects of drought on the susceptibility of trees to fire damage and post-fire mortality agents (e.g., bark beetles). Existing fire mortality models (e.g., FOFEM) were parameterized using fires that burned between the late 1980s and early 2000s (Hood and Lutes 2017), and it is not currently known whether mortality predictions from these models are sufficient for fires that burn under hotter and drier modern climates. Recent studies have revealed that drought alters the ability of trees to recover from fire damage (van Mantgem et al. 2013, 2018, Furniss et al. 2019), but the degree to which this may undermine existing mortality models has not yet been quantified.

Recent research has also begun to reveal that tree neighborhoods also mediate post-fire mortality; they do this directly through inter-tree competition for water and soil resources, as well as indirectly through host-specific pests and pathogens (Hood et al. 2018, van Mantgem et al. 2018, Furniss et al. 2020a). We leveraged existing stem-mapped datasets to characterize the local neighborhood conditions around each individual tree, and we used these data to generate local neighborhood metrics that served as a proxy for competitive stress, water availability, and insect selection pressure around each tree.

Interactions between fire, beetles, and drought are complex (Hood and Lutes 2017, Raffa et al. 2008, McDowell et al. 2008), and the timing and order of disturbance events can alter the nature of the disturbance interaction (Kane et al. 2017, Hood et al. 2018). For example, fire may decrease drought-related mortality through reduced competition for water (van Mantgem et al. 2016), but drought may increase fire-related mortality due to increased susceptibility to direct fire damage and reduced tree defenses (van Mantgem et al. 2013). Recent studies have begun to disentangle the two-way interactions between climate and fire (van Mantgem et al. 2013, Dillon et al. 2011), climate and bark beetles (Weed et al. 2013, Kolb et al. 2016), and fire and bark beetles (Breece et al. 2008, Youngblood et al. 2009), but some critical questions remain (Kane et al. 2017). This research directly targeted several knowledge gaps regarding two-way disturbance interactions, and it provided a rare factorial example of the three-way interaction between fire, climate, and bark beetles on mortality in the Sierra Nevada.

Quantifying the sensitivity of existing models to different climates and different forest density conditions is a top research priority as mortality models are a critical management tool, yet existing models may not be adequately adaptable to warmer future climates or altered forest structure. This research advanced the applied science of fire effects modeling by developing methods to incorporate climate parameters and susceptibility to beetle attack into fire effects models, and it contributes a basic understanding of the complex relationships between primary drivers of tree mortality in western forests (e.g., Kane et al. 2017, Stephens 2018).

Methods

Study Sites

We combined two longitudinal tree mortality datasets: the Sierra Nevada Forest Dynamics Plot Network (SNFDPN; van Mantgem and Stephenson 2007), and the Yosemite Forest Dynamics Plot (YFDP; Lutz et al. 2012) (Fig. 1). Within each of these study plots, all woody stems ≥1 cm DBH have been identified, tagged, and mapped. The plots were censused annually for new recruitment and mortality beginning in 1990 for the SNFDPN and 2011 for the YFDP, and have continued through 2021. The SNFDPN contains 18 1-ha plots (16,033 trees total) distributed throughout the lower montane mixed-conifer zone of Yosemite and Sequoia & Kings Canyon National Parks. Eight of the SNFDPN plots burned between 1990 and 2009 (Fig. 1) under climatic conditions including both wet and dry years. The YFDP is a single, 25.6-ha plot containing 34,458 pre-fire live trees that was burned under extreme drought conditions in the 2013 Rim Fire (Furniss et al. 2020b).

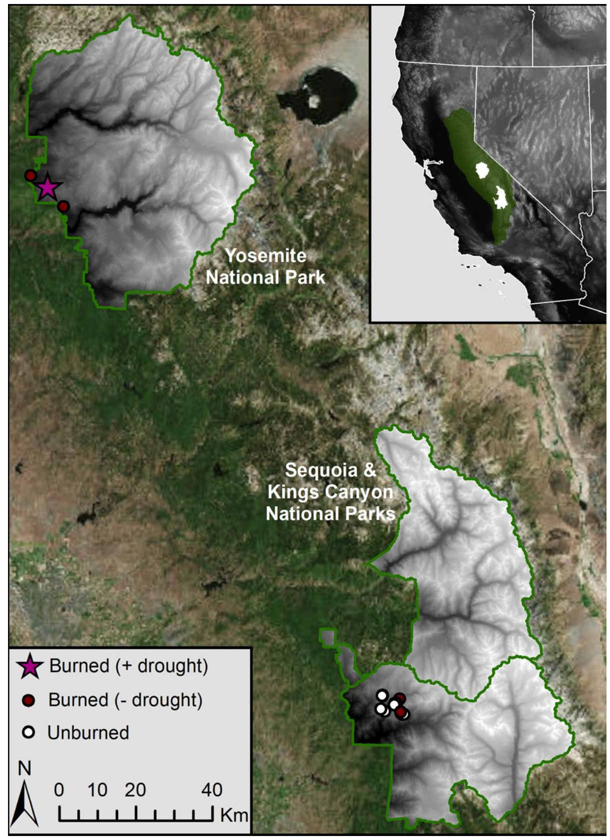

Figure 1. Locations of study sites in Yosemite and Sequoia & Kings Canyon National Parks. Dots indicate plot locations for 18 plots within the Sierra Nevada Forest Dynamics Plot Network, and the star represents location of the Yosemite Forest Dynamics Plot.

Field Measurements

During the annual mortality surveys, pathology exams were conducted for all newly dead trees within each plot. Factors associated with death were identified for each individual tree that died within that year by trained field technicians who removed bark on the bole and around the root crown to reveal evidence of pests and pathogens (see Das et al. 2016 and Furniss et al. 2020a for details). Bark beetles were identified to species based on the size and shape of the gallery, frass color, and actual beetles if present.

Study Design

We used generalized linear mixed models (GLMMs; details below) with a logit link to evaluate the effects of site-level 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.

The relative importance of site-level climate and local tree neighborhood variables 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. The base GLMM estimated probability of mortality (Pm_{ij}) for tree i in plot j as:

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

where β_0 is the intercept, b_0 are random intercept terms, b_{1Spp} is a random slope for each species, and $\beta_{1\text{-}2}$ are fitted coefficients for CVS and DBH.

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. We evaluated both overall drought-induced mortality as well as beetle-related mortality among *Pinus* that occurred during the drought.

Climate and local neighborhood variables

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 Wagtendonk et al. 2020) and tree mortality (van Mantgem and Stephenson 2007) in the Sierra Nevada. 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, inclusive of the month of the fire.

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 quantify density and competition influences around each tree (considering all neighbors and conspecifics only).

Results and Discussion

Pre-fire drought and tree crowding increased probability of fire-related mortality by 22% and 33%, respectively (Fig. 2, Table 1). Climate effects were most pronounced at low levels of fire damage (CVS ≤25%) where mortality risk was positively related to D_Δ. 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 compared with trees in denser neighborhoods (21% versus 54%, respectively, for a tree with 50% CVS, Table 1). Post-fire D_Δ and local conspecific BA also increased probability of successful post-fire beetle attack, especially at low levels of crown scorch (Fig. 2).

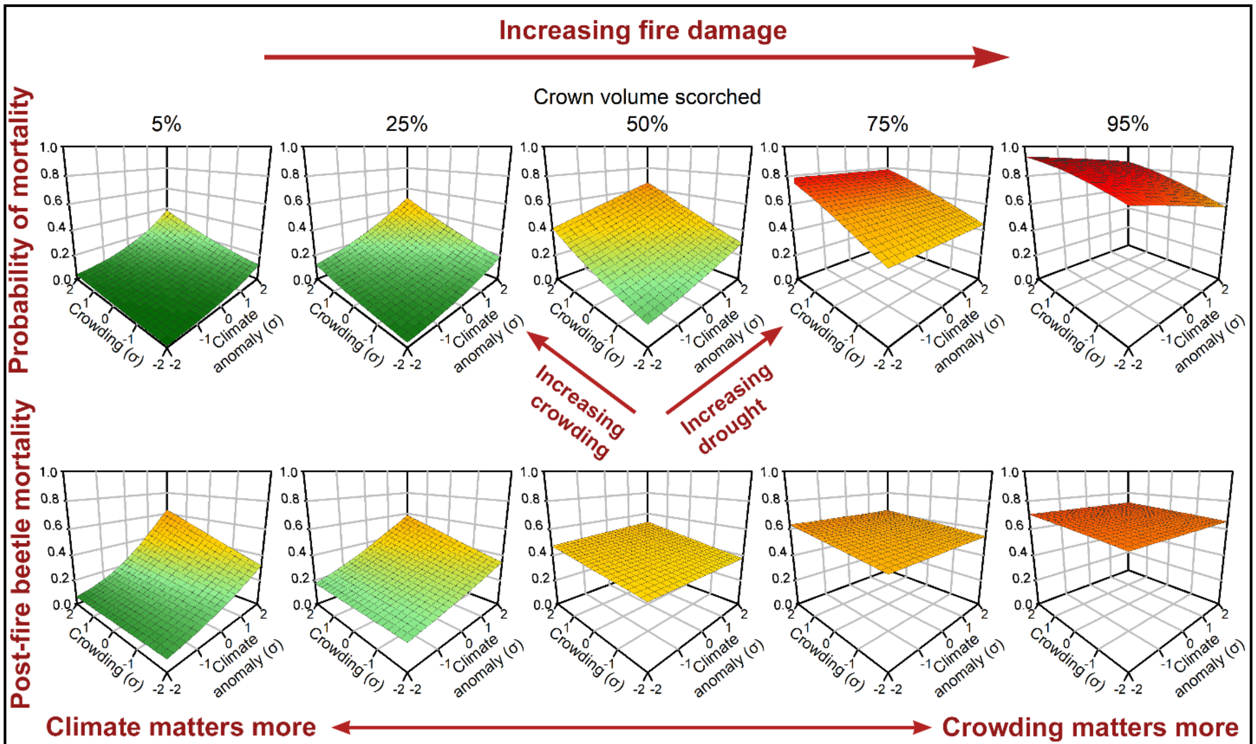

Figure 2. Net effects of crowding and climate on overall (top) and beetle-related (bottom) postfire mortality risk. Units for the x- and y-axes are standard deviations around the mean; actual values may be found in Appendix S1: Tables S1&S3. Color indicates probability of mortality (same as z-axis values). 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 DΔ (top) and 1-yr postfire DΔ (bottom). 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).

Table 1. Probability of mortality under various climate and neighborhood conditions, corresponding to the three-dimensional surface in Fig. 2 (top row, center panel). Values are model predictions from the best fit post-fire model that related probability of mortality to CVS, 3-yr pre-fire Pre-fire D_{Δ}, 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.

		Neighborhood		
		Open	Average	Dense
Climate	Wet	13.8%	25.2%	41.7%
	Average	20.7%	35.6%	53.9%
	Dry	29.9%	47.5%	65.7%

Drought-related mortality in plots unburned for at least 35 years was negatively correlated with elevation and positively correlated with stem density (Fig. 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. 3A), 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. 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 ($R^2 \sim 0$, $P > 0.1$; Fig. 3E, F, & 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. 3A & E, C & G).

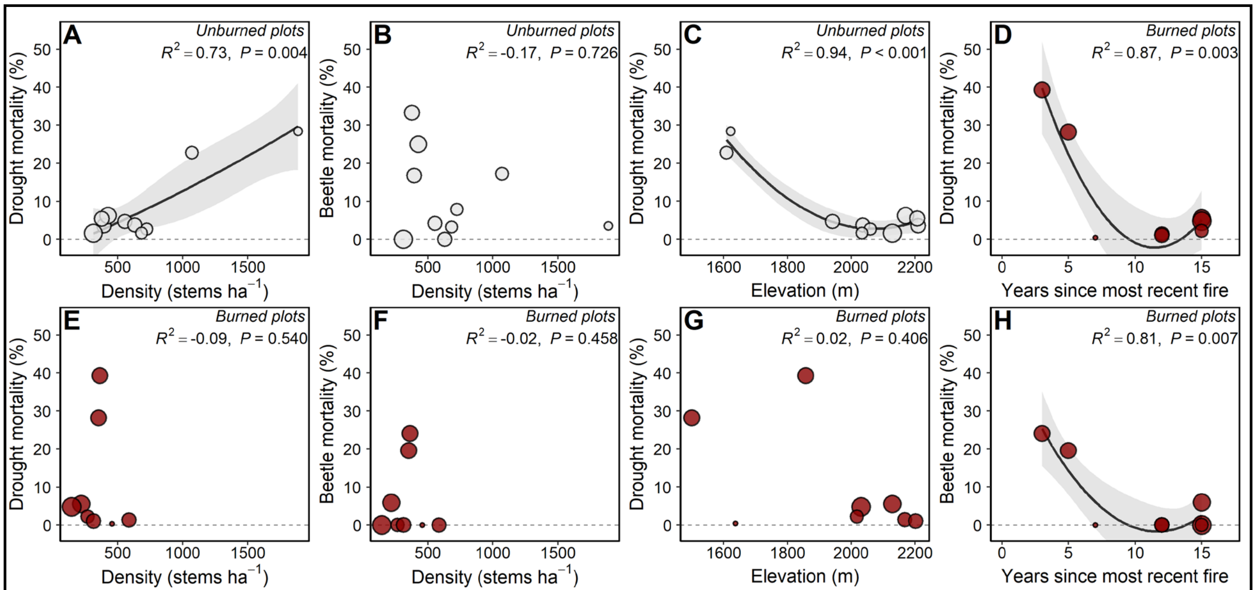

Figure 3. Relationships between drought-related mortality rate and stem density (A, B, E, F), elevation (C, G), and time since last fire (D, H). Point size indicates average DBH within each plot, color differentiates burned (red) from unburned (white) plots. The response variable in panels A, C, D, E, and G is drought mortality rate, while the response variable in B, F, and H is beetle-related mortality during the drought. R2 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.

This study provides an empirical framework for integrating previous research showing interactions between fire and climate (van Mantgem et al. 2013, 2018), local neighborhood effects (Restaino et al. 2019, Furniss et al. 2020a, 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 drier climatic conditions increase 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 neighborhood conditions can be equally important. The effects of drought (reduced plant-available water) are filtered through fine-grained ecological attributes including micro-topography, soil water-holding capacity, and forest density (affecting water demand), and these fine-grained conditions can potentially mediate the realized micro-environment that trees experience. Tree neighborhoods capture this net drought effect along with resource competition and spatially non-random mortality processes, all factors that are all closely linked to tree-to-tree variance in mortality risk (van Mantgem et al. 2018, Furniss et al. 2020a, Germain and Lutz 2021). Other studies have similarly 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 directly compare the relative magnitude of their effects. 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 in fire-prone, climate-limited forests.

Fire can confer either resistance (van Mantgem et al. 2016, Hood et al. 2016) or increased susceptibility (Breece et al. 2008, Furniss et al. 2020a, Knapp et al. 2021) to drought and bark beetles. Our results reconcile this apparent contradiction by identifying the time interval at which this relationship inverts (~7 years, in our study sites). 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 scorch-induced xylem deformation (Partelli-Feltrin et al. 2020). The time it takes to establish resistance to drought following fire (~7 years) is thus related to the time that it takes for post-fire mortality to subside to background levels (van Mantgem et al. [2011] found that it took 6 years in the SNFDP plots, and Furniss et al. [2020a] found that it took at least 5 years in the YFDP). The upper end of this time frame is likely influenced by the time it takes for post-fire regeneration of trees and shrubs to bring stand density, and associated demand for water and soil resources, back to pre-fire levels.

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. For example, Knapp et al. (2021) found elevated mortality rates in plots that burned 2-3 years before a 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-exclusion fire return interval for dry forests in the Sierra Nevada; this may be simply coincidental, but it invokes curiosity regarding the role of regular fire as a stabilizing process in droughty western forests.

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 CVS as the primary driver of post-fire mortality risk. Considering our model accuracy alone, it is currently unnecessary to incorporate climate and crowding as additional terms into management tools such as FOFEM. However, as average climatic conditions become drier it may become increasingly important to reparametrize fire effects models with trees that burn under "average" future conditions. The underlying relationships shown in our models portends a systematic increase in mortality risk as the climate becomes more droughty.

Conclusions and Management Implications

Here we show that advantageous local tree 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 (Fettig et al. 2007, 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.

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), and in this research 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.

These results provide empirical evidence for the efficacy of forest restoration treatments that is independent of historical reference conditions. This complements a considerable body of research regarding resilience at landscape scales (see Hessburg et al. 2019) by advancing our foundational understanding of the fine-scale ecological factors that mediate tree-level resistance and contribute to stand-level resilience to compound disturbance events. 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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Appendix A: Contact Information for Key Project Personnel

Tucker J. Furniss
ORISE Postdoctoral Fellow
USDA Forest Service
Pacific Northwest Research Station
Wenatchee, WA
E-mail: tucker.furniss@usda.gov

James A. Lutz
T.W. Daniel Associate Professor in Forestry
Wildland Resources Department
S.J. & Jessie E. Quinney College of Natural Resources and the Ecology Center
Utah State University
5230 Old Main Hill
Logan, UT 84322-5230
E-mail: james.lutz@usu.edu

Nathan Stephenson
Scientist Emeritus
Western Ecological Research Center
United States Geological Survey
nstephenson@usgs.gov

Appendix B: Completed Deliverables

Planned Deliverable	As Delivered	Delivery Date
Annual progress summary	Progress report submitted according to JFSP protocols	October 2020
Peer-reviewed publication	Furniss, T. J., A. J. Das, P. J. van Mantgem, N. L. Stephenson, and J. A. Lutz. In Press. *Crowding, climate, and the case for social distancing among trees*. Ecological Applications. https://doi.org/10.1002/eap.2507	December 2021
Presentation at *Association for Fire Ecology* conference	Furniss, T. J. and J. A. Lutz. 2021. *Translating error into ecology: What uncertainty in fire severity maps and mortality models can tell us about fire effects*. Organized oral session at the Association for Fire Ecology 9th International Fire Ecology and Management Congress. Nov. 30, 2021.	November 2021
Meeting with Yosemite Managers	PI Lutz met with Yosemite National Park Chief of Staff Joe Meyer to discuss research results.	May 21, 2021
Dissertation chapter	This project was the basis for Chapter V in *Big fires, big trees, and big plots: Enhancing our ecological understanding of fire with unprecedented field data*, a Dissertation produced by Tucker J. Furniss in partial fulfillment of the degree of Doctor of Philosophy at Utah State University.	April 2021
Final report	Submitted according to JFSP protocols by the project deadline.	December 2021

Appendix C: Metadata

No new data were collected for this project. Data used in the project, and associated metadata, are available to the public pending adherence to appropriate data use policies (USGS SM 502.8 for the SNFDPN, available at https://www2.usgs.gov/usgs-manual/500/502-8.html, and http://ctfs.si.edu/datarequest/ for the YFDP). Both SNFDPN and YFDP datasets are archived in accordance with the policies governing the organizations that manage the SNFDP and the YFDP longitudinal research programs.