Received: 27 September 2024 | Accepted: 8 October 2024

DOI: 10.1002/ecs2.70083

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Vegetation Ecology

Drought before fire increases tree mortality after fire

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Funding information
Joint Fire Science Program, Grant/Award Number: JFSP 16-1-04-8; U.S. Forest Service Forest Health Protection; U.S. Forest Service Rocky Mountain Research Station; U.S. Geological Survey's Ecosystems Mission Area; Corbett Fire Endowment

Handling Editor: Sunshine A. Van Bael

Abstract

Fire and drought are expected to increase in frequency and severity in temperate forests due to climate change. To evaluate whether drought increases the likelihood of post-fire tree mortality, we used a large database of tree survival and mortality from 32 years of wildland fires covering four dominant western North American conifers. We used Bayesian hierarchical modeling to predict the probability of individual tree mortality after fire based on species—*Pinus contorta* (lodgepole pine), *Abies concolor* (white fir), *Pseudotsuga menziesii* (Douglas-fir), and *Pinus ponderosa* (ponderosa pine)—bark thickness, bark char, percentage live tree crown scorched or consumed crown volume scorch (CVS), and mean annual climatic water deficit (CWD) anomalies the year pre-fire and fire year relative to the 1985–2015 reference period. Although *crown injury* was the primary determinant of tree mortality after fire, *drought* increased likelihood of death, with a 2-SD increase in CWD (+115.7) resulting in a 78% increase in the probability of mortality. We assessed the crown scorch level expected to result in >50% probability of mortality under different CWD scenarios: observed CWD, CWD of +2, and +4°C warming scenarios. Increased climatic moisture stress amplified tree death, reducing the threshold that causes tree mortality across all conifers under +4°C warming, with more subtle and species-specific reductions for the +2°C scenario. Models predicting post-fire tree mortality are components of global and regional carbon estimates, habitat suitability assessments, and forest management planning and decision support systems. The amplifying effects of drought on post-fire tree mortality and predicted future climates are likely to lead to higher tree mortality following fires in forested landscapes of western North America and may have cascading effects on ecosystem services and future forest resilience.

KEYWORDS
climate-mediated fire effects, climatic water deficit, disturbance interactions, drought, post-fire mortality, wildland fire

INTRODUCTION

Increases in tree mortality caused by wildfires and droughts are rapidly altering the resilience of forests across the planet (Falk et al., 2022). Changes in the structure, composition, and landscape configuration of dry forests in western North America have increased wildfire hazard and decreased ecological resilience to fire due to colonialism and associated disruptions of indigenous burning practices, extraction of large fire-resistant trees, grazing practices, and increases in fuel loadings and fuel connectivity due to fire exclusion and cool-wet climates that allowed for successful fire exclusion (Falk et al., 2022; Hessburg et al., 2019; Littell et al., 2009). Climate change is further altering historical fire regimes through regional and global increases in the length of the fire season, area burned, extreme single-day fire spread events, and the severity of fires (Coop et al., 2022; Parks & Abatzoglou, 2020). Additionally, climate change is directly impacting forests through increased drought-driven and insect-driven tree mortality (Anderegg et al., 2015), particularly through co-occurrence of extreme heat and drought, decreased growth, and decreased tree regeneration after disturbance (Davis et al., 2019, 2023; Hammond et al., 2022).

Drought and wildfire can have synergistic or antagonistic effects on tree mortality (Kane et al., 2017). For example, fire followed by drought may be antagonistic if reduced tree density from fire-related mortality decreases competition and thus moisture stress of surviving trees, reducing the probability of mortality from drought (Furniss et al., 2020, 2022; Tepley et al., 2020; van Mantgem et al., 2018). Conversely, there may also be synergies, such as drought-caused mortality increasing fuel loading and continuity, thereby increasing fire intensity and ensuing tree mortality (Stephens et al., 2022). Here, we test for a specific synergy: Does elevated drought stress increase the probability of post-fire tree mortality relative to wetter conditions?

Previous research has shown that fire-caused injury—especially tree crown scorch and crown consumption—can be used to predict the occurrence of immediate post-fire tree death with high accuracy (Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018; Varner et al., 2021). The models do not perform as well, however, in predicting post-fire tree survival (Cansler, Hood, van Mantgem, et al., 2020) or in delayed tree death 3–5 years after wildfire (Shearman et al., 2023). For trees with moderate levels of crown scorch or crown consumption, many interacting factors—pre-fire growth, drought stress, competitive stress, and post-fire bark beetle dynamics—can influence whether a tree survives or dies (Furniss et al., 2019, 2020; Hood & Bentz, 2007; Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018; Kane et al., 2017).

We expected that drought stress would elevate post-fire mortality, particularly in trees with moderate levels of fire-caused injury. This may occur through a variety of mechanisms, operating in both the presence and absence of fire, such as impaired physiological function due to the impacts of water stress on tree hydraulic systems and carbohydrate reserves (Hammond et al., 2019; Hood, 2021; Partelli-Feltrin et al., 2020; Sapes et al., 2019); higher fuel consumption because of low fuel moisture, which can lead to higher root and basal cambium death; and indirect effects such as increase prevalence or virulence of biotic stressors including bark beetles and pathogenic fungi (Caldeira, 2019; Desprez-Loustau et al., 2006; Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018; Huang et al., 2020; Wood et al., 2018). Previous empirical research has revealed associations between drought and post-fire tree mortality (Barker et al., 2022; Furniss et al., 2022; van Mantgem et al., 2013, 2018). By using a larger sample of fires—and thus climate variation—as well as a larger sample of individual trees from across large extents of species' native ranges, we address our core question: Does pre-fire drought increase the probability of post-fire tree mortality? We then explore how responses differ among species and project the interactive effects of fire-caused injury and pre-fire hot and dry conditions on tree mortality under two future ensemble climate projections.

METHODS

Data

To understand how climatic moisture stress impacts post-fire tree mortality, we use a large dataset drawn from the Fire and Tree Mortality Database (FTM) (Cansler, Hood, Varner, et al., 2020a, 2020b). The FTM was developed using data from multiple studies to evaluate and improve post-fire tree mortality models and includes field observation records from >160,000 individual trees impacted by fire. Samples cover most of the geographic range of the four focal species of this study: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Douglas ex Loudon), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr) (Appendix S1: Table S1). For inclusion in this study, we used observations from the FTM database that met these criteria: individual tree field-based observations of species and status (live/dead) within 1-year post-fire and in 3, 4, or 5 years post-fire, as well as field observations of (1) percentage crown volume scorch

(CVS), (2) presence/absence of bark char (BC), and (3) dbh (in centimeters). We then used dbh and species-specific bark thickness (BT) coefficients to calculate BT (in millimeters) (Cansler, Hood, Varner, et al., 2020a). We excluded observations of trees reburned in a second fire and limited the dataset to fires that had observations from at least 50 trees of any of the four focal tree species. These filters resulted in a dataset for this study of 66,278 trees across 154 fires that burned between 1984 and 2016.

Climate observations were drawn from monthly data from TerraClimate (Abatzoglou et al., 2018), sampled at fire locations provided in the FTM database. Climate variables were transformed into annual anomalies, based on 1985–2015 means, and summarized over 1- and 3-year pre-fire + year-of-fire and post-fire time windows. Random forests (RF, Breiman, 2001) was used to identify the interval with the closest relationship to post-fire mortality (Appendix S1). We identified a single climate variable used in subsequent predictive modeling: pre-fire 1 year + year-of-fire climatic water deficit (CWD; in millimeters of water). CWD was also conceptually appealing because it is associated with plant moisture stress (Stephenson, 1998), and exploratory analyses confirmed CWD as a consistently performing predictor among a suite of climate variables (Appendix S1). Because seasonal CWD values are highly correlated with annual values, and seasonality differed greatly among sites, we used annual CWD to account for inter-site variability. Our large sample of fires occurs across 25 separate years, with variation in pre-fire CWD both within and across years (Figure 1).

The choice of climate variables and periods over which they were summarized, as well as the model structure of the hierarchical Bayesian logistic regression (BLR) model (described below), was informed by exploratory analysis with RF. We initially assessed a large suite of climate variables, summarized over a variety of pre-fire and post-fire temporal windows (Appendix S1). The RF modeling showed (1) pre-fire climate anomalies were more strongly associated with post-fire mortality than post-fire climate anomalies, (2) only one pre-fire climate variable was needed to explain variance in post-fire tree mortality, (3) models needed to account for the time period over which tree mortality was both measured and occurred, (4) CVS and CWD had an interactive effect, and (5) model structure needed to account for potential random effects at the fire scale (Appendix S1: Figures S2–S4, Tables S2 and S3).

Empirical predictive modeling

We developed a hierarchical "BLR" (Gelman & Hill, 2006) to describe the effects of CVS, BT, BC, and 1-year pre-fire + year-of-fire CWD anomalies tree species, and a CVS:CWD interaction on the probability of mortality within 5 years of the fire (Appendix S1: Figure S1). We standardized all predictors prior to modeling by subtracting the mean and dividing by

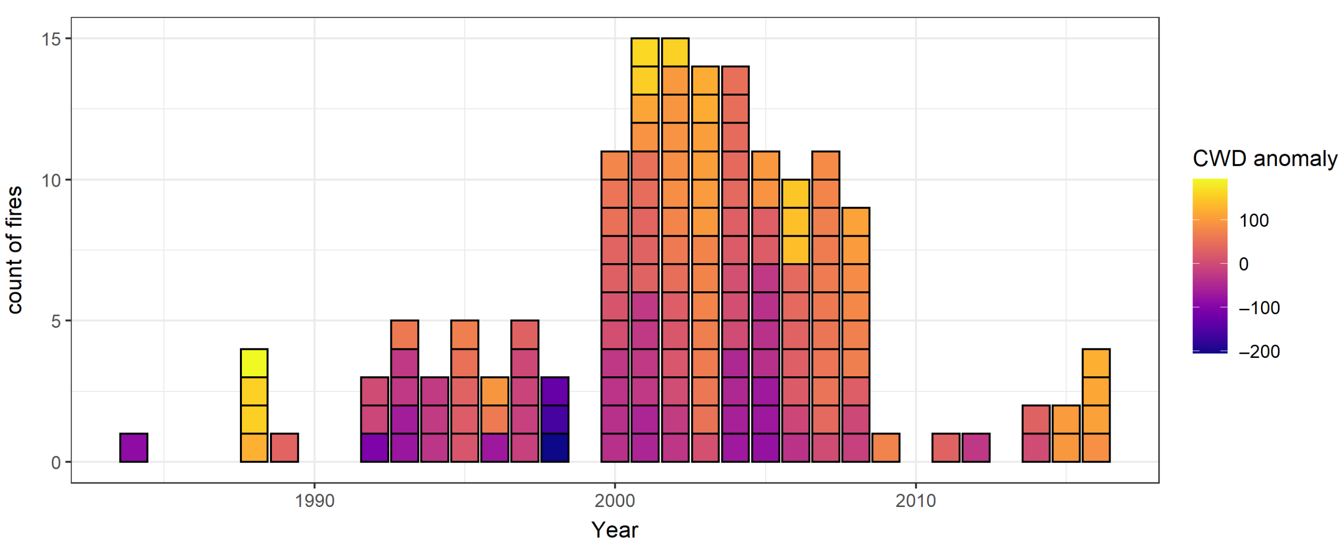

FIGURE 1 Bar graph showing the year of fire occurrence and the count of fires in each year. Each fire is represented by one stacked square, colored by the 1 year + year of fire climatic water deficit (CWD) anomaly. Greater CWD anomalies (warmer colors) represent warmer and drier conditions and associated increased drought. We use observations from 152 fires, from 25 separate fire-years occurring between 1984 and 2016, with the greatest within-year sample sizes and within-year variations in CWD anomalies occurring between 2000 and 2008.

twice the SD (Gelman & Hill, 2006). This model accounted for unequal post-fire sampling intervals by including observation interval (in years) as a penalty term on the probability of survival (Appendix S1: Figure S5). The model also included nested variable intercepts for fires (Appendix S1: Figure S6) and plots. We compared BLR models without and with species identity in the model and determined that inclusion of species improved model predictive accuracy (Appendix S1: Figure S7). Therefore, the BLR model included a species term with Douglas-fir as the reference species.

CWD was measured at the fire level, so we modeled the variable intercept for fire as a function of CWD (Gelman & Hill, 2006). The parameters are as follows: μ_{fire}, global intercept; α, the group-level intercepts; σ, SD; p, probability of mortality or survival; β, the coefficient for predictor variables;

$$\alpha_{\text{fire}} \sim \text{normal}(\mu_{\text{fire}}, \sigma_{\text{fire}})$$

$$\alpha_{\text{plot}} \sim \text{normal}(\alpha_{\text{fire}}, \sigma_{\text{plot}})$$

$$\begin{aligned}\text{linear predictor} = {} & \alpha_{\text{plot}} + \beta_{\text{BT}} \times \text{BT} + \beta_{\text{CVS}} \times \text{CVS} + \beta_{\text{BC}} \\ & \times \text{BC} + \beta_{\text{CWD}} \times \text{CWD} + \beta_{\text{CVS:CWD}} \\ & \times \text{CVS} : \text{CWD} + \beta_{\text{species}} \times \text{species}\end{aligned}$$

$$p_{\text{mortality}} = \frac{\exp(\text{linear predictor})}{1 + \exp(\text{linear predictor})}$$

$$p_{\text{survival}} = \left(1 - p_{\text{mortality}}\right)^{\text{yearly observation interval}}$$

$$p_{\text{mortality penalty}} \sim \text{bernoulli}(1 - p_{\text{survival}})$$

We used weakly informative priors, shown below. The priors for σ_{plot} and σ_{fire} were constrained to positive values.

$$\mu \sim \text{normal}(0, 3)$$

$$\alpha \sim \text{normal}(0, 3)$$

$$\sigma_{\text{plot}} \sim \text{cauchy}(0, 3)$$

$$\sigma_{\text{fire}} \sim \text{cauchy}(0, 3)$$

$$\beta \sim \text{normal}(0, 5)$$

We ran the model with four chains for 2000 iterations each. We evaluated model convergence with visual inspections of MCMC trace plots and ensured that $\widehat{R}$ was below 1.05 for all parameters.

We used posterior predictive checks (Gabry et al., 2019) to ensure that model predictions resembled the training data. We evaluated model performance using Brier scores and area under the receiver-operating characteristic curve (AUC). The Brier score is the mean squared error of model predictions and is calculated using the formula $\frac{1}{N}\sum_{i=1}^{N}(p_i - O_i)^2$, where p is the predicted probability and O is the observed outcome.

To put our results into the context of current and future climates, we estimated mortality probabilities across the range of CVS for three CWD anomaly scenarios: observed anomalies compared to a 1985–2015 reference period and +2°C and +4°C future scenarios (Appendix S1: Figures S9 and S10), based on ensemble model predictions for pseudo-years 1985–2015 from TerraClimate (Abatzoglou et al., 2018), which were calculated following methods in Qin et al. (2020). Then, we calculated the lowest CVS at which a median sized tree of each species would have ≥0.50 P_m (CVS P_{m50}) for 1985–2015, +2°C, and +4°C future scenarios. We defined median size based on the species-specific range included in the constrained FTM database.

RESULTS

Pre-fire drought increased the probability of post-fire tree mortality

Pre-fire drought increased the probability of fire-caused conifer mortality beyond what would be expected based on fire-caused injury alone. Posterior estimates for the odds ratio suggest that for a 2-SD increase in CWD (+115.7 mm), a tree was 78% more likely to die than without the increase in CWD, given a constant level of fire-caused injury. Specifically, the estimated increase in the log odds of the outcome (tree mortality) per unit increase in the value of the exposure (in this case a 2-SD increase in CWD) was 1.78, when CVS is held at the mean of 43% (Appendix S1: Figure S8). For Douglas-fir, ponderosa pine, and white fir with moderate levels of CVS (e.g., 50%), observed variation in CWD shifted their probability of mortality from <0.30 to >0.60 (Figure 2). Model uncertainty was low for all parameters (i.e., credible interval did not overlap zero), showing strong support that all predictors improved predictions of tree mortality and survival (Figure 3). CVS was the main variable influencing tree mortality after fire, with other continuous predictors (CWD, BT, and the CVS:CWD interaction) having similar sized effects at average CWD (Figure 3). The effect size of CWD alone and the

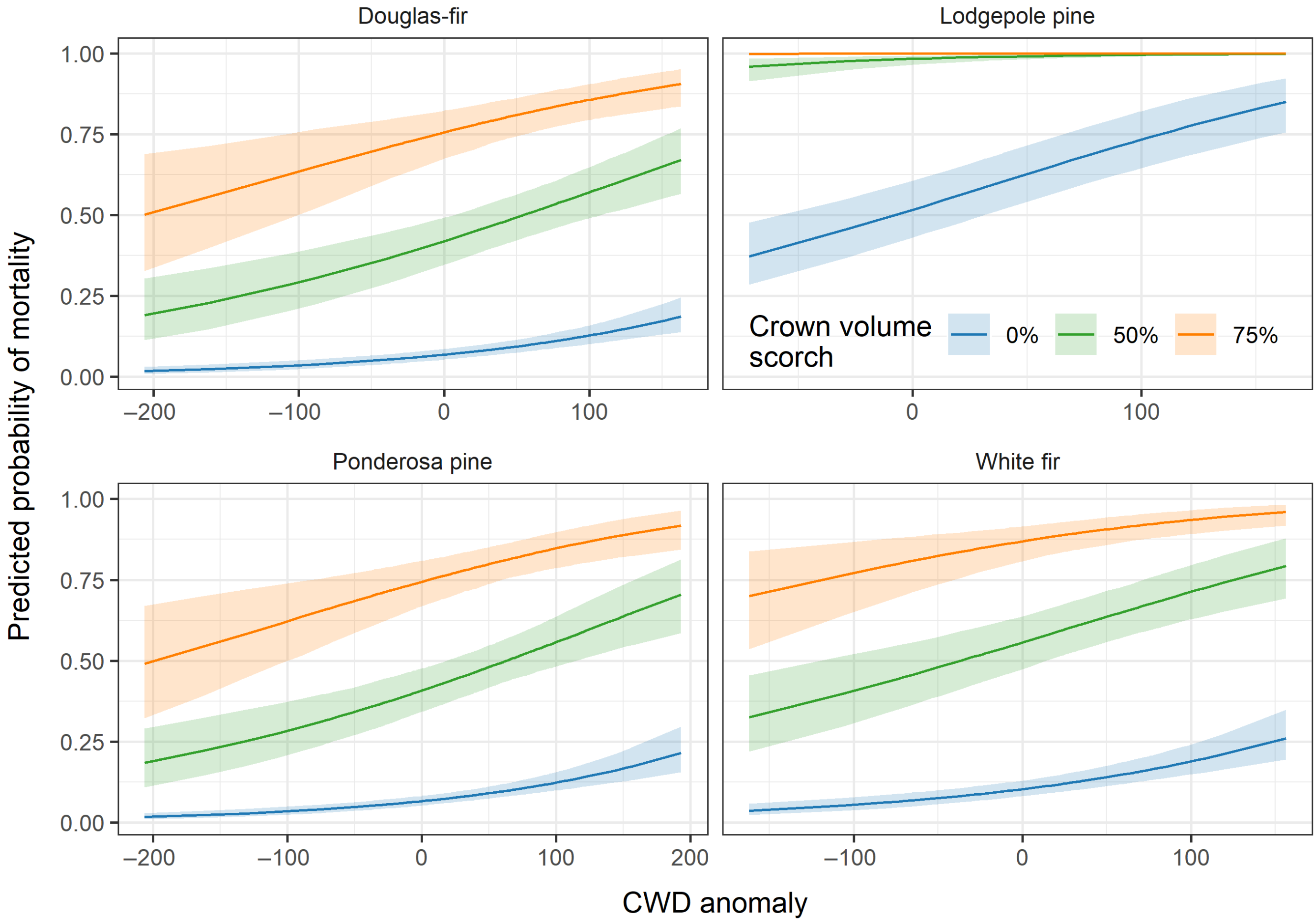

FIGURE 2 Interactions between crown volume scorch (0%, 50%, and 75%) and climatic water deficit (CWD) anomalies result in differing probability of individual tree mortality within 5 years of fire of four western North American conifers. Shaded areas show 95% credible intervals, specifically the 2.5 and 97.5 percentiles of the predicted probabilities from 2000 draws of the posterior.

CVS:CWD interaction were small compared to the main effect of CVS (Figures 2 and 3).

Sensitivity to drought and fire-caused injury differed among species

Model performance improved when species identity was included (Appendix S1: Figure S5), even though the model already included species-specific BT. Using wide-ranging Douglas-fir as the reference species, post-fire tree mortality was lower for ponderosa pine, but higher for white fir and lodgepole pine (Figure 3). CWD contributed to a switch between trees being predicted to survive ($P_m < 0.5$) versus die ($P_m > 0.5$) primarily at intermediate levels of fire-caused injury. This is shown in Figure 2, where P_m values have the biggest variation in response to CWD in trees with 50% CVS. The levels of fire-caused injury at which CWD affects P_m differed among species, with the thicker bark species of Douglas-fir, ponderosa pine, and white fir being more similar compared to thin-barked lodgepole pine (Figure 2).

Future climate may decrease tree resistance to fire and increase tree mortality

The crown scorch level projected to result in >50% P_m (CVS P_{m50}) was similar for the observed CWD anomalies and for 30-year average CWD under +2°C warming scenario ensemble means but decreased dramatically for 30-year average CWD under +4°C warming scenario ensemble means (Figure 4). The CVS P_{m50} for lodgepole pine did not vary among climate scenarios because lodgepole pine consistently had >50% P_m. Drought reduced tolerance to crown scorch for white fir, Douglas-fir, and ponderosa pine, particularly under the +4°C scenario (Figure 4). On average, across all

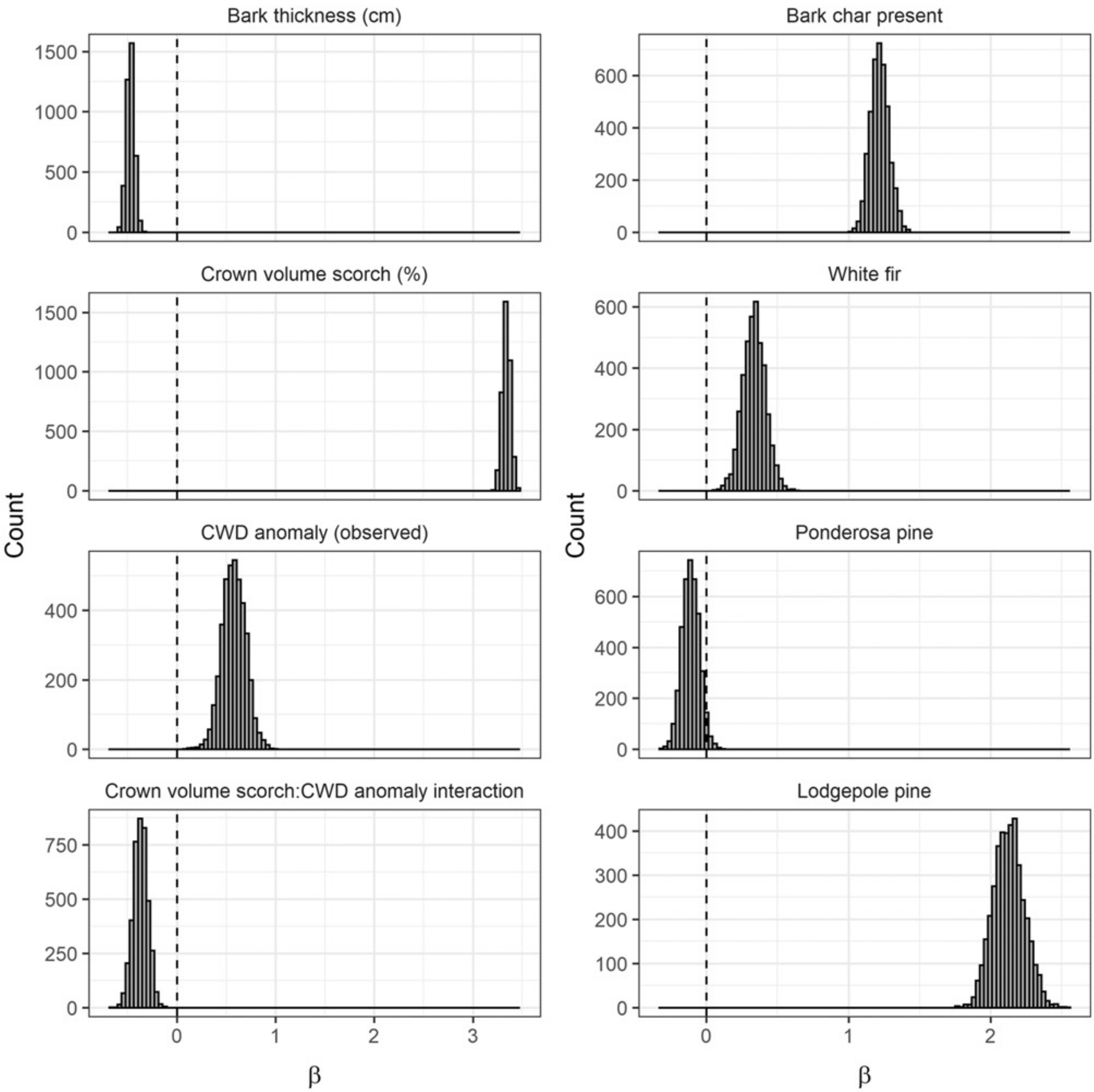

FIGURE 3 Posterior distributions for each fixed-effect parameter used in the hierarchical logistic regression model predicting the probability of individual tree mortality within 5 years of a fire for four common western North American conifers—ponderosa pine, Douglas-fir, white fir, and lodgepole pine. Probability distributions represent the relative credibility of each parameter value. Narrower distributions represent greater certainty in the parameter value. For continuous variables (left column), distributions above or below zero (dashed vertical line) indicate the variable increases or decreases, respectively, the probability of tree mortality. The bark char parameter (right column) represents the change in the probability of mortality when bark char is present; absent is the reference condition. Parameters for species (right column) indicate the change in the probability of mortality relative to Douglas-fir, the reference species. Tree observations were from the Fire and Tree Mortality database (Cansler, Hood, Varner, et al., 2020a, 2020b); bark thickness was modeled based on a linear relationship with observed diameters at breast height using a species-specific coefficient; climatic water deficit (CWD) anomalies were calculated based on annual data and 1985–2015 normals at each fire location ($n = 154$) using gridded data from TerraClimate (Abatzoglou et al., 2018).

observations, greater CWD under a +2°C scenario reduced the threshold of crown scorch needed to cause mortality (CVS P_{m50}) from 55% to 50% for ponderosa pine and from 45% to 40% for white fir but did not reduce CVS P_{m50} for Douglas-fir (Appendix S1: Table S4). The +4°C scenario resulted in much lower thresholds of CVS P_{m50} than the observed climate: from 55% to 40% for Douglas-fir, from 55% to 35% for ponderosa pine, and from 45% to 25% for white fir (Appendix S1: Table S4). White fir, ponderosa pine, and Douglas-fir had similar

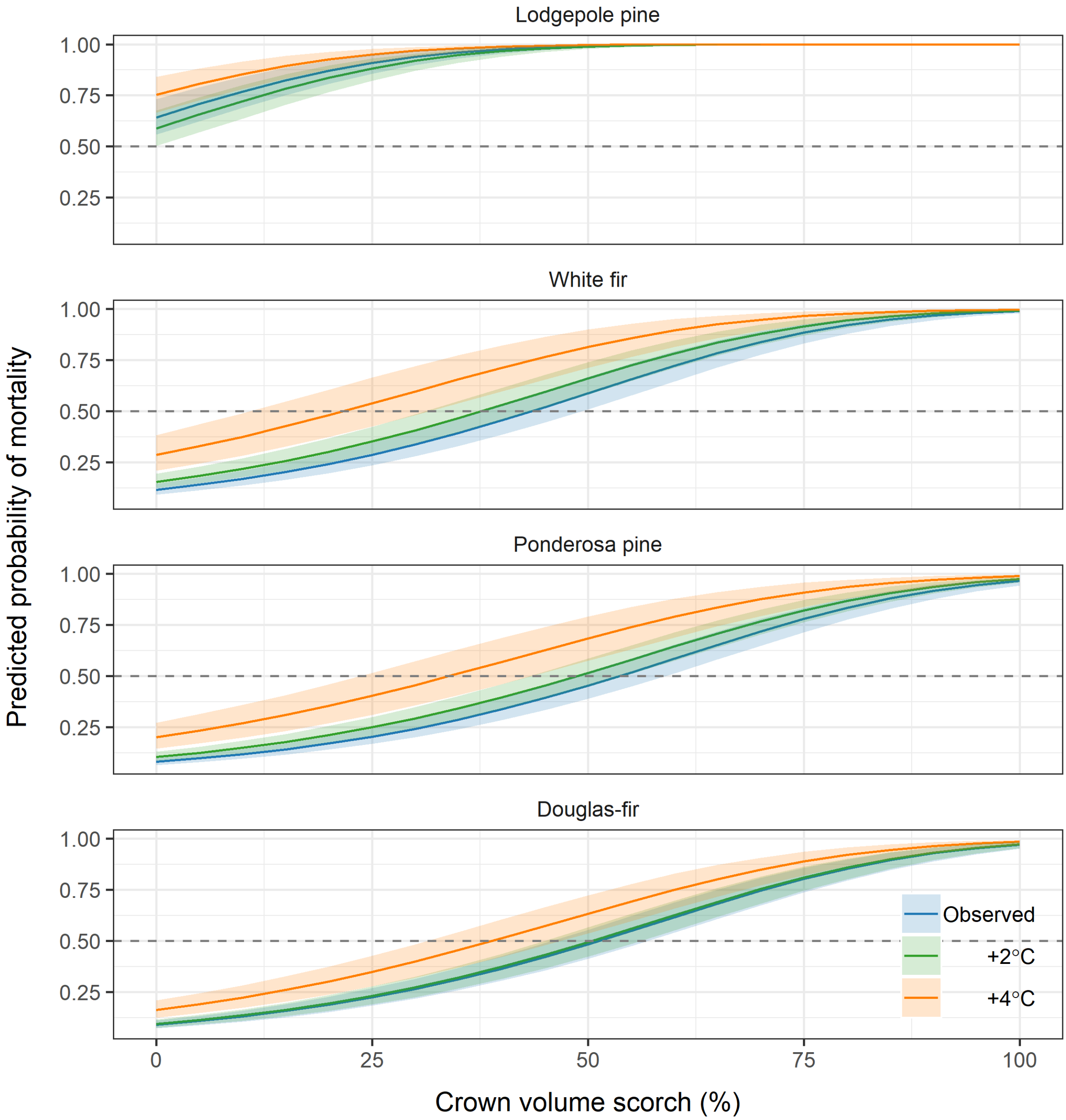

FIGURE 4 Predicted probabilities of tree mortality within 5 years of fire across the range of percent crown volume scorch for observed 1-year pre-fire + year of fire climate water deficit anomalies (blue), anomalies under +2°C (green), and +4°C (orange) warming scenarios. Shaded areas show 95% credible intervals, specifically the 2.5 and 97.5 percentiles of the predicted probabilities from 2000 draws of the posterior. Separation of the confidence bands illustrates the interaction between climate and fire-caused injury. Note that the confidence bands for the observed and +2°C scenarios overlap for Douglas-fir. Additional parameters including tree bark thickness and the presence or absence of bark char contributed to the variability. A probability of mortality ≥0.50 indicates a tree is more likely to die than survive within 5 years of the fire.

probabilities of mortality under current climates. White fir's P_m increased under both the +2 and +4°C scenarios, with white fir more likely to die from lower CVS levels under the mean change for +4°C scenario than Douglas-fir with the same BT (Appendix S1: Table S4). Ponderosa pine becomes more likely to die given the same level of CVS than Douglas-fir under the +4°C scenario (Figure 4; Appendix S1: Figure S11).

Projected impacts of future climate vary regionally

The potential effect of warming on post-fire tree mortality varied regionally in our analyses. Using down-scaled climate projections across the western United States (Abatzoglou et al., 2018), 30-year mean CWD under the +2°C scenario increases in some regions and decreases in others, but under the +4°C scenario, a drastic increase in CWD is predicted for the Southwestern United States (Appendix S1: Figure S10). To illustrate the projected responses, we mapped CVS P_{m50} for each fire location for median sized trees of each species for observed CWD, +2°C, and +4°C scenarios (Figure 5). The maps of fire-scale predictions of CVS P_{m50} show that for Douglas-fir, ponderosa pine, and white fir, predicted

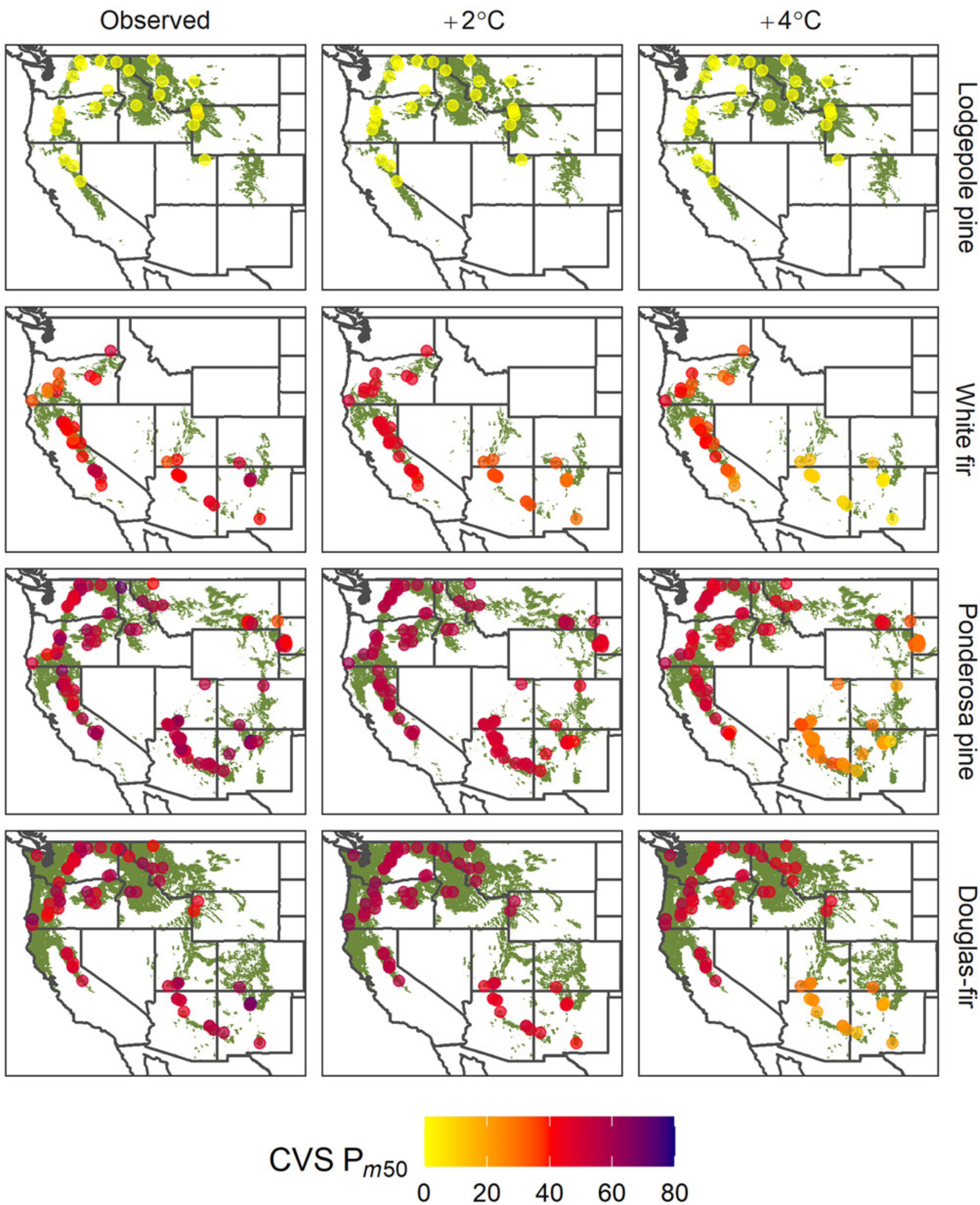

FIGURE 5 Legend on next page.

increases in CWD will decrease species resistance to fire. In other words, lower levels of CVS under a +4°C future climate will result in increased post-fire tree mortality compared to observed climate. CWDs are predicted to decrease, instead of increase, under the +2°C scenario in some parts of the Pacific Northwest (Appendix S1: Figure S10), resulting in predicted increases of CVS P_{m50} compared to the observed period for that region. This is contrasted by the predicted decrease in CVS P_{m50} in the southwest and Central Rockies, with the CVS P_{m50} >40% in most fire locations, reflecting the increase in CWD projected in that region. The larger increases in CWD projected under the +4°C scenario (Appendix S1: Figure S9)—particularly for the Southwestern United States (Appendix S1: Figure S10)—translated to large decreases in CVS P_{m50}. Corresponding figures for smaller (Appendix S1: Figure S12A) and larger trees (Appendix S1: Figure S12B) indicate that the greater overall sensitivity of smaller trees to CVS, and their small size means that they are also more sensitive to CWD.

DISCUSSION

Our results show how resilience of western North American conifer forests to fire may erode under climate change (Coop et al., 2020; Falk et al., 2022). Specifically, our results demonstrate that pre-fire drought can exacerbate post-fire delayed tree mortality, thereby increasing fire severity independent of fire intensity and associated direct fire-caused injuries. Because the distance to seed source and surviving tree cover are important determinants of post-fire conifer regeneration (Davis et al., 2023), our results also have implications for post-fire recovery of conifer forests in western North America. Increases in drought increase fire severity, as measured by post-fire tree mortality—an effect that amplifies under future climate projections. As climatic stress increases, Douglas-fir, ponderosa pine, and white fir with moderate crown scorch levels are less likely to survive. Our results expand on previous work (Barker et al., 2022; Furniss et al., 2020; van Mantgem et al., 2013) by showing that the implications of drought stress and fire-caused injury interactions differ among species across subcontinental scales.

Incorporating drought stress improves post-fire mortality predictions. Projected increases in CWD resulted in high levels of predicted tree mortality under the +4°C scenario, but we urge caution in applications of +4°C scenario projections because CWDs under that scenario were sometimes outside the ranges of observed CWD anomalies (Appendix S1: Figure S9). The purpose of tree mortality projections under the future climate scenarios was to put the effect of CWD on mortality in the context of current and possible future conditions. Nevertheless, under future projected climates, it may become necessary to incorporate climatic information into predictive models of post-fire tree mortality to achieve acceptable prediction accuracy. These extreme predictions will test empirical data, arguing for greater attention to process-based modeling approaches.

Pre-fire drought more strongly influences tree mortality than post-fire drought, in agreement with van Mantgem et al. (2013), although some (approximately 8%) of the same data were used in both studies. Models using post-fire climate variables had less support, in contrast to Barker et al. (2022), who found that moisture stress over a 10-year post-fire period had a weak positive association with mortality of trees that had high levels of crown injury, but also had a negative association with trees that had low levels of crown injury. Our exploratory RF models showed support for both pre- and post-fire CWD anomaly, although support for pre-fire CWD anomaly was stronger. As pre- and post-fire CWD anomaly were correlated, we opted to use only pre-fire CWD anomaly for our analyses. Future research using observations of pre-fire non-drought—post-fire drought combinations, for which we only had a small sample, would allow for a more robust assessment of post-fire drought and fire interactions on tree growth and mortality. However, this is a rare combination of conditions because cool, wet pre-fire conditions rarely lead to large

FIGURE 5 Maps illustrating the sensitivity to fire-caused injury, as indicated by the CVS P_{m50}, which is the percent crown volume scorched (CVS) at which the predicted probability of mortality = 0.50, for a medium-sized tree of each species under observed pre-fire climatic water deficit (CWD) anomalies and for +2°C (middle), and +4°C (right) warming scenarios. dbh of medium-sized trees: Douglas-fir = 31 cm; lodgepole pine = 19 cm; ponderosa pine = 25 cm; white fir = 30 cm. Appendix S1: Table S3 has additional summary statistics for each scenario. Lower CVS P_{m50} values (warmer colors) indicate that lower fire-caused injury results in tree mortality, due to decreased physiological fitness resulting from pre-fire moisture stress. Maps for small and large trees are shown in Appendix S1: Figure S12. Tree observations used to develop the model (n = 66,278) were from the Fire and Tree Mortality database (Cansler, Hood, Varner, et al., 2020a, 2020b), and CWD data and future projections at each fire location (n = 154) were from TerraClimate (Abatzoglou et al., 2018). Appendix S1: Figures S5 and S6 show predicted changes for small and large trees, respectively. Predictions were made using the median of the posterior for each parameter.

fire years in most conifer forests, with the exception of grass-dominated fuel beds (Littell et al., 2009).

Climate–fire-caused tree injury interactions are one of the many interactions between drought, fire, and vegetation across varying spatial and temporal scales. In temperate forests in North America, high-severity fire is driven by fuel aridity before and during fire and weather conducive to extreme single-day fire spread events (Coop et al., 2022; Parks & Abatzoglou, 2020). In our tree-scale models, some interactions between warm and dry pre-fire conditions, fire behavior, and resulting fire severity are implicit in the measured CVS: Greater fire intensity (unmeasured energy release) causes more crown consumption and scorch (measured fire injuries), and thus greater tree mortality (measured fire severity). Other interactions between drought and fire-caused injury are explicit: The models show that given the same level of CVS, warm and dry pre-fire conditions lead to higher tree mortality. Changes in fuel moisture may also affect root damage (Varner et al., 2007), which is only infrequently measured and not captured in this study. However, changes in fuel moisture are related to short-term fire weather (days or weeks prior to ignition) rather than longer term climatic conditions used in this study (1-year pre-fire and year-of-fire average conditions).

Tree mortality has been conceptualized as a process in which trees decline due to compounding stress from many factors (Axelson et al., 2020; Franklin et al., 1987; Manion, 1987). The conceptualization of mortality as resulting from a "decline spiral" is useful, although empirical support for "mortality syndromes"—specific groupings of contributing mortality agents—has been difficult to find (Das et al., 2016). There is substantial support that multiple stressors—competitive stress for water and light, bioclimatic setting, fungal pathogens, defoliators, and bark beetles—jointly contribute to tree mortality (Axelson et al., 2020; Breshears et al., 2018; Das et al., 2016; Franklin et al., 1987; Furniss et al., 2022; Manion, 1987). We have quantified the expressed impact of drought stress and fire-caused injury on tree mortality, but we do not quantify the impact of competition, bioclimatic setting, and biotic agents. Untangling the explicit roles of these interacting factors on tree mortality across large ranges of common species presents a challenge for future research. Future field-based research that includes collection of detailed information on factors that contribute to individual tree mortality is needed to continue improving our ecological understanding of tree mortality processes and to better inform predictive modeling and management of future fires and droughts.

The role of biotic agents under future climates is particularly uncertain. Our large sample of fires occurring over 32 years likely captures post-fire conditions over a range of bark beetle population pressures (Cansler, Hood, Varner, et al., 2020b). Importantly, the data included in our analysis were from trees that had some level of fire-caused tree injury and died after fire; any bark beetle attacks that occurred before fire were not included in the FTM database. Therefore, we know that fire contributed to observed mortality for all trees. While elevated bark beetle activity during drought coincident with fire may account for some of the elevated mortality risk captured in our model, it is unlikely that our results are driven solely or primarily by bark beetle outbreaks. Bark beetle–caused tree mortality has fluctuated greatly and asynchronously with fire-caused tree mortality over the 1985–2015 window of our study period (Hicke et al., 2016). Mountain pine beetle populations were elevated in the 1980s, declined in the 1990s, and then rose again in the mid-2000s (Raffa et al., 2008), while other western bark beetle outbreaks caused significant mortality in the mid-2010s (Fettig et al., 2022). Even when outbreaks occur, their impacts vary greatly across host ranges (Jarvis & Kulakowski, 2015).

Uncertainty in future predictions is due to uncertainty in the interactions between climate change and bark beetle population dynamics. Drought is an inciting factor for outbreaks of some species of bark beetles (Kolb et al., 2016; Raffa et al., 2008). Thus, it is possible that bark beetles may elevate mortality in fire-injured trees to a greater extent than is predicted by our model under future climates. Conversely, not all droughts are associated with outbreaks and drought-induced tree mortality also occurs in the absence of bark beetles (Adams et al., 2017). Bark beetle populations do not have a simple positive linear relationship with warmer and drier climates, and there may also be elevational and regional decreases in bark beetle activity in response to climatic changes (Bentz et al., 2010, 2016; Littell et al., 2010). The factors involved in initiating eruptive population increases are complex, with large uncertainties about how future climate will alter tree defenses and bark beetle fecundity that deserve further investigation (Anderegg et al., 2015; Bentz et al., 2010; Kolb et al., 2016).

We expected that due to interspecific trait variation (e.g., BT, bud size, hydraulic resistance to cavitation), there would be differences in species' ability to withstand both fire injury and climatic stress (Choat et al., 2012; Dickman et al., 2023; Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018; Piñol & Sala, 2000; Varner et al., 2021). The relative resistance of the four conifer species we evaluated to post-fire mortality matches known fire resistance traits (Stevens et al., 2020), revealing that under current climate, ponderosa pine is most resistant to fire, followed closely by Douglas-fir and white fir, while lodgepole pine is least resistant (Appendix S1:

Figure S11). Ponderosa pine produces thick bark rapidly with increasing tree size, self-prunes lower branches, and has protected buds, allowing the trees to regrow even when needles are entirely scorched (Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018). These traits allow ponderosa pine to survive higher CVS levels than the other species we examined. Douglas-fir and white fir have slower bark accumulation (but do develop thick bark when large), smaller buds more vulnerable to heating, and they are more shade tolerant, so do not self-prune to the extent ponderosa pine does (Stevens et al., 2020). The low resistance of lodgepole pine to fire is reflective of its different fire tolerance strategy than the other three species tested, which is to maximize regeneration ability after fire through serotinous cones (Schwilk & Ackerly, 2001). The importance of the species term in the model may also reflect inaccuracies in modeling BT based on a linear relationship with tree diameter (Pausas, 2015). For example, ponderosa pine and Douglas-fir have the same BT scaling coefficient in the first order fire effects model (FOFEM; Reinhardt & Dickinson, 2010)—used for prediction here—but Rodman et al. (2020) report that ponderosa pine produces thicker bark and more rapid height growth when young than Douglas-fir, conferring higher resistance to fire earlier in life. These ontogenetic differences and other species' traits (e.g., protected buds, bark rugosity, leaf/needle flammability, and xylem hydraulic properties) result in species-specific differences in fire responses (Bär et al., 2018, 2021; Dickman et al., 2023; Frejaville et al., 2013; Niccoli et al., 2023; Pile et al., 2017; Shearman & Varner, 2021; Stevens et al., 2020; Varner et al., 2022).

Studies of drought-induced tree mortality can provide insight into traits likely associated with resistance to fire. O'Brien et al. (2017) synthesize important species traits and environmental variables predictive of drought-induced tree mortality. In the temperate forests of our study, wood density, growth rate, point of 50% loss of hydraulic conductivity (P_{50}), leaf specific hydraulic conductivity (k_l), xylem architecture, and nonstructural carbohydrates are important drought resistance traits for conifers, while topography, site water content, and stem density are important environmental factors (O'Brien et al., 2017). Although less intensively studied, many of these traits have also been linked to resistance to fire. Repairing fire-caused injuries can reduce nonstructural carbohydrates (Reed & Hood, 2024) and compromise future defenses to fire-caused injuries (Pile et al., 2017; Varner et al., 2009). Fire can reduce hydraulic conductivity and P_{50} thresholds, making trees more vulnerable to future droughts (Bär et al., 2018; Partelli-Feltrin et al., 2020; West et al., 2016). Less is known about the physiological effects of pre-fire drought stress on long-term tree survival, but long-term moisture stress has been linked to increased vulnerability to mortality (Keen et al., 2022; Young et al., 2017). Based on studies of physiological effects of moisture stress, it is logical that the combination of pre-fire climatic moisture stress combined with fire-caused injuries would lead to increased tree mortality after fire as we observed. However, our data are not suitable for exploring these mechanisms of fire resistance and further research is needed, especially for predicting how species' resistance to fire may change under future climates. For example, our results suggest that under future climate conditions, ponderosa pine goes from being more resistant to CVS than Douglas-fir to slightly less resistant (Figure 4; Appendix S1: Figure S11). This deserves further exploration to confirm this pattern, to determine what mechanisms govern such shifts, and to be able to incorporate such changes into predictive models of post-fire tree mortality. Additionally, species-scale information may not account for all differences in traits, as there may be variation in genotypic and phenological sensitivity to both fire injury and moisture stress (Bär et al., 2021; Bär & Mayr, 2020). Future research could integrate intraspecific trait variation and draw on observations that cover the full geographic range of each species, allowing differences between genotypes and leading edge versus trailing edge sensitivity to climatic water stress to be assessed.

This study focused on four common conifers, but there is a great deal of variation in traits associated with tolerance to moisture stress and fire among tree species. How duration and intensity of droughts influence tree vigor and mortality varies based on physiological traits (Partelli-Feltrin et al., 2021). The impacts of fire are influenced by species traits related to flammability, resistance to heat injury, and ability to recover from injury (Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018; Partelli-Feltrin et al., 2021; Stevens et al., 2020). Angiosperms, not represented in this study, employ a range of strategies for surviving drought (Skelton et al., 2021), but as a group may be more susceptible to immediate damage to their xylem, yet also may be able to better repair damage (Choat et al., 2012). Likewise, the ability of many angiosperms to resprout decreases susceptibility to mortality from drought (Zeppel et al., 2015). Future research addressing interactions between drought and fire-caused injuries to determine tree survival or mortality should target a range of species covering a wider variety of drought-adapted and fire-adapted traits to understand how timing, intensity, and duration droughts—in combination with different types and levels of fire-caused injury—vary in response to species traits (Zylstra, 2021). Efforts could also incorporate data from trees that burned in recent record droughts in the western United States (post-2016) and more broadly across the planet where plant responses may differ from those of the temperate conifers documented here. Better elucidation of the physiological mechanisms influencing sensitivity to drought–fire interactions could lead to more fine-tuned post-fire climate adaptation strategies (Knapp et al., 2021; van Mantgem et al., 2021).

Management applications

Predictive modeling at stand, regional, and global scales

The interaction between warm and dry pre-fire climates and fire severity is unaccounted for in current tree, stand, landscape, or global simulations (Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018), confounding estimates of post-fire tree mortality, turnover between live and dead carbon pools, and overall forest resilience to fire. As we move into more anomalous climates, the limitations of empirical models, such as the one presented here, may become evident. Process-based models allow for exploration of the effects of moisture stress and drought on ecosystem processes (Kennedy et al., 2021; Thonicke et al., 2010), but their development is still dependent on and informed by observations. Thus, advancements to mechanistic models are likely to proceed in parallel with empirical research. Additional ecophysiological research that directly links fire-caused tree injury and plant moisture stress to physiological responses is needed to further develop more accurate process-based models (Dickman et al., 2023; Niccoli et al., 2023). Including interactions between pre-fire droughts and fire-caused injury in dynamic global vegetation models would allow broader hypothesis testing of how changes in climate may differentially affect post-fire mortality across regions and ecosystems. Earth system models and some landscape models predict post-fire mortality values within large grid cells (0.5°–2.5°) for tree cohorts using a simplified approach with constant parameters for scorch height and BT based on broad plant functional types or species groupings (Thonicke et al., 2010). We show that vulnerability to fire-caused injury and pre-fire climatic stress varies between our three thicker barked conifer species. Thus, regional and global simulation models could likely be better structured and parametrized if clearer linkages were made between fire- and drought-resistant plant traits—and their variation both across and within species—and the types and levels of fire-caused injury and moisture stress that lead to survival or mortality (Hantson et al., 2016).

Including pre-fire climate information when modeling post-fire tree mortality can also inform post-fire land management (Hood, Ilana, et al., 2018; Hood, Varner, et al., 2018; Larson et al., 2022). Post-fire salvage logging and hazard tree removal prescriptions are usually developed based on predictive modeling of immediate and delayed tree mortality, the accuracy of which would be improved if pre-fire climate information was incorporated—the importance of which will increase as drought intensifies with global climate change. The interactions between warm and dry pre-fire climates and fire-caused injury we document here have important implications for understanding tree mortality from prescribed burns, especially now when the United States is increasingly implementing prescribed burning as a tool to reduce fuel hazard and increase forest resilience (USDA, 2022).

Climate change adaptation

Our results show that pre-fire moisture stress contributes to post-fire tree mortality, particularly for smaller trees and trees with intermediate levels of fire-caused injury. We did not find evidence that larger or very large trees were more sensitive to pre-fire moisture stress, as has been found in studies focusing on hydraulic stress alone (Bennett et al., 2015). Fortunately, the scientific basis of management actions to moderate fire behavior, and thus reduce injury to trees and associated mortality (e.g., fire severity), is mature (Hessburg et al., 2019, 2021; Prichard et al., 2021). In dry, frequent-fire forests, there is strong evidence that reduction of surface fuel loadings, especially through prescribed fire, either alone or in combination with thinning, is an effective method of reducing mortality of mature trees and landscape-scale fire severity (Cansler et al., 2022; Kalies & Yocom Kent, 2016). Prescribed fire and thinning can increase tree growth even during droughts (Zald et al., 2022). Likewise, prescribed fire and thinning increase tree resistance to mortality from biotic causes (Crotteau et al., 2020; Hood et al., 2016) and could offset carbon losses from high-severity wildfires (Fargione et al., 2018). Silvicultural treatments and previous fires can increase tree resistance to subsequent bark beetle attacks (Hood et al., 2016; Knapp et al., 2021) and drought (Steel et al., 2021; van Mantgem et al., 2021) due to increased fire-induced defenses (Hood et al., 2015, 2016), lower tree density, and less competition for water (Furniss et al., 2020, 2022; Sturdevant et al., 2022). The details of treatment implementation matter, though. For example, prescribed fire can decrease tree growth by causing injury to surviving trees or can increase growth by decreasing local-neighborhood competition (Wenderott et al., 2022). In other cases, prescribed fire may not cause enough tree mortality to reduce density and decrease competition, resulting in negligible increases in growth compared to thinning, either alone or in combination with prescribed fire (Zald et al., 2022). Post-fire drought stress and long distances to conifer seed sources have been linked to low post-fire regeneration of conifers (Davis et al., 2019, 2023; Kemp et al., 2019; Povak et al., 2020; Stevens-Rumann & Morgan, 2019). Thus, reductions in post-fire tree mortality could improve the likelihood of post-fire conifer regeneration by retaining seed sources (Davis et al., 2023; Wolf et al., 2021). Therefore, in dry conifer forests of western North America, the greatest opportunity to reduce post-fire tree mortality and increase post-fire resilience is through management that reduces potential fire intensity, thus limiting injury to tree crowns.

Climate change mitigation

We found large, meaningful differences in predicted post-fire tree mortality between the +2 and +4°C warming scenarios, with dramatic declines in resilience in the Southwestern United States for the latter. Our results illustrate that limiting warming below 2°C could help avoid amplifying the feedback between stress caused by warm and dry pre-fire climates and fire-caused injury, which would reduce carbon storage through additional tree mortality.

AUTHOR CONTRIBUTIONS

Conceptualization, data curation, methodology, formal analysis, visualization, writing—original draft, and writing—review and editing: C. Alina Cansler. *Conceptualization, methodology, formal analysis, visualization, writing—original draft, and writing—review and editing*: Micah C. Wright. *Conceptualization, methodology, formal analysis, writing—original draft, writing—review and editing, and funding acquisition*: Phillip J. van Mantgem. *Methodology and writing—review and editing*: Timothy M. Shearman. *Conceptualization, writing—original draft, writing—review and editing, and funding acquisition*: J. Morgan Varner. *Conceptualization, data curation, methodology, visualization, writing—original draft, writing—review and editing, project administration, supervision, and funding acquisition*: Sharon M. Hood.

ACKNOWLEDGMENTS

We acknowledge funding from the Joint Fire Science Program under project JFSP 16-1-04-8, U.S. Forest Service Forest Health Protection, U.S. Forest Service Rocky Mountain Research Station, and U.S. Geological Survey's Ecosystems Mission Area. Maureen C. Kennedy, Donald McKenzie, Andrew J. Larson, and two anonymous reviewers provided constructive feedback that greatly improved this paper. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Individual tree observation data (Cansler, Hood, Varner, et al., 2020a, 2020b) are available from the Fire and Tree Mortality Database (FTM): https://doi.org/10.2737/RDS-2020-0001-2 and https://doi.org/10.1038/s41597-020-0522-7. Climate observations and climate projections (Abatzoglou et al., 2018) were drawn from monthly data from TerraClimate: https://doi.org/10.1038/sdata.2017.191.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Cansler, C. Alina, Micah C. Wright, Phillip J. van Mantgem, Timothy M. Shearman, J. Morgan Varner, and Sharon M. Hood. 2024. "Drought before Fire Increases Tree Mortality after Fire." *Ecosphere* 15(12): e70083. https://doi.org/10.1002/ecs2.70083