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Recent bark beetle outbreaks influence wildfire severity in mixed-conifer forests of the Sierra Nevada, California, USA

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Abstract. In temperate forests, elevated frequency of drought related disturbances will likely increase the incidence of interactions between disturbances such as bark beetle epidemics and wildfires. Our understanding of the influence of recent drought and insect-induced tree mortality on wildfire severity has largely lacked information from forests adapted to frequent fire. A recent unprecedented tree mortality event in California's Sierra Nevada provides an opportunity to examine this disturbance interaction in historically frequent-fire forests. Using field data collected within areas of recent tree mortality that subsequently burned in wildfire, we examined whether and under what conditions wildfire severity relates to severity of prefire tree mortality in Sierra Nevada mixed-conifer forests. We collected data on 180 plots within the 2015 Rough Fire and 2016 Cedar Fire footprints (California, USA). Our analyses identified prefire tree mortality as influential on all measures of wildfire severity (basal area killed by fire, RdNBR, and canopy torch) on the Cedar Fire, although it was less influential than fire weather (relative humidity). Prefire tree mortality was influential on two of three fire-severity measures on the Rough Fire, and was the most important predictor of basal area killed by fire; topographic position was influential on two metrics. On the Cedar Fire, the influence of prefire mortality on basal area killed by fire was greater under milder weather conditions. All measures of fire severity increased as prefire mortality increased up to prefire mortality levels of approximately 30–40%; further increases did not result in greater fire severity. The interacting disturbances shifted a pine-dominated system (Rough Fire) to a cedar–pine–fir system, while the pre-disturbance fir–cedar system (Cedar Fire) saw its dominant species unchanged. Managers of historically frequent-fire forests will benefit from utilizing this information when prioritizing fuels reduction treatments in areas of recent tree mortality, as it is the first empirical study to document a relationship between prefire mortality and subsequent wildfire severity in these systems. This study contributes to a growing body of evidence that the influence of prefire tree mortality on wildfire severity in temperate coniferous forests may depend on other conditions capable of driving extreme wildfire behavior, such as weather.

Key words: bark beetle; Dendroctonus*; disturbance interaction; fir engraver; mixed-conifer forest;* Scolytus*; tree mortality; western pine beetle; wildfire severity.*

Introduction

Drought-related disturbances are projected to increase in frequency in the future (Christensen et al. 2007, Intergovernmental Panel on Climate Change 2014, Seidl et al. 2017, Martinuzzi et al. 2019), leading to higher probability of disturbance interactions, where multiple disturbances occur on the same landscape within a short time period (Kane et al. 2017). Severity of drought related disturbances will likely increase with a changing climate as well (Seager et al. 2007, Allen et al. 2010, Millar and Stephenson 2015, Bowman et al. 2017), with severity defined here as the amount of biomass lost due to disturbance (Keeley 2009). Indeed, forests of western North America have already experienced elevated frequency and severity of two disturbances that can be caused or exacerbated by hot and dry conditions: widespread tree mortality due to drought and/or native bark beetle (Coleoptera: Curculionidae, Scolytinae) epidemics (Bentz 2009, van Mantgem et al. 2009, Allen et al. 2010, Asner et al. 2016) and severe wildfires (Miller et al. 2009*b*, Miller and Safford 2012). Resource managers are concerned about interactions between such climate-linked disturbances, out of fear of synergistic interactions whereby one disturbance exacerbates the effects of the next, and also because the ecological outcomes of such novel disturbance interactions within a changing climate are largely unknown.

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It is crucial that resource managers understand what factors lead to increases in fire severity over historical conditions so they can effectively utilize limited mitigation and prevention resources. Severe wildfires in areas adapted to largely low-severity fire can cause substantial changes to the landscape in the short and long term that affect biodiversity, soil stability, water quality, carbon balance, timber production, and recreational and aesthetic values (Maestrini et al. 2017, Underwood et al. 2018, Dove et al. 2020, Miller and Safford 2020). Until now, our understanding of the influence of recent drought- and insect-induced tree mortality on subsequent wildfire severity in western North America has been almost exclusively limited to mesic forests historically adapted to relatively infrequent, mixed- or high-severity wildfire (Hicke et al. 2012, Kane et al. 2017), but outcomes from those forests may not be directly applicable to drier forests intrinsically adapted to frequent, mostly low-severity fire (Stephens et al. 2018). We might expect difficulty detecting an effect of prefire dead canopy fuels on fire severity in a mesic forest adapted to infrequent, high-severity canopy fire, because the live forest was likely to burn at high severity anyway. Prefire tree mortality may affect fire severity more dramatically in a forest adapted to frequent, low-severity fire. Further, increases in fire severity in forests not adapted to large patches of high-severity fire (Steel et al. 2018) may have more serious consequences for ecosystem recovery than for their more mesic counterparts. A recent, unprecedented severe tree mortality event in the Sierra Nevada provides a novel opportunity to examine this relationship in frequent-fire forests.

Where severe bark beetle epidemics have been interacting with subsequent wildfires in the western United States for several decades (most prominently in the Rocky Mountains), a substantial body of research exists that examines the relationship between these disturbances. Most studies have not detected an increased likelihood of wildfire occurrence in bark beetle affected areas (Hart et al. 2015, Kane et al. 2017), but conclusions regarding effects on wildfire behavior and associated impacts to ecosystems (i.e., severity) are more nuanced. Some model predictions have found enhanced fire behavior (e.g., rate of spread, fire-line intensity, crown fire potential) in areas of recent tree mortality (“red phase,” when trees still support their dead leaves; Jenkins et al. 2008, Schoennagel et al. 2012, Sieg et al. 2017), which suggests fire severity would also be increased during this brief period. However, the few empirical studies of insect outbreaks and subsequent fire severity have either failed to find a significant effect (Bond et al. 2009, Harvey et al. 2013), found a negative effect (Meigs et al. 2016), or documented increased fire severity for a small minority of fire-severity metrics and only under limited but not consistent conditions (Harvey et al. 2014*a*,*b*, Andrus et al. 2016). Of these studies, only Bond et al. (2009) and Harvey et al. (2014*a*,*b*) separately address recent outbreaks (red phase) vs. older outbreaks (“grey phase,” when tree leaves and fine branches have been lost but large snags remain standing, or “tree-fall phase,” when large snags are falling to the forest floor), and none of them occurred under typical summer burning conditions in forests adapted to high frequency, low-severity fire.

The uncertain conclusions and paucity of empirical evidence regarding these interacting disturbances, combined with the novelty of severe drought- and insect-induced tree mortality events in dry mixed-conifer forests of California necessitate empirical research within these historically frequent-fire systems. To our knowledge, no field-based studies exist that examine the effects of severe tree mortality on wildfire severity in forests adapted to frequent, low-severity fire. Using data collected within areas of recent tree mortality that subsequently burned in wildfire, we examined whether and under what conditions wildfire severity relates to severity of recent prefire tree mortality in Sierra Nevada mixed-conifer forests. Using prefire conditions and fire-severity outcomes from two large, recent wildfires in the southern Sierra Nevada (2015 Rough Fire and 2016 Cedar Fire; California, USA), we sought to answer the following question: at the local (plot) level, does recent prefire tree mortality affect the severity of subsequent wildfires in Sierra Nevada mixed-conifer forests? Our overarching question is divided into three sub-questions. (1) Does prefire tree mortality influence wildfire severity, and what is the strength of its influence relative to topography, fire weather, and other aspects of vegetation? (2) Does the relationship between prefire tree mortality and fire severity depend on interactions with topography, fire weather, or vegetation characteristics? (3) How does the effect of prefire tree mortality on fire severity change as the severity of prefire mortality changes? We also quantify changes in dominant tree species composition resulting from these interacting disturbances.

Methods

Study site

The study was conducted within the postfire footprints of the ~60,000 ha 2015 Rough Fire and the ~12,000 ha 2016 Cedar Fire in the southern Sierra Nevada. Plots were located within the Sierra and Sequoia National Forests and the Giant Sequoia National Monument in mixed-conifer forest. Study sites were selected because they qualitatively represent typical dry mixed-conifer forest conditions of the Sierra Nevada in terms of management history and dominant vegetation, and because they encompass areas of tree mortality suitable for our study (see *Data collection*).

The forest type in the study area is mixed-conifer (North et al. 2016, Safford and Stevens 2017) and is dominated by white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and incense cedar (*Calocedrus decurrens*). Other common tree species include sugar pine (*P. lambertiana*) and California black oak (*Quercus kelloggii*). Prior to the drought and fire disturbances, the shade-intolerant ponderosa pine was the most common canopy tree species on the Rough Fire plots, and the shade-tolerant white fir was the most common canopy tree on the Cedar Fire plots. Stand basal area and plot-level tree density were slightly higher on the Cedar Fire than the Rough Fire (Table 1). Regional climate is of the Mediterranean type, with cold wet winters and warm dry summers, and the mean annual precipitation of ~108 cm falls mostly between November and May, with approximately equal amounts of rain and snow (Minnich 2007). Elevations ranged from 1,138 to 2,140 m on the Rough Fire (median = 1,702 m, average = 1,616 m), and on the Cedar Fire ranged from 1,604 to 2,330 m (median = 2,007 m, average = 1,982 m; Table 1). Slopes were variable but Cedar Fire plots had slightly steeper average and maximum slopes than Rough Fire plots (Table 1). Soils at both study sites are formed largely from granitic substrates and are typically moderately deep to deep and well drained, with some shallow, excessively well-drained soils on the Cedar Fire site (Giger and Schmitt 1983, Hanes et al. 1996, Soil Survey Staff 2019). Rock outcrops are occasional to common.

Mean fire-return intervals for Sierra Nevada mixed-conifer before Euroamerican settlement were between ~10 and 20 yr (Van de Water and Safford 2011) but the area was subject to cessation of native burning practices and fire-suppression policies beginning in the late 19th and early 20th centuries. Fire suppression and timber harvest generally led to increased tree densities, fewer large trees, a shift in species composition toward less fire-tolerant and more shade-tolerant species (Parsons and Debenedetti 1979, Collins et al. 2017, Safford and Stevens 2017), and a more homogeneous tree spatial arrangement (Lydersen et al. 2013). These changes in forest composition and structure have led to higher competition for water, greater potential drought stress, and susceptibility to bark beetle outbreaks (Young et al. 2017), and a fire regime that is characterized by notably less fire, but much more severe fire when it occurs, meaning greater loss of live biomass, than under conditions before Euroamerican settlement (Safford and Stevens 2017).

At the time of the Rough and Cedar Fires, much of California, including the southern Sierra Nevada, was experiencing its fourth and fifth consecutive years of severe drought. Tree mortality increased during each year of the drought but 2015 and 2016 saw extremely elevated levels of tree mortality statewide (an estimated 27.6 million trees died in 2015 and 62 million trees in 2016), and the southern Sierra Nevada was the region with the highest levels of mortality (Moore et al. 2016, 2017). Aerial detection surveyors attributed most of the prefire conifer mortality within both fire perimeters to mortality agents shown in Table 2 (USDA Forest Service Pacific Southwest Region 2018*a*).

Table 1. Plot-level predictor variables included in the random forest models for the 2015 Rough Fire (n = 50) and 2016 Cedar Fire (n = 130; California, USA).

Variable	Type	Rough Fire range (continuous) or observed values (categorical)	Cedar Fire range (continuous) or observed values (categorical)	Rough Fire mean (continuous) or mode (categorical)	Cedar fire mean (continuous) or mode (categorical)
Prefire tree mortality (plot-level percentage of prefire red-phase dead tree basal area) (%)	continuous	0–100	0–100	32.4	27.2
Elevation (m)	continuous	1,138–2,180	1,604–2,330	1,658	1,980
Slope (%)	continuous	4–59	8–80	31	42
Topographic position	categorical	valley bottom, lower, middle, upper, ridgetop	lower, middle, upper, ridgetop	middle slope	middle slope
Topographic relative moisture index (0 = xeric, 60 = mesic)	continuous	12–51	12–45	27	28
Relative humidity, RH (%)	continuous	15–32	12–29	20	16
Estimated prefire shrub cover % (0–10, 11–30, 31–60, 61–80, 81–100)	categorical	0–100	0–60	0–10	0–10
Live + dead tree density (no. trees ≥ 25 cm DBH in 0.04 ha plot)	continuous	2–21	4–25	7.4	9.7
Stand basal area (m^2/ha)	continuous	14–119	23–115	45	58
Dominant tree genus	categorical	*Abies*, *Calocedrus*, *Pinus*	*Abies*, *Calocedrus*, *Pinus*	*Pinus*	*Abies*
Ladder fuel density (no. trees >1.37 m tall and <25 cm DBH in 0.04 ha plot)	continuous	not sampled	0–56	not sampled	11.2
Presence in 1990 Stormy Fire footprint	categorical	not applicable	yes, no	not applicable	no

TABLE 2. The four insects most commonly listed as conifer mortality agents prefire (2010 through year of fire) within the 2015 Rough and 2016 Cedar Fire perimeters in the USDA Forest Service Aerial Detection Survey data set (USDA Forest Service Pacific Southwest Region 2018*a*), listed in descending order of mapped area.

Common name	Scientific name	Host species in study area
Western pine beetle	*Dendroctonus brevicomis*	*Pinus ponderosa*
Mountain pine beetle	*D. ponderosae*	*P. ponderosa*, *P. lambertiana*, *P. contorta*
Fir engraver	*Scolytus ventralis*	*Abies concolor*, *A. magnifica*
Jeffrey pine beetle	*D. jeffreyi*	*P. jeffreyi*

Note: Mortality of incense cedar was attributed to drought.

Twenty-eight of the 130 Cedar Fire plots were within the footprint of the 1990 Stormy Fire, which overlaps the eastern portion of the Cedar Fire footprint. Three of those plots occurred where the Stormy Fire burned at high severity (measured by remote sensing of biomass loss, specifically basal area mortality [Miller et al. 2009*a*]), five were where the vegetation was designated as unchanged by the Stormy Fire, and the remainder were in areas of low or moderate severity (USDA Forest Service Pacific Southwest Region 2018*b*). Almost all (24) of the plots burned by the Stormy Fire burned at high severity in the Cedar Fire. Four plots that burned in the Stormy Fire burned in 1924, but no other Cedar Fire plots were documented to have burned since 1878 (CA Dept. of Forestry and Fire Protection Fire and Resource Assessment Program 2018).

Most plots in the Rough Fire burned in wildfires in 1928 and/or 1955, but none were documented to have burned more recently (CA Dept. of Forestry and Fire Protection Fire and Resource Assessment Program 2018). In the Rough Fire, 32 plots burned at high severity, 14 at moderate severity, and 4 at low severity (USDA Forest Service Pacific Southwest Region 2018*b*).

Plots on the Rough Fire were distributed across seven burn dates from 24 August through 11 September 2015, and on the Cedar Fire across seven burn dates from 17–24 August 2016. Red flag warnings were not issued for any of these burn dates (Iowa State University Mesonet, *available online*),[4] but the majority of plots on both fires burned on days with rapid fire spread and large increases in area burned. Mean weather variables for each fire are shown in Table 3.

Data collection

Research plot centers were randomly selected from a grid of points with 400 m spacing constrained by the following criteria: (1) within 400 m of areas of conifer mortality (minimum 25 dead trees/ha) documented within 2 yr prior to fire by U.S. Forest Service Aerial Detection Surveys (Moore et al. 2016, 2017), to ensure plots were located in landscapes experiencing highly elevated tree mortality; (2) a minimum of 100 m from roads and postfire salvage harvesting; (3) outside of areas where prescribed burns or other direct fire-fighting activity occurred during the Rough and Cedar Fires, as determined through personal communications with U.S. Forest Service personnel; and (4) outside of riparian areas. The Rough Fire had additional accessibility constraints such as extremely steep slopes and areas without road access, and these areas were excluded from sampling.

Data were collected in late spring through mid-summer approximately 1 yr following wildfire, i.e., in 2016 on the Rough Fire (50 plots) and in 2017 on the Cedar Fire (130 plots). At each 11.3 m radius (~0.04 ha) circular plot, surveyors recorded aspect, slope, topographic position, an estimate of prefire shrub cover based on shrub stumps remaining postfire, and stand-level tree basal area using a 20 factor gauge (Table 1). We measured the following variables on all trees ≥25 cm (9.8 inch) diameter at breast height (DBH) on the 130 Cedar Fire plots and up to 10 randomly selected trees ≥25 cm DBH on the Rough Fire plots: tree species, DBH, percentage of tree crown that was torched (needles or leaves were consumed by fire), and mortality status (Table 4). On the Cedar Fire, we also recorded ladder fuel density, or the number of trees ≥1.37 m tall (4.5 feet) and <25 cm DBH. Only six out of 50 plots on the Rough Fire had >10 trees eligible for sampling, and the number of trees not sampled was recorded.

We worked with the USDA Forest Service (B. Bulaon, Forest Health Protection) to adapt established methods of determining mortality status (Harvey et al. 2013) to mixed-conifer forests under recent and current insect attack (Table 4). Surveyors observed all visible parts of trees for signs of insect infestation (boring dust, pitch tubes, etc.) using binoculars if necessary, and for dead or dying trees, removed bark samples to examine the cambium and inner bark for possible insect galleries. Mortality status of each tree was assigned according to the following categories: (1) dead ≥3 yr prior to fire (highly weathered/decayed), (2) red-phase dead at the time of fire (trees retaining red needles at the time of fire) due to recent insect attack, (3) red-phase dead at the time of fire without evidence of insect attack, (4) live at the time of fire and killed by fire, (5) live at the time of fire and subsequently killed by insects, (6) under insect attack but still retaining green needles at time of sampling, and (7) live at sampling, no evidence of insect attack, (8) unknown. See Appendix S1 for details on the numerous checks we conducted to ensure our classifications were accurate and that possible misclassifications would not

[4] https://mesonet.agron.iastate.edu/

TABLE 3. Summary of weather data for plot burn dates on the Rough and Cedar Fires, showing the mean daily value across sampled burn dates and the range of daily values in ().

Weather variable	Rough fire	Cedar fire
Air temperature	30.6 (23.3–33.9)°C, 87.0 (74.0–93.1)°F	30.2 (26.4–32.8)°C, 86.4 (79.6–91.1)°F
Relative humidity	22.6% (14.5–29.9)%	19.7% (12.2–29.0)%
Mean wind speed	5.0 (3.9–5.8) km/h, 3.1 (2.4–3.6) mi/h	11.2 (8.9–13.7) km/h, 7.0 (5.5–8.5) mi/h
Peak wind speed	13.0 (11.9–14.6) km/h, 8.1 (7.4–9.1) mi/h	24.5 (20.8–27.5) km/h, 15.2 (12.9–17.1) mi/h
10-h fuel moisture	5.1% (3.9–7.0)%	not available

Notes: Daily values are averaged from daytime hourly data obtained from the portable Remote Automated Weather Station installed within the 2015 Rough Fire perimeter and the four nearest permanent weather stations to the 2016 Cedar Fire (Johnsondale, River Kern, UHL/Hot Springs, and Wofford Heights).

TABLE 4. Criteria for designating mortality status of trees in the field postfire.

Category	Name	Criteria
1	older dead (gray phase)	dead at the time of sampling, highly decayed sapwood, char (if present) extends deep into sap or heartwood, cambium is fully dried, cambium surface molds dead and dry
2	recently dead prefire, killed by bark beetles (red phase)	dead at the time of sampling, BB (bark beetle) exit holes visible on bark but no postfire boring, dust present on charred bark, BB galleries underneath bark with few to no adults or brood present, woodpecker flecking on bark is charred (i.e., woodpecker activity occurred prefire)
3	recently dead prefire, not killed by bark beetles (red phase)	dead at sampling, no evidence of BB, cambium intermediate between moist and dry
4	killed by fire	dead at sampling, no BB galleries present under bark and no other evidence of BB, *or* displays signs of postfire BB activity in category 5 (below) but canopy torch is >95%, could be infested with woodborers or other insects known to attack dead trees, could have red turpentine beetle, cambium moist
5	killed by bark beetles postfire	infested with BB, with gallery development, boring dust, or resin on top of char, Woodpecker activity post-fire, revealing colored bark underneath flecked off char, may have associated woodborer evidence and/or RTB, canopy torch ≤ 95%, otherwise designated as killed by fire, regardless of postfire BB evidence
6	under current attack (green attack)	live at sampling (defined as having any green needles present), some crown fade may be present, evidence of current BB activity, e.g., fresh pitch tubes, clear pitch streaming, BB galleries with live adults or brood
7	no attack	live at sampling No evidence of insect attack

Note: For sprouting oak species, category 4 indicates top kill only and does not account for possible stump sprouting.

result in a type 1 error regarding a relationship between prefire tree mortality and wildfire severity.

Spatial and remote data

Plot burn date was determined using ArcGIS 10.5 (ESRI 2016) by overlaying plot locations on daily fire progression layers obtained through the National Interagency Fire Center website of incident-specific data (*available online*).[5]

Weather data obtained from the single portable Remote Automated Weather Station installed within the Rough Fire perimeter were provided by Sequoia National Forest staff. No portable weather stations were installed on the Cedar Fire, so weather data were averaged from the four nearest permanent stations (Johnsondale, River Kern, UHL/Hot Springs, and Wofford Heights). Each plot was assigned a value for temperature, wind speed, and relative humidity (RH) based on the daytime (10:00 – 17:00) average of hourly values for the plot burn date. On both fires, RH was highly negatively correlated with temperature, as expected, and highly positively correlated with wind speed, meaning lower wind speeds were recorded during days that were hotter and drier. Because daytime average hourly wind speeds were relatively low (3.9 to 5.8 km/h on the Rough

[5] http://ftp.nifc.gov/incident_specific_data/

Fire and 8.9 to 13.7 km/h on the Cedar Fire) and wind can be a highly localized variable, we chose RH as the single weather variable to represent overall weather conditions on each burn date.

Topographic Relative Moisture Index (TRMI, an index ranging from 0, xeric, to 60, mesic), which indicates relative soil moisture availability among sites in mountainous terrain, was calculated from four metrics based on the methods described in Parker (1982). We used field measurements of aspect, slope, and topographic position, and derived slope curvature values from a 10-m resolution digital elevation model of the project site using ArcGIS Desktop 10.5 (ESRI 2016).

A remotely sensed fire-severity metric, Relative differenced Normalized Burn Ratio (RdNBR) (Miller and Thode 2007), was obtained for each plot from a 30-m resolution raster data set of vegetation burn severity (USDA Forest Service Pacific Southwest Region 2018*b*). Extended assessment RdNBR values based on postfire imagery taken one year after fire were used. Bilinear interpolation, which uses the value of the four nearest pixel centroids to calculate a weighted average, was used to derive RdNBR values for each plot in ArcGIS Desktop 10.5 (ESRI 2016).

Analysis

We calculated basic summary statistics of tree mortality status by tree species, fire, and disturbance type to characterize the effects of each disturbance on dominant tree species composition. We conducted predictive analyses of plot-level fire severity for the Rough and Cedar Fires separately because of differences in weather conditions, plot elevations, and dominant tree species between fires.

The fire-severity metrics we analyzed were plot-level percentage of tree basal area killed by fire, (a field measurement of fire-caused tree mortality), remotely sensed RdNBR (a remotely sensed estimate of fire-caused conversion from live to dead biomass), and plot-level mean torch percent (a field measure of the percentage of live and dead tree canopy consumed by fire). We chose fire-severity metrics that focus on the tree canopy because that is the strata we expect red-phase tree mortality to primarily influence, since the red phase involves mostly changes to canopy fuels. We evaluated three fire-severity metrics to determine whether observed patterns hold across multiple ways of measuring biomass loss. We believe basal area killed by fire is our most biologically meaningful metric of fire severity because it is a direct measurement of conversion from live to dead biomass measured on the same scale as the predictors; RdNBR is measured on a different scale than our plots, and mean torch percent accounts for consumption of both live and dead fuels.

For our prefire mortality predictor variables, we grouped trees in the red phase at the time of fire due to insect and non-insect mortality (categories 2 and 3, Table 4) into a single category of red-phase dead at the time of fire (27.0% of sampled trees). We excluded trees that were designated as dead ≥3 yr prior to fire (3.2% of sampled trees) from this prefire mortality predictor metric to focus on effects of red-phase mortality, and because those trees represent background mortality not associated with the recent severe drought.

Other potential predictors of fire severity were elevation, slope, topographic position, TRMI, RH, estimated prefire shrub cover, tree density (live and dead combined), stand basal area (live and dead combined), dominant tree genus (*Pinus*, *Abies*, or *Calocedrus*), and the percentage of plot basal area in the red phase immediately prefire (hereafter red-phase basal area). For the Cedar Fire, we also included ladder fuel density (not recorded on the Rough Fire) and recent fire history (plot presence within the 1990 Stormy Fire footprint). We excluded Beers-transformed aspect (Beers et al. 1966) because it exceeded our correlation threshold (Spearman's $r \geq 0.7$) with TRMI. Red-phase basal area and the percentage of red-phase trees were very highly correlated (Spearman's $r = 0.99$ and 0.94 for Rough and Cedar Fires), so we excluded percent red-phase trees as a predictor variable. Ranges and means or modes for the 12 included predictor variables are shown in Table 1.

Does prefire tree mortality influence wildfire severity, and what is the strength of its influence relative to topography, fire weather, and other aspects of vegetation?

For each fire, we used random forest analysis to identify potentially influential topographic, weather, vegetation, and prefire tree mortality variables on our three fire-severity metrics: the percentage of live tree basal area killed by fire, RdNBR, and mean torch percent. We chose random forest because it is a nonparametric method well suited to model complex and nonlinear relationships without imposing distributional assumptions. We conducted three replicates of the random forest analysis for each fire-severity response variable, using the cforest function of the party package (Hothorn et al. 2019). We set a different random seed for each replicate and specified 5,000 trees. We then generated the conditional variable importance values for each replicate using the varimp function of the party package, which calculates importance by comparing model prediction accuracy before and after permutation of each predictor variable (Strobl et al. 2008); larger decreases in model accuracy after permutation of a variable corresponds to a higher importance value. We verified that importance rankings were stable for all replicates (Strobl et al. 2009). Variables were considered important if the importance value was greater than the absolute value of the lowest negative score, because values for unimportant variables are assumed to vary randomly around zero (Strobl et al. 2009). We estimated the proportion of variance each random forest model explained by calculating the out-of-bag R^2 (R^2_{oob}). Models with negative R^2_{oob} were not included in further analyses, as they were assumed to be poor performing and fitting to noise; any models with positive R^2_{oob} were retained, as they detected at least some reliable patterns in the data.

Does the relationship between prefire tree mortality and fire severity depend on interactions with topography, fire weather, or vegetation characteristics?

To identify possible hierarchical relationships between important variables that explained variation in fire severity, we conducted regression tree analysis using the nonparametric conditional inference tree technique from the party package (Hothorn et al. 2019) and included only those predictor variables identified as important by random forest analysis (Thompson and Spies 2009). Partitions are based on the lowest statistically significant P values ($\alpha = 0.1$) derived from Monte Carlo simulations. This method avoids both overfitting and a selection bias toward covariates with many possible splits, which are common to some other recursive partitioning methods (Strobl et al. 2009). We estimated the proportion of variance explained by each conditional inference tree by calculating the R^2_{oob}.

We also directly examined interactions of a priori interest using a generalized additive model (GAM), which uses smooth, nonlinear functions to balance over- and underfitting. We chose GAM because interaction terms can be specified in the model and visualized with three-dimensional plots, unlike our random forest variable importance metric that incorporates both interaction and main effects within a single importance value. Tree density can be correlated with bark beetle and drought-induced tree mortality (Fettig et al. 2007, Hayes et al. 2009, Van Gunst et al. 2016, Young et al. 2017, Restaino et al. 2019) as well as wildfire severity (Safford et al. 2009, 2012, Prichard and Kennedy 2014), so we examined the effect of any potential interaction between these predictors on a fire-severity response variable: the probability of fire-caused individual tree mortality. We also sought to investigate any potential interaction between fire weather and prefire tree mortality because several studies have documented differing effects of prefire mortality depending on fire weather conditions (Harvey et al., 2014*a*,*b*, Sieg et al. 2017).

We ran a full model GAM for each fire that included the same suite of predictor variables included in the random forest model plus the two interaction terms of interest (plot-level density of all trees and of prefire dead trees, and RH and density of prefire dead trees), using the package mgcv (Wood 2019). We then used the package MuMIn (Bartoń 2019) to search all possible predictor combinations for the model with the lowest Akaike information criterion (AIC). Our prefire mortality metric in this analysis was the number of prefire dead trees per plot instead of the percentage, to correspond with the binomial response variable of an individual live tree being killed by fire or not killed by fire. We specified a smooth function (s) for the main effects and a tensor interaction (ti) function for the interaction effects, which is used to separate individual effects from the interaction effects and is appropriate for variables on different scales (Wood 2017). We set the number of basis functions at 3 for interaction terms to reduce overfitting, and at 7 for RH on the Cedar Fire to not exceed the number of distinct observations. For the Rough Fire, we set the number of basis functions at 5 for all (s) terms so that the sum of all smooths would not exceed the total number of observations (50). We specified a logit link function and chose the method REML (restricted maximum likelihood) for estimation of variance components to reduce the underestimation bias common with maximum likelihood (Wood 2017).

How does the effect of prefire tree mortality on fire-severity change as the severity of prefire mortality changes?

We generated partial dependence plots for the random forest models with positive R^2_{oob} to examine whether the influence of the important predictor variables identified by random forest analysis varied over different levels of the predictor (Friedman 2001), using the edarf package (Jones and Linder 2017). Partial dependence analysis examines the effect of a variable on the predicted response when all other predictors are held constant at their means. Analyses were conducted in R version 3.6.1 (R Core Team 2019) and RStudio version 1.2.5001 (RStudio Team 2019).

Results

Tree mortality summary

Although both study sites were in Sierra Nevada mixed-conifer forest, the dominant pre-disturbance vegetation (live trees ≥25 cm DBH) differed. ponderosa pine was the most common tree species on the 50 Rough Fire plots (59.5% of 311 live trees), followed by incense cedar (15.4%) and white fir (13.5%; Fig. 1a). The 130 Cedar Fire plots had greater pre-disturbance dominance of shade-tolerant species, with white fir (54.5% of 1,237 live trees) and incense cedar (22.9%) being most common (Fig. 1b). Seventeen trees on the Rough fire were not identified with certainty as ponderosa pine or Jeffrey pine because they were dead at sampling and cones of both species were present; they are counted here as ponderosa pine.

Twenty-seven percent of all sampled trees were red-phase dead at the time of fire (31.9% on the Rough Fire and 25.7% on the Cedar Fire), and 69.9% of trees were live at the time of fire (Fig. 2). The remaining trees were dead ≥3 yr prior to fire. The mean plot-level proportion of trees in the red phase prefire was 35.3% on the Rough Fire and 24.7% on the Cedar Fire.

A lower rate of fire-caused mortality was recorded for Rough Fire trees (36.6% of live trees) than Cedar Fire

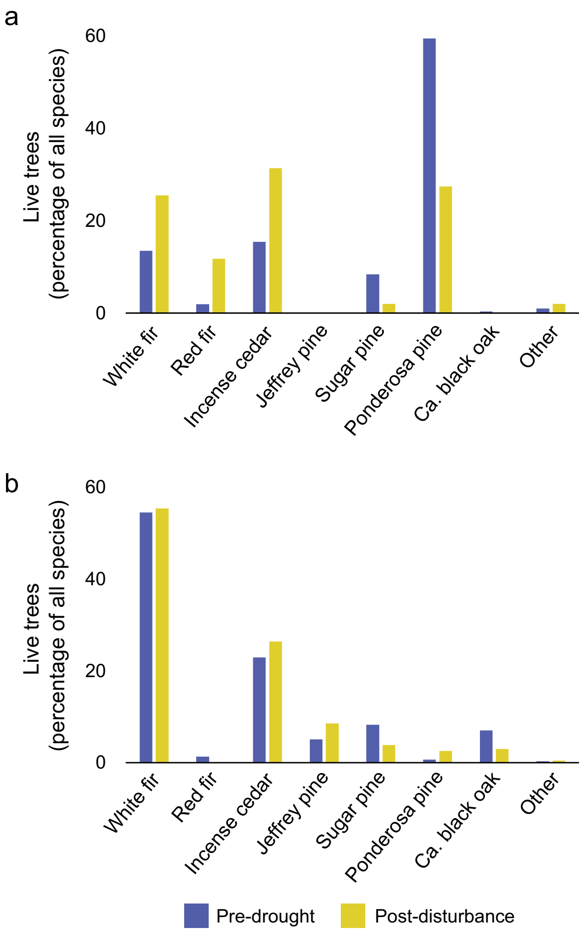

FIG. 1. Relative tree species composition (trees ≥ 25 cm DBH) for (a) 2015 Rough Fire plots and (b) 2016 Cedar Fire plots (California, USA) prior to the recent severe tree mortality event (pre-drought) and after the drought/bark beetle disturbance and subsequent wildfire (post-disturbance).

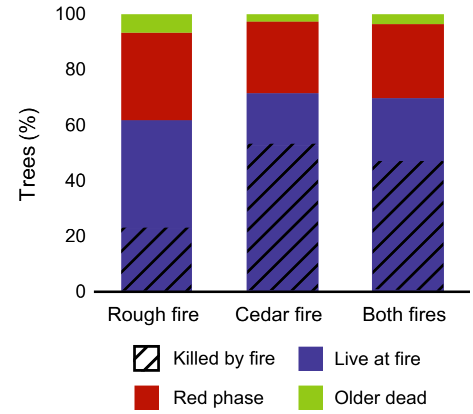

FIG. 2. Mortality status of trees at the time of fire for the 2015 Rough Fire, 2016 Cedar Fire, and both fires combined, and the proportion of trees killed by fire. Older dead and red-phase trees were dead at the time of fire.

trees (73.7% of live trees; Fig. 2), and mean plot-level fire-caused tree mortality also followed this pattern (37.3% and 77.5% of live trees, respectively). The median plot-level percentage of live trees killed by fire was 20.8% on the Rough Fire and 100% on the Cedar Fire.

Prefire mortality and fire-caused mortality were not distributed evenly among species: sugar pine, ponderosa pine, and white fir suffered the highest levels of prefire mortality, and incense cedar had the highest rate of fire-caused mortality (black oak was also top-killed at a high rate, but this species commonly resprouts after even severe fires; Table 5).

Live tree density was reduced by the insect and drought-induced mortality to 65.9% (Rough Fire) and 73.7% (Cedar Fire) of pre-drought live tree densities, then drastically reduced by fire and postfire bark beetle attack to 16.4% and 19.0% of pre-drought densities. The combined disturbances did not dramatically shift the overall tree species composition on the Cedar Fire, where white fir (55.3%) and incense cedar (26.4%) still made up the largest proportion of living trees. On the Rough Fire, the proportion of living incense cedar and white fir increased post-disturbance to 31.4% and 25.5% of all trees, while the proportion of ponderosa pine decreased from 59.5% to 27.5% (Fig. 1).

Influence of prefire tree mortality, topography, and fire weather on fire severity

Our prefire tree mortality measure was identified by random forest as influential to all three fire-severity metrics on the Cedar Fire (although it was less influential than RH) and to two of three fire-severity metrics on the Rough Fire, where it was the most important predictor of basal area killed by fire (Fig. 3). On the Rough Fire, topographic position was influential on basal area killed by fire and RdNBR, and on the Cedar fire, RH (representing general fire weather conditions and negatively associated with temperature) was the most influential variable to all three fire-severity metrics. Variance explained by the random forest models on the Cedar Fire was 21%, 22%, and 16% for percent of plot basal area killed by fire, RdNBR, and mean torch percent, respectively; and 5%, 1%, and −8% for the Rough Fire. The Rough Fire random forest model for mean torch percent was excluded from display and from further analyses because the negative R^2_{oob} value indicates the model was fitting noise.

Effects of fire weather, topography, and vegetation on the relationship between prefire tree mortality and fire severity

Regression tree analysis revealed that on the Cedar Fire, RH (our proxy for fire weather) was the primary variable associated with fire severity, and apparent thresholds of RH were identified under or over which other variables explained fire severity (Figs. 4–6). Red-phase basal area >13% was significantly associated with the percent basal area killed by fire when RH was

TABLE 5. Percentage of tree species within each mortality status class on the 2015 Rough and 2016 Cedar Fires combined.

Species common name	Older dead (%)	Red phase (%)	Killed by fire (%)	Killed by insects postfire (%)	Green attack (%)	No attack (%)
Incense cedar	4.1	2.3	71.0	0.0	0.3	22.3
Ponderosa pine	3.5	38.0	14.5	34.0	3.5	6.5
Jeffrey pine	1.6	14.1	46.9	6.3	9.4	21.9
White fir	2.5	33.5	44.6	0.0	1.8	17.7
Red fir	0.0	27.3	45.5	0.0	0.0	27.3
Sugar pine	1.5	65.4	16.2	9.2	1.5	6.2
California black oak	7.4	1.1	84.2	0.0	0.0	7.4

Notes: The "killed by fire" class indicates top kill and does not account for stump sprouting of California black oak; likely few of the oaks in this class were killed.

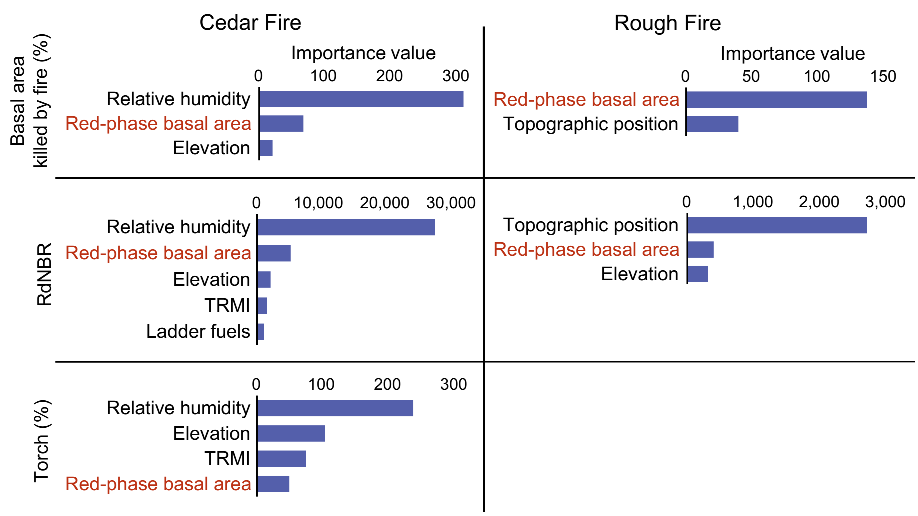

FIG. 3. Conditional permutation importance values of important predictor variables identified by the random forest model for fire-severity metrics measured for the 2016 Cedar Fire and 2015 Rough Fire. Fire-severity metrics are plot basal area killed by fire (%) for trees ≥25 cm diameter at breast height, RdNBR (a remotely sensed fire-severity metric), and mean canopy torch (percentage of needles or leaves consumed by fire; not included for the Rough Fire because out-of-bag R^2 [R^2_{oob}] was negative). Variables with importance values greater than the absolute value of the lowest negative importance value are considered influential to the fire-severity metric (only important variables are shown). Importance values are relative and not comparable across fires or severity metrics. TRMI, Topographic Relative Moisture Index.

>20.25% ($P = 0.008$; Fig. 4c), meaning that under milder fire weather, drought and insect-induced mortality was associated with higher fire severity. A low topographic moisture index was associated with high torch percent when RH was ≤20.25% ($P = 0.093$; Fig. 6a). On the Rough Fire, regression tree analysis identified red-phase basal area >23.5% as significantly associated with higher percent BA killed by fire ($P = 0.026$; Fig. 4a), but red-phase basal area was not identified as driving any of the splits between lower and higher fire severity as measured by RdNBR. Instead, topographic positions >3 (shoulder slope and ridgetop) were associated with higher fire severities ($P = 0.021$), and at low to mid topographic positions, elevation explained the split between higher and lower RdNBR ($P = 0.062$; Fig. 5a). The variance explained by regression trees for basal area killed by fire, RdNBR, and mean torch percent on the Cedar Fire was 33%, 29%, and 26%, respectively, and on the Rough Fire 24% and 41%, respectively (regression tree analysis for mean torch percent was not conducted).

On the Cedar Fire, partial dependence plots also reveal that RH had the greatest influence on fire severity; increases in RH were associated with decreases in fire severity for all three metrics, and the magnitude of change in fire severity associated with RH was greater than for any other explanatory variables, including red-phase basal area (Figs. 4–6). The lowest fire severities were associated with RH > 20% for all three metrics. On the Rough Fire, the highest topographic positions (shoulder slope and ridgetop) were associated with increased fire severity as measured by basal area killed by fire and RdNBR (Figs. 4, 5). The relationship between red-phase basal area and all fire-severity metrics followed a similar pattern on both fires, whereby increased fire severity was associated with a particular range of increased prefire mortality (Figs. 4–6). On the Cedar Fire, increases in fire severity occurred as red-phase basal area increased from ~15% to ~30% (torch percent) or ~40% (basal area killed by fire, RdNBR). On the

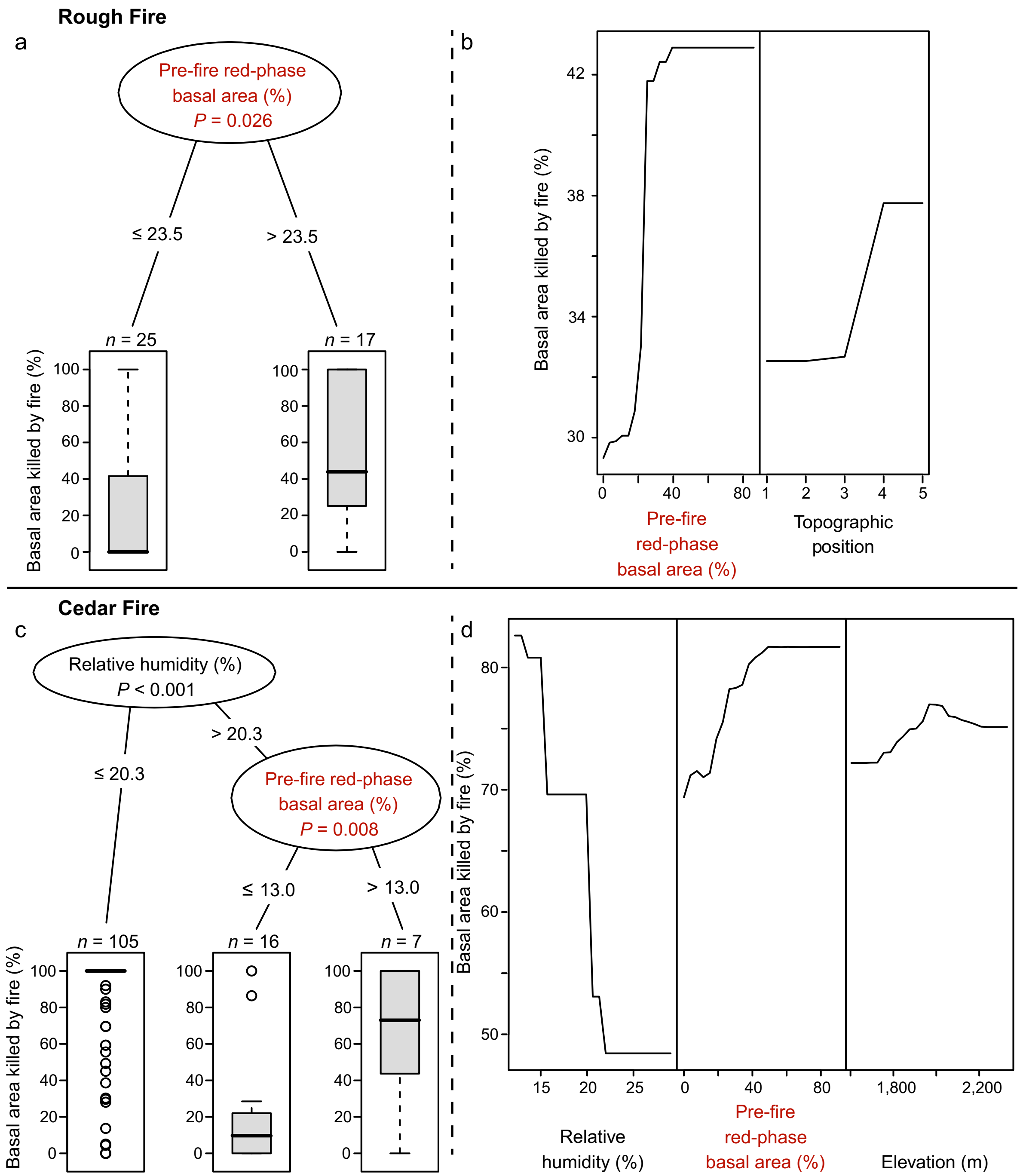

Fig. 4. (a, c) Regression trees and (b, d) partial dependence plots for the percentage of plot basal area killed by fire on the (a, b) 2015 Rough Fire and (c, d) 2016 Cedar Fire, using the predictor variables identified as important to this metric by the random forest model. On regression trees (a, c), n is the number of plots in each group, and P values at each node are from a Monte Carlo randomization test ($\alpha = 0.1$). On the box-plots, the center line is the median value, the box represents the interquartile range, the outer whiskers encompass the range of values excluding outliers, and open circles are outliers a distance >1.5 times the length of the interquartile range from the median. Partial dependence plots (b, d) characterize the dependence of model predictions on each influential variable. Topographic positions are (1) valley bottom, (2) lower slope, (3) middle slope, (4) upper slope, and (5) ridge top.

Rough Fire, basal area killed by fire increased as red-phase basal area increased from ~15% to ~40%, and RdNBR increased as red-phase basal area increased from 0% to ~25%. Increases in red-phase basal area above 30% or 40% were not associated with further increases in fire severity.

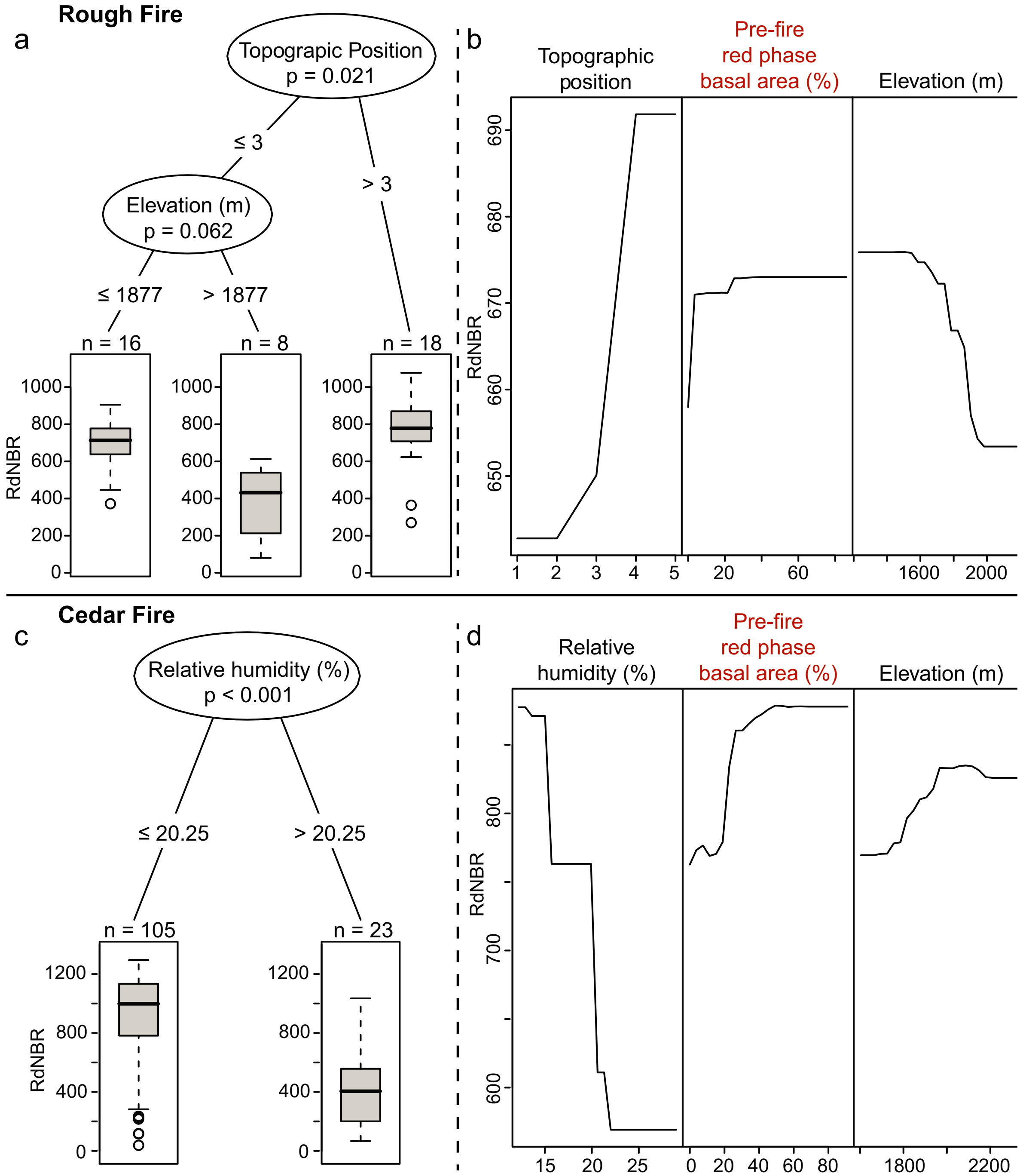

Fig. 5. (a, c) Regression trees and (b, d) partial dependence plots for the remotely sensed fire-severity metric, RdNBR, on the (a, b) 2015 Rough Fire and (c, d) 2016 Cedar Fire, using the predictor variables identified as important to this metric by the random forest model. Partial dependence plots for topographic relative moisture index and ladder fuels, important variables on the Cedar Fire, are not shown. On regression trees (a, c), n is the number of plots in each group, and P values at each node are from a Monte Carlo randomization test ($\alpha = 0.1$). On the box-plots, the center line is the median value, the box represents the interquartile range, the outer whiskers encompass the range of values excluding outliers, and open circles are outliers a distance >1.5 times the length of the interquartile range from the median. Partial dependence plots (b, d) characterize the dependence of model predictions on each influential variable. Topographic positions are (1) valley bottom, (2) lower slope, (3) middle slope, (4) upper slope, and (5) ridge top.

On the Cedar Fire, the best fit GAM for predicting probability of fire-caused individual tree mortality was a model that included all predictors except ladder fuels and presence in the Stormy Fire footprint main effects and the RH–prefire-dead-tree-density interaction (deviance explained = 84.5%; R^2 adjusted = 0.854). The

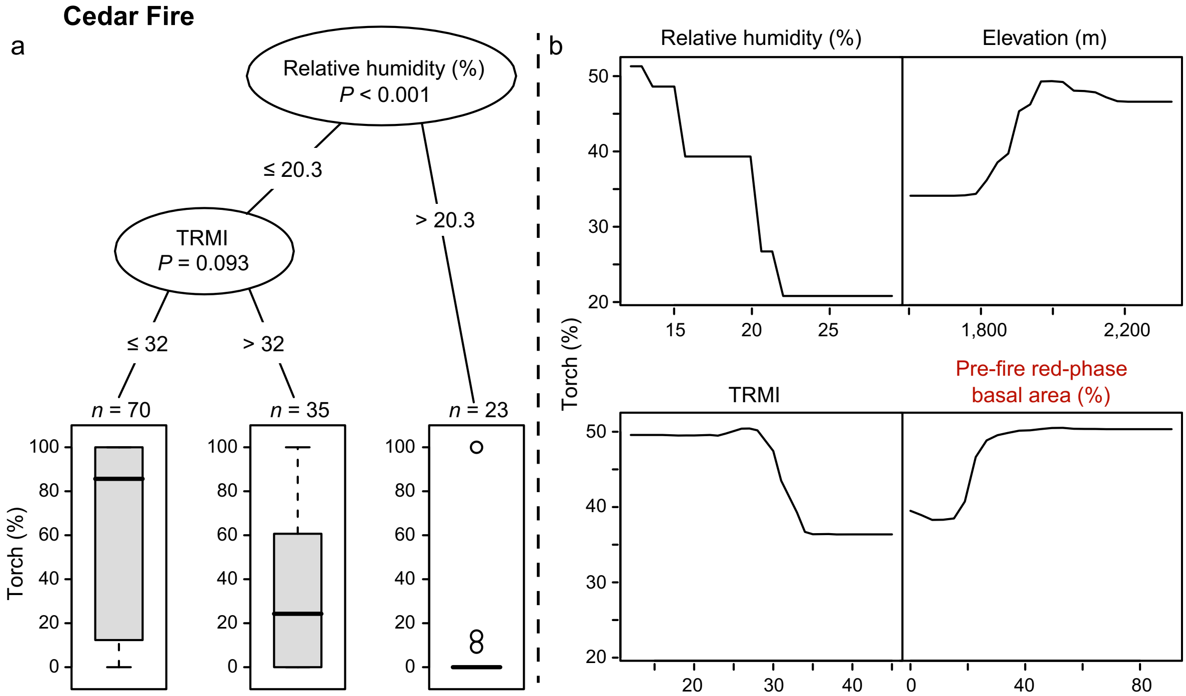

Fig. 6. (a) Regression tree and (b) partial dependence plots for mean canopy torch (needles or leaves consumed by fire) percent on the Cedar Fire, using the predictor variables identified as important to this metric by the random forest model. On the regression tree (a), *n* is the number of plots in each group, and *P* values at each node are from a Monte Carlo randomization test ($\alpha = 0.1$). On the box-plots, the center line is the median value, the box represents the interquartile range, the outer whiskers encompass the range of values excluding outliers, and open circles are outliers a distance >1.5 times the length of the interquartile range from the median. Partial dependence plots (b) characterize the dependence of model predictions on each influential variable. TRMI, Topographic Relative Moisture Index. Only one influential variable was identified for canopy torch on the Rough Fire; these analyses were not conducted.

interaction between total tree density and prefire mortality was included in the final model but was not significant, so we did not explore this interaction further. The interaction between RH and prefire mortality was significant ($P = 0.046$), but was not included in the final model with the lowest AIC.

On the Rough Fire, the best-fit GAM for predicting probability of fire-caused individual tree mortality was a model that included all variables except prefire shrub cover, elevation, and topographic position (deviance explained = 97.2%; R^2 adjusted = 0.988). The interaction between tree density and prefire tree mortality was not significant, so the interaction was not further examined. No clear patterns were evident when visualizing the interaction between RH and prefire tree mortality (see Appendix S1 for results).

Discussion

Key findings

We found support for a positive but nuanced relationship between prefire red-phase tree mortality severity and subsequent wildfire severity in Sierra Nevada mixed-conifer forests. Prefire tree mortality was associated with two of the three fire-severity metrics on the Rough Fire, and all of the fire-severity metrics on the Cedar Fire. Notably, on both fires, prefire tree mortality was associated with what we consider our most direct and biologically meaningful measure of fire severity: basal area killed by fire. On the Cedar Fire, weather was more strongly associated with fire severity, and prefire tree mortality had a stronger influence on basal area killed by fire when RH was high. On the Rough Fire, upper topographic positions were also consistently associated with our fire-severity metrics, but prefire tree mortality had the strongest association with basal area killed by fire, and the influence of prefire tree mortality did not appear to depend on topographic position. On both fires, increasing severity of bark beetle mortality was only associated with increased fire severity up to prefire mortality levels of 30-40% of plot basal area; increases in prefire mortality above this threshold were not associated with further increases in fire severity. Increases in fire severity were more pronounced when prefire tree mortality was above ~15% for most fire-severity metrics. The interacting disturbances drastically reduced forest cover on both fires and converted a system dominated by shade-intolerant and low-severity fire-adapted pines to a cedar–pine–fir-dominated system, while the fir–cedar system retained its overall tree species composition of shade-tolerant species.

Relationship between red-phase tree mortality and wildfire severity

Our finding that red-phase tree mortality severity is related to subsequent wildfire severity agrees with some modeling (Schoennagel et al. 2012, Hoffman et al. 2012, Sieg et al. 2017), remotely sensed (Prichard and Kennedy 2014), and observational (Metz et al. 2011, Harvey et al. 2014*a*) studies that found a similar positive relationship between recent tree mortality and wildfire severity, at least under certain conditions. Ours is the first to examine this relationship in dry mixed-conifer forests under typical summer burning conditions, and although Seig et al. (2017) modeled ponderosa pine forests of Arizona that have similarities to our pine-dominated Rough Fire plots, no studies in any region have examined this relationship in white-fir- and incense-cedar-dominated forests such as on the Cedar Fire.

This finding is also broadly consistent with previous research on mortality–wildfire interactions. Kane et al. (2017) note in their review that the few synergistic interactions between prefire tree mortality and wildfire severity that have been documented were in wildfires that occurred a short time after a moderate- to high-severity prefire mortality event (i.e., during the red phase), similar to the disturbances in our study. Studies that have not detected increased fire severity after bark beetle or drought-induced tree mortality were either not conducted in the red phase of mortality (Harvey et al. 2013), or lumped recent (red phase) and older (gray and/or tree-fall phase) prefire mortality together to reach that conclusion (Meigs et al. 2016), although there are studies that found little to no effect of prefire red-phase mortality on wildfire severity (Bond et al. 2009, Harvey et al. 2014*b*) or that documented limited evidence for positive effects in gray-phase mortality (Andrus et al. 2016).

Our study disagrees with the conclusions drawn from another dry mixed-conifer forest with a historically frequent-fire regime: Bond et al. (2009) reported results of a GIS-based analysis of very recent western-pine-beetle-driven mortality (aerial survey estimates) on fire severity (RdNBR) in the San Bernardino Mountains of California, and did not find an association between prefire tree mortality and wildfire severity. Three factors may have led to the lack of a detected association. First, the study fires occurred under extreme weather conditions, with strong desert "Santa Ana" winds (60–90 km/h sustained maximum wind speeds), low RH values (5–9%) and 10-h fuel moistures (1–3%), and daily maximum temperatures >35°C (data from nearby RAW stations). It is not surprising that, under Santa Ana conditions, in which fires often spread with little influence of fuel age or loading (Keeley et al. 2009), Bond et al. (2009) did not find any statistical relationship between prefire mortality and fire severity. Second, the density of prefire mortality (maximum 21.8 dead trees/ha) was much lower than in our study (123.5 and 148.2 dead trees/ha on the Rough and Cedar Fire plots according to the same aerial detection survey data used in their study) and may have been too low to influence wildfire severity and/or for an influence to be detected statistically. Finally, the airborne sketch-mapping procedure they used to estimate mortality density is not spatially accurate at the scale used in their analysis (USDA Forest Service Pacific Southwest Region 2018*a*).

Several possible mechanisms for a synergistic interaction between prefire tree mortality and fire severity have been proposed. Increased crown torching may result from aerial embers more easily igniting recently dead needles than green needles (Jolly et al. 2012), and indeed increased crown torching has been observed in recently dead trees in the Rocky Mountains (Page et al. 2013) and on the 2016 Cedar Fire studied here (Reiner et al. 2016). Enhanced ember production was observed in recently dead torching trees on the Cedar Fire (Reiner et al. 2016), further increasing chances for spot fires and aerial ignitions. Increased incidence of crown fire in dead trees may translate to increased mortality of nearby live trees through crown fire spread or heat transfer. Others have suggested that increased wind speed in areas of severe tree mortality may increase fire severity by enhancing fire behavior (Page and Jenkins 2007), but this pertains to later stages of an outbreak when needles have fallen from the canopy (gray stage) and was not likely a factor on our study sites.

Since water stress may increase beetle- and drought-caused mortality (Young et al. 2017) and fire-caused mortality (van Mantgem et al. 2013), it is possible that an association between the two disturbances is an artifact of localized water deficit or competitive water stress. However, our proxy for localized soil moisture (TRMI) was not correlated with red-phase mortality (Spearman's $r = -0.07$ and 0.21 for Rough and Cedar Fires), nor was plot-level tree density (Spearman's $r = -0.21$ and 0.18 for Rough and Cedar Fires). While drought- and stand-density-related water stress may have increased forest vulnerability to both prefire and fire-caused mortality at our study sites, our data do not support this association at the plot scale at which the relationship between red-phase mortality and wildfire severity was detected.

Effect of fire weather on wildfire severity

We were not surprised to find that the influence of prefire red-phase mortality on basal area killed by fire was greater under less-severe weather conditions, as fire weather is known to be a strong driver of fire severity. One possible reason why so few observational studies have detected a strong relationship between the two disturbances is that most large wildfires occur under extreme weather conditions in forests with dense stand conditions and, under these conditions, much of the forest may burn at high severity regardless of the mortality status of the trees (see, e.g., Bond et al. 2009). In areas of recent bark beetle mortality, Harvey et al. (2014*a*) and Andrus et al. (2016) only detected prefire mortality-driven increases in fire severity under moderate, but not severe, fire-weather conditions, and the increase in fire severity associated with recent tree mortality that Sieg et al. (2017) modeled became less pronounced as wind speeds increased. Together with our study, these results suggest that the role of prefire tree mortality in subsequent wildfire severity may be most pronounced when weather conditions are less than extreme. Our failure to detect an influence of fire weather on fire severity on the Rough Fire may have been due a low sample size of plots burning on days with higher RH, since we had only five plots with RH > 20%, as compared to 24 plots on the Cedar Fire.

Effect of topography on wildfire severity

On the Rough Fire, topographic position was associated with both basal area killed by fire and RdNBR. Topographic position has been documented to be associated with fire severity where topography is pronounced (Skinner et al. 2006, Estes et al. 2017), with higher severities on upper slopes. Yet our results do not clearly reveal whether upper topographic position or prefire tree mortality was the strongest driver of fire severity on the Rough Fire, nor were we able to tease apart the conditions under which each might have the strongest effects. There were relatively few plots on the Rough Fire ($n = 50$), possibly limiting the combinations of conditions present in our data. Topographic position was not included as a potential predictor in a previous analysis of the Rough Fire data (Stephens et al. 2018).

We did not detect an effect of topographic position on fire severity on the Cedar Fire. This may be due to the fact that the vast majority of Cedar Fire plots were located in the middle slope position and topographic variation was therefore low. The Rough Fire sample had much higher variation in topographic position.

Elevation had a differing effect on fire severity in each fire, with a positive association on the Cedar Fire up to about 2,000 m and a leveling off at higher elevations, and a negative association on the Rough Fire (but only with one severity metric, RdNBR). The difference may be due to the different dominant tree species composition on each fire, particularities of fire weather while different elevations were burning, or another factor we haven't identified. The effect of elevation was mild on the Cedar Fire (Figs. 4–6) and only associated with RdNBR on the Rough Fire (Fig. 5b), so we do not draw strong conclusions regarding elevation's relationship with fire severity from our results.

Observed thresholds of prefire tree mortality's effect on wildfire severity

We observed an upper threshold of prefire mortality severity, above which the positive relationship with fire severity did not hold, and this threshold was similar for both fires and for all metrics of fire severity (Figs. 4–6). Fire severity increased with increasing prefire tree mortality levels up to tree mortality of about 30–40%, but prefire mortality above this threshold was not associated with further increases in fire severity. This would not be explained by fire severity maxing out at complete canopy mortality above this threshold, because the effect of prefire mortality on fire severity plateaued well below complete fire-caused mortality on both fires. Nor is it due to limited observations of high levels of prefire mortality: the percentage of plots on the Rough and Cedar Fires with ≥30% prefire red-phase basal area mortality was 40% and 42%, respectively; 24% of plots on the Rough Fire and 12% of plots on the Cedar Fire had ≥70% prefire mortality. Further research is needed to understand the mechanisms behind this apparent threshold and whether it is common to other fires burning in red-phase tree mortality.

The partial dependence plots (Figs. 4–6) show that fire severity did not increase substantially due to prefire red-phase mortality below about 15%, except for RdNBR on the Rough Fire. This result may suggest a lower threshold of red-phase mortality severity under which effects of prefire mortality on wildfire severity are not detected. If such a threshold is corroborated in additional studies, it could signal to managers when a mortality event becomes severe enough to represent substantially elevated fire severity risk.

Interactions between prefire tree mortality and other variables

We used GAM to examine potential interactions between prefire mortality and each of two variables, RH and tree density, on fire-caused tree mortality for each fire. Only one of these four potential interactions was statistically significant in the final model: RH × prefire tree mortality on the Rough Fire. This interaction is difficult to interpret in an ecologically meaningful way, as it predicts the highest wildfire severity when prefire tree mortality is moderate and RH is very low or relatively high, and when prefire mortality is high and RH is low to moderate (see Appendix S1). The regression tree analysis did not investigate this interaction on the Rough Fire because RH was not one of the important variables identified by random forest analysis. The hierarchical relationship revealed by the regression tree between RH and prefire tree mortality on the Cedar Fire was corroborated by the GAM in that the interaction was significant in the full model, but the interaction term was not included in the final model as determined by lowest AIC. It is likely that the inclusion of this interaction term did not improve the model enough to overcome the penalty for the additional term.

Disturbance-driven changes in species composition

The interacting disturbances of severe drought/insect mortality and wildfire shifted a pine-dominated system to a cedar–pine–fir-dominated system, while the pre-disturbance fir–cedar system retained its overall species dominance. While the observed species are all common components of Sierra Nevada mixed-conifer forests, the shift away from pines equates to a shift away from shade-intolerant and fire-adapted species and toward shade-tolerant species that are less well adapted to frequent fire. Other studies of this bark beetle event have observed a similar shift toward dominance of incense cedar and white fir as large overstory pines were preferentially killed, and white fir and incense cedar dominated both new and advanced regeneration (Fettig et al. 2019, Young et al. 2019). These studies did not examine an interaction with wildfire and therefore implicate the prefire tree mortality event as the driver of the shift toward shade-tolerant species in the overstory that we observed. This conclusion is supported by the fact that ponderosa, Jeffrey, and sugar pines are the most fire-resistant tree species in our study area (Safford and Stevens 2017) and, after fires without antecedent drought/beetle mortality, they tend to be more common in severely burned plots than the fire intolerant species (Welch et al. 2016).

Study scope and limitations

These findings are directly relevant to dry mixed-conifer systems historically adapted to frequent fire but with highly altered stand structure and species composition due to decades of fire suppression and lack of cultural burning, and they pertain specifically to recent (ongoing and red phase) tree mortality events. Our measures of fire severity primarily reflect canopy fire severity and not surface fire severity (or soil burn severity; see Safford et al. 2008). The finding that the influence of prefire tree mortality on wildfire severity may depend on other site conditions capable of driving extreme fire behavior (i.e., weather and topography) is broadly relevant to temperate conifer forests experiencing these two interacting disturbances, as it contributes to a small but growing body of evidence observing similar dependencies.

Our analyses were conducted at the plot scale, or at the scale of individual trees when examining interactions with GAM. The relationship we observed between prefire tree mortality and wildfire severity was likely due to very localized effects of recently dead trees within a stand. It is possible that the red-phase mortality also had landscape level effects not investigated by our study, such as pockets of red-phase trees causing increased incidence of crown fire initiation and ember cast that spread into areas with lower prefire mortality. Further research could tease apart localized vs. landscape scale effects.

The variance explained by our random forest models for the Cedar Fire and for regression trees for both fires ranged from 16% to 41%, which is not surprising given the highly complex relationships between fire behavior and fuels, weather, and topography, and the limitations of our measurements. The random forest models for the Rough Fire explained very little variance (5% and 1%), possibly due to the low sample size. Clearly there is much variability that is not explained by our models. However, the intent of our models was to examine relationships, and the R^2_{oob} values do not change the interpretation of the ranking and relative influence of the variables we measured.

We acknowledge that fire weather can be a major driver of fire behavior and severity, yet plot-level fire weather is inherently difficult to quantify. Plot-level weather data may be mismatched with plot data temporally because we have hourly weather data but do not know what time of day our plots burned, and spatially because few weather stations were appropriate to each site, yet much microsite weather variability exists. While our fire weather metric (daytime average RH) provides a reasonable estimate of broad scale burning conditions, a more nuanced relationship between prefire mortality, fire weather, and fire severity might be detected with more spatially and temporally specific weather metrics (e.g., Viedma et al. 2020).

It is possible that a relationship existed in our plots between prefire shrub cover and wildfire severity, but went undetected in our models due to the coarseness of our metric (a categorical estimate of prefire shrub cover based on postfire observation of remaining shrub stumps). Shrub cover has been shown to influence wildfire severity in other mixed-conifer forests historically adapted to frequent fire (Lydersen et al. 2014, Coppoletta et al. 2016).

Management implications

Speculation until now on the red-phase-mortality and wildfire-severity relationship has been complicated by the ambivalent evidence drawn from substantially different forest systems. Our results demonstrate that in this dry mixed-conifer system, red-phase tree mortality does relate to increased subsequent wildfire severity. New pockets of pines continue to be killed by bark beetles throughout the Sierra Nevada, but the vast majority of trees killed in this mortality event have transitioned to the gray phase (dead needles and fine branches have dropped from tree canopies), and few host trees remain in the southern Sierra Nevada to sustain a near-future native bark-beetle epidemic of this scale (Fettig et al. [2019] observed up to 85% ponderosa pine mortality in some southern Sierra Nevada watersheds). However, current fir engraver mortality in the Sierra Nevada is high, and expanding areas of Jeffrey pine and sugar pine are being killed by *Dendroctonus* beetles in drier parts of the range. Because these forests are adapted to largely low-severity fire and were experiencing increased fire severity even before this unprecedented tree mortality event occurred (Steel et al. 2015, Safford and Stevens 2017), forest management is focused on increasing resistance to high-severity wildfire. Results of this study and others (e.g., Fettig et al. 2007, Stephens et al. 2018, Restaino et al. 2019, Young et al. 2019) suggest that resource managers should consider whether some level of dead-tree management in red-phase stands might result in more desirable forest conditions in the case of wildfire occurrence.

Along those lines, our results suggest that removal of recently dead trees from the landscape *may* reduce the severity of a subsequent wildfire by removing an extremely flammable canopy fuel, but further research is needed to solidify our understanding of the relative contributions of red-phase tree mortality, topography, and fire weather to wildfire severity in dry mixed-conifer forests. Forest managers also must weigh the chance that a wildfire will occur within the short red-phase window (usually 2–3 yr) against the need to spend limited fuels-reduction dollars elsewhere. Either way, what are now gray-phase trees will eventually fall to the forest floor, and high quantities of spatially continuous large downed fuels could have dramatic effects on surface-fire severity and fire control (Metz et al. 2011, Stephens et al. 2018). Several studies suggest the best course of action would be preventative forest density reduction measures that reduce forest susceptibility to future drought- and insect-induced tree mortality (Restaino et al. 2019, Fettig et al. 2019). Such pre-disturbance treatments are also likely to increase resistance and resilience to severe wildfire (Safford et al. 2012, McIver et al. 2013).

Summary of findings and future research

We found that prefire tree mortality relates to subsequent wildfire severity under certain environmental conditions that may differ between sites and wildfires and that, above 30–40% tree mortality, the influence on fire severity plateaus. We also found that these combined disturbances in Sierra Nevada mixed-conifer forests resulted in dominance by white fir and incense cedar in forests dominated by pines pre-disturbance, representing a shift from more fire-tolerant to less fire-tolerant species, while white fir and incense cedar maintained their dominance in forests where they dominated pre-disturbance.

To solidify our understanding of the magnitude of the effect of prefire red-phase tree mortality on wildfire in frequent-fire forests, additional studies should be conducted in a wider variety of locations and fire-weather conditions. Empirical research is needed on the relationship between gray-phase and tree-fall-phase mortality and wildfire severity in these systems, as well as direct observational research on fire behavior and intensity during wildfire events in red-phase and gray-phase mortality. Finally, the recovery trajectory of mixed-conifer forests subject to these interacting disturbances is unknown (but see Young et al. 2019), and monitoring should be conducted of vegetation regeneration and mechanisms driving observed patterns.

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Literature Cited

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Andrus, R. A., T. T. Veblen, B. J. Harvey, and S. J. Hart. 2016. Fire severity unaffected by spruce beetle outbreak in spruce–-fir forests in southwestern Colorado. Ecological Applications 26:700–711.

Asner, G. P., P. G. Brodrick, C. B. Anderson, N. Vaughn, D. E. Knapp, and R. E. Martin. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proceedings of the National Academy of Sciences USA 113: E249–E255.

Bartoń, K. 2019. MuMIn: multi-model inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Bentz, B. J. 2009. Bark beetle outbreaks in western North America: Causes and consequences. University of Utah Press, Salt Lake City, Utah, USA.

Bond, M. L., D. E. Lee, C. M. Bradley, and C. T. Hanson. 2009. Influence of pre-fire tree mortality on fire severity in conifer forests of the San Bernardino Mountains, California. Open Forest Science Journal 2009:41–47.

Bowman, D. M. J. S., G. J. Williamson, J. T. Abatzoglou, C. A. Kolden, M. A. Cochrane, and A. M. S. Smith. 2017. Human exposure and sensitivity to globally extreme wildfire events. Nature Ecology & Evolution 1:1–6.

CA Dept. of Forestry and Fire Protection Fire and Resource Assessment Program. 2018. Fire perimeters. https://frap.fire.ca.gov/mapping/gis-data/

Christensen, J. H., et al. 2007. Regional climate projections. Page 94 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Collins, B. M., D. L. Fry, J. M. Lydersen, R. Everett, and S. L. Stephens. 2017. Impacts of different land management histories on forest change. Ecological Applications 27:2475–2486.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Dove, N. C., H. D. Safford, G. N. Bohlman, B. L. Estes, and S. C. Hart. 2020. High-severity wildfire leads to multi-decadal impacts on soil biogeochemistry in mixed-conifer forests. Ecological Applications 30:e02072.

ESRI. 2016. ArcGIS desktop: Release 10.5. Environmental Systems Research Institute, Redlands, California, USA.

Estes, B. L., E. E. Knapp, C. N. Skinner, J. D. Miller, and H. K. Preisler. 2017. Factors influencing fire severity under moderate burning conditions in the Klamath Mountains, northern California, USA. Ecosphere 8:e01794.

Fettig, C. J., K. D. Klepzig, R. F. Billings, A. S. Munson, T. E. Nebeker, J. F. Negrón, and J. T. Nowak. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238:24–53.

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecology and Management 432:164–178.

Friedman, J. H. 2001. Greedy function approximation: a gradient boosting machine. Annals of Statistics 29:1189–1232.

Giger, D. R., and G. J. Schmitt. 1983. Soil survey of the Sierra National Forest area, California. USDA Forest Service. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/california/sierraNFCA1983/sierraNFCA1983-I.pdf

Hanes, R. O., S. E. Plocher, and D. Z. Martynn. 1996. Soil survey of Sequoia National Forest, California. USDA Forest Service Pacific Southwest Region. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/california/sequoiaNFCA1996/sequoiaNFCA1996-I.pdf

Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences USA 112:4375–4380.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. Ecology 94:2475–2486.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014*a*. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014*b*. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Norther Rockies. Proceedings of the National Academy of Sciences USA 111:15120–15125.

Hayes, C. J., C. J. Fettig, and L. D. Merrill. 2009. Evaluation of multiple funnel traps and stand characteristics for estimating western pine beetle-caused tree mortality. Journal of Economic Entomology 102:2170–2182.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hoffman, C., P. Morgan, W. Mell, R. Parsons, E. K. Strand, and S. Cook. 2012. Numerical simulation of crown fire hazard immediately after bark beetle-caused mortality in lodgepole pine forests. Forest Science 58:178–188.

Hothorn, T., K. Hornik, C. Strobl, and A. Zeileis. 2019. party: a laboratory for recursive partytioning. R package version 1.3.3. https://CRAN.R-project.org/package=party

Intergovernmental Panel on Climate Change. 2014. Climate change 2014: synthesis report. Page 151 *in* Core Writing Team, R. K. Pachauri, and L. A. Meyer, editors. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology and Management 254:16–34.

Jolly, W. M., R. A. Parsons, A. M. Hadlow, G. M. Cohn, S. S. McAllister, J. B. Popp, R. M. Hubbard, and J. F. Negron. 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. Forest Ecology and Management 269:52–59.

Jones, Z. M., and F. Linder. 2017. edarf: exploratory data analysis using random forests. R package version 1.1.1. https://CRAN.R-project.org/package=edarf

Kane, J. M., J. M. Varner, M. R. Metz, and P. J. van Mantgem. 2017. Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western US Forests. Forest Ecology and Management 405:188–199.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Keeley, J. E., H. D. Safford, C. J. Fotheringham, J. Franklin, and M. Moritz. 2009. The 2007 Southern California wildfires: lessons in complexity. Journal of Forestry 107:287–296.

Lydersen, J. M., M. P. North, and B. M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. Forest Ecology and Management 328:326–334.

Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. Forest Ecology and Management 304:370–382.

Maestrini, B., E. C. Alvey, M. D. Hurteau, H. Safford, and J. R. Miesel. 2017. Fire severity alters the distribution of pyrogenic carbon stocks across ecosystem pools in a Californian mixed-conifer forest: pyrogenic carbon stock and fire severity. Journal of Geophysical Research: Biogeosciences 122:2338–2355.

Martinuzzi, S., A. J. Allstadt, A. M. Pidgeon, C. H. Flather, W. M. Jolly, and V. C. Radeloff. 2019. Future changes in fire weather, spring droughts, and false springs across U.S. National Forests and Grasslands. Ecological Applications 29:e01904.

McIver, J. D., et al. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate study (FFS). International Journal of Wildland Fire 22:63.

Meigs, G. W., H. S. J. Zald, J. L. Campbell, W. S. Keeton, and R. E. Kennedy. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environmental Research Letters 11:45008.

Metz, M. R., K. M. Frangioso, R. K. Meentemeyer, and D. M. Rizzo. 2011. Interacting disturbances: wildfire severity affected by stage of forest disease invasion. Ecological Applications 21:313–320.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009*a*. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment 113:645–656.

Miller, J. D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. Fire Ecology 8:41–57.

Miller, J. D., and H. D. Safford. 2020. Are plant community responses to wildfire contingent upon historical disturbance regimes? Global Ecology and Biogeography 29:1621–1633.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009*b*. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16–32.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Minnich, R. A. 2007. Climate, paleoclimate, and paleovegetation. Pages 43–70 *in* M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. Third edition. University of California Press, Berkeley, California, USA.

Moore, J., M. Woods, and A. Ellis. 2016. 2015 Aerial survey results: California. USDA Forest Service Forest Health Monitoring Program, Davis, California, USA.

Moore, J., M. Woods, A. Ellis, and B. Moran. 2017. 2016 Aerial survey results: California. USDA Forest Service Forest Health Monitoring Program, Davis, California, USA.

North, M. P., B. M. Collins, H. D. Safford, and N. L. Stephenson. 2016. Montane forests. Pages 553–577 *in* H. A. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

Page, W. G., M. E. Alexander, and M. J. Jenkins. 2013. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. Forestry Chronicle 89:783–794.

Page, W. G., and M. J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. Forest Science 53:662–674.

Parker, A. J. 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Physical Geography 3:160–168.

Parsons, D. J., and S. H. Debenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21–33.

Prichard, S. J., and M. C. Kennedy. 2014. Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. Ecological Applications 24:571–590.

R Core Team 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reiner, A. L., M. Dickinson, M. Courson, K. Napier, T. Sexton, A. Miyagashima, R. Pasquale, and P. Riggan. 2016. Fire behavior in tree mortality: Cedar fire report. Fire Behavior and Assessment Team, US Forest Service PSW Region. https://www.fs.fed.us/adaptivemanagement/reports/fbat/CedarFireReport_29Sept2016.pdf

Restaino, C., D. J. N. Young, B. Estes, S. Gross, A. Wuenschel, M. Meyer, and H. Safford. 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. Ecological Applications 29:e01902.

RStudio Team. 2019. RStudio: integrated development for R. RStudio, Boston, Massachusetts, USA.

Safford, H. D., J. Miller, D. Schmidt, B. Roath, and A. Parsons. 2008. BAER soil burn severity maps do not measure fire effects to vegetation: A comment on Odion and Hanson (2006). Ecosystems 11:1–11.

Safford, H. D., D. A. Schmidt, and C. H. Carlson. 2009. Effects of fuel treatments on fire severity in an area of wildland–urban interface, Angora Fire, Lake Tahoe Basin, California. Forest Ecology and Management 258:773–787.

Safford, H. D., and J. T. Stevens. 2017. Natural Range of Variation for yellow pine and mixed-conifer forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California, USA. General Technical Report PSW-GTR-256. USDA Forest Service Pacific Southwest Research Station, Albany, California, USA.

Safford, H. D., J. T. Stevens, K. Merriam, M. D. Meyer, and A. M. Latimer. 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. Forest Ecology and Management 274:17–28.

Schoennagel, T., T. T. Veblen, J. F. Negron, and J. M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7:e30002.

Seager, R., et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Seidl, R., et al. 2017. Forest disturbances under climate change. Nature Climate Change 7:395–402.

Sieg, C. H., R. R. Linn, F. Pimont, C. M. Hoffman, J. D. McMillin, J. Winterkamp, and L. S. Baggett. 2017. Fires following bark beetles: factors controlling severity and disturbance interactions in ponderosa pine. Fire Ecology 13:1–23.

Skinner, C. N., A. H. Taylor, and J. K. Agee 2006. Klamath Mountain bioregion. Pages 170–194 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. The University of California Press, Berkeley, California, USA.

Soil Survey Staff. 2019. Gridded Soil Survey Geographic (gSSURGO) Database for California. USDA Natural Resources Conservation Service. https://gdg.sc.egov.usda.gov/

Steel, Z. L., M. J. Koontz, and H. D. Safford. 2018. The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. Landscape Ecology 33:1159–1176.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:8.

Stephens, S. L., B. M. Collins, C. J. Fettig, M. A. Finney, C. M. Hoffman, E. E. Knapp, M. P. North, H. Safford, and R. B. Wayman. 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. BioScience 68:77–88.

Strobl, C., A. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. Conditional variable importance for random forests. BMC Bioinformatics 9:307.

Strobl, C., T. Hothorn, and A. Zeileis. 2009. Party On! A new conditional variable importance measure for random forests available in the party package. Department of Statistics, University of Munich, Munich, Germany.

Thompson, J. R., and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management 258:1684–1694.

Underwood, E. C., H. D. Safford, N. A. Molinari, and J. E. Keeley, editors. 2018. Valuing chaparral: ecological, socioeconomic, and management perspectives. Springer, Cham, Switzerland.

USDA Forest Service Pacific Southwest Region. 2018*a*. Aerial Detection Survey GIS Data. https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046696

USDA Forest Service Pacific Southwest Region. 2018*b*. Vegetation burn severity—1985 to 2017. https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833

Van de Water, K. M., and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecology 7:26–58.

Van Gunst, K. J., P. J. Weisberg, J. Yang, and Y. C. Fan. 2016. Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality. Forest Ecology and Management 359:19–32.

van Mantgem, P. J., et al. 2009. Widespread increase of tree mortality rates in the Western United States. Science 323:521–524.

van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. Climatic stress increases forest fire severity across the western United States. Ecology Letters 16:1151–1156.

Viedma, O., F. Chico, J. Fernández, C. Madrigal, H. Safford, and J. Moreno. 2020. Disentangling the role of prefire vegetation vs. burning conditions on fire severity in a large forest fire in SE Spain. Remote Sensing of Environment 247:111891.

Wayman, R., and H. Safford 2020. Recent bark beetle outbreaks influence wildfire severity in mixed-conifer forests of the Sierra Nevada, California, USA. Dryad, data set. https://doi.org/10.25338/B8T92S

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7:29.

Wood, S. 2017. Generalized additive models: an introduction with R. Second edition. Taylor & Francis Group, Boca Raton, Florida, USA.

Wood, S. 2019. mgcv: mixed GAM computation vehicle with automatic smoothness estimation. R package version 1.8.28. https://CRAN.R-project.org/package=mgcv

Young, D. J. N., M. Meyer, B. Estes, S. Gross, A. Wuenschel, C. Restaino, and H. D. Safford. 2019. Forest recovery following extreme drought in California, USA : natural patterns and effects of pre-drought management. Ecological Applications 30:e02002.

Young, D. J. N., J. T. Stevens, J. M. Earles, J. Moore, A. Ellis, A. L. Jirka, and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecology Letters 20:78–86.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2287/full

Data Availability

Data are available from the Dryad Digital Repository (Wayman and Safford 2020): https://doi.org/10.25338/B8T92S.