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Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA

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Abstract. Extreme drought stress and associated bark beetle population growth contributed to an extensive tree mortality event in California, USA, resulting in more than 129 million trees dying between 2012 and 2016. Although drought is an important driver of this mortality event, past and ongoing fire suppression and the consequent densification of forests may have contributed. In some areas, land management agencies have worked to reduce stand density through mechanical treatments and prescribed fire to restore forests to less dense, more open conditions that are presumably more resilient to disturbance and changing climate. Here, we evaluate if stand structural conditions associated with treated (e.g., thinned and prescribed burned) forests in the Sierra Nevada of California conferred more resistance to the bark beetle epidemic and drought event of 2012–2016. We found that, compared to untreated units, treated units had lower stand densities, larger average tree diameters, and greater dominance of pines (*Pinus*), the historically dominant trees. For all tree species studied, mortality was substantially greater in climatically drier areas (i.e., lower elevations and latitudes). Both pine species studied (ponderosa pine [*Pinus ponderosa*] and sugar pine [*Pinus lambertiana*]) had greater mortality in areas where their diameters were larger, suggesting a size preference for their insect mortality agents. For ponderosa pine, the tree species experiencing greatest mortality, individual-tree mortality probability (for a given tree diameter) was significantly lower in treated stands. Ponderosa pine mortality was also positively related to density of medium- to large-sized conspecific trees, especially in areas with lower precipitation, suggesting that abundance of nearby host trees for insect mortality agents was an important determinant of pine mortality. Mortality of incense cedar (*Calocedrus decurrens*) and white fir (*Abies concolor*) was positively associated with basal area, suggesting sensitivity to competition during drought, but overall mortality was lower, likely because the most prevalent and effective mortality agents (the bark beetles *Dendroctonus brevicomis* and *D. ponderosae*) are associated specifically with pine species within our study region. Our findings suggest that forest thinning treatments are effective in reducing drought-related tree mortality in forests, and they underscore the important interaction between water and forest density in mediating bark beetle-caused mortality.

Key words: drought; forest thinning; precipitation; prescribed fire; Sierra Nevada; stand density; tree mortality.

INTRODUCTION

The 2012–2016 California drought may have been the most extreme in the last 1,000 yr (Griffin and Anchukaitis 2014, Robeson 2015), and an example of a "hot" drought where low levels of precipitation and high temperatures combine to increase drought intensity and amplify the ecological consequences (Overpeck 2013, Allen et al. 2015). Among the drought's many effects was the initiation of a severe tree mortality event (Paz-Kagan et al. 2017, Preisler et al. 2017, Young et al. 2017, Fettig et al. 2019). By December 2017, it was estimated that 129 million trees had died across the state, with the highest concentration along the west slope of the southern and central Sierra Nevada (USDA 2017). In this region, the primary mortality agents are bark

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beetles (Coleoptera: Curculionidae, Scolytinae; Fettig 2016) that have expanded their populations in large areas of water-stressed forest during the multi-year drought (Fettig et al. 2019). The western pine beetle (*Dendroctonus brevicomis*), which attacks ponderosa pine (*Pinus ponderosa*) was the primary driver of landscape-level mortality. However, the mountain pine beetle (*Dendroctonus ponderosae*), which attacks a number of pines (*Pinus* spp.), and the fir engraver beetle (*Scolytus ventralis*) have also played important roles (Fettig 2016).

Such high levels of tree mortality have caused widespread concern about the potential associated effects on watershed function, fire risk, and ecosystem resilience. One of the most economically important agricultural regions in North America is directly downstream of these affected forests and changes in the ecosystem structure and function of the watersheds upslope could have ripple effects on users across the state and nation (Brown et al. 2005, Bales et al. 2011). Firefighting agencies across the region have encountered intense burning conditions following extensive mortality. Mortality may modify the severity and behavior of wildfires, as dead and dying trees may contribute to fuel loading and continuity (Harvey et al. 2014, Stephens et al. 2018). The potential combination of drought-induced tree mortality and large, high-severity fires could precipitate major changes to ecosystem composition, structure, and function (McKenzie et al. 2008), as observed with other bark beetle outbreaks and mortality events (Morris et al. 2018). For example, some currently conifer-dominated landscapes are likely to transition to perpetual shrublands maintained by fire, while others may shift to hardwood-dominated systems that may be more tolerant of drought conditions and recurrent fire (Lenihan et al. 2008, Millar and Stephenson 2015, Tepley et al. 2017). Such structural and compositional changes may lead to changes in ecosystem function, with consequences for ecosystem services that humans depend on and value including ground and surface water provisioning, water and air quality, carbon sequestration, wildlife habitat, and recreational opportunities (Morris et al. 2018).

Mortality triggered by the 2012–2016 drought was concentrated in pines (particularly ponderosa pine), drier locations (generally lower elevations and latitudes), and larger trees (Paz-Kagan et al. 2017, Preisler et al. 2017, Young et al. 2017, Fettig et al. 2019). A coarse-scale analysis identified increased mortality in stands with more and/or larger trees, especially in dry sites, suggesting that water availability and competition for water play important roles in shaping susceptibility to bark beetles and ultimately tree mortality (Young et al. 2017). In addition to contributing to competition-related stress, high densities of conspecific trees may attract disproportionately high densities of one or more species of bark beetles that exhibit aggregation behavior (Thistle et al. 2004, Raffa et al. 2008). However, some recent plot-scale analyses in California (Fettig et al. 2019) and the western United States (van Mantgem et al. 2016) have found that individual tree mortality probability is negatively correlated with stand density (though in some cases only weakly), potentially indicating that, at more local scales, factors associated with stand density (such as site suitability) may affect stress and mortality in the opposite direction as competition. The influence of different stand variables also varies through the course of an infestation, which can complicate comparisons among studies (Egan et al. 2016). Some bark beetle species tend to target larger pines (generally >10 or 15 cm diameter), presumably because of their larger carbohydrate stores (Furniss and Carolin 2002). However, in some cases, the largest trees may be less prone to attack due to their ability to access deep water stores, though even these trees become susceptible in later outbreak stages (Egan et al. 2016).

Because of the potential for stand density to influence competition and mortality patterns, there has been substantial interest in using forest management interventions that reduce stand density and/or basal area (such as mechanical thinning and prescribed fire) to decrease the probability of drought-related mortality (Kolb et al. 2016). Over a century of fire suppression in western U.S. forests, combined with institutional barriers to other forms of management, have led to widespread densification (Dolanc et al. 2014, McIntyre et al. 2015), leaving forests more vulnerable to drought, fire, insects, and pathogens (Hessburg and Agee 2003, Hicke et al. 2016). Through the use of mechanical thinning, prescribed fire, and strategically managed wildfire, managers may begin to reverse this densification, restore historical stand structure and species composition, and increase the resilience of forests (Fettig 2012, North et al. 2012*b*). Nonetheless, because of the complex relationship between stand structure, climate, tree vigor, insects, and tree mortality, it is unclear whether mortality patterns will respond to direct manipulations of stand structure in the same way that they respond to existing structural variability. Some limited work to date has documented reduced mortality in stands that have been treated with mechanical thinning (Busse et al. 2009, Egan et al. 2010) or prescribed fire (van Mantgem et al. 2016), but no work to our knowledge has evaluated the impact of density reduction treatments during an extreme mortality episode triggered by a prolonged, global change-type drought.

In this study, we assess whether forest thinning and prescribed fire treatments reduced tree mortality resulting from the extreme 2012–2016 California drought. We studied the effect of pre-drought thinning treatments on forest mortality along a latitudinal and climatic gradient on the west slope of the southern and central Sierra Nevada in and near landscapes where the most extreme mortality occurred. We hypothesized that treated stands would have lower tree densities and that these lower tree densities would confer greater resistance to drought and beetle-driven tree mortality.

METHODS

Study site

The study site was located in the southern and central Sierra Nevada of California (Fig. 1). Climate across the study site is Mediterranean, with cool wet winters dominated by a low-pressure system in the Northern Pacific and warm dry summers dominated by high pressure. Summers are characterized by an annual drought period of approximately three to five months. Precipitation decreases from north to south with approximately twice as much precipitation in the northern Sierra Nevada as compared to the south. Our study focused on lower montane "mixed-conifer" forest, which adjoins foothill woodland at its lower edge and red fir (*Abies magnifica*)-dominated forest at its upper edge (van Wagtendonk 2018). Common tree species include ponderosa pine, sugar pine, incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and black oak (*Quercus kelloggii*). The historic mixed-conifer fire regime of frequent low-intensity fires has been replaced with infrequent, often stand-replacing fires, due largely to human management including past logging of most large trees, grazing, and long-term (and ongoing) fire suppression (Safford and Stevens 2017). As a result, forest structure has also experienced greatly reduced heterogeneity, with most stands today dominated by small and medium size-classes of shade tolerant conifers, particularly white fir and incense cedar (Knapp et al. 2013, Safford and Stevens 2017).

Field data

In 2017, we collected plot data at 10 pairs of sites (treated and untreated) in the central and southern Sierra Nevada, from the Eldorado National Forest in the north (NF; centroid 38.66° N, 120.46° W), to the Sierra National Forest in the south (37.03° N, 119.29° N; Fig. 1). Sites were located on lands administered by the United States Forest Service (USFS), National Park Service (NPS), and Bureau of Land Management (BLM). Treated areas were defined as areas that had received multiple thinning and/or fire (either prescribed fire or pile burning) treatments intended to substantially reduce stand density, primarily in the smaller tree size classes, and increase stand resilience. Treated stands were selected to meet the following conditions: (1) treatments involved multiple mechanical and/or prescribed burn treatments intended to increase stand resilience and health; (2) the treatments were completed after 2000 (i.e., such that the time between treatment and outbreak of the drought was within the mean fire return interval in these forests before the institution of fire suppression; Van de Water and Safford 2011); (3) the treated area was a minimum of 4 ha; (4) the area was composed primarily of yellow pine or mixed-conifer forest; (5) the area contained greater than background mortality (≥7 dead overstory trees/ha, as indicated by Aerial Detection Survey data and by USFS staff expert opinion); and (6) there was a nearby (<1 km away) untreated area that was abiotically comparable, to serve as a control. Data on treatments (date, location, size, and prescription)

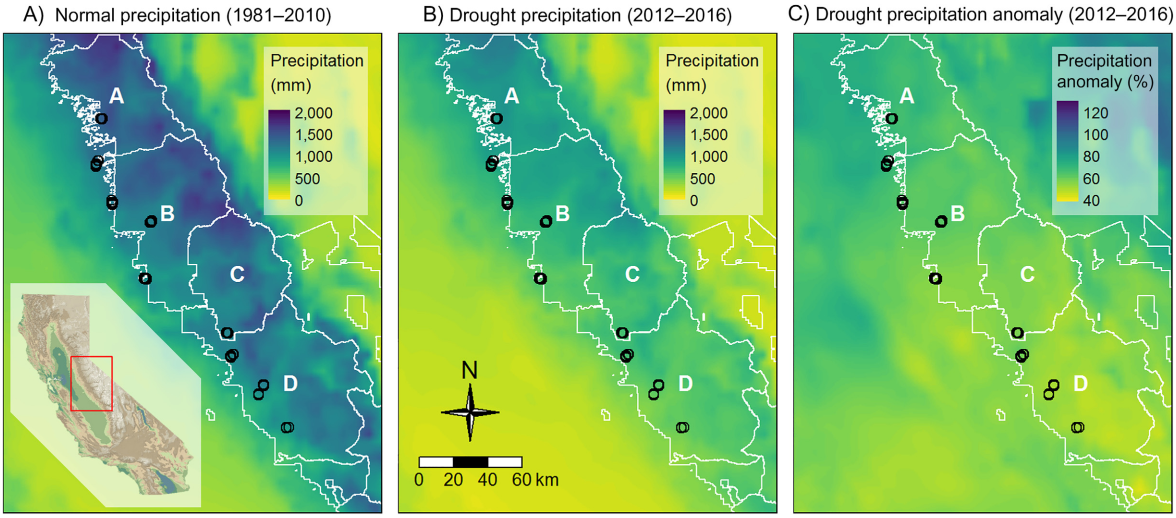
A) Normal precipitation (1981–2010)
B) Drought precipitation (2012–2016)
C) Drought precipitation anomaly (2012–2016)

FIG. 1. Location of study sites (black circles) relative to spatial variation in (A) normal annual precipitation from the period from 1981 to 2010, (B) mean annual precipitation during recent California drought (i.e., the water years ending in 2012 through 2016), and (C) mean precipitation anomaly (percentage of normal) during the drought. White outlines indicate National Forest and National Park boundaries, with units represented by letters: A, Eldorado National Forest; B, Stanislaus National Forest; C, Yosemite National Park; D, Sierra National Forest. The inset map in panel A shows the location of the study region within the state of California, USA.

were obtained from the USDA Forest Service Activity Tracking System (FACTS; USDA Forest Service 2016) and confirmed with local silviculture staff and via field visits. We collected data from all pairs of treated and untreated sites within our study region that met our criteria.

We overlaid a 50 × 50 m grid of points across all treated and paired untreated sites and randomly selected seven or eight of these points per area (treated or untreated) to serve as study plot locations, for a total of 159 plots. Untreated plots were located 50–1,000 m from treated stands and were paired with treated plots by slope, aspect, and successional stage. All plots were a minimum of 50 m from openings, roads, trails, and large canopy gaps associated with unproductive sites or recent disturbance (e.g., hazard tree removal, stand-replacing wildfire). Plot elevations ranged from 912 m to 1,677 m and average annual precipitation ranged from 830 to 1,270 mm (1981–2010; Prism Climate Group 2018), with the higher precipitation values at the northern sites (Fig. 1).

We surveyed vegetation in each study plot following a modified version of the USDA Forest Service common stand exam protocol (USDA Forest Service 2007). Trees (conifer and hardwood species) greater than 7.6 cm diameter at breast height (DBH) were sampled in a 12.6 m radius plot (500 m^2, 0.05 ha). For each tree sampled, species, DBH, and status (live, recently dead, and less recently dead) were recorded. We considered recently dead trees (those retaining at least some needles) as mortality potentially attributable to the 2012–2016 drought, whereas we assumed dead trees with no needles and few fine branches had died prior to the drought and thus excluded them from analyses (Keen 1929; sensu Egan et al. 2010).

Analysis

We tested the effect of treatment on stand structure and composition variables (tree density, basal area, mean tree diameter, and percentage of trees that are pines) at the plot level using simple generalized linear regressions with treated status (yes/no) as the only predictor. We modeled tree basal area and mean diameter using a Gaussian model, density (number of trees per plot) using a Poisson model, and percentage of trees that are pines (number of pines out of total number of trees) using a binomial model.

We used binomial regression to model species-specific individual-tree mortality probability for all trees with a diameter at breast height (DBH) > 7.6 cm. We conducted the analysis at the plot level and modeled mortality as the number of dead trees of the focal species out of the total number of trees of the focal species (with a separate model for each species). We selected as focal species the five most common tree species across all plots (ponderosa pine, sugar pine, white fir, incense cedar, and black oak), but we did not perform analyses for black oak because it experienced extremely low mortality (Table 1). We evaluated the following predictor variables: mean DBH of the focal species (to account for potential tree size preferences of insects (Fettig et al. 2019); basal area (BA) based on all tree species (as an index of competition); density (trees per hectare; TPH) of the focal species (using all trees, trees > 20 cm DBH, and trees > 30 cm DBH, as separate candidate metrics to represent density of hosts for insects based on previously observed patterns; Furniss and Carolin 2002, Fettig et al. 2019); 30-yr mean annual precipitation from 1981 to 2010; and the interaction of precipitation with the tree density and BA variables. We obtained precipitation values via bilinear interpolation from the PRISM 800-m resolution gridded 30-yr 1981–2010 normal precipitation data set (PRISM Climate Group 2018).

In modeling the response (individual-tree mortality probability), we evaluated all possible combinations of the candidate predictor variables (listed in previous paragraph), with the restriction that models could only include a maximum of one tree density (TPH) predictor. For each focal species, we selected the set of predictor variables yielding the lowest AIC value as the best-fit model (Appendix S1: Table S1). We refer to the resulting models as the “structure-based models” throughout the text. Next, to directly assess the effect of stand treatments (i.e., thinning and/or prescribed fire), we fit an additional set of models that excluded all stand structure variables and instead included a factorial (yes/no) variable for treated status (Appendix S1: Table S2). We refer to the resulting models as the “treated status-based models.”

We interpreted model coefficient magnitude and significance following a Bayesian framework. Assuming uniform priors, we simulated the posterior distribution of the coefficients and computed the mean and 95% credible interval (Gelman and Hill 2007). For ease of interpretation by readers familiar with frequentist statistics, we refer to parameters for which the credible interval excludes zero as “significant.”

TABLE 1. Tree counts and mortality rates across all study plots. Mortality is presented as the mean percentage of stems or basal area across all plots (in separate columns), with 25th and 75th percentiles in parentheses.

Species	Number of trees	Mortality by stems (%)	Mortality by basal area (%)
White fir	422	24 (0,37)	25 (0,42)
Incense cedar	1,310	21 (0,33)	22 (0,29)
Sugar pine	168	35 (0,78)	35 (0,86)
Ponderosa pine	1,095	40 (0,91)	42 (0,99)
Black oak	191	1 (0,0)	0 (0,0)

Notes: Mortality is presented as the mean percentage of stems or basal area across all plots (in separate columns), with 25th and 75th percentiles in parentheses.

We assessed goodness of model fit and discrimination by calculating McFadden's pseudo-R^2 (McFadden 1973) and by plotting the fitted vs. observed proportion of dead trees per plot for all plots with ≥ 4 trees. To visualize model fits, we used the best-fit models for each species to predict individual-tree mortality probability across a range of values of the relevant predictor variables, representative of the range of values observed across the data set. We tested for the presence of unexplained spatial autocorrelation in mortality patterns by computing Moran's I statistic (Moran 1950) for among-plot distances ranging from 50 to 2,000 m, in increments of 50 m, for the residuals of the best-fit ponderosa pine structure-based model. Spatial autocorrelation was minimal ($I < 0.2$ for all distance classes, and I did not decline with distance). We performed all analyses in R 3.5.0 (R Core Team 2018), using the packages lme4 (Bates et al. 2015) for fitting binomial models, MuMIn (Bartoń 2018) for performing model selection, and ncf (Bjørnstad 2018) for computing Moran's I.

Results

Mortality, stand structure, and composition

Across the study area, relative to untreated plots, treated plots had significantly lower basal area (mean 38 vs. 53 m^2/ha) and stem density (mean 325 vs. 601 trees/ha) and significantly greater mean tree diameter at breast height (mean 43 vs. 29 cm) and relative abundance of pines (mean 49% vs. 37% of stems; Fig. 2, Table 2). Across all study plots, ponderosa pine experienced the greatest mortality of all study species (mean 40% of trees > 7.6 cm DBH died), followed by sugar pine (35%), white fir (24%), incense cedar (21%), and black oak (1%; Table 1). The extent of mortality varied substantially among plots; for example, for ponderosa pine, the interquartile range (25th to 75th percentiles) of mortality spanned 0% to 91%.

Stand structure-based models

For ponderosa pine and incense cedar, stand structure and mean annual precipitation variables explained a substantial proportion of the variation in mortality among plots (pseudo-R^2 = 0.44 for ponderosa pine and 0.36 for incense cedar), while models for sugar pine and white fir explained less variation (pseudo-R^2 = 0.21 for sugar pine and 0.16 for white fir; Appendix S1: Fig. S1).

For all four conifer species, mortality increased significantly and substantially with decreasing normal precipitation (Figs. 3 and 4, Table 2). This effect was the strongest for ponderosa pine: at intermediate levels of all other predictors, mean model-predicted ponderosa pine mortality increased from 27% in wetter areas (1,144 mm normal annual precipitation, reflecting the 75th percentile of precipitation values across all study plots) to 59% in areas with low precipitation (998 mm, reflecting the 25th percentile; Fig. 3).

Although the best-fit models for all species included precipitation, the most important stand structure and composition variables varied by species (Appendix S1: Table S1).

Ponderosa pine.—For ponderosa pine, mortality was significantly greater in areas with greater mean diameter of ponderosa pine trees, all else equal. For example, in relatively dry conditions (998 mm normal annual precipitation), model-predicted ponderosa pine mortality increased from 36% in areas where mean ponderosa pine diameter was 15 cm to 79% in areas where mean ponderosa pine diameter was 90 cm, given average values of basal area and conspecific density (Fig. 3). Mortality was also significantly greater in areas with a greater density of conspecific trees (ponderosa pines) with DBH > 30 cm, all else equal. The best-fit model included a significant interaction between conspecific tree density and normal precipitation, whereby the relationship between conspecific tree density and mortality probability was strongly positive in dry areas and weak to slightly negative in wet areas (Fig. 3). In dry areas, predicted mean mortality probability ranged from 38% at low conspecific tree densities (25 trees over 30 cm DBH per hectare) to 72% at high conspecific densities (120 trees over 30 cm DBH per hectare; Fig. 3). Total tree basal area was also an important predictor of ponderosa pine mortality, but its effect also depended on normal precipitation: in wet areas, mortality probability increased slightly with increasing basal area, but in dry areas, mortality probability decreased with increasing basal area. The effect of basal area, while significant, was weak relative to the effects of precipitation and conspecific density (Fig. 3, Table 2).

Sugar pine.—As with ponderosa pine, mortality of sugar pine was significantly and substantially greater in areas with greater mean sugar pine diameter (Fig. 3). For example, under relatively dry conditions (998 mm normal annual precipitation), mean predicted sugar pine mortality increased from 35% in areas where mean sugar pine diameter was 15 cm to 77% in areas where mean sugar pine diameter was 90 cm, given average values of basal area and conspecific density (Fig. 3). Sugar pine mortality was significantly associated with interactions between precipitation and conspecific tree density and between precipitation and total basal area. However, the directions of these relationships were the reverse of those for ponderosa pine. Specifically, sugar pine mortality responded positively to increasing basal area in dry areas (from 45% at a basal area of 25 m^2/ha to 59% at 70 m^2/ha) and negatively to increasing basal area in wet areas (from 48% at a basal area of 25 m^2/ha to 20% at 70 m^2/ha; Fig. 3). In contrast, conspecific tree density was related negatively (though very weakly) to sugar pine mortality at low precipitation levels and positively to mortality at high precipitation levels. The best model for sugar pine was achieved by including the density of conspecifics > 20 cm, rather than > 30 cm as was the case

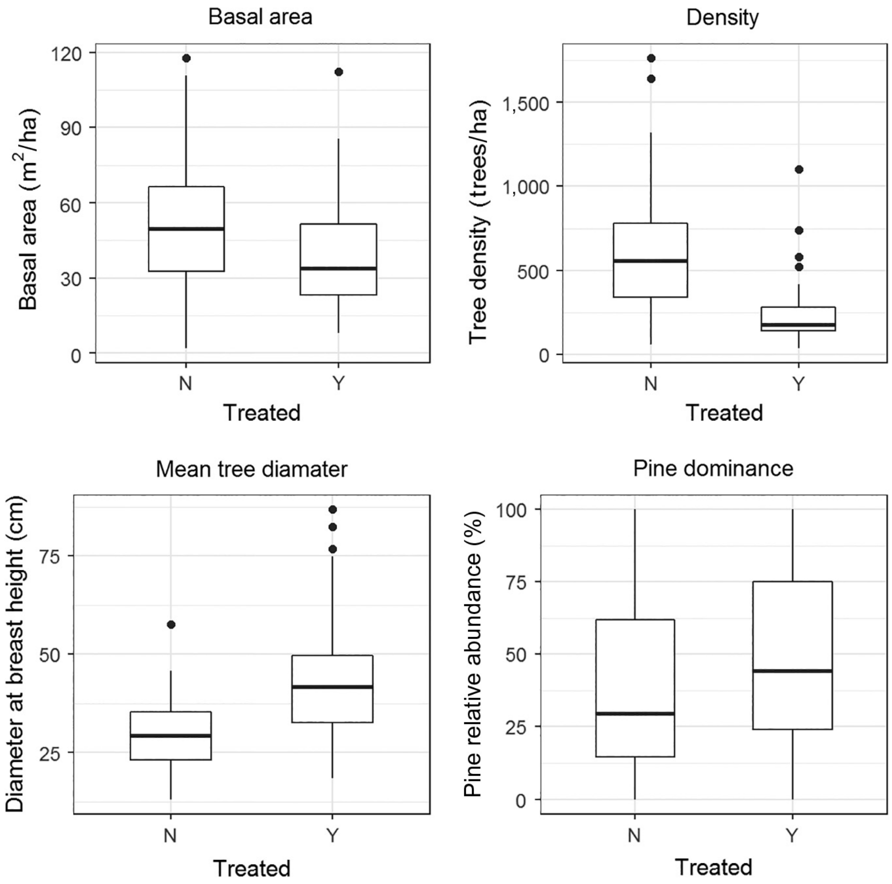

FIG. 2. Stand structure and composition values across all study plots, summarized by treated status. The heavy horizontal line depicts the median; the limits of the boxes depict the interquartile range; the whiskers indicate the largest and smallest values not more than 1.5 times the interquartile range beyond the limits of the boxes. Values represent the contribution of all trees > 7.6 cm diameter at breast height.

TABLE 2. Model coefficients (with 95% credible intervals in parentheses) for the best-fit structure-based mortality model for each species.

Species	Intercept	Basal area	Mean diameter	PPT†	Conspecific tree density (>30 cm)	Basal area × PPT	Conspecific tree density (>30 cm) × PPT	Conspecific tree density (>20 cm)	Conspecific tree density (>20 cm) × PPT
Ponderosa pine	**−0.5 (−0.69, −0.31)**	−0.15 (−0.36,0.07)	**0.38 (0.18,0.6)**	**−1.23 (−1.45, −1)**	**0.41 (0.27,0.54)**	**0.5 (0.32,0.68)**	**−1.02 (−1.26, −0.79)**	–	–
Sugar pine	**−0.55 (−1.04, −0.06)**	−0.44 (−0.99,0.11)	**0.79 (0.12,1.45)**	**−0.85 (−1.52, −0.24)**	–	**−0.96 (−1.86, −0.06)**	–	**0.75 (0.32,1.2)**	**1.09 (0.47,1.71)**
White fir	**−1.41 (−1.68, −1.16)**	**0.42 (0.13,0.73)**	–	**−0.82 (−1.15, −0.51)**	–	–	–	–	–
Incense cedar	**−2.1 (−2.35, −1.86)**	**0.59 (0.36,0.8)**	–	**−1.75 (−2.06, −1.46)**	**−0.46 (−0.63, −0.28)**	**0.51 (0.3,0.7)**	–	–	–

Notes: Each row reflects a separate model. Predictors were centered and standardized (by dividing by the standard deviation) prior to fitting models to facilitate interpretation of effect sizes. Coefficients with credible intervals that exclude zero are shown here in boldface type and interpreted as “significant” throughout the text. If the best-fit model for a given species did not include a given coefficient, the coefficient is shown here as a dash.

† PPT, mean annual precipitation climatic normal (1981–2010).

for ponderosa pine. Conspecific tree density was related less strongly to mortality than were precipitation, mean tree diameter, and basal area (Table 2).

White fir.—The best-fit model for white fir included only precipitation and basal area. White fir mortality increased significantly but moderately with increasing basal area. For example, in dry sites (998 mm normal annual precipitation), mean predicted white fir mortality increased from 22% at a basal area of 20 m^2/ha to 39% at a basal area of 80 m^2/ha (Fig. 4).

Incense cedar.—As with white fir, incense cedar mortality increased significantly (though weakly) with increasing basal area. Although there was also a significant positive interaction between precipitation and basal area (whereby the positive relationship between basal area and morality was stronger in wetter sites), this effect was not readily apparent because incense cedar mortality was so low in wetter sites (Fig. 4). In drier areas, mean predicted incense cedar mortality increased weakly from 24% at a basal area of 25 m^2/ha to 31% at a basal area of 65 m^2/ha. In contrast, incense cedar mortality was significantly (though weakly) negatively associated with conspecific tree density. As with ponderosa pine, incense cedar mortality was better explained by the density of conspecifics >30 cm, as opposed to >20 cm or >7.6 cm. However, the direction of the relationship between conspecific density and mortality was the reverse of what it was for ponderosa pine.

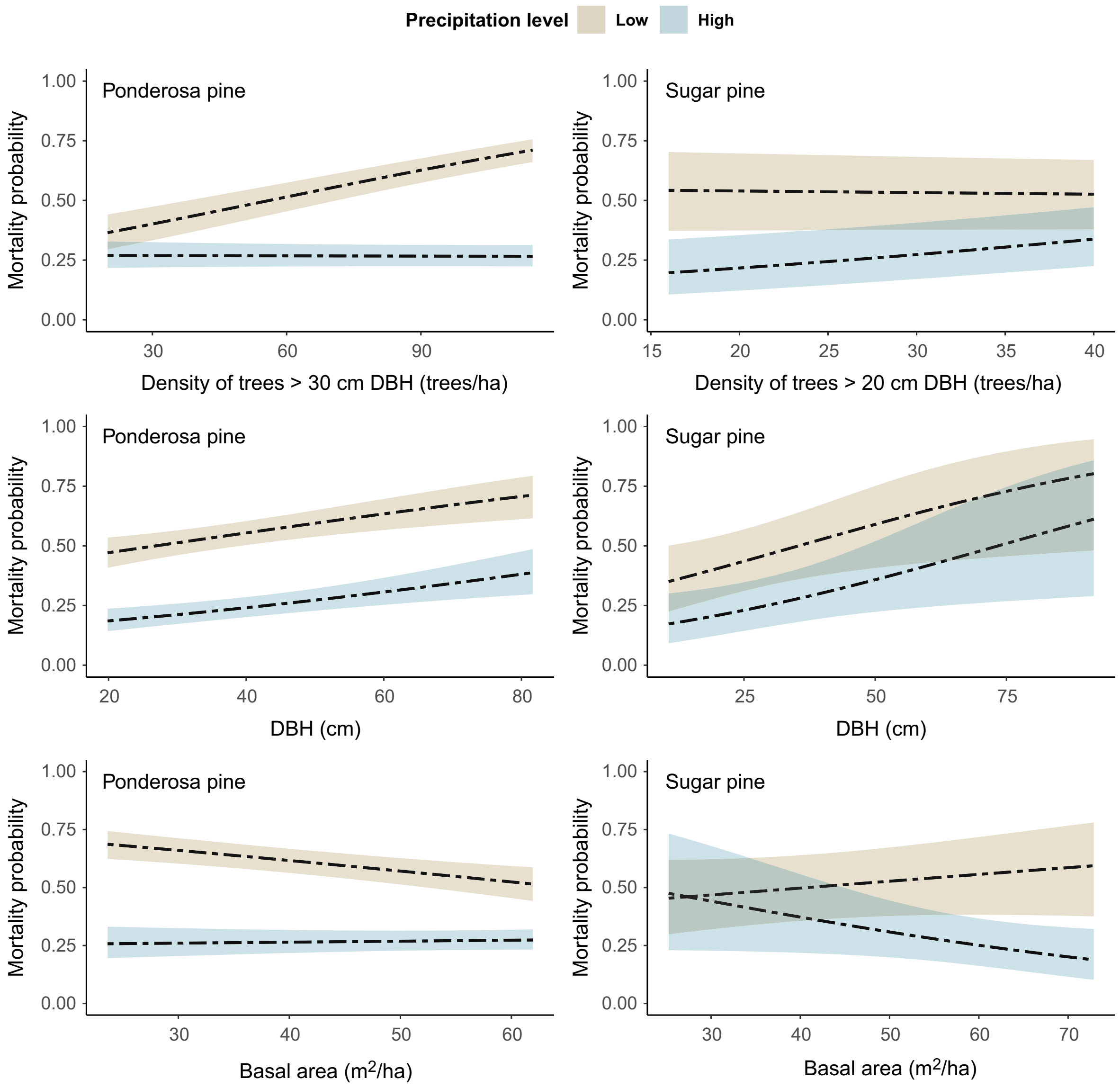

FIG. 3. Predictions from the statistical models explaining individual-tree mortality probability for ponderosa and sugar pines using tree density (trees > 30 cm and > 20 cm), diameter at breast height (DBH), and basal area. For both pine species, probability of mortality increases with increasing conspecific stand density and greater tree size and the increase in mortality is greatest in dry sites. Probability of mortality decreases as a function of basal area in dry conditions for ponderosa pine and in wet sites for sugar pine, suggesting that microsite conditions that favor more trees may buffer against drought conditions.

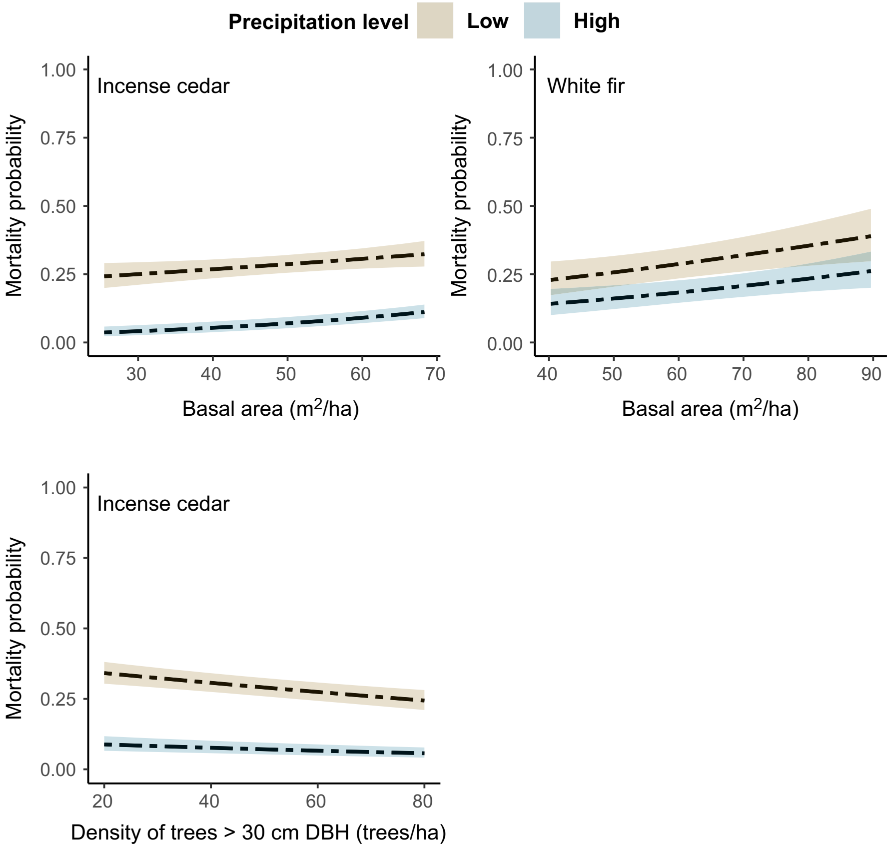

FIG. 4. Predictions from the statistical models explaining individual-tree mortality probability for incense cedar and white fir using basal area and trees density (>30 cm). Increasing basal area is associated with increased probability of mortality in both dry and wet sites.

Treatment-status-based models

We next directly tested the effect of stand density reduction treatments on tree mortality by fitting models explaining a tree's status (live or dead) given a plot's treated status (treated or untreated) and covariates (precipitation and plot-level mean diameter of the focal tree species). For ponderosa pine and incense cedar, these variables explained a substantial proportion of the variation in mortality among plots (pseudo-$R^2 = 0.33$ for ponderosa pine and 0.31 for incense cedar). They explained less variation in the other species (pseudo-$R^2 = 0.21$ for sugar pine and 0.16 for white fir).

The models identified a significant effect of treatment in reducing mortality for ponderosa pine (Fig. 5, Table 3). For example, in a relatively dry site (normal annual precipitation = 1,000 mm), mean predicted mortality probability of an intermediate-sized ponderosa pine dropped from 76% in untreated stands to 61% in treated stands. Sugar pine mortality was marginally but nonsignificantly lower in treated stands. For white fir and incense cedar, the best-fit models included a marginally significant interaction between treated status and normal precipitation (Table 4), whereby treatment was more effective at reducing mortality in wetter areas; however, this trend was not significant, and the overall effect of treatment was also weak and non-significant. Nonetheless, in the driest sites (but not intermediate or wet sites), predicted incense cedar mortality probability was substantially greater in treated vs. untreated areas, and the credible intervals of predicted mortality for treated and untreated stands did not overlap, suggesting the pattern is meaningful.

The treated status-based statistical models for all species detected and accounted for a significant negative relationship between mortality probability and normal precipitation (Table 3). Additionally, the model for ponderosa pine identified a moderate and significant positive relationship between diameter of ponderosa pine and mortality probability. The models for sugar pine and white fir identified a marginally significant positive relationship between mean diameter of the focal species and mortality probability. As with the structure-based model, including mean tree diameter did not improve the fit of the treatment-based model for incense cedar (Appendix S1: Table S2).

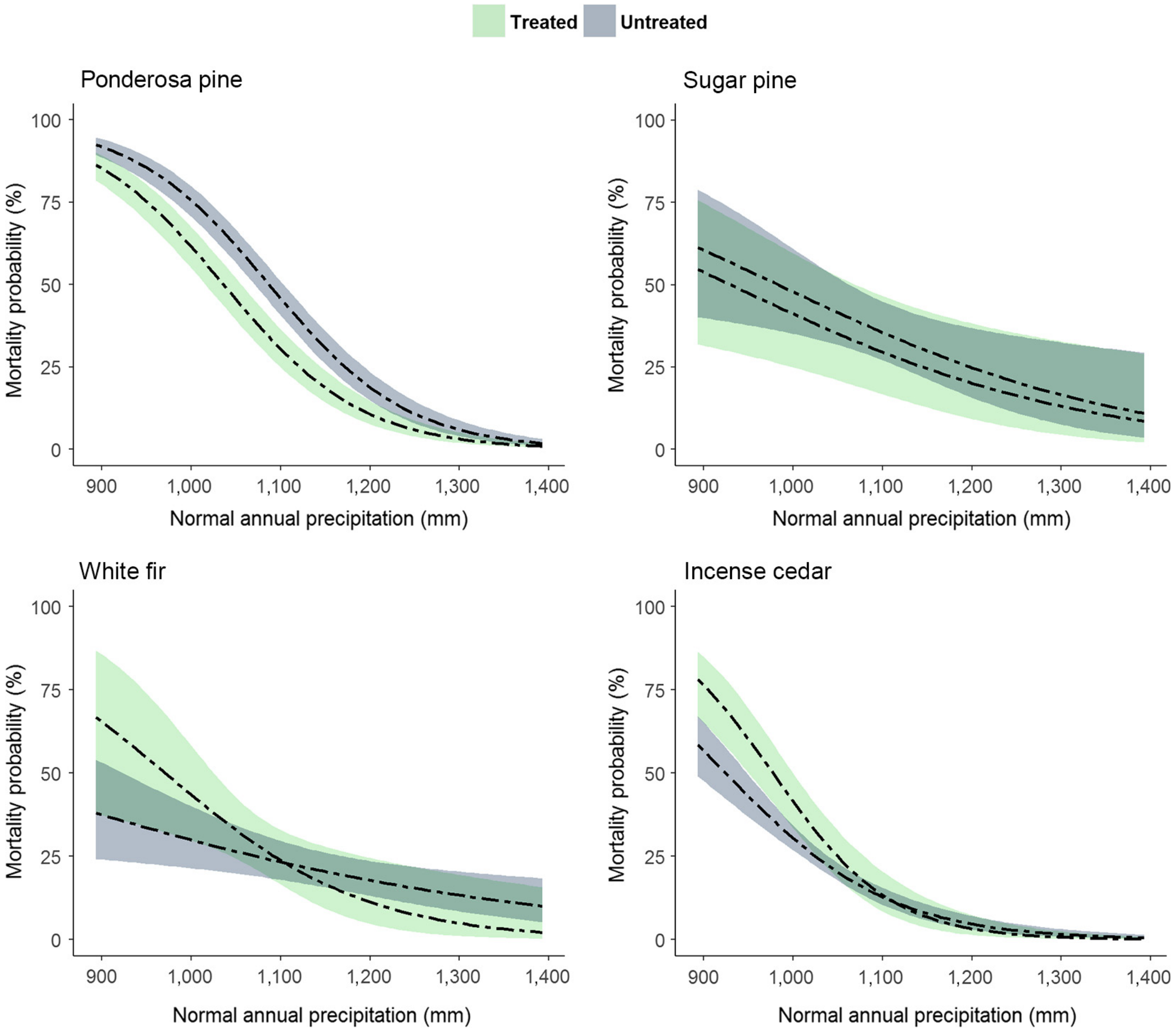

FIG. 5. Predictions from the statistical models explaining individual-tree mortality probability using treated status, precipitation, and mean plot-level tree diameter of the focal species. The shaded bands reflect the 95% credible interval capturing uncertainty in the model coefficients. For tree species for which diameter was included in the statistical model (ponderosa pine, sugar pine, and white fir), predictions are made at the mean diameter value across all plots. The range of precipitation values for which predictions are displayed represents the 2.5th to 97.5th percentiles across all plots.

TABLE 3. Model coefficients (and 95% credible intervals) for models testing the effect of treatment on stand structure and composition.

Metric	Intercept	Treated
Basal area	**52.73 (47.37,57.95)**	**−14.84 (−23.07, −6.98)**
Stem density	**3.4 (3.36,3.44)**	**−0.94 (−1.02, −0.87)**
Mean tree diameter	**29.37 (26.6,32)**	**14.12 (10.21,17.99)**
Proportion pine	**−0.57 (−0.65, −0.49)**	**0.27 (0.11,0.42)**

Notes: Each row reflects a separate model. Coefficients with credible intervals that exclude zero are shown here in boldface type and interpreted as "significant" throughout the text. Basal area and mean tree diameter were modeled using a Gaussian distribution, stem density was modeled using a Poisson distribution, and pine proportion was modeled using a binomial distribution.

DISCUSSION

Density reduction treatments were effective at altering stand structure and promoting resistance to drought. Treated units had fewer trees per hectare and less basal area. The effective reduction in stand density and basal area was important because it allowed a quantitative comparison of mortality patterns in treated and untreated stands that were presumably driven by a difference in density-dependent competition and abundance of host trees for insects. While mean annual precipitation was also strongly associated with mortality, it varied primarily over latitudinal and elevational gradients rather than finer spatial scales within forest landscapes (Fig. 1). In contrast, tree density and basal area, which are also important predictors of mortality

TABLE 4. Model coefficients (and 95% credible intervals) for the best-fit treatment status-based mortality model for each species.

Species	Intercept	Mean diameter	PPT†	Treated	PPT × Treated
Ponderosa pine	−0.03 (−0.24,0.18)	**0.69 (0.48,0.9)**	**−1.71 (−1.93, −1.48)**	**−0.66 (−1, −0.32)**	–
Sugar pine	**−0.58 (−0.99, −0.18)**	0.46 (−0.08,0.97)	**−0.64 (−1.1, −0.16)**	−0.27 (−1.19,0.55)	–
White fir	**−1.35 (−1.68, −1.04)**	0.26 (−0.05,0.55)	**−0.48 (−0.81, −0.13)**	−0.24 (−0.88,0.48)	−0.79 (−1.72,0.15)
Incense cedar	**−1.9 (−2.13, −1.68)**	–	**−1.45 (−1.79, −1.13)**	0.06 (−0.46,0.6)	−0.57 (−1.21,0.05)

Notes: Each row reflects a separate model. Predictors were centered and standardized (by dividing by the standard deviation) prior to fitting models to facilitate interpretation of effect sizes. Coefficients with credible intervals that exclude zero are shown here in boldface type and interpreted as "significant" throughout the text. If the best-fit model for a given species did not include a given coefficient, the coefficient is shown here as a dash.

† PPT, mean annual precipitation climatic normal (1981–2010).

patterns, vary at the stand scale and can be manipulated via forest restoration treatments. Our study provides evidence that treatment can be effective in increasing resistance to drought and beetle-induced mortality, even mortality resulting from a drought of historically unprecedented severity.

Conifer mortality was mainly associated with mean annual precipitation, number of conspecific trees per hectare, and/or basal area (depending on the species). All species exhibited greater mortality in normally drier sites (Fig. 3). In this particular drought event, drier areas experienced greater proportional reductions in precipitation (Fig. 1), such that increased mortality in dry sites also reflects increased mortality where drought was more intense. Greater mortality is often observed in drier sites and/or under more intense drought (Allen et al. 2015, Young et al. 2017, Fettig et al. 2019), both of which correspond with decreased water availability. Multiple consecutive drought years have been associated with dramatic increases in populations of some bark beetle species (Raffa et al. 2008, Egan et al. 2016), the proximate drivers of most mortality in this event (Fettig et al. 2019), likely because the beetles can more readily colonize and reproduce within trees that are weakened by drought.

In contrast to their unified responses along moisture gradients, species responded differentially to stand structure variables. Many of these differences can also be explained by the behavior and dynamics of the insects driving the mortality event. For example, both ponderosa and sugar pine exhibited increased mortality probability in stands with larger pines (even after accounting for the effects of basal area). Western pine beetle and mountain pine beetle, the most important insect pest species for these trees, are known to target larger trees as beetle outbreaks move into epidemic phases because the beetles can overwhelm the defense capabilities and access the larger carbohydrate stores of these larger trees (Safranyik and Wilson 2007, Egan et al. 2016). We did not observe a relationship between tree diameter and mortality probability in white fir and incense cedar, consistent with other studies observing no clear relationship between tree diameter (especially for trees > 20 cm dbh) and mortality in these shade-tolerant species (Egan et al. 2010, Pile et al. 2018, Fettig et al. 2019).

High conspecific tree density was strongly related to the highest probabilities of mortality for ponderosa pine (Fig. 3), consistent with previous research documenting increases in density-dependent mortality during extreme drought in the Sierra Nevada (Van Gunst et al. 2016, Young et al. 2017). Because we quantified tree density (TPH) using only trees of the focal species (e.g., of ponderosa pine trees when predicting ponderosa pine mortality), our metric may represent an influence of the density of trees that are hosts to insects more strongly than it represents competition. Numerous suitable host trees in close proximity can attract insects and facilitate their spread and population growth; other studies have found that density and proximity to brood trees is an important variable in predicting tree mortality (Egan et al. 2010, 2016). Nonetheless, even when conspecific tree density (presumably representing a host density effect) is important, the density of all species of trees (presumably representing a competition effect) can also be important (Hayes et al. 2009).

Among our study species, the relationship between conspecific tree density and mortality was by far the strongest in ponderosa pine, but it was present for this species only in dry areas (Fig. 3, Table 2), where trees were likely stressed prior to insect infestation. While there is greater dominance of pine in drier areas, our multiple-regression approach allows us to evaluate the effect of variation in pine dominance at a given precipitation level. The positive relationship between tree mortality and conspecific tree density that we observed in ponderosa pine is consistent with the behavior of western pine beetle, the primary proximal mortality agent for ponderosa pine in this event (Fettig et al. 2019), which uses aggregation behavior to target areas with suitable hosts (i.e., stressed trees of the appropriate species). Further supporting this interpretation, our model selection procedure consistently identified that mortality was best explained by the density of conspecifics > 20 cm diameter (in the case of sugar pine) or > 30 cm diameter (in the case of ponderosa pine) as opposed to > 7.6 cm diameter (i.e., all trees measured), consistent with the beetles' preference of larger trees (Furniss and Carolin

2002, Fettig 2018) and higher reproductive success where there is a higher density of suitable reproductive substrate.

Competition among trees is often better reflected by total tree basal area (and associated metrics like stand density index; SDI) than stand density (i.e., number of trees) alone, as basal area, SDI, and similar metrics incorporate both tree size and diameter (Avery and Burkhart 2002). Nonetheless, for ponderosa pine, basal area did not explain mortality in the direction we would expect if patterns were driven by competition: in dry sites, we observed (weak) declines in ponderosa pine mortality as basal area increased. We hypothesize that this relationship may be driven by microclimate variation at fine spatial scales: higher basal areas are often found in sites that have a more favorable microclimate and are consequently buffered from extreme drought effects. Fine-scale variation in site suitability (e.g., due to soils or micro-topography) would not be captured by coarse-scale climate variables. The important role of fine-scale variation in this relationship may explain why our results differ from those of coarser-scale studies that do identify a positive relationship between tree basal area and mortality (e.g., Young et al. 2017). Indeed, other recent plot-scale studies have identified a similar negative relationship between competition indices and individual-tree mortality probability (Fettig et al. 2019) or variables that explain mortality (e.g., growth rate; van Mantgem et al. 2016). In contrast to our observations in ponderosa pine, mortality of our other study species did respond to basal area variation in the direction expected (i.e., positively), either specifically in dry sites (in the case of sugar pine) or across all levels of precipitation (in the case of incense cedar and white fir). This may indicate that for these species, microsite buffering is less important than competition.

We also directly tested the effect of recent forest density reduction treatments on tree mortality. Our analysis revealed that for ponderosa pine, the species experiencing the greatest mortality, mortality probability for a tree of a given size was significantly, though moderately, reduced by treatment. The effectiveness of density reduction treatments in reducing mortality did not vary significantly with precipitation. We observed a similar relationship between treated status and mortality in sugar pine, though the effect was not significant. Our findings align with those of other studies, which have shown that mechanically thinned or prescribed-burned forests have healthier trees (Feeney et al. 1998, Stone et al. 1999, Fettig et al. 2007, Bradford and Bell 2017) and less mortality during drought (Busse et al. 2009, van Mantgem et al. 2016). However, our study is the first to our knowledge to evaluate effectiveness of density reduction treatments during an extreme mortality episode triggered by a prolonged, global change-type drought. For incense cedar, we observed a marginally significant interaction between treatment and precipitation, whereby forest density reduction treatment actually increased mortality in the driest areas (but not in wetter sites). We propose that treatment increased mortality of this shade-tolerant species via sudden changes in canopy microclimate conditions, including elevated exposure of formerly shaded trees to direct sunlight and increases in vapor pressure deficit and air temperature following thinning (Rambo and North 2009). These microclimate changes may increase evapotranspiration rates that lead to increased tree moisture stress and drought-related mortality (Allen et al. 2015). This interpretation is supported by the fact that the increase in mortality was greatest in dry sites, which represent relatively harsh growing conditions. In white fir, in contrast, we did not find a clear effect of treatment on mortality, consistent with other work finding little influence of thinning on drought-related mortality of white fir (Egan et al. 2010).

Management Implications

Forest management in the Sierra Nevada has long favored pines by removing more shade-tolerant species (e.g., white fir, incense cedar) that have grown more common due to fire suppression and are a large component of forest densification (Knapp et al. 2013). Moving forward, forest managers might consider cultivating a more diverse set of forest species to buffer against insects and pathogens that target individual species, particularly when they are at high densities, as well as projected increases in both drought and fire. For example, oaks (e.g., California black oak; canyon live oak, *Q. chrysolepis*), which were relatively underrepresented in our study sites (hardwood component averaged 8.2% across the entire study area), experienced very low mortality rates (Table 1) despite high levels of mortality in both shade-tolerant and shade-intolerant conifers in the drier portions of our study area. Transitions from pine to oak over the last century have been documented at lower elevations throughout California (Thorne et al. 2008, McIntyre et al. 2015). The promotion of oaks and other hardwoods in lower montane stands of the region may confer greater stand resistance to future hotter droughts and bark beetle outbreaks, as well as greater resilience to disturbances like fire, since most hardwood species resprout after topkill, resulting in the maintenance of key ecosystem services regardless of transitory changes in tree species composition (i.e., oaks replacing pines; Millar and Stephenson 2015). California managers can look to the Mediterranean Basin for inspiration and guidance in this respect. Here, where forests share climate and major tree genera with California forests, modern management and restoration strategies in semiarid landscapes are often focused on shifting the dominance of forests from pines to more resilient hardwood species like oaks and madrone (Vallejo et al. 2012, Safford and Vallejo, in review).

The recent drought in California was markedly outside of the 500–1,000 yr range of variability (Griffin and Anchukaitis 2014, Robeson 2015), and empirical temperature trends and modeled climate projections suggest forest ecosystems will experience increased weather variability in the future with notable increases in the frequency and duration of droughts (Cayan et al. 2008, Allen et al. 2015, Millar and Stephenson 2015). Despite these trends, forest managers favor relatively narrow restoration objectives (e.g., reducing ladder fuels, restoring high proportion of pines, managing stand densities based on static stocking thresholds) that inadvertently create stand conditions less susceptible to moisture stress and bark beetle attack under extreme drought conditions (Allen et al. 2015). In the current era of rapid environmental change, forest management would benefit from a revised approach that considers historic, current, and future conditions as a general guide, restores heterogeneity in forest conditions, reestablishes critical ecosystem processes (e.g., natural fire regimes), and increases adaptive capacity and resilience in “live” forests not heavily impacted by the 2012–2016 drought (Safford et al. 2012*a,b*, Stephens et al. 2018). In the future, large-scale and coordinated management efforts will likely be necessary to increase ecosystem patchiness and reduce the probability of synchronous disturbances that could push whole landscapes over ecological thresholds from which there may be no return (Betancourt 2012).

Moving forward, land management agencies must consider the pros and cons of managing succession and reinvigorating ecological processes (e.g., fire) vs. waiting for the next agent of biomass regulation to modify western forest landscapes in unexpected and largely undesired ways. Emphasizing landscape-scale restoration that reduces forest density and reintegrates low- and moderate-severity fire across large spatial scales rather than across smaller, disjointed units will be more efficacious (Stephens et al. 2016). Results from our southernmost study sites (Sierra NF), where only about 20% of forest landscapes are receiving restoration treatments (North et al. 2012*a*), underscores that current treatment rates are insufficient to mitigate the impacts of bigger, more severe fires, hotter droughts, and large-scale bark beetle outbreaks (Allen et al. 2015). The expanded use of wildland fire under moderate fire-weather conditions (e.g., Meyer 2015) coupled with strategic mechanical thinning and prescribed burning treatments may achieve large-scale fire regime restoration and increased forest resilience across entire forest landscapes (Stephens et al. 2016). Such large-scale restoration treatments have the best chance of mitigating the impacts of hotter droughts and insect outbreaks in California’s forest ecosystems.

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