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# Do forest fuel reduction treatments confer resistance to beetle infestation and drought mortality?

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**Abstract.** Climate change is amplifying the frequency and severity of droughts and wildfires in many forests. In the western United States, fuel reduction treatments, both mechanical and prescribed fire, are widely used to increase resilience to wildfire but their effect on resistance to drought and beetle mortality is not as well understood. We followed more than 10,000 mapped and tagged trees in a mixed-conifer forest following mechanical thinning and/or prescribed burning treatments in 2001 through the extreme 2012–2016 drought in California. Mortality varied by tree species from 3% of incense-cedar to 38% of red fir with proportionally higher mortality rates in the larger size classes for sugar pine, red fir, and white fir. Treatment reductions in stem density were associated with increased diameter growth and rapidly growing trees had lower rates of mortality. However, the ultimate effects of treatment on drought-related mortality varied greatly by treatment type. All species had neutral to reduced mortality rates following mechanical thinning alone, but treatments that included prescribed burning increased beetle infestation rates and increased mortality of red fir and sugar pine. Fuel reduction treatments appear to benefit some species such as Jeffrey pine, but can reduce resistance to extreme drought and beetle outbreaks in other species when treatments include prescribed burning. In a non-analog future, fuel reduction treatments may require modification to provide resistance to beetle infestation and severe droughts.

**Key words:** bark beetle; climate change; drought; fire suppression; forest restoration; resilience.

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## INTRODUCTION

The frequency and severity of forest disturbances are intensifying globally due to a combination of climate change, fire suppression, and past forest management (Millar et al. 2007, Flannigan et al. 2009, Allen et al. 2010, Abatzoglou and Williams 2016, Steel et al. 2018). Where such shifts result in tree mortality beyond historic norms, these changes will have important implications for ecosystem persistence, provisioning of ecosystem services, and biodiversity (Millar et al. 2007). Intensification of drought and accompanying beetle infestations are increasing in severity and extent in many western U.S. forests, and can change affected forests from carbon sinks to sources (Kurz et al. 2008, Hicke et al. 2012). In dry forests, drought stress is often exacerbated by past fire exclusion which has significantly increased tree density and competition for seasonally scarce soil moisture (Safford and Stevens 2017, Young et al. 2017). The recent 2012–2016 California drought, by some measures the most severe in the last 1000 yr (Griffin and Anchukaitis 2015), may provide a harbinger of the stress and mortality that many dry forests are likely to experience in coming decades. Over 150 million trees are estimated to have died during or shortly following this drought, most of them in the drier conditions of the southern Sierra Nevada (Asner et al. 2016, Stephens et al. 2018, USDA 2020).

At broad scales, forest density and climatic water deficit (Young et al. 2017) have been suggested as important influences on mortality. Forest density may have two potential pathways for affecting mortality: Higher density can lead to greater water competition and drought stress (Fettig et al. 2019), and higher density of conspecific trees can lead to greater beetle infestation (Smith et al. 2005). In many western U.S. forests, density reduction often occurs through mechanical thinning and/or prescribed burning treatments designed to reduce potential wildfire severity by removing ladder and surface fuels. These treatments may improve survival of some conifer species at least during the early years of prolonged droughts (van Mantgem et al. 2016, Restaino et al. 2019). However, we still lack a mechanistic understanding of how specific treatments indirectly influence conifer mortality as mediated by competition, pre-drought vigor, and beetle infestation. Fully understanding the influence of these factors on tree resilience or susceptibility to drought requires manipulative experiments accompanied by detailed physiographic information and longer-term sampling.

Drought mortality may result from a complex interaction of tree species, size, beetle infestation, and growth over time. To evaluate the effects of these factors and their interactions, we used data from an ongoing long-term study that manipulated forest density of an old-growth, mixed-conifer forest through replicated prescribed burning and thinning treatments 12 yr prior to the 2012–2016 drought. This provided a rare opportunity to monitor stand conditions and drought effects on more than 10,000 individual trees, to experimentally evaluate the ecological drivers of forest density and disturbance history on drought mortality, as well as efficacy of commonly applied fuel reduction and restoration treatments on drought mitigation. In particular, we tested the following proximate relationships: (1) How do fuels treatments influence forest density? (2) Does forest density and tree size affect tree growth (a surrogate for vigor)? (3) What are the drivers of beetle infestation? (4) What are the drivers of tree mortality during drought? Gaining a mechanistic understanding of the direct and indirect drivers of conifer mortality during droughts may aid efforts to maintain resilient forests in an age of increasingly severe disturbances.

## METHODS

### *Study area*

The Teakettle Experimental Forest (36°58′ N, 119°2′ W) is located in the High Sierra Ranger District of Sierra National Forest, in California's Sierra Nevada. Elevation of the forest ranges from 1880 to 2485 m. Soils are predominantly poorly developed and granite-based Inceptisols and Entisols with a coarse sandy loam texture and very low clay content. The climate is typical of the southern Sierra Nevada with hot, dry summers and cool, moist winters. Precipitation averages 1250 mm per year and falls mostly as snow between the months of November and April. Air temperatures range from a summer mean of 17.1°C to a winter mean of 1.2°C (North et al. 2002). The forest is composed of old-growth mixed conifer dominated by white fir (*Abies concolor*), red fir (*A. magnifica*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*). Hardwood species are primarily found in the understory and account for less than 1% of the total basal area of the forest (North et al. 2002). Prior to experimental treatments, white and red fir accounted for about 85% of the total basal area (North et al. 2002). Historically, fires occurred approximately every 17 years within the study area, but wildfire has been largely excluded since 1865 (North et al. 2005). There is no history of significant logging prior to the initiation of experimental thinning treatments, with the exception of limited hazard tree removal and some sugar pine removal as part of early white pine blister rust control efforts (North et al. 2002, Smith et al. 2005). As measured by the Palmer Drought Severity Index (PDSI), Teakettle and California more generally experienced drought conditions (negative PDSI values) starting in water year 2012 and ending in 2016 (https://www.ncdc.noaa.gov).

### *Treatments and field measurements*

Eighteen experimental plots were established in 1998 representing six burning and thinning treatments, each with three replicates. Thinning treatments were a no thin, a removal of most trees between 25 and 75 cm diameter at breast height (DBH) treatment (hereafter referred to as an understory thin), and a heavier thinning treatment, cutting all trees >25 cm DBH but leaving 20 large (>75 cm) evenly spaced trees per hectare (hereafter "overstory thin"). Thinning treatments were crossed with a binary unburned or prescribed burn treatment for a full factorial design. Plots were 200 × 200 m squares and included similar species compositions, densities, and patch types (e.g., closed canopy vs. open canopy) prior to treatment. Burn treatments were thinned in 2000 and burned in October of 2001, and unburned treatments were thinned in 2001. Full treatment details can be found in North et al. (2002).

Comprehensive plot surveys were conducted before and after thinning and burning treatments. Plots were subsequently revisited in 2011 and 2012, prior to the recent drought and again following the drought in 2017 and 2018. A second prescribed burn treatment was applied following the drought (Goodwin et al. 2020), but all burn plot survey data used here preceded that treatment. As part of the initial survey, each tree and snag larger than 5 cm DBH was identified to species, mapped using a surveyor's total station (accuracy ± 35 cm) and tagged. In subsequent surveys, as new individuals grew to at least 5 cm DBH they were likewise mapped and tagged. Among other metrics, the status (live or dead) and DBH were assessed during each survey. Beetle sign was assessed (presence of pitch tubes, boring dust, and frass on tree bole) for each plot at the end of the drought. For example, red turpentine beetle was distinguished from mountain pine beetle or Jeffrey pine beetle based on the location of the attack on the bole (<2–3 m base of trees) and the size of pitch tubes (2–5 cm diameter for red turpentine beetle; 0.5–1.8 cm in diameter for mountain and Jeffrey pine beetles). Only fresh pitch tubes and frass were recorded to avoid accidently capturing old beetle sign. While all field technicians were trained and checked in their beetle detection abilities, these tallies were made with visual estimates of bole damage irrespective of the level of beetle damage. This sampling limitation likely resulted in some false absences where beetle infestation was missed especially where infestation levels were low. For a small subset of dead trees with bark beetle sign, a section of bark ~2500 $cm^2$ was removed with a hatchet at ~2 m in height to examine the shape, orientation, and size of bark beetle galleries for confirming the accuracy of species identification based on bole surface characteristics. Mean annual solar radiation and topographic water index were calculated within a 10-m radius circle surrounding each tree using a lidar-derived digital surface model with a resolution of 1 m (Fricker et al. 2019).

Pre-drought density of live trees within 10 m of every live tree was calculated from the 2011 to 2012 survey data, both in terms of the number of neighboring trees and neighborhood tree basal area. The number of neighboring trees was split into small (<25 cm DBH) and moderate-large (≥25 cm DBH) size classes. Bark beetles are host-specific, with fir engraver (*Scolytus ventralis*) attacking red and white fir, Jeffrey pine beetle (*Dendroctonus jeffreyi*) attacking Jeffrey pines, mountain pine beetle (*D. ponderosae*) attacking sugar pine, and red turpentine beetle (*Dendroctonus valens*) attacking Jeffrey and sugar pine. Thus, for each tree the neighboring basal area of each beetle's host species and non-host species were calculated. The 10-m radius was selected based on analyses of local density effects on tree growth conducted in Sierra Nevada mixed-conifer forests (Das et al. 2008, 2011). The mean annual growth rate of an individual tree was calculated as the difference in diameter from the post-treatment measurement (2003 or 2004) and the pre-drought measurement (2011 or 2012) divided by the number of years between measurements. Growth was standardized by species and tree size and should be interpreted as growth anomaly where negative values represent below average and positive values above average growth, respectively. Whether a tree died during the drought was determined by a

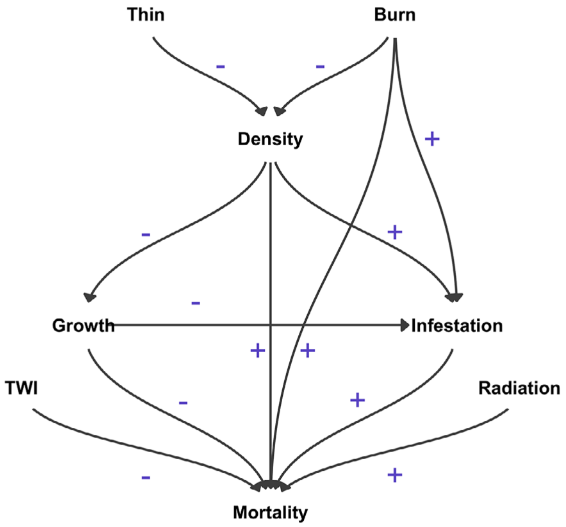

Fig. 1. Hypothesized causal model of drought mortality. Direct positive (+) and negative (−) effects are hypothesized for all five dominant conifer species at the Teakettle Experimental Forest. Many effects are allowed to vary by species and tree diameter (Equations 2–4). Topographic wetness index is abbreviated as TWI.

change in live to dead status between the pre- and post-drought (2017 or 2018) survey. We only evaluated trees recorded as alive in 2011.

### *Statistical analysis*

To evaluate the direct and indirect drivers of tree mortality during drought, we built a Bayesian multi-level and multivariate model. The multi-part structure of the model follows our four primary questions with (1) density, (2) growth, (3) beetle infestation, and (4) mortality submodels (Fig. 1).

$$\text{density}_{i,k} = \alpha_{\text{treatment}[i]} + \alpha_{\text{plot}[i]} \qquad (1)$$

We modeled neighborhood density around tree $i$ as a function of the six-level burning and thinning treatments. $\text{density}_{i,k}$ is a multivariate response with $k$ variables: number of small trees (<25 cm DBH), medium-large trees (≥25 cm DBH), as well as basal area (BA) of fir engraver hosts, red turpentine beetle hosts, mountain pine beetle hosts, Jeffrey pine beetle hosts, and BA of non-host species for each beetle. Basal area was used as a measure of density as it relates to beetle infestation rates as we hypothesized the amount of beetle habitat to be more important than the number of neighboring trees. On the other hand, we expected the number of individuals of different size classes to be better indicators of competitive pressure since mature trees and saplings draw water from different soil depths (Plamboeck et al. 2008). A varying intercept for plot ID was included here and in subsequent submodels to account for spatial non-independence of trees within plots. The log of all density metrics was used along with a gaussian error structure. We hypothesized treatments negatively affect stand density (Fig. 1).

$$\begin{aligned}\text{growth}_i = {} & (\alpha_0 + \beta_1 \times \text{density.sm}_i + \beta_2 \\ & \times \text{density.sm}_i \times \text{dbh}_i + \beta_3 \\ & \times \text{density.lg}_i + \beta_4 \times \text{density.lg}_i \\ & \times \text{dbh}_i) \times \beta\text{species}[i] + \beta\text{plot}[i]\end{aligned} \qquad (2)$$

We modeled growth of tree $i$ as a function of neighborhood density of small ($\text{density.sm}_i$) and medium-large ($\text{density.lg}_i$) trees, and the interaction of each trees' diameter ($\text{dbh}_i$) and neighborhood density. The model intercept $\alpha_0$ and slope parameters $\beta$ were allowed to vary by species as random effects. We tested different metrics of local density and found that the number of neighboring trees outperformed models using basal area when evaluating growth. Growth was modeled using a Gaussian error structure. We hypothesized greater neighborhood density decreases tree growth but that this affect is dependent on species and tree size (Fig. 1).

$$\begin{aligned}\text{logit}(\text{beetle}_{i,j}) = {} & \alpha_0 + (\beta_1 \times \text{Density.Host}_{i,j} + \beta_2 \\ & \times \text{Density.Other}_{i,j} + \beta_3 \times \text{dbh}_i \\ & + \beta_4 \times \text{growth}_i + \beta_5 \times \text{burn}_i) \\ & \times \beta\text{species}[i,j] + \beta\text{plot}[i]\end{aligned} \qquad (3)$$

The likelihood of infestation by beetle $j$ at tree $i$ was modeled as a function of the log basal area of a beetle's host species ($\text{Density.Host}_{i,j}$), log basal area of non-host species ($\text{Density.Other}_{i,j}$), diameter of the focal tree ($\text{dbh}_i$), the pre-drought growth of the focal tree ($\text{growth}_i$), and whether the tree experienced prescribed burning ($\text{burn}_i$).

Where a beetle species has multiple conifer hosts (i.e., fir engraver infests both white and red fir, and red turpentine beetle infests both sugar and Jeffrey pines), the slope parameters were allowed to vary by species as random effects. The likelihood of infestation was modeled using a binomial error structure with a logit link. We hypothesized greater host density to increase the probability of infestation, non-host density to have no effect, and larger trees to be infested at greater rates. We also hypothesized trees previously exposed to prescribed fire may be infested more often because fire damage can facilitate beetle attack, although such effects are typically observed within 5 yr of treatment (Schwilk et al. 2006, Youngblood et al. 2009, Fig. 1).

$$\begin{aligned}\text{logit(mortality)} &= (\alpha_0 + \beta_1 \times \text{growth}_i + \beta_2 \times \text{burn}_i \\ &+ \beta_3 \times \text{denstiy.sm}_i + \beta_4 \times \text{denstiy.sm}_i \times \text{dbh}_i \\ &+ \beta_5 \times \text{denstiy.lg}_i + \beta_6 \times \text{denstiy.lg}_i \times \text{dbh}_i \\ &+ \beta_7 \times \text{solar}_i + \beta_8 \times \text{TWI}_i) \times \beta\text{species}[i] \\ &+ \beta\text{beetle}[j] \times \beta\text{species}[i,j] + \beta\text{plot}[i]\end{aligned} \tag{4}$$

The likelihood of mortality of tree *i* was modeled as a function of a tree's pre-drought growth rate ($\text{growth}_i$), density of small ($\text{density.sm}_i$) and medium-large competitors ($\text{density.lg}_i$), the interaction with density and focal tree diameter ($\text{dbh}_i$), whether the tree experienced prescribed burning ($\text{burn}_i$), mean annual solar radiation ($\text{solar}_i$), topographic wetness index ($\text{TWI}_i$), and whether beetle infestation was noted during 2017–2018 surveys. βbeetle[*j*] × βspecies[*i, j*] represented an additive vector of beetle-conifer pairs where the effect of a beetle species is evaluated only for host conifer species. For example, the likelihood of Jeffrey pine mortality included effects of red turpentine and Jeffrey pine beetles but not fir engraver or mountain pine beetles. We included $\text{burn}_i$ as a predictor of drought mortality to account for any non-beetle related effects not accounted for elsewhere in our model, particularly for incense-cedar which exhibited little evidence of important drought-related beetles such as cedar bark beetles (*Phloeosinus* spp.). Likewise, we included a direct effect of neighborhood density as a predictor of mortality to account for any effects not captured by pre-drought growth anomaly. For example, at some densities competition for water may not result in reduced growth in average years but becomes limiting under extreme drought conditions. The intercept $\alpha_0$ and slope effects β were allowed to vary by species as random effects. The likelihood of mortality was modeled using a binomial error structure with a logit link. We hypothesized faster growing, un-infested and unburned trees with fewer neighbors are less likely to die during a drought. Further, we expected trees located in areas with lower solar radiation and higher values of TWI to die less often (Fig. 1).

In addition to evaluating each hypothesized cause and effect relationship (Fig. 1), we used the full model to simulate the indirect effects of thinning and prescribed burning on drought-related mortality. This was analyzed by fitting the model 1000 times for each combination of stand treatment, conifer species, and two tree sizes (25 and 75 cm DBH). Uncertainty associated with each model parameter and submodel was propagated through the hypothesized chain of causation to avoid underestimating the total uncertainty between treatment and mortality. The result of these simulations is posterior prediction distributions of the probability of mortality for each scenario. For each species and size, the effect of treatment is expressed as the difference in these distributions from the control scenario.

We report mortality rates of all monitored trees (14,764) below but for modeling we omitted trees along plot edges (i.e., within 10 m) where neighborhood density could not be calculated fully. This reduced our sample size to a total of 10,510 trees (Table 1). Probabilistic statements in the results are calculated using model posterior distributions. For example, contrasts between categories (e.g., density within untreated vs. overstory thinned plots) were calculated as the difference between category posteriors. The probability an effect was positive (or negative) was calculated as the proportion of the parameter posterior distribution above (or below) zero. The model was fit using the brms and rstan packages (Bürkner 2017, Stan Development Team 2018) in the R statistical environment (R Core Team 2019). The full joint model was run with 3 chains, each for 3000 samples with a warmup of 1500 samples and 4500 total post-warmup samples. Traceplots and R-hat values were assessed for proper mixing and model convergence. Full model code and data can be found in Data S1.

Table 1. Summary statistics of trees used in statistical modeling.

| Characteristic | Incense-cedar | Jeffrey pine | Sugar pine | White fir | Red fir |
|---|---|---|---|---|---|
| Diameter at breast height (cm) | 24 (15, 41) | 50 (20, 94) | 31 (18, 92) | 23 (13, 39) | 21 (12, 47) |
| Growth ($cm^2$/yr) | 14 (4, 34) | 18 (6, 43) | 25 (8, 76) | 14 (5, 32) | 12 (4, 35) |
| No. neighboring trees | 10 (6, 16) | 6 (2, 10) | 9 (5, 15) | 12 (7, 19) | 12 (8, 17) |
| Neighborhood basal area ($m^2$) | 1.3 (0.5, 2.3) | 0.7 (0.2, 1.5) | 1.2 (0.4, 2.3) | 1.6 (0.8, 2.7) | 1.9 (1.0, 2.9) |
| Topographic water index | 3.6 (3.3, 3.9) | 3.4 (3.1, 3.7) | 3.5 (3.3, 3.8) | 3.5 (3.3, 3.8) | 3.7 (3.4, 4.0) |
| Annual solar radiation (MWH/$m^2$) | 1.67 (1.63, 1.70) | 1.68 (1.61, 1.72) | 1.66 (1.60, 1.69) | 1.66 (1.59, 1.69) | 1.62 (1.54, 1.69) |
| Observed beetle infestation (%) | 11.7 | 15.6 | 11.4 | 25.3 | 35.0 |
| No. of trees | 1736 | 467 | 901 | 6892 | 514 |

*Note:* The median (50% inter-quantile range) of diameter at breast height, pre-drought growth rate, number of neighboring trees, neighborhood basal area within a 10-m radius, topographic wetness index, solar radiation, percent of trees infested, and number of trees analyzed are reported for the five common conifer species assessed.

## RESULTS

### *Mortality and infestation rates*

Overall, the percentage of trees that died during the drought was low for incense-cedar (3%), and Jeffrey pine (8%), and relatively high for sugar pine (24%), white fir (34%), and red fir (38%). Mortality rates were often lowest for both firs and incense-cedar with moderate diameters at breast height (25–50 and 50–75 cm DBH). Sugar pines experienced high rates of mortality among larger diameter trees (≥50 cm DBH), and Jeffrey pines showed little variation in mortality across size classes (Fig. 2; Appendix S1: Table S1).

Jeffrey pine mortality was 7% when no beetle infestation was observed, 10% when only Jeffrey pine beetle was observed, 15% when only red turpentine beetle was observed, and 14% among individuals infested by both beetle species. Un-infested sugar pine mortality was 20%, 25% when only mountain pine beetle was observed, 37% when only red turpentine beetle was observed, and 100% when trees were infested by both beetle species. Observed mortality rates of white fir increased from 25% among un-infested trees to 55% among fir engraver infested trees, while red fir saw a similar but greater increase from 24% to 65% between the un-infested and infested groups, respectively. No important drought-associated insect infestations were observed among incense-cedars.

### *Treatment effects on density*

Neighborhood density within a 10-m radius a decade following treatments was lowest in thinned and burned plots. The number of small neighboring trees (<25 cm DBH) was highest within the unburned/understory thin with a median (*M*) of 8 and 50th inter-quantile range (Q50) of 4–14 neighbors. We observed median small tree densities of 3 (Q50: 1–7) in the burn/understory thin and 4 (Q50: 2–8) in the unburned/overstory thin plots, both of which were consistently lower than the controls with 98% (burn/understory thin) and 94% (unburned/overstory thin) probabilities (Pr.). Burning and overstory thinning created the lowest small tree density (*M*: 1, Q50: 0–3) and was statistically lower than the unburned/overstory thin treatment (Pr. 99%; Fig. 3A; Appendix S1: Table S2). Trees within the control plots had the most medium-large (≥25 cm DBH) neighbors (*M*: 6, Q50: 4–9), while trees within burn/overstory thin plots had the fewest medium-large neighbors (*M*: 2, Q50: 1–3; Fig. 3B). Relative to the control, the model estimated the density of medium to large neighbors decreased for all thinning treatments with a greater than 99% probability, but there was no meaningful difference when a stand was burned but not thinned (Fig. 3B; Appendix S1: Table S2).

Treatments reduced neighborhood basal area of fir engraver host species (white and red firs) but had little effect on pine beetle host species (i.e., Jeffrey and sugar pines). Observed neighborhood basal area of fir engraver hosts was highest in the controls with a median of 1.3 $m^2$ within 10-m radius (Q50: 0.6–2.2) and lowest in burned/overstory thin treatments (*M*: 0.1, Q50: 0–0.5; Appendix S1: Table S2). Relative to the control, there was little evidence fir engraver host basal area was affected by the burn/no thin treatment, there was a likely negative effect of the

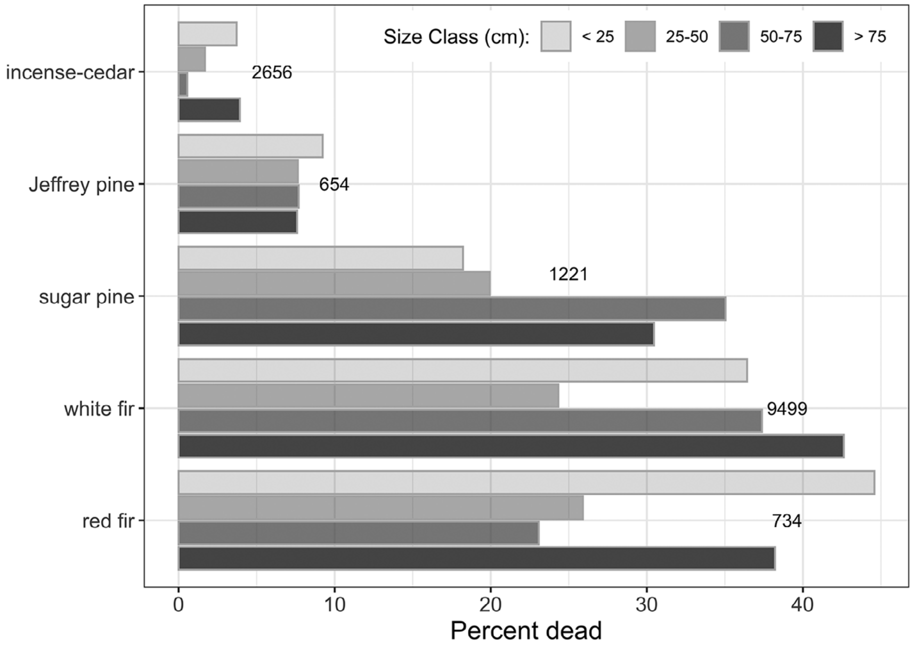

Fig. 2. Mortality of five conifer species during the 2012–2016 drought, summarized by diameter at breast height size class. Total number of monitored trees for each species is printed to the right of the bars. Tabulated mortality rates by species, size class, and treatment can be found in Appendix S1: Table S1.

unburned/understory thin treatment (Pr. 92%), and clear negative effects of the three more intense treatments (Pr. >99%; Fig. 3C). For red turpentine beetle, basal area was reduced in the burned/understory thin and burned/overstory thin treatments only (Pr. >97%; Fig. 3D). Observed neighborhood basal area of Jeffrey pine beetle hosts was low to nonexistent ($M = 0$; Appendix S1: Table S2), with no clear effect of any treatment (Pr. <90%; Fig. 3E). Neighborhood basal area of mountain pine beetle hosts (i.e., sugar pines) was reduced by the burned/understory thin and burned/overstory thin treatments (Pr. >98%; Fig. 3F). Effects of treatment on non-host basal area of all three pine beetles mirrored those on host species of fir engraver (Fig. 3C–F).

### Density effects on growth

The effect of neighborhood density on conifer growth during the drought was dependent on the size of the focal tree as well as the size of nearby competitors. The growth of small sugar pine, incense-cedar, white fir, and red fir was lower when surrounded by both small and medium-large neighbors (Pr. >95%; Fig. 4A, B). For these four species, effect sizes of small competitors were most negative when the focal tree was small (Fig. 4A) and declined as focal tree diameter increased (i.e., the density:dbh interaction was positive). For larger incense-cedar, sugar pine, and red fir, the effect on growth became negligible, while the estimated effect on white fir switches sign completely (Fig. 4C). Medium-large competitors were estimated to negatively affect growth of large focal trees of all species (Pr. >95%) with the potential exception of large red firs (Fig. 4B, D). Neighborhood density of either size class had no discernible effect on small Jeffrey pines but clear negative effects on large Jeffrey pines (Pr. >95%; Fig. 4).

### Effects on beetle infestation

Large sugar pines were infested at greater rates than small trees by both red turpentine and mountain pine beetles (Pr. ≥99%), although the absolute infestation rate of mountain pine beetle was lower. Large Jeffrey pines were similarly infested at higher rates than small individuals by red turpentine beetles (Pr. 99%) and likely by Jeffrey pine beetles (Pr. 94%). Fir trees showed the

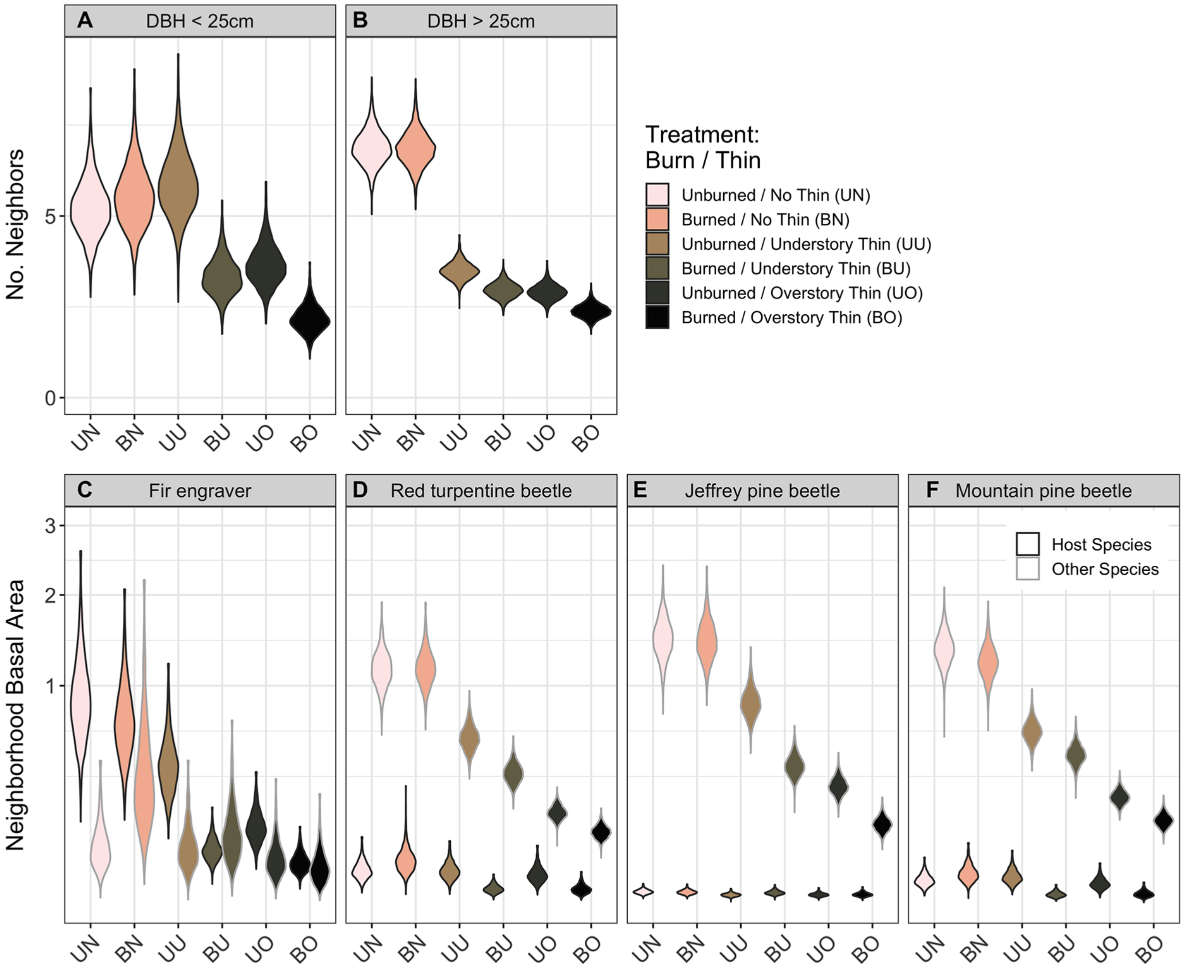

Fig. 3. Estimated neighborhood density within 10 m under different forestry treatments. Density is measured as the number of (A) small (<25 cm diameter at breast height [DBH]) and (B) medium-large (≥25 cm DBH) trees, and (C–F) basal area ($m^2$) of beetle host species.

opposite trend with smaller individuals being infested by fir engraver at higher rates than large individuals (Pr. ≥97%; Fig. 5A). Tree growth clearly affected infestation probability in two cases with vigorous white fir showing lower rates of infestation of fir engraver, and vigorous sugar pines exhibiting higher rates of mountain pine beetle infestation (Pr. >99%; Fig. 5B). Neighborhood host density increased the likelihood of fir engraver infestation for both fir species and of red turpentine beetle for Jeffrey pine (Pr. ≥98%). Being in a burned plot increased the infestation rate of both sugar pine associated beetle species and of fir engraver in the case of red fir (Pr. ≥98%). White fir was expected to see greater infestation rates of fir engraver in burned plots as well but with greater model uncertainty (Pr. 93%; Fig. 5D). Neighborhood density of non-host conifers showed no clear effect on infestation probability (Appendix S1).

### *Effects on conifer mortality*

Pre-drought growth anomaly and whether a tree showed signs of beetle infestation were often strong predictors of tree mortality. The infestation effect of both red turpentine beetle and mountain pine beetle and their interaction on sugar pine mortality were clearly (Pr. >99%) positive. When other predictors are held at their mean values, our model predicted sugar pines

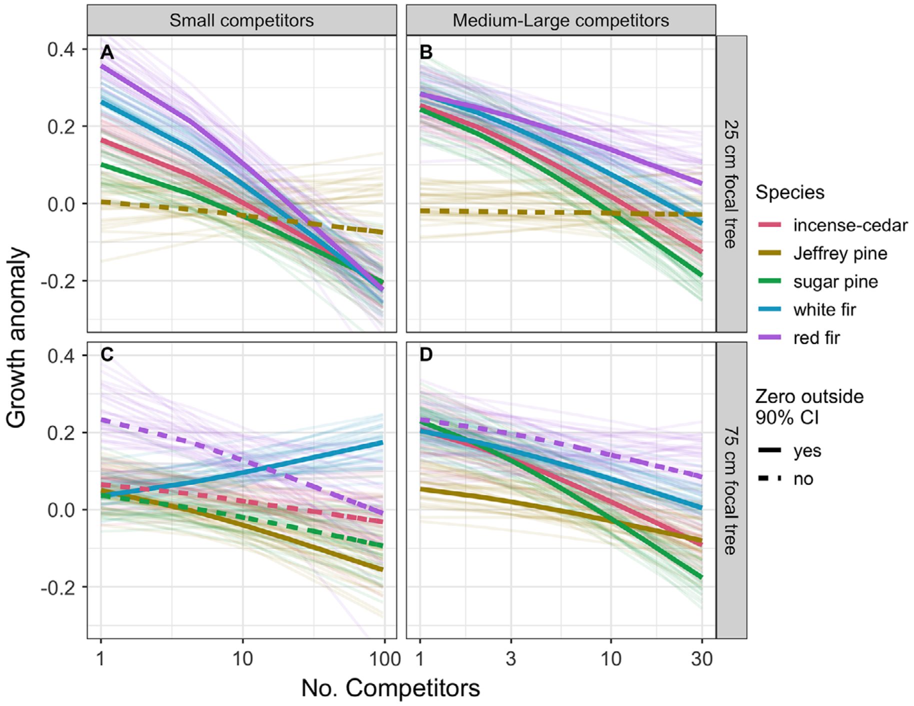

Fig. 4. Effects of neighborhood density on individual tree growth. The number of competing neighbors of two size classes (columns) interacts with the diameter at breast height (DBH) of the focal tree. DBH of the focal tree is modeled as a continuous variable but is fixed at 25 cm DBH and 75 cm DBH to illustrate this interaction. Thick lines show mean effect estimates with solid lines representing relationships where the 90% credible interval of the effect estimate does not include zero. To illustrate the spread of credible effects, 30 model posterior draws are also shown as faint lines. Neighborhood density was calculated as the number of small (<25 cm DBH) and medium-large (≥25 cm DBH) trees within a 10-m radius of a focal tree.

with no sign of infestation to have a median (*M*) mortality rate of 19% (90% prediction interval: 14–25%). Being infested by only red turpentine beetle increased the probability of mortality to 39% (PI: 22–57%), and only mountain pine beetle increase predicted mortality rate to 27% (PI: 12–40%). When both beetles are observed, mortality is expected for a strong majority of sugar pines (*M*: 98%; PI: 93–100%). Similarly, being infested by fir engraver increased expected fir mortality rates from a median of 25% (PI: 20–32%) for un-infested white firs to 58% (PI: 50–56%) in infested trees and from 27% (PI: 19–37%) in un-infested red fir to 74% (PI: 64–82%) for infested trees. There was no apparent effect of infestation on Jeffrey pine mortality, and no important drought-related pests were observed among incense-cedars (Fig. 6A).

All five conifer species assessed showed strongly decreasing rates of mortality with increased pre-drought growth rates (Pr. >99%), although the benefit of pre-drought vigor was markedly lower for sugar pine as compared to other species (Fig. 6B). After accounting for density-influenced growth, neighborhood density of medium-large (≥25 cm DBH) trees was positively related to mortality for white fir (Pr. >99%) and Jeffrey Pine (Pr. 98%) with the magnitude of the effect varying little with the size of focal tree (Fig. 6C). Conversely, white fir mortality was lower when density of small (<25 cm DBH) neighbors was high. No other species showed clear direct effects of small tree density on mortality (Data S1). The topographic variables of solar radiation and topographic water index (TWI) rarely influenced conifer mortality.

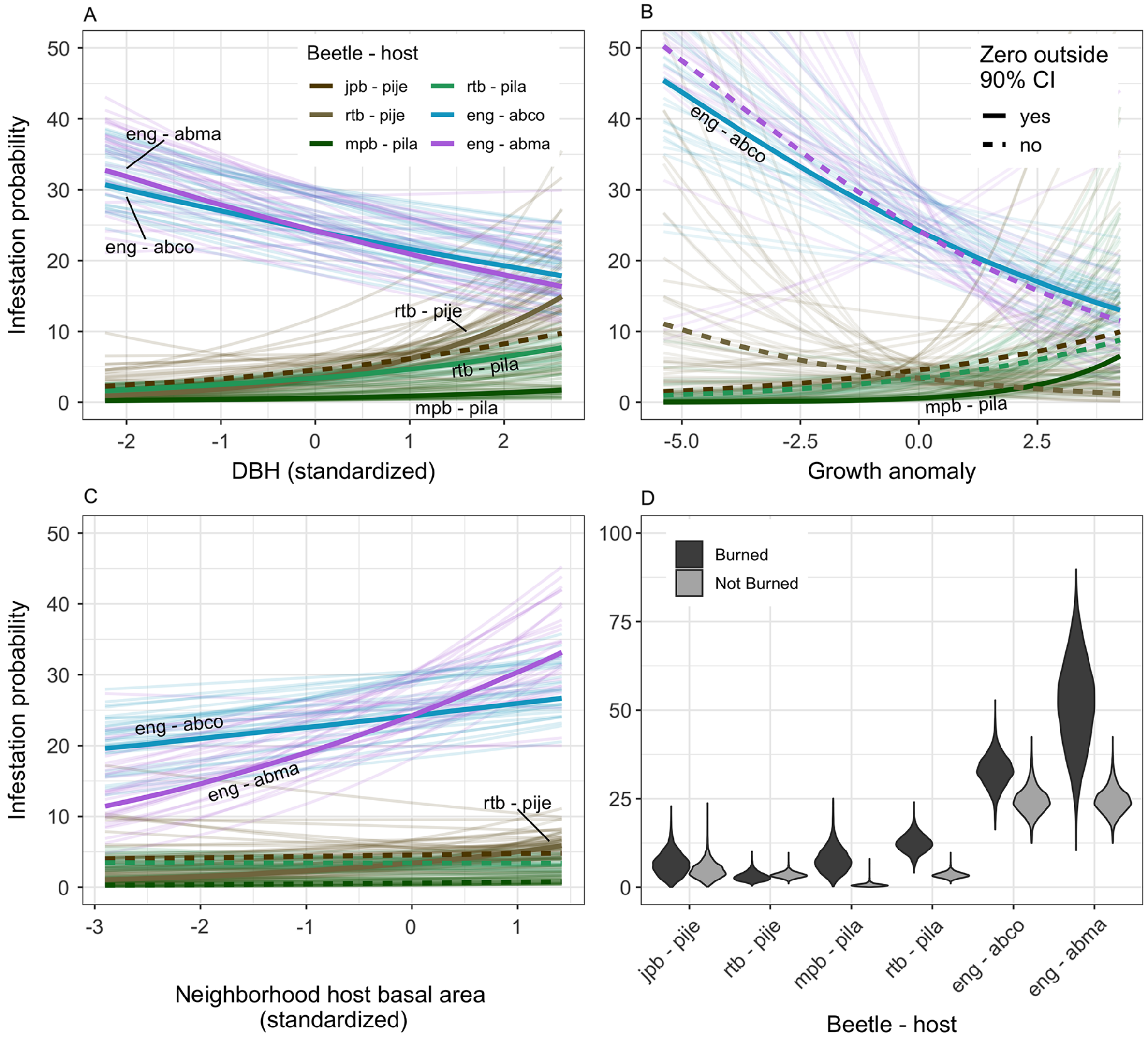

Fig. 5. Marginal effects on beetle infestation. (A) Tree diameter at breast height (DBH), (B) pre-drought tree growth relative to an individual's size and species average, (C) host species basal area within a 10-m radius, and (D) whether a tree experienced a prescribed burn treatment. Beetle and tree species abbreviations are jpb for Jeffrey pine beetle; rtb for red turpentine beetle; mpb for mountain pine beetle; eng for fir engraver; pije for Pinus jeffreyi (Jeffrey pine); pila for Pinus lambertiana (sugar pine); abco for Abies concolor (white fir); and abma for Abies magnifica (red fir). For (A–C), thick lines show mean effect estimates with labeled solid lines represent relationships where the 90% credible interval does not include zero. To illustrate the spread of credible effects, 30 model posterior draws are also drawn as faint lines. Note the *y*-axis scale differs for (D).

Incense-cedar were more likely to die at low levels of TWI (Pr. 97%), and white fir were more likely to die in areas with high solar radiation (Pr. 95%). Being in a burned plot may directly increase mortality for incense-cedar (Pr. 94%) and sugar pine (Pr. 92%; Data S1).

### *Indirect effects of treatment on mortality*

Model predictions showed the indirect effect of treatments on drought-related mortality varied among species and occasionally by tree size (Fig. 7). Our relatively smaller sample sizes for Jeffrey pine and red fir limited the power of some

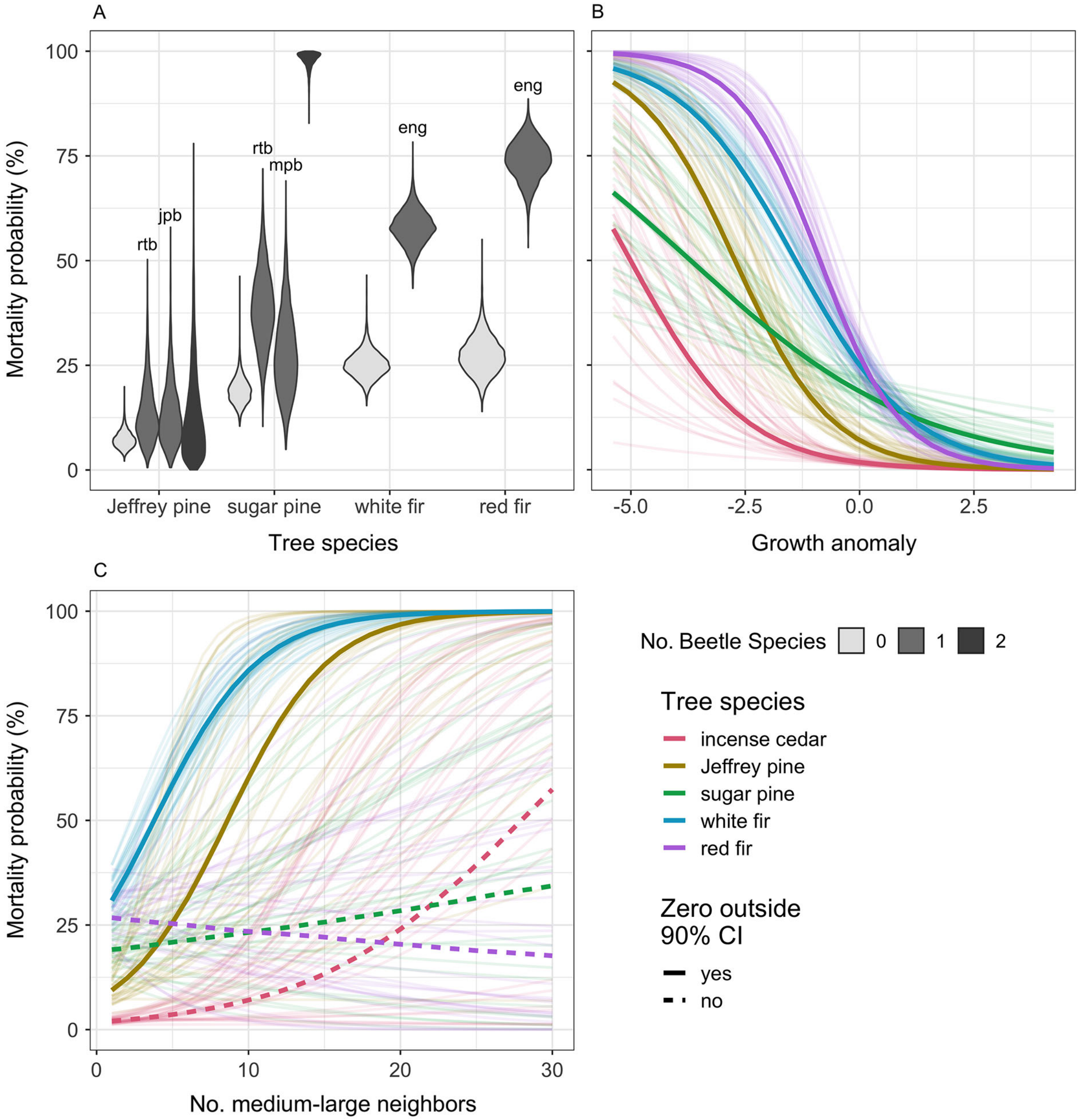

Fig. 6. Direct drivers of mortality. Marginal effects of (A) beetle infestation, (B) pre-drought tree growth relative to an individual's size and species average, and (C) density of medium-large neighbors on an average sized focal tree. Beetle species abbreviations are jpb for Jeffrey pine beetle; rtb for red turpentine beetle; mpb for mountain pine beetle; and eng for fir engraver. For (B) and (C), thick lines show mean effect estimates with solid lines representing relationships where the 90% credible interval does not include zero. To illustrate the spread of credible effects, 30 model posterior draws are also drawn as faint lines.

of our analyses when the data were parsed by tree size and treatment type (Appendix S1: Table S1). Relative to the controls, mortality of small (25 cm DBH) incense-cedars was reduced when stands had been thinned and increased when burned, although absolute effect sizes are low

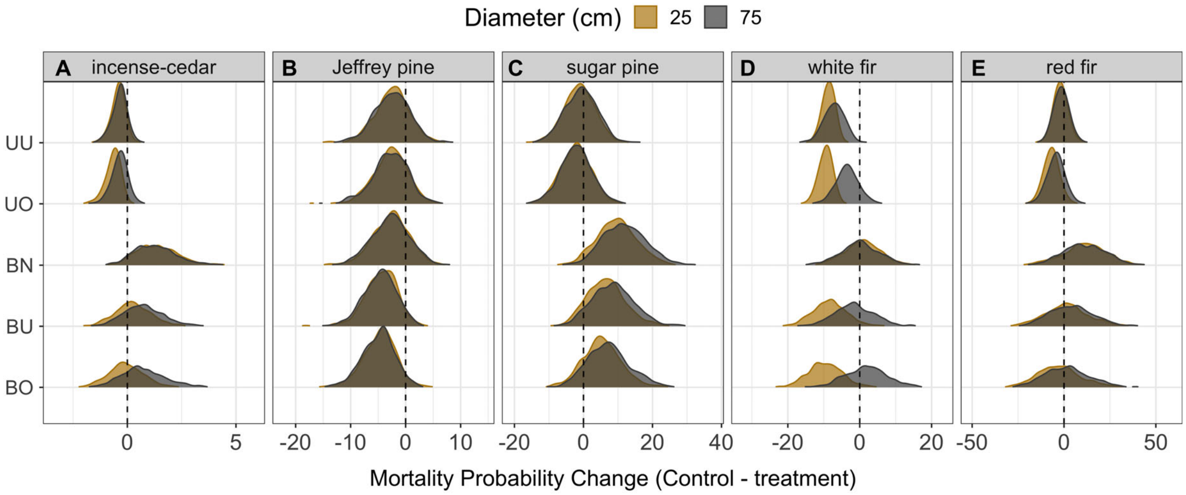

Fig. 7. Indirect effect of forest treatment on drought mortality. (A) incense-cedar, (B) Jeffrey pine, (C) sugar pine, (D) white fir, and (E) red fir. Treatment abbreviations are UU for Unburned/Understory Thin; UO for Unburned/Overstory Thin; BN for Burned/No Thin; BU for Burned/Understory Thin; and BO for Burned/Overstory Thin. Value distributions represent change in probability of mortality relative to controls for two tree sizes. The scale of the *x*-axis varies among species.

given low rates of incense-cedar mortality generally. Small incense-cedars were predicted to die 0.4% (90% PI: 0.0, 1.0%) less often on average (μ) with understory thinning and 0.6% (PI: 0.2, 1.3%) when heavily thinned, but are predicted to die 1.4% (PI: 0.0, 3.1%) more often when burned only. Mortality differed little from controls when thinning and burning were combined (Fig. 7A). Drought mortality of Jeffrey pines of all sizes was predicted to decrease for all treatments with the effect size and model certainty increasing with increasing intensity of treatment. Burned / overstory thin treatments were predicted to produce the greatest decrease in mortality rates for both large (μ: 4.7%; PI: 0.4, 9.9%) and small (μ: 4.5%; PI: 0.2, 10.1%) Jeffrey pines (Fig. 7B). Sugar pine saw little effect of thinning on drought mortality when unaccompanied by prescribed burning, but showed large increases in mortality within prescribed burn plots. Relative to controls, mortality of large sugar pines was predicted to increase by 11.7% (PI: 2.2, 22.5%) within burned / no thin plots, and somewhat lower and less certain increases for burned / understory thin (μ: 8.4%; PI: −1.3, 18.9%) and burned/overstory thinned plots (μ: 7.0%; PI: −2.2, 18.2%). Predicted increases in mortality due to burning were marginally lower for small sugar pines (Fig. 7C). Thinning treatments appear to have reduced drought-related mortality for white fir with the greatest reduction in mortality rate for large trees occurring in understory thin treatments (μ: 7.0%; PI: 2.4, 11.8%) and in overstory treatments for small trees (μ: 9.4%; PI: 6.6, 12.7%; Fig. 7D). Thinning may have reduced and burning may have increased drought mortality of red fir, although model uncertainty was high. Relative to controls, mortality of large red firs was predicted to decrease the most in unburned/ overstory thinned stands by 4.2% on average (PI: −3.2, 11.9%). Burned/no thin treatments were predicted to increase mortality of large red firs by 10.7% on average but with a wide prediction interval (PI: −7.6, 30.7%; Fig. 7E).

## DISCUSSION

Trees can die during drought through water stress alone or through a combination of water stress and infestation of drought-associated beetle pests (Stephenson et al. 2019). The long-term study at Teakettle Experimental Forest and California's historic 2012–2016 drought provided an opportunity to test these two inter-related pathways by manipulating stand densities and compositions through mechanical thinning and prescribed burning. Generally, we found that trees with a less dense competitive environment (i.e., fewer neighbors) were more vigorous prior to the drought, which translated to lower probability of mortality. Trees with greater neighborhood basal area of conifers that host the same beetle species were often infested at greater rates than relatively isolated individuals and were more likely to die during the drought. Surprisingly for some species, having experienced a prescribed burn more than a decade prior to the drought increased the likelihood of beetle infestation and ultimately the probability of mortality. This effect was especially strong for large sugar pines. Jeffrey pines appear to benefit most consistently from both thinning and prescribed burning treatments designed to reduce stand density and increase forest resilience to disturbance.

Forest thinning treatments a decade before the drought provided some decrease in drought mortality (Fig. 7). There could be several reasons for this modest response, but three in particular may be influential. First, fuel reduction treatments designed to mitigate wildfire hazard by reducing crown density and increasing height to live crown may not alter forest structure in a way that reduces drought-related conifer mortality. Treatments to increase resilience to beetle infestation focus on reducing host tree density and increasing residual tree spacing, improving tree vigor by reducing stand basal area, selective removal of low vigor trees, and increasing stand-level heterogeneity (Fettig et al. 2007, North 2012, Gillette et al. 2014). The unburned overstory treatment tested here most resembles this approach and our results suggest this would most benefit Jeffrey pines and small diameter white fir (Fig. 7). Second, modest mortality reductions may be attributable to the relatively small size of the plots (4 ha) and the fact that they were imbedded in a larger, fire-suppressed landscape with high beetle populations. Specifically, the 18 experimental plots assessed encompassed a total of 60 ha, which equates to just 0.05% of the 1300-ha Teakettle Experimental Forest. Beetle outbreak severity in the Sierra Nevada varied with latitude and elevation (Fettig et al. 2019), and these broadscale differences can overwhelm local factors such as reduced neighborhood competition and low conspecific density that otherwise increase tree resistance to beetle mortality. Third, the magnitude and duration of the unprecedented 2012–2016 drought (Griffin and Anchukaitis 2015) may have exhausted tree defenses against beetles (i.e., nonstructural carbohydrate storage; He et al. 2020) to an extent that overrode treatment benefits. One element of California's drought that may have made its impact so severe was the timing of warm temperatures and water scarcity during winter and early spring when substantial growth occurs in Mediterranean forests (Earles et al. 2018). Ultimately, the compounding effects of prescribed fire, followed by drought and beetle attack, may have depleted tree defenses (Piper and Paula 2020), a potential harbinger of many forest's limited resilience to multiple stresses in a non-analog future.

### *Pathways to persistence or mortality*

A reduction in stand density and the competitive environment often results in increased vigor among surviving trees. One exception to this generalization was a tendency of large white firs to grow relatively rapidly among higher density of small trees (<25 cm DBH; Fig. 4C). Previous Teakettle research found white fir basal area was positively associated with thicker soils (Meyer et al. 2007) which hold more water. This suggests that at least for large white fir, increased competition from small neighbors may be offset by higher productivity sites on which this greater density occurs. Pre-drought growth also affected beetle infestation rates in two instances with vigorous white firs infested by fir engraver at lower rates and vigorous sugar pines infested by mountain pine beetle at higher rates (Fig. 5B). The white fir–fir engraver relationship is consistent with much of the literature (Ferrell et al. 1994, Hood and Sala 2015), but the sugar pine–mountain pine beetle result is surprising. Two potential explanations for this unexpected finding are that there exists a trade-off between growth and defense in sugar pines (Mata et al. 2017), while the greater phloem thickness associated with pines released from competition constitutes a more attractive resource, which could be overwhelmed during outbreak conditions (Lahr and Sala 2014, Bentz et al. 2015).

Fuel treatments also likely affected beetle infestation in two ways. First, the direct effect of prescribed burning was positively associated with beetle infestation in sugar pines, and red firs (Fig. 8), consistent with previous Teakettle research which found bark beetle attack was higher in burned than unburned plots three years after treatment (Maloney et al. 2008). Research in other mixed-conifer and ponderosa pine forests has also found higher rates of bark beetle attack following damage from prescribed fire (McHugh et al. 2003, Breece et al. 2008, Fettig et al. 2010, Collins et al. 2014). Subsequently, fire induced damage may facilitate future beetle attack among trees whose defenses were weakened by past prescribed fire (Parker et al. 2006). However, increased infestation rates following prescribed burning are typically short lived (i.e., within the first 5 yr) and result in limited tree mortality (Stephens et al. 2012, Fettig and McKelvey 2014). Such strong effects a decade following burning are surprising and perhaps another result of the unprecedented severity of the 2012–2016 drought. Second, neighborhood density of beetle host trees was positively associated with beetle infestation rates in the case of fir engraver for both white and red firs (Smith et al. 2005), and red turpentine beetle in the case of Jeffrey pine (Egan et al. 2016). Non-host density did not affect beetle infestation. Fir engraver was observed more often in small firs, while red turpentine beetle infested large pines, and mountain pine beetle infested large sugar pines at higher rates. Thus, treatments that reduce stand density can indirectly reduce the likelihood of beetle infestation in some cases, but how the treatments affect stand composition and demography is also important. For example, removal of pines would not alter fir engraver infestation rates but reducing the density of white or red firs would.

Both pre-drought tree growth and observed beetle infestation during the drought were strong predictors of tree mortality. For all species, slowly growing trees were more likely to die during the drought while rapidly growing trees frequently survived (Fig. 8). Beyond these generalized responses, there were substantial differences by species. Jeffrey pine did not show increased mortality rates even when infested by red turpentine and Jeffrey pine beetle (Fig. 8B). This resistance to beetle infestation could be related to Jeffrey pine being less drought stressed because their roots can access deep (>4 m) water in fissures within the granitic bedrock (Hubbert et al. 2001, Hurteau et al. 2007). The reduction in drought mortality attributable to pre-drought growth was weaker for sugar pine than other species (Fig. 6B), and more vigorous individuals were more likely to be infested by mountain pine beetle (Fig. 5B). Although incense-cedar can potentially be colonized and killed by cedar bark beetles (*Phloeosinus* spp.), these species were generally not considered an important causal agent of tree mortality during prior droughts in the Sierra Nevada (Fettig and Mortenson 2018). Cedar mortality was mostly driven by dry sites and fire (Fig. 8A).

Variation in the microclimate has also been proposed as an important driver of drought mortality (Restaino et al. 2019). While we did not test the influence of edaphic factors such as soil depth or texture, we tested the effects of topographic water index and solar radiation on tree mortality and found no consistent effects. The largely weak effects of these microclimate variables suggest that variation in climate may be more important at broad scales where variation in moisture availability and drought stress is greater (Young et al. 2017). At fine scales, topography may influence baseline species composition and density, while local stand density and burn history are the primary indirect drivers of drought mortality.

### *Management challenges*

Density reduction treatments that rely on mechanical thinning alone had neutral to positive effects on conifer survival during the 2012–2016 drought (Figs. 7, 8). The overstory treatment that removed medium to large trees (e.g., ≥25 cm) was most beneficial to residual individuals, suggesting such a strategy could be used broadly to increase drought resilience for some species (i.e., Jeffrey pine and white fir). While removal of smaller trees (e.g., ≤25 cm) may be less effective at mitigating drought mortality, treatments focused on ladder and surface fuels may still be preferred when considering non-drought objectives such as reducing fire hazard or maintaining wildlife habitat (Stephens et al. 2012).

Prescribed burning appears less effective than mechanical thinning at reducing drought mortality and in some cases can lead to higher beetle infestation and mortality rates (Fig. 8). This is

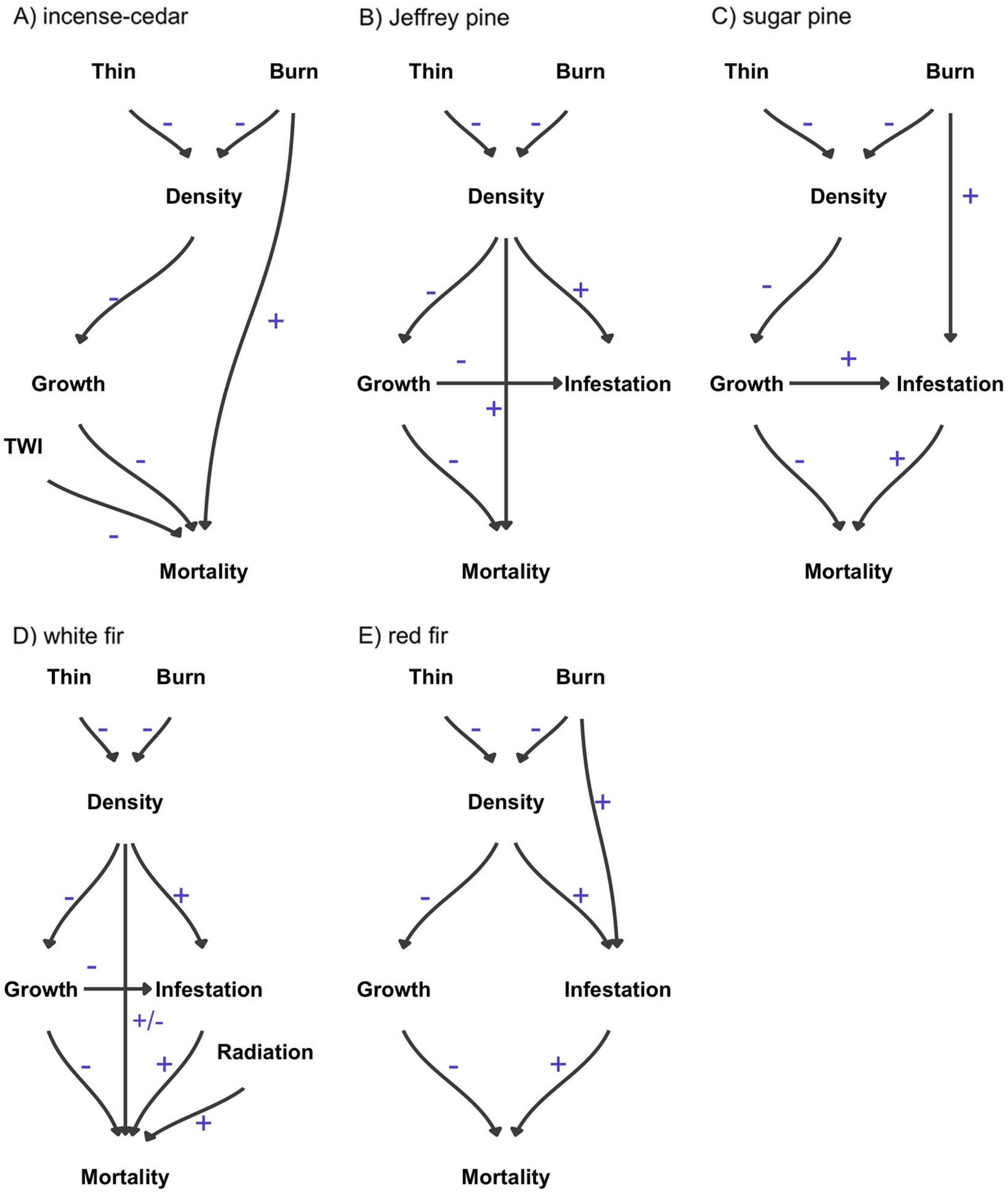

Fig. 8. Causal pathways of drought mortality for (A) incense-cedar, (B) Jeffrey pine, (C) sugar pine, (D) white fir, and (E) red fir. Only links and effect directions are shown when certainty is high (≥95% probability of an effect).

most striking in the case of large sugar pines which died at much higher rates in prescribed burn plots during the drought. The negative effect of burning on tree survival is somewhat surprising given that the fire regime under which these forests developed was characterized by frequent (i.e., 11–17 yr) low- to moderate-severity fire (North et al. 2005, Safford and Stevens 2017), and that the prescribed burn occurred approximately a decade prior to the drought. Further, van Mantgem et al. (2016) observed decreased tree mortality associated with prescribed fire elsewhere in the Sierra Nevada following the initial two years of California's drought, and Meyer et al. (2019) found no difference in mortality between paired burned and unburned plots in red fir forests during the middle and late periods of the drought. The forests Meyer et al. (2019) sampled were at higher elevations than Teakettle where soil moisture is substantially higher and temperatures lower. The results presented here could be unique to the Teakettle Experimental Forest, but we suspect they are more likely attributable to the historic severity of the 2012–2016 drought. When beetle populations are less than epidemic such as at higher elevations, during moderate droughts, or early in severe droughts, previous fire and its associated reduced density may be neutral or ameliorating for conifer mortality. Our sugar pine results may indicate a tipping point beyond which the combination of extreme water stress from drought, bark beetle outbreaks, and fire result in increasingly high rates of tree mortality (Nesmith et al. 2015), and subsequent forest structural changes outside the natural range of variation (Young et al. 2020). These results suggest cautious low-intensity and small (i.e., stand) scale prescribed burning, as it is often applied by managers, may only benefit forests under short duration drought stress while contributing to higher mortality in red fir and sugar pine during prolonged and exceptional droughts. High mortality rates of large sugar pines may be related to prescribed fires consumption of deep litter and duff layers that have accumulated around the base of pine species under fire suppression, suggesting removal of litter and duff through raking could protect individual trees. Nesmith et al. (2010) found raking increased survival and reduced bark beetle activity when fire intensity was moderate (<80% crown scorch) and when fuel depth was ≥30 cm. Thus, protecting individual trees of high ecological value may be possible prior to prescribed burns. However, such targeted measures are infeasible at broad scales in fire-prone landscapes of the Sierra Nevada. In the long run, retaining sugar pine in these pyrogenic landscapes may hinge on fostering sunny, bare mineral soil conditions favorable for sugar pine regeneration and in the future reducing surface fuels on a regular basis.

Treatment effects on large diameter trees are often the focus of management restoration efforts since these structures have been reduced from past logging, take a long time to develop, and are associated with important ecosystem services (e.g., sensitive species habitat and carbon storage). Treatments using only thinning consistently reduced mortality of large (>75 cm DBH) trees across species, albeit with different effect sizes. For incense-cedar and especially white fir, there was a greater reduction in mortality for small versus large trees, which are often the target of fuel reduction treatments. Prescribed fire has mixed effects, reducing mortality of large Jeffrey pine and slightly reducing small white fir mortality when combined with thinning, but increasing mortality of large red fir, incense-cedar, and significantly increasing large sugar pine mortality. While prescribed burning is an important tool for increasing resistance to wildfire (Stephens and Moghaddas 2005, Prichard et al. 2010), our results suggest such fuel treatments do not necessarily also instill drought resistance. There is general benefit to all species in reducing density, but the means (i.e., mechanical vs. prescribed fire) of treatment matters, suggesting caution in widespread use of fire in drought-prone areas where managers want to retain large sugar pines and red fir.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3344/full