RESEARCH ARTICLE

# Tree mortality response to drought-density interactions suggests opportunities to enhance drought resistance

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## Abstract

1. The future of dry forests around the world is uncertain given predictions that rising temperatures and enhanced aridity will increase drought-induced tree mortality. Using forest management and ecological restoration to reduce density and competition for water offers one of the few pathways that forests managers can potentially minimize drought-induced tree mortality. Competition for water during drought leads to elevated tree mortality in dense stands, although the influence of density on heat-induced stress and the durations of hot or dry conditions that most impact mortality remain unclear.

2. Understanding how competition interacts with hot-drought stress is essential to recognize how, where and how much reducing density can help sustain dry forests in a rapidly changing world. Here, we integrated repeat measurements of 28,881 ponderosa pine trees across the western US (2000–2017) with soil moisture estimates from a water balance model to examine how annual mortality responds to competition, temperature and soil moisture conditions.

3. Tree mortality responded most strongly to basal area, and was elevated in places with high mean temperatures, unusually hot 7-year high temperature anomalies, and unusually dry 8-year low soil moisture anomalies. Mortality was also lower in places that experienced unusually wet 3-year soil moisture anomalies between measurements. Importantly, we found that basal area interacts with temperature and soil moisture, exacerbating mortality during times of stress imposed by high temperature or low moisture.

4. *Synthesis and applications.* Our results imply that a 50% reduction in forest basal area could reduce drought-driven tree mortality by 20%–80%. The largest impacts of density reduction are seen in areas with high current basal area and places that experience high temperatures and/or severe multiyear droughts. These interactions between competition and drought are critical to understand past and future patterns of tree mortality in the context of climate change, and provide information for resource managers seeking to enhance dry forest drought resistance.

## 1 | INTRODUCTION

Forests in semi-arid and dry sub-humid climates occupy >25 million km$^2$ and represent nearly 30% of total global forest area (Andrews et al., 2020). The sustainability of these dry forests is uncertain given rising temperatures and enhanced aridity (Anderegg et al., 2019). In coming decades, the structure, composition and distribution of dry forests will be determined by how these tree populations respond to disturbance, management and drought (McDowell et al., 2020). As temperatures rise, overall aridity increases, and droughts potentially become more frequent and severe (Bradford et al., 2020). Expected impacts to dry forests include decreased regeneration, including after wildfires and other disturbance events (Batllori et al., 2020; Petrie et al., 2017), more pronounced declines in growth during hot–dry drought events (Bradford, Andrews, Robles, et al., 2021; Williams et al., 2013), and elevated tree mortality rates due to drought, wildfires and insect outbreaks (Allen et al., 2010; McNellis et al., 2021).

Of all these impacts, elevated tree mortality, in response to drought and often interacting with insect outbreaks, may play a particularly large role in shaping the future of dry forests. Droughts can be defined in many ways (Crimmins et al., 2017). Conditions with the greatest adverse impact on forests are expected to involve 'hot droughts', which combine high temperatures, and associated high atmospheric demand for moisture, with low soil moisture availability. Predicting tree mortality has proven difficult (Rowland et al., 2021) and the specific physiological mechanisms responsible for tree mortality resulting from these hot droughts are still being investigated (Breshears et al., 2018; Choat et al., 2018). Nevertheless, tree mortality associated with hot drought has been clearly demonstrated in both manipulative experiments (Adams et al., 2017) and observational studies (Paz-Kagan et al., 2017), and is expected in increase as temperatures rise (Allen et al., 2010; Bradford & Bell, 2017; McNellis et al., 2021).

In addition to drought, tree mortality is influenced by competition among trees for scarce water resources, and competition will shape how tree mortality responds to future hot droughts. Competition between trees has long been recognized as a dominant driver of tree mortality (Hille Ris Lambers et al., 2002; Peet & Christensen, 1987). Competition provides the foundation for forest self-thinning curves defining maximum sustainable number and size of trees (Westoby, 1984), and stand density indexes (Reineke, 1933). Competition may be even more important in coming decades as climate change and enhanced climate variability promote mismatches between forest structure and moisture availability (Jump et al., 2017). Competitive intensity in forests is often quantified by basal area density (BA: cross-sectional area of trees per unit ground area), a metric that represents the number and size of trees. High BA, even in old growth forests, has been positively related to high tree mortality rates (Bradford & Bell, 2017; Das et al., 2011; Venturas et al., 2020). In addition, forest treatments that reduce BA, often implemented to decrease wildfire risk, have been shown to minimize both drought-induced reductions in tree growth that typically precede mortality (Bottero et al., 2017; Bradford, Andrews, Robles, et al.,2021), and to reduce long-term mortality rates (Powers et al., 2010; Restaino et al., 2019). Despite the recognized influence of basal area on tree response to drought (Young et al., 2017) and observations of rising forest basal area in recent decades (Rautiainen et al., 2011), few studies have examined how basal area interacts with specific drought conditions to determine tree mortality.

Evaluating the potential benefits reducing forest density requires both identifying the specific characteristics of hot-drought events that drive mortality and understanding how competition interacts with those drought conditions. By definition, hot droughts include high temperature and low moisture, but the duration and severity of hot and dry conditions that most influence tree mortality (e.g. short-term extreme heat waves vs. prolonged soil moisture deficits) remains unclear. Reducing forest BA to moderate competition does not mitigate drought-induced tree mortality uniformly across dry forests (Van Gunst et al., 2016), presumably because competition does not exacerbate the adverse impacts of all types of hot-drought stress equally. Competition and moisture limitation are likely interconnected, because more trees, and thus increased competition, result in more water consumption through transpiration, and less moisture resources available to each tree (Davis Kimberley et al., 2018; McDowell et al., 2006). Assessing these potentially divergent interactions between competition and components of hot–dry stress is crucial to understanding the long-term benefits of density reduction in the context of climate change projections that include rising temperatures and uncertain trajectories for soil moisture and ecological drought (Bradford, Schlaepfer, et al., 2020).

Here, we investigate the effects of competition and drought, including their interactions, on tree mortality in ponderosa pine *Pinus ponderosa* forests across the western U.S.. Mortality of ponderosa pine has been related to several aspects of drought and water balance and was generally higher in dry places (Fettig et al., 2019; Paz-Kagan et al., 2017). Ponderosa pine forests include a wide range of basal area conditions (Figure 1b) and are the target of widespread restoration efforts initiated in response to a century of fire suppression which has led to overly dense forest conditions (Covington & Moore, 1994; Reynolds et al., 2013) and enhanced risk of catastrophic wildfires. These restoration efforts include multi-landscape, multi-owner initiatives, such as the Collaborative Forest Landscape Restoration Program (https://www.fs.fed.us/restoration/CFLRP/) which represents some of the largest active ecological restoration efforts in the world and in western North America (Figure 1a).

**(a) FIA plots**



**(b) Current basal area (m²/ha)**

**(c) TEMP$_{MEAN}$ (°C)**

**(d) SWA$_{MEAN}$ (cm)**
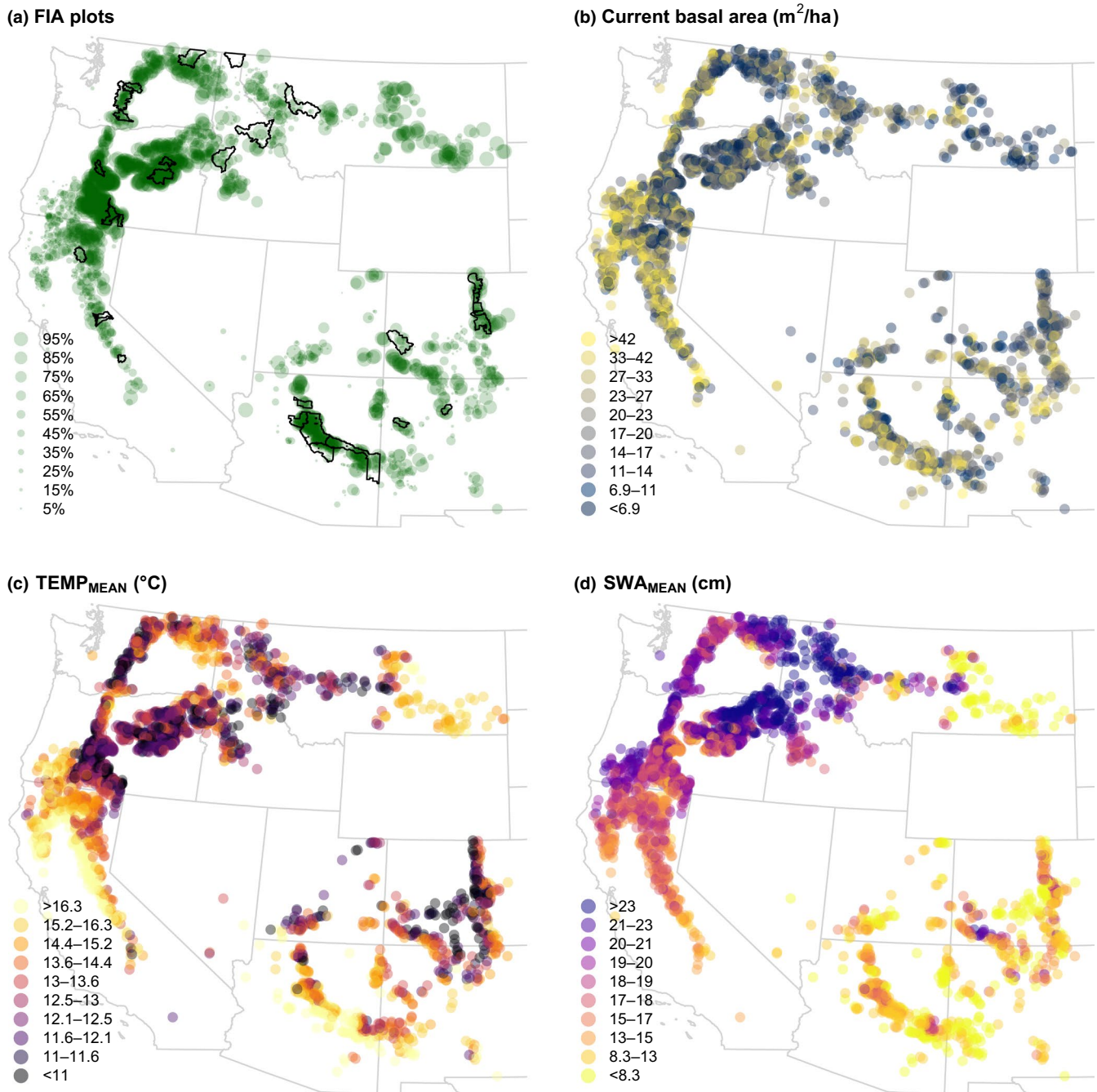
**FIGURE 1** Conditions at forest monitoring plots, including (a) locations (symbol size depicts proportion of total plot basal area represented by ponderosa pine); (b) current basal area; (c) long-term mean growing season temperature (TEMP$_{MEAN}$), and (d) long-term mean growing season soil water availability (SWA$_{MEAN}$). Black polygons in (a) are Collaborative Forest Landscape Restoration Projects

We integrated observations from 28,881 ponderosa pine trees with soil moisture from a $CO_2$ sensitive ecosystem water balance model (Schlaepfer & Murphy, 2018) to assess how competition interacts with various types of heat and drought stress to influence tree mortality. Our objectives were as follows: (a) define conceptual models for tree mortality that represent competing hypotheses about the importance of long-term average conditions, multiyear anomalies, single-year anomalies, competition, and interactions between competition and environmental conditions; (b) determine the support for each hypothesis by quantitatively comparing model performance in explaining observations of mortality across the western U.S.; and (c) utilize the best performing model to identify locations where forest management may be most impactful, assessed both as locations where current forest structural conditions are promoting high competition-driven mortality, as well as locations with climate conditions that create high overall sensitivity of mortality to competition.

## 2 | MATERIALS AND METHODS

### 2.1 | Data description and variable selection

We assessed ponderosa pine mortality in plots maintained by the US Forest Service Forest Inventory and Analysis program (FIA: http://www.fia.fs.fed.us/; Bechtold & Patterson, 2005). We excluded plots with recorded fire-caused mortality or tree harvesting, resulting in 28,881 trees within 3,101 FIA plots in the Washington, Oregon, California, Idaho, Nevada, Montana, Utah, Colorado, Arizona and New Mexico with at least one ponderosa pine tree measured at least twice. Plots were measured 10 years apart; the first measurement occurred between 2000 and 2007. We used plot-level tree basal area (BA; $m^2$/ha) as a measure of competitive intensity, calculated as the sum of cross-sectional area of all trees per unit ground area.

To calculate hot-drought conditions, we used the SOILWAT2 ecosystem water balance model (Schlaepfer & Murphy, 2018), with temperature and precipitation data from DayMET (daymet.ornl.org) extracted between 1979 and 2018. SOILWAT2 is a daily time-step, multiple layer, process-based ecosystem water balance model (Bradford et al., 2014). Soil texture by plot was extracted (by FIA staff) from ISRIC 250m v5 (Hengl et al., 2017) in three layers (0–15, 15–60 and 60–200 cm), or until soil profile depth. To evaluate the impact of BA on mortality, we eliminated the influence of BA on estimated drought conditions by applying constant values for BA (median value; 20 $m^2$/ha) at each plot in the ecohydrology model. Tree biomass and percent live biomass were determined from plot data and equations in Jenkins et al. (2003), and averaged across plots. Leaf area index and grass fraction were determined from Flathers et al. (2016).

We used the RSFSW2 R package (Schlaepfer & Andrews, 2018) to calculate available soil moisture (SWA) as extractible water before all soil layers reached a soil water potential of −3.0 MPa. SWA values remove the effect of local soil conditions on residual moisture held below −3.0 MPa, and are useful for comparing across sites and minimizing the effect of uncertainty in local soil conditions. We focused on growing season (April–September) air temperature and SWA. Because mortality can be influenced by hot–dry conditions over several years or within a single year, we defined covariates (Table 1) that include long-term (1980–2018) mean temperature and SWA, as well as high temperature and low SWA anomalies, calculated as difference between the most extreme (e.g. highest temperature or lowest SWA) value between plot measurements for any single year (1-year anomaly) or multiple consecutive years (multiyear anomalies), and the long-term mean value. Anomalies represent the extreme events with recognized influence over tree mortality (Adams et al., 2017) that occurred between periodic measurements. We quantified collinearity among temperature and SWA anomalies for interval lengths from 1 to 10 years, and identified that 8-year low SWA and 7-year high temperature anomalies minimize collinearity with each other and with single-year anomalies (Figure S1). To explore the potential moderating effect of wet periods, we also calculated the highest 3-year SWA anomaly. Among these covariates, substantial collinearity existed between the 1- and 8-year low SWA anomalies, between the 1- and 7-year high temperature anomalies, and between the 7-year high temperature and high PET term (Figure S1), so we did not use these pairs of covariates in the same model. We included tree size in all models. We considered covariates based on the forest drought severity index (see Supporting Information) but growing season temperature and soil water availability yielded better performance (Table S1), so we defined candidate models (Table S2) representing hypotheses about combinations of long-term average conditions, multiyear anomalies, single-year anomalies, competition, and interactions between competition and environmental conditions.

**TABLE 1** Covariates representing competition and environmental conditions incorporated into candidate statistical models for ponderosa pine mortality

| Category | Covariate abbreviation | Covariate description |
|---|---|---|
| Tree size | $TREE_{DBH}$ | Tree diameter at 1.37 m (included in all models) |
| Competition (Basal area) | BA | Sum of tree cross-sectional basal area at 1.37 m height ($m^2$/ha) |
| Climate | $SWA_{MEAN}$ | Mean April–September soil water availability from 1980 to 2018 (cm) |
| | $TEMP_{MEAN}$ | Average April–September air temperature from 1980 to 2018 (°C) |
| Multiyear hot–dry anomalies | $SWA_{8YMIN}$ | Lowest April–September soil water availability during a consecutive 8-year period between measurements (cm) |
| | $TEMP_{7YMAX}$ | Highest April–September temperature during a consecutive 7-year period between measurements (°C) |
| Single-year hot–dry anomalies | $SWA_{1YMIN}$ | Lowest April–September soil water availability during a single year between measurements (cm) |
| | $TEMP_{1YMAX}$ | Highest April–September temperature during a single year between measurements (°C) |
| Multiyear wet anomaly | $SWA_{3YMAX}$ | Highest April–September soil water availability during a consecutive 3-year period between measurements (cm) |

## 2.2 | Statistical modelling and verification

We modelled survival probability for the 10 years between plot measurements following the approach described in detail in Shriver et al. (2021) and the Supporting Information. Briefly, individual tree survival between measurements was modelled as a function of plot-level environmental conditions and basal area, as well as individual-level tree diameter. Spatial random effects were included using a predictive process model (Latimer et al., 2009) which address the computational challenges of fitting spatial models to large datasets by reducing point locations (i.e. plots) to a lesser number of constituent knots that encapsulate the landscape of spatially autocorrelated processes not explained by covariates. We fit models with Hamiltonian Monte Carlo (HMC) with two chains, 5,000 iterations each, 2,500 for warmup. Model comparison was done with DIC, and the model with lowest DIC was validated for predictive performance using posterior predictive checks, which indicated good agreement between model predictions and data ($p = 0.53$; Figure S2). We partitioned the variance in estimated survival into the proportion explained by fixed (covariates) and random effects following the approach of Gelman and Pardoe (2006). Even across the broad geographical distribution of ponderosa pine and the suite of other local factors that influence tree survival (aspect, bark beetles, etc.), fixed effects in the model accounted for 29% (90% CI: 20%–38%) of overall observed variability in survival probability at the individual tree level, a proportion that is consistent with other mixed-effect ecological studies (Clark et al., 2010).

## 2.3 | Geographical assessment of mortality patterns

10-year survival rates ($S$) were converted into annualized mortality rates ($M$) using the equation:

$$M = 1 - S^{(1/10)}.$$

We used our top performing model to identify areas with climate where reducing BA most enhances survival by quantifying the difference between survival at a fixed high (30 m$^2$/ha; 75th percentile of current BA among plots) versus low (13 m$^2$/ha; 25th percentile), and by calculating for each plot the basal area that would result in estimated long-term mortality rate of 0.5% (van Mantgem et al., 2009). In addition, we identified locations where density reduction would most enhance ponderosa pine survival, given current stand structural conditions, by contrasting survival for each FIA plot at current BA versus survival at 50% of current BA.

# 3 | RESULTS

In our best model, variation in ponderosa pine mortality was primarily attributable to a positive relationship with basal area (BA; Figure 2a; Table S3). The positive effect of BA on mortality became especially pronounced above ~30 m$^2$/ha BA. In addition to BA, our best model for ponderosa pine mortality included mean temperature and SWA (TEMP$_{MEAN}$ and SWA$_{MEAN}$), 7-year high temperature anomaly (TEMP$_{7YMAX}$), 8-year low SWA anomaly (SWA$_{8YMIN}$) and a 3-year high soil moisture anomaly (SWA$_{3YMAX}$; Table S2, Model 5.3, Table S3). Mortality was positively related to both TEMP$_{MEAN}$ and TEMP$_{7YMAX}$, indicating that mortality was greater in places with higher TEMP$_{MEAN}$ and places that experienced unusually high TEMP$_{7YMAX}$ between measurement periods (Figure 2c,e). Mortality was strongly and negatively related to soil moisture anomalies, both SWA$_{8YMIN}$ and SWA$_{3YMAX}$ (Figure 2b,f), indicating that mortality was higher in locations that experienced an unusually dry 8-year period, and was lower in locations that experienced an unusually wet 3-year interval. Our results suggest strong support for the importance of SWA$_{3YMAX}$, which was consistently negatively related to mortality, and substantially improved model performance in all models where it was included. SWA$_{MEAN}$ was included in the best performing model, although this variable displayed only a slight positive relationship with mortality (Figure 2d; Table S3).

Comparing alternative models underscores the importance of BA and provides insight into the duration of temperature and soil moisture anomalies that most influence mortality. Compared to a model with only SWA$_{MEAN}$ and TEMP$_{MEAN}$, including BA substantially increased model performance (ΔDIC of ~200; Table S2). The positive BA–mortality relationships in models with BA (Figure S3) indicate consistent evidence for lower mortality when BA is lower. While TEMP$_{7YMAX}$ and TEMP$_{1YMAX}$ contributed similar improvements to models, TEMP$_{7YMAX}$ performed better when interacting with BA. SWA$_{8YMIN}$ clearly and consistently improved models more than single-year low soil moisture anomalies (ΔDIC of best model with SWA$_{1YMIN}$ = 5.8, Table S2). Strong performance of two models other than the best model illustrates some uncertainty in the optimal combination of covariates: models without TEMP$_{1YMAX}$ or SWA$_{8YMIN}$ performed only slightly worse than our best model (ΔDIC = 1.8, Table S2).

Interactions with competition were critical to understand how mortality responded to drought. In our best model, BA interacted with both long-term conditions (TEMP$_{MEAN}$ and SWA$_{MEAN}$), as well as multiyear anomalies (TEMP$_{7YMAX}$ and SWA$_{8YMIN}$). The importance of interactions between basal area and environmental conditions was demonstrated by the >11 DIC units difference between models with no interactions (Table S2, models 4.0 and 4.1) and similar models with BA interactions (model 5.3). In addition, coefficients for BA and the interactions between BA and these covariates all clearly diverged from zero (Figure S3). For example, the TEMP$_{MEAN}$ coefficient was uncertain in model 1.0 without the BA interaction, but was consistently positive in model 1.1 (Figure S3). By contrast, SWA$_{MEAN}$ was negatively related to mortality when considered without the BA interaction in model 1.0, but the coefficient became uncertain when interacting with BA in model 1.1 (Figure S3), demonstrating how the sensitivity of mortality to competition is influenced by temperature and drought. Differences in mortality rate between high and low basal areas were greater in warmer locations (e.g. those with higher
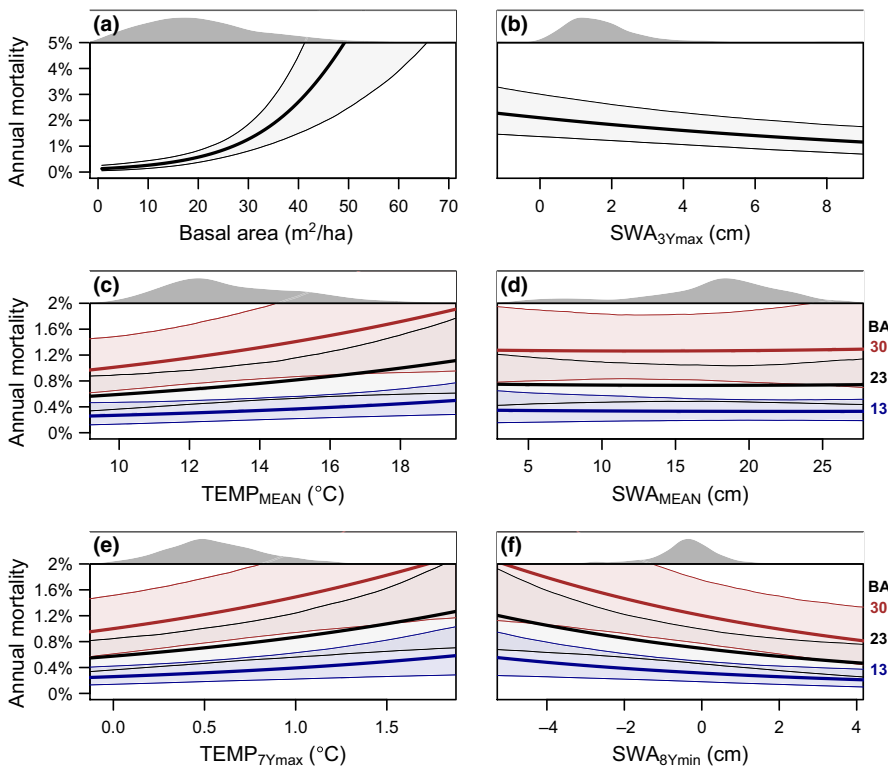
**FIGURE 2** Modelled marginal effects of ponderosa pine tree mortality response to (a) plot basal area, (b) 3-year high soil water anomaly, (c) long-term mean temperature, (d) long-term mean soil water, (e) 7-year high temperature anomaly and (f) 8-year low soil water availability anomaly. Estimated mortality in (c)–(f) three basal area levels: 13 (blue), 23 (black) and 30 (red) m²/ha (25th, 50th and 75th percentiles, respectively, of observed basal areas). Thin lines (outsides of shaded areas around each dark line) are 90% credible intervals estimated from posterior parameter distributions. Grey histograms illustrate the covariate's distribution across all plots examined. All relationships are depicted for a tree of 24 cm DBH (median in the dataset)

$TEMP_{MEAN}$ or $TEMP_{7YMAX}$; Figure 2c,e) and drier locations (e.g. those with lower $SWA_{8YMIN}$; Figure 2b).
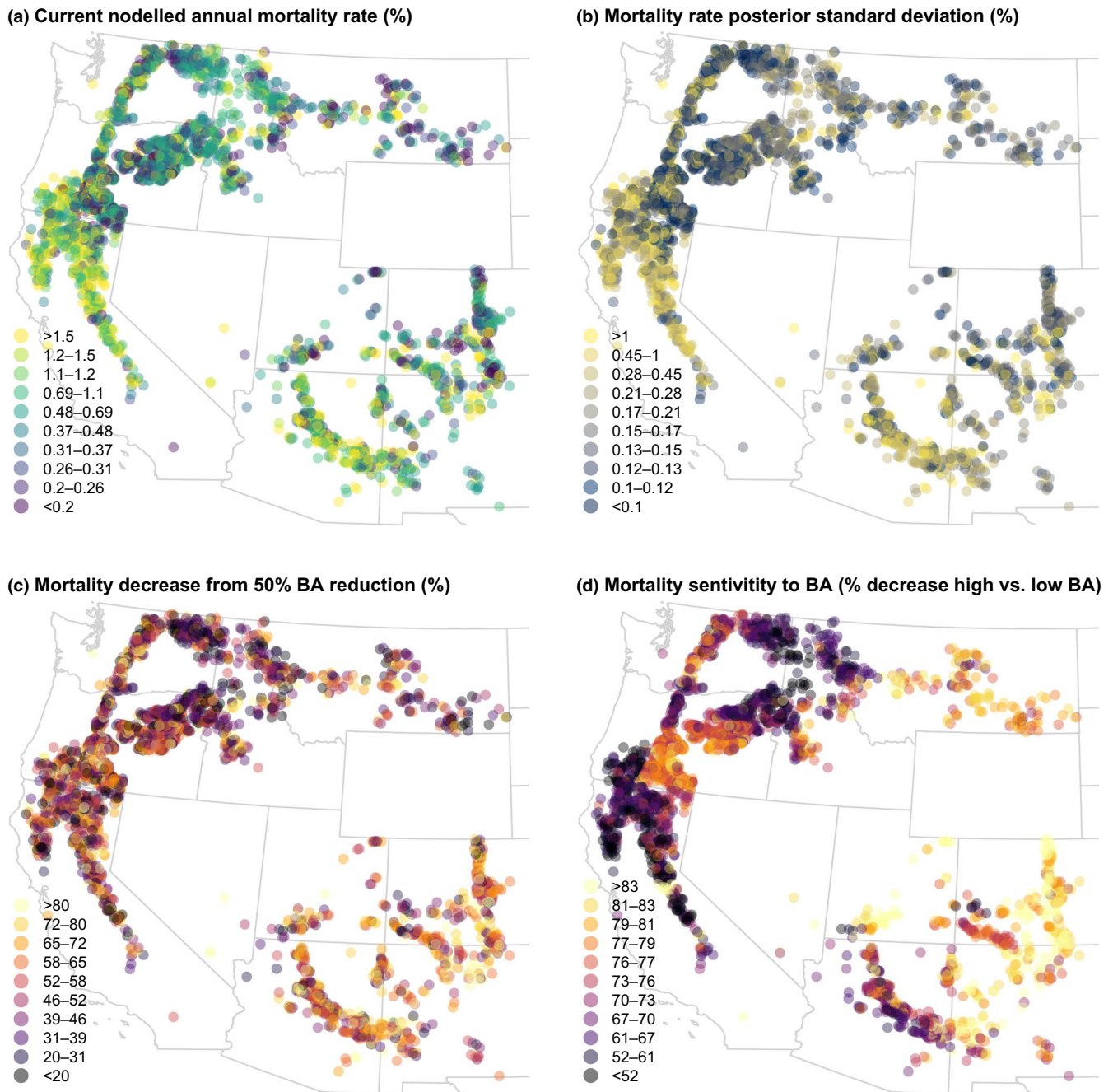
By contrasting mortality under current observed BA (Figure 3a) with mortality at 50% of current BA, we identify locations where current BA (Figure 1b) may promote high mortality (Figure S4). Decreases in mortality from a 50% decrease in basal area were relatively evenly distributed across the range of ponderosa pine, and especially prevalent in the southwest states (Figure 3c). These are areas with high current BA where reducing current BA would have the largest influence, and are generally the same locations that will require the largest reductions in BA to support long-term average mortality rates of 0.5% (Figure S4c). Mortality sensitivity to basal area can be approximated by contrasting mortality from our best model assuming fixed low versus high BA (Figure S4). Areas with the greatest estimated sensitivity include much of the Southwest U.S., eastern Montana and central Oregon (Figure 3d). These areas have climate, particularly high mean temperatures, in which competition has the largest influence on mortality and include California, the southern ranges of Arizona and New Mexico, and eastern Montana (Figure 1d).

## 4 | DISCUSSION

Drought-driven tree mortality is increasing around the world (Allen et al., 2010). Despite growing drought severity in recent decades (Ficklin et al., 2015), the strong relationship between mortality and BA in our results underscores the dominant influence of competition on tree mortality (Venturas et al., 2020), and highlights the potential

opportunities for management to enhance forest drought resistance, defined here following the ideas of Holling (1973) as the ability of forests to retain their structure during drought conditions. While stress induced by hot–dry conditions enhances mortality (Allen et al., 2010), our results help identify the specific drought characteristics that promote mortality in ponderosa pine. The similar performance of 1- and 7-year temperature anomalies is expected given the high correlation between temperature anomalies of differing lengths (Figure S1), and suggests that representing the specific duration of heat waves may not be essential to accurately understand mortality impacts of high temperature events. Our finding of enhanced mortality in places with both warmer long-term climate conditions and hotter temperature anomalies is consistent with previous studies (Adams et al., 2017; Breshears et al., 2018). By contrast, our incorporation of water balance modelling to assess the influence of soil moisture availability on tree mortality over a broad geographical extent, and to contrast varying types of droughts, is relatively new. We found that mortality is more influenced by dry soil anomalies over multiple years than over a single year, and that a 3-year wet period can mitigate mortality. Both insights should be useful for modelling tree mortality under future climate scenarios.

Representing these interactions between drought and competition may enhance the accuracy of ecosystem models, improve projections of long-term climate change impacts on forest distribution and structure, and identify potential management strategies for mitigation. In particular, the positive influence of high temperature (means and anomalies) implies that mortality will increase under warming conditions expected in coming decades, consistent with other studies. In addition, the strong influence of low soil moisture

### (a) Current nodelled annual mortality rate (%)



| | |
|---|---|
| | >1.5 |
| | 1.2–1.5 |
| | 1.1–1.2 |
| | 0.69–1.1 |
| | 0.48–0.69 |
| | 0.37–0.48 |
| | 0.31–0.37 |
| | 0.26–0.31 |
| | 0.2–0.26 |
| | <0.2 |

### (b) Mortality rate posterior standard deviation (%)



| | |
|---|---|
| | >1 |
| | 0.45–1 |
| | 0.28–0.45 |
| | 0.21–0.28 |
| | 0.17–0.21 |
| | 0.15–0.17 |
| | 0.13–0.15 |
| | 0.12–0.13 |
| | 0.1–0.12 |
| | <0.1 |

### (c) Mortality decrease from 50% BA reduction (%)



| | |
|---|---|
| | >80 |
| | 72–80 |
| | 65–72 |
| | 58–65 |
| | 52–58 |
| | 46–52 |
| | 39–46 |
| | 31–39 |
| | 20–31 |
| | <20 |

### (d) Mortality sentivitity to BA (% decrease high vs. low BA)



| | |
|---|---|
| | >83 |
| | 81–83 |
| | 79–81 |
| | 77–79 |
| | 76–77 |
| | 73–76 |
| | 70–73 |
| | 67–70 |
| | 61–67 |
| | 52–61 |
| | <52 |

**FIGURE 3** Geographical patterns of (a) current modelled annual ponderosa pine mortality (posterior mean from $n = 5,000$), (b) standard deviation of posterior mortality estimates for each plot, (c) percent decrease in annual mortality rate between current BA and 50% of current BA, and (d) the sensitivity of mortality to differences in basal area, calculated as the % decrease in mortality between fixed high and low BA levels (30 and 13 $m^2$/ha, respectively)

conditions suggests that future increases in frequency and severity of hot and/or dry events, including multiyear droughts could elevate tree mortality.

Competition is a recognized driver of tree mortality (Hille Ris Lambers et al., 2002; Peet & Christensen, 1987), and interactions between competition and drought identified here can help forest managers anticipate patterns of tree mortality under a changing climate (Jump et al., 2017). Moderating competitive intensity by reducing BA can reduce drought-induced tree growth declines

(Bottero et al., 2017; Gleason et al., 2017) and general patterns of mortality (Powers et al., 2010; Restaino et al., 2019). However, understanding how the influence of competition on mortality varies across climatic gradients and under different types of drought events is limited. We demonstrated this variation, represented by interactions between BA and environmental conditions, notably mean temperature and anomalies in temperature and soil moisture. These interactions illustrate that competition has greater influence on mortality under both hot and dry conditions. Previous

studies have demonstrated tree growth response to interactions between competition and hot–dry stress (Andrews et al., 2020; Gleason et al., 2017; McCauley et al., 2019), and our findings show that those interactive effects extend to tree mortality and apply to stress experienced during high temperatures and during low soil moisture.

Interactions between competition and drought provide information for near-term forest management. In particular, the response of mortality to drought-density interactions reinforces the climate adaptation benefits of ongoing forest landscape restoration (Stoddard et al., 2021) that is increasingly widespread in ponderosa pine forests (Figure 1a). Increasing BA in the late 20th century over many forests in the western U.S. (Rautiainen et al., 2011), particularly in ponderosa pine forests (Covington & Moore, 1994; Reynolds et al., 2013), prompted restoration projects designed to reduce forest density, promote structural conditions consistent with the historical range of variability, and mitigate the risk of catastrophic wildfires that lead to rapid loss of forest cover and ecosystem carbon (McCauley et al., 2019). The interactions demonstrated here between competition and hot drought provide quantitative information about how density reduction enabled by these restoration projects, initially designed for other purposes, will also help buffer forests against heat- and drought-driven tree mortality that is increasing in forests around the world (Allen et al., 2010). In addition, these results identify areas where BA reduction may be most useful for enhancing dry forest sustainability. Geographical patterns in estimated benefits of reducing current BA (Figure 3c,d) and in overall climate-driven sensitivity of mortality to basal area (Figure 3e) may be useful for prioritizing future restoration projects. Our results suggest that substantial reduction in BA may be necessary to moderate drought-induced mortality (Figure S4c). These treatments would alter forest structure, and the impact of those changes need to be weighed against the benefits of imposing treatments. Although severe mortality events driven by hot droughts and insects would also reduce BA, restoration treatments may include benefits like selecting the trees to removed or retain, and avoiding rapid increases in fuel loads after mortality.

Although our focus was assessing how BA and drought combine to influence tree mortality, our data include the effects of insect activity. Tree mortality is often elevated by the combination of both drought and insects (Anderegg et al., 2015). Mortality events driven by these drought–insect combinations have been demonstrated in many areas, including in ponderosa pine forests within our study area and sampling period (Fettig et al., 2019; Stephenson et al., 2019). Including these recent insect outbreaks in the data we examined ensures that our results about how mortality responds to drought type and basal area are relevant even in the context of substantial insect activity. Specifically, the potential for reducing BA to decrease tree mortality encompasses the influence of both drought (whose effects may be exacerbated by high BA due to competition) and insect dynamics (whose effects may be exacerbated by BA due to insect population dynamics not directly related to tree competition). Unlike insects, we attempted to avoid including other mortality agents by excluding plots with wildfire or harvesting. As a result, our overall average mortality rate of ~0.8% per year (5th–95th percentile = 0.14% and 1.8% per year) is an estimate of background mortality and may be less than other studies of ponderosa pine mortality (Ganey & Vojta, 2011). Drought contributes to wildfire activity (Hicke et al., 2016), underscoring the need to untangle the interacting influences of these multiple mortality agents. In addition, our results may not fully account for the consequences of actual temporal changes in climate and/or forest because we utilized a space-for-time substitution, which has recognized limitations in modelling climate-induced changes in tree mortality with a single remeasurement of FIA plots (Dietze & Moorcroft, 2011).

Forest managers have relatively few proven strategies to enhance near-term drought resistance of intact dry forests to rising temperatures and more extreme droughts. Long-term forest management strategies for climate adaptation include harvesting and/or planting to shift composition towards tree species with higher drought tolerance (Paz-Kagan et al., 2017) or to promote forests with higher diversity in species composition or functional traits (Anderegg et al., 2016). Reducing BA in existing forests is a complementary and feasible strategy that our results suggest will have long-term benefits. The interactions identified here provide insight into the types of drought that most influence tree mortality, and how those drought conditions can be minimized by moderating competitive intensity. Specifically, BA reduction can enhance resistance to hot conditions and to multiyear drought events, whose frequency and severity are also expected to be increased as a result of elevated hydro-climatic variability (Swain et al., 2018). This elevated hydro-climate variability may create more multiyear wet periods that could enhance mortality in subsequent droughts by promoting structural overshoot (Jump et al., 2017), further highlighting the benefits of density reduction. Predictions of multiyear wet periods (Liu & Di Lorenzo, 2018) may represent important opportunities for intensive management (e.g. thinning) to promote forest structural conditions with high resilience to hot droughts (Bradford et al., 2018). Our findings that basal area interacts strongly with multiyear drought, and that 3-year wet periods partially mitigate ponderosa pine mortality, provide evidence that both the interactions and the occurrence of wet periods may be useful focal points for additional synthesis and analysis.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

J.B.B., R.K.S., M.D.R., L.A.M., T.J.W. and M.C. conceived the ideas and designed the methodology; D.M.B., R.K.S., C.A.A. and J.B.B. collected the data, including compiling publicly available data; J.B.B., R.K.S., C.A.A. and L.A.M. analysed the data; J.B.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Related datasets have been published and are available via the US Geological Survey ScienceBase https://doi.org/10.5066/P92HBML8 (Bradford et al., 2021).

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