A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area

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Increasing aridity as a result of climate change is expected to exacerbate tree mortality. Reducing forest basal area – the cross-sectional area of tree stems within a given ground area – can decrease tree competition, which may reduce drought-induced tree mortality. However, neither the magnitude of expected mortality increases, nor the potential effectiveness of basal area reduction, has been quantified in dryland forests such as those of the drought-prone Southwest US. We used thousands of repeatedly measured forest plots to show that unusually warm and dry conditions are related to high tree mortality rates and that mortality is positively related to basal area. Those relationships suggest that while increasing high temperature extremes forecasted by climate models may lead to elevated tree mortality during the 21st century, future tree mortality might be partly ameliorated by reducing stand basal area. This adaptive forest management strategy may provide a window of opportunity for forest managers and policy makers to guide forest transitions to species and/or genotypes more suited to future climates.

Climate change is expected to enhance aridity and drought severity in forests around the globe, likely resulting in elevated tree mortality (Allen *et al.* 2010, 2015; Choat *et al.* 2012). Drought impacts are anticipated to be especially severe in dry forest systems, including those in the US Southwest, where pronounced drought and associated reductions in water availability to plants and ecosystems have emerged as predominant characteristics of climate at the beginning of the 21st century (Cayan *et al.* 2010; Seager and Vecchi 2010; Cook *et al.* 2015). Climate model predictions suggest that warming and drying conditions will characterize the Southwest through the remainder of the century (Seager and Vecchi 2010).

In the past few decades, drought-driven tree mortality has received substantial scientific attention (reviewed by Allen *et al.* [2015]), and a growing body of results provides insight into both the physiological processes that occur before and during mortality and the environmental conditions that trigger mortality events. Drought stress emerges as plants experience an increasing gradient between atmospheric demand for water (quantified by vapor pressure deficit; VPD) and soil water availability (quantified by soil water potential; SWP) (McDowell *et al.* 2008). VPD and SWP have been identified as two effective empirical predictors of atmospheric demand for water (McDowell *et al.* 2013, 2016; Williams *et al.* 2013)

and soil moisture limitation, respectively. VPD increases with rising temperature and falling relative humidity, elevating the rate at which water is lost from leaves. Soil water availability decreases as soils become dry during drought periods, contributing to tree stress through hydraulic failure associated with extreme drought and/or carbon starvation during prolonged drought (McDowell *et al.* 2008). In either case, prolonged exposure to extremely hot and dry conditions can lead to eventual tree mortality.

Air temperature, particularly the occurrence of unusually warm conditions, is closely related to VPD at broad spatial and temporal scales and is therefore a useful predictor of atmospheric demand for water and associated drought stress and mortality (McDowell *et al.* 2013; Williams *et al.* 2013). Likewise, precipitation patterns, particularly the occurrence of prolonged dry periods, provide an easily accessible, albeit imperfect, measure of soil water availability. Many details about the environmental drivers and physiology of tree mortality are still being examined (Meir *et al.* 2015), and the importance of interactions between these processes and other stressors (eg insect and disease outbreaks), remains a major focus of ongoing research (Anderegg *et al.* 2015). Nevertheless, these general principles provide a powerful theoretical framework for assessing the future impacts of changing climatic conditions on tree mortality (Allen *et al.* 2015).

As the potentially dramatic impacts of climate change on tree mortality become clear (Allen *et al.* 2015), forest managers and policy makers need strategies to minimize the consequences for tree populations and avoid catastrophic tree die-offs that can contribute to severe wildfire and flood events (Millar *et al.* 2007). One potentially promising

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Figure 1. *(a and b) Naturally occurring variability in forest basal area apparent in* Pinus ponderosa *forests of northern Arizona. Note mortality in the high basal area stand in (b). Results presented here from widespread forest inventory data suggest that tree mortality is greater in high basal area stands.*

approach is to reduce forest basal area (quantified as summed cross-sectional area of all trees within a fixed area at a height of approximately 1.37 m, a metric that is reflective of both the number and size of trees; Figure 1), which effectively increases water availability to remaining trees and has the potential to ameliorate drought stress (Breda *et al.* 2006; McDowell *et al.* 2006). Although basal area reduction has been shown to improve tree resistance and resilience to drought (D'Amato *et al.* 2013) and to decrease mortality rates in experimental settings (Powers *et al.* 2010), the utility of basal area reduction for minimizing drought impacts in natural forests remains relatively unexplored (Clark *et al.* [2016] but see Elkin *et al.* [2015]), especially in dry forests like those of the Southwest US that may be particularly vulnerable to drought.

Here, we quantify mortality patterns in three of the most abundant low-elevation forest tree species of the Southwest: Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and pinyon pine (*Pinus edulis*). We focus on these species because they comprise much of the warmer, drier forests of the Southwest where drought-induced mortality has been observed in the past and is expected to increase in coming decades (Williams *et al.* 2013). We used a dataset of 1854 repeatedly measured forest inventory plots in the Southwest US (Figure 2) encompassing 29,308 individuals of these three species to quantify how tree mortality related to temperature and precipitation extremes and assess whether basal area reduction can mitigate expected climate-driven increases in tree mortality.

■ **Materials and methods**

Mortality data

We compiled forest inventory data from 1854 plots from the US Forest Service Forest Inventory and Analysis Program, which were measured at least twice between 1995 and 2012 in Arizona, New Mexico, Utah, Colorado, and Wyoming. We used individual tree data to ensure that subsequent measurements relate to the same tree by matching tree species, confirming that initial diameter and diameter change were reasonable (eg tree diameter changes less than –2.5 cm or greater than 12.5 cm were carefully inspected and excluded if other data, such as tree heights, species codes, etc, appeared suspect), and that tree location within the plot is within measurement error (<1-m difference between observations, similar to Pollard *et al.* [2003]). For each tree species, we examined mortality only in plots with at least five individuals of that species and with less than 80% stem mortality for the focal species to avoid plots that experienced stand-replacing disturbance events. We examined three species: *P menziesii* (represented by 421 plots; 5861 trees; 5105 survived; 756 died), *P ponderosa* (805 plots; 13,139 trees; 11,674 survived; 1465 died), and *P edulis* (763 plots; 10,308 trees; 8495 survived; 1813 died).

Climate extremes data

For each plot, we extracted 4-km interpolated monthly precipitation and mean temperature data for 1980–2010 from PRISM (PRISM Climate Group, Oregon State University, prism.oregonstate.edu), and calculated temperature mean and precipitation sum by season (winter: DJF; spring: MAM; summer: JJA; fall: SON [the three-letter sequences correspond to the first letters of month names]). For climate data extractions, publically available plot coordinates were used, which incorporate error designed to protect plot locations for privacy purposes (Woudenberg *et al.* 2010). We calculated

weather extremes as the highest and lowest individual temperature and precipitation values for each season in the interval between plot measurement. We confirmed that weather extremes are not correlated with plot basal area (WebFigure 1), simplifying interpretation of individual relationships between extremes and mortality and/or between basal area and mortality.

Analysis of mortality relationship with climate and stand basal area

Following the methods developed by Bell *et al.* (2015), we estimated annual mortality rates (M_R) for each plot from observed mortality (M_{dt}) over the years between measurements (dt) as

$$M_R = 1 - (1 - M_{dt})^{\frac{1}{dt}}$$

We characterized the relationship between M_R and climate or stand structure drivers (x) for each plot i using a logit link function as

$$logit(M_R) = \beta_0 + \beta_1 x_i$$

We used the *optim* function in R (R Core Team 2015) to identify the maximum likelihood estimates for logistic regression intercept and slope parameters β_0 and β_1, respectively, that minimize the negative log-likelihood. Non-parametric bootstrap sampling (5000 samples) was used to estimate the mean parameter estimates and credible intervals. We quantified the relationship between mortality and climatic extremes, including maximum annual temperature observed between measurements (highly correlated with other temperature metrics) and minimum seasonal precipitation observed between measurements for winter, spring, summer, and fall. We also quantified the relationship between mortality and stand basal area (WebFigure 3). We focused on extremes of temperature and precipitation rather than more derived climate metrics such as VPD or the forest drought severity index, which is based on VPD (Williams *et al.* 2013), for two reasons. First, at the broad spatial and relatively long temporal resolutions that we examined, those metrics were highly correlated with temperature extremes. In fact, relationships between VPD and mortality (not shown) were similar to relationships based on temperature, and temperature extremes are more easily interpreted. Second, measures of VPD that differ meaningfully from temperature require estimates of relative humidity, which is unavailable in the down-scaled future climate data we used, limiting our ability to accurately forecast VPD. We quantified how mortality relates to four potential candidate models defined by minimum precipitation in each of the four seasons (each in a separate model) along with maximum annual temperature and stand basal area (both in all models). We utilize the best model (that is, the model with the
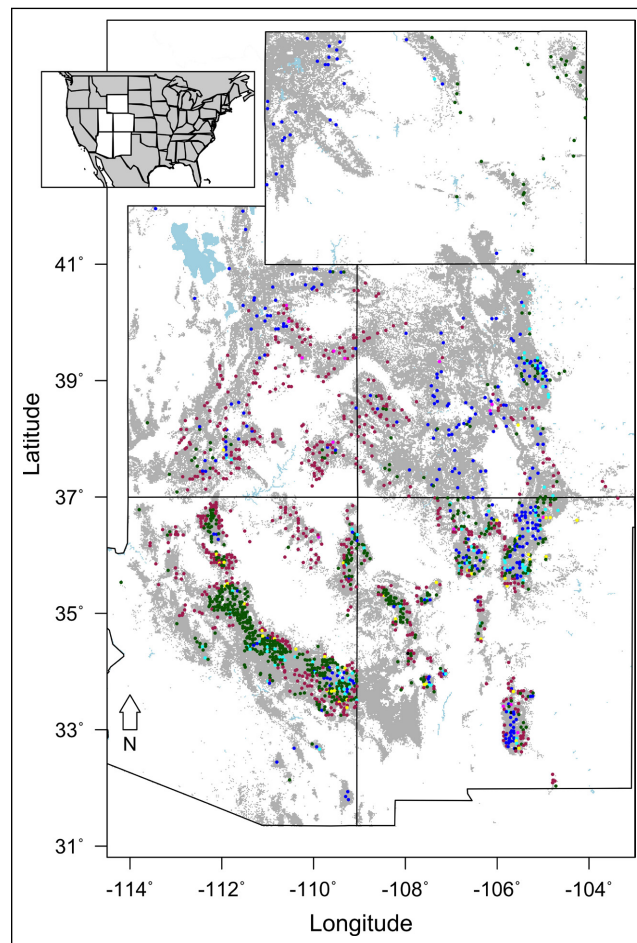

Figure 2. Locations of forest inventory plots used (blue, Pseudotsuga menziesii; green, Pinus ponderosa; maroon, Pinus edulis). Plots used for more than one species are colored with a combination of primary colors (yellow for both P ponderosa and P edulis, cyan for both P menziesii and P ponderosa, magenta for both P menziesii and P edulis). Gray indicates forested areas (data from USDA Forest Service: http://data.fs.usda.gov/geodata/rastergateway/biomass).

lowest Bayesian information criterion) as an overall representation of mortality response to climatic extremes and stand structure. Models with interactions among temperature, precipitation, and basal area predictors did not improve model performance.

Future climate data

To evaluate future climatic conditions, we synthesized monthly temperature and precipitation predictions from 10 general circulation models (GCMs) for the areas occupied by these species for 30-year periods in the middle and end of the 21st century. We used future monthly climate data from the bias correction and spatial disaggregation (BCSD)–downscaled Coupled Model Intercomparison Project Phase 5 (CMIP5) Climate and Hydrology Projections archive at http://gdo-dcp.ucllnl.org/downscaled_cmip_projections. We examined data from

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each GCM for two representative concentration pathways (RCP4.5 and RCP8.5). We focus on RCP8.5; results of mortality predictions for RCP4.5 are available in WebFigure 4. We selected GCMs based on their performance in the western US (Rupp *et al.* 2013) and to be representative of the families of existing GCMs (Knutti *et al.* 2013). For each plot, we extracted monthly temperature and precipitation forecasts for three time periods: 1970–2000 (historical), 2020–2050 (mid-century), and 2069–2099 (late-century) and calculated the mid- and late-century changes as differences from current conditions for both mean and extreme seasonal conditions. These differences were applied to monthly PRISM datasets to estimate future long-term mean and extreme seasonal temperature or precipitation. We calculated ensemble ranks for each climatic extreme variable and report the minimum (1st ranked GCM; lowest value), median (average of 5th and 6th ranked GCMs), and maximum (10th ranked GCM; highest value) for the middle and end of the 21st century (WebFigures 5 and 6).

Future mortality

We applied the forecasts of future climate extremes to the best mortality model for each species to estimate future mortality rates under climate-change scenarios. We developed ensemble predictions of plot-level future mortality based on all 10 GCMs and report minimum, median, and maximum mortality values under both time periods (WebFigure 7). We quantified future mortality rates for the median climate ensemble under low, current, and high basal area conditions (represented by the 20th, 50th, and 80th percentile of current total basal area distribution for all plots examined for each species).

■ Results and discussion

These repeat forest inventory measurements indicated that tree mortality was positively related to temperature extremes. For all three species, mortality was higher in locations within each species' range that experienced higher maximum annual temperature conditions between inventory measurements (WebTable 3 and WebFigure 3). Because long-term annual or seasonal temperature conditions (and annual or seasonal temperature extremes) are all highly correlated (WebTable 1), locations with high maximum annual temperature (observed here to have high mortality) are also generally those with the highest long-term temperature. The consistent and strong positive relationship between temperature extremes and tree mortality corresponds with a growing body of work identifying the adverse impacts of high temperatures on tree growth and mortality (eg Allen *et al.* 2010, 2015; Williams *et al.* 2013; McDowell *et al.* 2016).

Relationships between tree mortality and precipitation extremes were more variable across species and among seasons, reflecting lower, and in some cases negative,

correlations among extreme and long-term precipitation at seasonal and annual time frames (WebTables 2 and 3). For all three species, mortality was negatively related to minimum winter and spring precipitation, indicating higher mortality in locations that experienced especially dry winter and spring conditions between inventory measurements. Precipitation extremes in summer and fall, by contrast, were more inconsistently related to mortality (WebFigure 3). While mortality of *P menziesii* was not significantly related to minimum precipitation in either summer or fall, mortality of *P ponderosa* was positively related to moisture during both periods; by comparison, mortality of *P edulis* displayed a weak positive relationship with minimum summer precipitation and a weak negative relationship with minimum fall precipitation. We found that low precipitation extremes generally had the strongest and most consistent relationship with mortality in the lower-elevation species *P ponderosa* and particularly *P edulis* (Figure 3 and WebFigure 3), whose growth and mortality are highly sensitive to drought and even specific precipitation thresholds (Clifford *et al.* 2013; Macalady and Bugmann 2014).

For all three species, the relationships between mortality and climate conditions described above suggest that mortality is likely to increase under future conditions. Increasing temperatures are typically the most consistent and reliable component of climate-change forecasts (WebFigures 5 and 6), and all GCMs anticipate substantial increases in the temperature of unusually hot years for the areas covered by these species. Average maximum annual temperature extremes (over a 30-year time period) for *P menziesii*, *P ponderosa*, and *P edulis* are currently 6.9°C, 9.3°C, and 10.4°C, respectively. Forecasts for 30-year maximum annual temperature extremes under the RCP8.5 scenario for plots occupied by these tree species suggest increases of ~2.8°C (GCM range: 1.6°C to 3.4°C) by the middle of the 21st century and ~6.3°C (GCM range: 4.9°C to 7.7°C) by the end of the 21st century (WebFigure 5).

When combined with maximum annual temperature and stand basal area, the most explanatory precipitation predictors of tree mortality were relatively weak relationships with minimum spring precipitation for *P menziesii* and *P ponderosa* and a stronger negative relationship with minimum winter precipitation for *P edulis* (Figure 3). Forecasts for precipitation change, in contrast with temperature, are more variable across seasons and among GCMs. For *P menziesii* plots, minimum spring precipitation (currently 20.6 mm) is forecasted to increase approximately 12 mm by mid-century (GCM range: –10 mm to 34 mm) and increase 4 mm by the end of the century (GCM range: –16 mm to 44 mm; WebFigure 5). For *P ponderosa* plots, minimum spring precipitation (currently 26.2 mm) is largely unchanged (1 mm increase) by mid-century (GCM range: –10 mm to 11 mm) and slightly decreased (–4 mm) by the end of the century (GCM range: –14 mm to 8.3 mm). Minimum winter precipitation for *P edulis*

plots (currently 18.5 mm) is expected to increase 9 mm (GCM range: –5 mm to 22 mm) by mid-century and 5 mm by the end of the century (GCM range: –9 mm to 25 mm).

To estimate potential future rates of tree mortality, we identified the most explanatory statistical model for mortality that includes maximum annual temperature, stand basal area, and minimum seasonal precipitation in one of the four seasons (WebTable 3 and WebFigure 2). Applying these models to future climatic conditions suggests that although predictions for minimum winter and spring precipitation extremes are not as consistent as predictions for temperature, the modest potential increases in spring precipitation anticipated for *P menziesii* are unlikely to substantially moderate the negative impact of rising temperatures, and the expected decreases in winter precipitation for *P edulis* will likely exacerbate mortality increases (Figure 3). The current average annual tree mortality rate based on the inventory data for *P menziesii* is 1.4%, while future rates based on future climate under the RCP8.5 scenario (assuming unchanged basal area) are 1.77% by mid-century (GCM range: 1.6% to 1.79%) and 2.58% by late-century (GCM range: 2.2% to 2.9%; Figure 3). Changes in mortality are more substantial for both *P ponderosa* and *P edulis*. Current annual mortality for *P ponderosa* is 1.3% compared to an estimated 2.5% by mid-century (GCM range: 1.9% to 2.8%) and 5.6% by late-century (GCM range: 4.1% to 7.6%). Current *P edulis* mortality is 2.0%, while future estimates are 3.5% by mid-century (GCM range: 2.5% to 4.1%) and 7.7% by late-century (GCM range: 6.4% to 11.7%). Our estimates of current mortality rates are consistent with other assessments and may already reflect increases over the past several decades (van Mantgem *et al.* 2009).

Our data also suggest that, ignoring climatic influences, mortality is positively related to stand basal area for both *P menziesii* and *P ponderosa* and not strongly related to

Figure 3. *Relationship between tree mortality and climatic extremes (a, c, e) and estimated mortality rates for all plots under current and potential future climate conditions (b, d, f). Left: modeled annual tree mortality rates (green = low mortality, magenta = high mortality) for each inventory plot shown as a point within the climate space defined by maximum annual temperature and the most predictive minimum seasonal precipitation variable. Future climatic conditions for the climatic extremes during the middle and end of the 21st century are shown by light blue and dark blue isolines, respectively. Right: boxplots of modeled mortality rates under current conditions (gray) and future climatic conditions (RCP8.5; median GCM) expected during the middle and end of the 21st century (light and dark blue, respectively). Narrow boxes on left (yellow outline) and right (green outline) of each set illustrate mortality under low and high basal area, defined as the 20th and 80th percentile of the plot basal areas, respectively, for each species. Inset shows the basal area (BA) coefficient distribution from 5000 iterations in the full model, illustrating support for a positive relationship between basal area and mortality.*

basal area for *P edulis* (WebTable 3 and WebFigure 3). When climate and basal area are simultaneously considered by mortality models that include stand basal
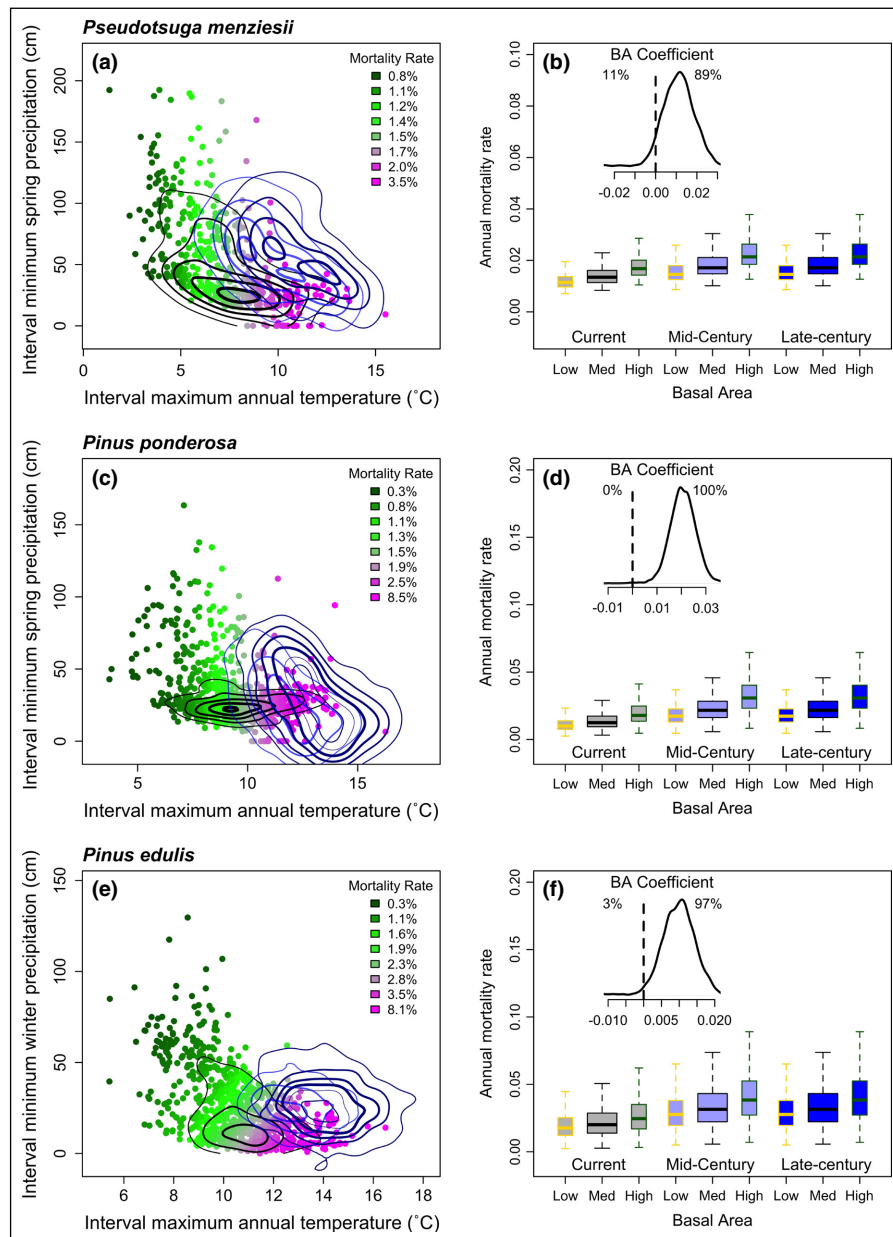
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area, maximum annual temperature, and minimum winter or spring precipitation, basal area has a clear positive effect on mortality in all three species (WebTable 3), suggesting that managing forests at lower basal area can help minimize tree mortality. We estimated mortality rates under low, median, and high basal area conditions (defined as the 20%, 50%, and 80% percentile of current basal area in plots for each species) and contrasted future mortality estimates under low basal area conditions with median and high basal area to provide a measure of the mitigation potential of managing stands at lower basal area. For *P menziesii*, managing stands at low basal area could avoid 70% to 86% (median and high basal area, respectively) of anticipated mortality increases in mid-century and 31% to 54% of anticipated increases by the last 30 years of the 21st century. For *P ponderosa*, managing for low basal area could avoid 42% to 70% of mid-century mortality increases and 25% to 51% of late-century mortality increases. Basal area reduction may be somewhat less effective for avoiding *P edulis* mortality; low basal areas could avoid 30% to 55% of mid-century mortality increases and 16% to 34% of late-century increases.

While the forest inventory data used in this analysis provide an invaluable perspective on patterns and controls of tree mortality, these widely distributed, infrequently measured data are inherently limited in their ability to characterize detailed physiological links between environmental conditions and tree mortality – a notoriously complex physiological process (McDowell *et al*. 2013) that is additionally obfuscated at landscape and regional scales by insect and disease dynamics (Anderegg *et al*. 2015). Ideally, our analysis could have relied on site-specific direct measurements of both VPD and soil moisture conditions. In the absence of such data, we relied on relatively simple metrics of climate extremes and focused here on the potential impact of stand basal area. Despite the substantial variability in these data and the challenges of representing mortality, we found a consistent positive relationship between basal area and mortality rates (Figure 3; insets in right-hand column). Although the observational nature of these data limit our ability to be unequivocal about the link between basal area and mortality, the impact of basal area cannot be accounted for by climatic means or extremes (WebFigure 1), and the consistency of this relationship with the few studies that have examined mortality in long-term basal area manipulation experiments (eg Powers *et al*. 2010) supports the inference that decreasing basal area is likely to be an effective strategy for ameliorating tree mortality. While we examined plot basal area here, other aspects of forest structure may influence forest vulnerability to climatic extremes, including stem density and stand age, which can be related (Lutz and Halpern 2006), as well as tree height (Sperry *et al*. 2002).

The effect of basal area on mortality rates, and therefore the amelioration potential of managing forests for low basal area, is greater for climate extremes expected in the middle of the 21st century and lower by the end of the century, presumably because the more substantial long-term climatic changes include severe conditions where basal area reduction is less able to moderate drought stress. Similarly, simulation studies in Europe indicated that thinning effectively delayed climate-induced mortality by several decades, which can allow forest management to create opportunities for immigration of more drought-tolerant tree species into stressed forests (Elkin *et al*. 2015). Likewise, managing forests at low basal area will likely have even higher mitigation potential for the more moderate RCP4.5 scenario (WebFigure 4). While high tree mortality rates expected for high basal area stands in the 21st century could have the potential benefit of allowing only drought-adapted trees to persist, they also have the potential negative consequence of rapidly changing forest structure, function, and ecosystem service delivery (Clark *et al*. 2016). These results suggest that basal area reduction may be most useful in the relatively near-term, potentially providing forest managers with a window of opportunity to promote species and genotypes that are more appropriately adapted to emerging climatic conditions.

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■ Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1445/suppinfo