

LETTER

Long-term climate and competition explain forest mortality patterns under extreme drought

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Abstract

Rising temperatures are amplifying drought-induced stress and mortality in forests globally. It remains uncertain, however, whether tree mortality across drought-stricken landscapes will be concentrated in particular climatic and competitive environments. We investigated the effects of long-term average climate [i.e. 35-year mean annual climatic water deficit (CWD)] and competition (i.e. tree basal area) on tree mortality patterns, using extensive aerial mortality surveys conducted throughout the forests of California during a 4-year statewide extreme drought lasting from 2012 to 2015. During this period, tree mortality increased by an order of magnitude, typically from tens to hundreds of dead trees per km², rising dramatically during the fourth year of drought. Mortality rates increased independently with average CWD and with basal area, and they increased disproportionately in areas that were both dry and dense. These results can assist forest managers and policy-makers in identifying the most drought-vulnerable forests across broad geographic areas.

Keywords

California, climate, climatic water deficit, competition, drought, forest, mortality, stress, tree.

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INTRODUCTION

Major drought-induced tree mortality events have the potential to dramatically alter the structure and distribution of forests globally (Allen *et al.* 2010). As droughts become hotter and more frequent with climate change, their effects on tree mortality may have profound implications for carbon storage and other ecosystem services provided by forests (Allen *et al.* 2015; Millar & Stephenson 2015). Drought events often impact forests across large geographic areas that have substantial spatial variation in average climate and competitive environments (Allen *et al.* 2010). At this regional scale, the influence of average climate, competition, and their interaction on tree mortality during drought remains poorly understood (Clark *et al.* 2016).

Along spatial gradients of climatic aridity, one might expect tree vulnerability to drought to be either greater in wetter sites, greater in drier sites, or largely independent of aridity (Clark *et al.* 2016). Tree architecture and physiology respond to environmental conditions through both adaptation and plasticity (Franks *et al.* 2013), and trees in climatically cooler and/or wetter sites may have low water use efficiency, high leaf-area index, or other attributes that disproportionately reduce growth or increase mortality when a drought does occur (Field *et al.* 1983; Clark *et al.* 2014). Conversely, trees in climatically warmer and/or drier sites may exist closer to

the absolute climatic limits of forest biomes that are constrained by water availability (Stephenson 1990), thus making them more vulnerable to droughts despite potential adaptations such as increased water use efficiency (Field *et al.* 1983). For instance, individual-based and plot-based studies of long-term tree mortality along climatic gradients often observe greater mortality in sites with higher average temperatures and lower average precipitation (Lines *et al.* 2010; Ruiz-Benito *et al.* 2013; Zhang *et al.* 2015). Similarly, drought-induced mortality may increase at the hot, dry limit of an individual tree species' range (Allen & Breshears 1998; Millar *et al.* 2012; Anderegg *et al.* 2015a).

Forest structure mediates the effect of average climate on drought-induced forest mortality, because individual trees respond to climate and resource limitation differently depending on their competitive environment (Clark *et al.* 2016). Higher levels of competition within a forest stand can increase mortality probability (Das *et al.* 2011; Dietze & Moorcroft 2011; Ruiz-Benito *et al.* 2013; Zhang *et al.* 2015; Van Mantgem *et al.* 2016), likely compounding the effects of drought on mortality, particularly where water is a limiting resource. However, studies of tree mortality responses to drought often do not explicitly distinguish the effects of local climate and competitive environment under drought conditions (Price *et al.* 2015; Zhang *et al.* 2015), although such interactions are known to drive the sensitivity of individual trees to drought

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(Clark *et al.* 2016). Thus, our understanding of the influence of forest structure and climate (and their interaction) on mortality during drought remains extremely limited at a regional scale, in part because spatial data on drought-related tree mortality at this scale covering multiple years and prolonged droughts are scarce.

We address these knowledge gaps using spatially explicit data on forest mortality, structure, and climate from a broad geographic region (the state of California) prior to and during a recent extreme drought. California forests encompass large gradients in climate and structure and are representative of the challenges faced by many forests in western North America, where extensive fire suppression, logging, and grazing for over a century have led to large increases in tree density and stand basal area in many locations (Knapp *et al.* 2013; McIntyre *et al.* 2015; Safford & Stevens in press). These changes have likely increased forest vulnerability to stressors such as bark beetles, wildfire, and drought (Millar & Stephenson 2015). Exemplifying this vulnerability, California experienced a historically extreme drought from 2012 to 2015 that caused the Governor's office to declare a state of emergency due to dramatic increases in tree mortality (Brown 2015).

The cumulative 3-year drought spanning the 2012–2014 water years (October 2011–September 2014) was among the most extreme in California's recorded history by any measure, and potentially the most extreme in the past millennium, depending on the reconstruction methodology and climate data used (Griffin & Anchukaitis 2014; Swain *et al.* 2014; Robeson 2015; Williams *et al.* 2015). The drought continued during the 2015 water year (October 2014–September 2015), making the cumulative 4-year drought from 2012–2015 likely unprecedented in at least the past 1200 years, at least for central and southern California (Robeson 2015). Given the projected increases in temperature due to climate change, California's 2012–2015 drought may represent an increasingly

common condition in which warmer temperatures coincide with periodically occurring dry years (Berg & Hall 2015), contributing to increasing physiological stress in trees (Williams *et al.* 2015).

Dramatic reductions in live forest canopy water content – a potential precursor to mortality – have been observed in many areas of the state (Asner *et al.* 2016), but no study to date has directly examined potential environmental drivers of actual tree mortality during this drought. We used comprehensive statewide annual aerial mortality surveys conducted by the U.S. Forest Service from 2009 through 2015, combined with regional-scale data on climatic water deficit (CWD) and forest basal area, to ask (1) Does drought equally impact mortality of trees inhabiting climatically wet and dry forests, or is it concentrated in particular climatic regions? and (2) Does the influence of competition on drought-related mortality depend on average site climate?

Because the drought affected forests with a wide range of mean annual CWD and stand basal area (Fig. 1), we can directly observe tree mortality responses to extreme drought, link these responses to long-term site climate and tree competition, and gain valuable insights into likely forest responses to future drought as the climate continues to change.

MATERIAL AND METHODS

Mortality data

Annually, the United States Forest Service Pacific Southwest Region Aerial Detection and Monitoring Program (ADMP) flies a small aircraft over the majority of the forested areas of the state of California and defines geospatial polygons that represent aerially observed recent tree mortality (U.S. Forest Service 2016). The polygons are produced by aerial observers by carefully drawing outlines on digital aerial imagery around

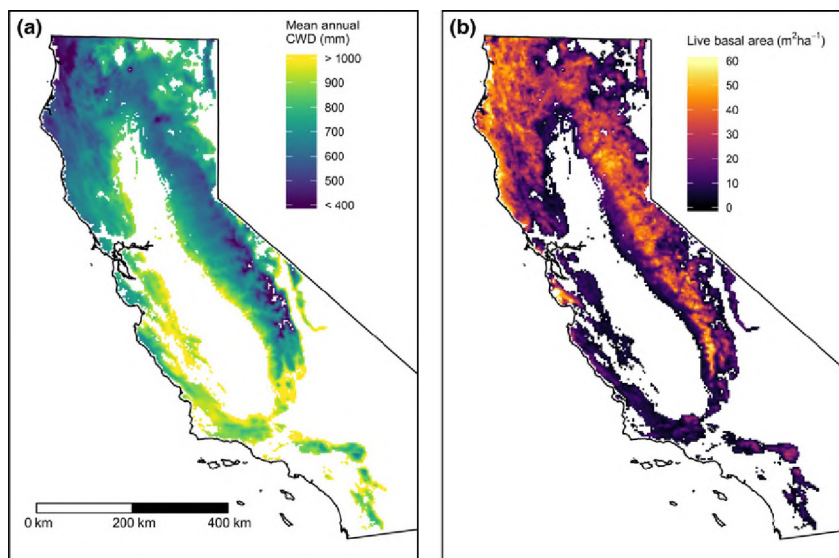


Figure 1 Mean annual climatic water deficit (CWD) for the 1981–2015 period (a) and live basal area (b) for all 3.5 km grid cells that were surveyed for mortality in at least 1 year between 2009 and 2015. In (a), cells with CWD > 1000 mm year⁻¹ (7% of cells) were set equal to 1000 mm year⁻¹, and cells with CWD < 400 mm year⁻¹ (1% of cells) were set to 400 mm year⁻¹ to highlight contrasts within and among regions.

the locations where recent mortality is observed on the ground. Each mapped polygon is assigned attributes, including estimated number and density of trees that died during the preceding year and the inferred cause of mortality. Although the ADMP covered most of the forested area of the state annually from 2009 to 2015, the exact coverage varied from year to year (Fig. S1).

For each survey year from 2009 to 2015, we converted the ADMP survey data into a raster layer (grid) with a 3.5 km resolution (see Appendix S1 for details on rasterization). For this analysis of broad-scale patterns of forest response along large climatic gradients, we considered mortality of all tree species and did not distinguish among species. Our analysis considered all forested areas and forest community types covered by the aerial survey in each year. Across all 7 years analysed, the surveyed area consisted of the following forest type groups as defined by the Society of American Foresters (Eyre 1980) and mapped by the U.S. Forest Service (2008): California mixed-conifer (39% of surveyed area), western oak (21%), ponderosa pine (11%), fir/spruce/mountain hemlock (8%), tanoak/laurel (6%), lodgepole pine (5%), pinyon/juniper (5%), Douglas-fir (3%), and eight other groups each representing < 2% of surveyed area. We considered all surveyed 3.5 km grid cells having a basal area of $\geq 2 \text{ m}^2 \text{ ha}^{-1}$ as 'forested' (see 'Forest structure data', below) and included them in our analysis, though we excluded ADMP polygons that were very small and/or had very low mortality density, as well as those attributing mortality to agents that have little if any association with drought (e.g. wind and bears) (see Appendix S1).

Climate data

We sought to explain spatial variation in tree mortality in each year using mean annual climatic water deficit (CWD), a representation of the water stress experienced by plants. CWD reflects the amount by which evapotranspiration is restricted due to water limitation (Stephenson 1990). We modelled CWD using a modified Thornthwaite approach (Willmott *et al.* 1985), which integrates monthly temperature and precipitation and modelled hydrological processes, including snow accumulation and melt, soil water storage, runoff, and evaporation to derive monthly estimates of potential evapotranspiration (PET), actual evapotranspiration (AET), and CWD (which is calculated as the difference between PET and AET). The modified Thornthwaite approach has been used in numerous recent studies of plant–climate relationships (e.g. Van Mantgem & Stephenson 2007; Gavin 2009; Stephenson & Das 2011; Smith *et al.* 2015).

As inputs to the water balance model, we used 2.5 arc-min ($\sim 4 \text{ km}$) grids of estimated monthly precipitation from September 1980 to September 2015 developed by the PRISM Climate Group (2016) and 30 arc-sec ($\sim 800 \text{ m}$) grids of estimated monthly temperature from September 1980 to September 2015 (which we aggregated to the same $\sim 4 \text{ km}$ grid as the precipitation data) from the TopoWx data set (Oyler *et al.* 2014). We assumed that soils had a constant water holding capacity of 150 mm throughout the study area (*sensu* Stephenson & Das 2011). We modelled the monthly CWD for each

$\sim 4 \text{ km}$ climate grid cell, and we used bilinear interpolation to downscale the monthly CWD grids to match the 3.5 km resolution of the mortality grid (described above). For each resulting grid cell, we calculated the total annual water-year (October–September) CWD for each year from 1981 to 2015, and we calculated a 35-year climatic normal (mean annual) CWD for each cell by averaging the total annual water-year CWD across all years. For each year, we also quantified each grid cell's CWD anomaly, or departure from long-term mean annual CWD, by calculating its *z*-score: the difference between the year's mean annual CWD and the 35-year mean CWD, divided by the standard deviation in CWD across all 35 years in that grid cell. Thus, in our model, we use 'mean annual CWD' to represent the *average climatic water deficit* of a particular grid cell (i.e. spatial variability in CWD), and 'CWD anomaly' to represent the *departure* of CWD from average conditions in a given year for a particular grid cell (i.e. a proxy for temporal variability in drought severity).

Forest structure data

The likelihood that a given tree will die may be higher in denser stands due to stronger competition for resources (Das *et al.* 2011). To account for this phenomenon, we included tree basal area as a covariate in our model. Basal area is an imperfect index of competition, as the number, size, and identity of competitors can also influence mortality. However, basal area is a widely used and highly relevant single metric of competition, as it integrates both number and size of trees. We obtained values from a gridded data set of basal area imputed to a 30 m resolution for all forested areas of the state using extensive field plot data, remotely sensed imagery, and climate data (GNN data set; LEMMA group 2015; see Appendix S1 for further details). The GNN data set also provides a modelled layer of tree density (trees per hectare), but validation tests found it to be substantially less accurate than the basal area layer (see Appendix S1). A possible alternative explanation for observing greater absolute mortality in stands with higher basal area is simply that there are more trees available to die in those stands. If such a sampling effect were driving the association between basal area and mortality, however, we would expect a correlation between the total number of trees in a grid cell (from the GNN data set) and number of dead trees counted there (from the aerial survey data set). We found no such association ($R^2 = 0.0003$ for 2015; Fig. S3) and proceeded to use basal area as our indicator of tree competition.

Statistical analyses

We performed all statistical analyses in R (R Core Team 2016). For each year from 2009 to 2015, we used a separate statistical model to explain annual tree mortality within a given grid cell using mean annual CWD (calculated as described above), stand basal area (in $\text{m}^2 \text{ ha}^{-1}$; derived from the GNN data set), and the CWD anomaly for the year and grid cell in question. We included the latter variable to account for the fact that the annual CWD values for different grid cells in a given year may depart more or less from their

35-year average value, despite similar drought patterns across the state (for the magnitude of this within-year deviation, see the shaded bands in Fig. 2a). Because the data were highly zero-inflated, we modelled the occurrence of mortality and the amount of mortality where it occurred as separate processes using a hurdle model, which consisted of a logistic model with a logit link to explain presence or absence of any mortality and a Gaussian model to explain the (log-transformed) density of dead trees for grid cells in which mortality was observed. This approach permitted evaluation of whether similar processes could explain both the occurrence and amount of mortality.

We considered each cell in our 3.5 km grid (with associated climate data, total live tree basal area, and number of dead trees per hectare) as a data point, though we omitted all cells with a basal area $< 2 \text{ m}^2 \text{ ha}^{-1}$ in order to exclude non-forested areas. To identify the appropriate set of predictor variables for the logistic and Gaussian components of the hurdle models, we computed the BIC of models for the full 2015 mortality data set based on systematically chosen subsets of the following set of predictor variables: mean annual CWD, basal area, CWD anomaly, (mean annual CWD)², (basal area)², and (mean annual CWD) \times (basal area) (Table S1). We selected the set that resulted in the lowest BIC value for each sub-model of the hurdle model (Table S1). For the Gaussian sub-model, the full predictor set minimised BIC,

while for the logistic model, the full predictor set minus the (mean annual CWD)² term minimised BIC. We used these predictor sets for the Gaussian and logistic models, respectively, for each of the 7 years, with a separate hurdle model fit for each year (Table S2). We fit models using the 'lm' function in R for the Gaussian models and the 'glm' function for the logistic models. We used the same model structure for all years to facilitate evaluation of the relative influence of predictors across years. We used centred and standardised predictor variables for each regression model, with the exception of the CWD anomaly term, which already represents the centred and standardised departure of each grid cell's annual CWD from its mean CWD. The predictor variables had low to moderate collinearity (Fig. S4), and the variance inflation factors (VIFs) for all parameters across all models were low (< 5). We examined model fits and predictions across a range of basal area and mean annual CWD values (see Appendix S1).

We additionally fit Bayesian spatial regression models to test the robustness of our logistic and linear regressions by evaluating the effect of spatial autocorrelation on the estimated variances for model coefficients. Modelling autocorrelation in this way adjusts the confidence intervals around estimated coefficients to take into account the fact that the model residuals have some degree of spatial autocorrelation at small scales (for spatial model methods and results, see Appendix S2). Here, we present the results of the non-spatial

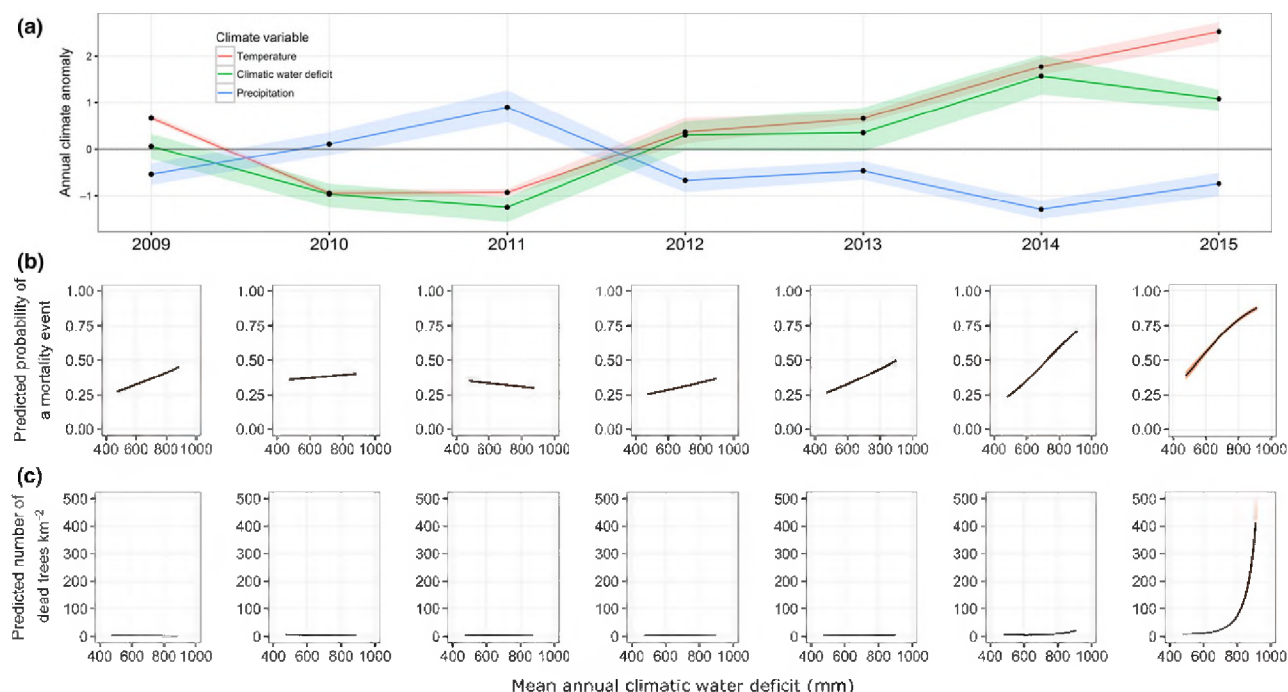


Figure 2 Annual climate anomaly (a) and model-predicted probability (b) and amount (c) of tree mortality for 7 years of aerial mortality survey data. Mortality probability and amount were predicted along a range of mean annual climatic water deficit (CWD) values (x -axes), holding basal area at $20 \text{ m}^2 \text{ ha}^{-1}$ (an intermediate value) and holding the CWD anomaly at its statewide mean for each respective year. Anomalies in (a) are represented as mean z -scores of annual climate in all 3.5 km grid cells, with positive numbers indicating larger than average values. Lines in each panel represent the median; bands represent the 25th–75th percentile range in the data set in panel (a) and 95% confidence intervals for the response in panels (b) and (c). The range of mean annual CWD displayed in panels (b) and (c) represents the range of values observed in the data set for cells with a basal area of $20 \pm 3 \text{ m}^2 \text{ ha}^{-1}$ in each respective year, omitting the upper and lower 1st percentiles of mean annual CWD values due to sparseness of data at these extremes.

models because they were qualitatively consistent with those of the spatial models and appear to more realistically capture the effects of spatially clustered variation in climate (for further discussion, see Appendix S2).

Forest deficit-competition index

Within our study area, mean annual CWD is negatively correlated with basal area (Fig. S4), indicating that stands with higher basal area tend to occupy sites with lower mean annual CWD (e.g. climatically wetter sites). Nonetheless, stands of any given basal area can be found across a fairly wide range of mean annual CWD values (Fig. 3b). We wanted to explore the utility of a single metric that indicates the degree of water stress *vis-à-vis* the level of competition for water within each of our grid cells as a potentially useful tool to visualize the regional interaction between competition and climate that we modelled above. We developed a forest deficit-competition index (FDCI) to represent, in a single variable, the combined effects of competition and mean annual CWD. The FDCI of a focal grid cell is calculated by first identifying all other grid cells within the study region with a similar live basal area (within a standardised bin width of $\pm 2.5 \text{ m}^2 \text{ ha}^{-1}$ of the

focal cell), then determining the cumulative distribution of mean annual CWD values represented by those other grid cells, and finally determining which quantile of that distribution the mean annual CWD of the focal cell falls into (range 0–1). For example, a forested grid cell with a mean annual CWD of 750 mm and live basal area of $20 \text{ m}^2 \text{ ha}^{-1}$ has an FDCI of 0.80, indicating that its mean annual CWD is higher than 80% of grid cells with a live basal area between 17.5 and $22.5 \text{ m}^2 \text{ ha}^{-1}$ and therefore is towards the drier end of possible climates that can support a stand of that basal area. Thus, the FDCI is interpreted as an indicator of how close a stand is to its climatic ‘dry margin’, given its basal area. We used linear regression (with and without a quadratic term) to evaluate the ability of FDCI to explain the observed number of dead trees per km^2 in 2015, the year with the greatest amount of mortality.

RESULTS

Mortality patterns recorded by the U.S. Forest Service aerial surveys varied substantially in location and amount between 2009 and 2015, with generally higher amounts of mortality in later years as the drought progressed (Fig. S1). The mortality

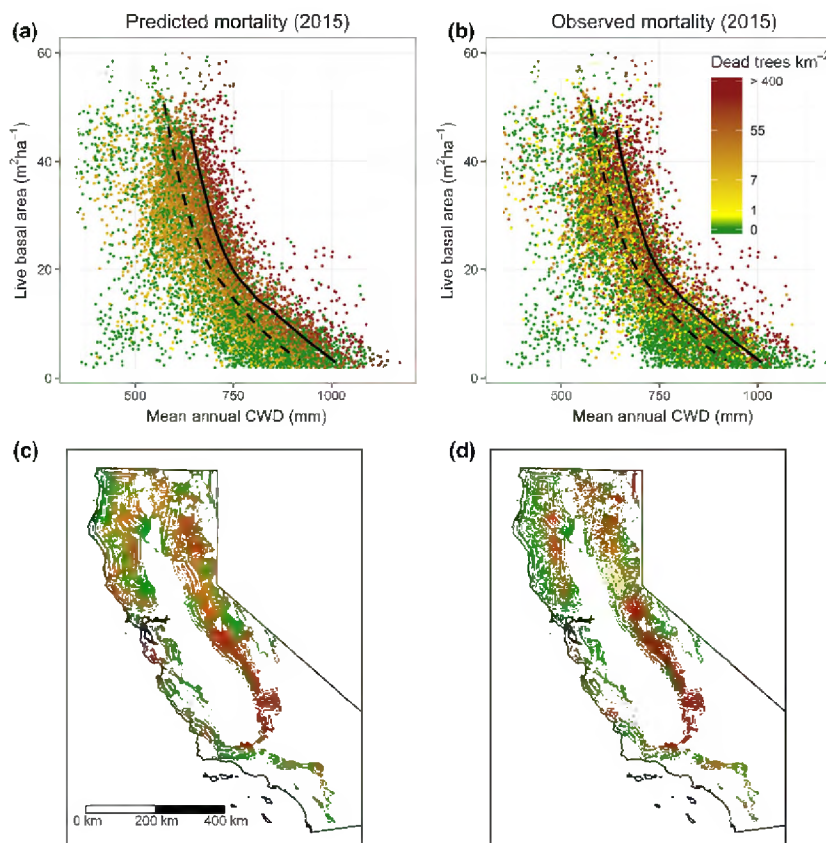


Figure 3 Predicted (a and c) and observed (b and d) number of dead trees per km^2 for each surveyed grid cell in the 2015 data set (the year with the greatest mortality) relative to mean annual climatic water deficit (CWD) and basal area (a and b) and plotted in geographic space (c and d). We simulated the presence or absence of mortality using the fitted logistic model; for grid cells that were assigned mortality, we subsequently used the fitted Gaussian model to predict the amount of mortality. Grid cells with > 400 dead trees per km^2 were set to 400 trees per km^2 in order to highlight differences in intermediate values. The solid curve in (a) and (b) represents a forest deficit-competition index (FDCI) value of 0.8, and the dashed curve represents an FDCI value of 0.5.

surveys conducted in 2010 and 2011 followed a period of relatively cool, moist conditions throughout California (Fig. 2a). In these years, the median predicted probability of observing any mortality in a given 3.5 km grid cell with 20 m² ha⁻¹ of basal area (hereafter referred to as 'intermediate basal area') was relatively low (between *c.* 30% and 40%) and was only weakly related to mean annual CWD across the landscape (Fig. 2b). With the onset of the drought in the 2012 water year (October 2011–September 2012), predicted mortality probability began to increase substantially, particularly in sites with high mean annual CWD (Fig. 2b). For a grid cell with intermediate basal area, the median predicted probability of observing mortality reached 87% by 2015 at a mean annual CWD of 900 mm, but at a mean annual CWD of 500 mm, it remained under 45%, similar to the probability before the drought.

When mortality occurred, the amount of mortality also increased and became positively associated with the mean annual CWD as the drought progressed (Fig. 2c). Between 2009 and 2014, the median predicted amount of mortality for a stand of intermediate basal area was < 25 dead trees per km² regardless of mean annual CWD. Thus, even in areas that experienced some tree mortality, the amount of mortality remained at relatively low levels through 2014. In 2015, in contrast, median predicted mortality for stands of intermediate basal area dramatically increased to *c.* 345 dead trees per km² at a mean annual CWD of 900 mm, although uncertainty in predictions was high (Fig. 2c). In 2015, mean annual CWD and CWD anomaly were both positive predictors of mortality amount, with mean annual CWD having a larger effect (Table S2). Areas with high mean annual CWD following 4 years of severe drought experienced substantially more tree mortality than areas with low mean annual CWD, where mortality remained similar to pre-drought levels (Fig. 2c).

In addition to mean annual CWD, basal area was an important positive predictor of mortality in 2015 (Fig. 3; Table S2). Our model (Fig. 3a) and the data (Fig. 3b) both suggest that stands with low live basal area (e.g. 10 m² ha⁻¹) can exist at relatively high mean annual CWD (e.g. > 750 mm) without experiencing substantial drought-related mortality. However, in stands with intermediate to high basal area (e.g. > 30 m² ha⁻¹), substantial mortality occurred even in locations with moderate mean annual CWD (e.g. > 600 mm). We also observed a positive interaction between basal area and mean annual CWD, whereby increasing mean annual CWD has a stronger effect on mortality amount in areas with greater basal area (Fig. S2, Table S1). Our models explained a substantial amount of variation in mortality patterns (2015 binomial model AUC: 0.74; 2015 Gaussian model adjusted *R*²: 0.20).

As a test of the robustness of the patterns we report, we also fit Bayesian spatial models, specified using the same hurdle model structure and predictor variables sets, for each year from 2009 to 2015. The spatial models were consistent with the non-spatial logistic and linear regressions: coefficients for mean annual CWD and basal area remained strong, with credible intervals generally excluding zero, particularly in the later years of the drought (see Appendix S2; Table S3).

The FDCI performed reasonably well as a single-variable predictor of mortality during 2015. The best model of FDCI had a quadratic term and clearly showed an increase in mortality amount with higher FDCI values (*R*² = 0.14; Fig. 4), thus indicating that mortality was greater in areas that had high CWD for a given basal area. While the FDCI model performed better than a null model of mortality in 2015 (Δ BIC = 852), it performed worse than the full interaction model analysed above (Δ BIC = -309).

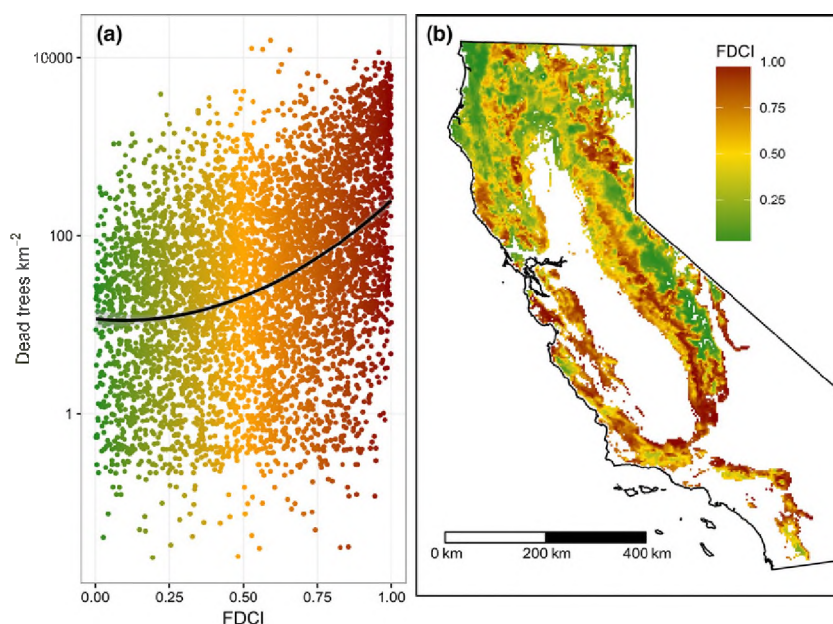


Figure 4 The relationship between the number of dead trees per km² in 2015 (log scale) and the forest deficit-competition index (FDCI), with a quadratic regression best-fit curve and 95% confidence bands (a), and the FDCI plotted in geographic space (b). Panel (a) includes all forested cells that were surveyed in 2015. Panel (b) includes all forested cells that were surveyed for mortality in at least 1 year between 2009 and 2015. The colour scheme identifies areas with high FDCI shown in red, as a predictor of mortality (a) and across geographic space (b).

DISCUSSION

Trees often exhibit strong local adaptation along climatic gradients (e.g. St Clair *et al.* 2005; Wang *et al.* 2010), and some global-scale physiological work suggests that the extent of adaptation and/or acclimation among species is so great that many tree species are similarly susceptible to drought stress regardless of the climate in which they occur (Choat *et al.* 2012). However, we found that during extreme drought, mortality was substantially greater in areas with higher mean annual CWD (i.e. areas that are on average hotter and drier). Our finding highlights the existence of limits to local adaptation and/or acclimation: trees in the driest sites appear to exist close to their limits of climatic tolerance, while populations in wetter sites may have larger physiological buffers. Thus, observations of greater drought-related tree mortality in more arid sites on smaller geographic scales (e.g. Allen & Breshears 1998; Millar *et al.* 2012; Anderegg *et al.* 2015b) also appear to hold across a range of forest types at a broad geographic scale.

For a given amount of water input, the presence of more and/or larger trees within a given area implies less water available per tree, and thus the positive association between live basal area and mortality that we observed may represent water-mediated competition. This interpretation is further supported by the positive interaction between live basal area and mean annual CWD in our models, particularly in the mortality amount (Gaussian) model in 2015 (Table S2); competition appears to have a stronger influence on drought-related mortality in areas that are already more climatically water-limited. An alternative explanation for our observation of greater mortality at higher live tree basal area values is that there may be more trees available to die in denser stands. However, several lines of reasoning suggest such a sampling effect is of less importance in our data: (1) the association between the modelled density of live trees and the observed density of dead trees is very weak and negative (see Methods; Fig. S3); (2) the positive effect of live tree basal area on mortality amount is greater in sites with higher CWD (as opposed to constant across all levels of CWD; Fig. S2b); and (3) mortality amount was by far most strongly associated with basal area in 2015, when mortality was the greatest; the amount of mortality that occurred in wetter, earlier years was much less sensitive to basal area (Table S2).

Because aggressive fire suppression over the past century has made the dry mixed-conifer forests of California much denser than they were historically (Safford & Stevens *in press*) and thus increased competition among trees, it is likely that the amount of drought-related stress and mortality in these areas is higher than it would be under a natural high-frequency, low-severity fire regime that maintains forests at lower density (Van Mantgem *et al.* 2016). Nonetheless, our results suggest that management to reduce the density of fire-suppressed stands – a common priority for restoring forest resilience and mitigating wildfire risk – may have the additional benefit of reducing the probability of drought-related mortality. Removing smaller trees prior to drought may even help to prevent the mortality of larger trees during drought (Thomas & Waring 2015; Van Mantgem *et al.* 2016). Alternatively, in at least some cases, drought-related mortality may

itself reduce stand densities to levels more comparable to historical densities (Potter 2016).

Despite the drought's long duration, high levels of tree mortality – and a strong dependence of mortality on mean annual CWD – were not apparent until the fourth year of drought (2015; Fig. 2). Other studies have observed a lagged mortality response to drought (e.g. Das *et al.* 2013). Such a delayed response may be due to the fact that trees can store carbohydrates as starch, allowing them to maintain baseline metabolic processes for some period of time in the absence of sufficient water for photosynthesis (McDowell *et al.* 2008), or it may arise from the cumulative effects of hydraulic damage on photosynthetic capacity (Anderegg *et al.* 2015b). In addition, delayed mortality may result from a lagged increase in pest and/or pathogen abundance and damage in response to tree defenses being weakened by drought (Franklin *et al.* 1987). Although mortality was most substantial in the fourth year of the drought, it is possible that the trees that died in 2015 were already weakened by 3 years of low water availability and resulting infestations and infections by pests and pathogens. Bark beetle activity in particular is well known to be correlated with drought severity and forest density (i.e. competition) (Fettig *et al.* 2007; Millar & Stephenson 2015), and it is likely that pests such as bark beetles were the proximate cause of much of the mortality observed in our study. Because pests often attack previously weakened trees (Millar & Stephenson 2015), some of the mortality observed in 2015 would likely have occurred even had the drought not persisted for a fourth year. Similarly, the negative impact of the drought on tree vitality may lead to decreased growth and elevated levels of mortality that persist for years following the drought (Berdanier & Clark 2015).

The forest deficit-competition index (FDCI) represents the quantile of CWD for a focal grid cell relative to the CWD of all other grid cells having a similar live basal area. As a single variable, FDCI had less explanatory power than the full model that included basal area, mean annual CWD, and CWD anomaly. Nonetheless, a simple index such as FDCI may be useful as a qualitative tool to identify particularly drought-vulnerable forests across a landscape (Fig. 4). For instance, in 2015, the predicted FDCI value associated with > 100 dead trees per km² was ~ 0.8 (Fig. 4a), and the 20% of grid cells at and beyond this FDCI threshold accounted for ~ 60% of the total tree mortality observed in 2015 (Fig. 3a). Thus, forest stands that have mean annual CWD > 80% of other stands with the same basal area may contribute disproportionately to mortality during extreme drought. The spatial configuration of FDCI across the state of California (Fig. 4b) is also closely aligned with observed areas of high mortality in 2015 (Fig. 3d). This index could thus be used to guide strategic, targeted management activities on a relatively small fraction of the landscape (e.g. areas where FDCI > 0.8) that could lead to a disproportionate reduction in future drought-related mortality. Given that current drought-induced mortality is already reducing live basal area, however, it will be important to consider post-drought live basal area in identifying areas for treatment and also to evaluate whether remaining live trees in these vulnerable areas are stressed beyond a threshold from which they can recover (Asner *et al.* 2016).

The response of forests to this extreme event can help in anticipating and preparing for the impacts of climate change. The relatively predictable spatial and temporal concentration of high tree mortality levels may aid forest conservation and management, because composition and structural change may occur slowly in some forests even during extreme drought, allowing management efforts to be focused on other higher vulnerability areas. This study also highlights the vital importance of consistent, large-scale monitoring of forest ecosystems. Given the outsized influence of extreme events on the stability and functioning of these ecosystems, and the uneven distribution of vulnerability in space and time, occasional or patchy surveys may miss the key signals that are essential for understanding and managing forest change.

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AUTHOR CONTRIBUTIONS

DJNY, JTS and JME conceived of the study; JM, AE, and AJ collected mortality data; DJNY, JTS, JME and AML performed analyses; and DJNY, JTS, JME, JM and AML wrote the manuscript.

DATA ACCESSIBILITY

The data set used for this analysis, the code used to generate this data set from public data sources, and the code used to perform statistical analyses are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7vt36>.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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