

Future vulnerability mapping based on response to extreme climate events: Dieback thresholds in an endemic California oak

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Abstract

Aim: This study presents a bioclimate modelling approach, using responses to extreme climate events, rather than historical distributional associations, to project future species vulnerability and refugia. We aim to illustrate the compounding effects of groundwater loss and climate on species vulnerability.

Location: California, USA.

Methods: As a case study, we used the 2012–2015 California drought and resulting extensive dieback of blue oak (*Quercus douglasii*). We used aerial dieback surveys, downscaled climate data and subsurface water change data to develop boosted regression tree models identifying key thresholds associated with dieback throughout the blue oak distribution. We (1) combined observed dieback–climatic threshold relationships with climate futures to anticipate future areas of vulnerability and (2) used satellite-derived measurements of subsurface water loss in drought/dieback modelling to capture the mediating effect of groundwater on species response to climatic drought.

Results: A model including climate, climate anomalies and subsurface water change explained 46% of the variability in dieback. Precipitation in 2015 and subsurface water change accounted for 62.6% of the modelled probability of dieback. We found an interaction between precipitation and subsurface water in which dieback probability increased with low precipitation and subsurface water loss. The relationship between precipitation and dieback was nonlinear, with 99% of dieback occurring in areas that received <363 mm precipitation. Based on a MIROC_rcp85 future climate scenario, relative to historical conditions, 13% of the blue oak distribution is predicted to experience more frequent years below this precipitation threshold by mid-century and 81% by end of century.

Main conclusions: As ongoing climate change and extreme events impact ecological processes, the identification of thresholds associated with observed dieback may be combined with climate futures to help identify vulnerable populations and refugia and prioritize climate change-related conservation efforts.

*Brittini Brown and Blair McLaughlin should be considered joint first authors.

KEYWORDS

climate change, drought, forest dieback, groundwater, *Quercus douglasii*, refugia, vulnerability mapping

1 | INTRODUCTION

For many forests globally, a changing climate likely will bring more frequent and intense dry periods and greater vapour pressure deficits (Luce et al., 2016), and climate change already is contributing to increased drought, heat stress and related forest dieback in many parts of the world (Allen, Breshears, & McDowell, 2015; Allen et al., 2010; Anderegg, Anderegg, Abatzoglou, Hausladen, & Berry, 2013; Van Mantgem et al., 2009; Williams et al., 2010). Climate models project that in the future, these kinds of drought events will become more intense and frequent in many ecosystems (IPCC 2014). Climate change-adaptive forest management will be a critical component of biodiversity and ecosystem service conservation over the next century, and accessible modelling tools are needed to support land management decisions (Heller and Zavaleta 2009).

The use of correlative bioclimatic models to tease apart biotic relationships and interactions, and thereby help to address land management decisions by providing guidance on where species' distributions may shift over time, has flourished in recent decades (Guisan & Thuiller, 2005). Several different methods are utilized (Elith et al., 2006), but all use known occurrence records to produce statistical associations with abiotic variables of interest (Guisan & Thuiller, 2005). Challenges with assumptions and remaining uncertainties in these models have been extensively reviewed (Araujo & Guisan, 2006; Guisan & Thuiller, 2005; Jiménez-Valverde, Lobo, & Hortal, 2008; Pearson & Dawson, 2003). More diverse modelling approaches have been developed in an effort to address these concerns and increase the accuracy of predictions. These include incorporating the effects of biotic interactions (Giannini, Chapman, Saraiva, Alves-dos Santos, & Biesmeijer, 2013; Staniczenko, Sivasubramaniam, Suttle, & Pearson, 2017), dispersal in process-based simulations (Svenning et al., 2014), observed long-term relationships between population demographics and climate (Wolf, Snyder, Sydeman, Doak, & Croll, 2010), and demographic and landscape processes in hybrid models (Franklin, 2013). In this study, we utilize boosted regression tree (BRT) modelling to identify climatic and hydrologic threshold dieback responses to an extreme drought event, combined with a simplified bioclimatic model based on these empirical dieback thresholds to estimate future species vulnerability under climate change. This approach is relatively accessible to managers, avoids some of the limitations associated with models based on historical distribution data and provides more current, empirically defensible estimates of potentially vulnerable and refugial locations.

California's 2012–2015 extreme drought, attributed in part to anthropogenic warming (Diffenbaugh, Swain, & Touma, 2015), provided a prescient look at the potential biological impacts of climatic drying, likely to occur over the next century (Flint & Flint, 2012).

This drought was related to the death of an estimated 100 million trees (USDA Forest Service 2016). Coates, Dennison, Roberts, and Roth (2015) found a reduction in relative green vegetation fraction in grey pine (*Pinus sabiniana*), California sycamore (*Platanus racemosa*), coast live oak (*Quercus agrifolia*), blue oak (*Quercus douglasii*), California bay laurel (*Umbellularia californica*) and chaparral species. Water stress associated with this drought has been linked to chaparral species mortality and changes in stand structure (Venturas et al., 2016). Ray (2016) found increased vulnerability among giant sequoia (*Sequoiadendron giganteum*). Nearly 10.6 million ha of California forests experienced loss in canopy water content in a variety of forest types including coastal redwood, pinyon-juniper, lodgepole pine, red fir and black oak (Asner et al., 2016). This extreme climate and vegetation response event presents an opportunity to test the modelling approach outlined above. We use the endemic California blue oak, for which dieback patterns have not been directly assessed previously, as a case study for this approach and as a proxy for the potential behaviour of other deep-rooted species in water-limited ecosystems.

Blue oak, an iconic, long-lived tree with significant cultural and ecological value, is one of many species with narrow ranges that are at increased risk for habitat loss and fragmentation resulting from a changing climate (Morueta-Holme, Fløjgaard, & Svenning, 2010). Long-lived, sessile species with relatively short dispersal distances and long generation times, such as trees, may face substantial barriers to migration or adaptation (Ackerly et al., 2010; Allen & Breshears, 1998). Like many deep-rooted trees (Canadell et al., 1996), blue oaks may depend heavily on subsurface sources to meet water requirements (Miller, Chen, Rubin, Ma, & Baldocchi, 2010). Groundwater levels in California have declined dramatically in recent decades (Wang, Lin, Gillies, & Hakala, 2016), potentially increasing blue oak's vulnerability to episodes of low rainfall. Previous bioclimatic models predict that blue oak will be lost in much of its current distribution (Kueppers, Snyder, Sloan, Zavaleta, & Fulfrost, 2005), and studies already have observed reduced survival in areas projected to experience climate change-related contraction (McLaughlin, Morozumi, MacKenzie, Cole, & Gennet, 2014). Drought stressors likely will compound ongoing threats of restricted blue oak seedling establishment and sapling recruitment (Davis et al., 2016; McLaughlin & Zavaleta, 2013; McLaughlin et al., 2014; Tyler, Kuhn, & Davis, 2006), and habitat loss and fragmentation (Bolsinger, 1988).

Using aerial mortality surveys (USDA Forest Service 2015) and satellite-derived GRACE data on change in terrestrial water storage, we explored the impacts of climate and hydrologic parameters on distribution-wide blue oak dieback patterns. Although GRACE data have been used previously for general drought monitoring (Ning, Ishidaira, Udmale, & Ichikawa, 2015; Velicogna, Kimball, & Kim, 2015;

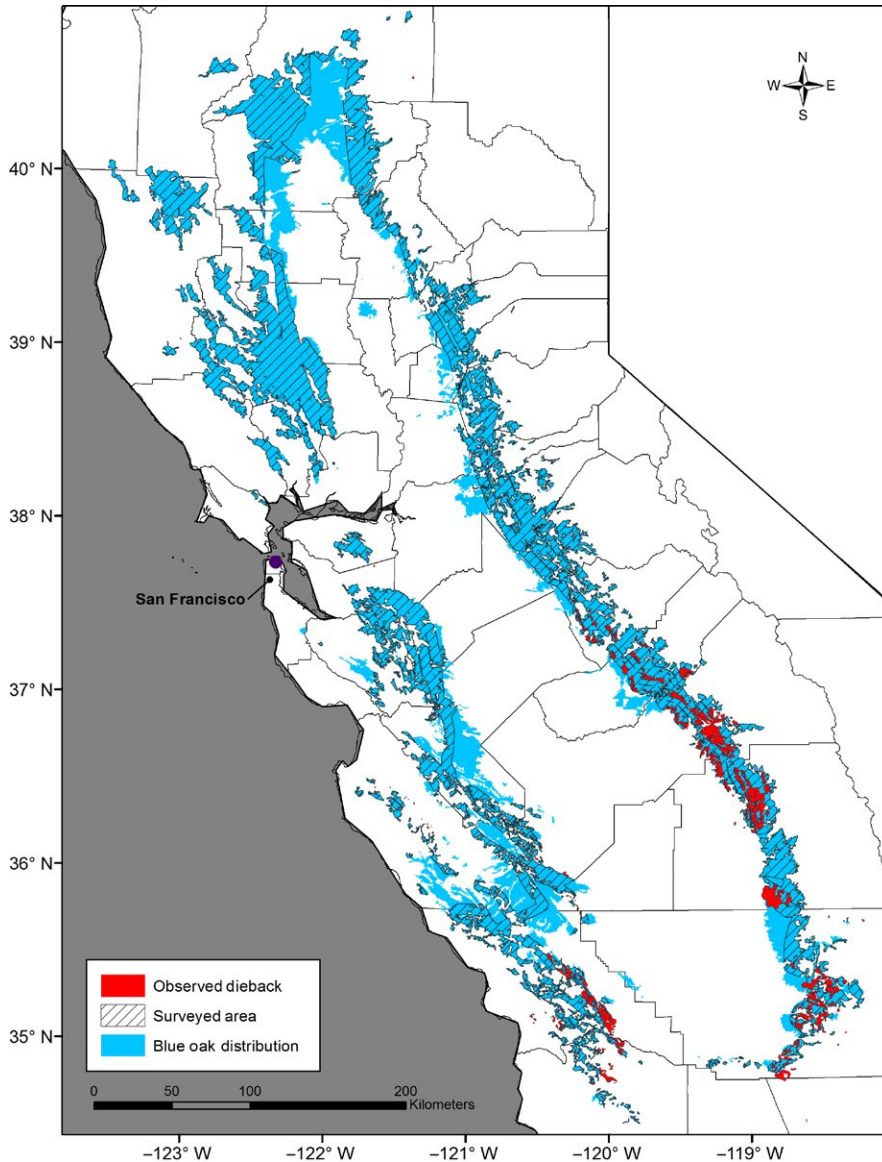


FIGURE 1 Map of California showing the blue oak distribution in blue, the extent of the USFS aerial mortality surveys hatched, and the observed dieback from USFS aerial mortality surveys in red

Wang et al., 2016), our work illustrates a novel approach of using this data as a predictor of individual species' distributional dieback patterns. To help inform climate-adaptive management over the next century, we present future "climate vulnerability maps" based on the climate/dieback thresholds identified in our data. Given that there have been multiple increased stressors in ecosystems over the past century, maps based on such current observed dieback data, rather than on historical distributional associations, may capture a more realistic perspective on future vulnerability of long-lived species.

2 | MATERIALS AND METHODS

2.1 | Study system

The blue oak distribution, covering nearly 1.2 million ha in California, encircles the Central Valley and includes the Coast Ranges and lower western foothills of the Sierra Nevada Range (Figure 1). Blue oak is a slow-growing, winter deciduous species with an average life span of

150 years. Blue oak grows in a Mediterranean climate in which most precipitation typically falls between October and March (Major, 1988).

2.2 | Distribution data and study area

The blue oak distribution was derived using vegetative distribution data from the California GAP Analysis database (Davis et al., 1998). The database uses the California Natural Diversity Database or "Holland" system to describe vegetation at the community level. Database polygons, ranging from a few (16.5 ha) to thousands (40,672.9) of hectares (mean 1,409.8 ha), may contain up to three plant community types. We limited our definition of distribution to polygons in which blue oak was identified as the dominant or co-dominant species within the primary or secondary cover type. Doing so reduced instances in our data where blue oak occurred, but was not a significant component of the canopy. We limited our study area to locations surveyed by the 2015 USDA Forest Service Aerial

Detection Monitoring campaign (USDA Forest Service 2015), which was conducted in an effort to quantify mortality in tree species across California. Aerial surveys in which a surveyor record observations of tree dieback and species from a low flying airplane occurred between June and August 2015, a period after which blue oaks had reached full leaf out and before leaf senescence. Areas where the aerial surveyors identified blue oak dieback outside of the California GAP distribution were added into the study area. We classified areas as “dieback” when blue oak was identified by aerial surveyors as the host species with a damage type of either “mortality,” “discoloration,” “defoliation” or “dieback”; categories that indicate the tree experienced very poor canopy health, indistinguishable from mortality (J. Moore, personal communication Feb 2016). Areas of the blue oak distribution not identified as one of the above dieback categories were classified as “non-dieback.” The “dieback” category does not definitively indicate mortality (which cannot be confirmed in oaks without ground-level surveying), but indicates severe stress, lack of leaf out and possible mortality. Our study area encompassed 79% of the total blue oak distribution (2,742,630 ha). We then converted dieback distribution data from polygons to points using a 270-m resolution grid in ArcGIS (ESRI, 2016), matching the resolution of the climatic data used in analyses. Dieback points were assigned if a portion of the dieback polygon covered >25% of the grid cell, non-dieback points were assigned throughout the remaining study area. Points falling within water bodies were removed from the dataset.

2.3 | Climate and water data

We used water year climate data (e.g., Oct 2014–Sept 2015) from the California Climate Commons database (California Landscape Conservation Cooperative, 2017) where PRISM data (PRISM Climate Group 2015) have been downscaled to a 270-m resolution grid which incorporated hydrology dates back to 1896 (Flint & Flint, 2012). We derived 11 climatic variables from this dataset (Table 1) likely to influence climate-driven dieback in blue oak. We examined climate variables over six timeframes to assess time lags or compounding impacts of multiple years of drought (Table 1). In addition, we calculated two historical comparison parameters for each variable: a continuous climate anomaly variable and a binary novel climate variable. Climate anomaly values were calculated as the difference between 1951–1980 average (a baseline adopted by the Intergovernmental Panel on Climate Change IPCC 2014) and 2015. We defined a novel climate as a cell that in 2015 was hotter or drier than previously recorded before the drought onset (i.e., 1896–2011). For anomaly variables, positive values indicate stronger recent drought conditions (e.g., anomalously low precipitation and anomalously high temperatures are both represented by positive values).

We also examined the change in subsurface water storage (cm water thickness), obtained from NASA’s GRACE satellite (Swenson, 2012) at a 55-km resolution. The variable differs from the hydrologic component of the climate water deficit (CWD) downscaled climate data, which incorporates changes in shallow soil moisture but does not capture changes in deeper groundwater. The GRACE satellite

TABLE 1 Eleven climate variables derived from BCM, used in initial determination of model variables. Each climate variable was calculated across six absolute (2015, 2013–2014, 2013–2015, 2011–2015, 1981–2010 and 1951–1980) and two historical comparison (Anomaly and Novel) timeframes

Climate variable	Description
Climate water deficit (CWD) (mm)	Difference between potential and actual evapotranspiration
Annual precipitation (mm)	Cumulative yearly precipitation by water year
Spring precipitation (mm)	Cumulative precipitation for March, April and May
Fall precipitation (mm)	Cumulative precipitation for September, October and November
Winter precipitation (mm)	Cumulative precipitation for December of the previous year and January and February of the current year
Spring temperature (°C)	Average of March, April, May max temperatures
Summer temperature (°C)	Average of June, July, August max temperatures
Fall temperature (°C)	Average of September, October, November max temperatures
Growing season temperature (°C)	Average of March–November max temperatures
Spring-summer temperature (°C)	Average of March–August max temperatures
Summer-fall temperature (°C)	Average of June–November max temperatures

measures monthly changes in Earth’s gravitational field, which are used to estimate the total amount of water stored in a region as ice, snow, surface water and groundwater. We used GRACE data collected in August 2015 when most of the blue oak distribution was entering its driest period. During this summer period in our study area, snow and ice were not present, and the influence of surface water was limited since stream flow during that time was minimal. Therefore, the GRACE data were representative of change in subsurface water. While these changes may not represent changes in plant available water if sources beyond the reach of plant roots were tapped through intensive agricultural irrigation oriented pumping, the majority of our study area is rangeland; therefore, irrigation withdrawals for agriculture should have had minimal impact. Change in surface water values represents the difference between August 2015 and the available pre-drought baseline (mean of August 2004–2009).

2.4 | Modelling and statistical analysis

We used a threshold of 0.7 to identify highly correlated predictor variables and avoid issues of collinearity in the models, following

the recommendations of Dormann et al. (2013). We removed highly correlated variables in three steps. First, using logistic regression, we determined the time frame and historical comparison parameter for each climate variable that had the strongest relationship with dieback. We compared each variable in a single parameter model to a null model, and the time frame or historical parameter for each climate variable with the lowest Bayesian information criterion (BIC) was retained. Second, we removed any remaining highly correlated variables, retaining composite over seasonal measures (e.g., annual precipitation over winter precipitation). Using this methodology, our climatic model variables were 2015 water year precipitation (hereafter "2015 precipitation"), 2013–2014 average max summer-fall temperature, summer-fall temperature novel climate, CWD anomaly (water year) and spring temperature anomaly. Finally, we determined that there was no strong correlation between our remaining climatic variables and the change in subsurface water variable. Variables in the final model were all correlated by <0.64 .

To address possible spatial autocorrelation in our model (Dormann et al., 2007), we generated eight spatially balanced datasets and tested the robustness of our model to reduction in spatial structure. To generate these spatially balanced datasets, we used generalized random tessellation stratification (Stevens & Olsen, 2004) within the R package `SPSURVEY` (Kincaid & Olsen, 2015). We ensured that the eight datasets maintained the same ratio of dieback to non-dieback points as the original dataset but were thinned to 490 randomly selected dieback and 9,310 non-dieback points.

We used BRTs to model dieback because they handle complex ecological relationships well (Elith et al., 2006), allowing for nonlinear relationships and fitting interactions automatically (Elith, Leathwick, & Hastie, 2008; Leathwick, Elith, Francis, Hastie, & Taylor, 2006). Using methods from Elith et al. (2008), we found optimal values of learning rate (a shrinkage parameter), tree complexity (interaction depth) and bag fraction (proportion of randomly selected data at each model iteration), which were 0.01, 5 and 0.5, respectively. We first modelled the relationship between dieback (presence/absence) and our five independent predictor variables across the entire study area using the binomial family. We then re-fit the same model using our eight spatially balanced datasets. Variables not robust to removal of spatial structure in the data (e.g., direction of relationship with dieback varying across spatially balanced datasets) were removed from the model.

We used the area under the curve (AUC), deviance explained and root mean square error (RMSE) to evaluate model fit and predictive performance. BRTs calculate AUC by withholding test data (controlled by the bag fraction) with each new tree in the model to determine the model's predictive ability (Elith et al., 2008). An AUC of 0.5 indicates the model cannot predict better than random, while an AUC of 1 indicates perfect prediction, a possible indication of overfitting (Fielding & Bell, 1997). Overfitting is reduced in the BRT modelling process using the bagging fraction to randomly sample half the data for tree fitting at each step and using a low learning rate to shrink the contribution of each tree (Elith et al., 2008).

All analyses, except where indicated, were performed in R 3.3.2 (R Core Team 2016) using the `RASTER` 2.5-8 (Hijmans, 2016), `MAPTOOLS` 0.8-40 (Bivand & Lewin-Koh, 2016), `RGDAL` 1.2-3 (Bivand, Keitt, & Rowlingson, 2016), `GBM` 2.2.1 (Ridgeway, 2015) and `DISMO` 1.1-4 (Hijmans, Phillips, Leathwick, & Elith, 2016) packages.

2.5 | Future vulnerability mapping

For future vulnerability mapping, we examined the modelled threshold value for the increased probability of dieback occurrence of 2015 precipitation. We downloaded monthly `MIROC_rcp85` and `MPI_rcp45` climate scenario precipitation projections from the 2014 Basin Characterization Model dataset at 270-m resolution (California Landscape Conservation Cooperative, 2017; Flint & Flint, 2012). `MIROC_rcp85` represents a very dry climatic change scenario, and `MPI_rcp45` represents a milder, very wet scenario. For both scenarios, we computed total precipitation for each water year and calculated the number of times each pixel went below the 2015 precipitation threshold (363 mm) over the 30-year baseline (1951–1980), as well as the total number of times precipitation was predicted to be below the threshold over two 30-year futures (2021–2050 and 2070–2099). We analysed both scenarios to illustrate the range of potential climatic futures. However, in the main results of the paper, we focus on the `rcp85` projections because we are attempting to conservatively identify regional refugia, and because our future model does not account for other factors that likely will increase plant drought stress such as projected increasing groundwater loss (Taylor et al., 2013) and higher temperatures (Flint & Flint, 2012).

3 | RESULTS

In 2015, aerial surveys identified 5.52% (151,381 ha) of the blue oak study area as experiencing dieback. Over 99% of the distribution had a lower 2015 precipitation (Figure 2) and 92% had higher 2013–2014 summer-fall temperatures than the 30-year normal. However, only a small percentage of the distribution experienced novel climate in 2015 compared to 1896–2011. (0.5% experienced novel precipitation and 1.8% novel temperatures). Total August 2015 water storage levels were an average of 24 cm below the 2004–2009 pre-drought baseline.

3.1 | Model results

The final model included five variables (2015 precipitation, 2013–14 summer-fall temperature, CWD anomaly, spring precipitation anomaly, and change in subsurface water) and explained 46% of the variability in dieback across the distribution (AUC = 0.958, RMSE = 0.143, Figure 3). Relationships between dieback and model variables were robust to removal of spatial structure within the data (Appendix S1: Figure S2). Nearly 63% of modelled dieback probability was explained by 2015 precipitation (33%) and change in subsurface water

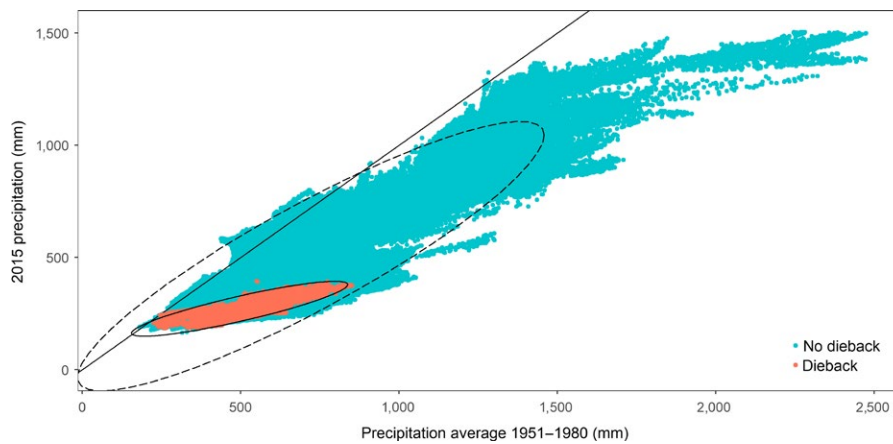


FIGURE 2 Precipitation in 2015 (mm) and mean precipitation from 1951–1980 (mm) (water years) for all climate cells (270 m) across the surveyed area of the blue oak distribution, with observed dieback in red and no observed dieback in blue. Ellipses represent 95 % confidence intervals (solid: observed dieback, dashed: no observed dieback). Solid black line represents a one-to-one line. Over 99% of the points were below the one-to-one line, indicating 2015 was drier than normal in most areas [Colour figure can be viewed at wileyonlinelibrary.com]

(29.6%). Partial dependence plots of these variables indicated that nonlinear, threshold-based relationships existed (Figure 4), and although non-dieback points did occur below the thresholds, few dieback points existed above them. For 2015 precipitation, we saw a severe increase in dieback probability when the total precipitation fell below 363 mm (Figure 4). This threshold was calculated as the 99th percentile of 2015 precipitation, which also coincided with the precipitation value that corresponded to the greatest drop in the marginal probability of dieback (Figure 4). No dieback occurred above 395 mm. The likelihood of dieback also increased dramatically as subsurface water loss exceeded 30 cm (Figure 4). Precipitation in 2015 interacted with subsurface water loss (Figure 5) to cause an increase in dieback probability when precipitation was below 395 mm and loss in subsurface water was >30 cm.

The remaining three model variables, spring temperature anomaly, 2013–14 summer–fall temperature and CWD anomaly, explained 15.7%, 12.7% and 9%, respectively, of modelled dieback probability. We saw a slight increase in the likelihood of dieback as average 2013–14 summer–fall temperature increased above 25°C (Figure 4) and an increase in dieback probability with more anomalous spring temperatures (Figure 4) until 2.3°C at which point anomalous values

became rare (Figure S1). Dieback probability also began to increase when CWD anomaly reached ~100 mm (Figure 4) and continued until anomalous CWD became rare near ~300 mm (Figure S1).

The variable summer–fall temperature novel climate was dropped from the final model because it was not robust to the thinned, spatially balanced datasets. After removal of this parameter, partial dependence plot trends between the final spatially balanced dataset and the full dataset were similar (Figure S2).

3.2 | Future vulnerability

During historical baseline conditions (year 1951 to 1980), 23% (7,970 km²) of the blue oak distribution never experienced annual precipitation below the threshold (363 mm). Although this percentage is predicted to increase to ~31% (10,660 km²) by mid-century (2021–2050) under the MIROC_rcp85 scenario, it is predicted to shrink to 11% (3,640 km²) of the range by end century (year 2070–2090) (Figure 6). Of particular interest are areas that have historically remained above the precipitation threshold but are projected to go below in the future. While these areas comprise only ~1% of the range by mid-century, they are predicted

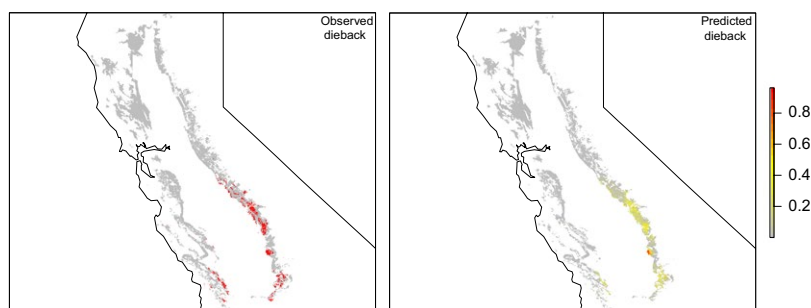


FIGURE 3 Comparison of observed dieback (left) and modelled dieback probability (right) across the blue oak distribution. Dieback was modelled using a binomial boosted regression tree model. The legend indicates high (red) to low (grey) probabilities of dieback. On average, our model predicted $30 \pm 6\%$ probability of dieback within observed dieback areas [Colour figure can be viewed at wileyonlinelibrary.com]

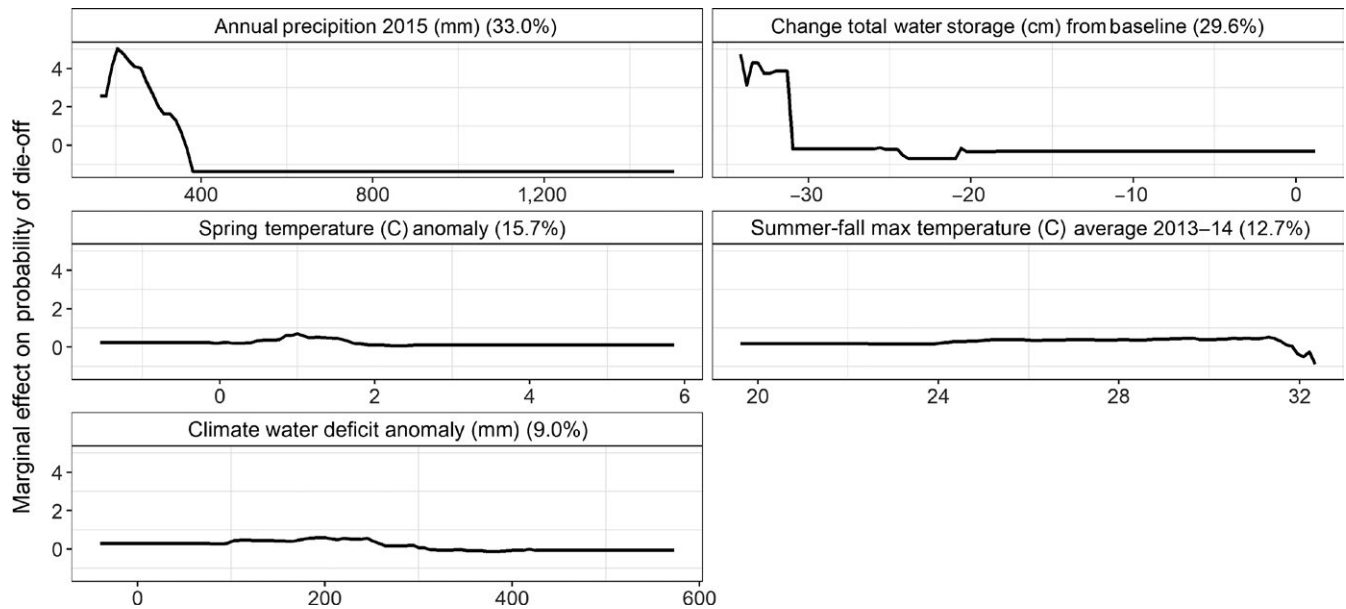


FIGURE 4 Model partial dependence plots, showing the contribution of each variable (with all other variables at their means) to the total model fitted function on the y-axis, variable scale range on the x-axis. Percentages are estimated percentage of the total model variance explained by that variable. Two variables, 2015 precipitation (water year) and change in subsurface water, explain nearly 63% of dieback probability in our model

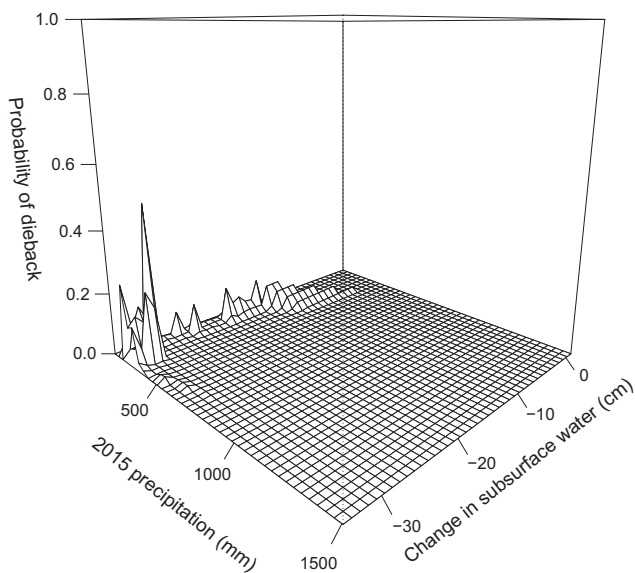


FIGURE 5 Modelled interaction between change in subsurface water from baseline (cm) on the x-axis, 2015 precipitation (mm) (water year) on the y-axis and probability of dieback on the z-axis. All values are fitted values from the boosted regression tree model relating the presence and absence of dieback in blue oak to climate and change in subsurface water variables. Low 2015 precipitation and high loss of subsurface water interact to increase the probability of dieback

to increase by an order of magnitude to 13% by end of century. Additionally, by mid-century 13%, and by end of century 81%, of the total blue oak distribution is predicted to have more frequent below threshold drought years relative to baseline conditions

(Figure 6). For corresponding data for an alternative wet MPI_rcp45 future scenario, see Figure S3, and for absolute projected future values for both scenarios, see Figure S4.

4 | DISCUSSION

4.1 | Groundwater loss and vulnerability to climatic drought

Patterns of blue oak dieback in our analysis were largely a result of an interaction between annual water year precipitation and subsurface water change, with the highest likelihood of dieback occurring in areas with low precipitation and high subsurface water loss. While precipitation was the strongest predictor of dieback, subsurface water loss explained nearly as much variation in dieback probability. Because of the cryptic nature of subsurface water change, ecologists have been challenged to evaluate the impacts of groundwater loss on ecosystems. Datasets like GRACE data represents a new potential tool to evaluate deep-rooted species response to change in subsurface water at the distribution scale. For deep-rooted, water-limited plants in areas projected to become drier in the future, groundwater loss represents a potentially exacerbating driver of vulnerability to climate change.

Data from numerous wells across California, as well as GRACE data, indicate that subsurface water storage in the state has declined dramatically since the beginning of the twenty-first century (Wang et al., 2016), up to $31 \pm 3 \text{ km}^3$ between 2006–2012 (Famiglietti et al. 2014; Scanlon, Longuevegne, & Long, 2012). Estimates from 2014 alone indicate that the drought resulted in an additional 6.3 km^3 of groundwater depletion (Howitt, Medellin-Azuara, MacEwan, Lund,

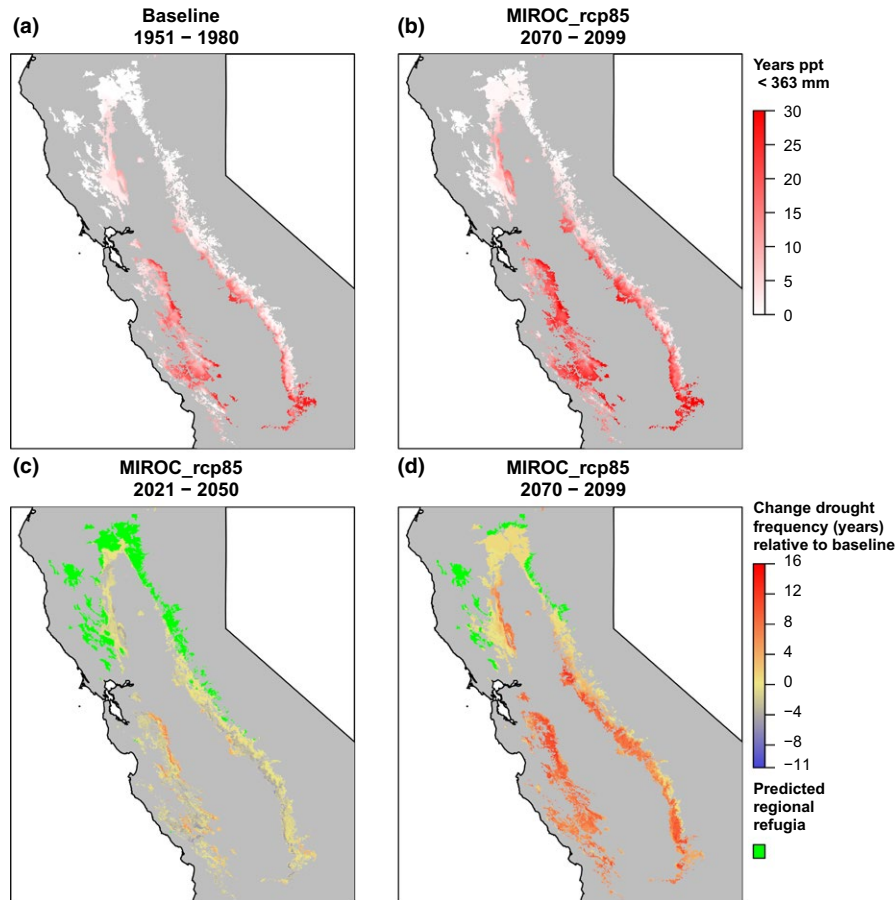


FIGURE 6 Map of current blue oak distribution showing (a) number of years when precipitation is below the 363 mm threshold during historical baseline conditions (1951–1980) and (b) at end of century (2070–2099), (c) change in number of years below threshold relative to baseline conditions for mid-century (2021–2050) predictions and (d) end-of-century predictions. Futures are based on a dry MIROC_rcp85 scenario. In (c) and (d), green colouring indicates refugial areas where annual precipitation remains consistently above the 363 mm threshold

& Sumner, 2014), largely due to higher agricultural withdrawals necessitated by low precipitation. The demonstrated importance of groundwater hydrology to blue oak survival at the broad scale suggests that local variation in subsurface water availability (influenced by local landscape features such as perched riparian aquifers or soil depth) may also impact dieback within populations.

Blue oak and closely related oaks can depend heavily on subsurface water sources, particularly during drought and the driest part of the growing season: nearly 80% of blue oak water requirements were met by deep water sources during summer months (Miller et al., 2010). In a historical survivorship study, the highest mortality of adult valley oak (*Quercus lobata*, a close relative of blue oak with a similar geographic distribution) was associated with the lowest groundwater levels (Brown & Davis, 1991). Blue oak has been shown to obtain water from different depths during different times of the year, using higher amounts of shallow soil water in the beginning of the growing season and transitioning to deep water sources as shallow soil water becomes less available during the summer dry period (Miller et al., 2010). A similar progression to deeper water sources throughout the growing season has been observed in other species in seasonally dry ecosystems (Ellsworth & Sternberg, 2014;

Weekley, Gagnon, Menges, Quintana-Ascencio, & Saha, 2007). Low precipitation and higher growing season temperatures may deplete shallow water sources earlier in the season, causing species to tap into deeper water sources earlier and for a longer overall period of time.

Our results suggest that the effects of subsurface water loss on blue oak dieback were nonlinear, showing a threshold at approximately -30 cm after which the probability of dieback rose steeply. Similar threshold-based relationships between groundwater availability and dieback have been found in eucalyptus species in Australia (Kath et al., 2014). Because of this threshold-based response, we may see little to no warning of increasingly depleted groundwater effects on ecosystems before dieback occurs.

4.2 | Modelled climate parameters

Precipitation in 2015 played an overwhelmingly important role in blue oak dieback, consistent with previous studies identifying precipitation as a dominant climatic driver of blue oak growth and survival (Kertis et al., 1993; Kueppers et al., 2005). Low precipitation and subsurface water loss both can reduce plant water availability,

increasing the likelihood of hydraulic failure, a frequent driver of tree mortality (Adams et al., 2009). We found that dieback probability increased dramatically when annual precipitation fell below 363 mm and that almost no dieback occurred above this precipitation value. Thus, 363 mm appears to be a threshold under which blue oaks become increasingly vulnerable to climate-related dieback and over which they are much less vulnerable. However, local climatic adaptation may occur (Rice, Gordon, Hardison, & Welker, 1991; Sork et al., 2010), and thus, population or region-specific thresholds may exist (i.e., populations in historically highly xeric areas of the distribution may have a lower precipitation/dieback threshold than populations in historically more mesic areas). For the purposes of this study, to conservatively identify refugia, 363 mm is used as a distribution-wide safety threshold, above which drought-related dieback appears unlikely. However, this value is likely not a fixed, independent boundary and the possibility of variable local thresholds below this value deserves further investigation.

Summer-fall high temperatures also increased the likelihood of blue oak dieback. Increased summer and fall temperatures increase ecosystem evapotranspiration, exacerbating the water deficits caused by low precipitation. Maximum temperatures directly impact physiological functions such as respiration and photosynthetic capacity and increase mortality risk for trees (McDowell et al., 2008) and may play a particularly important role in tree mortality under low water conditions (Adams et al., 2009). As such, the likelihood of dieback in our model rose slightly as 2013–2014 summer-fall temperature increased above 25°C. In our model, the relationship between 2013–2014 summer-fall temperatures and dieback probability dropped off after ~31.5°C because the frequency of temperatures above 31.5°C decreased to <4.5% of observed dieback points (Figure S1).

It was not only absolute climate values during drought years that predicted dieback but also climate anomalies—the drought years' climate value relative to the historical climate for a particular population. Spring temperature and CWD anomalies showed small effects on dieback probability. The hump-shaped relationship between these climate anomalies and probability of dieback (Figure 4) represents a sharp decline in the frequency of occurrence at the high values, rather than a quadratic relationship (Figure S1). Earlier spring warming results in a longer growing season and can lead to prolonged or earlier drought stress (Hongyan et al., 2013; Piao, Fang, Zhou, Ciais, & Zhu, 2006; Wu, Liu, Wang, & Deng, 2013). CWD integrates temperature, precipitation, and surface and shallow soil hydrologic processes (Flint, Flint, Thorne, & Boynton, 2013; Willmott, Rowe, & Mintz, 1985), making it a useful measure of plant water deficit integrated across these variables.

That the *degree of change* in these climate parameters may be predictive of dieback suggests the possibility of local climate adaptation of blue oak. Limited experimental work on local adaptation in blue oak indicates that water use efficiency (WUE) may differ across populations, with higher WUE in more xeric parts of the distribution (Rice et al., 1991). Regional populations have distinct genetics and that local adaptation within these regions has occurred (Rice,

Richards, & Matzner, 1997); however, genetic variation within populations may be large enough to obscure definitive ecotypes or ecoclines (McBride, Norberg, Bertenshaw, Kloss, & Mossadegh, 1997; Riggs, Millar, & Delany, 1991). In valley oak, separate genetic clusters were identified and linked to limited gene flow (Grivet, Sork, Westfall, & Davis, 2008). Sork et al. (2010) found that genetic structure in valley oak had a strong association with climatic gradients, suggesting the likelihood of local adaptation to climate. Given their close phylogenetic relationship and similar geographic distribution, genetic structure similar to that of valley oak may exist in blue oak.

4.3 | Model limitations

Aerial survey data are expected to have some collector error; however, to verify general data accuracy, we explored the relationship between NDVI and areas categorized with and without dieback. We found that NDVI was lower in observed dieback than in non-dieback areas (Appendix S1). Non-climatic factors, absent from our analysis, that may have contributed to dieback include biotic interactions (Buse, Dury, Woodburn, Perrins, & Good, 1999; Pearse, Funk, Kraft, & Koenig, 2015), potential local genetic variation (Sork et al., 2010), soil characteristics that impact plant water availability, and the varied topography and geology of the region (Norris & Webb, 1990).

4.4 | Future vulnerability

Blue oak likely will become more vulnerable to drought-related stressors over the next century. We demonstrate the use of observed thresholds to identify populations likely to be susceptible to dieback currently and over the next century. For accessibility, we used a simplified model with a single-year threshold; however, locally, other factors may be important including local adaptation, microtopographic conditions, soil characteristics, hydrology and exposure to extended, multiyear drought. Our vulnerability maps *are not intended to predict survival* (many areas with precipitation under our threshold did not experience dieback) but rather to identify where vulnerable areas are and may exist over the next century. Vulnerable areas would be good candidates for climate change adaptation planning, particularly if climate continues to become drier as projected (Flint & Flint, 2012). For example, these areas would benefit from more rigorous groundwater monitoring and conservation to minimize confounding stressors. Populations in these areas also should be considered for genetic material collection to ensure preservation of the dry-adapted parts of the species genome for future restoration. Potential climate change refugia (McLaughlin et al., 2017; Morelli et al. 2017) in these areas may be particularly important to identify and protect.

Our vulnerability maps provide complementary information to bioclimate models predicting range shifts based on species' historical distributional associations with climate. Because our maps are based on current empirical dieback data, they may be particularly useful in mapping vulnerability for long-lived, non-mobile species, such as trees, that experience compounded impacts of climate and other

ongoing water-related environmental stressors (such as invasive competitors for water, changes in hydrology or ground-level ozone exposure that can inhibit stomatal closure and increase transpiration). Under these circumstances, historical climate associations may underpredict potential vulnerability as they do not account for potentially narrower climatic tolerances in populations experiencing such compounded stressors. For example, in our study, blue oak in areas with less groundwater loss were able to tolerate drier climatic conditions, whereas trees in areas with high groundwater loss experienced dieback at higher precipitation levels.

Our threshold-based vulnerability maps also have the advantage of simplicity and accessibility. We explicitly chose to use a single strongly predictive threshold metric (precipitation) rather than a full climate modelling exercise with the full suite of predictive climate variables, to simplify map output. While our future predictions give guidelines on where areas below the threshold exist now or may exist in the future, the metric is sufficiently simple that managers could tailor the recommendations based on the current and future climate conditions in their locations.

We present vulnerability maps based on a dry rcp85 future scenario (Figure 6, see Appendix S1: Figure S3 for an alternative wet future scenario) because (1) we cannot account for future groundwater loss, which likely will intensify with climate change (Taylor et al., 2013) and increase drought vulnerability; (2) because they are based on a precipitation threshold, our maps do not account for predicted rising regional temperatures (Flint & Flint, 2012), which will increase overall evapotranspiration and drought vulnerability (Diffenbaugh et al., 2015); and (3) the maps from the rcp85 scenario provide a conservative estimate of regional refugia (areas projected not to cross the precipitation threshold over the next century). To illustrate the range of possible futures, we also analysed the rcp45 wet future scenario (Appendix S1: Figure S3), which shows qualitatively similar geographic patterns of refugia by end of century (located in the northern part of the species distribution), but substantially more refugial area than the rcp85 scenario.

Under the rcp85 scenario, major changes in the extent of the blue oak distribution that experiences rainfall years under the distribution-wide 363 mm precipitation threshold appear by the end of the century. Between 2070–2099, many areas that had historically remained above the threshold are predicted to cross it. Precipitation years below the threshold also showed increased frequency in 81% of the distribution by end of century. The frequency of dry years is particularly important given that multiple years of prolonged drought stress can increase the likelihood of mortality (Allen et al., 2015). Pockets of regional refugia (areas predicted always to stay above threshold) are predicted in the north coastal, north-central and northern Sierra areas of the distribution.

5 | CONCLUSIONS

Ongoing climate change and extreme climatic events give us an opportunity to improve understanding of where species may be

vulnerable and where they are likely to persist based on empirical threshold response data. Our model indicated that reductions in groundwater may interact with low precipitation to increase dieback risk for blue oak. These factors showed nonlinear threshold relationships with dieback, and as such were used with futures scenarios to suggest areas of likely vulnerability or refugia. While the GRACE data provide a useful new tool to track species responses to groundwater change, higher resolution groundwater data also are needed to understand groundwater impacts and conservation potential at a local level. Improved groundwater monitoring and conservation will be critical to climate-adaptive conservation in these ecosystems.

Climatic conditions such as those seen during California's recent extreme drought are likely to increase in many parts of the world (IPCC 2014); global groundwater withdrawals are, likewise, projected to increase with climate change (IPCC 2014, Taylor et al., 2013). In many parts of the earth, similar to observed effects on blue oak during the CA drought, drying climatic conditions and subsurface water loss may combine to intensify dieback in deep-rooted trees in water-limited ecosystems. Under circumstances in which strong threshold-based species climate/dieback relationships can be identified, vulnerability mapping based on observed thresholds can help prioritize regional refugia protection, as well as climate change-related conservation efforts within vulnerable areas such as monitoring, protection of microrefugia, genetic material preservation and consideration of alternative species for restoration.

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DATA ACCESSIBILITY

All data used in this study are publicly available as cited in the methods. No new data were collected.

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REFERENCES

- Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change implications for conservation biogeography. *Diversity and Distributions*, *16*, 476–487. <https://doi.org/10.1111/j.1472-4642.2010.00654.x>
- Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., ... Huxman, T. E. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Science*, *106*, 7063–7066. <https://doi.org/10.1073/pnas.0901438106>
- Allen, C. D., & Breshears, D. D. (1998). Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Science*, *95*, 14839–14842. <https://doi.org/10.1073/pnas.95.25.14839>
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*, 129. <https://doi.org/10.1890/ES15-00203.1>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderegg, L. D. L., Anderegg, W., Abatzoglou, J., Hausladen, A. M., & Berry, J. A. (2013). Drought characteristics' role in widespread aspen forest mortality across Colorado, USA. *Global Change Biology*, *19*, 1526–1537. <https://doi.org/10.1111/gcb.12146>
- Araujo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*(10), 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Asner, G. P., Brodrick, P. G., Anderson, C. B., Vaughn, N., Knapp, D. E., & Martin, R. E. (2016). Progressive forest canopy water loss during the 2012–2015 California drought. *Proceedings of the National Academy of Sciences*, *113*, E249–E255. <https://doi.org/10.1073/pnas.1523397113>
- Bivand, R., Keitt, T., & Rowlingson, B. (2016). rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 1.2-3. Retrieved from <https://CRAN.R-project.org/package=rgdal>
- Bivand, R., & Lewin-Koh, N. (2016). mapproj: Tools for Reading and Handling Spatial Objects. R package version 0.8-40. Retrieved from <https://CRAN.R-project.org/package=mapproj>
- Bolsinger, C. L. (1988). The hardwoods of California's timberlands, woodlands, and savannas. Resource Bulletin PNW-RB-148. Portland (OR): Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture.
- Brown, F. W., & Davis, R. W. (1991). Historical mortality of valley oak (*Quercus lobata*, Née) in the Santa Ynez Valley, Santa Barbara County, 1938–1989. In Standiford, Richard B., tech. coord. Proceedings of the symposium on oak woodlands and hardwood rangeland management; Davis, California Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. pp. 202–207.
- Buse, A., Dury, S. J., Woodburn, R. J. W., Perrins, C. M., & Good, J. E. G. (1999). Effects of elevated temperature on multi-species interactions: The case of Pedunculate Oak, Winter Month, and Tits. *Functional Ecology*, *13*, 74–82. <https://doi.org/10.1046/j.1365-2435.1999.00010.x>
- California Landscape Conservation Cooperative. (2017). Climate Commons Dataset Catalog. Retrieved from <http://climate.calcommons.org/lists/datasets>
- Canadell, J., Jackson, R., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E.-D. (1996). Maximum rooting depth of vegetation types at the global scale. *Oecologia*, *108*, 583–595. <https://doi.org/10.1007/BF00329030>
- Coates, A. R., Dennison, P. E., Roberts, D. A., & Roth, K. L. (2015). Monitoring the impacts of severe drought on Southern California chaparral species using hyperspectral and thermal infrared imagery. *Remote Sensing*, *7*, 14276–14291. <https://doi.org/10.3390/rs71114276>
- Davis, F. W., Stoms, D. M., Hollander, A. D., Thomas, K. A., Stine, P. A., Odion, D., ... Graae, J. (1998). The California Gap Analysis Project – Final Report. University of California, Santa Barbara, CA. Retrieved from http://legacy.biogeog.ucsb.edu/projects/gap/gap_rep.html
- Davis, F. W., Sweet, L. C., Serra-Diaz, J. M., Franklin, J., McCullough, I., Flint, A., ... Mortiz, M. A. (2016). Shrinking windows of opportunity for oak seedling establishment in southern California Mountains. *Ecosphere*, *7*, e01573. <https://doi.org/10.1002/ecs2.1573>
- Diffenbaugh, N. S., Swain, D. L., & Touma, D. (2015). Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences*, *112*, 3931–3936. <https://doi.org/10.1073/pnas.1422385112>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Dormann, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., ... Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, *30*, 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., ... Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*, 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Ellsworth, P. Z., & Sternberg, L. S. L. (2014). Seasonal water use by deciduous and evergreen woody species in a scrub community is based on water availability and root distribution. *Ecohydrology*, *8*, 538–551.
- ESRI. (2016). ArcGIS Desktop: Release 10.4. Redlands, CA: Environmental Systems Research Institute.
- Famiglietti, J. S. (2014). The global groundwater crisis. *Nature Climate Change*, *4*, 945–948. <https://doi.org/10.1038/nclimate2425>
- Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, *24*, 38–49. <https://doi.org/10.1017/S0376892997000088>
- Flint, L. E., & Flint, A. L. (2012). Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. *Ecological Processes*, *1*, 2. <https://doi.org/10.1186/2192-1709-1-2>
- Flint, L. E., Flint, A. L., Thorne, J. H., & Boynton, R. (2013). Fine-scale hydrologic modeling for regional landscape applications: The California Basin Characterization Model development and performance. *Ecological Processes*, *2*, 25. <https://doi.org/10.1186/2192-1709-2-25>
- Franklin, J. (2013). Species distribution models in conservation biogeography: Developments and challenges. *Diversity and Distributions*, *19*, 1217–1223. <https://doi.org/10.1111/ddi.12125>
- Giannini, T. C., Chapman, D. S., Saraiva, A. M., Alves-dos Santos, I., & Biesmeijer, J. C. (2013). Improving species distribution models using biotic interactions: A case study of parasites, pollinators and plants. *Ecography*, *36*, 649–656. <https://doi.org/10.1111/j.1600-0587.2012.07191.x>
- Grivet, D., Sork, V. L., Westfall, R. D., & Davis, F. W. (2008). Conserving the evolutionary potential of California valley oak (*Quercus lobata* Née): A multivariate genetic approach to

- conservation planning. *Molecular Ecology*, 17, 139–156. <https://doi.org/10.1111/j.1365-294X.2007.03498.x>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, 142, 14–32.
- Hijmans, R. J. (2016). raster: Geographic Data Analysis and Modeling. R package version 2.5-8. Retrieved from <https://CRAN.R-project.org/package=raster>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2016). dismo: Species Distribution Modeling. R package version 1.1-1. Retrieved from <https://cran.r>
- Hongyan, L., Williams, A. P., Allen, C. D., Guo, D., Wu, X., Anenkhonov, O. A., ... Badmaeva, N. K. (2013). Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. *Global Change Biology*, 19, 2500–2510.
- Howitt, R., Medellín-Azuara, J., MacEwan, D., Lund, J., & Sumner, D. (2014). Economic analysis of the 2014 drought for California agriculture. Center for Watershed Sciences, University of California, Davis, 20 pp.
- IPCC (Intergovernmental Panel on Climate Change). (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R. K. & Meyer, L. A. (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Jiménez-Valverde, A., Lobo, J. M., & Hortal, J. (2008). Not as good as they seem: The importance of concepts in species distribution modelling. *Diversity and Distributions*, 14(6), 885–890. <https://doi.org/10.1111/j.1472-4642.2008.00496.x>
- Kath, J., Reardon-Smith, K., Le Brocque, A. F., Dyer, F. J., Dafny, E., Fritz, L., & Batterham, M. (2014). Groundwater decline and tree change in floodplain landscapes: Identifying non-linear threshold responses in canopy conditions. *Global Ecology and Conservation*, 2, 148–160. <https://doi.org/10.1016/j.gecco.2014.09.002>
- Kertis, J. A., Gross, R., Peterson, D. L., Arbaugh, M. J., Standiford, R. B., & McCreary, D. D. (1993). Growth trends of blue oak (*Quercus douglasii*) in California. *Canadian Journal of Forest Research*, 23, 1720–1724. <https://doi.org/10.1139/x93-215>
- Kincaid, T. M., & Olsen, A. R. (2015). spsurvey: spatial survey design and analysis. R package version 3.1. Retrieved from <https://cran.r>
- Kueppers, L. M., Snyder, M. A., Sloan, L. C., Zavaleta, E. S., & Fulfrost, B. (2005). Modeled regional climate change and California endemic oak ranges. *Proceedings of the National Academy of Sciences*, 102, 16281–16286. <https://doi.org/10.1073/pnas.0501427102>
- Leathwick, J. R., Elith, J., Francis, M. P., Hastie, T., & Taylor, P. (2006). Variation in demersal fish species richness in the oceans surrounding New Zealand: An analysis using boosted regression trees. *Marine Ecology Progress Series*, 321, 267–281. <https://doi.org/10.3354/meps321267>
- Luce, C. H., Vose, J. M., Pederson, N., Campbell, J., Millar, C., Kormos, P., & Woods, R. (2016). Contributing factors for drought in the United States forest ecosystems under projected future climates and their uncertainty. *Forest Ecology and Management*, 380, 299–308. <https://doi.org/10.1016/j.foreco.2016.05.020>
- Major, J. (1988). California climate in relation to vegetation. In M. Barbour & J. Major (Eds.), *Terrestrial vegetation of California* (pp. 11–74). Sacramento, CA: Native Plant Society of California.
- McBride, J. R., Norberg, E., Bertenshaw, J., Kloss, S., & Mossadegh, A. (1997). Genetic variation in shoot growth phenology, and mineral accumulation of northern and central Sierra Nevada foothill populations of blue oak. In: Pillsbury, N. H., Verner, J., & Tietje, W. D., technical coordinators. Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues; 1996 March 19–22; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 117–125.
- McDowell, N. G., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- McLaughlin, B. C., Ackerly, D. D., Klos, Z. P., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, 23, 2941–2961. <https://doi.org/10.1111/gcb.13629>
- McLaughlin, B. C., Morozumi, C. N., MacKenzie, J., Cole, A., & Gennet, S. (2014). Demography linked to climate change projections in an ecoregional case study: Integrating forecasts and field data. *Ecosphere*, 5, 85. <https://doi.org/10.1890/ES13-00403.1>
- McLaughlin, B. C., & Zavaleta, E. S. (2013). Shifting bottom-up and top-down regulation of oak recruitment across a regional resource gradient. *Global Ecology and Biogeography*, 22, 718–727. <https://doi.org/10.1111/geb.12028>
- Miller, G. R., Chen, X., Rubin, Y., Ma, S., & Baldocchi, D. D. (2010). Groundwater uptake by woody vegetation in a semiarid oak savanna. *Water Resources Research*, 46, W10503.
- Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., ... Beissinger, S. R. (2017). Correction: managing climate change refugia for climate adaptation. *PLoS ONE*, 12, e0169725. <https://doi.org/10.1371/journal.pone.0169725>
- Moruet-Holme, N., Fløjgaard, C., & Svenning, J. C. (2010). Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS ONE*, 5, e10360. <https://doi.org/10.1371/journal.pone.0010360>
- Ning, S., Ishidaira, H., Udmale, P., & Ichikawa, Y. (2015). Remote sensing based analysis of recent variations in water resources and vegetation of a semi-arid region. *Water*, 7, 6039–6055. <https://doi.org/10.3390/w7116039>
- Norris, R. M., & Webb, R. W. (1990). *Geology of California*, 2nd edn. Somerset, NJ: John Wiley Sons, Inc.
- Pearse, I. S., Funk, K. A., Kraft, T. S., & Koenig, W. D. (2015). Lagged effects of early-season herbivores on valley oak fecundity. *Oecologia*, 178, 361–368. <https://doi.org/10.1007/s00442-014-3193-2>
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12(5), 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Piao, S. L., Fang, J. Y., Zhou, L. M., Ciais, P., & Zhu, B. (2006). Variations in satellite-derived phenology in China's temperate vegetation. *Global Change Biology*, 14, 1–17.
- PRISM Climate Group. (2015). Oregon State University. Retrieved from <http://prism.oregonstate.edu>
- R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>
- Ray, R. L. (2016). Moisture stress indicators in giant sequoia groves in the southern Sierra Nevada of California, USA. *Vadose Zone Journal*, 15, 1–19. <https://doi.org/10.2136/vzj2016.03.0018>
- Rice, K. J., Gordon, D. R., Hardison, J. L., & Welker, J. M. (1991). Intraspecific phenotypic variation and ecological genetics of blue oak (*Quercus douglasii* Hook. & Arn.). In Standiford, R. B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31–November 2; Davis, California. Gen. Tech. Rep. PSW-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture: 59–62.
- Rice, K. J., Richards, J. H., & Matzner, S. L. (1997). Patterns and processes of adaptation in blue oak seedlings. In: Pillsbury, N. H., Verner, J.,

- Tietje, W. D., technical coordinators. Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues; 1996 March 19–22; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 109–115.
- Ridgeway, G. (2015). gbm: Generalized Boosted Regression Models. R package version 2.1.1. Retrieved from [https://cran.r-](https://cran.r-project.org/web/packages/gbm/index.html)
- Riggs, L. A., Millar, C. I., & Delany, D. L. (1991). Genetic variation sampled in three California oaks. In: Standiford, R. B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31–November 2; Davis, CA. Gen. Tech. Rep. PSW-126. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 233–234.
- Scanlon, B. R., Longuevergne, L., & Long, D. (2012). Ground referencing GRACE satellite estimates of groundwater storage change in the California Central Valley, USA. *Water Resources Research*, 48, W04520.
- Sork, V. L., Davis, F. W., Westfall, R., Flint, A., Ikegami, M., Wang, H., & Grivet, D. (2010). Gene movement and genetic association with regional climate gradients in California valley oak (*Quercus lobata* Née) in the face of climate change. *Molecular Ecology*, 19, 3806–3823. <https://doi.org/10.1111/j.1365-294X.2010.04726.x>
- Staniczenko, P. P. A., Sivasubramaniam, P., Suttle, K. B., & Pearson, R. G. (2017). Linking macroecology and community ecology: Refining predictions of species distribution using biotic interaction networks. *Ecology Letters*, 20, 693–707. <https://doi.org/10.1111/ele.12770>
- Stevens, D. L., & Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association*, 99, 262–278. <https://doi.org/10.1198/016214504000000250>
- Svenning, J. C., Gravel, D., Holt, R. D., Schurr, F. M., Thuiller, W., Münkemüller, T., ... Normand, S. (2014). The influence of interspecific interactions on species range expansion rates. *Ecography*, 37, 1198–1209. <https://doi.org/10.1111/j.1600-0587.2013.00574.x>
- Swenson, S. C. (2012). GRACE monthly land water mass grids NETCDF RELEASE 5.0. Ver. 5.0. PO.DAAC, CA, USA. Retrieved from <https://doi.org/10.5067/telnd-nc005.f>
- Taylor, R. G., Scanlon, B., Döll, P., Rodell, M., vanBeek, R., Wada, Y., ... Treidel, H. (2013). Ground water and climate change. *Nature Climate Change*, 3, 322–329. <https://doi.org/10.1038/nclimate1744>
- Tyler, C. M., Kuhn, B., & Davis, F. W. (2006). Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology*, 81, 127–152. <https://doi.org/10.1086/506025>
- USDA Forest Service. (2015). 2015 Forest Health and Protection Aerial Detection Survey. Retrieved from www.fs.usda.gov/detail/r5/forest-grasslandhealth/
- USDA Forest Service. (2016). New Aerial Survey Identifies More Than 100 Million Dead Trees in California. Retrieved from <https://www.fs.fed.us/news/releases/new-aerial-survey-identifies-more-100-million-dead-trees-california>
- Van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fule, P. Z., ... Veblen, T. T. (2009). Widespread increase of tree mortality rates in the western United States. *Science*, 323, 521–524. <https://doi.org/10.1126/science.1165000>
- Velicogna, G. A., Kimball, J. S., & Kim, Y. (2015). Impact of changes in GRACE derived terrestrial water storage on vegetation growth in Eurasia. *Environmental Research Letters*, 10, 124024.
- Venturas, M. D., MacKinnon, E. D., Dario, H. L., Jacobsen, A. L., Pratt, R. B., & Davis, S. D. (2016). Chaparral shrub hydraulic traits, size, and life history types related to species mortality during California's historic drought of 2014. *PLoS ONE*, 11, e0159145. <https://doi.org/10.1371/journal.pone.0159145>
- Wang, S. Y. S., Lin, Y. H., Gillies, R. R., & Hakala, K. (2016). Indications for protracted groundwater depletion after drought over the Central Valley of California. *Journal of Hydrometeorology*, 17, 947–955. <https://doi.org/10.1175/JHM-D-15-0105.1>
- Weekley, C. W., Gagnon, D., Menges, E. S., Quintana-Ascencio, P. F., & Saha, S. (2007). Variation in soil moisture in relation to rainfall, vegetation, gaps, and time-since-fire in Florida scrub. *Ecoscience*, 14, 377–386. [https://doi.org/10.2980/1195-6860\(2007\)14\[377:VISMIR\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[377:VISMIR]2.0.CO;2)
- Williams, A. P., Allen, C. D., Millar, C. I., Swetnam, T. W., Michaelsen, J., Still, C. J., & Leavitt, S. W. (2010). Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences*, 107, 21289–21294. <https://doi.org/10.1073/pnas.0914211107>
- Willmott, C. J., Rowe, C. M., & Mintz, Y. (1985). Climatology of the terrestrial seasonal water cycle. *Journal of Climatology*, 5, 589–606. <https://doi.org/10.1002/joc.3370050602>
- Wolf, S. G., Snyder, M. A., Sydemann, W. J., Doak, D. F., & Croll, D. A. (2010). Predicting population consequences of ocean climate change for an ecosystem sentinel, the seabird Cassin's auklet. *Global Change Biology*, 16, 1923–1935. <https://doi.org/10.1111/j.1365-2486.2010.02194.x>
- Wu, X., Liu, H., Wang, Y., & Deng, M. (2013). Prolonged limitation of tree growth due to warmer spring in semi-arid mountain forests of Tianshan, northwest China. *Environmental Research Letters*, 8, 024016. <https://doi.org/10.1088/1748-9326/8/2/024016>

BIOSKETCH

This study represents an effort to utilize large-scale data to better understand distribution-wide effects of climate and subsurface water change on deep-rooted species. Our research fits into a larger attempt to identify ongoing impacts and anticipate future impacts of climate change on species distributions (www.blairmclaughlin.org, <https://naiamoruetaholme.wordpress.com>). This work is included in BJB's MS thesis.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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