Climate and Water Availability Contribute to Die-Off Patterns in an Endemic California
Oak

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AUTHORIZATION TO SUBMIT THESIS

This thesis of Brittni JoAnn Brown, submitted for the degree of Master of Science with a major in Natural Resources and titled "Climate and Water Availability Contribute to Die-Off Patterns in an Endemic California Oak," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

I used Forest Service aerial die-off surveys, downscaled PRISM climate data, and GRACE groundwater change data to develop boosted regression tree models identifying key variables and thresholds associated with die-off occurance throughout blue oak (*Quercus douglasii*) distribution. Precipitation in 2015 below 400mm, spring temperature anomalies, 2013-14 summer-fall temperatures, climate water deficit anomalies, and loss of total water storage below 30cm of baseline were associated with increased die-off probability. Model results indicate blue oak is highly influenced by water availability as precipitation and groundwater, and to a lesser extent, elevated temperatures, and temperature anomalies especially in the southeastern portion of their range. Drought frequency and intensity are projected to increase and may threaten the species' survival given its restricted range and high habitat fragmentation. Knowledge of the climatic and hydrologic variables linked to blue oak die-off will help prioritize climate change related conservation efforts.

ACKNOWLEDGEMENTS

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CHAPTER 1

BLUE OAK ECOLOGY AND RESEARCH BACKGROUND

Anthropogenic climate change is having a substantial impact on biodiversity (IPCC 2014) leading to a wide array of disturbances that alter composition and productivity of ecosystems (Easterling et al. 2000) and contribute to observed range contractions or expansions of numerous plant and animal species (Thomas 2010; Chen et al. 2011; Morueta-Holme et al. 2015). A changing climate is also linked to increased drought, heat stress, and forest die-off across varying elevations, latitudinal gradients, and habitat types worldwide (Van Mantgem et al. 2009; Williams et al. 2010; Allen et al. 2010, 2015; Anderegg et al. 2013). Forest die-off is often linked either directly or indirectly to increasing temperatures or variability in the timing or amount of precipitation in studies documenting the phenomena. Extensive drought and heat related vegetation mortality (Allen et al. 2010) could create a chain reaction of rapid alterations in ecosystems.

Beginning in 2011 and continuing through early 2016, California entered a severe drought marked by record setting low precipitation accumulation, less than 34% of average (Swain et al. 2014). Drought conditions became so severe that a state of emergency was declared in early 2014, causing citizens to cut urban water usage, farmers to reduce river water consumption, and environmental flow mandates to become hotly contested. The drought also marked extreme climatic conditions for many of the plant species that make California a biodiversity hotspot (Myers et al. 2000), conditions which will likely intensify as climate change continues (Diffenbaugh et al. 2015). Laser and satellite monitoring between 2012 and 2015 estimated nearly 10.6 million hectares of California forests had experienced measurable loss in canopy water content (Asner et al. 2016). Recent estimates from the Forest Service approximate 102 million trees died as a result of the drought (USDA Forest Service 2016), predominately in the southern Sierra Nevada, Tehachapi, Transverse, and Southern Coast Ranges. Research on California tree and shrub species indicated the drought has had a profound impact on ecological functions (Ray 2016; Venturas et al. 2016), and had been associated with reductions in species richness and cover (Copeland et al. 2016). Coates et al. (2015) found a reduction in relative green vegetation fraction in grey pine (*Pinus sabiniana*), California sycamore (*Platanus racemose*), coast live oak (*Quercus agrifolia*), blue oak (*Quercus douglasii*), California bay laurel (*Umbellularia californica*), and a number of chaparral species. Asner et al. (2016) noted major decreases in canopy water content in a variety of different forest types including coastal redwood, pinyon-juniper, lodgepole pine, red fir, and black oak forests.

Blue oak, one of the most iconic foothill trees in California, experienced severe die-off throughout portions of its distribution as a result of the drought. Blue oaks are one of several oak species endemic to the Coast Ranges and western foothills of the Sierra Nevada in California, which as a group, make up nearly a quarter of the woody plant biomass in the state (Pavlik et al. 1991). The species is common throughout its approximately 3-million-acre distribution which generally encircles the Central Valley, California's famous agricultural region. Isolated populations exist in the Siskiyou, Trinity, and Kalamath mountains as well as on Santa Cruz and Santa Catalina islands; it is thought these may have been historical introductions by Native American tribes (Griffin & Critchfield 1972). Blue oak is not often found above 1,200 m (3,900 ft), but has been known to extend into higher elevations in the southernmost portions of its distribution (McDonald 1990). In the northern region of the distribution climate conditions tend to be cooler and wetter than in the southern regions where summer temperatures can reach 38°C for weeks at a time (Pavlik et al. 1991). Annual precipitation varies across the distribution from an average of 500 mm in the south to 1000 mm in the north (McDonald 1990). Most precipitation occurs during the winter months followed by a dry summer, which is typical of a Mediterranean climate (Major et al. 1988). Blue oak occurs in a variety of habitat types ranging from savannas where distance between trees is substantial to densely packed blue oak-dominated woodlands. Blue oak co-occurs with grey pine and other oak species in many areas of its distribution. Historically, understory vegetation was likely composed of native bunch grasses, but has since been irreversibly converted to annual non-native grasses (Keeley et al. 2003).

Blue oak is a masting species, with mast years occurring approximately every 3 years if climatic condtions are met (Koenig et al. 1991). Pollination of blue oak occurs through wind dispersal. Acorns are popular food sources for wildlife and many are cached and never retrieved, providing a good conditions for emergence. Blue oak acorns typically begin germinating immediately after they have dropped when the fall rainy season begins (Matsuda et al. 1987), therefore, a seed bank does not develop. Outside of wildlife consumption, acorns are also highly susceptible to fungal damage (Matsuda et al. 1987), which may contribute to the lack of seed banking in the species.

A number of adaptations enable blue oak to survive hot, dry summers including thick blue-green leaves with small stomatal openings (Abrams 1990) and high water use efficiency (Xu & Baldocchi 2003), especially after reaching maturity (Matzner et al. 2003). As soil water deficits become more severe during the dry months, blue oak has been shown to utilize hydraulic lift to bring water to more accessible soil layers (Ishikawa & Bledsoe 2000). Spatial distribution of fine root structure also appears to be optimized to meet climatic constraints and physical settings associated with individual

trees (Koteen et al. 2015). Blue oak is winter dormant and drought deciduous (McCreary 1990), meaning in years of inadequate climatic conditions blue oak will not leaf-out, instead waiting for better conditions in the following year. It is unknown how many consecutive years blue oak can survive without leafing-out. As such, die-off in blue oak does not necessarily indicate mortality.

Prior to European settlement, low-intensity fires occurred on a decadal average (Sandiford et al. 2012), many of which may have been intentionally set by Native American tribes to manage weevils in acorn crops and produce sprouts for basketry (Anderson 2007). Conversion of understory vegetation to annual grasses have greatly altered the fire regime and intensity within blue oak distribution. Bark of blue oak is thin, especially in seedlings and saplings which are susceptible to top-kill in low- and moderate-severity fires (Fry 2002; Horney et al. 2002). Mature blue oaks typically survive low-intensity fires, but are frequently killed in high-severity fires or those with sustained heat (Plumb 1980). In low-severity fires, blue oak is capable of sprouting from the crown or root bole.

The species has cultural significance; as an iconic feature on the landscape it is popular with outdoor enthusiasts and amateur botanists because of its easily identifiable features. Ranchers also heavily value the tree for its ability to provide fodder in the form of acorns and shade during the hot summer months for cattle. Furthermore, blue oak was highly valued among local indigenous peoples who used its acorns to create flour and wood for building material, utensils, baskets, and fuel (Anderson & Moratto 1996).

Blue oak also plays an important ecological role, serving as a keystone species within its ecosystem. Acorn masts produced by blue oak serve as a key food source to wildlife species including bears, ungulates, and a variety of rodents and birds (Pavlik et al. 1991). A number of small mammals, birds, and reptiles (Block & Morrison 1990) utilize blue oak forests for habitat; for instance, California spotted owls (*Strix occidentalis occidentalis*) and purple martins (*Progne subis*) both use blue oak woodlands for nesting (Steger et al. 1997; Williams 2002). Hydraulic lift by blue oak redistributes water to higher soil levels where it is accessible by understory vegetation with less extensive root systems during dry summer months (Ishikawa & Bledsoe 2000). The tree also serves an important role in erosion prevention (Brooks & Merenlender 2001) and improvement of soil quality and fertility (Camping et al. 2002).

Endemic species, and those with restricted ranges, are at increased risk for habitat loss and fragmentation as a result of a changing climate (Morueta-Holme et al. 2010), land use change (Sunny

et al. 2015), and environmental degradation (Rosenzweig & Neofotis 2013; Pinna et al. 2015). In addition, long-lived, sessile species with relatively short dispersal distances and long generation times face substantial barriers to migration into suitable habitat or adaptation to changing climatic conditions (Ackerly et al. 2010, Allen & Breshears 1998). Blue oak is one of many endemic species in California facing this predicament. The tree lives an average of 100 years, although tree cores have been taken from live trees between 300 and 500 years of age (McDonald 1990), and is slow growing, taking decades to reach full maturity (Koenig & Knops 2007).

Climate change has been projected to cause losses in the majority of the current blue oak distribution (Kueppers et al. 2005). Decreases in survival have already been observed in parts of the range projected to contract (McLaughlin et al. 2014). These findings have increased ongoing conservation concerns about low recruitment (Tyler et al. 2006; Zavaleta et al. 2007) and habitat loss and fragmentation due to agriculture and development (Bolsinger 1988). Low recruitment has been linked to many biotic factors throughout the distribution including high levels of cattle and wildlife seed predation (Davis et al. 1991; Hall et al. 1992) and increased resource competition with annual grasses (Gordon & Rice 2000). Blue oak is thought to be one of the hardiest oaks in California and the most capable of surviving high temperature and extended drought (Schoenherr 1992), making its response to the recent drought particularly disturbing.

In this paper I present an analysis of drought-related die-off patterns of blue oak using US Forest Service aerial mortality surveys (USDA Forest Service 2015). I consider the impacts of absolute climate values, climate anomalies, subsurface water storage losses, and fog abundance. Although the importance of fog as a potential water source has been studied in some coastal California species (Dawson et al. 1998; Corbin et al. 2005; Fischer et al. 2009, 2016; Baguskas et al. 2014, 2016; Emery et al. 2016), there have been no reports that I know of on fog influence in blue oak ecosystems. While groundwater has been reported as an important water source for blue oaks (Miller et al. 2010), its influence has not been explored at the distribution scale in relation to die-off patterns. I hypothesize that blue oak die-off patterns will be influenced most greatly by water availability variables in the analysis. I seek to 1) characterize the extent of die-off across the species distribution, 2) model climate and water variables that contribute to die-off, and 3) identify vulnerable populations and examine the management implications of the results.

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CHAPTER 2

CLIMATE AND WATER AVAILABILITY CONTRIBUTE TO DIE-OFF PATTERNS IN AN ENDEMIC CALIFORNIA OAK

Brittni J. Brown

ABSTRACT

Drought conditions in the state of California reached extraordinary levels between 2012 and 2015, resulting in extensive die-off of blue oak (*Quercus douglasii*), an iconic, locally widespread tree endemic to the state. I used Forest Service aerial die-off survey data, downscaled PRISM climate data, and GRACE groundwater change data to develop boosted regression tree models identifying key variables and thresholds associated with the occurrence of die-off throughout blue oak distribution. Precipitation in 2015 below 400 mm, increased loss of total water storage below 30 cm of baseline, spring temperature anomalies, 2013-14 summer-fall temperatures, and climate water deficit anomalies were important indicators of die-off probability. I also explored decadal fog averages as a potential variable in future models. Results indicate that blue oaks are highly influenced by water availability in the forms of precipitation, climate water deficit anomalies, and groundwater, and to a lesser extent to temperatures including elevated temperatures, and temperature anomalies especially in the southeastern portion of their range. Fog showed some potential as a variable when data becomes more available. Drought frequency and intensity are projected to increase with climate change and may threaten the species' survival given its restricted range and high habitat fragmentation. Knowledge of the climatic and hydrologic variables associated with die-off will help prioritize climate change related conservation efforts.

INTRODUCTION

Anthropogenic global climate change is having a substantial impact on biodiversity (IPCC 2014). With it comes a wide array of disturbances altering composition and productivity of ecosystems (Easterling et al. 2000), and contributing to observed range contractions or expansions of numerous species over recent decades (Thomas 2010; Chen et al. 2011; Morueta-Holme at al. 2015). Climate change is leading to increased drought, heat stress, and forest die-off in many parts of the world (Van Mantgem et al. 2009; Williams et al. 2010; Allen et al. 2010, 2015; Anderegg et al. 2013). Extensive

drought and heat related vegetation mortality (Allen et al. 2010) could create a chain reaction of rapid alterations in ecosystems.

Beginning in 2011 and continuing through early 2016, California entered a severe drought marked by record setting low precipitation accumulation, less than 34% of average (Swain et al. 2014). Drought conditions became so severe that a state of emergency was declared in early 2014. The drought also marked extreme climatic conditions for many plant species, which will likely intensify as climate change continues (Diffenbaugh et al. 2015). Laser and satellite monitoring between 2012 and 2015 estimated nearly 10.6 million hectares of California forests had experienced measurable loss in canopy water content (Asner et al. 2016). The most recent estimate from the Forest Service approximate 102 million trees died as a result of the drought (USDA Forest Service 2016), predominately in the southern Sierra Nevada, Tehachapi, Transverse, and Southern Coast Ranges. Research on other tree and shrub species indicate the drought has had a profound impact on ecological functions (Ray 2016; Venturas et al. 2016), and had been associated with reductions in species richness and cover (Copeland et al. 2016). Coates et al. (2015) found a reduction in relative green vegetation fraction in grey pine (*Pinus sabiniana*), California sycamore (*Platanus racemose*), coast live oak (*Quercus agrifolia*), blue oak (*Quercus douglasii*), California bay laurel (*Umbellularia californica*), and a number of chaparral species. Asner et al. (2016) noted major decreases in canopy water content in a variety of different forest types including coastal redwood, pinyon-juniper, lodgepole pine, red fir, and black oak forests.

Endemic species, and those with narrow ranges, are at increased risk for habitat loss and fragmentation as a result of a changing climate (Morueta-Holme et al. 2010), land use change (Sunny et al. 2015), and environmental degradation (Rosenzweig & Neofotis 2013; Pinna et al. 2015). In addition, long-lived, sessile species with relatively short dispersal distances and long generation times face substantial barriers to migration into suitable habitat or adaptation to changing climatic conditions (Allen & Breshears 1998; Ackerly et al. 2010). Blue oak, an iconic and high value species which can take many decades to reach maturity (Koenig & Knops 2007), is one of many endemic species in California facing this predicament.

Climate change has been projected to cause losses in the majority of the current blue oak distribution (Kueppers et al. 2005). Decreases in survival have already been observed in parts of the range projected to contract (McLaughlin et al. 2014). These findings have increased ongoing conservation concerns about low recruitment (Tyler et al. 2006; Zavaleta et al. 2007) and habitat loss and fragmentation due to agriculture and development (Bolsinger 1988). Historically, blue oak was

thought to be one of the hardiest oaks in California and the most capable of surviving high temperature and extended drought (Schoenherr 1992).

In this paper I present an analysis of drought-related die-off patterns of blue oak using US Forest Service aerial mortality surveys (USDA Forest Service 2015). I consider the impacts of absolute climate values, climate anomalies, subsurface water storage losses, and fog abundance. Although the importance of fog as a potential water source has been studied in some coastal California species (Dawson et al. 1998; Corbin et al. 2005; Fischer et al. 2009, 2016; Baguskas et al. 2014, 2016; Emery et al. 2016) there have been no reports that I know of on fog influence in blue oak ecosystems. While groundwater has been reported as an important water source for blue oaks (Miller et al. 2010), its influence has not been explored at the distribution scale in relation to die-off patterns. I hypothesize that blue oak die-off patterns will be influenced most by water availability variables in the analysis. I seek to 1) characterize the extent of die-off across the species distribution, 2) model climate and water variables that contribute to die-off, and 3) identify vulnerable populations and examine the management implications of the results.

METHODS

Study system

The blue oak distribution, covering nearly 1.2 million hectares, generally encircles the Central Valley and includes the Coast Ranges and lower western foothills of the Sierra Nevada in California (Figure 1). Blue oaks are a slow growing, winter deciduous species with an average lifespan of 150 years, and are adapted in some areas to hot dry climates where average summer temperatures may exceed 38°C for weeks at a time (Pavlik 1991). Blue oak grows in a Mediterranean climate in which most precipitation falls between October and March (Major 1988), during the period when blue oak is dormant or just beginning to leaf-out.

Distribution data and study area

To define the blue oak distribution, species occurrences were derived from vegetation distribution data where blue oak was identified as the dominant or co-dominant species in the primary or secondary cover type by the California GAP Analysis database (Davis et al. 1998). To define the study area, using ArcGIS (ESRI 2016), the blue oak distribution was clipped to areas surveyed by the USDA Forest Service Aerial Detection Monitoring campaign (USDA Forest Service 2015). The study area encompassed 79% of the blue oak distribution (2,742,630 ha). This area was surveyed between

June and October 2015, a time period after which blue oaks had reached full leaf out and before leaf drop. Areas where the aerial surveys identified blue oak die-off outside of the California GAP distribution were added into the study area. Distribution data was converted to points spaced at 270x270 m to match the resolution of the climatic data used in analyses, and points falling within water bodies were removed from the data set. I classified areas as 'die-off' when blue oaks were identified by the aerial surveys as the host species with a damage type labeled as either 'mortality,' 'discoloration,' 'defoliation,' or 'die-off;' categories that indicate the tree is experiencing very poor canopy health, indistinguishable from mortality (J. Moore, personal communication Feb 2016) (Figure 2). I classified areas as 'non-die-off' when they were not identified by the aerial surveys under one of the above categories. Blue oak is a drought deciduous species (McCreary 1990), meaning it may not leaf-out in years of inadequate climatic conditions, instead waiting for better conditions in the following year. It is unknown how many consecutive years blue oak can survive without leafing-out and, as such, die-off in blue oak does not necessarily indicate mortality.

Climate and water data

Climate data was downloaded from the California Climate Commons database where PRISM data (PRISM Climate Group 2015) has been downscaled to a 270x270m grid dating back to 1896 (Flint & Flint 2012). I derived eleven climatic variables from this dataset (Table 1) likely to influence climate-driven die-off in blue oaks. A broad pool of climate variables was initially examined so climate-driven impacts could be assessed over a variety of different seasons. I was interested in capturing potential time lags or compounding impacts of multiple years of drought, therefore each climate variable was also examined over six absolute time frames (Table 1). In addition, I calculated two historical comparison parameters for each variable: climate anomalies and novel annual climates. Anomaly values were calculated as the difference between climate normals and 2015 values. Climate normals are averaged data from 1951-1980, a baseline adopted by the Intergovernmental Panel on Climate Change (IPCC) (IPCC 2014). For all anomaly variables, positive values indicate stronger recent drought conditions (e.g. anomalous low precipitation and anomalous high temperatures are represented by positive values). A novel climate was defined as a cell that in 2015 was hotter or drier than ever previously observed (1896-2011). Novel climate values were calculated as the difference between a 2015 climate value and the hottest or driest value for the same area on record. Positive values for all variables indicate a novel climate.

Two additional hydrologic variables were examined. The first, change in total water storage (cm water thickness), was downloaded from NASA's GRACE satellite (Swenson & Wahr 2006; Landerer

& Swenson 2012; Swenson 2012) at a 55km resolution. The satellite measures changes in Earth's gravitational field to estimate the amount of water stored in a region as ice, snow, surface water, and groundwater, and how water level changes on a monthly basis. Summer snow and ice was not present and surface water availability was limited in the study area, therefore, this data was representative of change in subsurface water storage. GRACE data was downloaded from August 2015 when most of the distribution was entering its driest period. Changes in total water storage are between 2015 and the mean of 2004-2009.

Second, I evaluated decadal average fog coverage at 4km resolution (Torregrosa et al. 2015), available on the California Climate Commons database (California Landscape Conservation Cooperation 2017). Decadal fog data was an average of 1999-2009 summer fog rates in hours/day. The dataset is only available for northern and coastal portion of blue oak distribution (Figure 1), therefore the analysis of fog was only exploratory, completed on a geographic data subset referred to as the 'fog subset.' The fog subset covered 61% (1,674,460 ha) of the blue oak distribution, and 6.4% (9,677 ha) of total identified die-off area. I compared hours of daily fog of die-off and non-die-off areas by comparing 99% confidence intervals of each category. To account for differences in sample size between die-off (n = 721) and non-die-off (n = 275,170), 10,000 random samples of 721 die-off and non-die-off points to compare confidence intervals were used. The p value reported is equal to the number of time confidence intervals overlapped divided by the number of iterations (10,000).

Modeling and statistical analysis

Highly correlated variables were removed ($R^2 > 0.8$) in three steps to account for collinearity, which can have a profound effect on ecological models (Dormann et al. 2013). First, I determined the time frame and historical comparison parameter for each climate variable that had the strongest relationship with die-off (Supplementary Table 2.1 & 2.2) using logistic regression. Each parameter was compared 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, I removed any remaining highly correlated variables, retaining composite over seasonal measures (e.g. annual precipitation over winter precipitation). Using this methodology, the climatic model variables were 2015 annual precipitation, 2013-2014 average max summer-fall temperature, summer-fall temperature novel climate, climate water deficit anomaly, and spring precipitation anomaly. Finally, I examined the correlation between the remaining climatic variables, GRACE, and decadal fog, none of which were highly correlated.

To address possible spatial autocorrelation in the model, which can be an issue leading to Type I errors and resulting poor model interpretation (Dormann et al. 2007), I generated eight spatially balanced datasets to test the robustness of the full model with fewer samples. The datasets maintained the same ratio of die-off to non-die-off points as the original dataset but were thinned to 490 randomly selected die-off points. I used generalized random tessellation stratification (Stevens & Olsen 2004) within the R package *spsurvey* (Kincaid & Olsen 2015) to generate spatially balanced datasets.

I used boosted regression trees (BRTs) to model die-off because they handle complex ecological relationships well (Elith et al. 2006), allowing for non-linear relationships and including model interactions automatically (Leathwick et al. 2006; Elith et al. 2008). Using methods from Elith et al. (2008), I found optimal values of learning rate (a shrinkage parameter) (Figure 3), tree complexity (interaction depth) and bag fraction (the proportion of randomly selected data at each modeling iteration) which were 0.01, 5 and 0.5 respectively. The model used climatic and subsurface water data available for the full stay area, hereafter referred to as the full model. The model used the binomial family with the presence or absence of die-off as the response variable. Finally, I compared the optimal full model output with models using our 8 spatially balanced datasets; variables not robust to removal of spatial structure in the data (e.g. direction of relationship with die-off varying across spatially balanced datasets) were removed in the full model.

Model fit and predictive performance were evaluated using area under the curve (AUC), deviance explained, root mean square error and Pearson's correlation coefficient (between observed and fitted values). BRTs calculate AUC by withholding test data (controlled by the bag fraction) with each new tree in the model to determine predictive ability (Elith et al. 2008). An AUC value of 0.5 indicates that the model cannot predict any better than random, while an AUC of 1 indicates perfect prediction, which can be an indication of over-fitting (Fielding & Bell 1997). Over-fitting is reduced in the BRT modeling process by 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 version 3.3.2 (R Core Team 2016) using the *gbm* version 2.2.1 (Ridgeway 2015) and *dismo* version 1.1-4 (Hijmans et al. 2016) packages.

Remotely sensed data

Because aerial surveys have a high potential for human error, I verified the surveys by examining blue oak die-off using Landsat 8 Reflectance Data remote sensing products (USGS 2016A) and normalized difference water index (NDVI). Similar verifications of aerial surveys have been

conducted in aspen stands in Colorado and the surveys were shown to be visually comparable to remote sensing imagery (Worrall et al. 2008; Huang & Anderegg 2012). The remotely sensed analysis was limited to areas of the distribution identified as explicitly 'blue oak woodland' in the California GAP Analysis database to limit potentially confounding influence by co-occurring tree species. The Reflectance Data product was chosen because it has already been radiometrically corrected and accounts for atmospheric effects, illumination, and viewing geometry (USGS 2016B), reducing user post-processing requirements distinctively.

Data was downloaded over a two-week period in August 2015 (Julian days 223-237), a time when most understory plants have senesced while blue oak is still leafed out. Cloud cover between years used in analysis was minimal within the study area. One tile - 2015 path 45 row 32 - was too cloudy for analysis so the first clear image closest to our two-week analysis window was substituted. I removed clouds using the provided cloud mask from each tile, as well as any oversaturated pixels (value > 10000) before mosaicking into one image. I compared the NDVI of die-off and non-die-off areas by comparing 99% confidence intervals of each category. Due to the difference in sample sizes between the die-off (n = 7282) and non-die-off (n = 97628), 10,000 random samples of 200 die-off and 200 non-die-off points were taken, then compared their 99% confidence intervals. I generated subsets of 200 points each to avoid confidence intervals that were inflated by large sample sizes. The reported p value is equal to the number of times the confidence intervals overlapped, divided by the number of iterations (10,000).

RESULTS

Across the majority of the blue oak distribution, 2015 was hotter and drier than the 30-year normal. Over 99.36% of the distribution had a lower annual precipitation (Figure 4) and 91.56% had higher average max summer-fall temperatures in 2015 than the 30-year normal. Only a small percentage of the distribution experienced novel annual climates in 2015 (0.5% experienced novel precipitation and 1.8% novel temperatures). Total August 2015 water storage levels, derived from the GRACE data, were generally lower than the 2004-2009 baseline (min: -34.2 cm, max: 1.2 cm, mean: -24.0 cm).

In 2015, aerial surveys identified 5.52% (151,381 ha) of the blue oak study area as experiencing die-off. Approximately 50% of this area was identified in the California GAP database as blue oak woodlands. NDVI was significantly lower in observed die-off locations (0.30 ± 0.01) within the woodlands than in non-die-off locations (0.38 ± 0.2; $P < 0.001$; Figure 5). Only 7.5% of observed die-off areas fell within the 99% confidence intervals of the NDVI values within non-die-off areas. This

indicated trees within observed die-off areas were indeed less green than trees in non-die-off locations.

Full model

The final full model included five variables (2015 precipitation, 2013-2014 average max summer-fall temperature, climate water deficit anomaly, and spring temperature anomaly, and change in total water storage), and explained 46% of the variability in die-off across the distribution (AUC = 0.958, RMSE = 0.143, R^2 = 0.574). One-third (33%) of the variability within the full model was explained by 2015 precipitation, followed by change in total water storage (29.6%), spring temperature anomaly (15.7%), 2013-14 summer-fall temperature (12.7%), and climate water deficit anomaly (9%). Partial dependence plots of the model variables (Figure 6) indicated that non-linear, threshold-based relationships existed within the data. Although non-die-off points occurred above these thresholds, few die-off points existed above them. For 2015 precipitation, a severe increase in die-off probability occurred when the total precipitation fell below 400 mm. The likelihood of die-off increased dramatically as change in baseline total water storage levels fell below -30cm. Slight growth in the likelihood of die-off occurred as average 2013-2014 summer-fall temperature increased above 25^0C, and an increase in die-off probability with more anomalous spring temperatures, although the effect disappeared after 2.3^0C anomaly due to the rarity of anomalous temperatures above this value (Figure 7). Die-off probability also began to increase when climate water deficit anomaly reached ~100 mm and continued until anomalous climate water deficit became rare near ~300 mm (Figure 7). The strongest modeled interaction was between precipitation in 2015 and change in total water storage (Figure 8) to cause an increase in the probability of die-off when precipitation was below 450 mm. The variable summer-fall temperature novel climate was dropped from the final models because it was not robust to the thinned, spatially balanced datasets. After removal of this parameter, the final spatially balanced dataset explained 39% of the total die-off variability (AUC = 0.933, RMSE = 0.159, R^2 = 0.703). Partial dependence plot trends between the final spatially balanced dataset (Figure 6) and the full dataset were qualitatively similar. Fitted values of the full model (Figure 9) over the blue oak distribution predicted observed die-off with 30 ± 6% confidence on average (max = 97%, min = 0%).

Fog subset

Analysis of fog in die-off and non-die-off areas of the fog subset indicated that die-off was not present when average hours of fog per day was greater than 3.2, though hours of daily fog ranged

from 1.9 to 9.4. Fog in die-off areas occurred for an average of 2.74 ± 0.022 hours per day, whereas in non-die-off areas fog occurred for an average of 2.88 ± 0.057 hours per day (P = 0.007).

DISCUSSION

Our analysis indicates patterns of blue oak die-off may be greatly influenced by limited water availability both in the form of annual precipitation and total water storage. To a lesser extent recent mid-late season high temperatures, anomalous increases in spring temperature, and anomalously high climate water deficit also increased the likelihood of die-off. Fog could be playing a protective role, decreasing the likelihood of die-off. Although GRACE data has been used previously for general drought monitoring (Ning et al. 2015; Velicogna et al. 2015; Wang et al. 2016), this work illustrates a novel analysis of drought-related die-off patterns of blue oak using climatic variables and subsurface water storage data.

Climatic relationships with blue oak die-off

Consistent with previous studies identifying precipitation as a dominant climatic factor for blue oak growth and survival (Kertis et al. 1993; Kueppers et al. 2005), the results indicated that 2015 annual precipitation played an overwhelmingly important role in die-off. Die-off probability increased dramatically in the full model when precipitation fell below approximately 400 mm annually, but almost no die-off occurred above this precipitation value. Thus, 400 mm may represent a threshold under which blue oak systems become vulnerable to die-off. Given projections for increased regional climatic drying (Flint & Flint 2012), blue oak populations in xeric parts of the distribution or in areas projected to drop below the 400 mm threshold may become increasingly vulnerable in the future. Annual precipitation in 2015 was likely chosen over other time frames because 2015 data represented the third year of a three-year drought, after which trees would have been highly stressed and vulnerable to another year of low precipitation.

Increased summer and fall temperatures increase ecosystem evapotranspiration, likely exacerbating the plant water deficits caused by low precipitation. Maximum temperatures directly impact physiological functions such as respiration and photosynthetic capability and increase mortality risk for trees (McDowell et al. 2008). High temperatures may play a particularly important role in tree mortality under water deficit conditions (Adams et al. 2009). As such, the likelihood of die-off in the full model slowly increased as summer-fall temperature max averages in 2013-14 increased above 25^0C. The majority of 2015 aerial surveys were completed before late summer, making 2015 summer-fall max average temperatures irrelevant as a key variable in the model. In our full model,

the relationship between summer-fall temperatures in 2013-14 and die-off probability dropped off after 31.5^{0}C because the frequency of temperatures this high decreased to less than 4.5% of observed die-off points (Figure 7).

In addition to absolute climate values, I also found that certain climate anomalies increased the likelihood of die-off. The fact that *change* in these climate variables rather than their absolute values predicted die-off suggests the possibility of local climate adaptation, either physiological or evolutionary, in blue oak. These small changes over time contributing to an increased likelihood of die-off would likely have not been captured using only absolute time frames, which may explain model inclusion. Limited 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). Common garden studies have suggested that regional populations have distinct genetics and that local adaptation within these regions has occurred (Rice et al. 1997), however genetic variation within populations may be large enough to potentially obscure definitive ecotypes or ecoclines (Riggs et al. 1991; McBride et al. 1997). In valley oak (*Quercus lobata*) separate genetic clusters have been identified and linked to limited gene flow (Grivet et al. 2008), especially in the southernmost portion of the distribution where the Transverse Range may limit dispersal (Ashley et al. 2015). 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, it is possible that a genetic structure similar to that of valley oak may exist in blue oak.

Die-off probability was associated with anomalously high spring temperatures. Warmer temperatures contribute to earlier arrival of spring events (Parmesan & Yohe 2003; Schwartz et al. 2006), likely to cause earlier leaf-out for many tree species (Parmesan 2007). Earlier leaf-out was linked to altered trophic relationships and more insect damage in valley oak (Pearse et al. 2015). In other Mediterranean oaks, mast-seeding was most strongly related to precipitation and water deficit, but appeared to increase with warmer spring temperatures (Perez-Ramos et al. 2015), potentially directing more resources toward reproduction. Spring warming trends often result in a longer growing season and can lead to prolonged or earlier drought stress (Piao et al. 2006; Hongyan et al. 2013). Wu et al. (2013) found early spring warming increased soil water deficit and decreased growth in semi-arid forests in the Tianshan Mountains of northwestern China. In blue oak woodlands, anomalous spring temperatures may increase already limited annual water demands. The model output showed a hump shaped relationship between die-off probability and spring temperature anomaly because the frequency of anomalous spring temperatures declined above 1^{0}C, and accounted for less than 2.5% of

observed die-off points above 2 ^{0}C (Figure 7), leading to a decrease in contribution to die-off probability.

An increase in die-off probability as anomalous climate water deficits increased over 100 mm also occurred. Climate water deficit variables help to integrate temperature, precipitation, and surface and shallow soil hydrological processes (Willmott et al. 1985), making it a useful measure of anomalous plant water deficit integrated across these variables. Young et al. (2017) found that between 2012 and 2015 statewide mortality in Californian forests increased with higher 35-year averages of climate water deficit, and that in 2015 mortality probability in Californian forests reached 87% when mean annual climate water deficit was greater than 900 mm. The relationship between die-off probability and climate water deficit anomalies in the model was also hump shaped because the frequency of anomalous climate water deficits declines above 200 mm; only 2% of observed die-off points were above 300 mm (Figure 7).

Die-off-groundwater relationship

Blue oak appears to be dependent on deep water sources in certain populations during certain time periods. Blue oak has been shown to obtain water from different depths during different times of the year (Miller et al. 2010), with higher percentages of water use coming from shallow soil water in the beginning of the growing season and transitioning to deep water sources as shallow soil water becomes insufficient during the summer dry period. Nearly 80% of blue oak water requirements were met by deep water sources during summer months (Miller et al. 2010). A similar progression to deeper water sources throughout the growing season has been observed in multiple species in dry seasonal ecosystems (Weekley et al. 2007; Ellsworth & Sternberg 2014). Low precipitation may cause these species to tap into deeper water sources earlier in the year. In a historical survivorship study on closely related valley oak, the highest mortality of overlapped with years with the lowest groundwater levels (Brown & Davis 1991).

GRACE measurements and data from numerous wells across California indicate groundwater storage in the state has declined dramatically since the beginning the twenty-first century (Wang et al. 2016), up to 31 ± 3 km^3 between 2006 and 2012 (Famiglietti et al. 2011; Scanlon et al. 2012). Estimates from 2014 alone indicate the drought resulted in an additional 6.3 km^3 of groundwater depletion (Howitt et al. 2014), largely as a result of higher agricultural withdrawals necessitated by low precipitation. Change in total water storage from a pre-drought baseline (2004-2009) had a clear threshold after which most die-off occurred in the full model, approximately -30 cm. After this point, the probability of die-off rose substantially, indicating that a nonlinear relationship may exist between groundwater

levels and blue oak vulnerability to die-off. Similar threshold-based relationships between groundwater availability and die-off have been found previously in eucalyptus species in Australia (Kath et al. 2014).

Fog in subset

Fog and other forms of occult precipitation have a significant impact on water, energy and nutrient flux in coastal ecosystems (Torregrosa et al. 2015), and have been shown to impact soil moisture availability (Dawson 1998), reduce transpiration and evaporative water losses (Barradas & Glez-Medellín 1999; Ritter et al. 2009), and enable foliar water uptake (Limm et al. 2009; Emery 2016). Numerous studies evaluating coastal species, such as redwood (*Sequoia sempervirens*) (Burgess & Dawson 2004), Bishop pine (*Pinus muricata)* (Fischer et al. 2009, 2016), and various shrubs (Emery 2016) have found that fog plays an important role in maintaining water balance and buffering species from low precipitation and drought (Baguskas et al. 2014). However, no research, as far as I know, has previously been conducted on fog effects on oak woodland condition or die-off. An exploratory analysis indicated that higher fog presence and duration may reduce the negative effects of low precipitation, although this effect was small. Annual fog data covering the full study area was not available, therefore the fog data used in the analysis represented an average of fog abundance across a decade rather than specific drought years. However, these data likely represented relative fog abundance across the fog subset as fog patterns tend to be correlated from year to year (Torregrosa et al. 2015). The results indicate that further research is warranted on the role of occult precipitation in blue oak ecosystem water balance and vulnerability to die-off.

Model evaluation and limitations

The full model explained 46% of the deviance in die-off occurrence. In comparison, in a study using differing methods examining aspen stands across Colorado, climate parameters explained 32% of predicted versus observed mortality levels (Anderegg et al. 2013). The full model predicted, on average, $30 \pm 6\%$ probability of die-off within observed die-off areas, with an AUC of 0.958. The use of BRTs allowed more flexibility in modeling non-linear relationships between die-off and climatic and water-related variables, including identifying threshold relationships. The analysis was limited to only climate and water variable across the distribution, and therefore did not take into account other potential influencers of die-off. Non-climatic factors contributing to die-off that likely account for some unexplained variance in the models also include biotic interactions (Buse et al. 1999; Pearse et al. 2015), the greatly varied topography and geology of the region, fire ecology, and low spatial resolution of subsurface water storage data.

In the full model, relationships between die-off and climate variables were robust to removal of spatial structure within the data, as illustrated by the eight models with spatially thinned data (Figure 6). Fog analysis was limited by the extent of the fog predictor variable that was available and low number of die-off points within the available area (< 0.3 % of total points). For this reason, I restricted interpretations of fog relationships to an exploratory analysis of fog role in die-off patterns, rather than using it in model prediction.

Despite some expected data collector error in long distance aerial surveying, there was a difference in NDVI between observed die-off and non-die-off woodland areas, which made up 50% of observed die-off. Observed die-off had a NDVI of 0.30 ± 0.01, while non-die-off areas had a NDVI of 0.38 ± 0.02 in blue oak woodlands. NDVI is one of the most well-known and robust remotely sensed vegetation indices (Ogaya et al. 2015; Coates et al. 2016), and the analysis of the differences in NDVI between areas identified by aerial surveys as having blue die-off versus no die-off confirm the value of the aerial surveys.

Conservation implications and conclusions

There is consensus that global surface temperatures will increase (IPCC 2014) and despite variable projections for future precipitation rates (Seager et al. 2012), much of blue oak distribution is projected to experience drier annual conditions because of increase evapotranspiration due to warming temperatures (Flint & Flint 2012). For blue oak forests this will likely mean 1) droughts and unusually hot periods will become hotter, 2) vapor pressure deficit will become more severe, and 3) less precipitation will fall as snow (Luce et al. 2016). Climatic conditions such as those seen during California's recent extreme drought are likely to become more frequent. Populations, especially in the xeric portions of the distribution, will likely become increasingly vulnerable to die-off, and poor regeneration (McLaughlin & Zavaleta 2013; McLaughlin et al. 2014). Shrinking windows for seedling establishment in the southernmost part of the distribution have been linked with climate water deficits and, to a lesser degree, high temperatures (Davis et al. 2016).

These xeric regions, where die-off already has begun, make up the "trailing edge" of the blue oak distribution. As climate continues to change, blue oak may become extirpated from these regions except in areas of refugia (Keppel et al. 2012), likely to fall near consistent sources of groundwater (McLaughlin et al. 2017) where the trees are capable of meeting water demands in the context of projected higher and more frequent climatic drought. It will be important for land managers in xeric regions to prioritize blue oak conservation within refugia. California is known for its large urban populations, significant economic activity, and productive agricultural regions, all of which compete

with natural systems for finite freshwater resources. In 2014 alone, groundwater pumping increased by 6.3 km^3 (Howitt et al. 2014) to compensate for drought conditions, reducing aquifer levels drastically. Implementation of long-term groundwater conservation is essential for natural resource management under future climatic scenarios, and land managers may collaborate with private land owners where possible to implement groundwater conservation projects designed to replenish deep water supplies.

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Table 1. Eleven climate variables derived from downscaled PRISM climate parameters, used in initial determination of model variables

Climate Variable: 2015, 2013-2014, 2013-2015, 2011-2015, 1981-2010, 1951-1980, Anomaly, Novel	**Description**
Climate Water Deficit (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

Table 2. Step 1 of removal of highly correlated variables. Each variable was first tested in a GLM against a null model; BIC was used to determine how much it contributed to model improvement. For each climate parameter (e.g. CWD) the time frame with the lowest BIC was selected to move on to step 2. To be sure time frames were highly correlated, we ran Pearson correlation tests to examine the relationship between the chosen variable (value of 1) and the other time frames for each climate parameter. Variable abbreviations are as follows: climate water deficit (CWD), annual precipitation (AP), spring precipitation (PMAM), fall precipitation (PSON), winter precipitation (PDJF), spring temperature (TMAM), summer temperature (TJJA), fall temperature (TSON), growing season temperature (TGS), spring-summer temperature (TSS), summer-fall temperature (TSF).

Variable	Pearson Correlation	BIC against null model
CWD 2015 (15)	0.978	81680.45
CWD Average 2013-2014 (1314)	1	79813.11
CWD Average 2013-2015 (1315)	0.996	80365.80
CWD Average 2011-2015 (1115)	0.991	82312.35
CWD Average 1981-2010 (8110)	0.965	83435.82
CWD Average 1951-1980 (5180)	0.959	83173.04
AP 15	1	81876.33
AP 1314	0.963	86999.63
AP 1315	0.984	85186.89
AP 1115	0.949	90282.08
AP 8110	0.904	90897.81
AP 5180	0.899	91273.71
PMAM 15	0.865	90948.77
PMAM 1314	0.953	91281.50
PMAM1315	1	89867.52
PMAM 1115	0.977	91261.57
PMAM 8110	0.887	94782.68
PMAM 5180	0.836	97201.14
PSON 14	0.977	89517.00
PSON 1314	0.980	90283.83
PSON 1214	1	86138.84
PSON 1014	-	
PSON 8110	0.936	90872.98
PSON 5180	0.945	88166.94
PDJF 15	1	76568.72
PDJF 1314	0.877	86629.64
PDJF 1315	0.947	82214.75
PDJF 1115	0.865	90451.27
PDJF 8110	0.832	88845.63
PDJF 5180	0.817	89792.66
TMAM 15	0.945	99249.57
TMAM 1314	0.997	97703.69
TMAM 1315	0.991	98235.15
TMAM 1115	1	96454.35
TMAM 8110	0.953	97350.67
TMAM 5180	0.936	98462.28
TJJA 15	0.980	97395.62
TJJA 1314	0.997	92523.19
TJJA 1315	0.997	94396.43
TJJA 1115	1	93255.26
TJJA 8110	0.917	93881.64
TJJA 5180	0.899	95908.36

TSON 14	1	90364.75
TSON 1314	0.978	94798.25
TSON 1214	0.975	94483.29
TSON 1014	0.962	95583.40
TSON 8110	0.892	97208.58
TSON 5180	0.886	97485.39
TGS 15	0.989	95753.48
TGS 1314	0.998	94554.81
TGS 1315	0.996	95742.55
TGS 1115	1	94141.57
TGS 8110	0.939	95982.54
TGS 5180	0.925	97178.94
TSS 15	0.965	98316.94
TSS 1314	0.998	94775.77
TSS 1315	0.994	96133.72
TSS 1115	1	94280.69
TSS 8110	0.941	95507.11
TSS 5180	0.926	97188.51
TSF 1314	1	92737.90
TSF 1315	0.997	94204.49
TSF 1115	0.998	93075.62
TSF 8110	0.922	95272.31
TSF 5180	0.908	96433.27

Table 3. Step 1 of removal of highly correlated variables. Each variable was first tested in a GLM against a null model; BIC was used to determine how much it contributed to model improvement. For each climate parameter (e.g. CWD) the historical variable with the lowest BIC was selected to move on to step 2. Variable abbreviations are as follows: climate water deficit (CWD), annual precipitation (AP), spring precipitation (PMAM), fall precipitation (PSON), winter precipitation (PDJF), spring temperature (TMAM), summer temperature (TJJA), fall temperature (TSON), growing season temperature (TGS), spring-summer temperature (TSS), summer-fall temperature (TSF).

Variable	Pearson Correlation	BIC against null model
CWD Anomaly	1	96849.61
CWD Novel Climate	0.651	100107.55
AP Anomaly	0.120	100161.49
AP Novel Climate	1	84107.92
PMAM Anomaly	0.600	99932.41
PMAM Novel Climate	1	93795.33
PSON Anomaly	0.658	99115.14
PSON Novel Climate	1	90139.45
PDJF Anomaly	0.130	100170.72
PDJF Novel Climate	1	80791.59
TMAM Anomaly	1	96628.77
TMAM Novel Climate	0.600	98704.82
TJJA Anomaly	1	97925.94
TJJA Novel Climate	0.927	100156.23
TSON Anomaly	0.886	95107.30
TSON Novel Climate	1	91479.34
TGS Anomaly	0.834	100029.27
TGS Novel Climate	1	97258.90
TSS Anomaly	1	97132.73
TSS Novel Climate	0.876	99808.54
TSF Anomaly	0.899	99819.19
TSF Novel Climate	1	96475.62
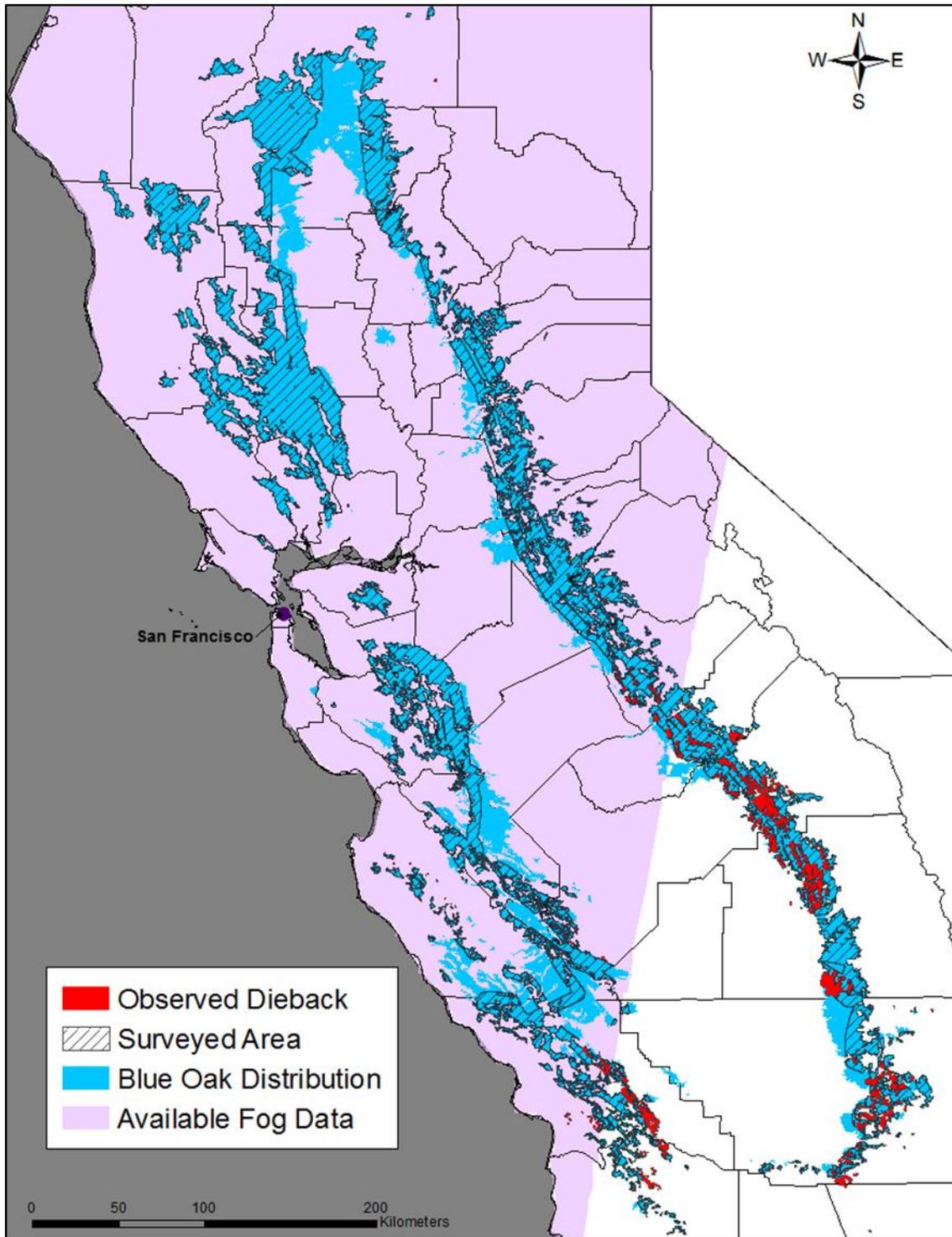
Figure 1. Map of California showing the blue oak distribution in blue, the extent of the USFS aerial mortality surveys, hatched, the observed die-off from USFS aerial mortality surveys in red, available fog data and area of distribution used in the fog subset model.

Figure 2. An example of a healthy, fully leafed out blue oak (top) versus a blue oak experiencing die-off (bottom).
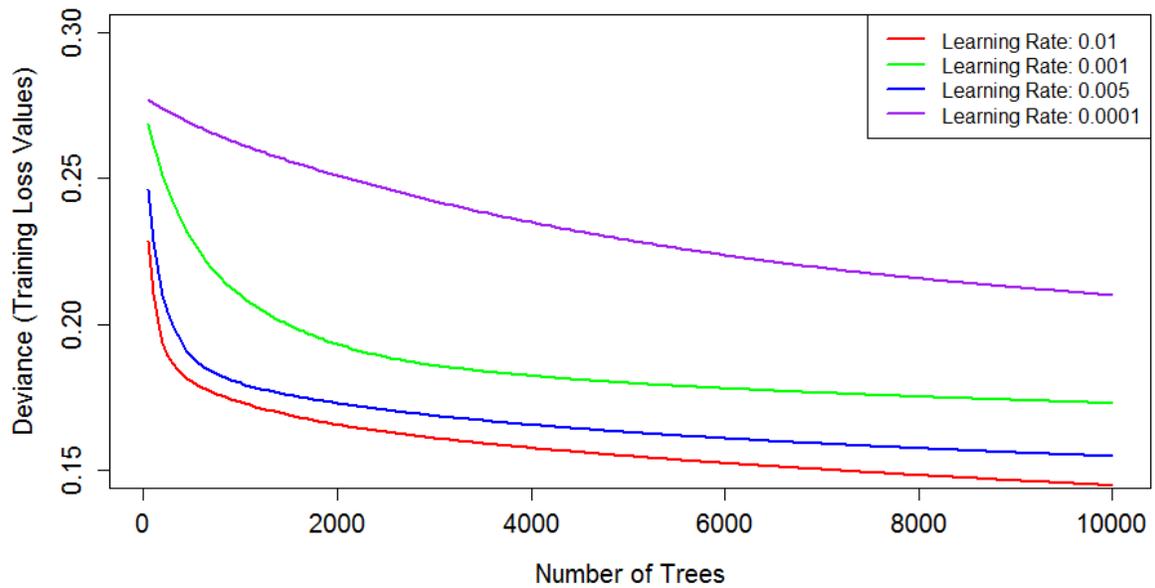
Figure 3. Remaining unexplained deviance after 10,000 trees at four different learning rates (0.01 red; 0.001 green; 0.005 blue; 0.0001 purple). X axis is number of trees examined, y axis in the remaining unexplained deviance.
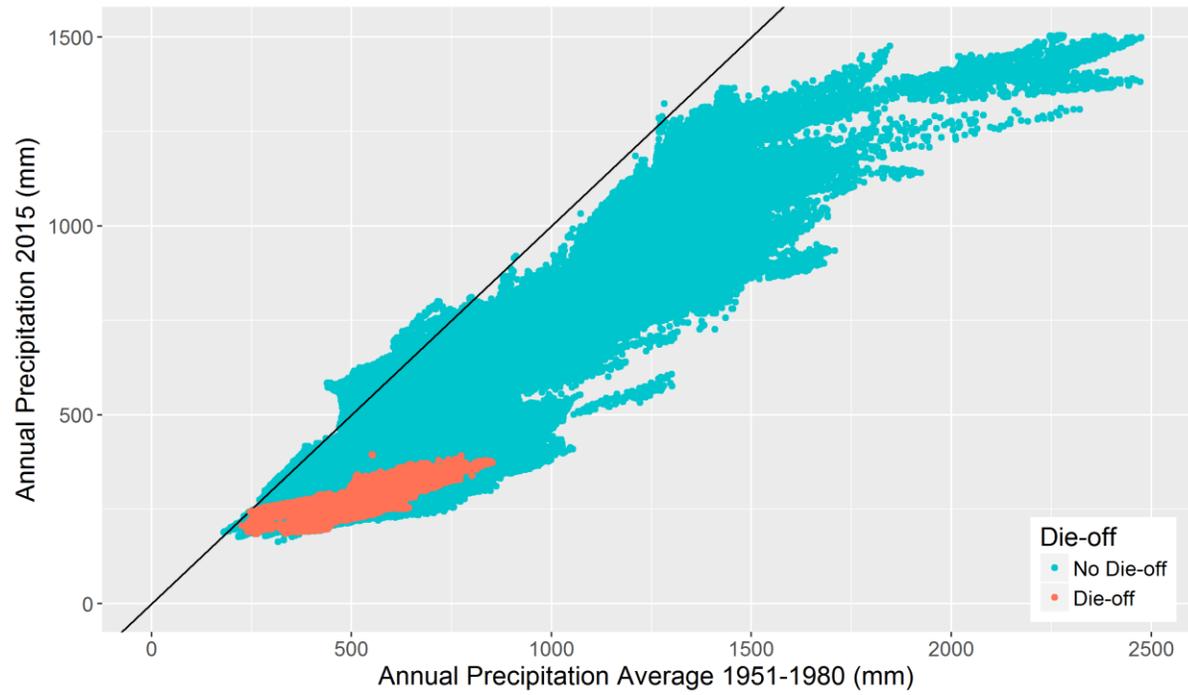
Figure 4. 2015 annual precipitation (mm) and mean annual precipitation from 1951-1980 (mm) for all climate cells (270 m) across the surveyed area of the blue oak distribution, with observed die-off in red and no observed die-off in blue. Black line represents a one-to-one line.
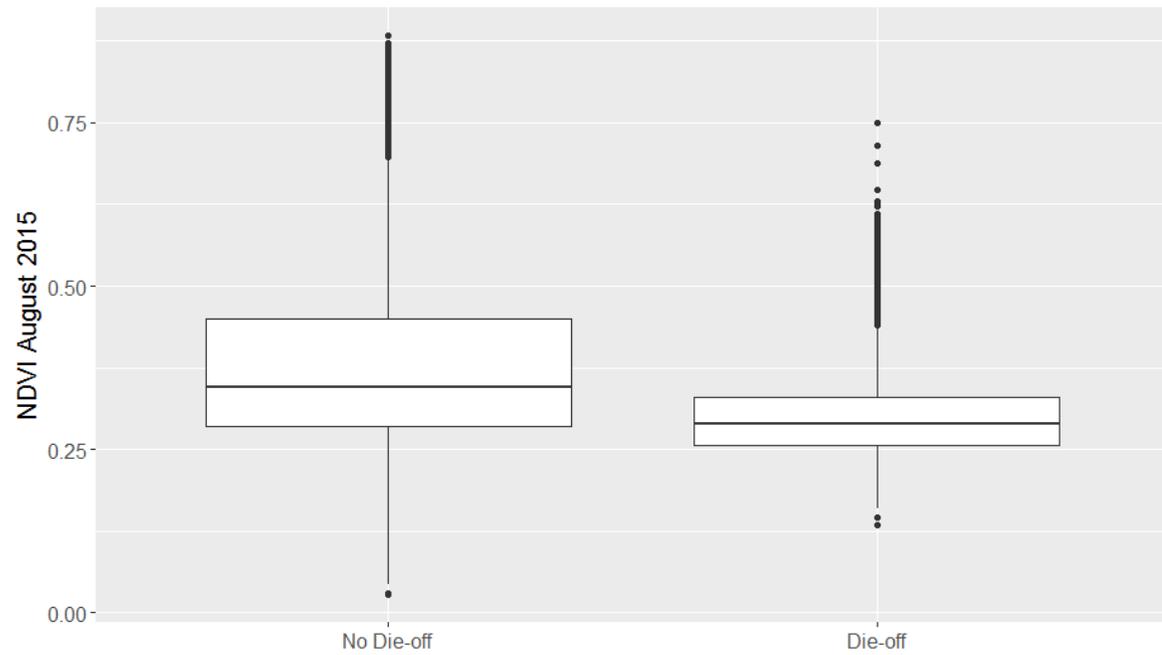
Figure 5. Measured differences in NDVI in blue oak woodlands. X axis is presence or absence of die-off, y axis is NDVI in August 2015 (non die-off = 0.38 ± 0.13; die-off = 0.30 ± 0.07).
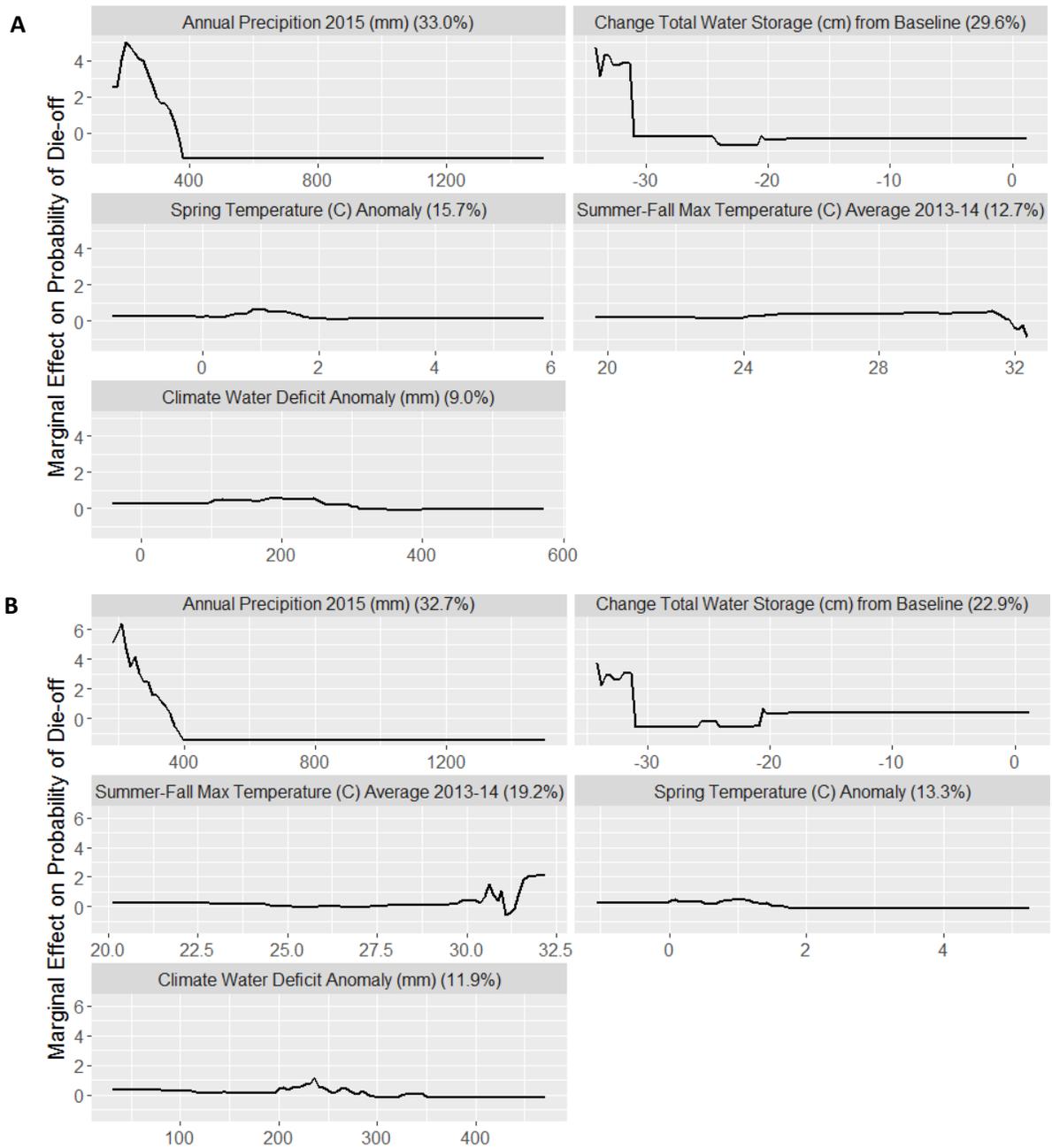
Figure 6.(A) Full model partial dependence plots isolate the contribution of each variable to the total model fitted function on the y axis, variable scale range on the x axis. Percentages are estimated contribution of the variable to the full model. (B) Partial dependence plot of the final spatially balanced, thinned model used to test the robustness of the full model.
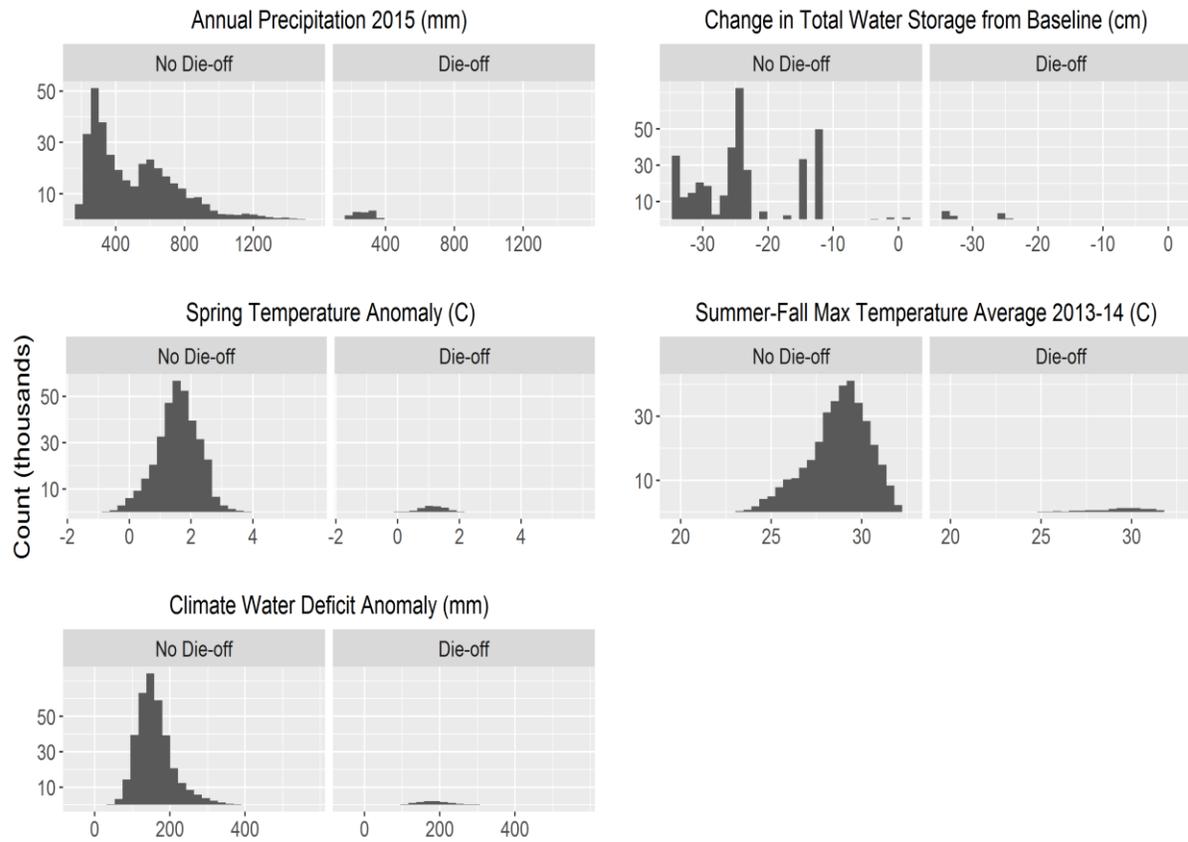
Figure 7: Histograms of the variable value distribution in the full model variables differentiated by observed die-off and non-die-off. The y axis is point count in thousands of points, x axis is the value of the variable.
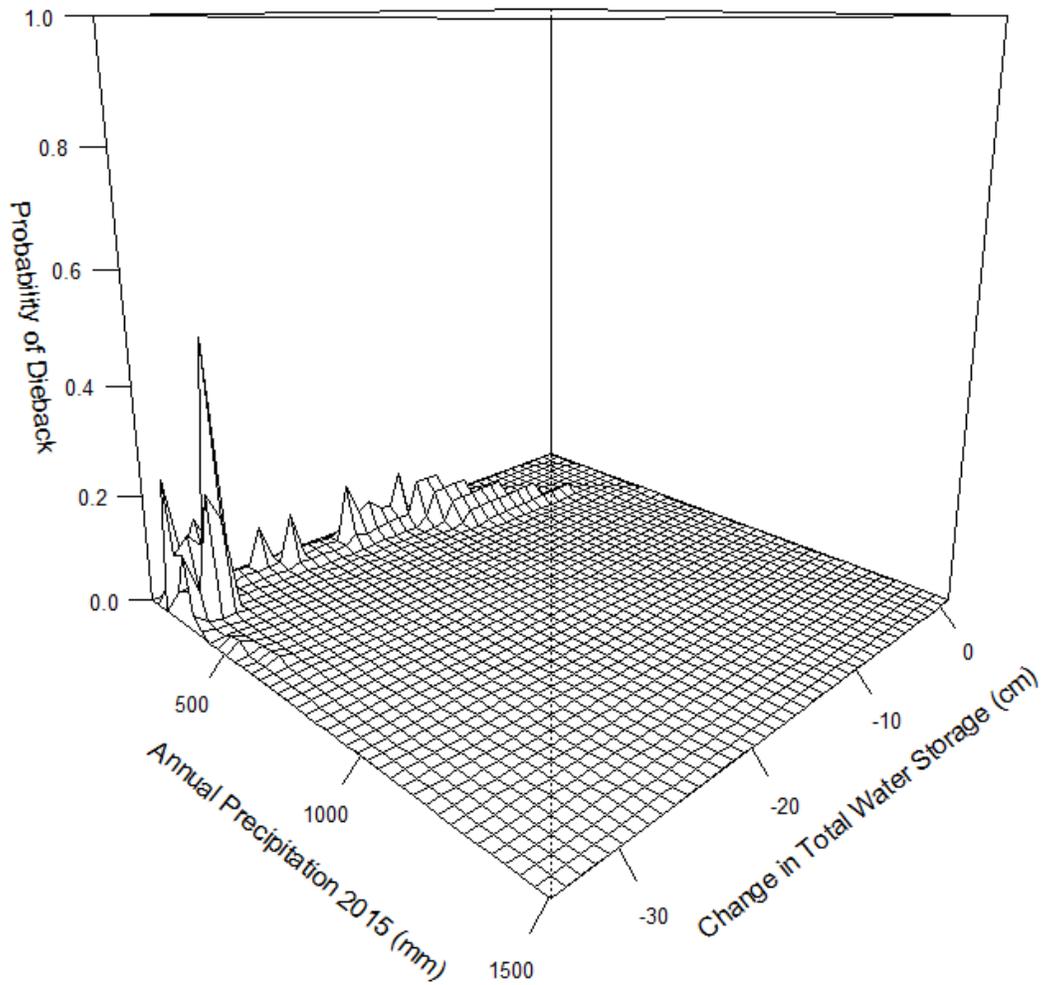
Figure 8. Modelled interaction between change in total water storage from baseline (cm) on the x axis, 2015 precipitation (mm) on the y axis, and probability of die-off on the z axis. All values are fitted values from the full BRT model relating presence and absence of die-off in blue oak to climate and water storage variables.
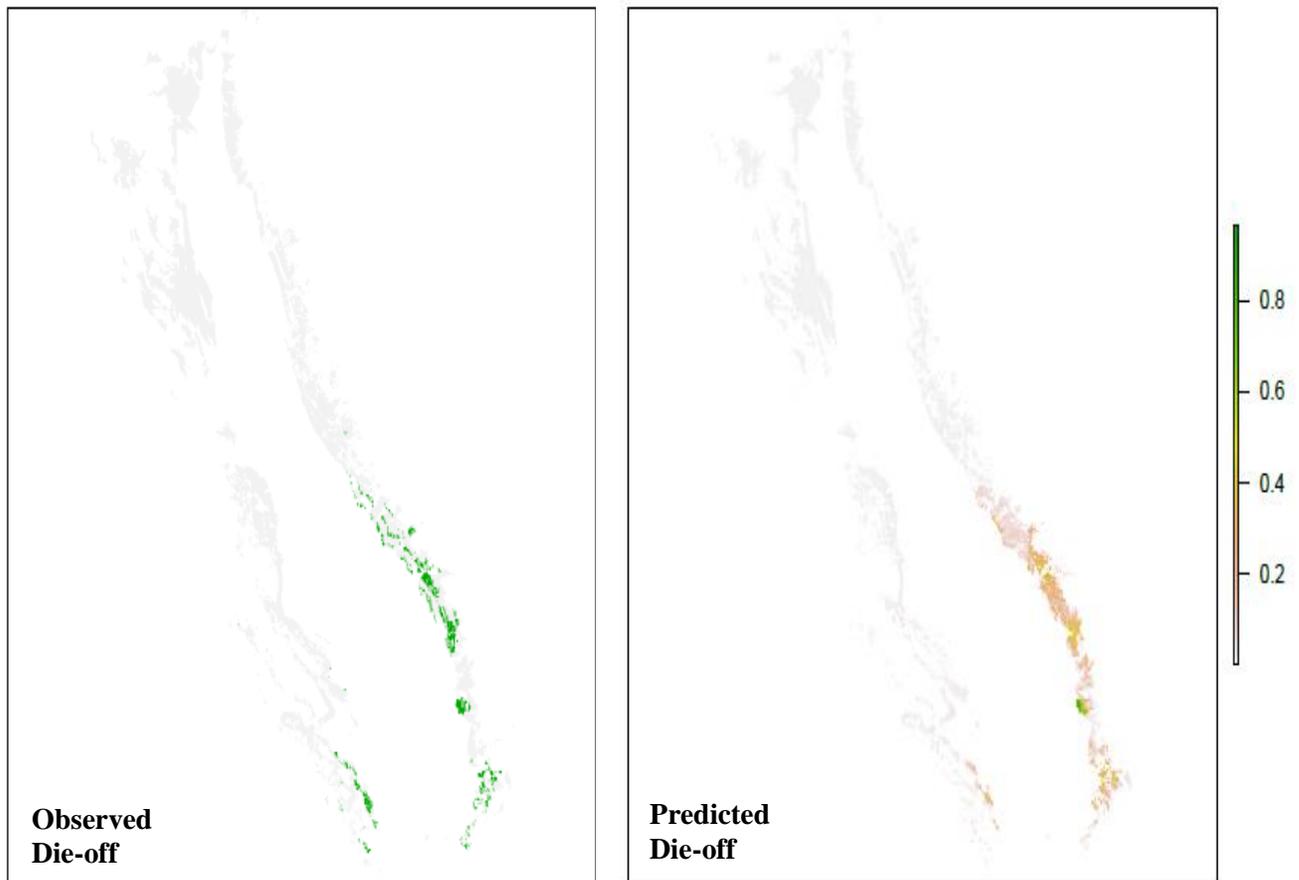
Figure 9: Full model fitted values of the blue oak distribution. Observed die-off on left, modelled die-off probability on right. Legend indicates confidence of die-off probability prediction.