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TREE MORTALITY IN BLUE OAK WOODLAND DURING EXTREME DROUGHT IN SEQUOIA NATIONAL PARK, CALIFORNIA

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ABSTRACT

Blue oak woodlands in California have been a focus of conservation concern for many years. Numerous studies have found that existing seedling and sapling numbers are inadequate to sustain current populations, and recent work has suggested that blue oak woodlands might be particularly vulnerable to a warming climate. California has recently experienced a drought of historically unprecedented severity, resulting in the mortality of tens of millions of trees, including an apparent spike in mortality in oak communities. Here we present the results of a survey of tree mortality and composition in blue oak woodlands in Sequoia National Park. We found that 18% (95% CI = 14–24,) of all standing trees and 23% (95% CI = 17–30) of standing *Quercus douglasii* Hook. & Arn. (blue oak) were dead, substantially higher than proportions of dead trees recorded in pre-drought datasets, which showed 4% (95% CI = 2–9) standing dead for all trees and 5% (95% CI = 4–7) dead or 8% (95% CI = 4–16) standing dead for blue oak. Furthermore, much of this mortality appeared to be recent. Based on foliage or fine twig retention, 19% (95% CI = 14–26) of blue oak and 23% (95% CI = 16–31) of *Quercus wislizeni* A. DC. (interior live oak) appear to have died recently. In contrast, only 5% (95% CI = 3–8) of *Aesculus californica* (Spach) Nutt. (California buckeye) and 5% (95% CI = 2–11) of *Fraxinus dipetala* Hook. & Arn. (California ash) appear to have died recently. Even after such high mortality, with blue oak basal area dropping by 26% (from 9.5 m^2/ha [95% CI = 7.4–11.6] to 7.0 m^2/ha [95% CI = 5.3–8.7]), blue oak remains the dominant species in these ecosystems. However, given the lack of recruitment and the apparent vulnerability to extreme drought, blue oak populations may be at risk for severe decline if such mortality events become more frequent.

Key Words: blue oak, drought, *Quercus douglasii*, tree mortality, Sequoia National Park.

Oak woodlands are an iconic part of the California landscape and have been a focus of conservation concern for many years (Waddell and Barrett 2005). In fact, hardwood forests in general comprise an estimated 40% of forested area in California and provide many benefits to the state, including grazing, forest products, biodiversity, and recreational opportunities. Blue oak woodland, which forms a peripheral ring around California's Central Valley, is the most common hardwood forest type, covering an estimated 1.23 million hectares (Waddell and Barrett 2005).

Numerous studies have noted an apparent lack of recruitment in blue oak woodlands, with seedling and sapling numbers seemingly inadequate to sustain existing populations (Bolsinger 1988; Swiecki et al. 1997; Waddell and Barrett 2005). Tree ring studies have supported this contention, finding little recruitment after an apparent regeneration peak in the mid-1800's and early 1900's (White 1966; McClaran and Bartolome 1989; Mensing 1992; Gervais 2006; Stahle et al. 2013). Although interpretation of the regeneration peak itself is somewhat complicated by a tendency for blue oak to resprout and by its variable and very slow height growth, there seems to be general agreement on the lack of adequate recruitment, at least in some areas, since that time (Mensing 1992; Swiecki and Bernhardt 1998; Koenig and Knops 2007; Stahle et al. 2013). Various explanations for this regeneration gap have been investigated, including fire suppression, competition from non-native annual grasses, grazing, and land use changes (McClaran 1986a, b; Gordon et al. 1989; Allen-Diaz and Bartolome 1992; Mensing 1992; Swiecki et al. 1993; Gordon and Rice 2000; Swiecki and Bernhardt 2002).

More recently, there has been heightened concern that blue oak might be at particular risk in a warming climate. Research suggests that suitable habitat for blue oak might shrink by over 50% by the end of the century, while also shifting northward (Kueppers et al. 2005). As with all forests, oak woodlands are likely to be vulnerable to the increasingly severe and potentially more frequent droughts that accompany warming temperatures (Brown et al. 2018). For example, reports indicate that the recent California drought (2012 through 2016) resulted in the mortality of over 100 million trees, including high levels of mortality in oak woodlands (Moore et al. 2017, 2018). The drought was the most extreme in the ~120-year instrumental record, partly as a consequence of the associated higher temperatures (AghaKouchak et al. 2014; Griffin and Anchukaitis 2014; Williams et al. 2015).

With recruitment lacking and the mature tree population suffering heightened mortality, the blue oak woodlands ecosystem merits particular attention. Yet, while there have been extensive examinations of recruitment and periodic surveys of blue oak woodland extent and overall changes in growing-stock volume (e.g., Waddell and Barrett 2005), there have been very few examinations of individual tree mortality through time and, to date, no detailed on the ground assessments of woodland mortality during the recent drought. Aerial surveys of mortality for blue oak are complicated by the species' adaptive habit of dropping foliage in response to drought, and, while the U.S. Forest Service aerial team did do a special survey of oaks in 2016 and 2017 to confirm increased mortality, the authors of those survey reports indicated that the special survey was not comprehensive and that levels of oak mortality were likely greatly under-reported (Moore et al. 2017, 2018).

In Sequoia National Park, blue oak woodlands are a prominent feature of the foothills portion of the park and represent an often understudied part of the park's landscape. During the drought, oak mortality in and around the park visibly increased, causing concern among park managers about the state of the ecosystem. Therefore, in 2017, we surveyed a representative sample of 30 plots distributed throughout the blue oak woodland alliance to estimate tree mortality during the drought and to capture the current species composition and size structure.

Here, we report the results of the survey and compare them with previous datasets from the park's blue oak woodlands. We find that mortality among oak species appears to have been high during the drought, while non-oak species appear to have been less affected. As a result, oak populations dropped more substantially than other species, but, given the large dominance of blue oak in these ecosystems, relative species structure and composition did not change dramatically.

METHODS

Site Description

Within Sequoia National Park, the blue oak woodland alliance is located in the foothills between 418 and 1462 m in elevation and occupies about 880 ha. The climate is Mediterranean, with hot, dry summers and cool, wet winters. Average annual precipitation is 66 cm, with a mean annual temperature of 17.4°C (Western Regional Climate Center 2018). About 240 ha (27%) of the woodland has been managed as a pasture since at least 1920 (Bartolome et al. 2016). Nine of our 30 sample plots (see below) were located in the pasture. Over the last century, 703 ha of the woodland has burned at least once, but only 22 ha have burned in the last two decades. These more recent fires were prescribed burns initiated by park staff to reduce fuels, generally for the purpose of protecting existing infrastructure. None of our data collection was located in these more recent burns. As an additional precaution, we examined whether there were any relationships between the numbers or proportions of standing dead and the time since last fire and found no significant results. Therefore, we did not consider fire further. Common tree species in the woodland include *Quercus douglasii* Hook. & Arn. (blue oak), *Quercus wislizeni* A. DC. (interior live oak), *Aesculus californica* (Spach) Nutt. (California buckeye), *Fraxinus dipetala* Hook. & Arn. (California ash), and *Cercocarpus betuloides* Nutt. (mountain mahogany).

Data Collection

In the spring of 2017, we surveyed 30 plots (hereafter referred to as 'drought plots') to provide an unbiased characterization of tree mortality, by species and size class, across the blue oak woodlands in Sequoia National Park. Our study area was defined as the blue oak woodland alliance (Fig. 1), as indicated by the park vegetation map. Plot locations were selected *a priori* using Generalized Random Tessellation (GRTS) sampling, which provides a spatially balanced sample that has a true probability design, allowing valid inference for the entire study area (Stevens and Olsen 2004). In the field, plot centers were determined using a proximity alarm on handheld GPS units, with the alarm sounding when proximity to the predetermined GRTS location was within the measurement error of the device. Plots were defined as the area within a 17.84 m horizontal radius (determined by electronic rangefinders) from these plot centers, yielding 0.1 ha sample areas. Precise plot locations were determined using a JAVAD Triumph-2 GPS unit that, after post-processing, determined actual locations with sub-meter accuracy. We attempted to sample 41 plots, but six plots could not be reached safely and five plots overlapped a road, leaving a total of 30 sampled plots for analysis. We failed to get precise GPS coordinate for two plots due

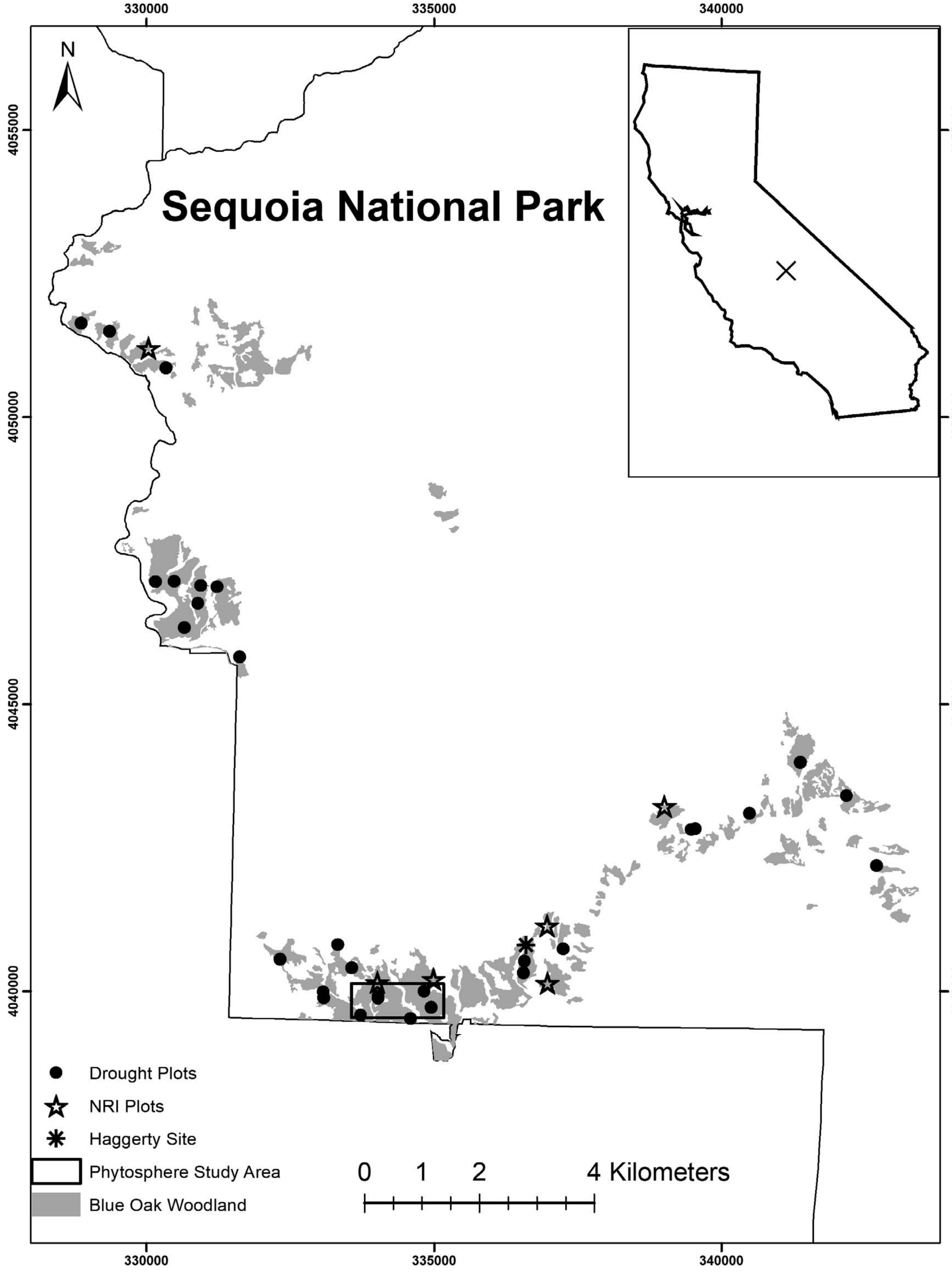

FIG. 1. Map of study area and study sites. Boundary shown on the larger map is the Sequoia National Park boundary. Coordinates are UTM, NAD83, Zone 11N.

to inadequate data collection. For the remaining 28 plots, our plot centers were never more than 10 m from the GRTS target, and the average difference in location was 5.3 m.

Within each plot, we surveyed live trees and standing dead trees that had a trunk diameter at breast height (1.37 m along the length of the trunk) of at least 2 cm. "Standing" was defined as any tree leaning less than 45 degrees from vertical and retaining at least 1.37 m of trunk length. For each tree, we recorded the species, trunk diameter at breast height (DBH; in 5 cm classes), and condition (living or dead). We defined a tree to include any stem that reached breast height regardless of whether it shared a base with another tree (i.e., structural individuals rather than genetic individuals). Dead trees were further classified according to foliage and fine twig retention to provide some indication of which trees had died more recently (see Table S1 in Supplemental Material). Samples sizes and frequency of occurrence (by plot) are given in Table S2.

Comparison Datasets

An issue with rapid 'snapshot' surveys of mortality is that, in the absence of tree rings, it is generally difficult or impossible to determine the exact year of death of standing dead trees, making it a challenge to determine with confidence whether a large number of standing dead trees represents high mortality or low rates of tree fall. Therefore, we identified three existing, pre-drought datasets with data on dead trees from blue oak woodlands in the park and used them for comparison with our drought plot data (Table 1). If drought mortality was high, we would expect the number of standing dead trees estimated from the drought plots to be substantially higher than the number of dead recorded prior to the drought.

Our most robust (in terms of sample size) pre-drought dataset was collected in 1992 as part of a statewide study on the status of blue oak sapling recruitment and regeneration (hereafter referred to as the Phytosphere dataset, after the name of the organization that collected the data). The study used 15 locations throughout the range of blue oak woodlands in California (Swiecki et al. 1993). One of those locations was in Sequoia National Park and was not only in our study area, but overlapped several of the drought plots that were in the pasture (Fig. 1). The Phytosphere data were collected inside a randomly placed sampling grid, which consisted of a series of parallel transects 100 m apart. Plots were placed at 80 m intervals along these transects until 100 plots had been sampled (Swiecki et al. 1993). Plots were circular with a 16 m radius (0.08 ha). Data collection was focused on seedlings and saplings, however, counts of live and dead blue oak trees were also collected, with a tree being defined as any individual at least 3 cm in DBH at 140 cm above ground level. The Phytosphere data included any dead tree that, based on wood degradation, appeared to have died in the last 30 years, regardless of whether it was standing. For this analysis, we have also included their 1 to 3 cm DBH sapling class (which was designated S3 in the Phytosphere data). The Phytosphere data provide a robust estimate of the proportion of dead blue oak in 1992 (although not by tree size).

TABLE 1. DATASET DESCRIPTIONS. Asterisk (*) indicates that only nine of the Haggerty Plots contained trees.

Dataset	Year	# of plots	Plot size (ha)
Drought Plots (Current Dataset)	2017	30	0.10
Phytosphere Plots	1992	100	0.08
NRI Plots	1986–1987	6	0.10
Haggerty Plots	1987	10*	0.05

Methods differed somewhat between our drought plots and the Phytosphere data. The Phytosphere protocol used a slightly taller definition of breast height (140 cm versus 137 cm) and, with the inclusion of the S3 class, a slightly smaller diameter cutoff (1 cm versus 2 cm). This probably results in a trivial overestimate of overall blue oak density relative to our drought plot data, as only 2 saplings fell in the S3 class for the entire Phytosphere dataset. Furthermore, as the drought plot dataset only included standing dead trees, the comparison with the Phytosphere set will be conservative with respect to detecting an increase in mortality during the drought.

The second set of pre-drought comparison data was from the Natural Resources Inventory (NRI) program, which was a park-wide survey of vascular plants in Sequoia and Kings Canyon National Parks (Graber et al. 1993). As part of the program, park staff installed circular, 0.1 ha plots throughout the parks near 1-km UTM grid intersections. Six of those plots fell inside our blue oak woodland study area and were surveyed in 1986 and 1987. As part of the survey, all standing trees, defined as stems at least 1.3 m in height, were recorded and measured for DBH to the nearest 1 cm. Live trees were identified to species, but dead trees were simply identified as 'snags'. These plots provide a pre-drought comparison of standing dead by size class (though not by species). Again, there is a small difference in the definition of breast height which could lead to small discrepancies between datasets.

The third comparison set was from data collected by P. K. Haggerty as part of a study to assess the damage and recovery of blue oak woodland after a wildfire in Sequoia National Park in 1987 (Haggerty 1991, 1994). As part of that study, she used a control site that had not burned. We use that site here as our pre-drought comparison. Data were taken in ten circular, 0.05 ha plots, only nine of which contained trees. In each plot, all standing live and dead trees at least 1.37 m in height were recorded, identified to species, and measured for DBH. Because of limited

Table 2. Percent Standing Dead By Foliage And Twig Retention Category For Drought Plots. Numbers in parentheses describe the 95% confidence interval of the estimate. The few unexpected small increases in percent of standing dead for the last column are due to changes in the estimation of the random plot effect. A '0' without confidence intervals indicates no dead trees in that sample.

Species	Size class (cm)	Any foliage or fine twig retention	Any foliage retention or fine twig retention in ≥⅓ of the canopy	Any foliage retention or fine twig retention in ≥⅔ of the canopy
Blue oak	All	18.9 (13.6 to 25.8)	16.6 (11.1 to 24.2)	15.7 (10.3 to 23.4)
	2–10	19.8 (9.7 to 36.2)	15.6 (6.7 to 32.0)	16.6 (7.2 to 34.0)
	10–20	17.8 (10.8 to 28.0)	15.4 (8.6 to 26.0)	13.6 (7.4 to 23.8)
	20–40	15.1 (9.7 to 22.8)	13.3 (7.9 to 21.4)	12.6 (7.4 to 20.6)
	≥40	30.1 (18.5 to 45.0)	26.8 (15.3 to 42.7)	26.3 (14.8 to 42.3)
Interior live oak	All	22.6 (15.9 to 31.1)	20.8 (13.6 to 30.5)	20.8 (13.3 to 31.0)
	2–10	13.6 (8.8 to 20.6)	12.1 (7.2 to 19.6)	11.8 (6.9 to 19.5)
	10–20	51.7 (36.4 to 66.7)	49.0 (32.5 to 65.7)	49.3 (32.4 to 66.4)
	≥20	46.6 (28.8 to 65.4)	46.1 (27.1 to 66.3)	46.9 (27.3 to 67.5)
California buckeye	All	4.6 (2.8 to 7.6)	1.7 (0.8 to 3.5)	1.1 (0.4 to 2.7)
	2–10	6 (3.5 to 10.2)	2.3 (1.0 to 5.0)	1.4 (0.5 to 3.5)
	10–20	2.6 (0.8 to 8.4)	1.8 (0.4 to 7.7)	1.8 (0.4 to 7.7)
	≥20	0.9 (0.1 to 6.8)	0	0
California ash	All	4.9 (2.1 to 11.1)	3.3 (1.2 to 8.8)	3.8 (1.3 to 10.2)
Other	All	10.5 (5.7 to 18.7)	9.4 (4.8 to 17.7)	9.9 (5.0 to 18.9)

sample sizes, we were only able to use blue oak for purposes of comparing mortality with our current dataset.

Analyses

In order to assess the level of mortality during the drought, we compared the number of dead trees between pre-drought datasets and our drought dataset. We also estimated the proportion of recent dead (based on foliage and twig retention) in the drought dataset. Finally, we examined apparent changes in species composition due to mortality during the drought.

We separately examined any species with at least 100 stems in our drought plot dataset, lumping the rest into an 'Other' category. To examine size structure and species composition, we divided the trees within a species into the following DBH classes: ≥2 and <10 cm, ≥10 and <20 cm, ≥20 and <40 cm, and ≥40 cm. We assessed composition within these species and size class combinations before and after likely recent mortality to examine drought induced changes in composition. For mortality analyses, we required a minimum of 30 trees within a species and size class. Therefore, when necessary, we lumped adjacent size classes for mortality analyses to achieve adequate sample sizes.

We estimated mortality (i.e., proportion of standing dead) using generalized linear mixed effect models with a binomial distribution and a logit link (i.e., a mixed effects logistic regression). Species or the combination of species and size class (with each species and size class combination considered as a separate category) were used as categorical predictors, and plot identity was used as the random effect. We estimated the proportion of standing dead for both all dead trees and for apparently recently dead trees. Recently dead trees were defined as those retaining any leaves or fine twigs (though we also analyzed the data using more strict definitions of recently dead as shown in Table 2). For other datasets, we only estimated all dead (Phytosphere dataset) or standing dead, as we did not have data on leaf or twig retention. Because information depth varied by dataset (e.g., size class, species identity), we performed additional analyses as necessary on our drought plot data in order to match those from the comparison sets.

We estimated the average species and size composition by fitting negative binomial models, with count of trees within a plot as the dependent variable and species or species and size class combination as categorical predictors. Due to the highly variable spatial structure of these woodlands, means and medians often differed substantially. For example, certain species occurred infrequently in our plots but, when they occurred, were present in high numbers (Table S2), leading to a relatively high average but a very low median.

All analyses were performed in R 3.1.1 using the *MASS* and *lme4* packages (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

All Dead

Our estimates of the proportion of standing dead trees in the drought plots, 18.4% (95% CI = 13.7–24.2) of all standing trees and 22.7% (95% CI = 17.0–29.5) of standing blue oak, were three to five times higher than estimates of dead trees from any of the pre-drought comparison datasets (Table 3, Table S3). This was also true within size classes (Table 3,

TABLE 3. PRE-DROUGHT MORTALITY COMPARISONS. The data in this table include all dead trees, rather than just those that still retain foliage and fine twigs (i.e., those that have likely died more recently). The numbers in parentheses are 95% confidence intervals. The Haggerty and NRI datasets included only standing dead trees. The Phytosphere dataset also included fallen dead trees. Asterisk (*) indicates a subset of landscape plots (six plots in total) that occur in or near the Phytosphere study area.

Pre-drought comparison dataset	Type of dead	Pre-drought dead (%)	Drought standing dead (%)
Phytosphere (all sizes)	Blue oak	5.2 (4.1–6.5)	22.7 (17.0–29.5) 25.7 (17.0–36.8)*
Haggerty (all sizes)	Blue oak standing	7.6 (3.4–16.2)	22.7 (17.0–29.5)
Haggerty (2–<20 cm)	Blue oak standing	4.4 (1.4–13.0)	26.4 (17.8–37.2)
Haggerty (≥20 cm)	Blue oak standing	15.2 (6.5–31.6)	23.4 (16.5–32.0)
NRI (all sizes)	All standing	3.9 (1.6–9.0)	18.4 (13.7–24.2)
NRI (2–<20 cm)	All standing	3.0 (0.7–11.2)	16.8 (12.3–15.3)
NRI (≥20 cm)	All standing	4.9 (1.6–14.2)	21.1 (15.3–28.0)

Table S4), with the exception of large blue oak in the Haggerty dataset where confidence intervals from our drought plots and pre-drought data overlapped. In the case of the Phytosphere data, we were also able to compare results against a subset of our drought plots that occurred within or near the Phytosphere study area and found our estimates for the proportion of standing dead trees, 25.7% (95% CI = 17.0–36.8), to be nearly five times Phytosphere estimates of dead trees from prior to the drought. This is an especially notable increase, given that the Phytosphere data included both standing and fallen blue oaks. These results are also consistent with numbers from two recently installed long-term monitoring plots in the park (Appendix 1), where the proportion of all standing dead were 34.2% (95% CI = 27.5–41.6) and 15.0% (95% CI = 11.6–19.2) and the proportion of blue oak standing dead were 34.0% (95% CI = 27.4 41.4) and 20.4% (95% CI = 16.7–24.7).

Recently Dead

Since our pre-drought standing dead estimates are from data collected two to three decades prior to the drought, an alternative explanation for the increase in standing dead might be a more gradual accumulation of standing dead over a period of many years rather than a spike during the recent drought. While this seems unlikely, as it would also imply a substantial change in the fall rate of dead trees, we also analyzed standing dead for our drought plots based on foliage and twig retention, as trees that retain foliage and twigs presumably died more recently. If we restrict our analysis only to live trees and dead trees that have retained foliage or fine twigs (Table 2, Fig. 2), we find that the numbers of standing dead are still high relative to pre-drought datasets, with 14.0% (95% CI = 9.7–19.9) of all trees being recently dead. For oak species, recently dead trees account for 18.9% (95% CI = 13.6–25.8) and 22.6% (95% CI = 15.9–31.1) of standing blue oak and interior live oak respectively (Fig. 2, Table 2, Table S3). Recent mortality was also high among 'Other' species (10.5% [95% CI = 5.7–17.7] of standing stems), driven primarily by mortality in canyon live oak (*Quercus chrysolepis* Liebm.), which is at the lower end of its elevational range in blue oak woodland and occurs only rarely. In contrast, only 4.6% (95% CI = 2.8–7.6) of California buckeye and 4.9% (95% CI = 2.1–11.1) California ash trees appear to have died recently.

For blue oak, interior live oak, and California buckeye, our sample sizes of more recently dead trees were large enough for analyses by size class. Recent blue oak mortality was high across all size classes, with a higher average mortality rate in trees greater than 40 cm DBH (Fig. 3, Table S4), although there is considerable overlap in the confidence intervals among size classes. Interior live oak had substantially higher mortality rates for trees greater than 10 cm in DBH. California buckeye had low mortality across the size classes, with some indication of decreasing

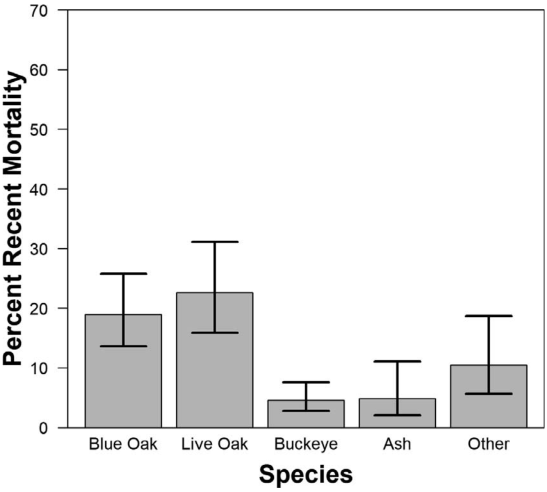

FIG. 2. Percent recent mortality by species in the drought plots, obtained by restricting the drought plot dataset to live trees and recently dead trees. Recently dead trees were defined as standing dead trees that retain foliage or fine twigs. Error bars are 95% confidence intervals.

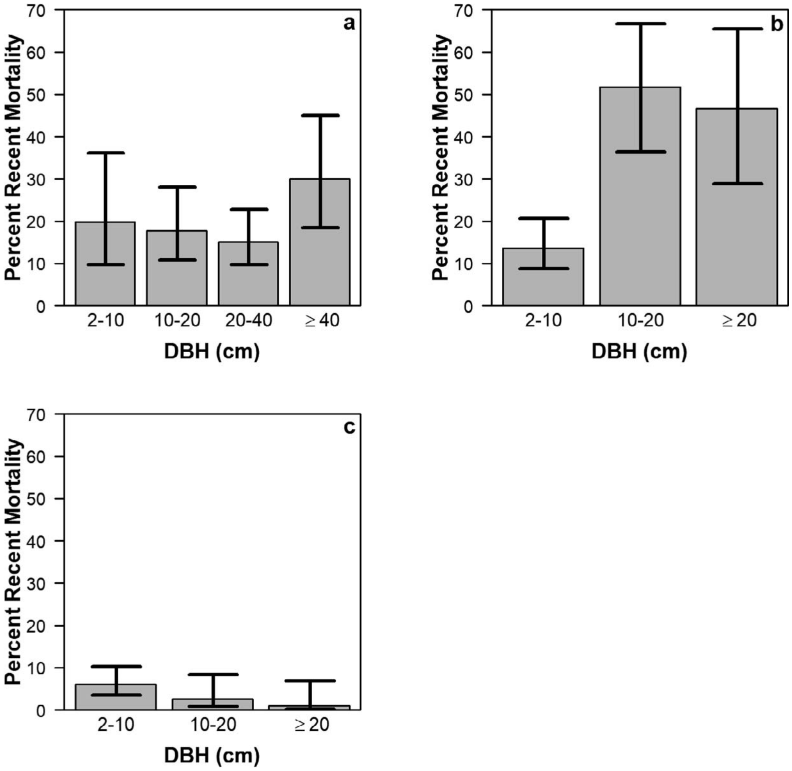

FIG. 3. Percent of recent mortality by size class for a) blue oak; b) interior live oak; and c) California buckeye. Error bars are 95% confidence intervals. Estimates were obtained by only considering live and recently dead trees in the drought plot dataset. Recently dead trees were defined as standing dead trees that retain foliage or fine twigs.

mortality with size. However, any size-related trends in buckeye mortality are obscured by the relatively large confidence intervals for this species.

These numbers do not change substantially if we further restrict our sample to standing dead that either retain foliage or retain at least ⅓ or ⅔ of their fine twigs (Table 2), again suggesting that a majority of the standing dead trees have died recently. In addition, these results are consistent with estimates from our recently installed long-term plots, where we find a similarly high occurrence of standing dead blue and live oak with foliage and fine twig retention (Appendix 1, Fig. S1).

Species Composition and Size Structure

Unsurprisingly, blue oak dominates these woodlands in basal area (Fig. 4, Table S5), with most blue oak stems being in the ≥20 to <40 cm size class (Fig. 5, Table S6). This dominance remains even after the substantial apparent losses due to mortality during the drought, with average blue oak basal area in our drought plots dropping by 26%, from 9.5 m^2/ha (95% CI = 7.4–11.6), when including live and recently dead trees, to 7.0 m^2/ha (95% CI = 5.3–8.7), when only including live trees.

While the average number of interior live oak and California buckeye are higher than the average number of blue oak (Fig. 4, Table S5), their stems tend to be small (Fig. 5, Table S6) and occur only in rare, dense patches, hence the large disparity between mean and median densities for these species. In contrast, small blue oak are found only rarely (Fig. 5). Overall, median blue oak density is much higher than all other species combined. Importantly, in this study, we counted structural individuals (ramets) rather than genetic individuals (genets), and many of the interior live oak, California buckeye, and California ash stems are from small clumps of stems that originate from the same base.

DISCUSSION

Mortality

Aerial surveys suggest that recent drought mortality in the blue oak woodlands of California has been high (Moore et al. 2017). Our data in Sequoia National Park bear out that assessment, indicating far higher numbers of dead trees after the onset of the drought than prior to it, with nearly 20% of standing blue oak apparently having died recently. Mortality rates appear to have been even higher among interior live oak, while other major woodland species appeared less affected.

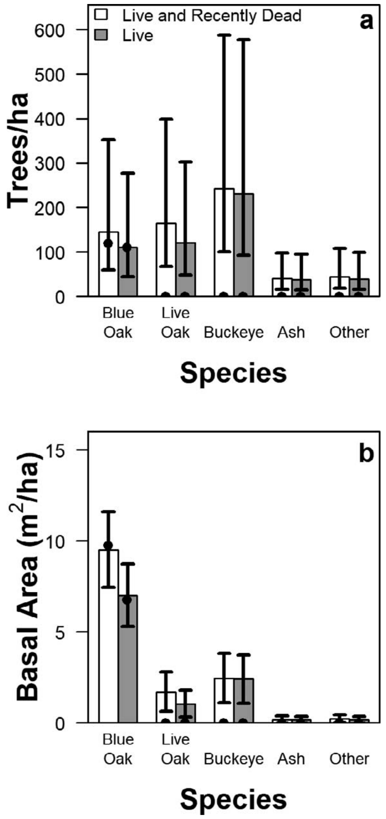

FIG. 4. Blue oak woodland composition, including a) average density and b) average basal area by species for living and recently dead trees combined and living trees alone. Recently dead trees are defined as those dead trees that retain foliage or fine twigs. The combination of living and dead trees can be considered as an estimate of living trees prior to drought mortality. Error bars are 95% confidence intervals. Black dots are medians.

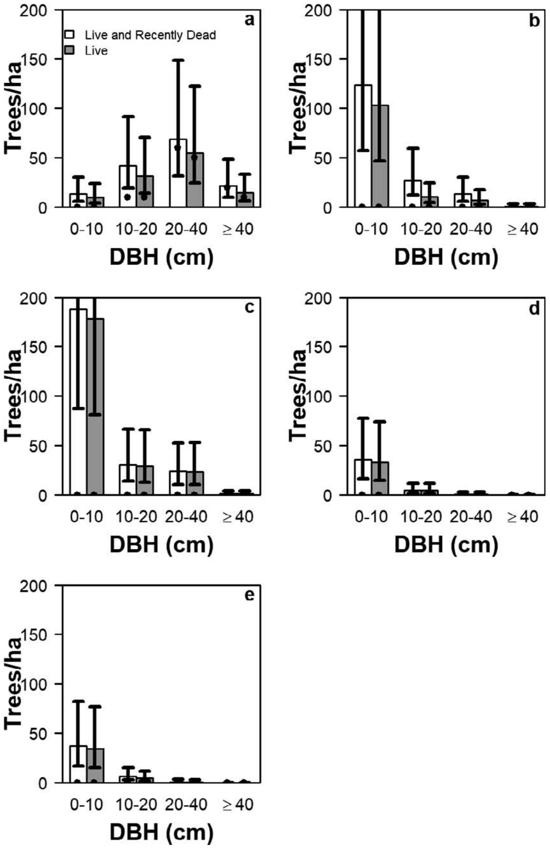

FIG. 5. Average density by size class for live and recently dead trees combined and live trees for a) blue oak, b) interior live oak, c) California buckeye, d) California ash, and e) Other species (see main text), as estimated from the drought plots. Recent mortality is defined as standing dead trees that retain foliage or fine twigs. Error bars are 95% confidence intervals. Black dots are medians.

This assessment is further supported by blue oak woodland data from other parts of California, which show that blue oak woodlands typically had much smaller pre-drought populations of dead trees than we found in our drought plots. For example, for all 15 sites from across California in the full Phytosphere dataset (Swiecki et al. 1993), dead blue oak varied between 2.3% and 10.8% of all trees, with an average of 5.9%, even including both fallen and standing dead. This compares to 25.7% for our drought plots, which only include standing dead. A nest site study at the San Joaquin Experimental Range in the Sierra Nevada in the 1980s reported 1.1% and 1.2% of standing trees with a DBH $>$ 8 cm (all species) were dead in their two plots (Waters et al. 1990), and another habitat study in San Luis Obispo, CA in 1995 found that standing dead comprised between 6.7 and 8.8% of standing trees with DBH $\geq$ 5.1 cm (Tietje et al. 1997). These numbers compare to 19.7% or 23.9% for lower size limits of 5 cm and 10 cm respectively in our plots. Finally, in a recent study on the effect of mistletoe on California oaks (Koenig et al. 2018), of a set of 257 blue oak trees, mostly greater than 20 cm DBH and all of which had been tracked since at least 1999, only 6 trees (2.3%) had died as of 2016, suggesting a low mortality rate over a long time period. However, the results do not indicate high mortality among these sample trees during the drought.

Overall, the weight of evidence strongly suggests that the recent drought has dramatically increased (probably quadrupling) the number of dead trees in blue oak woodlands in Sequoia National Park, particularly among oak species.

Surprisingly, our estimates of mortality for the other relatively abundant species, California buckeye and California ash, were much lower than for oak species. Unfortunately, we are not aware of any other studies assessing mortality or relative drought tolerance for buckeye and ash. In the case of ash, the lack of apparent response may be a tendency for the species to prefer riparian areas, perhaps biasing occurrence to parts of the landscape with higher moisture availability. That said, our sample size for ash was modest, and the species only occurred in 5 of our 30 plots (Table S2). Therefore, our ash mortality estimates should be treated with some caution.

For buckeye, we had a robust sample (794 trees), and the species occurred in over 40% of our plots, making our estimates of mortality less prone to sampling error. Furthermore, there was little visual evidence of elevated mortality among buckeye in the park generally. This suggests that buckeye may simply be more drought tolerant than either of the oak species, though such a determination would require further research.

Composition

Recent mortality has clearly reduced the biomass and density of blue oak and interior live oak in the woodlands at Sequoia National Park (Fig. 4). Nonetheless, even accounting for mortality, blue oak remained the dominant species by basal area and, for trees >10 cm DBH, by density. In contrast, and in keeping with the well-documented lack of recruitment for blue oak in blue oak woodlands generally, smaller size classes were dominated by other species, both before and after the drought.

While our analyses focused on standing dead trees, estimates of overall composition from all the Sequoia National Park datasets we used were fairly consistent. Estimates of blue oak densities from the Phytosphere, Haggerty, and NRI datasets were 159 trees/ha, 212 trees/ha, and 98 tree/ha respectively, all well within the uncertainty range of the density estimates of live and recently dead trees from our landscape dataset (Fig. 4). These estimates are also consistent with the data used to develop the vegetation map in the parks, which gave an estimate for blue oak density of 115 trees/ha. We did not use this last dataset in our main analysis because it lacked information on dead trees. Note that, as described in the Methods, there are small differences in DBH cutoffs among our datasets, which in some circumstances can result in large differences in density estimates. That said, for blue oak, due to the low abundance of saplings and smaller trees, these small discrepancies in DBH cutoffs are unlikely to have had a substantial effect.

All of these results are in stark contrast to those reported by Vankat and Major (1978) and Roy et al. (1999), who estimated average blue oak densities in the park at 600 trees/ha or more. This is well outside the 95% confidence interval of our estimate of average density from our data and is, in fact, outside the entire range of densities from our plots (Fig. 4b). Moreover, the estimate differs substantially from those obtained from every other dataset collected in blue oak woodlands in the park. This difference is almost certainly a result of a bias in the Vankat and Major (1978) and Roy et al. (1999) datasets, including possible 'majestic forest bias' and a bias in their sampling design (Appendix 2).

Conclusions

Our surveys suggest that a substantial percentage of canopy blue oak in Sequoia National Park died during the drought, and, given indications from aerial data, this is likely a pattern repeated in many blue oak woodlands, particularly in the southern half of their distribution in California (Brown et al. 2018). But while the mortality was substantial and particularly concentrated within oak species in our study area, this has not changed the general character of the woodland. Blue oaks still dominate our study landscape, and the large majority of trees survived. In other words, drought mortality, while dramatic, has not led to type conversion, at least in the short term.

However, in the longer term, such mortality events may have important consequences. As documented above, there is ample evidence that blue oaks are not regenerating at a rate that can sustain existing populations, even without massive losses. Our results indicate that nearly a fifth of the blue oaks in Sequoia National Park may have died during the drought, without much prospect for replacement. If such droughts occur with increased frequency (e.g., Allen et al. 2010) and without a concomitant increase in regeneration, blue oaks could decline in prominence.

How the effects of increased drought frequency and severity play out across the range of blue oak woodlands will likely vary by locale. The blue oak stand at Sequoia National Park was among the most xeric of the 15 blue oak locations included in the Phytosphere data, due to a combination of high insolation, low soil available water holding capacity, and high evapotranspiration relative to annual precipitation (Swiecki et al. 1993). In xeric locations, blue oak regeneration tends to be restricted to the most mesic sites, such as north-facing slopes, patches of deeper soil, and wetter topographic positions (Swiecki and Bernhardt 1998). Changes in climate that further increase evapotranspiration or result in longer and more severe droughts are likely to further limit the likelihood that gaps created by overstory blue oak mortality will be filled by blue oak advance regeneration. The expected result is that blue oak would continue to decline at xeric locations such as this. In more mesic locations, blue oak recruitment is more likely to be limited by dense canopies of competitors, such as interior live oak, and tends to be restricted to more xeric sites where competition with less drought-tolerant species is reduced. In mesic locations, especially in the wetter northern portion of its range, blue oak may have more opportunities for recruitment in a warmer and drier climate if its less drought tolerant competitors are suppressed. Furthermore, the recent drought was most severe in the southern part of the blue oak range (e.g., Williams et al. 2015), so drought-related mortality may also be less intense in more mesic locations.

Blue oak woodlands are an important and iconic part of the California landscape. Our work here, combined with decades of previous work on blue oak regeneration, support the contention that these ecosystems may be particularly vulnerable in a warming climate. Going forward, it behooves us to give these woodlands increased attention, including effective and consistent monitoring of adult trees. Such information is likely to be critical not only for understanding changes in these woodlands, but also for informing management decisions, whether intended to boost resilience in these systems or to facilitate change.

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APPENDIX 1

LONG-TERM MONITORING PLOTS

While several research and monitoring projects have been located in blue oak woodlands over the history of Sequoia National Park, no ongoing or systematic assessment of the woodlands' conditions had been conducted in many years. To help fill this gap, in addition to the drought plots described in the main text, we established two 2.25-ha permanent plots (named 'BOF' and 'DOP') that will be used for long-term population monitoring and as a venue for citizen science. These plots were not randomly located. Instead, we chose accessible locations with an abundance of blue oak. Both plots are located in Sequoia National Park's pasture area (see Methods). Accessibility was critical to ensure that long-term monitoring is feasible, especially given that much of the future monitoring may rely on volunteers. We chose areas with abundant blue oak so that we had an adequate population for tracking trends. For the BOF plot, average slope was 8.4°, ranging from 2° to 21°, and average aspect was 171°, ranging from 3° to 348°. For the DOP plot, average slope was 13.5°, ranging from 3° to 25°, and average aspect was 118°, ranging from 0° to 352°. Slope and aspect were obtained using GIS layers provided by Sequoia National Park.

The long-term plots are square, with 150 m sides (errors in mapping resulted in the plots deviating modestly from perfect squares). Mapping of plot boundaries and trees was accomplished using the GPS and rangefinder on a Trimble Geo 7X handheld with a Zephyr Model 2 antenna. Every living tree inside the plot boundaries with a diameter at breast height (DBH) $\geq$ 2 cm was tagged, mapped, measured for diameter, and identified to species. In addition, in order to provide a comparison between the long-term and our drought plots, we surveyed all the standing dead trees using the same protocol as within the drought plots. Going forward, long-term plots will be visited every year to check for mortality and to map and measure recruitment. Trees that die will be evaluated for factors associated with mortality (e.g., beetles, fungal pathogens, suppression), and we will record any conditions on live trees that might contribute to future mortality (see Das et al. 2016). Every five years, every living tree will be re-measured for diameter.

In order to compare mortality and composition between our drought and long-term plots, we needed to describe variability within the long-term plots in a way that was comparable to the 0.10 ha drought plots. This required subdividing each long-term plot into smaller subunits. As there is not a simple method for splitting a 150 m X 150 m plot into precisely 0.10 ha plots without excluding a substantial portion of the plot or resorting to very odd combinations of plot shapes, we instead split each long-term plot into twenty-five 0.09 ha square subplots (30 m x 30 m). These subplots vary in size somewhat, as the established plots were not precisely square, but all of the subplots deviate by less than 10% from 0.09 ha.

Mortality patterns in the long-term plots reflected the broader landscape pattern indicated by the drought plots. For the BOF and DOP plots respectively, the proportion of all standing dead were 34.2% (95% CI = 27.5–41.6) and 15.0% (95% CI = 11.6–19.2), and the proportion of blue oak standing dead were 34.0% (95% CI = 27.4%–41.4%) and 20.4% (95% CI = 16.7–24.7). Likely recent mortality (including trees with foliage or fine twig retention) was also high for blue oak in the long-term plots, with a mean of 30.1% at BOF and 18.5% at DOP (Fig. S1a). In the DOP plot, where sample sizes of California buckeye and California ash were adequate for analysis, we found low mortality rates (0.8% and 2.0% respectively, Fig. S1a), in keeping with the pattern on the broader landscape. Mortality of 'Other' species was very high (33.3%, Fig. S1a) in the DOP plot, even compared to the broader landscape, and this high mortality was entirely within the population of mountain mahogany in the plot. Sample sizes of interior live oak were too small to analyze formally in either long-term plot, but 35% of the 40 interior live oak stems that occurred in the long-term plots were dead. Mortality of blue oak was high across size classes (Fig. S1b), although sample sizes in the smallest and larger size classes were limited.

Both of our long-term plots have higher blue oak densities and basal areas than our estimates for the landscape as a whole from the drought plots (Figs. S2 and S3), although variability across the landscape and within the long-term plots is large. As with the drought plots, our long-term plots are dominated by blue oak, with most of the blue oak concentrated in the middle size classes (Fig. S4). Live oak and other species occurred less frequently in our plots than the landscape as a whole, with the BOF plot being nearly exclusively populated by blue oak. The DOP plot had a relatively high concentration of California ash compared to the landscape, but California ash was still a small component of the overall species composition.

Overall, the similarity in mortality patterns between our long-term and drought plots suggest that these plots might serve as reasonable representatives of mortality rates as they are monitored into the future. However, they are probably not effective guides to species composition or changes in species composition through time. Not surprisingly, given our selection criteria, blue oaks appear to be more dense in the long-term plots than the landscape as a whole, and other, smaller-stature species occur less frequently than the average.

Nonetheless, the long-term plots should serve as excellent sentinels for detecting large-scale changes in blue oak populations (particularly increases in mortality rate), and, as venues for citizen science, they have already demonstrated great potential, with National Park Service staff already leading several volunteer groups to measure and re-measure tree diameters. At the very least, they can serve as a key component in an effective monitoring program of blue oak woodlands at Sequoia National Park.

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APPENDIX 2

BIAS IN VANKAT AND MAJOR (1978) AND ROY ET AL. (1999) DATASETS

Blue oak density estimates from Vankat and Major (1978) and Roy et al. (1999) are almost certainly gross overestimates, given the large disparity between their estimates and those from all other blue oak woodland datasets collected in the park. The cause of this overestimation is probably due in part to "majestic forest bias", since the Vankat plots were placed subjectively and such placement can easily fall prey to choosing locations with higher than average densities (e.g., Phillips et al. 2004). Simply placing plots to include several blue oak trees– instead of the single tree that they might have expected with random placement of their 0.01 ha plots– would lead to large overestimates, since each additional tree would add 100 trees per hectare.

In addition, there is a bias in their sampling design that would be synergistic with a majestic forest bias. Vankat and Major (1978) and Roy et al. (1999) used band transects to estimate density, including any tree "rooted" inside the transect, regardless of whether the center of the tree fell within the transect and without any procedure for eliminating overestimation due to such "boundary trees". For example, in order to avoid overestimates, it is common practice to only include boundary trees on one side of the transect (i.e., half the boundary trees) or to only include boundary trees whose center falls within the plot. Lacking such procedures could easily lead to large overestimates, given, as noted above, that each extra tree adds 100 trees per hectare to their estimates. Being 2 m by 50 m, their transects had a high edge to area ratio and therefore would have been particularly prone to including edge trees.

Roy et al. (1999) acknowledge the sampling bias, suggesting that it might lead to "slight" overestimates of basal area, but they provide no explanation for why they think the bias would be slight. In fact, the basal area estimates provide an additional clue. Vankat and Major (1978) report basal area estimates obtained by using wedge prisms, a plotless estimator that would not be subject to edge bias. They reported a basal area estimate of 11.85 m^2/ha for blue oak in blue oak woodlands in 1969, which is consistent with our own basal area estimates (Fig. 4, main text). Roy et al. (1999), however, calculated basal area using plot data, including recalculating it for the Vankat and Major (1978) data from 1969. This recalculation gave an estimate of 21 m^2/ha, nearly double the prism estimate for the same time period.

Unfortunately, one would expect these biases throughout their dataset, making their estimates of density unreliable for all forest types in the parks.

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