

Communication

Drought Impacts and Compounding Mortality on Forest Trees in the Southern Sierra Nevada

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Abstract: The increase in compounding disturbances, such as “hotter droughts” coupled with insect outbreaks, has significant impacts on the integrity of forested ecosystems and their subsequent management for important ecosystem services and multiple-use objectives. In the Southern Sierra Nevada, years of severe drought have resulted in unprecedented tree mortality across this mountainous landscape. Additionally, past land management practices, including fire suppression, have led to overly stocked, homogenous forest stand structures, dominated by small diameter, shade-tolerant and fire-intolerant tree species. Thus, the current condition of the landscape has further increased the susceptibility of forest trees to multiple stressors. We sought to determine the effects of extreme drought and insect outbreaks on tree mortality and their influence on forest stand structure and composition. To characterize mortality patterns, we monitored the condition of mature forest trees (>25.4 cm diameter at breast height) across 255 monitoring plots with four repeated measurements from 2015 through 2017. Tree mortality varied by species and through time. Reductions in pine species (*Pinus lambertiana* Douglas and *P. ponderosa* Lawson & C. Lawson) occurred earlier in the study period than *Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr. or *Calocedrus decurrens* (Torr.) Florin. Across species, larger tree size, most often associated with tree height, was consistently related to increased survival in mature, overstory trees. As expected, sites with greater pine stocking and subsequently more bark beetle (Curculionidae: Scolytinae) host availability had increased pine mortality, especially for *P. ponderosa*. For *Abies concolor*, lower overstory basal area increased tree survival for this species. This study highlights the importance of effective forest monitoring, especially during a period of unprecedented ecological change as the compounding disturbance had a disproportional effect on pine species in smaller diameter classes. Proactive forest management may be necessary to maintain and promote these ecologically important species in heterogeneous mixtures across the landscape.

Keywords: Ponderosa pine; Sugar pine; White fir; Red fir; California black oak; Incense-cedar; Collaborative Forest Landscape Restoration Project; adaptive management; monitoring

1. Introduction

Globally, the increasing frequency, severity, and duration of drought due to climate change has a significant impact on forested communities [1–3]. Impacts of drought can be local or transcend landscapes [4–8]. The effects can range from stressed trees that are more susceptible to secondary mortality to wholesale shifts in forest structure, composition, and function [2]. Extensive tree mortality on public lands may impact recreational activities, threaten human safety, change ecological conditions, diminish sensitive wildlife habitats, and increase fire hazard and risk. Although drought is a natural disturbance in many forested ecosystems, exceptional drought events are becoming more frequent and severe with increasing global temperatures and the interaction of stressors [9]. Determining the role of factors contributing to tree mortality may aid forest management prioritization as droughts become more recurrent and severe.

In the western US, drought-induced stand replacement mortality events are becoming commonplace [10]. Additionally, drought associated with warmer annual minimum temperatures, and longer, hotter summers are highly correlated with bark beetle (Curculionidae: Scolytinae) outbreaks [11]. In particular, from 2012 through 2016, California experienced an episode of prolonged, extreme drought [5,12], followed by a wet winter in 2016–2017 that was well above seasonal averages. In contrast, the 20th century was characterized as an unusually wet period in the dendrochronological record in the Southern Sierra Nevada range [13], with the lack of snow (snow water equivalent) in 2015, unprecedented in the past 500 years [14]. Additionally, warming climate trends and the associated “hotter drought” during the period of 2012–2016 was considered to be unprecedented in the previous 1200 years or more [15]. Although the recent wet winter was able to reverse the drought status, the Sierra Nevada mountain range had already experienced rapid increases in tree mortality, with over 129 million dead trees in California in 2016 [16]. Moreover, although rainfall amounts eased drought conditions, moisture stress from a warmer climate will continue to persist in this region due to increasing atmospheric demand.

Drought and bark beetle outbreaks that result in tree mortality are natural disturbance processes in the mixed-conifer forests of the Sierra Nevada [17]. However, human activities (e.g., fire exclusion, historic logging) have greatly altered these communities, resulting in changes to forest composition and structure, including a higher representation of fire-sensitive and shade-tolerant species (e.g., *Calocedrus decurrens* (Torr.) Florin and *Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr., higher stand densities, and increased stand homogenization [18,19]. These conditions result in greater mortality rates than were seen historically or in recent decades [19,20]. For example, tree size is often correlated with drought induced mortality, and large trees are consistently cited as more prone to mortality during drought across a wide range of forest types and topographic conditions [21], in part owing to the tendency of bark beetles (such as western pine beetle, *Dendroctonus brevicornis*; or mountain pine beetle, *D. ponderosae*) to target larger diameter pines [22,23]. In addition, high stand densities are often associated with increased tree mortality, especially on low quality sites [21,24], such as those with higher climatic water deficit. Stands dominated by a relatively higher host density of pines may be more prone to insect attack, especially if the stands are even-aged [22]. In many cases, forest management (e.g., silvicultural manipulation) that substantially reduce stand densities can decrease moisture stress in coniferous forest ecosystems, leading to increased rates of tree survivorship and growth [25]. However, climatic events, such as severe drought and subsequent insect outbreaks, may supersede or dampen the effects of site level treatments.

Effective monitoring programs are critical to adaptive management, especially with alterations in the structure, composition, and function of forests from compounding disturbances. Monitoring is an important component of any adaptive management process and functions to advise future action, including forest management decision-making and priority setting. This is particularly evident when science is slow to provide data-driven strategies under rapidly changing environmental conditions, such as recent landscape-scale tree mortality event in California.

By 2014, bark beetle induced mortality was evident in the Southern Sierra Nevada on *Pinus ponderosa* Lawson & C. Lawson and *P. lambertiana* Douglas at lower elevations (~1220 m). At the onset of the rapid

increase in tree mortality, monitoring plots were established in early 2015 to assess drought impacts to forest structure and composition within the Dinkey Collaborative Forest Landscape Restoration Project (Dinkey CFLRP). These monitoring plots were re-inventoried four times over the course of two years (2015–2017), providing a rare opportunity to observe the impact of drought to forest trees as it occurred. Prior to extensive tree mortality, collaborative restoration activities focused on reducing the density of smaller diameter, shade-tolerant, and fire-sensitive species and promoting shade-intolerant, more fire-tolerant pine species (i.e., *Pinus ponderosa* and *P. lambertiana*) through green tree thinning, fuels reduction, and prescribed surface fire to create stand and landscape heterogeneity largely based on topographic and landscape position [26]. An essential monitoring question of the collaborative focused on changes in forest composition and structure with the tree mortality event.

The objectives of this study were to evaluate the effects of compounding drought- and insect-induced tree mortality in the Southern Sierra Nevada. We sought to characterize: (1) overstory mortality by species; (2) changes in overall stand structure and composition; and (3) the factors associated with survival during the initial onset of mortality from compounding disturbances and after drought conditions were alleviated.

2. Materials and Methods

2.1. Study Site

The study took place on the High Sierra Ranger District of the Sierra National Forest within the Dinkey Collaborative Forest Landscape Restoration Project (CFLRP) boundary (Figure 1). The Sierra National Forest is located in the southern Sierra Nevada mountain range of California. The Dinkey CFLRP is located approximately 60 miles (95 km) east of Fresno, California. The landscape-level collaborative project was established in 2010 and was one of the first projects funded by Title IV of the Omnibus Public Land Management Act of 2009 and lies entirely within the High Sierra Ranger District [27]. Climate in this area is characterized as montane Mediterranean, with warm dry summers and cool wet winters. Most precipitation falls from October to April with 70% falling as snow [28]. Soils are in the Gerle–Cagwin families association with a coarse, sandy loam texture, low clay content and water holding capacity, and well-drained, Holland families association with a fine loam texture. Both families are developed primarily from granitic parent material [29].

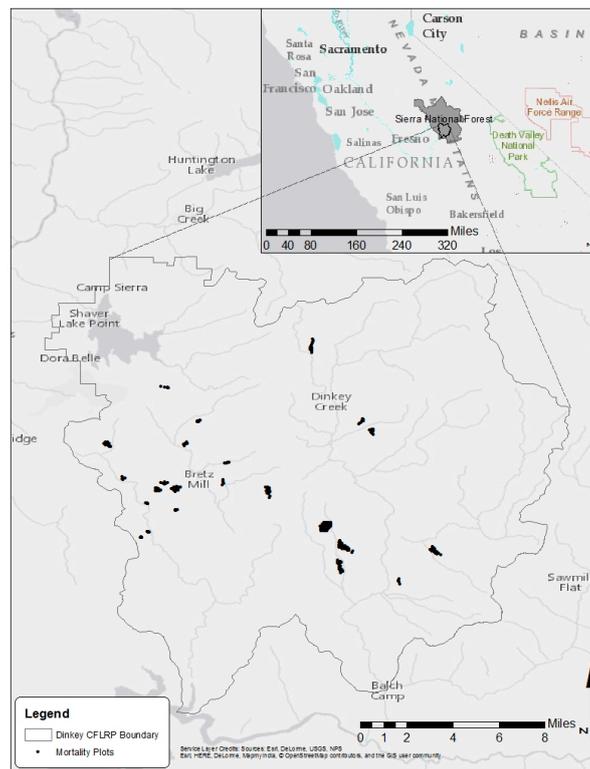


Figure 1. Map of the 255 mortality plot locations measured four times from 2015 through 2017 within the Dinkey Collaborative Forest Landscape Restoration Project (CFLRP). The Dinkey CFLRP resides entirely within the Sierra National Forest in the Southern Sierra Nevada of California.

2.2. Plot Establishment and Field Measurements

Forest monitoring plots were established in stands outside any recent or active management areas, stratified by forest type, and observed mortality classes based on 2015 USDA Forest Service, Forest Health Monitoring aerial detection surveys (ADS). We divided the ADS data into five mortality classes (low to very high) based upon a visual assessment of dead trees per hectare. We limited plot selection to the elevational range of *P. ponderosa* and mixed conifer zones. Potential polygons with more than 10% tree cover were included in the selection tool. This process identified 24 polygons for measurement ranging in size from 2 to 38 hectares. A randomly placed grid was used to identify plot locations within each of the polygons. This process yielded 255 plots.

In the spring of 2015 (SPR15), plots were established using a 40-factor angle gauge prism. Although fixed-area plot sampling is preferable for repeated measurements in scientific design, this study was originally established for rapid assessment monitoring by forest managers and was subsequently expanded once overstory mortality in the region became an increasing concern. In the summer of 2015 (SUM15), we permanently tagged trees greater than 25.4 cm in DBH (diameter at breast height) that were contained in the variable-radius plots and recorded each for DBH (cm), height (m), species, and status (dead or alive). Height was determined using a laser range finder and rounded to the nearest half meter. We re-assessed survivorship of each individual in the summer of 2015 (SUM15), the summer of 2016 (SUM16), and the summer of 2017 (SUM17).

2.3. Mortality by Species and Size

For analysis, we only included overstory trees greater than 25.4 cm in DBH (referred to hereafter as ‘overstory’). We only included overstory trees because as they are mostly of reproductive size, dominant or co-dominant trees, represent the minimum DBH usually impacted by bark beetles, and they are of high interest to forest managers in the region. The range of the monitored overstory trees reflected

their general size distribution within the southern Sierra Nevada (Table 1). We also excluded species with an insufficient sample size, resulting in only *A. concolor*, *A. magnifica* A. Murray bis, *C. decurrens*, *P. lambertiana*, *P. ponderosa*, and *Quercus kelloggii* Newberry being included in analysis. Changes in trees per hectare by measurement time and species was modeled using stand-level averages analyzed with a repeated-measures SAS GLIMMIX procedure (SAS Institute Inc., Cary, NC). The distribution of the response variable (trees per hectare) was assessed for normality prior to analysis and was subsequently fit with a negative binomial discrete response variable distribution within the GLIMMIX model. Using the SAS UNIVARIATE procedure, the residuals were tested visually for normality and using Shapiro–Wilk and Levene’s homogeneity of variance test statistics. We assessed the change in plot-level proportional composition from SPR2015 to SUM17 with a one-way ANOVA. Effects were considered significant if $p \leq 0.05$ and means and standard errors are reported in their original units. Mean tree DBH and height by species of survivors in overstory were compared in SPR15 and SUM17 using PROC GLM.

To assess our third objective, to determine factors predicting overstory mortality by species in SPR15 and SUM17, we used individual tree characteristics produced by field measurements (tree height (HGT), tree DBH) and stand variables. Specifically, measures of competition and host density including total trees per hectare (TPH), basal area of overstory trees (BA), and the proportion of basal area in overstory pines (PINE). A logistic regression model with a binary response variable for survivorship (0 dead, 1 alive) for the first and last measurement times was fit using the SAS GLIMMIX procedure. An individual tree was nested within plot as a random factor in the logistic model. Mortality in SPR15 included all measured individuals. For SUM17, we excluded individuals that were recorded as dead in the prior measurement periods allowing for analysis on the variables with potential influence on survivorship in SUM17. Each p -value less than 0.05 was considered evidence of a significant factor in survivorship.

Table 1. The original number of overstory study trees (greater than 25.4 cm in diameter at breast height (DBH)) and the mean (\bar{n}) number of trees per plot recorded in Spring 2015 (both dead and alive) by species and monitored from 2015 to 2017. Tree measurements include their mean (SD) DBH (cm), height (m), average plot trees per hectare (TPH), average plot basal area per hectare (m^2/ha ; BA), and elevation range recorded (m) across 255 plots within the Dinkey Collaborative Forest Landscape Restoration Project of the Southern Sierra Nevada.

Species (Species Code)	<i>n</i>	Plot \bar{n} (Range)	DBH (cm)	Height (m)	TPH	BA (m^2/ha)	Elevation (m)
<i>Abies concolor</i> (ABCO)	451	1.90 (0–15)	65.9 (19.8)	31 (10)	141 (139)	31.1 (20.5)	1190–2255
<i>Abies magnifica</i> (ABMA)	37	0.16 (0–9)	81.1 (33.2)	37 (14)	140 (125)	41.3 (26.0)	2100–2255
<i>Calocedrus decurrens</i> (CADE)	220	0.93 (0–8)	61.4 (26.8)	23 (9)	91 (83)	16.7 (10.9)	915–2040
<i>Pinus lambertiana</i> (PILA)	107	0.45 (0–5)	91.2 (31.5)	37 (12)	36 (40)	13.8 (8.1)	1160–2195
<i>Pinus ponderosa</i> (PIPO)	316	1.33 (0–11)	68.0 (24.6)	33 (11)	91 (90)	20.9 (16.8)	915–1950
<i>Quercus kelloggii</i> (QUKE)	73	0.31 (0–3)	59.6 (21.4)	17 (6)	86 (89)	14.1 (6.7)	915–2070

3. Results

Species responded differently through time. Reductions in density from 2015 to 2017 were significant by species ($F = 11.9; p < 0.01$), time ($F = 8.7; p < 0.01$), and the interaction of species by time ($F = 3.3; p < 0.01$) with the exception of both *A. magnifica* and *Q. kelloggii*, which remained stable from 2015 through 2017 (Figure 2). The greatest net reductions were in the smallest diameter size classes (Figure 3). However, although mean DBH and height did increase for some species, no species differed significantly in tree size from SPR15 to SUM17 (Table 2).

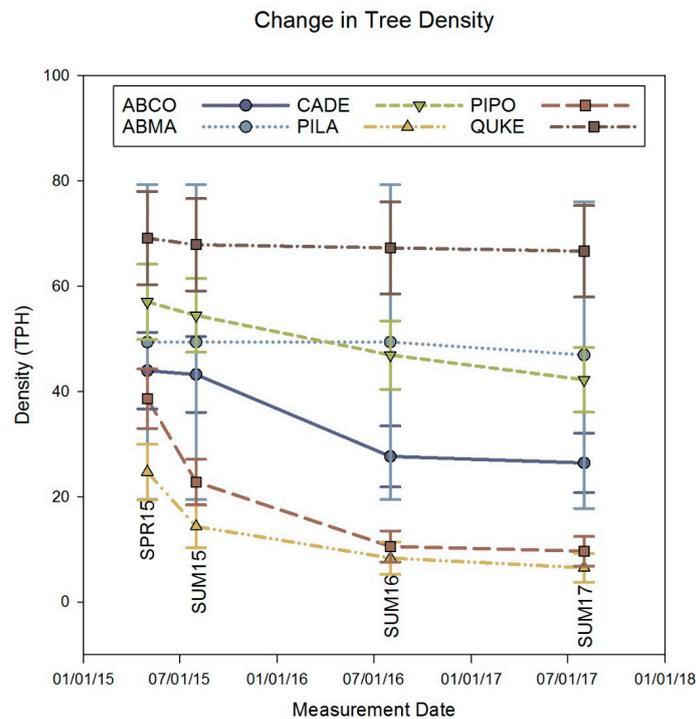


Figure 2. Mean (\pm 95% confidence interval (CI)) overstory (>25.4 cm DBH) density (trees per hectare) by species from Spring 2015 through Summer 2017 recorded across 255 plots in the Southern Sierra Nevada. Measurement periods refer to: SPR15—Spring 2015; SUM15—Summer 2015; SUM16—Summer 2016; and SUM17—Summer 2017.

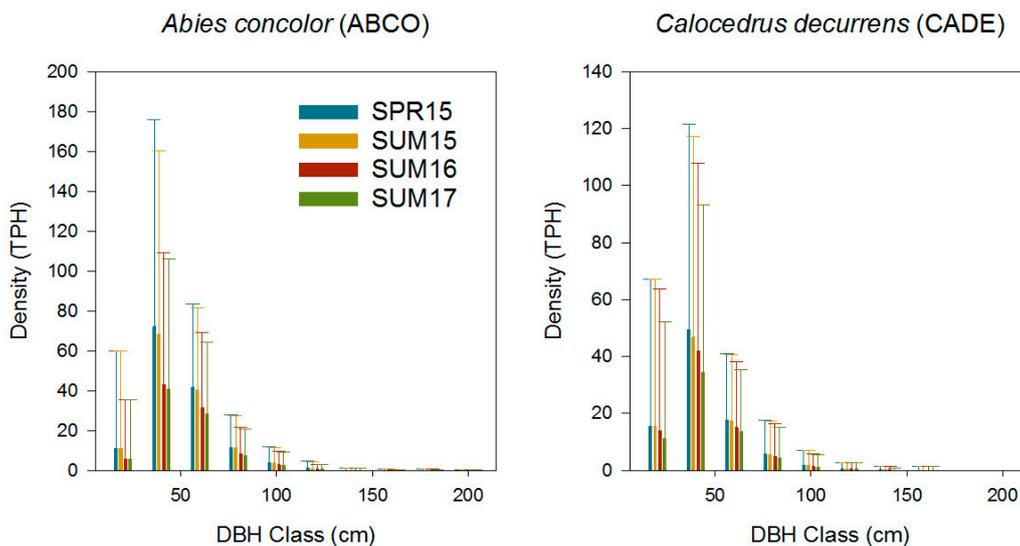


Figure 3. Cont.

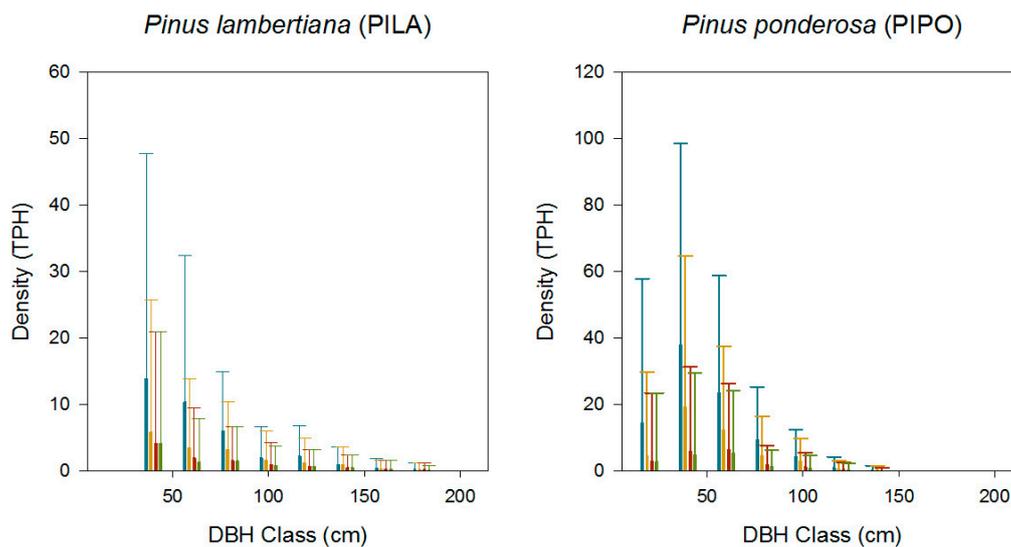


Figure 3. Diameter distribution (20 cm diameter classes) by species recorded as alive in Spring 2015 (SPR15—blue bar), Summer 2015 (SUM15—gold bar), Summer 2016 (SUM16—red bar), and Summer 2017 (SUM17—green bar) in the Southern Sierra Nevada.

Table 2. Mean and standard deviation (range) of DBH and height for living overstory trees (>25.4 cm DBH) in spring 2015 and summer 2017. DBH and height were not statistically different between measurement periods for any subject.

Species ¹	<i>n</i>		DBH (cm)		HEIGHT (m)	
	2015	2017	SPRING 2015	SUMMER 2017	SPRING 2015	SUMMER 2017
ABCO	372	237	64.5 ± 26.9 (26.9–203.7)	68.1 ± 25.9 (26.9–198.6)	32 ± 9 (10–58)	32 ± 9 (10–57)
ABMA	36	34	84.3 ± 38.9 (30.5–154.7)	84.6 ± 39.4 (30.5–154.7)	37 ± 14 (13–70)	37 ± 14 (13–70)
CADE	205	154	62.5 ± 28.5 (25.7–160.5)	63.5 ± 29.0 (25.7–160.5)	24 ± 9 (8–49)	24 ± 9 (8–49)
PILA	69	23	91.2 ± 36.3 (36.1–176.5)	105.2 ± 38.6 (36.1–173.5)	40 ± 11 (19–60)	45 ± 11 (21–60)
PIPO	228	44	68.3 ± 25.7 (27.2–149.3)	71.6 ± 26.2 (27.2–127.5)	34 ± 11 (13–65)	34 ± 10 (19–63)
QUKE	69	66	58.4 ± 24.6 (26.7–152.1)	58.9 ± 24.9 (26.7–152.2)	17 ± 6 (4–37)	17 ± 6 (4–37)

¹ABCO = *Abies concolor*; ABMA = *Abies magnifica*; CADE = *Calocedrus decurrens*; PILA = *Pinus lambertiana*; PIPO = *Pinus ponderosa*; QUKE = *Quercus kelloggii*.

3.1. *Abies Concolor*

Between SPR15 and SUM15, there were no significant reductions in the density of *A. concolor* ($t = 0.19$; $p = 0.85$; Figure 2). However, mortality increased from SUM15 to SUM16 ($t = 3.69$; $p < 0.01$), with no additional reductions in white fir density from SUM16 to SUM17 ($t = 0.33$; $p = 0.74$). The proportion of *A. concolor* plot-level composition from 2015 (0.56 ± 0.03) to 2017 (0.49 ± 0.03) was non-significant ($F = 1.7$; $p = 0.18$). In SPR15, survivorship increased with increasing tree height (Figure 4; Table 3) and decreasing overstory basal area (Figure 5; Table 3). However, although survivorship decreased more than 20% with DBH, it was non-significant. In SUM17, height was positively associated with survivorship. Similar to SPR15, lower initial stand basal area (Figure 5; Table 3) was associated with increased survivorship. DBH ($p = 0.91$) and the proportion of pine ($p = 0.92$) stocking did not influence *A. concolor* survival.

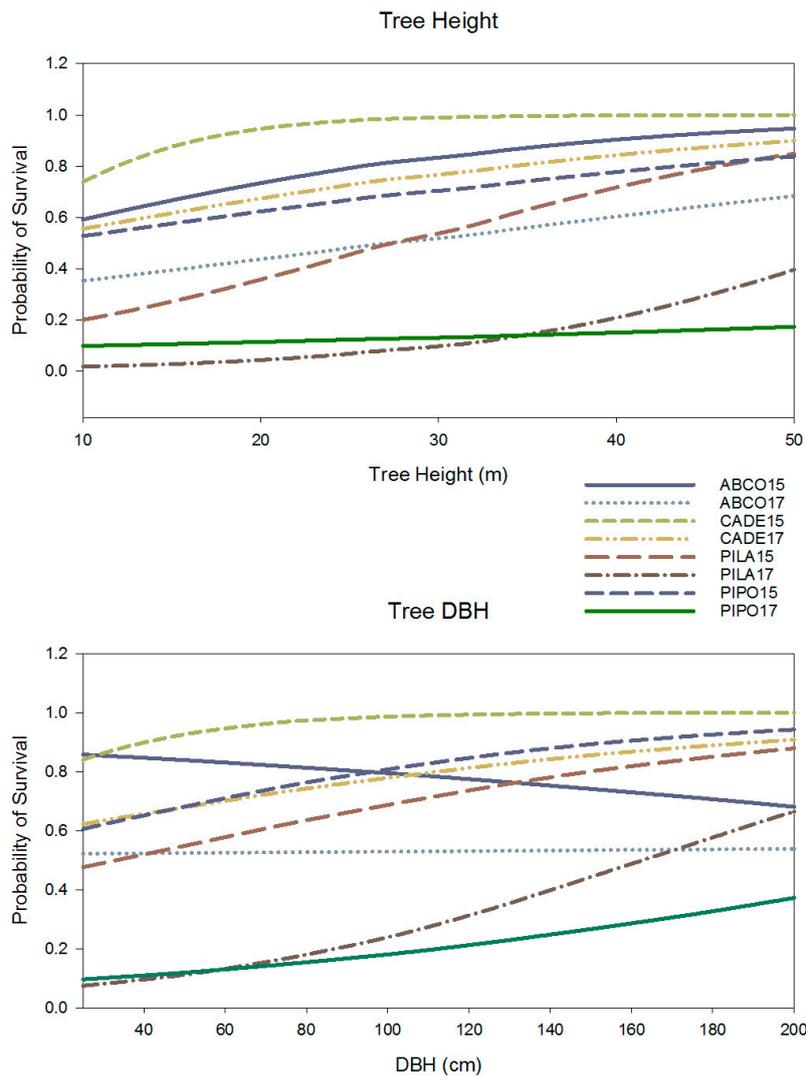


Figure 4. Probability of survival by species based on logistic regression for individual tree height (upper insert; m) and tree DBH (lower insert; cm) in Spring 2015 and Summer 2017 in the Southern Sierra Nevada. *Abies concolor*, ABCO; *Calocedrus decurrens*, CADE; *Pinus lambertiana*, PILA; *Pinus ponderosa*, PIPO.

Table 3. Logistic model estimates (HGT = tree height; DBH = tree diameter at breast height; BA = basal area per hectare of overstory trees; PINE = proportion of overstory pine in basal area) and model *p*-values for the probability of survival in the Spring of 2015 (SPR15) and Summer of 2017 (SUM17) by species. Number of individuals (*n*) includes both living and dead trees surveyed during that measurement period. Values in highlighted in bold are significant at a *p*-value less than an alpha of 0.05.

Spring 2015									
Species ¹	<i>n</i>	HGT		DBH		BA		PINE	
		estimate	<i>p</i> -value	estimate	<i>p</i> -value	estimate	<i>p</i> -value	estimate	<i>p</i> -value
ABCO	451	0.0193	< 0.001	−0.0151	0.1684	−0.0041	< 0.001	0.3112	0.6160
CADE	220	0.0552	< 0.001	0.0905	0.0080	−0.0052	0.0232	−1.1009	0.3247
PILA	107	0.0239	< 0.001	0.0302	0.0450	0.0005	0.7557	−0.4358	0.6148
PIPO	316	0.0118	0.0011	0.0108	0.0085	0.0040	0.0012	−0.7481	0.1181
Summer 2017									
ABCO	259	0.0106	0.0004	0.0009	0.9119	−0.0016	0.0275	0.0455	0.9214
CADE	177	0.0151	0.0045	0.0260	0.0648	0.0010	0.4276	−0.4724	0.4559
PILA	26	0.0272	< 0.001	0.0466	0.0046	0.0045	0.0326	−1.4459	0.1843
PIPO	57	−2.3702	0.2606	0.0250	0.1110	0.0025	0.0852	−3.0229	< 0.001

¹ABCO = *Abies concolor*; CADE = *Calocedrus decurrens*; PILA = *Pinus lambertiana*; PIPO = *Pinus ponderosa*.

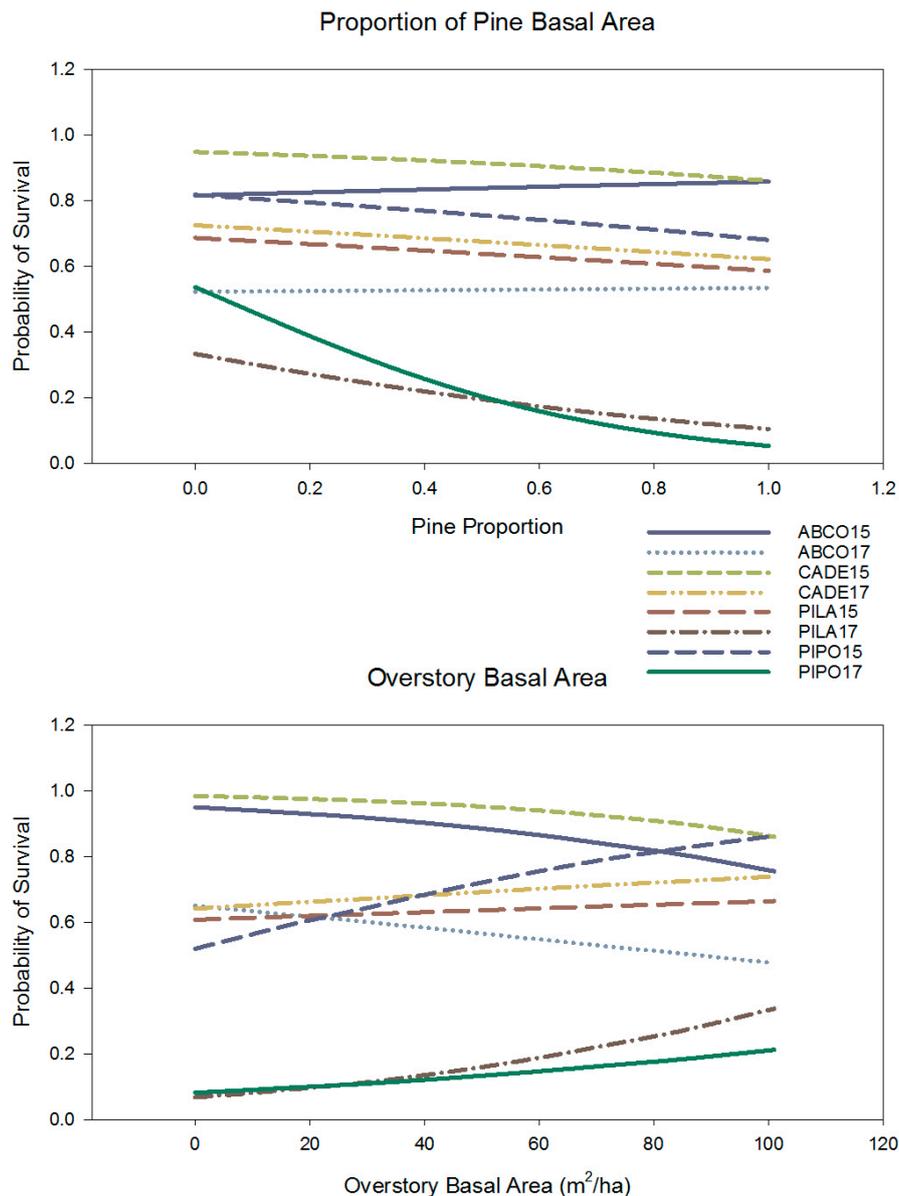


Figure 5. Probability of survival by species based on logistic regression of plot level proportion of pine overstory basal area (upper insert; scaled from 0.0–1.0, with 1.0 equally all basal area in pine) and total overstory basal area (lower insert; m²/ha) in Spring 2015 and Summer 2017 in the Southern Sierra Nevada. *Abies concolor*, ABCO; *Caleocedrus decurrens*, CADE; *Pinus lambertiana*, PILA; *Pinus ponderosa*, PIPO.

3.2. *Calocedrus Decurrens*

Overall, there were significant reductions in the density of *C. decurrens* from the initial measurement time in SPR15 to the final measurement in SUM17 ($t = 2.3$; $p = 0.02$); however, between measurement times, mortality was not significant. Similar to *A. concolor*, the proportion of *C. decurrens* plot-level composition between 2015 (0.51 ± 0.03) and 2017 (0.51 ± 0.03) was non-significant ($F = 0.0$; $p = 0.91$). In SPR15, increasing tree height (Figure 4; Table 3) and DBH were associated with tree survival. In addition, individual sites with lower overstory basal area had greater probability of survival (Figure 5; Table 3). Similarly, in SUM17, increased tree height (Figure 4; Table 3) was associated with survival. However, in SUM17, increasing DBH (Figure 4; Table 3) and basal area per hectare (BA; Figure 5) were not associated with survival. The proportion of pine stocking was not influential for *C. decurrens* survival in either SPR15 or SUM17 (Figure 5; Table 3).

3.3. *Pinus Lambertiana*

Pinus lambertiana density declined initially from SPR15 to SUM15 ($t = 2.55$; $p = 0.01$) with additional reductions from SUM15 to SUM16 ($t = 2.14$; $p = 0.03$). Those that survived to SUM16 remained stable until SUM17 ($t = 1.04$; $p = 0.30$). Plot-level proportional composition of *P. lambertiana* was not statistically significant between 2015 (0.15 ± 0.03) and 2017 (0.10 ± 0.03) ($F = 1.5$; $p = 0.22$). In SPR15, increasing tree height (Figure 4; Table 3) and DBH were positively associated with survival. However, increasing basal area and decreasing pine proportion (Figure 5; Table 3) were not significant factors associated with survivorship. In SUM17, *P. lambertiana* survival was positively associated with increasing tree height (Figure 4; Table 3), DBH, and BA (Figure 5). The negative association of the portion of pine stocking in SUM17 was non-significant (Table 3).

3.4. *Pinus Ponderosa*

Pinus ponderosa had similar initial reductions in density as *P. lambertiana* with significant mortality from SPR15 to SUM15 ($t = 4.8$; $p < 0.01$) and additional mortality from SUM15 to SUM16 ($t = 4.66$; $p < 0.01$). However, those that remained in SUM16 remained stable to SUM17 ($t = 0.51$; $p = 0.61$). At the plot-level, the proportional contribution of *P. ponderosa* to overall composition was significantly greater in 2015 (0.39 ± 0.03) than in 2017 (0.17 ± 0.03) ($F = 24.7$; $p < 0.01$). In SPR15, increasing tree height (Figure 4; Table 3), DBH, and BA (Figure 5) were positively associated with tree survival. Initially in SPR15, the proportion of pine was not associated with survivorship. However, by SUM17, the proportion of pine stocking was negatively associated with tree survival (Figure 5; Table 3). In contrast to SPR15, by SUM17, height, DBH, and BA were not significant factors in tree survival (Table 3).

4. Discussion

Most drought-related tree mortality studies occur following drought, or with large gaps in time between sampling, not as the mortality was unfolding. This short-term monitoring study provided a rare opportunity to study individual tree mortality as drought progressed, despite limitations inherent to monitoring progressive tree mortality. For example, given the design, we were unable to elucidate whether changes in tree status (live versus dead) were the result of morphological or physiological changes in response to severe drought, insect attack that likely contributed to the high levels of pine mortality, increased water stress associated with regional climate warming, or some combination of these mortality agents. However, in an era of novel and compounding disturbances, effective and long-term monitoring networks will be an important component of adaptive forest management.

In the Sierra Nevada Mountains, drought and tree mortality are highly correlated [30]. Based on our monitoring data, species differed in their susceptibility to mortality both temporally and by tree characteristics. Across species, a positive relationship between tree size and survival was consistent among our study species. Guarín and Taylor [30] reported that across sites tree mortality was greater for small and intermediate size classes (5 to 45.7 cm DBH) than for large (> 45.7 cm DBH) trees, except for *P. ponderosa*. Similarly, in terms of TPH, trees from smaller diameter classes, were disproportionately impacted throughout the mortality event and as tree size increased, survivorship also increased. Interestingly, other studies from the region report that stands with a greater mean diameter of *P. ponderosa* and *P. lambertiana* experienced greater levels of tree mortality than stands with smaller diameter pines [25], suggesting that tree mortality patterns may be scale-dependent. Further, since we were able to track mortality annually with individual tree data, the factors related to individual survivorship year to year may be different from those including all mortality across years [31]. Being tall was more consistently associated with survivorship than larger tree diameter across species. In Mediterranean climates, ontogenetic life stage may determine susceptibility of mortality from drought; larger trees were less prone to drought-related death while seedlings experienced greater mortality [21,32,33]. In addition, greater mortality of smaller diameter *C. decurrens* following the drought may be attributed to lower drought tolerance in small-diameter stems, possibly due to sunscald of this shade-tolerant species following overstory canopy mortality [34], or increased activity of cedar

bark beetles (*Phloeosinus* spp.) that appeared to target smaller stems as their numbers increased with progressing drought.

Both pine species were dramatically impacted during the short timeframe from May to August 2015, continuing into 2016, whereas *A. concolor* and *C. decurrens* mortality occurred later. Although both species are considered drought intolerant in comparison to *P. lambertiana* and *P. ponderosa* [35], bark beetles likely were the major contributor to the rapid initial mortality in both pine species especially in the medium to large (≥ 25 cm DBH) size classes [36]. This shift in tree species composition impacted by insects is consistent from previous intensive droughts [37,38], and the proportion of pine stocking was most influential on *P. ponderosa* survival in our study.

High densities of host tree species are associated with high levels of mortality from insect outbreaks. This is due to increased intraspecific competition and greater available breeding space and habitat for tree insects. The reduced pine mortality on sites with increased BA in our study could be attributed to more productive sites supporting greater BA and increased species diversity. Especially in higher-elevation, mixed conifer stands, increased buffering from moisture stress on productive sites and lower host densities may help to reduce drought effects and pine mortality. Climate change is also expected to affect bark beetle outbreaks with warmer winter weather associated with higher populations [22] and increased climatic water deficit may result in reduced defense mechanisms to bark beetle attack [39,40]. Zhang et al. [41] reported that stands exceeding a stand density index (SDI) of 202 (or approximately 12.1 m² of basal area) experienced significant bark beetle mortality. Preisler et al. [42] suggest that due to the extreme drought, a higher proportion of mortality is likely driven by drought than bark beetles alone, but areas affected by mortality prior to the drought ('beetle pressure') were highly correlated to subsequent mortality in neighboring areas.

Using the resilience approach suggested by Millar et al. [43] and Scott et al. [44], which includes promoting patterns of high structural and compositional spatial heterogeneity [45], the results of our study can help guide forest management in drought-prone forest ecosystems. First, larger trees had higher initial survivorship, so stand density management prior to the onset of the drought that accelerates large tree height and diameter growth may increase stand resistance to future droughts and moisture stress. This would require sufficient reductions in stand densities to levels within the natural range of variation [19] to reduce the risk of compounding disturbance on *P. ponderosa* and *P. lambertiana* [25]. Second, promoting mixed species stands to reduce host density and increase stand and landscape heterogeneity could further increase stand resistance and resilience to future droughts and insect attacks, especially in stands dominated by *P. ponderosa*. In addition, drought-tolerant *Quercus* species may have a greater role in the resilience of mixed conifer forests. Further, reforestation and thinning treatments may need to be altered and locations planned based on abiotic conditions. Lastly, as the frequency and duration of drought events are expected to increase with climate warming, approaches to forest management will need to adapt to changing ecological conditions. Our study highlights the importance of integrating repeated, systematic monitoring into adaptive forest management, especially with increasing stressors and environmental change.

5. Conclusions

In our study, tree species, such as *P. ponderosa*, were severely impacted by the compounding disturbances of drought and bark beetle outbreaks. However, the surviving *P. ponderosa* overstory trees may also have drought-tolerance traits that could be important for recruitment. Increased overstory basal area and the proportion of pine stocking were also indicative of higher mortality, especially for pine species. Prioritizing reductions in stand density prior to drought may help to alleviate individual tree stress. Additionally, tree diversity at the stand level may reduce the impact of bark beetles on pine species by reducing the proximity of available host species. Management to promote more heterogeneous stand structures and composition, including reducing the proportion of basal area occupied by pine, may provide increased resilience to drought and related stressors.

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