

Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. [☆]



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ABSTRACT

Much of California, U.S. experienced a severe drought in 2012–2015 inciting a large tree mortality event in the central and southern Sierra Nevada. We assessed causal agents and rates of tree mortality, and short-term impacts to forest structure and composition based on a network of 11.3-m fixed-radius plots installed within three elevation bands on the Eldorado, Stanislaus, Sierra and Sequoia National Forests (914–1219, 1219–1524 and 1524–1829 m on the Eldorado, Stanislaus, Sierra; 1219–1524, 1524–1829, and 1829–2134 m on the Sequoia), where tree mortality was most severe. About 48.9% of trees died between 2014 and 2017. Tree mortality ranged from $46.1 \pm 3.3\%$ on the Eldorado National Forest to $58.7 \pm 3.7\%$ on the Sierra National Forest. Significantly higher levels of tree mortality occurred in the low elevation band ($60.4 \pm 3.0\%$) compared to the high elevation band ($46.1 \pm 2.9\%$). Ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., exhibited the highest levels of tree mortality (89.6%), with 39.4% of plots losing all *P. ponderosa*. Mortality of *P. ponderosa* was highest at the lowest elevations, concentrated in larger-diameter trees, and attributed primarily to colonization by western pine beetle, *Dendroctonus brevicomis* LeConte. About 89% of *P. ponderosa* in the three largest diameter classes were killed, representing loss of an important structural component of these forests with implications to wildlife species of conservation concern. Sugar pine, *P. lambertiana* Dougl., exhibited the second highest levels of tree mortality (48.1%). Mortality of *P. lambertiana* was concentrated in the mid-diameter classes and attributed primarily to colonization by mountain pine beetle, *D. ponderosae* Hopkins. White fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., and incense cedar, *Calocedrus decurrens* (Torr.) Florin, exhibited 26.3% and 23.2% mortality, respectively. Only one *Quercus* died. Tree mortality (numbers of trees killed) was positively correlated with tree density and slope. A time lag was observed between the occurrence of drought and the majority of tree mortality. Tree regeneration (seedlings and saplings) was dominated by *C. decurrens* and *Quercus* spp., representing a potential long-term shift in composition from forests that were dominated by *P. ponderosa*. About 22.2% of plots contained plant species considered invasive, including cheatgrass, *Bromus tectorum* L., ripgut brome, *Bromus diandrus* Roth, bull thistle, *Cirsium vulgare* (Savi) Ten., and yellow star-thistle, *Centaurea solstitialis* L. The implications of these and other results to recovery and management of drought-impacted forests in the central and southern Sierra Nevada are discussed.

1. Introduction

Much of the western slope of the Sierra Nevada experiences a “Mediterranean-type climate”, indicative of an annual dry period characterized by hot, dry summers followed by an annual wet period characterized by cool, moist winters. While droughts have had an important influence on this region for millennia (Cook et al., 2007), the

most recent drought (2012–2015) was characterized by large precipitation deficits and abnormally high temperatures during both the wet and dry seasons (Aghakouchak et al., 2014; Williams et al., 2015), and in some areas is thought to be the most severe in 1200 years (Griffin and Anchukaitis, 2014). In particular, 2014 is noted for the lowest Palmer Drought Severity Index recorded for 1895–2017, when instrumental records were widely available (www.ncdc.noaa.gov/cag/). The

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2012–2015 drought resulted in progressive canopy water stress of at least 888 million trees and severe canopy water stress of at least 58 million trees (Asner et al., 2016), substantial mortality of dominant and co-dominant trees (Brodrick and Asner, 2017), and impacts to many ecological goods and services. The level of tree mortality observed is considered by some to be unprecedented (Stephens et al., 2018), and over time will influence the frequency and severity of other disturbances. For example, Stephens et al. (2018) concluded that a greater potential for “mass fires” exists in future decades driven by the amount, size and continuity of dry combustible woody fuels, which could produce large, severe and uncontrollable wildfires.

In 2015, the USDA Forest Service Aerial Detection Survey (ADS), the group responsible for conducting annually surveys of insect and disease conditions, first reported extensive tree mortality in the central and southern Sierra Nevada, and estimated 29 million trees died in California due to drought and outbreaks of native bark beetles. Winter 2015–2016 brought near normal precipitation to much of central and northern California, but drought stress remained high in many areas of the central and southern Sierra Nevada (U.S. Drought Monitor-California, 3 May 2016, extreme and exceptional categories; <http://droughtmonitor.unl.edu>). ADS estimated an additional 62 million trees died in 2016 and 27 million trees in 2017, bringing the total to at least 129 million trees since 2010 (California Department of Forestry and Fire Protection, 2018) (Fig. 1). Much of the mortality occurred in and around the wildland urban interface, putting significant infrastructure and lives at risk (California Tree Mortality Task Force, 2018).

While ~200 species of bark beetles are native to California only a handful is capable of causing tree mortality (Fettig, 2016). Trees of all species, ages and size classes may be colonized and killed, but each bark beetle species exhibits unique host preferences, life history traits, and impacts. In most cases, the resultant tree mortality goes unnoticed until an outbreak occurs, which generally requires several years of favorable weather conducive to beetle survival and population growth, and an abundance of susceptible hosts (Bentz et al., 2010). In particular, drought is an important factor inciting outbreaks of several notable species, including fir engraver, *Scolytus ventralis* LeConte, Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins, mountain pine beetle, *D. ponderosae* Hopkins, western pine beetle, *D. brevicomis* LeConte, and several engraver beetles, *Ips* spp. A recent synthesis reported a non-linear relationship between drought intensity and outbreaks of aggressive bark beetles (i.e., those species capable of causing extensive levels of tree mortality) where moderate drought reduces bark beetle population performance and subsequent tree mortality, and severe drought increases bark beetle performance and tree mortality (Kolb et al., 2016).

The primary objective of our research was to determine causes and rates of tree mortality within three elevation bands on the Eldorado, Stanislaus, Sierra and Sequoia National Forests (Fig. 2), and to describe short-term impacts to forest structure and composition. These national



Fig. 1. Tree mortality on the Sequoia National Forest, California, U.S., 12 April 2017. (Photo: C. Fettig, USDA Forest Service).

forests are the four most southerly on the western slope of the Sierra Nevada, and experienced the highest levels of tree mortality (California Department of Forestry and Fire Protection, 2018). Herein, we concentrate on impacts to tree size, density and species diversity, and provide baseline data on tree regeneration and invasive weeds. The network of plots created provides opportunities for monitoring other changes over time (e.g., fuels and snag demography).

2. Materials and methods

2.1. Study area and plot selection

A network of 180 11.3-m fixed-radius plots (0.041-ha) was established on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, 2016–2017 (Fig. 2). Fifteen plots (three groups of five plots) were distributed in each of three elevation bands on each national forest: 914–1219 m, 1219–1524 m and 1524–1829 m on the Eldorado, Stanislaus, and Sierra, and 1219–1524 m, 1524–1829 m, and 1829–2134 m on the Sequoia. The Sequoia National Forest is the most southerly in our network, and ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws., seldom grows there below ~1524 m elevation, which explains the increase in elevation bands. Individual plots ranged from 929 m elevation on the Georgetown Ranger District, Eldorado National Forest (UTM: 10S 693967 4307517) to 2006 m elevation on the Western Divide Ranger District, Sequoia National Forest (UTM: 11S 358511 3988017). For inclusion in the network, plots were required to be $\geq 35\%$ *P. ponderosa* by basal area, to contain $\geq 10\%$ *P. ponderosa* mortality in the last two years (as determined by presence of crown fade, Section 2.2), and unburned in the last decade. Plots meeting these criteria were randomly selected within groups, but separated by ≥ 100 m. Groups within elevation bands were separated by > 1.6 km.

2.2. Data collection and analyses

On each plot, trees ≥ 6.35 cm dbh (diameter at breast height, 1.37 m in height) were numbered, geo-referenced to plot center, and the species, dbh, condition (live or dead, based on the presence or absence of crown fade), cause of death (if applicable), and year of death (if applicable) were recorded. For trees that died prior to plot establishment, year of death was estimated based on the color of faded needles in the crown and degree of needle retention (i.e., 1 year prior, $> 90\%$ retention of yellow and/or red needles; 2 years prior, $\geq 50\text{--}90\%$ retention of red needles; ≥ 3 years prior, $< 50\%$ retention of red and/or gray needles) (Miller and Keen, 1960; Fettig et al., 2008). Very few trees (< 50 , across the network) died ≥ 3 years prior to plot establishment, and were ignored. For trees that died after plot establishment, year of death was recorded as the year before crown fade was observed (e.g., in 2016 for trees colonized by bark beetles that year, but that first exhibited crown fade in early 2017). Each plot was surveyed once annually, usually in April–June.

For dead trees, a section of bark ~ 625 cm² was removed with a hatchet at ~ 2 m in height on the north and south aspects to determine if bark beetle galleries were present. The shape, distribution and orientation of galleries are commonly used to distinguish among bark beetle species (Furniss and Carolin, 1977). In some cases, deceased bark beetles were present beneath the bark to supplement identifications based on gallery formation. The precise role of each bark beetle species in contributing to tree mortality is generally unknown. In some cases (e.g., *D. brevicomis*), trees must have enough green phloem for successful colonization and brood production to occur (Miller and Keen, 1960). In other cases (e.g., *Ips* and *Scolytus*), successful brood production may also occur in dead and dying trees (Furniss and Carolin, 1977). We attributed tree mortality to colonization by *D. brevicomis*, *D. ponderosae*, California fivespined ips, *Ips paraconfusus* Lanier, pine engraver, *I. pini* (Say), *S. ventralis*, and cedar bark beetles, *Phloeosinus* spp., only when parental and brood galleries were observed in or beneath the



Fig. 2. Distribution of experimental plots on the Eldorado (green points), Stanislaus (black points), Sierra (orange points), and Sequoia (red points) National Forests, California, U.S. Several points overlap due to spatial scale ($n = 45$ per national forest). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sections of bark removed despite the presence of other potential diagnostic characteristics (e.g., pitch tubes higher on the tree bole). As such, our estimates of levels of tree mortality attributed to bark beetles are conservative. *Dendroctonus brevicomis* and *D. ponderosae* were observed infesting the same *P. ponderosa* on 22 occasions, and in these cases we attributed tree mortality to *D. brevicomis* (Fettig et al., 2008). Tree mortality was attributed to *Ips* spp. only when evidence of *D. brevicomis* and *D. ponderosae* was absent and *Ips* spp. were present. Suppression was assigned as the cause of death when evidence of other contributing factors (e.g., bark beetles, pathogens, and mechanical damage) was absent, and if little or no direct sunlight was received from above or on the sides of the crown (USDA Forest Service, 2018). In some cases, a contributing factor could not be identified, and cause of death was recorded as unknown.

A 0.004-ha (3.6-m radius) subplot was established at the center of each plot to estimate seedling (≤ 0.3 m tall) and sapling (> 0.3 m tall to < 6.35 cm dbh) abundance by species, and ground and shrub cover. A complete census of each plot (0.041-ha) was conducted for invasive plants listed as “currently causing damage in California” (California Invasive Plant Inventory, 2016). The primary variables of interest were the causes and mean percentages of trees killed within 12.7-cm diameter classes (mid-points = 12.7, 25.4, 38.1, 50.8, 63.5, and > 69.9 cm). When appropriate, we used a two-way analysis of variance (ANOVA) to test for significance, but transformed data rarely met assumptions of normality and homoscedasticity. As such, the non-parametric Kruskal–Wallis test on ranks was used. On occasion, linear regressions were used to study the relationship between levels of tree

mortality and predictor (independent) variables.

3. Results and discussion

3.1. Conditions in 2014

At the beginning of this study, a total of 3909 trees occurred across the network including 1891 *P. ponderosa*, 1370 incense cedar, *Calocedrus decurrens* (Torr.) Florin, 247 *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., 162 sugar pine, *P. lambertiana* Dougl., 139 California black oak, *Quercus kelloggii* (Newb.), 64 canyon live oak, *Quercus chrysolepis* (Liebm.), 17 Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, nine gray pine, *P. sabiniana* Douglas ex D. Don, eight Jeffrey pine, *P. jeffreyi* Balf., one Pacific madrone, *Arbutus menziesii* Pursh, and one interior live oak, *Quercus wislizeni* A. DC. No significant differences were observed for measures of tree size or stand density among national forests ($P > 0.05$, all cases) (Table 1, 2014). A significantly higher proportion of *A. concolor* occurred on the Sequoia compared to the Stanislaus and Sierra ($H = 14.8$, $df = 3$, $P = 0.002$), and of *Q. chrysolepis* on the Sierra compared to the Eldorado and Sequoia ($H = 15.2$, $df = 3$, $P = 0.002$) (Table 1, 2014). No other significant differences were observed among national forests. All national forests were dominated by *P. ponderosa*.

Among elevation bands, mean QMD was higher in the mid-elevation band than the low elevation band ($H = 7.1$, $df = 2$, $P = 0.029$), and more trees occurred in the high elevation band than the low elevation band ($H = 6.8$, $df = 2$, $P = 0.034$). Basal area ($H = 14.4$, $df = 2$,

Table 1
Conditions on four national forests in the central and southern Sierra Nevada, California, U.S.

	Eldorado	Stanislaus	Sierra	Sequoia	All
Elevation (m)	1369 ± 35	1324 ± 32	1398 ± 33	1716 ± 31	1452 ± 20
Aspect (°)	187 ± 10	186 ± 15	178 ± 13	163 ± 13	179 ± 6
Slope (°)	17 ± 1	15 ± 1	20 ± 2	16 ± 1	17 ± 1
2014 ¹					
Mean dbh (cm)	36.4 ± 1.7 a	35.9 ± 1.7 a	32.8 ± 1.4 a	33.1 ± 1.4 a	34.5 ± 0.8
Quadratic mean diameter (cm)	41.7 ± 1.8 a	39.9 ± 1.7 a	37.2 ± 1.3 a	37.5 ± 1.4 a	39.1 ± 0.8
Trees per ha	539.8 ± 52.0 a	529.9 ± 46.1 a	556.8 ± 46.8 a	520.0 ± 38.8 a	536.6 ± 22.9
Basal area (m ² per ha)	63.7 ± 4.6 a	58.2 ± 3.8 a	53.1 ± 3.2 a	52.6 ± 3.6 a	56.9 ± 1.9
Stand density index	418.6 ± 28.1 a	390.0 ± 24.4 a	367.4 ± 20.5 a	359.6 ± 21.7 a	383.9 ± 12.0
% <i>Pinus ponderosa</i>	60.3 ± 4.2 a	53.3 ± 3.3 a	57.0 ± 3.9 a	48.9 ± 3.6 a	54.9 ± 1.9
% <i>Calocedrus decurrens</i>	26.0 ± 3.4 a	30.9 ± 3.1 a	28.8 ± 3.5 a	30.7 ± 3.4 a	29.1 ± 1.9
% <i>Abies concolor</i>	7.4 ± 1.8 ab	4.0 ± 1.4 b	3.1 ± 1.4 b	9.3 ± 1.6 a	6.0 ± 0.8
% <i>Pinus lambertiana</i>	3.2 ± 0.9 a	5.5 ± 1.2 a	5.7 ± 1.5 a	2.4 ± 0.8 a	4.2 ± 0.6
% <i>Quercus kelloggii</i>	1.4 ± 0.6 a	3.3 ± 0.8 a	1.8 ± 0.5 a	5.5 ± 1.8 a	3.0 ± 0.5
% <i>Quercus chrysolepis</i>	0.1 ± 0.1 b	2.5 ± 0.9 ab	3.7 ± 1.5 a	0.4 ± 0.3 b	1.7 ± 0.5
2017 ¹					
Mean dbh (cm)	28.0 ± 2.0 a	25.5 ± 1.6 ab	19.8 ± 1.6 b	23.3 ± 1.7 ab	24.1 ± 0.9
Quadratic mean diameter (cm)	31.5 ± 2.1 a	29.0 ± 1.8 ab	22.2 ± 1.8 b	26.0 ± 1.8 ab	27.2 ± 1.0
Trees per ha	325.1 ± 42.7 a	253.1 ± 29.7 a	262.5 ± 37.3 a	260.8 ± 30.8 a	275.4 ± 17.7
Basal area (m ² per ha)	23.8 ± 3.2 a	16.3 ± 2.0 ab	10.7 ± 1.6 b	15.2 ± 1.7 ab	16.5 ± 1.5
Stand density index	170.1 ± 21.3 a	120.4 ± 14.1 ab	86.4 ± 11.9 b	115.4 ± 12.6 ab	123.1 ± 8.0
% <i>Pinus ponderosa</i>	39.5 ± 5.8 a	22.2 ± 4.0 ab	20.0 ± 4.2 ab	15.9 ± 3.1 b	24.4 ± 2.3
% <i>Calocedrus decurrens</i>	38.8 ± 4.9 a	47.0 ± 4.8 a	44.7 ± 4.9 a	38.8 ± 4.9 a	44.5 ± 2.4
% <i>Abies concolor</i>	9.1 ± 2.4 a	6.6 ± 2.2 a	3.7 ± 1.6 a	10.7 ± 2.4 a	7.5 ± 1.1
% <i>Pinus lambertiana</i>	5.7 ± 2.0 a	6.3 ± 1.9 a	3.4 ± 1.7 a	1.5 ± 0.5 a	4.2 ± 0.8
% <i>Quercus kelloggii</i>	2.1 ± 0.9 a	9.7 ± 3.2 a	5.1 ± 1.7 a	11.6 ± 3.6 a	7.2 ± 1.3
% <i>Quercus chrysolepis</i>	0.1 ± 0.1 b	7.3 ± 2.9 a	7.8 ± 3.0 a	1.2 ± 0.8 b	4.1 ± 1.1

Values are mean ± SEM based on 45 11.3-m fixed-radius plots per national forest, live trees ≥ 6.35 cm dbh (diameter at breast height, 1.37 m). Means ± SEM followed by the same letter within rows are not significantly different ($P > 0.05$).

¹ Only species with ≥ 25 individuals are represented (based on numbers of trees).

$P < 0.001$) and SDI ($H = 13.5$, $df = 2$, $P = 0.001$) were higher in the mid- and high elevation bands compared to the low elevation band (Table 2, 2014). Elevation has long been recognized as a driver of plant composition, and in the Sierra Nevada results in greater *Pinus* and *Quercus* dominance at lower elevations and greater *Abies* dominance at higher elevations (Show and Kotok, 1929). We observed significantly higher proportions of *A. concolor* in the mid- and high elevation bands compared to the low elevation band ($H = 17.1$, $df = 2$, $P < 0.001$), and of *Q. chrysolepis* at the low elevation band compared to the mid- and high elevation bands ($H = 14.3$, $df = 2$, $P < 0.001$) (Table 2, 2014). No other significant differences were observed among elevation bands. All elevation bands were dominated by *P. ponderosa*.

Several reconstructions of historic forest conditions have been completed for mixed-conifer forests in the central and southern Sierra Nevada (e.g., Collins et al., 2011, 2015; Lydersen et al., 2013). Collins et al. (2015) reconstructed portions of Stanislaus National Forest and Yosemite National Park (776–2140 m elevation) from historic timber inventories, and reported forests in the early 20th century were of low density containing 25–79 trees per ha and 8–30 m² per ha of basal area. Safford and Stevens (2017) reported mixed-conifer forests in California averaged 159 stems per ha and 35 m² per ha of basal area. Our plots were heavily departed from these historic conditions (e.g., mean numbers of live trees ranged from 520.0 ± 38.8 per ha on the Sequoia to 556.8 ± 46.8 per ha on the Sierra; Table 1, 2014), which is usually attributed to suppression of wildfires in the modern era. For millennia, frequent, low-moderate intensity wildfires sculpted these landscapes reducing the quantity and continuity of surface and ladder fuels and the proportion of shade tolerant and fire intolerant tree species, such as *A. concolor* (Scholl and Taylor, 2010). Variability that provided diverse habitats and microclimates and fostered resilience to a variety of stressors and disturbances has also been lost (Lydersen et al., 2013).

3.2. Conditions in 2017

About 48.9% of trees (1912 trees) died between 2014 and 2017 (Fig. 3). Most tree mortality occurred in 2015 and 2016 after the drought subsided ($H = 119.1$, $df = 3$, $P < 0.001$) (Fig. 3), a trend observed in other drought-impacted forests in the region. For example, Kane et al. (2014) reported relationships between tree mortality and most climatic variables (e.g., temperature, precipitation, Palmer Drought Severity Index) were lagged 1–4 years in northern Arizona, U.S. Tree mortality (numbers of trees killed) was positively correlated with stand density (Section 3.3) and slope ($F_{1, 178} = 10.5$, $P = 0.001$, $R^2 = 0.06$), but not aspect ($F_{1, 178} = 0.6$, $P = 0.44$). Tree mortality among national forests ranged from 46.1 ± 3.3% on the Eldorado to 58.7 ± 3.7% on the Sierra, but no significant differences were observed among national forests ($H = 7.5$, $df = 3$, $P = 0.06$). Significantly higher levels of tree mortality occurred in the low elevation band (60.4 ± 3.0%) compared to the high elevation band (46.1 ± 2.9%) ($H = 11.5$, $df = 2$, $P = 0.003$). No other significant differences were observed among elevation bands (mid- = 54.4 ± 2.5%). Paz-Kagan et al. (2017) used high-fidelity imaging spectroscopy and light detection and ranging (LiDAR) to estimate levels of tree mortality in response to recent drought stress in Sequoia National Park. Higher levels of tree mortality were observed at lower elevations, and on southwest and west-facing slopes. In our study, 10 plots suffered 100% tree mortality and only one of these occurred in the high elevation band.

Significant declines in tree size (dbh, $H = 69.4$, $df = 1$, $P < 0.001$; QMD, $H = 75.2$, $df = 1$, $P < 0.001$) and stand density (trees per ha, $H = 81.8$, $df = 1$, $P < 0.001$; basal area, $H = 198.4$, $df = 1$, $P < 0.001$; SDI, $H = 193.7$, $df = 1$, $P < 0.001$) were observed between 2014 and 2017 (Table 1, 2017). Mean dbh ($H = 9.5$, $df = 3$, $P = 0.024$), mean QMD ($H = 11.1$, $df = 3$, $P = 0.011$), mean basal area ($H = 13.5$, $df = 3$, $P = 0.004$), and mean SDI ($H = 10.1$, $df = 3$, $P = 0.018$) were higher on the Eldorado than the Sierra (Table 1, 2017). A higher proportion of *P. ponderosa* occurred on the Eldorado

Table 2
Conditions within three elevation bands on four national forests in the central and southern Sierra Nevada, California, U.S.

	Low	Mid	High
Elevation (m)	1184 ± 23	1477 ± 22	1694 ± 20
Aspect (°)	148 ± 15	207 ± 8	181 ± 6
Slope (°)	18 ± 1	16 ± 1	17 ± 1
2014 ¹			
Mean dbh (cm)	33.4 ± 1.3 a	37.0 ± 1.4 a	33.3 ± 1.3 a
Quadratic mean diameter (cm)	37.6 ± 1.3 b	41.7 ± 1.3 a	38.0 ± 1.4 ab
Trees per ha	496.3 ± 43.1 b	513.2 ± 35.0 ab	600.5 ± 40.0 a
Basal area (m ² per ha)	47.4 ± 3.0 b	62.8 ± 3.5 a	62.8 ± 3.5 a
Stand density index	327.5 ± 20.7 b	412.4 ± 20.8 a	411.8 ± 19.1 a
% <i>Pinus ponderosa</i> ¹	57.2 ± 3.5 a	54.1 ± 3.4 a	53.3 ± 2.9 a
% <i>Calocedrus decurrens</i> ¹	26.5 ± 3.3 a	32.3 ± 2.9 a	28.4 ± 2.5 a
% <i>Abies concolor</i> ¹	2.9 ± 1.2 b	6.4 ± 1.3 a	8.5 ± 1.5 a
% <i>Pinus lambertiana</i> ¹	3.4 ± 1.0 a	4.2 ± 0.9 a	5.0 ± 1.1 a
% <i>Quercus kelloggii</i> ¹	3.5 ± 1.2 a	1.6 ± 0.4 a	3.9 ± 1.0 a
% <i>Quercus chrysolepis</i> ¹	3.9 ± 1.3 a	0.7 ± 0.4 b	0.4 ± 0.2 b
2017 ¹			
Mean dbh (cm)	21.7 ± 1.7 a	26.3 ± 1.6 a	24.4 ± 1.2 a
Quadratic mean diameter (cm)	23.7 ± 1.8 b	30.1 ± 1.8 a	27.8 ± 1.3 ab
Trees per ha	224.0 ± 31.2 b	251.6 ± 24.5 ab	350.5 ± 33.7 a
Basal area (m ² per ha)	10.8 ± 1.5 b	17.3 ± 1.7 a	21.4 ± 2.4 a
Stand density index	83.8 ± 10.9 b	125.4 ± 11.8 a	160.0 ± 16.4 a
% <i>Pinus ponderosa</i> ¹	23.2 ± 4.4 a	25.6 ± 4.0 a	24.4 ± 3.4 a
% <i>Calocedrus decurrens</i> ¹	35.2 ± 4.8 b	50.3 ± 4.1 a	47.9 ± 3.7 ab
% <i>Abies concolor</i> ¹	2.5 ± 1.4 b	7.1 ± 1.5 a	13.0 ± 2.4 a
% <i>Pinus lambertiana</i> ¹	4.3 ± 1.4 a	5.7 ± 1.6 a	2.6 ± 1.3 a
% <i>Quercus kelloggii</i> ¹	10.9 ± 3.4 a	3.2 ± 0.9 a	10.9 ± 2.9 a
% <i>Quercus chrysolepis</i> ¹	8.9 ± 2.8 a	2.5 ± 1.5 b	1.9 ± 0.8 b

Values are mean ± SEM, based on 60 11.3-m fixed-radius plots per elevation band, live trees ≥ 6.35 cm dbh (diameter at breast height, 1.37 m). Means ± SEM followed by the same letter within rows are not significantly different ($P > 0.05$).

Low = 914–1218 m on all national forests, except Sequoia (1219–1524 m); mid- = 1219–1524 m, except Sequoia (1524–1829 m); high = 1524–1829 m, except Sequoia (1829–2134 m).

¹ Only species with ≥ 25 individuals are represented (based on numbers of trees).

than the Sequoia ($H = 9.9$, $df = 3$, $P = 0.02$), and of *Q. chrysolepis* on the Stanislaus and Sierra compared to the Eldorado and Sequoia ($H = 15.4$, $df = 3$, $P = 0.002$) (Table 1, 2017). No other significant differences were observed among national forests. Since mortality was concentrated in *P. ponderosa*, *P. lambertiana* and *A. concolor* (Sections 3.2.1, 3.2.2, 3.2.3), substantial increases in the proportion of *C. decurrens* and *Quercus* spp. were observed. All national forests were dominated by *C. decurrens*, except Eldorado.

Among elevation bands, mean QMD was higher in the mid-elevation band than the low elevation band ($H = 7.9$, $df = 2$, $P = 0.002$); more trees occurred in the high elevation band than the low elevation band ($H = 11.9$, $df = 2$, $P = 0.003$); and basal area ($H = 17.2$, $df = 2$, $P < 0.001$) and SDI ($H = 17.5$, $df = 2$, $P < 0.001$) were higher in the mid- and high elevation bands compared to the low elevation band (Table 2, 2017). We also observed higher proportions of *A. concolor* in the mid- and high elevation bands compared to the low elevation band ($H = 21.9$, $df = 2$, $P < 0.001$), and of *Q. chrysolepis* at the low elevation band compared to the mid- and high elevation bands ($H = 14.4$, $df = 2$, $P < 0.001$) (Table 2, 2017). These relationships are similar to those observed in 2014. About 50% of trees in the mid-elevation band was represented by *C. decurrens*, which was higher than observed in the low elevation band ($H = 7.0$, $df = 2$, $P = 0.03$). No other significant differences were observed among elevation bands. All elevation bands were dominated by *C. decurrens*.

One might conclude the changes observed between 2014 and 2017 helped produce more resilient forest conditions. However, current structure and composition differs from what might be considered resilient in a historical context despite the substantial declines in stand density. For example, extensive areas exist where most of the largest trees have been killed, including most *Pinus*. These are not the same trees that would have been removed historically by low-moderate intensity wildfires, or targeted for removal in fuel reduction or forest restoration projects in more contemporary times (Stephens et al., 2012). Large unburned areas of dead trees may produce succession patterns favoring shade-tolerant and hardwood tree regeneration, limited shrub growth, and accumulation of large woody surface fuels that will likely kill regenerating forests when wildfires occur. Furthermore, the scale of tree mortality entrenches the homogeneity produced by fire suppression, reducing the fine-scale heterogeneity that contributes to resilience. Loss of the large-tree component exacerbates concerns

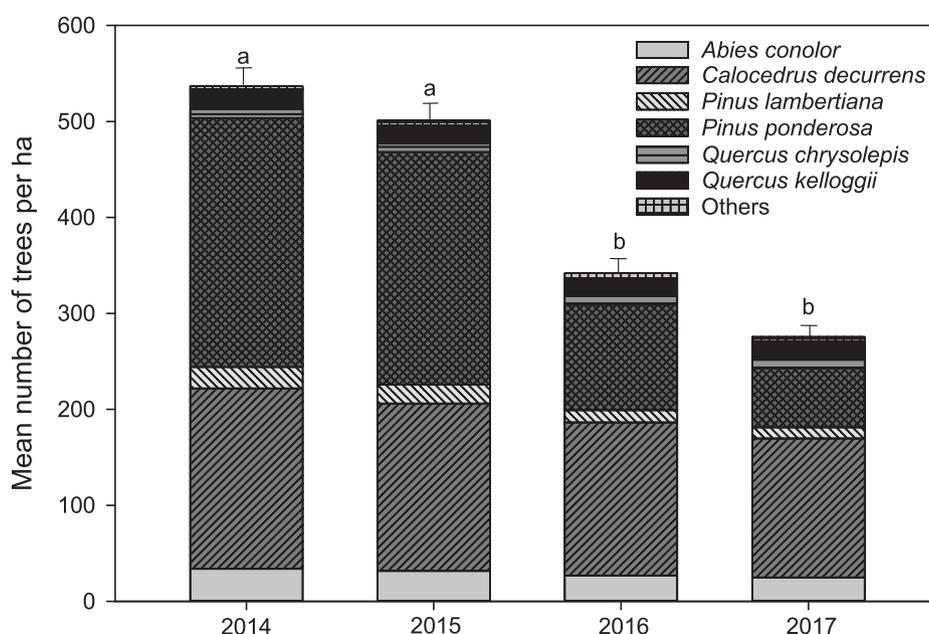


Fig. 3. Mean number of trees per ha (+SEM) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S., 2014–2017. Means (+SEM) followed by the same number are not significantly different ($P > 0.05$).

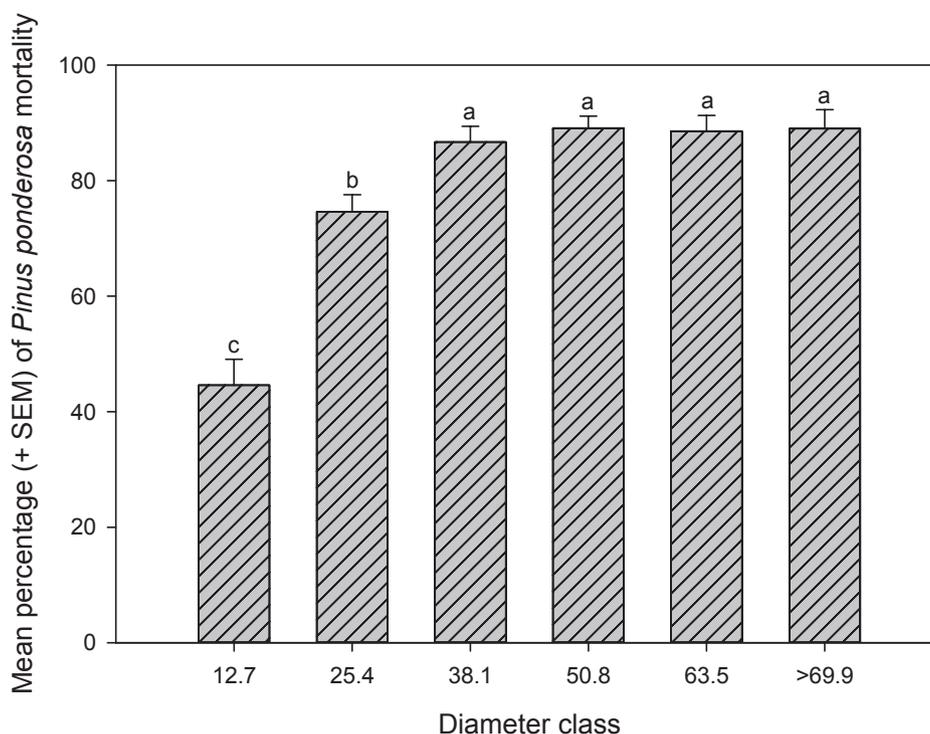


Fig. 4. Mortality of *Pinus ponderosa* by diameter class (mid-point of 12.7-cm diameter classes, except for largest) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. Means (+SEM) followed by the same letter are not significantly different ($P > 0.05$).

regarding habitat needs for some wildlife species, notably the California spotted owl, *Strix occidentalis occidentalis* (Xántus) (Jones et al., 2018). *Strix occidentalis occidentalis*, a species of conservation concern, prefers large trees and snags embedded in forests of complex structure. It will take decades to centuries for this structure to return.

3.2.1. *Pinus ponderosa*

Pinus ponderosa exhibited the highest levels of tree mortality observed (1695 trees, 89.6% of *P. ponderosa*) (Fig. 4). Mortality on a per plot basis ranged from 18.2% (one plot, 1330 m on the Eldorado) to 100% (71 plots). Significantly higher levels of *P. ponderosa* mortality occurred on the Sequoia ($85.4 \pm 2.6\%$) and Sierra ($84.1 \pm 3.0\%$) compared to the Eldorado ($70.3 \pm 3.9\%$) ($H = 9.9$, $df = 3$, $P = 0.02$). No other significant differences were observed among forests (Stanislaus, $81.5 \pm 3.0\%$). Significantly higher levels of *P. ponderosa* mortality occurred at the lowest elevations ($85.5 \pm 2.4\%$) compared to the highest elevations ($73.9 \pm 3.3\%$) ($H = 7.3$, $df = 2$, $P = 0.03$). No other significant differences were observed among elevation bands (mid-, $81.5 \pm 2.6\%$). These differences likely result from drought stress being more severe at lower elevations and latitudes (Asner et al., 2016). Mortality was most severe in 2015–2016 (Fig. 3), concentrated in the larger-diameter classes ($H = 118.7$, $df = 5$, $P < 0.001$) (Fig. 4), and attributed primarily to *D. brevicomis* (Fig. 5). No mortality occurred in *P. ponderosa* ≤ 10.0 cm dbh. This is not surprising as *D. brevicomis* exhibits a preference for colonizing large-diameter *P. ponderosa* (> 50 cm dbh) (Miller and Keen, 1960).

Like most conifers, *P. ponderosa* is capable of mobilizing large amounts of oleoresin following wounding, which constitutes its primary defense against bark beetles (Franceschi et al., 2005). Drought reduces carbon assimilation, water transport, and thus synthesis and mobilization of oleoresin (McDowell et al., 2011; Sala et al., 2012). Elevated temperatures and forest densification (Section 3.4) enhance the effect (Young et al., 2017) due to increases in maintenance respiration and evaporative demand (Ryan, 1991). As such, droughts occurring during warm periods are generally more damaging to plants than those occurring during cool periods (Breshears et al., 2005; Adams et al., 2009).

In most of California, *D. brevicomis* completes two and a partial third generation annually, but considerable variation in flight activity occurs (Fettig et al., 2004, 2005). Warm temperatures may increase the length of flight activity and voltinism of bark beetles. For example, high summer temperatures have been documented to prevent facultative prepupal diapause in spruce beetle, *Dendroctonus rufipennis* Kirby, allowing *D. rufipennis* to complete their life cycle in one year compared to two years when diapause is invoked (Hansen and Bentz, 2003). This and other factors have resulted in increased levels of tree mortality attributed to *D. rufipennis* in recent years (Hart et al., 2017). While it is possible voltinism is increasing in populations of *D. brevicomis* in the central and southern Sierra Nevada (B.M.B., pers. observ.), we attribute the large amounts of *P. ponderosa* mortality observed to declines in host resistance due to severe drought stress and forest densification (Section 3.3).

On occasion, mortality of *P. ponderosa* was attributed to *D. ponderosae* (14 trees) and *Ips* spp. (36 trees), but in these cases mortality was concentrated in the smaller-diameter classes (Fig. 5). *Dendroctonus ponderosae*, *I. paraconfusus* and *I. pini* are also important disturbance agents in the Sierra Nevada, but unlike *D. brevicomis* colonize other *Pinus* in addition to *P. ponderosa* (Fettig, 2016). In California, *D. ponderosae* infestations in *P. ponderosa* are typically confined to smaller (< 31.8 cm dbh) trees, and its role is often secondary to that of *D. brevicomis*, particularly in larger-diameter trees (Fettig and McKelvey, 2014). This is consistent with our observations (Fig. 5). However, given the species notable reputation as a disturbance agent (Negrón and Fettig, 2014), the paucity of mortality attributed to *D. ponderosae* is somewhat surprising and likely attributed to being outcompeted by *D. brevicomis* for drought-stressed trees. *Ips* spp. generally colonize slash, saplings, and weakened trees. Colonization rates are negatively correlated with tree diameter in *P. ponderosa* (Kolb et al., 2006), and trees 5–20 cm dbh are most frequently colonized as observed in our study (Fig. 5).

The Transverse and Peninsular mountain ranges of southern California experienced a similar outbreak of *D. brevicomis* in the early 2000s that resulted in substantial mortality of large-diameter

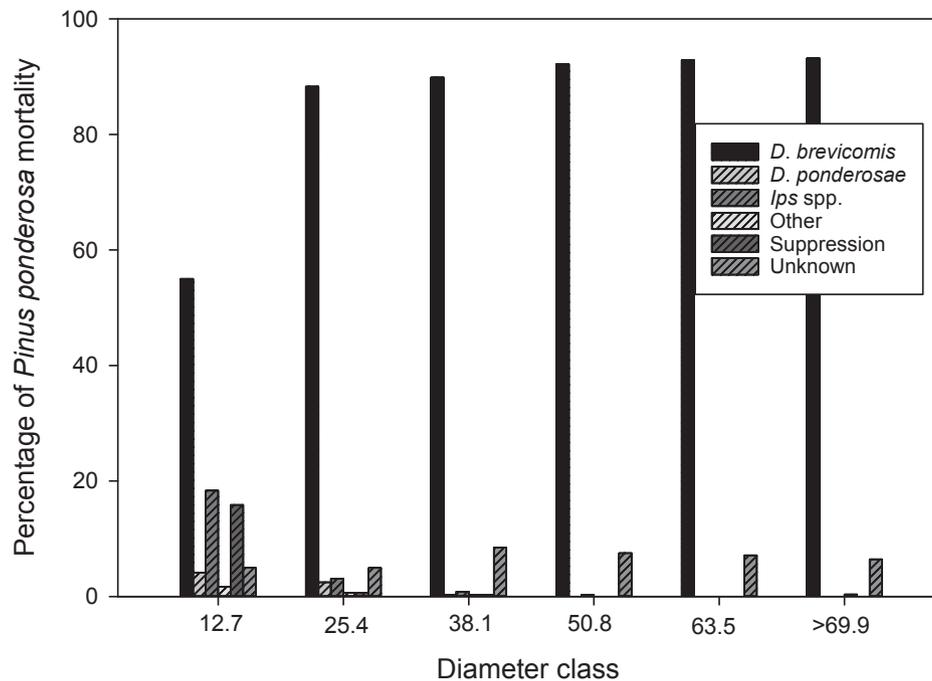


Fig. 5. Causes of *Pinus ponderosa* mortality by diameter class (mid-point of 12.7-cm diameter classes) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. Other includes root diseases and breakage due to wind.

(> 43.2 cm dbh) *P. ponderosa* and Coulter pine, *P. coulteri* D. Don (Fettig, 2018). Precipitation was the lowest in recorded history the year prior to the outbreak (Minnich et al., 2016), and was associated with a regional drought event that extended throughout much of the southwestern U.S. Air pollutants and root diseases were important inciting and contributing factors (Grulke et al., 1998; Jones et al., 2004). Concerns regarding hazard trees, fire risk, transportation and accessibility, and power line maintenance were paramount (Fettig, 2018), similar to areas most affected by this outbreak (www.fire.ca.gov/treetaskforce/).

3.2.2. *Pinus lambertiana*

Pinus lambertiana exhibited the second highest levels of tree mortality observed (78 trees, 48.1% of *P. lambertiana*) (Fig. 6). Mortality on a per plot basis ranged from 0% (31 plots) to 100% (21 plots), while 113 plots had no *P. lambertiana*. Mortality of *P. lambertiana* ranged from $16.1 \pm 9.7\%$ on the Eldorado to $51.0 \pm 8.6\%$ on the Sierra, but no significant differences were observed among national forests ($H = 6.6$, $df = 3$, $P = 0.09$). Furthermore, no significant differences were observed among elevation bands ($H = 0.7$, $df = 2$, $P = 0.71$). Mortality was concentrated in the mid-diameter classes (Fig. 6) ($H = 20.7$, $df = 5$, $P < 0.001$), and primarily attributed to *D. ponderosae* (Fig. 7). Mortality of only one *P. lambertiana* was attributed to *Cronartium ribicola* J.C. Fisch, the invasive pathogen that causes white pine blister rust. While all size classes of *P. lambertiana* are susceptible to white pine blister rust, smaller trees most frequently suffer lethal stem cankers (Maloney et al., 2011). It is thought that drought results in less rust infection (Kolb et al., 2016) due to the moist conditions required for disease progression (Van Arsdell et al., 1956). White pine blister rust and fire exclusion appear to be having significant impacts on *P. lambertiana* populations in the Sierra Nevada (van Mantegm et al., 2004) only to be exacerbated by this tree mortality event. This is concerning given the limited *P. lambertiana* regeneration observed (Table 3).

3.2.3. *Abies concolor*

Abies concolor exhibited the third highest levels of tree mortality (65 trees, 26.3% of *A. concolor*) (Fig. 8). Mortality on a per plot basis ranged from 0% (35 plots) to 100% (10 plots), while 114 plots had no *A. concolor*. Mortality of *A. concolor* ranged from $9.3 \pm 5.6\%$ on the

Stanislaus to $39.9 \pm 8.1\%$ on the Sequoia, but no significant differences were observed among national forests ($H = 4.6$, $df = 3$, $P = 0.20$). Furthermore, no significant differences were observed among elevation bands ($H = 4.6$, $df = 2$, $P = 0.10$). Mortality tended to be concentrated in the mid-diameter classes, but no significant differences were observed among diameter classes ($H = 7.6$, $df = 5$, $P = 0.18$). Mortality was primarily attributed to *S. ventralis* (Fig. 9). Outbreaks of *S. ventralis* are often associated with trees stressed by drought, defoliation, root pathogens or other factors (Ferrell et al., 1994).

3.2.4. *Calocedrus decurrens*

About 23.2% (318 trees) of *C. decurrens* died (Fig. 10). Mortality on a per plot basis ranged from 0% (72 plots) to 100% (11 plots), while 30 plots had no *C. decurrens*. Mortality of *C. decurrens* ranged from $13.7 \pm 3.8\%$ on the Eldorado to $26.6 \pm 5.5\%$ on the Stanislaus, but no significant differences were observed among national forests ($H = 3.3$, $df = 3$, $P = 0.35$). Significantly higher levels of mortality occurred in the low ($40.1 \pm 5.9\%$) compared to the high elevation band ($7.9 \pm 2.2\%$) ($H = 24.9$, $df = 2$, $P < 0.001$). No other significant differences were observed among elevation bands (mid-, $22.1 \pm 3.6\%$). No trends were observed among diameter classes (Fig. 10). Most mortality was attributed to suppression, however in larger trees mortality was often classified as unknown (Fig. 11). In both cases, drought was likely a significant contributing factor.

The bark beetle genus *Phloeosinus* contains several species in North America that colonize the twigs, branches and stems of trees weakened by drought or other factors (Fettig, 2016). Surprisingly, only five trees were colonized and killed by *Phloeosinus* spp. (Fig. 11), which likely underrepresents the true contribution of this species as sampling was limited to the tree bole. While *Phloeosinus* spp. are generally not considered an important cause of tree mortality, droughts in the Sierra Nevada during the 1980s and then again in the early 2000s resulted in significant branch flagging and some tree mortality attributed to western cedar bark beetle, *Ph. punctatus* LeConte (USDA Forest Service, 2003). Stephenson et al., (2018) reported drought-induced dieback of giant sequoia, *Sequoiadendron giganteum* Lindl. (Buchholz), crowns in Sequoia and Kings Canyon National Parks in 2014. *Phloeosinus* spp.

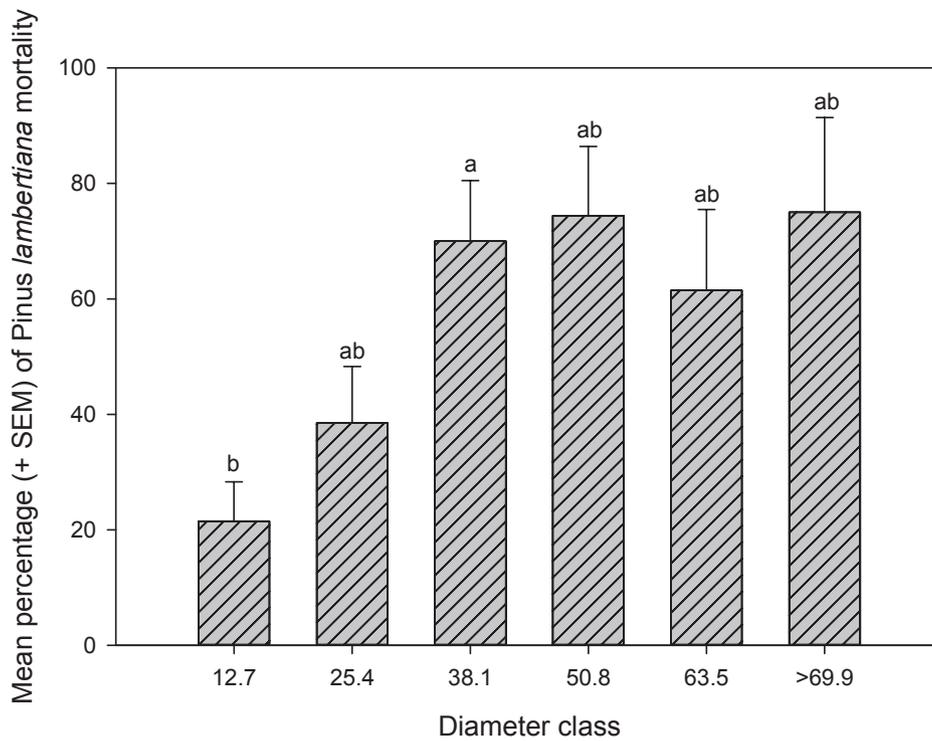


Fig. 6. Mortality of *Pinus lambertiana* by diameter class (mid-point of 12.7-cm diameter classes, except for largest) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. Means (+SEM) followed by the same letter are not significantly different ($P > 0.05$).

colonized some trees, but mortality was limited and the role of *Phloeosinus* spp. in contributing to tree mortality was unclear (Stephenson et al., 2018).

3.2.5. *Quercus* spp

Quercus are resistant to drought as they tend to be deep rooted, and form substantial mycorrhizal associations that enhance soil moisture uptake (Allen, 2015). *Quercus chrysolepis* and *Q. wislizeni* are evergreen,

and have sclerophyllous leaf structures that reduce evapotranspiration (Plumb and Gomez, 1983). *Quercus kelloggii* is deciduous, and may prematurely drop leaves to reduce evapotranspiration during periods of drought (McCreary, 2012). Despite this, it is surprising that only one *Quercus* (*Q. kelloggii*) died given the amount of mortality observed in other tree species. This is in contrast to a large oak decline event that occurred in the Ozark Mountains, U.S. during drought in the early 2000s. There, red oak borer, *Enaphalodes rufulus* (Haldeman), a native

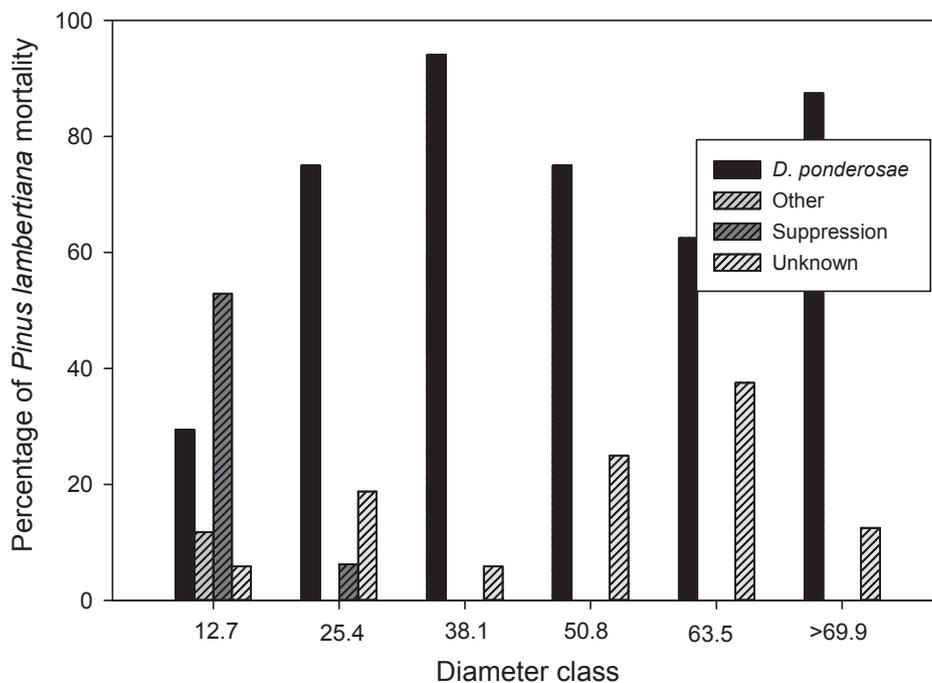


Fig. 7. Causes of *Pinus lambertiana* mortality by diameter class (mid-point of 12.7-cm diameter classes) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. Other includes *Cronartium ribicola* and *Ips* spp.

Table 3
Tree regeneration on four national forests in the central and southern Sierra Nevada, California, U.S.

	Eldorado	Stanislaus	Sierra	Sequoia	All
Seedlings ¹ per ha					
<i>Abies concolor</i>	366.4 ± 268.0 a	185.9 ± 90.6 a	93.0 ± 49.0 a	246.1 ± 75.0 a	222.8 ± 73.9
<i>Calocedrus decurrens</i>	229.7 ± 69.2 a	989.7 ± 306.7 a	262.5 ± 72.7 a	792.9 ± 235.6 a	568.7 ± 102.1
<i>Pinus lambertiana</i>	142.2 ± 41.7 a	185.9 ± 107.5 a	131.2 ± 58.8 a	10.9 ± 7.6 b	117.6 ± 32.5
<i>Pinus ponderosa</i>	311.7 ± 120.2 a	196.9 ± 86.6 a	153.1 ± 70.1 a	109.4 ± 30.0 a	192.8 ± 41.7
<i>Pseudotsuga menziesii</i>	131.2 ± 64.3 a	5.5 ± 5.5 b	0.0 ± 0.0 b	0.0 ± 0.0 b	34.2 ± 16.5
<i>Quercus chrysolepis</i>	10.9 ± 7.6 b	267.9 ± 102.5 a	350.0 ± 163.2 a	27.3 ± 22.4 b	164.2 ± 49.4
<i>Quercus kelloggii</i>	251.5 ± 85.1 a	404.6 ± 124.9 a	360.9 ± 218.4 a	246.1 ± 70.4 a	315.8 ± 68.3
All ³	1449.1 ± 387.8 a	2242.0 ± 474.5 a	1356.1 ± 372.3 a	1432.7 ± 302.5 a	1620.0 ± 194.8
Saplings ² per ha					
<i>Abies concolor</i>	180.5 ± 85.5 a	776.5 ± 392.2 a	125.8 ± 64.3 a	120.3 ± 44.7 a	300.8 ± 103.5
<i>Calocedrus decurrens</i>	355.4 ± 102.7 a	918.7 ± 311.0 a	541.4 ± 135.4 a	1203.0 ± 610.4 a	754.6 ± 176.7
<i>Pinus lambertiana</i>	93.0 ± 38.5 a	87.5 ± 42.2 a	76.6 ± 24.5 a	10.9 ± 7.6 a	67.0 ± 15.7
<i>Pinus ponderosa</i>	350.0 ± 120.8 a	328.1 ± 151.4 a	224.2 ± 121.1 a	76.6 ± 34.8 a	244.7 ± 57.9
<i>Pseudotsuga menziesii</i>	71.1 ± 44.0 a	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 b	17.8 ± 11.1
<i>Quercus chrysolepis</i>	98.4 ± 47.2 b	393.7 ± 134.4 a	284.3 ± 79.0 b	169.5 ± 72.9 b	236.5 ± 45.0
<i>Quercus kelloggii</i>	131.2 ± 46.0 a	388.2 ± 128.4 a	202.3 ± 70.1 a	153.1 ± 49.0 a	218.7 ± 40.6
All ³	1317.8 ± 258.1 b	2985.6 ± 673.6 a	1536.6 ± 314.7 ab	1771.7 ± 611.3 b	1902.9 ± 251.7

Values are mean ± SEM, based on one 0.004-ha subplot per 11.3-m fixed-radius plot.

¹ Height ≤ 0.3 m.

² Height > 0.3 m and dbh (diameter at breast height, 1.37 m) < 6.35 cm.

³ Includes infrequently encountered species *Cornus nuttallii*, *Arbutus menziesii*, *Notholithocarpus densiflorus*, *Pinus sabiniana*, and *Quercus wislizeni*.

wood-boring beetle previously recorded only at endemic levels, contributed to substantial levels of tree mortality (Stephen et al., 2001). The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, an invasive insect first associated with dying *Quercus* in San Diego County in 2008 (Coleman and Seybold, 2008), has caused mortality of large numbers of *Quercus* in southern California, but is not established in the Sierra Nevada. The species colonizes *Q. kelloggii* and *Q. chrysolepis*, among others, and represents a significant threat. Infestations appear to be incited by drought, and it has been demonstrated that *A. auroguttatus* enhances drought stress in infested hosts (Coleman et al., 2011).

3.3. Tree mortality and density

We observed significant positive relationships between the number of trees and the number of trees killed ($F_{1, 178} = 143.2$, $P > 0.001$, $R^2 = 0.45$, Fig. 12), basal area and the number of trees killed ($F_{1, 178} = 18.5$, $P < 0.001$, $R^2 = 0.10$), and SDI and the number of trees killed ($F_{1, 178} = 45.9$, $P < 0.001$, $R^2 = 0.21$). Hayes et al., (2009) reported basal area and SDI were strong predictors of levels of tree mortality attributed to *D. brevicornis* in California ($R^2 > 0.90$). In their study, plots with the highest densities experienced the highest levels of tree mortality on both an absolute (number of trees killed) and proportional (% mortality) basis. We observed a significant negative

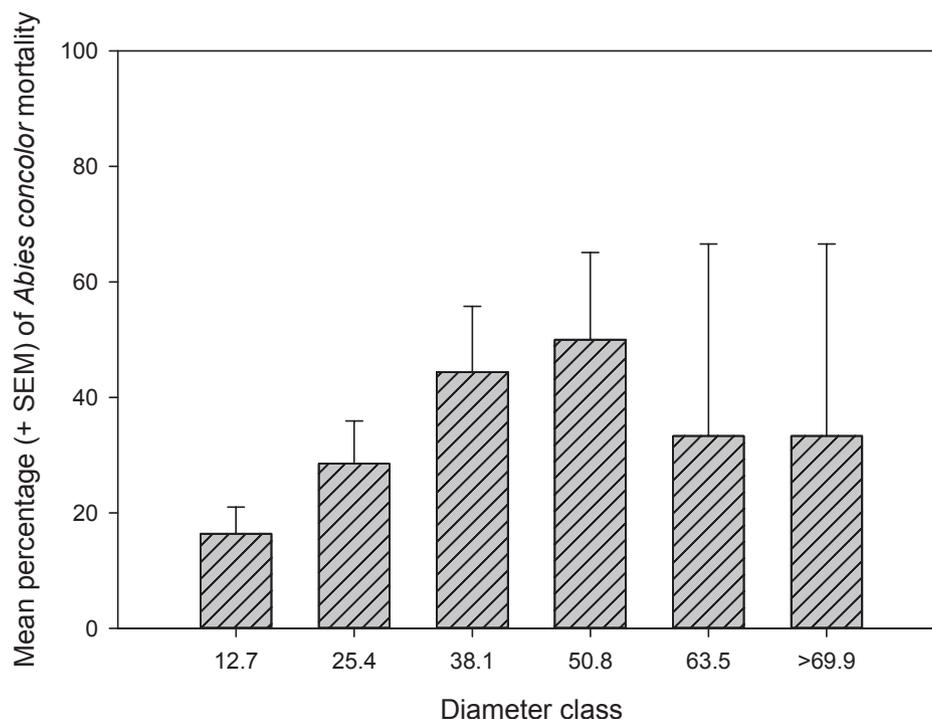


Fig. 8. Mortality of *Abies concolor* by diameter class (mid-point of 12.7-cm diameter classes, except for largest) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. No significant differences were observed ($P > 0.05$).

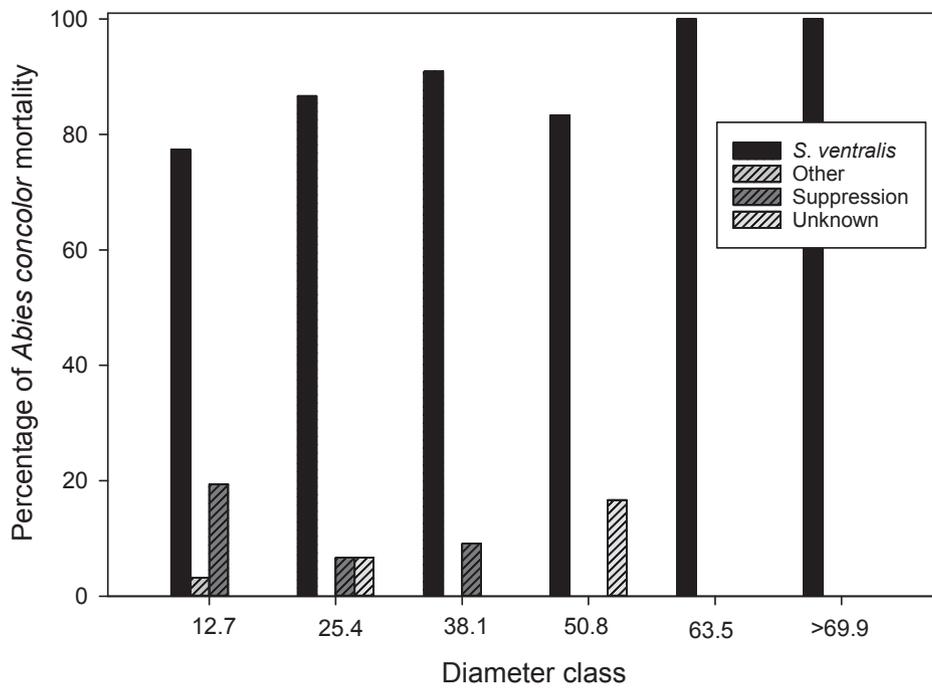


Fig. 9. Causes of *Abies concolor* mortality by diameter class (mid-point of 12.7-cm diameter classes) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. Other includes root diseases.

relationship between the number of trees and proportion of trees killed ($F_{1, 178} = 30.1, P > 0.001, R^2 = 0.15$), and a negative relationship between SDI and the proportion of trees killed ($F_{1, 178} = 6.9, P < 0.001, R^2 = 0.04$), although neither explained much variation. In our study, density-dependent mortality of trees may have been masked by severe drought stress as observed in other systems (e.g., Floyd et al.,

2009). Simply put, relative competition (e.g., for soil moisture) becomes less important during severe drought when few resources are available to any trees. Hayes et al., (2009) attributed the relationship between stand density and tree mortality to impacts on individual tree vigor and water availability (e.g., Kolb et al., 1998; Sala et al., 2005; Wallin et al., 2008), and pheromone plume distributions (Thistle et al.,

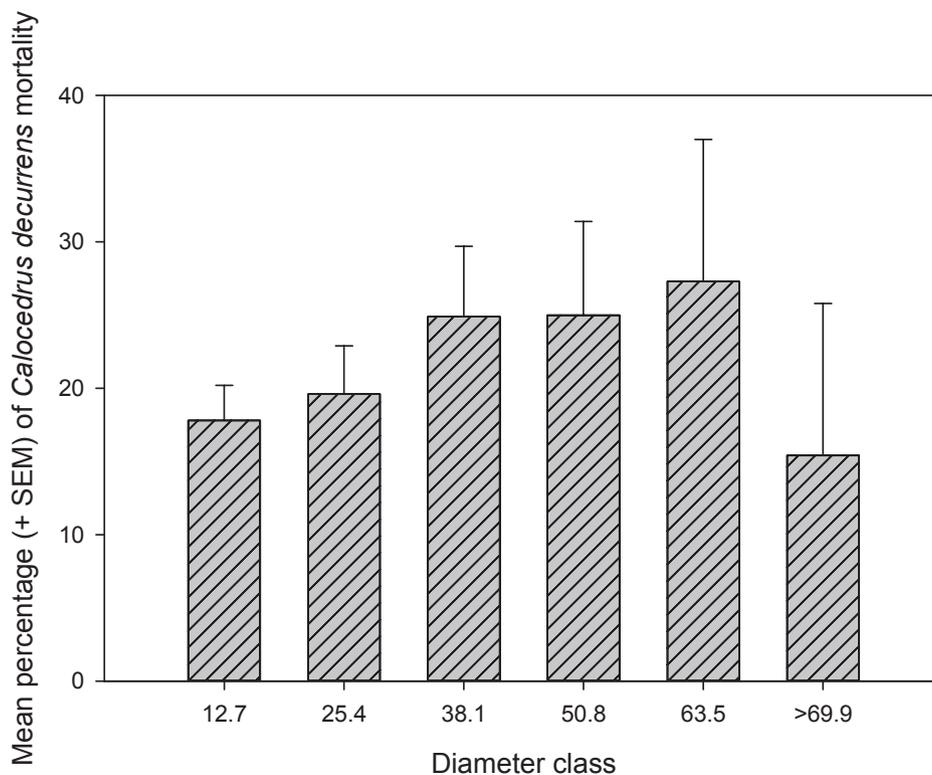


Fig. 10. Mortality of *Calocedrus decurrens* by diameter class (mid-point of 12.7-cm diameter classes, except for largest) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S. No significant differences were observed ($P > 0.05$).

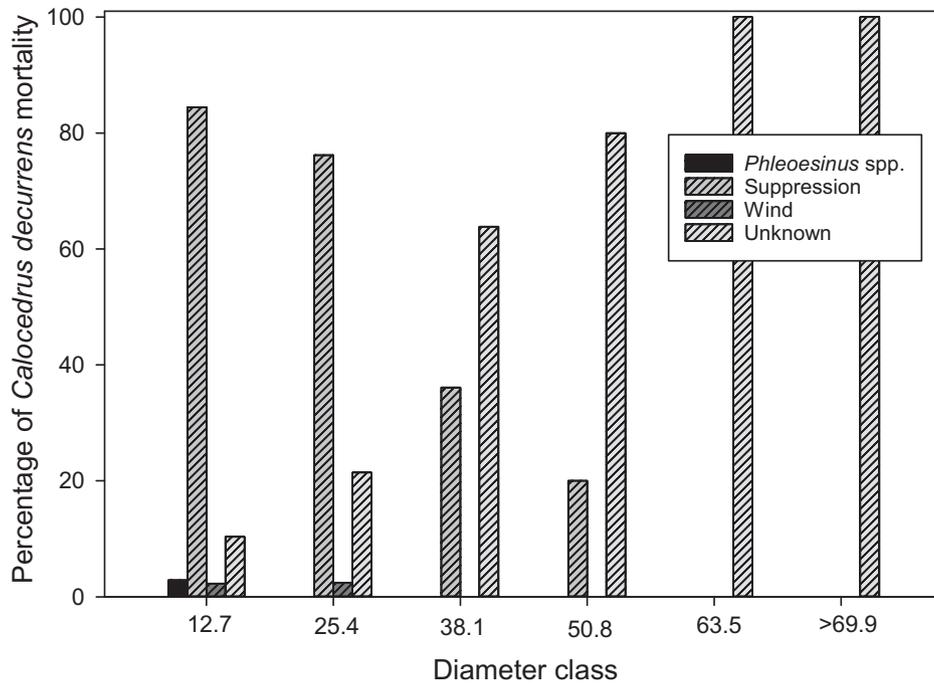


Fig. 11. Causes of *Calocedrus decurrens* mortality by diameter class (mid-point of 12.7-cm diameter classes) on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S.

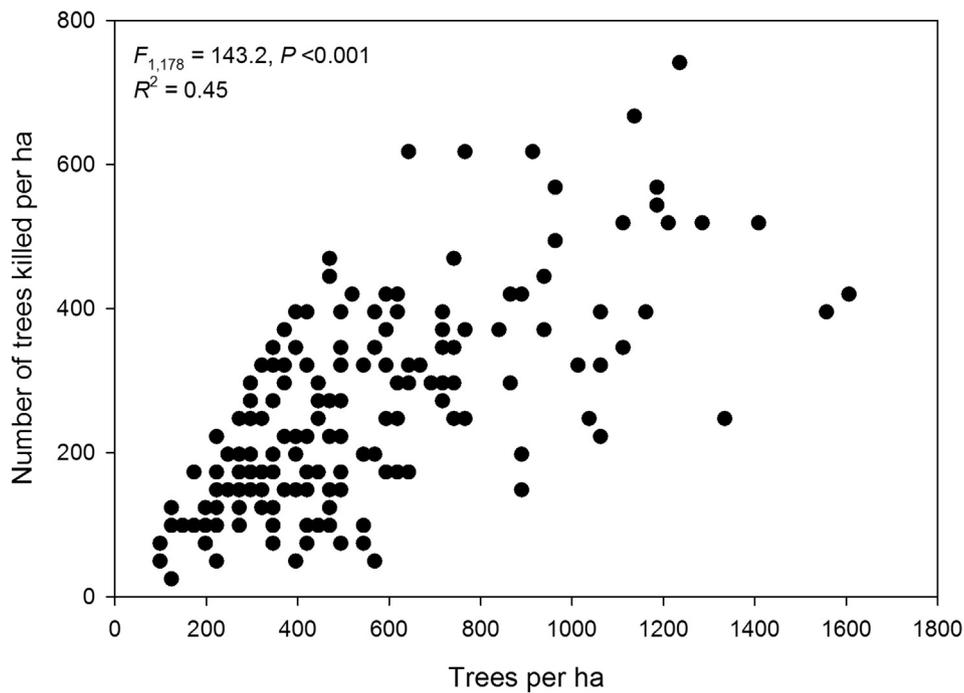


Fig. 12. Relationship between number of trees and number of trees killed on the Eldorado, Stanislaus, Sierra and Sequoia National Forests, California, U.S.

2004). They reported measures of tree competition were better predictors of tree mortality than measures of host availability recorded as basal area of *P. ponderosa* and numbers of *P. ponderosa*. Similar, we found measures of host availability explained less variation than measures of stand density (data not shown). Negrón et al., (2009) reported the probability of *P. ponderosa* mortality caused by bark beetles was positively correlated with tree density during drought in Arizona.

Fiddler et al., (1989) showed that thinning significantly reduced the amount of *P. ponderosa* mortality attributed to bark beetles in California. No tree mortality occurred in stands of < 9 m² per ha of basal

area, which agrees with the optimal stocking level of 11 m² per ha as described by Oliver (1979a, 1995). In our study, only one plot had ≤ 11 m² per ha of basal area in 2014. Oliver (1995) reported maximum SDI (365) for even-aged *P. ponderosa* stands in northern California was regulated by bark beetles. A SDI value of 230 defined a threshold for a zone of imminent bark beetle-caused tree mortality within which endemic populations killed a few trees, but net stand growth was positive. Only 27 plots had SDI values ≤ 230 and only half (91 plots) had SDI values ≤ 365 in 2014. Based on these thresholds, the majority of our plots would have been classified as “susceptible” to mortality by bark

beetles, and those that were not existed as small islands in a larger landscape mostly classified as “susceptible”, which likely increased their susceptibility due to contagion (Miller and Keen, 1960). In 2017, 84 plots had $\leq 11 \text{ m}^2/\text{ha}$ of basal area, and 175 plots had SDI values ≤ 365 . Based on these data, most plots would now be classified as of “low susceptibility”. As such, we expect to observe little tree mortality attributed to bark beetles during the next several years, especially in reference to *D. brevicornis* given the paucity of suitable hosts that remain (Fig. 4).

3.4. Seedlings and saplings

Tree regeneration was dominated by *C. decurrens* with few significant differences observed (Table 3). Of note, significantly fewer *P. lambertiana* seedlings occurred on the Sequoia than other national forests ($H = 11.2$, $df = 3$, $P = 0.011$), and of *Q. chrysolepis* on the Eldorado and Sequoia compared to the Sierra and Stanislaus ($H = 20.0$, $df = 3$, $P < 0.001$) (Table 3). Significantly more *A. concolor* seedlings occurred at the mid- (295.3 ± 83.7) and high elevation bands (348.6 ± 203.6) compared to the low elevation band (24.6 ± 17.3) ($H = 12.0$, $df = 2$, $P = 0.003$), which corresponds with dominance of overstory *A. concolor* (Tables 1 and 2). Significantly more *Q. chrysolepis* seedlings occurred at the low (242 ± 79.4) and mid-elevation band (246.1 ± 123.4) compared to the high elevation band (4.1 ± 4.1) ($H = 15.4$, $df = 2$, $P < 0.001$). Seedlings were dominated by shade-intermediate, shade-intolerant and shade-tolerant species, including *C. decurrens*, *Q. kelloggii* and *A. concolor*, respectively.

Significantly higher numbers of saplings occurred on the Stanislaus than the Eldorado and Sequoia ($H = 9.9$, $df = 3$, $P = 0.019$) (Table 3). Of note among elevation bands, significantly more *A. concolor* saplings occurred at the mid- (360.9 ± 154.7) and high elevation bands (488.0 ± 264.0) compared to the low elevation band (53.3 ± 45.3) ($H = 11.5$, $df = 2$, $P = 0.003$); more *Q. chrysolepis* saplings occurred at the low elevation band (504.4 ± 113.9) compared to the high elevation band (20.5 ± 10.6) ($H = 7.1$, $df = 2$, $P = 0.03$); and more *Q. kelloggii* saplings occurred at the low (291.2 ± 93.3) and mid-elevation band (274.8 ± 68.5) compared to the high elevation band (90.3 ± 34.6) ($H = 7.1$, $df = 2$, $P = 0.03$). In general, saplings were dominated by *C. decurrens*, *A. concolor*, and *P. ponderosa* (Table 3).

The relative densities of tree species in the understory differed from those in the overstory. For example, the density of *A. concolor*, *C. decurrens* and *Quercus* spp. was much greater in the understory than in the overstory, as has been reported elsewhere in the Sierra Nevada (Gray et al., 2005). *Calocedrus decurrens* seedlings and saplings are generally considered more drought tolerant than the other conifers (Pharis, 1966), but respond more slowly to release and are often heavily browsed by deer, *Odocoileus hemionus* Raf. (Powers and Oliver, 1990). Competition for light and soil moisture are primary factors limiting tree regeneration in the Sierra Nevada (Van Pelt and Franklin, 2000), especially in mixed-conifer stands. However, the higher light environment in the understory resulting from mortality of the overstory may kill some of the advanced regeneration that has mostly shade foliage (Boardman, 1977), but surviving individuals are likely to have more favorable growing conditions due to reduced competition for soil moisture. In the near-term, substantial litter and duff accumulations from the abundance of dead trees will likely further favor establishment of tree species other than *P. ponderosa*, due to its seed bed requirements (Powers and Oliver, 1990).

3.5. Shrubs, forbs, grasses and invasive weeds

Mountain misery or bearclover, *Chamaebatia foliolosa* Benth., whiteleaf manzanita, *Arctostaphylos viscida* Parry, and greenleaf manzanita, *Ar. patula* Greene, were the most abundant shrubs (Table 4). Competition by *Chamaebatia foliolosa* and *Arctostaphylos* spp. has been demonstrated to reduce *P. ponderosa* seedling survival and growth in

multiple studies (Oliver 1979b; Tappeiner and Radosevich, 1982; White and Newton, 1989). We observed little mortality of shrubs, which are capable of capturing and uptaking soil moisture at much lower concentrations than most trees, buffering shrubs from drought stress (Hurteau and North, 2008). Cover by forbs and grasses was variable throughout the network (Table 4), but more forbs were observed on the Sierra than the Stanislaus ($H = 13.1$, $df = 3$, $P = 0.004$). Bare ground accounted for only $0.3 \pm 0.1\%$ (Table 4). Among elevation bands, more grass cover occurred on the low ($10.9 \pm 2.3\%$) and mid-elevation bands ($8.0 \pm 1.7\%$) compared to the high elevation band ($3.3 \pm 1.0\%$) ($H = 27.6$, $df = 2$, $P < 0.001$), and more forbs occurred at the low elevation band ($8.7 \pm 1.8\%$) compared to the high elevation band ($5.0 \pm 1.3\%$) ($H = 12.3$, $df = 2$, $P = 0.003$). Litter occurred at higher levels on the high elevation band ($58.7 \pm 4.4\%$) compared to the low ($43.0 \pm 4.4\%$) ($H = 7.7$, $df = 2$, $P = 0.02$), where higher tree densities were observed (Tables 1 and 2). More bare ground occurred at the high elevation band ($0.6 \pm 0.2\%$) compared to the low ($0.02 \pm 0.02\%$) and mid-elevation bands ($0.2 \pm 0.09\%$) ($H = 13.0$, $df = 2$, $P = 0.001$).

Many disturbances promote plant invasions by increasing resource availability and decreasing plant competition. Surprisingly, previous studies of bark beetle-impacted landscapes in the western U.S. have reported few increases in invasive plants (Fettig et al., 2015). In our study, 40 plots contained species considered invasive, causing damage, or having the potential to cause damage (www.cal-ipc.org/ip/inventory/index.php 2016). Cheatgrass, *Bromus tectorum* L., was the most common (17 plots). Others included ripgut brome, *Bromus diandrus* Roth (9 plots), bull thistle, *Cirsium vulgare* (Savi) Ten. (8 plots), Johnsongrass, *Sorghum halepense* (L.) Pers. (4 plots), yellow star-thistle, *Centaurea solstitialis* L. (3 plots), mullein, *Verbascum thapsus* L. (2 plots), and Himalayan blackberry, *Rubus armeniacus* Focke (1 plot). Future surveys will facilitate a better understanding of the impacts of this mortality event on the distribution and abundance of invasive plants.

4. Conclusions

Droughts accompanied by warmer temperatures (i.e., “hotter droughts” or “global change-type droughts”) are increasingly recognized as important drivers of tree mortality not only in the western U.S. (Fettig et al., 2013; Crockett and Westerling, 2018), but worldwide (Allen et al., 2010, 2015; Hartmann et al., 2018). In short, warming amplifies chronic and acute water stress, and increases the incidence and severity of forest disturbances and drought-induced mortality of forest vegetation. During recent decades, tree mortality attributed to bark beetles has exceeded that by wildfires in the western U.S. (Hicke et al., 2016) raising concerns about the sustainability of some forests (Morris et al., 2018). In our study, 48.9% of trees died in a period of three years, most of which were *P. ponderosa* in the larger-diameter classes. Accordingly, we observed immediate shifts in forest structure and compositions, with a decline in the relative proportion of *P. ponderosa* and increases in the relative proportions of *C. decurrens*, *Q. kelloggii* and *Q. chrysolepis*. Tree regeneration was dominated by *C. decurrens* and *Quercus* spp., however additional surveys are required to get a better understanding of recruitment of these species to the mid- and overstory. In the absence of management intervention, we expect to see some type conversions (e.g., to *Cedrus* and *Quercus* or shrublands), particularly in the lower elevations of the southern Sierra Nevada where mortality of dominant and co-dominant trees was most severe.

Recently, the California Tree Mortality Task Force (2017) released recommendations for comprehensive restoration of the Sierra Nevada. Key elements of their plan include: (1) increasing the pace and scale of thinning, prescribed burning and managed wildfire, (2) rebuilding California’s forest products industry to facilitate adequate biomass removals, (3) improving forest structure for wildlife habitat, (4) restoring ecologically-sensitive areas (e.g., meadows), (5) facilitating important legislative and administrative reforms that act as barriers to project

Table 4
Ground cover percent on four national forests in the central and southern Sierra Nevada, California, USA.

	Eldorado	Stanislaus	Sierra	Sequoia	All
Shrubs	34.6 ± 5.2 a	39.3 ± 4.8 a	32.4 ± 5.2 a	32.9 ± 4.8 a	34.8 ± 2.5
<i>Chamaebatia foliolosa</i>	26.6 ± 5.0 a	31.6 ± 4.8 a	24.2 ± 5.1 a	24.2 ± 4.1 a	26.7 ± 2.4
<i>Arctostaphylos viscida</i>	0.8 ± 0.5 a	0.8 ± 0.6 a	3.3 ± 0.9 a	3.5 ± 1.4 a	2.1 ± 0.5
<i>Arctostaphylos patula</i>	0.0 ± 0.0 a	0.4 ± 0.2 a	0.0 ± 0.0 a	2.2 ± 0.8 a	0.7 ± 0.2
Forbs	7.0 ± 2.5 ab	3.0 ± 0.9 b	7.6 ± 1.6 a	9.6 ± 2.1 ab	6.8 ± 0.9
Grasses	6.1 ± 1.7 a	4.2 ± 1.4 a	8.2 ± 1.7 a	11.3 ± 3.0 a	7.4 ± 1.0
Bare ground	0.3 ± 0.1 a	0.5 ± 0.3 a	0.1 ± 0.1 a	0.2 ± 0.1 a	0.3 ± 0.1

Values are mean ± SEM, based on one 0.004-ha subplot per 11.3-m fixed-radius plot. Most abundant shrub species shown.

implementation, and (6) monitoring and adaptive management. In areas where substantial tree mortality has not yet occurred (e.g., some mid- to high elevations of the Eldorado), forest managers might reduce stand densities to increase the resilience of forests to drought and disturbances incited by drought (North et al., 2015a; Kolb et al., 2016; Fettig et al., 2018a) by use of mechanical thinning and/or fire, the latter either prescribed or managed wildfires (North et al., 2015b). To that end, Goulden and Bales, (2014) showed that evapotranspiration increases exponentially with increased Normalized Difference Vegetation Index (NDVI, a measure of forest greenness and density) supporting the value of thinning to reduce drought stress in the southern Sierra Nevada, and a recent study of the Illilouette Creek Basin in Yosemite National Park found increases in wetness occurred following 40 years of managed wildfire (Boisramé et al., 2017). Numerous other studies have demonstrated the effectiveness of thinning to increase resistance and resilience to bark beetles (Fettig et al., 2007) and wildfire (McIver et al., 2013). There are other tools available (e.g., insecticides and semi-chemicals) to protect individual trees (e.g., blister rust-resistant *P. lambertiana*) or stands of trees from mortality attributed bark beetles during periods of drought (Fettig and Hilszczański, 2015). To that end, it is likely that stocking thresholds (e.g., Oliver, 1995) will need to be lowered to maintain adequate levels of resistance and resilience under increased levels of drought stress projected for this region (Difffenbaugh et al., 2015). High variability thinning (focused on spatial complexity) coupled with prescribed burning may best align forests in the central and southern Sierra Nevada with historical conditions, which were known to be more resilient to drought and disturbances incited by drought (Knapp et al., 2017).

Tree mortality resulting from colonization of native bark beetles is an important part of the ecology of these forests. Some level of tree mortality is desirable and often results in a mosaic of age classes and tree species compositions that increases resistance and resilience to multiple disturbances (Fettig, 2012). This differs from impacts associated with large-scale outbreaks, which may negatively impact several ecological goods and services, including timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, biodiversity, endangered species, carbon sequestration and storage, and cultural resources, among many others (Morris et al., 2018). It is important to note that the ecology and impact of bark beetles is also influenced by other biotic, abiotic, and anthropogenic (e.g., management activities and land use patterns) disturbances that also directly influence successional pathways. To our knowledge, this is the most severe outbreak of *D. brevicomis* in recorded history, and among the largest for any bark beetle in recent decades in the western U.S. (Fettig et al., 2018b). Furthermore, much of the tree mortality occurred in and near the wildland urban interface (California Tree Mortality Task Force, 2018), which may foreshadow impacts of future outbreaks of *D. brevicomis* (and other species) as human populations shift from the eastern to western U.S. (U.S. Census Bureau, 2012). It also highlights increased mortality risks for trees during severe droughts, particularly under warmer temperatures attributed to climate change (Clark et al., 2016; Crockett and Westerling, 2018). In the future, it is likely that more frequent extreme weather events will increase

the frequency and magnitude of severe ecological disturbances in many forests, driving rapid and often persistent changes in forest structure, composition and function across large landscapes.

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