

Which trees die during drought? The key role of insect host-tree selection

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Abstract

1. During drought, the tree subpopulations (such as size or vigour classes) that suffer disproportionate mortality can be conceptually arrayed along a continuum defined by the actions of biotic agents, particularly insects. At one extreme, stress dominates: insects are absent or simply kill the most physiologically stressed trees. At the opposite extreme, host selection dominates: outbreaking insects kill trees independently of their stress, instead selecting trees based on size or other traits. Intermediate responses are also possible. Yet for mixed-species forests, we lack a broad understanding of the relative importance of insects in determining exactly which subpopulations of trees suffer disproportionate mortality during drought, and whether these subpopulations differ among co-occurring tree species.
2. During an extreme drought, we documented the roles of native bark beetles in the mortality of five tree species in California's Sierra Nevada. We analysed the patterns and agents of tree mortality in 12 permanent plots and the patterns of mortality in 89 temporary plots.
3. Most tree mortality was associated with bark beetles. However, the growth rates (an indicator of chronic stress) and sizes of trees that suffered greatest bark beetle-related mortality differed sharply among tree taxa, variously conforming with domination by stress (*Abies concolor*), domination by host selection (*Pinus lambertiana* and *P. ponderosa*) or a mix of the two (*Calocedrus decurrens*). *Quercus kelloggii* mortality remained relatively low. Thus, even during extreme drought substantial proportions of stressed trees survived because they were of sizes that mostly avoided fatal insect attack. Conversely, substantial proportions of comparatively unstressed trees died because they were of sizes that were selectively killed by outbreaking insects.
4. *Synthesis*. Native bark beetles were primarily responsible for determining which subpopulations of trees suffered greatest mortality during drought. However, idiosyncratic host-tree selection by the different bark beetle taxa meant that the

Stephenson and Das contributed equally to this work.

tree subpopulations suffering greatest mortality differed strikingly among tree taxa—for example, high mortality of small trees of one species, but of large trees of another. If idiosyncratic host-tree selection by biotic mortality agents proves to be a generally common phenomenon, it could help explain weak broadscale correlations between tree traits and tree mortality during drought.

KEYWORDS

bark beetle, drought, forest dieback, forest disturbance, insect outbreak, stress, temperate forest, tree mortality

1 | INTRODUCTION

Extensive tree mortality during recent hotter droughts—droughts in which unusually high temperatures exacerbate the effects of low precipitation—has contributed to renewed interest in the patterns and mechanisms of tree mortality during drought (Allen, Breshears, & McDowell, 2015). Yet even in forests experiencing severe, multi-year drought, the proportion of trees that dies rarely exceeds one half (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Zhang, Shao, Jia, & Wei, 2017). Within a given tree species, the subset of trees that dies is not random; rather, some subpopulations of trees—often defined by size and vigour—typically suffer greater drought mortality than others (O'Brien et al., 2017). These vulnerable subpopulations, in turn, are generally thought to be determined by (a) the magnitude of direct physiological stress (such as hydraulic failure or carbon starvation) suffered by trees in the subpopulations, (b) attack by biotic agents (insects and pathogens) or (c) both (Aguadé, Poyatos, Gómez, Oliva, & Martínez-Vilalta, 2015; Gaylord, Kolb, & McDowell, 2015; Hartmann et al., 2018; McDowell et al., 2008, 2011; McDowell, Ryan, Zeppel, & Tissue, 2013). Importantly, stress alone does not always predict which trees die: as elaborated below, some insects can selectively attack and kill trees based on tree traits other than, or in addition to, physiological stress. Thus, in addition to requiring a robust understanding of tree physiology, our ability to forecast the effects of climatic changes on forests also requires a robust understanding of the varying roles and importance of tree-killing insects.

Yet despite well-documented interactions between drought and insects (Anderegg et al., 2015; Jactel et al., 2012; Kolb et al., 2016; Seidl et al., 2017; Weed, Ayres, & Hicke, 2013), we currently lack broad generalizations about the variable roles of insects in determining which subpopulations of trees suffer greatest mortality. Conceptually, the effects of insects can be arranged along a continuum (Figure 1). At one extreme, stress dominates: insects may be absent or may simply be the final agent that kills the subpopulations of trees that have already been most weakened by physiological stress. That is, insect attack might effectively lower the stress threshold that trees can survive, but physiological stress still accurately predicts which trees live or die. Evidence supporting this end of the continuum comes, for example, from observations that chronically

stressed trees, as indicated by persistent slow growth preceding drought, often have higher mortality rates during drought—with or without insect attack—than their less stressed neighbours (e.g. Pedersen, 1998; Suarez, Ghermandi, & Kitzberger, 2004; Kane & Kolb, 2014; Gaylord et al., 2015; Cailleret et al., 2017). Chronically stressed trees enter a drought already exhibiting some of the same hydraulic, carbon gain and defensive problems that the drought will only serve to exacerbate (see Section 4.2).

At the other extreme, insect host-tree selection that is unrelated to tree stress determines which subpopulations of trees suffer greatest mortality during drought. A drought-triggered insect outbreak might initiate in stressed trees and then spread to include unstressed trees, but be limited mostly to trees with traits that best meet the insects' host needs (Figure 1). While insects proximately use an array of visual, olfactory, gustatory and tactile cues to select which trees to attack (Raffa, Andersson, & Schlyter, 2016), ultimately the selected trees often fall into easily identified subpopulations, such as distinct size classes. When host selection dominates, the subset of trees that dies becomes decoupled from the magnitude of physiological stress trees experience; that is, some of the least stressed trees may die (because they are of sizes successfully attacked by outbreaking insects), and some of the most stressed trees may survive (because they are of sizes that are rarely successfully attacked by outbreaking insects). This end of the continuum has been represented, for example, by some recent drought-triggered bark beetle outbreaks in western North America. These outbreaks often spread from stressed trees to healthier trees and continued for many years after the droughts ended, with beetles disproportionately killing larger trees (Creeden, Hicke, & Buotte, 2014; Pfeifer, Hicke, & Meddens, 2011; Raffa et al., 2008). In some cases, rather than insects killing trees independent of the trees' stress, insects can even disproportionately kill the most vigorous, least stressed trees (Boone, Aukema, Bohlmann, Carroll, & Raffa, 2011; Cooper, Reed, & Ballantyne, 2018; de la Mata, Hood, & Sala, 2017); we consider this to be an additional manifestation of domination by host selection.

Intermediate positions between the extremes are also possible. For example, within a given tree species, insects might selectively kill a particular size class of trees, but only the most stressed trees within that size class (Figure 1). Additionally, although, for simplicity, Figure 1 illustrates sharply defined subpopulations killed by insects,

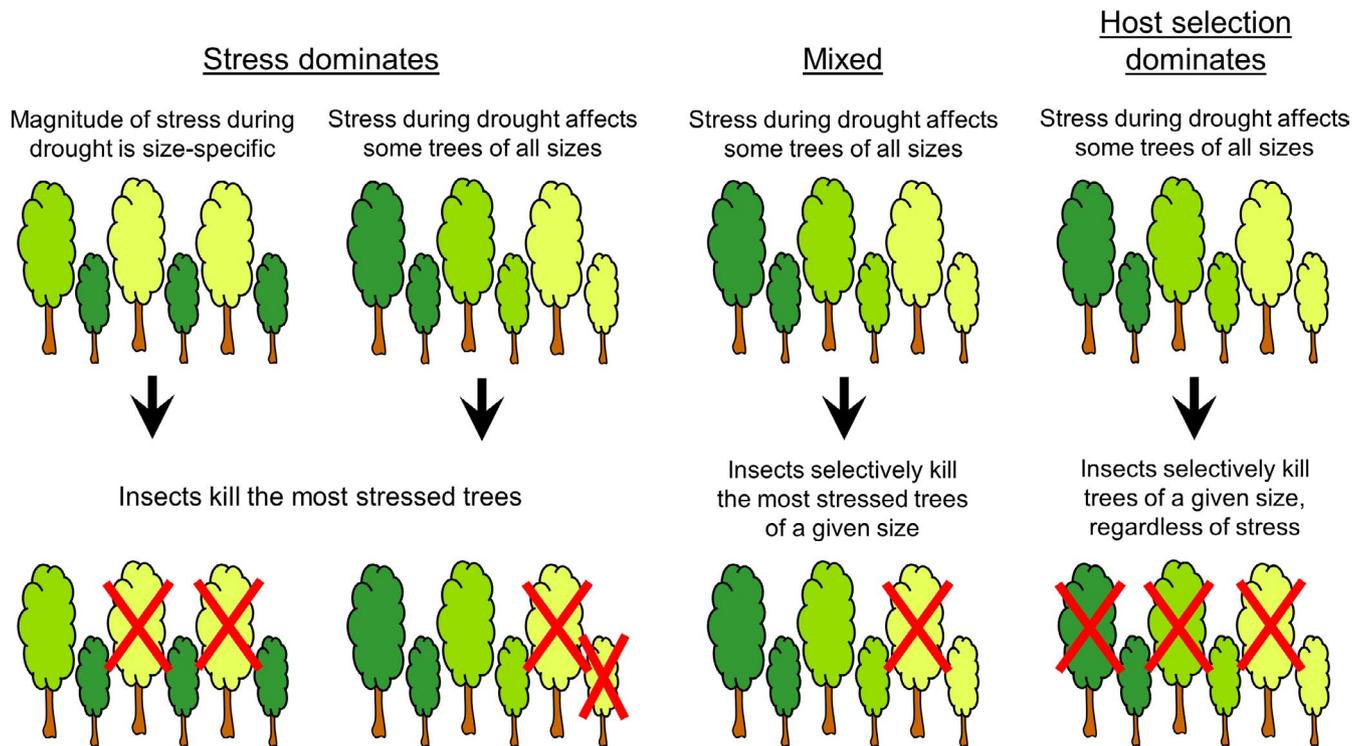


FIGURE 1 Example roles of insects in determining which subpopulations of trees suffer greatest mortality during drought. Shades of green indicate the magnitude of stress experienced by trees, from low (dark green) to high (light green). At one extreme (stress dominates), insects disproportionately kill the most stressed trees (indicated by the red Xs). The most stressed trees could predominantly occur in a particular size class (cf. Bennett et al., 2015; McDowell & Allen, 2015) or could occur in trees of all sizes. At the opposite extreme (host selection dominates), insects disproportionately kill trees within a particular size class regardless of their stress. Mixed responses are also possible, in which insects disproportionately kill trees within a particular size class, but only the most stressed trees of that size. Several other possibilities could be illustrated, such as mortality dominating in the smallest rather than largest trees, or outbreaking insects preferentially killing the most vigorous (least stressed) trees during drought (see Section 1)

the magnitude of insect-induced mortality could fall along a continuum. That is, although trees of all sizes or stress levels could suffer elevated mortality from insect attack during drought, certain sizes or stress levels could be disproportionately affected.

The continuum represented in Figure 1 helps highlight questions relevant to modelling and forecasting the effects of climatic changes on forests (Fisher et al., 2018; Hartmann et al., 2018; McDowell et al., 2011; McDowell, Fisher, et al., 2013). For example, at continental and global scales, how common are various positions along the continuum between domination by stress and domination by host selection? Are particular sizes of trees predictably more vulnerable to drought (cf. Bennett et al., 2015; Hember, Kurtz, & Coops, 2017)? If so, how does this depend on specific mechanisms of tree mortality? Do the answers to these questions vary geographically, or among phylogenetically related groups of tree taxa? These and related questions have gained additional importance in light of increasing reports of damaging insect outbreaks—often associated with novel environmental conditions, including hotter droughts—by native species that previously were considered to be innocuous (Haavik, Billings, Guldin, & Stephen, 2015; Kolb et al., 2016; Weed et al., 2013).

Our ability to confidently answer such questions has been limited by the paucity of relevant studies. Of the many studies worldwide that have quantified drought-related tree mortality (e.g. as

summarized in Allen et al., 2010; Allen et al., 2015; Hartmann et al., 2018), few have thoroughly documented the role of tree-killing insects (see the reviews by Raffa et al., 2008; Anderegg et al., 2015). Particularly rare are studies that have reported insect-induced tree mortality, or lack thereof, relative to both tree size and magnitude of stress (cf. Figure 1). Of those few, most have focused on a single tree species and (or) a single insect species (e.g. Miller & Keen, 1960; Boone et al., 2011). We thus lack the kinds of insights that could be gained by elucidating the role of an array of insect taxa in the mortality of several different co-occurring tree species, all during the same drought.

To begin filling some of these knowledge gaps, we took advantage of California's 2012–2016 hotter drought. The drought was the most extreme in the ~120-year instrumental record (and perhaps much longer), and its record-breaking severity was partly a consequence of higher temperatures (AghaKouchak, Cheng, Mazdiyasi, & Farahmand, 2014; Diffenbaugh, Swain, & Touma, 2015; Griffin & Anchukaitis, 2014; Williams et al., 2015). Within California, drought-related tree mortality was greatest in the region that included our study: the low-elevation forests of the southern Sierra Nevada (Byer & Jin, 2017; Moore, Woods, Ellis, & Moran, 2018; Potter, 2017), which are dominated by mixtures of several co-occurring tree species (Fites-Kaufman, Rundel, Stephenson, & Weixelman, 2007). Each

of the five dominant tree species in our study was associated with its own set of native bark beetle taxa, allowing us to document several spatially and temporally co-occurring sets of drought–insect interactions. Specifically, we wished to address the following questions: How important were insects in determining which trees died during drought? Was the answer consistent among tree species? What are implications for our understanding of the patterns and mechanisms of tree mortality during drought?

2 | MATERIALS AND METHODS

2.1 | Study area and environment

Our study area was in old-growth, all-aged mixed conifer forests (Fites-Kaufman et al., 2007) in the Kaweah River watershed of Sequoia National Park, California (36.6° N, 118.8° W) (Figure S1). Sampled elevations ranged from 1,535 to 2,405 m. The climate is montane Mediterranean, with warm, dry summers and cool, wet winters in which ~25%–60% of annual precipitation (which averages 1,100–1,400 mm) falls as snow, depending on elevation (Stephenson, 1988). Historical mean annual temperature declines from ~11°C at 1,500 m to ~6°C at 2,400 m.

Soils are largely derived from granitic parent material, but in a few areas from metamorphic substrates like marble. Parts of the southern Sierra Nevada's forested zone have a weathered regolith >10 m deep (Holbrook et al., 2014), and through the dry summer months, deeply rooted trees regularly transpire a quantity of water that is equivalent to what would be held in at least the top several metres of the regolith (Kelly & Goulden, 2016; Klos et al., 2018; Witty, Graham, Hubbert, Doolittle, & Wald, 2003). At the opposite extreme, other parts of the forested zone have almost no regolith (Hahm, Riebe, Lukens, & Araki, 2014; Klos et al., 2018), and thus little summer water availability for trees of any size. For any regolith depth, topographic position, topographic convergence and proximity to water may create substantial additional spatial heterogeneity in water availability for both large and small trees (e.g. Urban, Miller, Halpin, & Stephenson, 2000; Paz-Kagan et al., 2017; Klos et al., 2018). This fine-scale variation in water availability likely contributed to a broad range of moisture stress experienced by individual trees of all sizes, both before and during the drought.

2.2 | Time periods analysed

We wished to compare tree mortality and its causes during drought and non-drought periods. Choices of these study periods were informed by past work showing that tree mortality in our mixed conifer forests is best correlated with drought averaged over the current and preceding 2 years (Das, Stephenson, Flint, Das, & van Mantgem, 2013). Accordingly, we defined study periods by using trailing 3-year running means of summer (June–August) self-calibrated Palmer Drought Severity Index (PDSI), calculated from the Palmer's Z-index data developed for Williams et al. (2017) and standardized to a 1921–2000 baseline period. Values were calculated for a 236,600-ha quadrilateral

that encompassed the mixed conifer forest zone of Sequoia and Kings Canyon national parks (see Stephenson et al., 2018).

Although California's meteorological drought (below-average annual precipitation) spanned 2012–2016, our running mean PDSI values suggested that 2014 would be the effective start of the drought for tree mortality, and that the effects would continue through 2017 (Figure 2). Indeed, our lowest elevation intensive plots (described below) began to show increased mortality in 2014, and by 2017, most of these plots were experiencing mortality that was well above average. We thus chose 2014–2017 as our focal years for drought-related tree mortality.

For comparison with the 2014–2017 drought period, we selected 2004–2007 as a baseline non-drought period likely dominated by typical low levels of background tree mortality. Running mean PDSI values for 2004–2007 were near zero (indicating neither excessive drought nor excessive moisture) and followed 9 years of relatively benign climate (Figure 2).

2.3 | Plot types and tree species analysed

An existing network of long-term forest monitoring plots (Das, Stephenson, & Davis, 2016)—referred to here as our 'intensive plots'—provided the detailed data needed to quantify factors contributing to tree mortality, both during and preceding the drought, by tree species, size class and growth rate. These plots thus provided the foundation for addressing our primary questions.

However, we also wished to address the possibility that data from the intensive plots alone might not adequately reflect size-specific tree mortality at a landscape scale. Specifically, our intensive plots were not randomly located (locations had been chosen decades earlier based on accessibility and species compositions representative

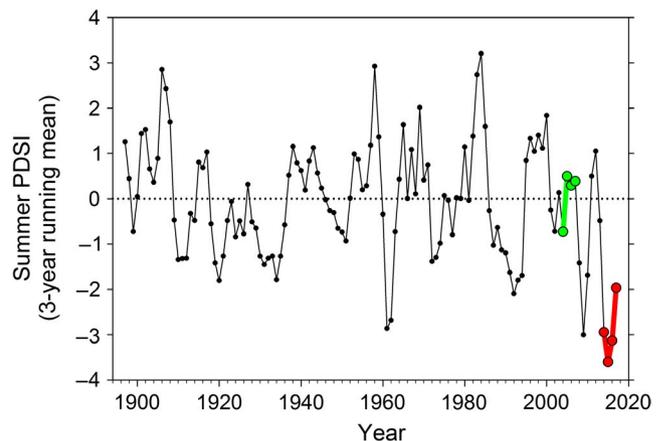


FIGURE 2 Three-year running mean of re-standardized, self-calibrated summer (June–August) Palmer Drought Severity Index (PDSI) from 1897 to 2017 for the study region. PDSI values that are more negative indicate more severe drought. The 2014–2017 drought period is highlighted in red; 2015, 2016 and 2014 were, respectively, the first, second and fourth most severe 3-year mean drought years in the 121-year record. The 2004–2007 reference period for non-drought (background) tree mortality is highlighted in green

of dominant forest types), and the 12 intensive plots that met our criteria for analysis (Section 2.4) might inadequately capture spatial variation in forest structure, composition and mortality during the drought. In 2016, we therefore additionally sampled 89 randomly located 'landscape plots' (Section 2.5).

Data from the two kinds of plots differed somewhat spatially and temporally. While the elevational ranges overlapped, the intensive plots included higher elevations (1,618–2,405 m) than the landscape plots (1,535–1,826 m) (Figure S1). As appropriate, we considered this difference when interpreting results. Additionally, data from the intensive plots spanned the 2014–2017 drought years, whereas data from the landscape plots spanned 2014–2016 (a consequence of funding and staffing). When we reanalysed the intensive plot data only for 2014–2016, to match the landscape plot sampling period, we found that our broad conclusions remained the same; we therefore present the full 2014–2017 analyses for the intensive plots.

We limited our study to the five tree species that each had >500 living and dead individuals in our landscape plots: *Abies concolor*, *Calocedrus decurrens*, *Pinus lambertiana*, *P. ponderosa* and *Quercus kelloggii*.

2.4 | Intensive plot methods

Our permanent 0.9- to 2.5-ha intensive plots (Table S1) were established between 1982 and 2001. Every living tree ≥ 1.37 m tall was mapped, tagged and assessed annually for mortality through 2017, with trunk diameters remeasured at ~5-year intervals (Das et al., 2016). Out of our broader permanent plot network, we used only the 12 plots that had not experienced fire since establishment and that also included at least 10 trees belonging to one or more of our five focal species.

Every tree in our intensive plots that had died since its previous annual visit was thoroughly assessed for 'mortality factors'—agents that potentially contributed to the tree's death (see Das et al., 2016 for details). Assessments included reviewing comments about a given tree's condition (including ongoing insect attacks) in previous years; examination for external indicators of poor health, damage or biotic attack (e.g. thinning crown foliage, pitch tubes, fungal conks); bark removal at different locations to find and identify beetle galleries and to search for signs of fungal attack; and some minor excavation and bark removal around the base to look for evidence of fungal attack (such as mycelia or rhizomorphs of *Armillaria*). Personnel conducting the assessments received intensive annual training, including a short field course led by the regional U.S. Forest Service pathologist and entomologist (author BMB is the entomologist), who were also consulted throughout the field season when their expertise was needed.

We listed bark beetles (Curculionidae: Scolytinae) as mortality factors if, upon peeling bark from a recently dead tree, we saw characteristic galleries (tunnels) at densities capable of contributing to a tree's death. The bark beetle taxa we encountered are reported in Section 3.2; our reasons for concluding that bark beetles were the probable proximate cause of tree mortality are discussed in Section 4.3. Without attempting to identify species, we listed bark beetles

as suspected mortality factors when we could see, at heights above which we could safely remove bark, various combinations of extensive pitching, apparent bark beetle exit holes, extensive insect frass, bright red foliage and abundant holes created by woodpeckers seeking beetle larvae. Only 6.7% of our bark beetle records fell in the 'suspected' category, and unless otherwise indicated, our analyses of bark beetle-related mortality include this category.

2.5 | Landscape plot methods

From 15 June to 26 October 2016, we established circular 0.1-ha landscape plots in old-growth mixed conifer forest within a relatively accessible 1,705-ha area between 1,524 and 1,829 m (5,000–6,000 ft) elevation in Sequoia National Park, California (Figure S1). Forests at these low elevations in the southern Sierra Nevada experienced some of the greatest tree mortality in California during the drought (Byer & Jin, 2017; Moore et al., 2018; Paz-Kagan et al., 2017; Potter, 2017). Plot locations were selected a priori using Generalized Random Tessellation sampling (GRTS), which provides a spatially balanced sample that has a true probability design, allowing valid inference for the entire study area (Stevens & Olsen, 2004). In the field, plot centres were determined using a proximity alarm on handheld GPS units, with the alarm sounding when proximity to the predetermined GRTS location was within the measurement error of the device. Plots were then defined as the area within a 17.84 m horizontal radius (determined by electronic rangefinders) from these plot centres. High-precision plot centre locations were then determined using a JAVAD Triumph-2 GPS unit that, after post-processing, determined actual locations with submeter accuracy. Established plot centres usually were quite close to the predetermined GRTS targets; for example, our original GRTS targets fell within established plot boundaries 93% of the time. We attempted to establish 98 plots, but six plots could not be reached safely, and three plots overlapped roads, leaving 89 plots for analysis.

Within each landscape plot, we recorded the species, trunk diameter at breast height (DBH; breast height = 1.37 m) by 5-cm classes and condition (living or dead) of all standing conifers >0 cm DBH and all standing angiosperms ≥ 5 cm DBH. 'Standing' was defined as any tree leaning less than 45 degrees from vertical and at least 1.37 m in length. In the landscape plots, we did not determine tree growth rates (such as from increment cores) or factors contributing to each tree's death, both of which would have been prohibitively time-consuming.

Each dead tree was further classified according to its foliage and fine twig retention (Table S2) to allow us to estimate year of death (Section 2.7). Of the 10,117 trees of all species sampled in the landscape plots, 2,836 were dead.

2.6 | Intensive plot analyses

Within each tree species (or genus), we analysed trees grouped by size, and by size and growth rate, both during the drought (2014–2017) and non-drought (2004–2007) periods. For analyses by size

alone, we used four diameter classes (cf. Das et al., 2016): >0 to 10 cm (≥ 5 to 10 cm for *Q. kelloggii*, to match the landscape plots), ≥ 10 to < 20 cm, ≥ 20 to < 50 cm and ≥ 50 cm. For analyses in which we additionally classified trees by growth rates, small sample sizes meant we used only two diameter classes: < 20 cm and ≥ 20 cm DBH. We calculated diameter growth rates from the two most recent consecutive trunk diameter measurements (excluding trees with growth rates < -2 mm/year and > 20 mm/year; cf. Das & Stephenson, 2015) and classified trees into three growth-rate classes we had previously defined using data that preceded the drought (Das et al., 2016): < 0.5 mm/year (high chronic stress; mortality rates were high), ≥ 0.5 mm/year and ≤ 4.0 mm/year (intermediate stress; mortality rates declined rapidly with increasing growth rate) and > 4.0 mm/year (low stress; mortality rates were low and largely independent of growth rate). Elsewhere we have demonstrated that, for our species, absolute diameter growth rate is a better predictor of tree mortality than other common growth metrics, such as basal area increment (Das & Stephenson, 2015).

As we calculated growth rates from each tree's two most recent diameter measurements, taken at ~ 5 -year intervals, growth rates associated with the 2004–2007 and 2014–2017 mortality intervals often included at least some growth that occurred both before and during those intervals. For example, for a tree that died in 2016, the two most recent diameter measurements might have occurred in 2009 and 2014, so that its growth included 4 years preceding the 2014–2017 mortality interval and 1 year early in the interval. We re-analysed the data using only growth calculated from diameter measurements preceding the 2014–2017 drought interval, finding no differences in our broad results and conclusions. This was expected, given the tendency in our study species for a given tree's growth during a particular 5-year interval to be predictive of its growth during the next 5-year interval (e.g. van Mantgem & Stephenson, 2005). That is, slow growth generally reflected chronic stress that preceded the drought and continued into the drought.

We set a minimum requirement of 20 trees in a group (a particular combination of species, size class and growth-rate class) for analysis and presentation of results. As the total sample of only 184 *P. ponderosa* in our intensive plots (Table S1, Figure S2) yielded many size and growth-rate classes with < 20 trees, we combined the two *Pinus* species for analyses involving the intensive plots. Combining the two *Pinus* species was justified because (a) bark beetle species in the genus *Dendroctonus*, which exhibited similar host selection preferences (Section 4.3), heavily dominated mortality in both species and, accordingly, (b) other studies during the same drought found (as we did in our landscape plots; Section 3.3) similar size-specific mortality patterns in the two *Pinus* species (Fettig, Mortenson, Bulaon, & Foulk, 2019; Pile, Meyer, Rojas, & Roe, 2018). After combining the two *Pinus* species, only a few groups—all in *Q. kelloggii*—did not meet the 20-tree threshold.

Within individual tree species and size classes, we calculated the proportions of trees that died in association with various mortality factors (cf. Das et al., 2016). If bark beetles occurred in association with additional mortality factors on a tree, we considered bark

beetles to be the proximate cause of tree mortality (see Section 4.3). The most common additional mortality factor associated with bark beetles was suppression (nearly 40% of trees with bark beetles), which contributes to the long-term chronic stress that we addressed in our growth-rate analyses. Other mortality factors associated with bark beetles (in $\sim 12\%$ of trees with bark beetles) were either unlikely to be proximate causes of mortality (such as past physical damage) or could have been co-contributors to mortality (such as pathogens).

To test for differences in mortality rates between various groups (e.g. proportions of small *A. concolor* killed by bark beetles in 2014–2017 vs. 2004–2007), we used Fisher's exact test for the contingency table of numbers of trees by status (killed by bark beetles or not killed by bark beetles) at the end of the periods of interest.

2.7 | Landscape plot analyses

Data from our landscape plots provided a snapshot in time, during the summer of 2016, of numbers of living and dead trees by species and size class, with each dead tree classified according to its foliage or fine twig retention (Table S2). However, unlike our intensive plots, we did not know the precise year of mortality for dead trees in our landscape plots, meaning that some of the dead trees undoubtedly died prior to the drought and were thus irrelevant to our analyses. We therefore developed an approach to calculate the probability that a given tree died prior to the drought (see the Supporting Information). The key data allowing us to accomplish this came from the intensive plots where, extending back decades, we knew the exact years of death for 2,297 standing dead trees of our five target species (Das et al., 2016; van Mantgem & Stephenson, 2007). In the summer of 2016, we classified each of these trees according to the same foliage and fine twig retention classes we used in the landscape plots, allowing us to fit probability distributions for year of tree death as functions of species and foliage or twig retention class, and thus to calculate the probability that a tree in the landscape plots had died prior to the drought. Given that probability, we then fit a mixed effects logistic model to estimate the probability that the tree had died in 2014–2016, using species-size categories as predictors and plot as a random effect. All parameters were fit as part of Bayesian models using a Markov Chain Monte Carlo approach. We analysed drought mortality in the same four DBH classes as the intensive plots. Analyses were performed using R 3.1.1 with the coda, rjags and R2jags packages in combination with JAGS 4.2.0 (Plummer, 2015; R Core Team, 2014). Details are provided in the Supporting Information.

3 | RESULTS

3.1 | Overall drought mortality

In the intensive plots, of the 8,522 focal species trees alive in 2013, 22.6% died in 2014–2017. Of those deaths, 73.5% were associated with bark beetles, and 83.6% with biotic mortality agents in general (comprising bark beetles, other insects [particularly bark weevils] and fungal pathogens [particularly rots]). In the landscape plots, from all 8,555

living and dead focal species trees, we estimated that 20.1% (95% credible interval = 17.2%–23.3%) of those alive in 2013 died in 2014–2016. Overall percentage mortality in the two plot types was similar despite the different time periods sampled (4 vs. 3 years), probably because the intensive plots included higher elevations where mortality was lower (Figure S1), and perhaps because the relative proportions of the five focal species differed between the plot types (Figure S2).

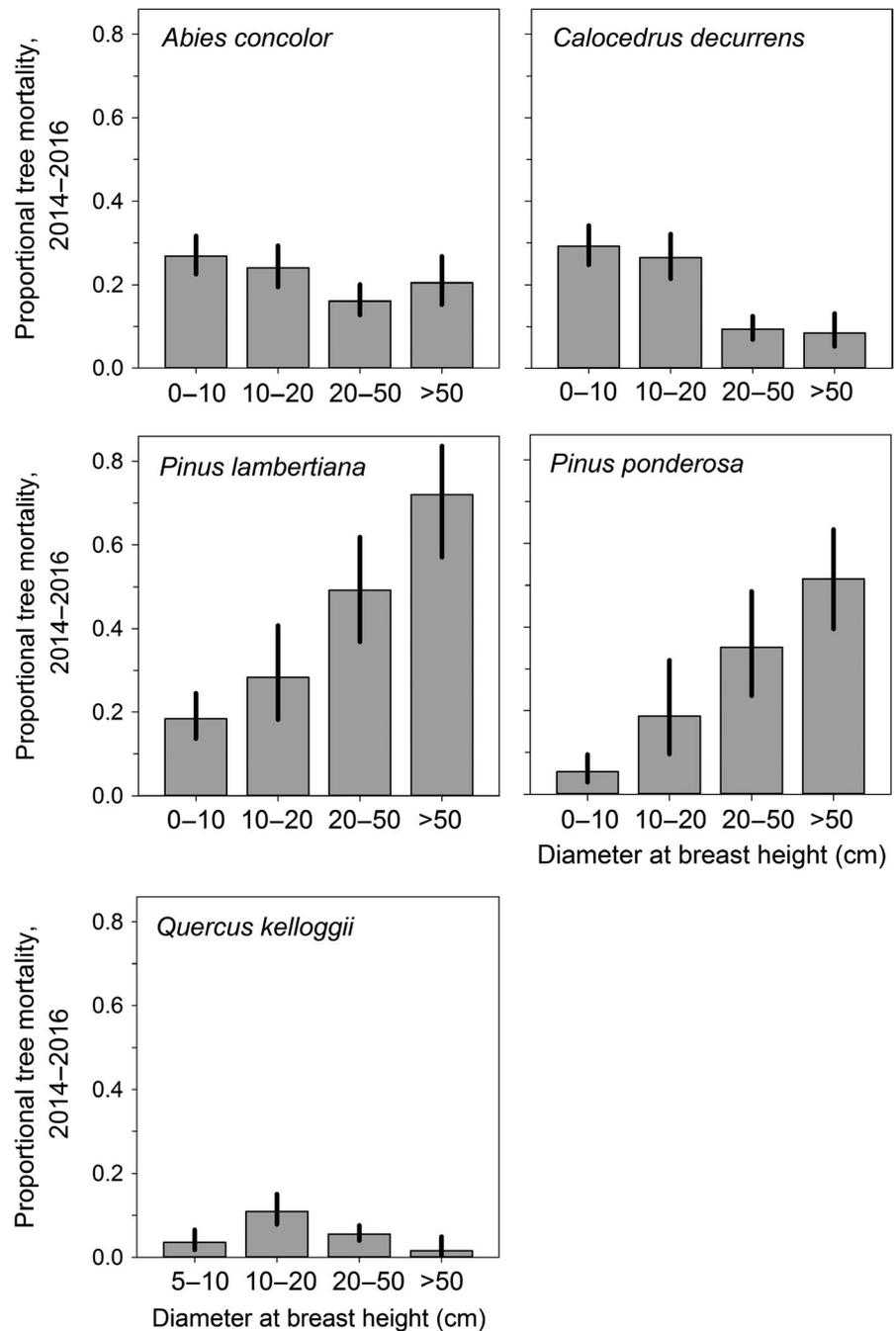
3.2 | Bark beetle taxa encountered

In our intensive plots, three native bark beetle genera—*Scolytus*, *Phloeosinus* and *Dendroctonus*—were found in 96.3% of trees that had confirmed bark beetles as a mortality factor. Three species of

Scolytus, *S. praeceps*, *S. subscaber* and *S. ventralis*, attacked *A. concolor*. Up to six *Phloeosinus* species may have attacked *C. decurrens* (Furniss & Carolin, 1977), but we did not attempt to distinguish among them; galleries of the genus are distinctive, but those of the individual species are not. Attacks on *P. lambertiana* were overwhelmingly by *Dendroctonus ponderosae*, often in association with *D. valens*. *Pinus ponderosa* was mostly attacked by *D. brevicomis* (occasionally *D. ponderosae*), also often in association with *D. valens*. For both species of *Pinus*, we suspect that *Ips* may sometimes have been active in the crowns at heights we could not reach.

In the absence of the three dominant bark beetle genera, 1.3%, 0.7%, 0.6% and 1.1% of all trees with confirmed bark beetles hosted *Pseudopityophthorus* (in *Q. kelloggii*), *Ips* (in small *Pinus*),

FIGURE 3 Proportions of trees that died from 2014 to 2016 by species and size class, as estimated from the 89 randomly located landscape plots. Error bars represent 95% credible intervals calculated from the Bayesian model and incorporate both sampling uncertainty and classification uncertainty, as described in the Supporting Information



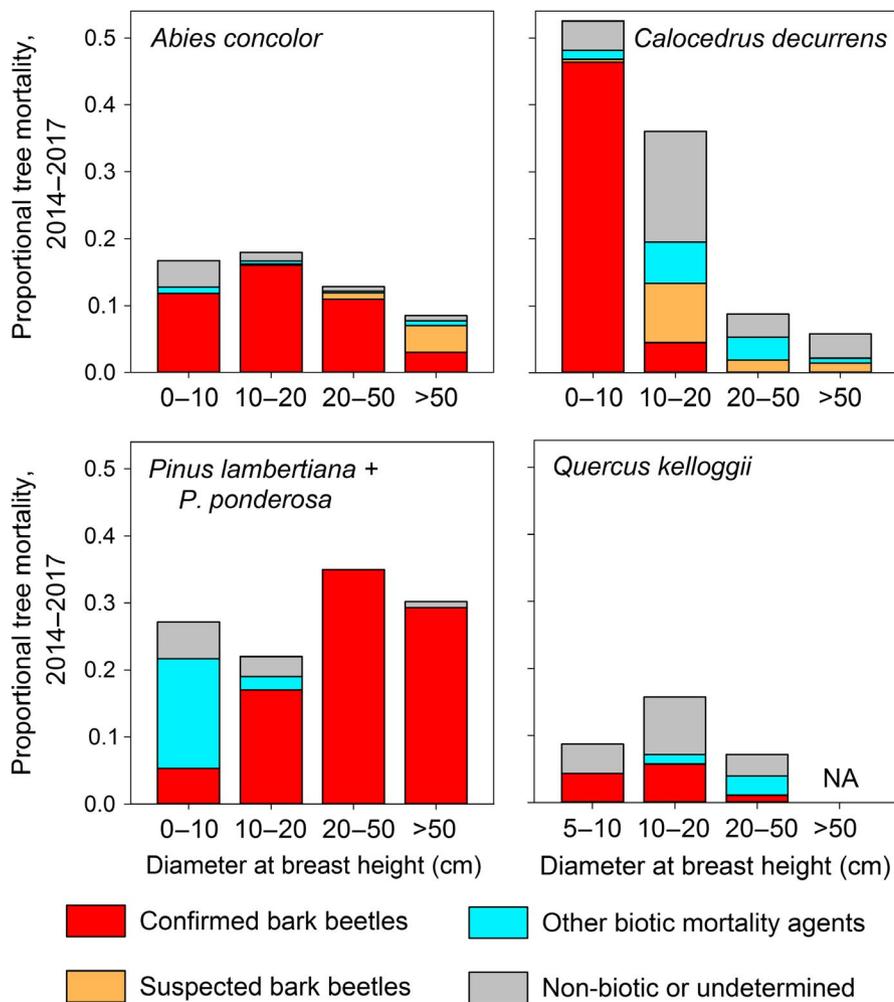


FIGURE 4 Proportions of trees that died in the 12 intensive plots from 2014 to 2017, by species and size class. Factors contributing to tree mortality (confirmed bark beetles, suspected bark beetles, other biotic agents and non-biotic or undetermined mortality agents) are indicated. 'NA' indicates that *Quercus kelloggii* ≥ 50 cm diameter at breast height were not analysed because the sample fell below our 20-tree threshold

Pityophthorus (in small *A. concolor* and *Pinus*) or unspecified bark beetles respectively.

3.3 | Size-specific mortality and mortality factors

In the 89 landscape plots—designed to give an unbiased snapshot of tree mortality by size class across a 1,705-ha area—the sizes of trees suffering greatest mortality during 2014–2016 differed markedly among species (Figure 3). In *C. decurrens*, mortality was $>3\times$ greater in small trees than in large trees; in *P. lambertiana* and *P. ponderosa*, mortality was greater in large trees than in small trees (nearly $4\times$ and $10\times$ differences respectively); and in *A. concolor* and *Q. kelloggii*, mortality was relatively evenly distributed among size classes, with *Q. kelloggii* mortality being notably low in all size classes.

In the 12 intensive plots, *A. concolor*, *C. decurrens* and *Q. kelloggii* showed patterns of tree mortality qualitatively similar to those in the landscape plots (Figure 4). However, rather than increasing with tree size, overall *Pinus* mortality during drought showed no clear trend in the intensive plots (Figure 4). This is almost certainly an artefact of the small number of intensive plots available to sample spatially clumped and variable mortality across the landscape; just as we found in our landscape plots, other assessments of tree mortality during the drought found that *Pinus* mortality increased with

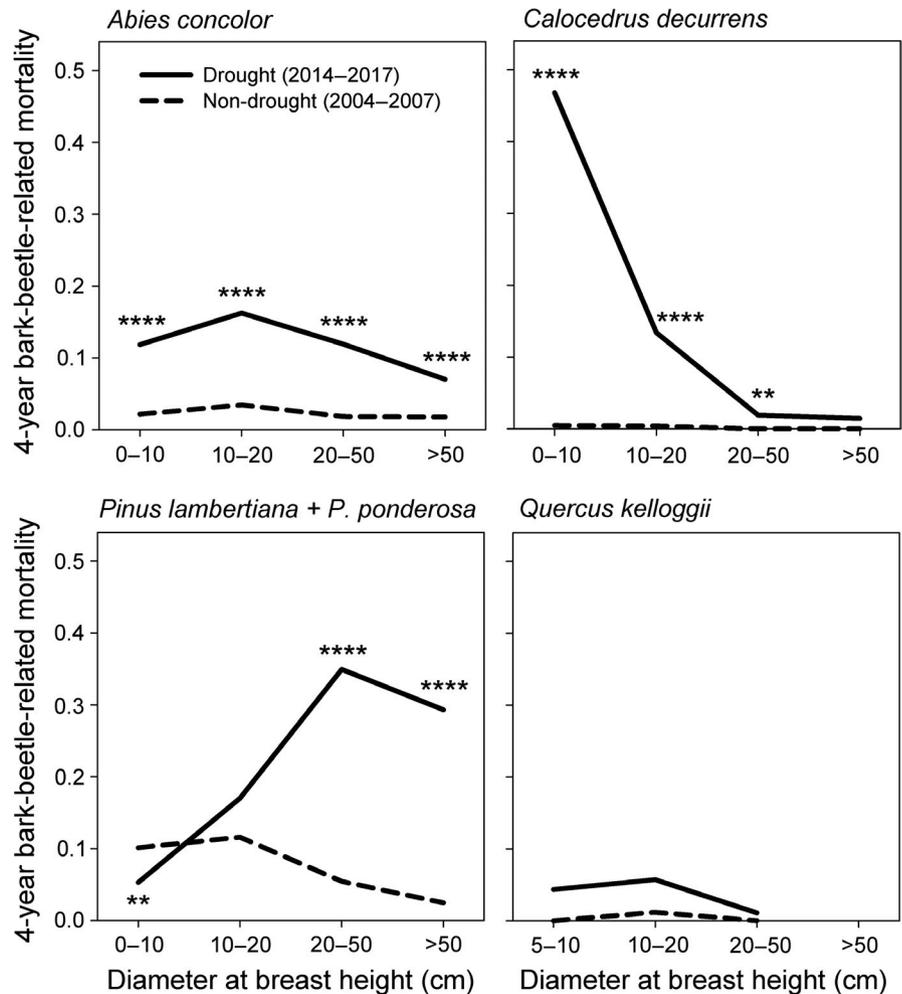
tree size (Pile et al., 2018; Fettig et al., 2019; also see the Supporting Information). Additionally, when only bark beetle-related mortality was considered in the intensive plots, *Pinus* mortality increased with size (Figure 4; Section 3.4).

Data from the intensive plots showed that, across many of the tree species and size classes, biotic agents—particularly bark beetles—were the dominant mortality factors during the drought (Figure 4). Biotic mortality agents other than bark beetles mostly comprised other insects and rots. In the smallest *Pinus*, the large proportion of biotic deaths not associated with bark beetles was mostly from *Pissodes schwarzi* (Yosemite bark weevil; Curculionidae: Molytinae). Non-biotic mortality factors included suppression, mechanical failure (uprooted, broken or crushed) and unidentified mortality agents (cf. Das et al., 2016).

3.4 | Relationships between tree size and bark beetle-related mortality during the drought and non-drought periods

Compared to the non-drought period, *Scolytus*-related mortality of *A. concolor* was significantly higher in all size classes during the drought (Figure 5). Some of the relative uniformity across size classes of *A. concolor*'s bark beetle-related mortality during the drought is

FIGURE 5 Size-specific tree mortality associated with bark beetles in the intensive plots during the drought and non-drought periods. Asterisks indicate that, for the particular size class of trees indicated, bark beetle-related mortality during the drought period (2014–2017, solid line) significantly differed from that of the non-drought period (2004–2007, dashed line) (Fisher's exact test: ** $p < 0.01$; **** $p < 0.0001$)



a consequence of the complementary effects of different *Scolytus* species successfully attacking different size classes of *A. concolor* (Section 4.3; Figure S3).

During the non-drought period, *Phloeosinus* contributed trivially to *C. decurrens* mortality, with <1% of trees dying in association with *Phloeosinus* attack, all <20 cm DBH. However, during the drought, overall *C. decurrens* mortality associated with *Phloeosinus* increased by roughly two orders of magnitude. Although a few *C. decurrens* ≥ 20 cm died in association with *Phloeosinus* during the drought, the most dramatic increases in *Phloeosinus*-related mortality were in trees <20 cm, with nearly half of the smallest *C. decurrens* (<10 cm) in the intensive plots dying in association with the beetle (Figure 5).

Of particular note is the reversal in the sizes of *Pinus* successfully attacked by *Dendroctonus* before and during drought (Figure 5). Before the drought, small *Pinus* (<20 cm DBH) had significantly higher bark beetle-related mortality rates than large *Pinus* (≥ 20 cm DBH) ($p = 0.0018$, Fisher's exact test). The opposite was true during the drought ($p < 0.0001$). Notably, bark beetle-related mortality in the smallest *Pinus* size class (<10 cm DBH) was significantly lower, not higher, during the drought than non-drought period ($p = 0.0031$; Figure 5).

Finally, *Pseudopityophthorus* was associated with greater overall *Q. kelloggii* mortality during the drought than non-drought period

($p = 0.0097$, Fisher's exact test), although mortality was low and differences between the time periods were not statistically significant within individual size classes (Figure 5). Even when all sources of mortality (not just bark beetles) are considered, overall *Q. kelloggii* mortality remained relatively low during the drought (Figures 3 and 4).

3.5 | Relationships between tree growth rate and bark beetle-related mortality during the drought and non-drought periods

For our 2014–2017 analyses, intermediate diameter growth rates (≥ 0.5 to ≤ 4.0 mm/year) were the most common growth rates in both large and small trees of all taxa, averaging 66% of trees (Figure S4). In small trees (<20 cm DBH), slowly growing trees (<0.5 mm/year) were always more common than rapidly growing trees (>4.0 mm/year), averaging 26% and 5% respectively. In large trees (≥ 20 cm DBH), slowly growing trees were usually, but not always, less common than rapidly growing trees (averaging 13% and 24% of large trees respectively) (Figure S4). *Quercus kelloggii* had notably low proportions of rapidly growing trees in either size class; however, this almost certainly does not reflect a paucity of vigorous *Q. kelloggii* in the population (see the Supporting Information). All the preceding patterns were similar to those of our 2004–2007 analyses,

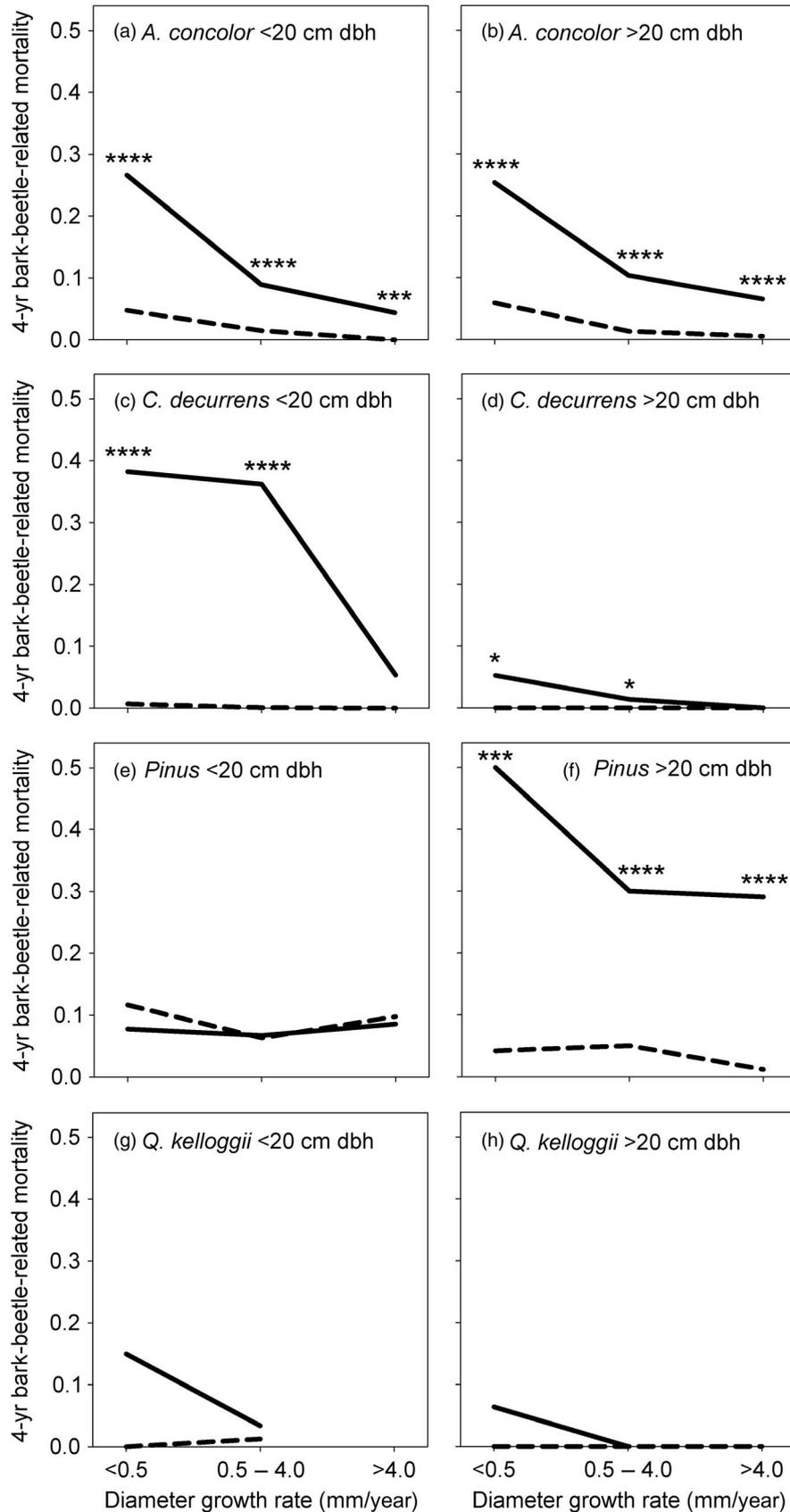


FIGURE 6 Size- and growth-rate-specific tree mortality associated with bark beetles in the intensive plots during the drought and non-drought periods. Asterisks indicate that, for the particular size and growth-rate class of trees indicated, bark beetle-related mortality during the drought period (2014–2017, solid line) significantly differed from that of the non-drought period (2004–2007, dashed line) (Fisher's exact test: * $p < 0.05$; *** $p < 0.001$; **** $p < 0.0001$). (a) *A. concolor* <20 cm DBH. (b) *A. concolor* ≥ 20 cm DBH. (c) *C. decurrens* <20 cm DBH. (d) *C. decurrens* ≥ 20 cm DBH. (e) *Pinus* <20 cm DBH. (f) *Pinus* ≥ 20 cm DBH. (g) *Q. kelloggii* <20 cm DBH. (h) *Q. kelloggii* ≥ 20 cm DBH

suggesting long-term continuity in the relative proportions of trees in different growth-rate classes.

Just as the sizes of trees suffering greatest bark beetle-related mortality differed markedly among species (Figure 5), so did the growth rates (Figure 6). Regardless of size, during the drought, only the slowest growing *A. concolor* had bark beetle-related mortality exceeding 25%—significantly higher than trees with intermediate or high growth rates ($p < 0.0001$, Fisher's exact test). At the opposite extreme, the elevated mortality experienced by large *Pinus* may have been independent of growth rate; all growth-rate classes had bark beetle-related mortality exceeding 25%, and mortality of large *Pinus* during the drought did not significantly differ in pairwise comparisons among the growth-rate classes ($p > 0.05$). *Pinus* <20 cm DBH did not show elevated mortality in any growth-rate class (Figure 6e).

In contrast to either *A. concolor* or *Pinus*, small *C. decurrens* with both slow and intermediate growth rates had strongly elevated bark beetle-related mortality during the drought (Figure 6c). Mortality in these two growth-rate classes significantly exceeded that of small, rapidly growing *C. decurrens* ($p < 0.0001$), the last of which was not detectably elevated compared to mortality in the non-drought period ($p = 0.25$). In contrast, among large *C. decurrens*, bark beetle-related mortality was only slightly elevated during the drought, in trees with low and intermediate growth rates (Figure 6d).

Sample sizes were <20 for rapidly growing *Q. kelloggii* (both large and small trees), limiting our analyses to those with slow and intermediate growth rates. Mortality during the drought never exceeded 15% in any group and in large trees was significantly higher than during non-drought conditions in trees with slow rather than intermediate growth rates ($p = 0.0042$).

3.6 | Summarizing the results

To create a simple summary figure for comparison with Figure 1, we began with the size and growth-rate results from our intensive plots (Figure 6), in which bark beetle-related mortality during the 2014–2017 drought years fell into two distinct groups: >25% (range = 25.4%–50.0%, mean = 33.7%, $n = 7$ taxon-specific size and growth-rate classes) and $\leq 15\%$ (range = 0% to 15.0%, mean = 6.0%, $n = 15$ taxon-specific size and growth-rate classes). Within each tree species, mortality in each class with >25% mortality significantly exceeded that of every other class (each class with $\leq 15\%$ mortality) (Fisher's exact test, $p < 0.0001$ for all pairwise, within-species group comparisons except those that included small, rapidly growing pines, for which $p < 0.001$ to 0.02). As described in the Supporting Information, we checked these intensive plot results for consistency with the size-specific mortality in our randomly located landscape plots, concluding that results were broadly consistent. Additionally, as described in the Supporting Information, we estimated that the likely mortality class of vigorous *Q. kelloggii*—which in our intensive plot had samples below our 20-tree threshold for analysis—was low. The resulting figure highlights substantial differences among tree taxa in the sizes and chronic stress classes of trees that suffered the greatest bark beetle-related mortality during the drought (Figure 7).

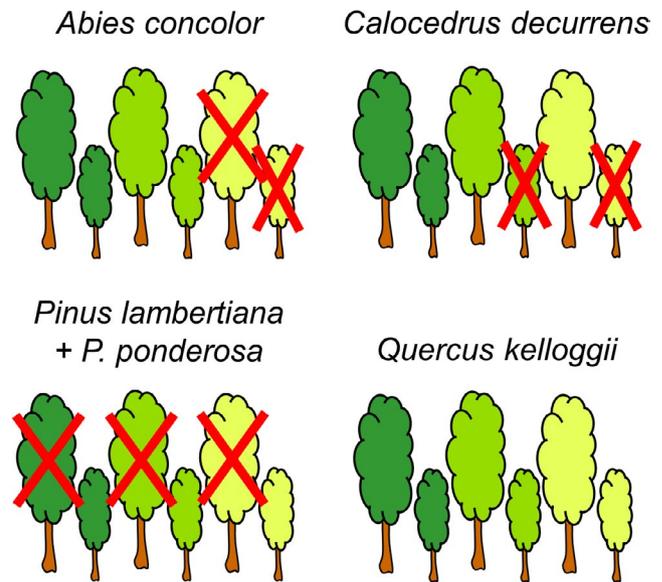


FIGURE 7 Summary of observed tree mortality associated with bark beetles during the drought, for comparison with Figure 1. Small and large tree symbols represent trees <20 cm and ≥ 20 cm diameter at breast height respectively. Shades of green indicate magnitude of chronic stress (as indicated by 5-year growth rates), ranging from low (dark green) to high (light green). Trees with and without red Xs indicate size and stress classes that suffered, respectively, 25%–50% (mean = 34%) and 0%–15% (mean = 6%) mortality associated with bark beetles (see Section 3.6 for details)

4 | DISCUSSION

4.1 | Summary interpretation of results

Preceding California's extreme drought, individual trees of all species and size classes suffered a range of chronic stress, from low to severe. During the drought, trees in all chronic stress classes likely experienced additional acute physiological stress—such as by partial hydraulic failure and (or) carbon limitation—which helped predispose them to outbreaking native bark beetles. However, bark beetles successfully attacked and killed trees according to taxon-specific host-tree selection, so that the specific sizes and chronic stress classes of trees experiencing greatest mortality varied widely among tree species (Figure 7). For the remainder of the Discussion, we consider evidence and observations relevant to this interpretation, and place our results within the broader context of other studies of the patterns and mechanisms of tree mortality during drought.

4.2 | Chronic and acute stress

Although we lack direct measurements of the physiological status of our 8,522 intensive plot study trees before or during the drought, our growth-rate metric of chronic stress almost certainly serves as a reasonable proxy of which trees suffered the greatest acute stress during the drought. Preceding drought, the magnitude of stress experienced by individual trees in a forest typically already spans the

entire spectrum from little or no stress to chronically high stress, the latter usually resulting from some combination of competition, poor local site conditions (such as shallow or nutrient-poor soils), past physical damage, the effects of past droughts, ongoing attack by root pathogens, etc. Chronically stressed trees, as indicated by persistent slow growth preceding drought, often have higher average mortality rates during drought than their less stressed (rapidly growing) neighbours (e.g. Pedersen, 1998; Suarez et al., 2004; Kane & Kolb, 2014; Gaylord et al., 2015; Cailleret et al., 2017). A growing body of evidence further suggests that, relative to their less stressed neighbours, chronically stressed trees can have xylem architecture (such as narrow tracheids or pits in conifers) that reduces their hydraulic conductivity; greater hydraulic failure (cavitation) preceding and during drought; greater diffusional constraints on gas exchange (limiting carbon fixation); and reduced defences (such as fewer or narrower resin ducts) (Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015; Ferrenberg, Kane, & Mitton, 2014; Gaylord et al., 2015; Gessler et al., 2018; Hereş, Camarero, López, & Martínez-Vilalta, 2014; Linares & Camarero, 2012; Pellizzari, Camarero, Gazol, Sangüesa-Barreda, & Carrer, 2016; Poyatos, Aguadé, Galiano, Mencuccini, & Martínez-Vilalta, 2013). That is, chronically stressed trees enter a drought already exhibiting some of the same hydraulic, carbon gain and defensive problems that the drought will only serve to exacerbate.

4.3 | Bark beetles as selective mortality agents

For trees with bark beetles listed as mortality factors (potential contributors to tree mortality), three lines of evidence collectively suggest that the beetles were usually the proximate cause of tree mortality. First, most of our dominant bark beetle taxa have previously been reported as capable of killing trees, especially during drought (see the following paragraphs). Second, across tree species and size classes, nearly all dead trees with bark beetles showed evidence of attacks of a magnitude sufficient to kill the trees, such as dense concentrations of pitch tubes, frass or beetle exit holes on the bark exterior, and inner bark beetle galleries at densities sufficient to severely disrupt or halt phloem function. Finally, it is implausible that the contrasting mortality patterns we observed (Figure 7) can be explained as a direct consequence of acute physiological stress, whereas they are easily explained as consequences of bark beetle host selection. For example, for acute physiological stress to have produced the patterns, the trees suffering the most acute stress during drought would have to include the smallest, most chronically stressed trees in one species, but the largest, least chronically stressed trees in another. Certainly, our tree taxa differ in xylem resistance to embolism and strategies for surviving water stress (e.g. Choat et al., 2012; Brodribb, McAdam, Jordan, & Martins, 2014), but we know of no plausible mechanism by which these physiological differences alone would result in the strikingly different species-specific relationships among size, chronic stress and mortality that we found.

Our results are compatible with previous findings suggesting a strong role for bark beetles in determining which subpopulations

of trees die. *Abies concolor* was notable in having three species of *Scolytus* that selectively killed trees experiencing high chronic stress, but predominantly trees within different size classes (individually, the 'mixed' response in Figure 1; see Figure S3). *Scolytus ventralis* is known both for killing larger, less vigorous trees and for undergoing outbreaks during drought, while *S. praeceps* tends to kill smaller suppressed trees (Berryman & Ferrell, 1988; Ferrell, Otrosina, & Demars, 1994; Furniss & Carolin, 1977; Struble, 1957). Although *S. subscaber* 'frequently attacks the main trunk of suppressed trees under 4 inches [10 cm] in diameter' (Struble, 1957), we are unaware of reports explicitly stating whether, under either non-drought or drought conditions, it kills such trees, fails to kill them or simply invades them after they are already nearing death from other causes. Regardless, during the extreme drought, we often found abundant beetle entrance holes on the main stems of small, living *A. concolor* that retained their full complement of apparently healthy green foliage. These trees subsequently died and yielded dense *S. subscaber* galleries, suggesting *S. subscaber* was the likely proximate cause of mortality. The combined effect of the mixed responses of the three *Scolytus* species was that high proportions of *Abies concolor* of all sizes died, with the net effect that *A. concolor* mortality was consistent with a dominant role for stress (Figure 7).

The genus *Phloeosinus*—sometimes identified to species as *Ph. punctatus*—has been known to kill even apparently healthy *C. decurrens*, particularly during drought (Fettig, 2016; Fettig et al., 2019; Schubert, 1957). *Phloeosinus* disproportionately killed small *C. decurrens*, even though chronically stressed large *C. decurrens* were also available on the landscape. We suspect that, like some other bark beetle taxa (e.g. Kolb, Guerard, Hofstetter, & Wagner, 2006), *Phloeosinus* were able to successfully bore through the thin, papery bark of small *C. decurrens*, but not the thicker woody bark of the main stems of large *C. decurrens*. This interpretation is consistent with our observations that *Phloeosinus* sometimes attacked the thin-barked branches of large *C. decurrens* and, by successfully attacking many branches, may have contributed to the deaths of some large trees. Thus, during the drought, the behaviour of *Phloeosinus* on *C. decurrens* was consistent with a mixed response (Figure 1); *Phloeosinus* selectively killed trees experiencing high and moderate chronic stress, but mostly those within a particular size class.

Previous work has found, as we did, that, during outbreaks, the dominant bark beetles in our two *Pinus* species (*Dendroctonus ponderosae* and *D. brevicomis*) expand their successful attacks from smaller or less vigorous trees to additionally include larger, vigorous trees (e.g. Bleiker, O'Brien, Smith, & Carroll, 2014; Boone et al., 2011; Miller & Keen, 1960; Negrón, Allen, Cook, & Withrow, 2008; Safranyik & Carroll, 2006). The decline in *Dendroctonus* attacks on *Pinus* <10 cm DBH during the drought (Figure 5) likely reflects the outbreaking beetles' improved ability to successfully mass attack large trees, which are their preferred hosts (e.g. Amman & Cole, 1983; Safranyik & Carroll, 2006). Thus, during drought, the behaviour of *Dendroctonus* on *Pinus* in our study area was consistent with a dominant role for host selection (Figure 1).

Collectively, our results suggest particularly strong interactions between drought and insects, in which the absence of either drought or insects would have resulted in substantially reduced tree mortality (cf. Anderegg et al., 2015). First, bark beetle-related mortality was much lower in the absence of drought, even though the same beetle taxa were present at endemic levels and were killing some trees (dashed lines in Figures 5 and 6). Second, despite the drought's historically unprecedented severity, some size classes of trees showed low, near-endemic levels of mortality even for trees suffering high chronic stress—such as large *C. decurrens* and small *Pinus*—despite substantially elevated mortality in other size classes of the same species (Figures 5 and 6). Additionally, a separate study (Stephenson et al., 2018) reported extremely low overall mortality (<1%) of *Sequoiadendron giganteum* during the drought, even though mortality was elevated in co-occurring tree species that were attacked by outbreaking bark beetles. The most parsimonious explanation of these collective observations is that, by themselves, the direct physiological effects of the drought did not contribute substantially to elevating tree mortality. Only the combined, non-additive effects of both acute drought stress and bark beetles resulted in greatly elevated mortality.

4.4 | Relationship to other studies of tree growth rate or size

In the absence of an existing broad review of drought-related tree mortality relative to both growth rate and size simultaneously (cf. Figures 1 and 7), we compare our findings with those of reviews and syntheses that considered growth rates and size separately. Cailleret et al. (2017) provided a broad, multi-continent synthesis of the relationship between tree growth rates and probability of mortality, concluding that growth-based mortality algorithms may have limited success in predicting tree mortality 'in case of intense drought or bark-beetle outbreaks', reflecting their observation that chronic slow growth was sometimes, but not always, predictive of tree mortality under those circumstances. These observations are consistent with our results and with those of other studies showing that insect-induced mortality is sometimes decoupled from chronic tree stress (Section 1 and Figures 1 and 7).

For comparisons with studies of tree size, we only considered studies that, like ours, (a) presented mortality rates for individual tree species (because mixed-species mortality rates can mask potentially dramatic differences among species), and (b) presented results as absolute mortality rates (because proportional changes in mortality rates do not reliably identify which size classes of trees are most affected by drought; see the Supporting Information). Condit, Hubbell, and Foster (1995) presented mortality rates in two size classes for 130 Panamanian tree species, with mortality rates during drought increasing with tree size for 43% of species and decreasing for 57%. However, sample sizes for most species were small, suggesting that a reanalysis might find that patterns for many of these species were not statistically significant. For six temperate tree species—mostly conifers—in North America,

South America, and Europe, the studies compiled by Bennett et al. (2015) found that absolute mortality rates increased with tree size for three species, decreased for two and, depending on location, either increased or decreased for one (see the Supporting Information for details). For 18 species in northeastern Australia, Fensham, Fraser, MacDermott, and Firn (2015) found that mortality rate during drought increased with size for seven species, decreased for three and showed no significant relationship for the remaining eight. Finally, Hember et al. (2017) presented size-specific drought responses for 64 tree species across North America. Although results varied depending on drought metric, roughly comparable proportions of species had absolute changes in mortality rates that increased, decreased or showed no trend with tree size. Thus, a broad array of geographically dispersed studies has found, as we did, a variety of size-specific tree mortality patterns during drought, with different species variously having mortality rates that increased, decreased or did not vary with tree size.

The global synthesis by Bennett et al. (2015) has been cited as evidence that large trees are more vulnerable to drought mortality than small trees (see the Supporting Information for details). However, as the authors noted, the overall positive relationship they found between tree size and absolute mortality rate was driven by instances in which bark beetles were reported as contributing to mortality. Specifically, the pattern was driven by *Pinus edulis* and *P. ponderosa* at eight sites in the southwestern United States; mortality rate increased with size for both species, as it did for *P. lambertiana* and *P. ponderosa* in the Sierra Nevada (Section 3.3). Thus, the overall relationship the authors found for absolute mortality rate appears to be a consequence of insect host-tree selection in two *Pinus* species. When we couple this observation with the evidence summarized in the preceding paragraph, it seems premature to conclude that large trees are broadly more vulnerable to drought mortality than small trees.

Although many studies have documented a variety of size-specific tree mortality patterns during drought, we cannot yet draw broad generalizations about the possible role of insects or other biotic agents in driving those patterns. Most of the original studies either did not mention biotic agents or mentioned them only in passing; that is, the potential role of biotic agents appears not to have been rigorously assessed (but see, e.g., Marchetti, Worrall, & Eager, 2011; Wood, Knapp, Muzika, Stambaugh, & Gu, 2018). However, observed patterns of size-specific mortality can still offer insights. For example, for stress to be the sole explanation of the patterns of tree mortality during drought, we would need to explain why large trees suffer the most drought stress in some species, but small trees do in other species, even in cases in which the species are growing immediately adjacent to one another (Section 4.3). A plausible alternative explanation is that insect or pathogen host selection for trees of different sizes may be common enough to contribute to the observed variety of patterns.

4.5 | Relationship to studies of tree hydraulic failure

In several recent studies (e.g. Rowland et al., 2015; Anderegg et al., 2016; Adams et al., 2017; Choat et al., 2018), hydraulic failure has

received particular support as a contributor to tree mortality during drought. At first glance, these studies could be taken as evidence that stress dominates (Figure 1); that is, they could be taken to suggest that if biotic agents play a role in tree mortality, it is largely by acting as the final agents killing those trees that are already the most stressed by drought-induced hydraulic failure. However, closer examination shows that the studies are compatible with potentially significant roles for insect host selection, in which insects selectively kill only a subset of all stressed trees and may sometimes even kill substantial proportions of unstressed trees.

For example, a recent global analysis showed that tree mortality rates during drought were correlated with certain species-specific hydraulic traits (Anderegg et al., 2016). We take this key finding at face value—as evidence that species-specific hydraulic traits can directly or indirectly contribute to tree survival or mortality during drought. However, at broad scales, the hydraulic traits explained a relatively small proportion of variance in mortality rates. We suggest that at least some of the unexplained variance might be attributable to variation among tree species and size classes in the importance of insects and pathogens in contributing to tree mortality (see Section 5).

Another recent multispecies synthesis found that hydraulic failure was a ubiquitous feature of drought-induced mortality (Adams et al., 2017). However, most studies in the synthesis were experimental droughts imposed on potted seedlings or saplings, and thus cannot broadly address mortality mechanisms among different sizes of trees experiencing drought in their natural environments, exposed to their natural enemies.

When an Amazonian tropical forest plot was subjected to long-term experimental drought, hydraulic failure was implicated as the primary driver of mortality (Rowland et al., 2015). Finding no difference in leaf area lost to herbivores between the control and droughted plots, the authors suggested that folivory was not a dominant contributor to drought-related mortality. However, we caution against taking this as evidence that biotic agents are generally not significant contributors to drought-related tree mortality in the tropics. First, the 1-ha area of experimental drought may simply have been too small to initiate and support an insect outbreak; during some natural droughts in tropical forests, generalized folivore outbreaks have been reported (Van Bael et al., 2004). More important, folivory is typically not a significant source of tree mortality compared to bark beetles or wood borers (see the summaries in Nair, 2007; Stephenson et al., 2011; Anderegg et al., 2015; Das et al., 2016). However, Rowland et al. (2015) gave no indication that they assessed bark beetles or wood borers. Yet several species of tropical bark beetles and wood borers undergo outbreaks (Dyer, Carson, & Leigh, 2012; Nair, 2007), and different tropical insect species can preferentially attack trees of different sizes (Nair, 2007). However, we are unaware of systematic evaluations of a full array of biotic mortality agents during drought in the tropics, and this remains a priority for tropical forest research.

Finally, we consider whether our observation of low drought mortality of *Q. kelloggii* (a deciduous angiosperm) relative to the other four tree species (all evergreen gymnosperms) might reflect

broad differences in hydraulic architecture and strategies between angiosperms and gymnosperms and consequent vulnerability to insect attack. Although we cannot definitively answer this question, circumstantial evidence suggests this is not the case. First, as mentioned in Section 4.3, an evergreen gymnosperm not analysed here, *S. giganteum*, had extremely low mortality (<1%) during the drought (Stephenson et al., 2018), even though mortality was elevated in *A. concolor* and *P. lambertiana* growing mixed with *S. giganteum*. Second, two other angiosperms in the genus *Quercus* (*Q. douglasii* [deciduous] and *Q. wislizeni* [evergreen]), which mostly occur at elevations lower than we sampled, had at least some size classes with estimated drought mortality >25% (A. J. Das & N. L. Stephenson, unpublished data; also see Brown, McLaughlin, Blakey, & Morueta-Holme, 2018). (However, these low-elevation *Quercus* may have experienced more severe drought stress than *Q. kelloggii*.) Finally, elsewhere in North America, outbreaks of native insects during drought have sometimes driven exceptionally high *Quercus* mortality (Haavik et al., 2015). The low *Q. kelloggii* mortality we observed may at least partly have been a consequence of the inability of *Pseudopityophthorus* bark beetles to overwhelm any of *Q. kelloggii*'s size or vigour classes.

5 | CONCLUSIONS

Even though the drought was the most severe in our study region's historical record, most tree mortality appears to have proximately resulted from bark beetles rather than the direct physiological effects of drought. Perhaps the most striking features of the mortality were the sharp differences among tree taxa both in the magnitude of tree mortality and in the subpopulations of trees that suffered greatest mortality (Figures 3 and 4). Those differences were largely driven by the idiosyncratic host-tree selection of the different bark beetle taxa.

If, similar to our findings, a large fraction of biotic mortality agents worldwide proves to have idiosyncratic host-tree selection and effects, this could help explain at least some of the large unexplained variance typically found in correlations between tree traits and tree mortality during drought. These correlations often focus on tree traits thought to be related to hydraulic function during drought, such as xylem architecture, vulnerability to embolism, wood density, specific leaf area and tree diameter or height (e.g. Bennett et al., 2015; Anderegg et al., 2016; Greenwood et al., 2017; O'Brien et al., 2017; Zhang et al., 2017). First, in comparisons among tree species, such correlations would be weakened if ecological and evolutionary contingencies have resulted in some tree species being associated with more lethal biotic mortality agents than others, unrelated to the species' hydraulic traits. Second, in comparisons within tree species, biotic mortality agents could selectively kill subpopulations of trees that do not necessarily correspond to those most vulnerable to direct physiological stress, instead selecting trees based on other traits. Finally, correlations could be weakened if the relative effects of biotic mortality agents vary unpredictably in space and time. Specifically, insect (and probably pathogen) outbreaks are functions

of complex interactions, thresholds and feedbacks among biotic and abiotic factors (Barbosa, Letourneau, & Agrawal, 2012; Bentz et al., 2010; Ferrenberg, 2016; Raffa et al., 2008; Rouault et al., 2006; Ryan, Sapes, Sala, & Hood, 2015). Contingencies of outbreak dynamics could mean that, both among and within tree species, the relative proportions of trees dying might vary seemingly idiosyncratically during different droughts in the same forest, or at different forest locations during the same drought, depending on which potentially outbreaking insects or pathogens may be favoured or disfavoured by current local conditions.

The preceding possibilities suggest that our ability to use species traits or tree traits alone to predict drought-related tree mortality may be limited. Yet, we currently cannot make reliable generalizations because, except for a few economically important tree species and particularly aggressive bark beetle species (Weed et al., 2013), the effects of biotic mortality agents are rarely systematically documented among different tree subpopulations. Nevertheless, both insects and pathogens are commonly implicated as contributing to tree mortality during drought (e.g. Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini, 2006; Raffa et al., 2008; Marchetti et al., 2011; Seidl, Schelhaas, & Lexer, 2011; Jactel et al., 2012; Weed et al., 2013; Anderegg et al., 2015; Haavik et al., 2015; Kolb et al., 2016; Kautz, Meddens, Hall, & Arneith, 2017; Seidl et al., 2017; Wood et al., 2018). Furthermore, in addition to being well documented in some insects (Section 4.3), size-specific host-tree selection might even occur in some pathogens (see Marchetti et al., 2011; Wood et al., 2018).

Our findings thus highlight a general need for improved assessments of the roles of biotic mortality agents during drought in forests worldwide, particularly in mixed-species forests that allow comparison among co-occurring tree species during the same drought. Because biotic agents can be difficult to detect and identify, assessments will usually require close collaboration with forest entomologists and pathologists. Some existing publications offer brief statements that no signs of biotic agents were observed, but without descriptions of methods such statements cannot automatically be taken as evidence that biotic mortality agents were absent. At a minimum, descriptions of methods should include how many trees were assessed, how soon after mortality they were assessed, and how they were assessed, including whether bark was removed to reveal possible evidence of the agents (e.g. García de la Serrana, Vilagrosa, & Alloza, 2015; Fettig et al., 2019).

Under novel environmental conditions, formerly innocuous insects and pathogens can unexpectedly emerge as significant agents of tree mortality (Haavik et al., 2015; Kolb et al., 2016; Weed et al., 2013), highlighting the importance of remaining alert for such novelty during mortality assessments. For example, most bark weevils in the genus *Pissodes* have not been considered important tree killers (Furniss & Carolin, 1977). Yet during California's exceptional drought, we judged that *P. schwarzi* became an important mortality agent of small *Pinus* in our study area (Section 3.3), and a similar conclusion was reached for small *Pinus contorta* during a recent hotter drought in British Columbia (Joy & Maclauchlan, 2000). If the emergence of novel mortality

agents—whether native or introduced—proves to be largely unpredictable, we can expect further limitations to our ability to predict tree mortality in a changing climate.

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AUTHORS' CONTRIBUTIONS

N.L.S. and A.J.D. conceived the ideas; N.L.S., A.J.D. and J.L.Y. designed methodology; B.M.B. trained personnel in insect identification and assisted in identifications; N.J.A., A.J.D. and N.L.S. collected the data; A.J.D., N.L.S. and N.J.A. analysed the data; N.L.S. and A.J.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available on ScienceBase: <https://doi.org/10.5066/P99RNGXH> (Das, Stephenson, & Ampersee, 2019).

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SUPPORTING INFORMATION

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

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