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Ancient trees and modern wildfires: Declining resilience to wildfire in the highly fire-adapted giant sequoia

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ABSTRACT

Ancient giant sequoias *Sequoiadendron giganteum* (Lindl.) J. Buchholz are highly valued trees with limited distribution. They are the most massive trees on earth, and they have exceptional longevity (>3,000 years). Given their extraordinary resilience to wildfire, insects, and disease, most managers hoped giant sequoias would be resistant to anthropogenic change. However, the warming climate and fire exclusion-caused fuel build-up has dramatically increased the amount of high-intensity wildfire in giant sequoia groves since 2015. To better understand recent wildfire effects on large, legacy giant sequoia trees, we surveyed high- and moderate-severity fire areas in groves that burned in three wildfires between 2015 and 2017. Within areas classified as high severity via remote sensing, ~84% of the 162 large sequoias (>1.2 m diameter at breast height) were killed; in moderate severity, ~28% of the 239 large sequoias were killed. These rates varied between fires but overall were at the lower end of the mortality range that has been documented in Sierra Nevada mixed-conifer forests. Across all three fire areas, we found large sequoia mortality was linked with presence of significant prior fire damage to the lower tree bole (i.e., fire scars or "catfaces"), lower crown ratios, and lower elevations. At Black Mountain Grove, we tracked trees through time and found total crown damage and the presence of fire scars were the best predictors of mortality by year three, where large sequoias sustained up to ~ 85% crown damage before succumbing to injury. There, 52 of 204 trees were dead one-year postfire, with 71 dead by year three. Overall, these fires caused significant and concerning mortality levels of these ancient trees, and yet the impact on sequoia groves between 2015 and 2017 was dwarfed in comparison to the more recent 2020 Castle Fire, 2021 Windy Fire and 2021 KNP Complex Fire. With the push to increase forest and fuel treatments to reduce catastrophic fire risk across the Western U.S., more immediate triage to protect irreplaceable resources is needed as fire activity rapidly increases. Our study suggests that prioritizing management action that creates fire resilience in unburned groves, and maintains the fuel reduction benefits accrued by past treatments and lower severity wildfires, will be critical to avoid continued losses of these exceptional, irreplaceable old growth forests.

1. Introduction

Rising temperatures and the legacy of human land uses that characterize the Anthropocene are having impacts on forests worldwide. Drought and hotter temperatures have been linked to extensive forest dieback and mortality (Allen et al., 2010; Anderegg et al., 2015, 2012), and more frequent and severe fires are related to increasing temperatures and the subsequent effect on vapor pressure deficit (Westerling et al., 2006; Williams et al., 2019). In forests with historically frequent, predominantly low-severity fire regimes, the modern management paradigm of excluding fire has also increased fuel loads, which is contributing to increased fire severity and greater extents of high-severity fire that exceed what would have occurred historically (Miller et al., 2009b; Parks and Abatzoglou, 2020; Safford and Stevens, 2017; Stevens et al., 2017). Mature forests are rapidly declining in response to cascading climate and fire regime shifts, which in turn is significantly

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impacting ecosystem services such as carbon storage, biodiversity, and hydrologic and watershed function (Anderegg et al., 2020; Turner, 2010). Another emerging threat of the Anthropocene is the loss of biodiversity, particularly in areas with rapid rates of ecological change (Johnson et al., 2017). Past management legacies and the warming climate are increasingly taking a toll on individual species, and species with limited distributions are likely to be at most risk (Pimm et al., 2014). The iconic giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz) is one such species that is increasingly facing novel threats as a result of anthropogenic change.

Giant sequoias are not currently designated as rare, but they are limited in distribution within the mixed-conifer forests of the Sierra Nevada mountains of California, USA. They occur in ~ 70 distinct groves covering only ~ 12,000 ha, most of which are in the southern Sierra Nevada (Hart, 2020). Culturally, they have been highly valued by American Indians throughout the Sierra Nevada for generations (Franco, Jr., 1994; Rueger, 1994); more recently they have been drawing visitors from around the globe (Tweed, 2016). They are primarily valued for their longevity and immense size, with the oldest known individual dated to ~ 3,200 years old, and the largest specimen measured at roughly 11 m in diameter and 95 m tall (Hartesveldt et al., 1975). Their longevity is also important for understanding the connection between life history strategies, disturbance regimes and their possible future modifications (Piovesan and Biondi, 2021), and their massive size translates to significant carbon storage capacity, where old-growth giant sequoia forests are second only to coast redwood (*Sequoia sempervirens* (D. Don) Endl.) in carbon storage per hectare globally (Sillett et al., 2019).

Giant sequoia longevity is generally attributed to their resistance to pests, disease and in particular, wildfire. They have extraordinarily thick bark (up to 0.6 m in some cases) that protects the cambium from the heat of a wildfire, self-pruning branches, and semi-serotinous cones (Hartesveldt et al., 1975; Kilgore and Taylor, 1979). Because of their longevity, they also provide some of the oldest tree ring-based fire history chronologies available, which document frequent fire over 1,400 years in five different groves. Though this frequency varied with climate, prior to the onset of the contemporary fire exclusion era in the late 19th century, the longest fire free period observed across the five groves sampled was 30 years (Swetnam, 1993). At the individual tree scale, fires occurred roughly every 15 years (Swetnam et al., 2009). This frequency shaped a fire regime dominated by low to moderate severity fire, with some smaller patches of high intensity fire that created canopy gaps necessary for regeneration (Stephenson et al., 1991). With Euro-American settlement in the late 19th century, American Indian cultural burning was prohibited and lightning-ignited wildfires were suppressed, dramatically reducing fire frequencies. Given the species' longevity and past fire frequencies, it is reasonable to assume that many of the older, legacy trees have lived through many dozens of fires that burned under a wide range of climatic conditions in their lifetimes, making the contemporary fire exclusion era truly anomalous for these trees (Swetnam, 1993).

Anthropogenic changes are negatively impacting giant sequoia groves in several ways. First, fire exclusion has resulted in scant giant sequoia regeneration in most groves due to their semi-serotinous cones and shade intolerance, raising concerns about overstory recruitment through time (Stephenson, 1994). The lack of fire has also dramatically increased fuel loads, a pattern that is well documented in both giant sequoia groves and in other frequent-fire forests throughout the west (Fulé et al., 2004; Greenberg and Collins, 2021; Parsons and DeBenedetti, 1979). Although a few groves, primarily in National Parks, have been regularly prescribed burned since the 1970 s, prior to 2015 most groves (~90%) had not experienced fire in over a century (York et al., 2013). Climate change has also been linked with extensive foliage dieback during the 2012–2016 "hotter drought" (Stephenson et al., 2018). While foliage dieback is an effective strategy to reduce water loss via stomata during times of water stress, it had not been previously documented in giant sequoia, and is a bellwether that these long-lived trees are beginning to be impacted by climate change. The hotter drought also may have shifted giant sequoia interactions with the native *Phloeosinus* beetle, where greater water stress enabled the beetles to attack some trees; research into this topic currently underway (Nate Stephenson and Thomas S. Davis, personal communication).

Of all threats to the persistence of the old-growth giant sequoia forests, perhaps the most immediate threat is the warming climate's interaction with increased fuel loads and drought stress, which is leading to increased fire activity and fire severity (Lydersen et al., 2017; Miller et al., 2009b; Parks and Abatzoglou, 2020; van Mantgem et al., 2018). While this trend has been underway for some time throughout the western US, it has only more recently been observed in giant sequoia groves. During a period that covered roughly the first century of fire exclusion (1910 to 2014), wildfire burned ~ 19% of the giant sequoia range; in just the last six years (2015–2021), ~65% of the range has burned in wildfires (Fire and Resource Assessment Program, 2020; Hart, 2020). Fire severity has also been on the rise; between 1984 and 2014, when burn severity maps from satellite imagery became widely available (Miller and Thode, 2007), ~1 ha was detected as having burned at high severity. From 2015 through 2021 ~1,600 ha burned at high severity.

Where recent wildfires within giant sequoia groves burned at lower intensity, they have likely been largely restorative and within the natural range of variability (Haase and Sackett, 1998; Kilgore, 1970; Kilgore and Sando, 1975). These fires are similar to management-ignited prescribed fires which cause minimal to no large sequoia mortality; where the rare mortality does occur in these types of fires, it is generally from structural failure, where cumulative structural injury from 100 s of years of fires eventually result in tree fall (Weatherspoon, 1990). However, despite significant research on the impacts of high-severity fire effects in mixed-conifer forests of the region (Collins and Roller, 2013; Shive et al., 2018; Stevens et al., 2017; Welch et al., 2016), little is known about the extent of direct, fire-caused mortality in large, legacy giant sequoias, primarily because the occurrence of extensive high severity areas in sequoia groves is relatively new in the modern era. Our primary objective in this study is to quantify these impacts and better understand both the rates and drivers of mortality.

Tree mortality after wildfire is often assessed via remotely-sensed burn severity maps, which are generated by differencing pre- and postfire LANDSAT images. The differenced images are then linked to existing metrics, such as the Composite Burn Index (CBI), and classified into severity classes (generally undetected change, low, moderate and high) based on established relationships with field plots (Miller and Thode, 2007). CBI maps classified as high severity in Sierran mixed conifer have been linked with stand-replacing fire (i.e., >95% canopy cover loss (Miller et al., 2009a)); this class has also been characterized as having > 75% tree mortality (Monitoring Trends in Burn Severity, 2022). Within the high severity class, any mortality < 100% suggests that there is at least some live foliage retained postfire; in forests this is most likely found in surviving portions of tree crowns, given that crown fires rarely occur independently of surface fires that also consume surface and ladder fuels (Scott and Reinhardt, 2001). Given giant sequoia's exceptional fire adaptations and height, we suspected that any live foliage that remains in high severity areas of sequoia groves could be concentrated in the upper crowns of large giant sequoia, increasing their potential for survival. This could effectively increase the survival rate for giant sequoia over that estimated for mixed -conifer forests, in which giant sequoia groves co-occur. In addition, although the basic drivers of fire behavior and severity are understood to be fuels, weather and topography, we don't have basic information about where on the landscape these exceptionally fire-adapted trees might be most susceptible, or what individual tree characteristics increase the risk of mortality.

Moreover, the total mortality from a fire event includes immediate tree death and delayed mortality, the latter of which is not well captured in burn severity maps that are derived either immediately after fire or one-year postfire (Miller and Quayle, 2015; Miller and Thode, 2007). Immediate tree death in giant sequoia is the result of the total loss of photosynthetic tissue, since these trees cannot sprout after top kill; though they do sprout epicormically, this generally occurs on trees that had also retained some green foliage in their crowns postfire (Hartesveldt et al., 1975). Delayed mortality is also expected through time, where trees retain some green needles but have sustained significant fire injury (i.e. the direct impacts of a fire on plants, generally called "first order fire effects") that either predisposes the tree to other stressors, such as drought stress or bark beetles, or that takes time to fully manifest (Hood et al., 2018).

There is substantial literature linking the degree of fire injury to tree mortality for individual species (Hood et al., 2018) and developing predictive models that can be used in applications that support forest management (Cansler et al., 2020a), such as the First Order Fire Effects Model (FOFEM; Keane and Lutes 2020). Important predictors of postfire tree mortality include crown scorch (needles killed from the heat of a fire), overall crown damage (which includes both crown scorch and crown torch, where the needles are consumed), bark char and cambium damage. The amount of damage that a tree can sustain and still survive varies greatly by species; to date, ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) have received the most research attention in the US (Cansler et al., 2020b; Woolley et al., 2012). In giant sequoias, only one study has examined delayed mortality after fire, with a focus on

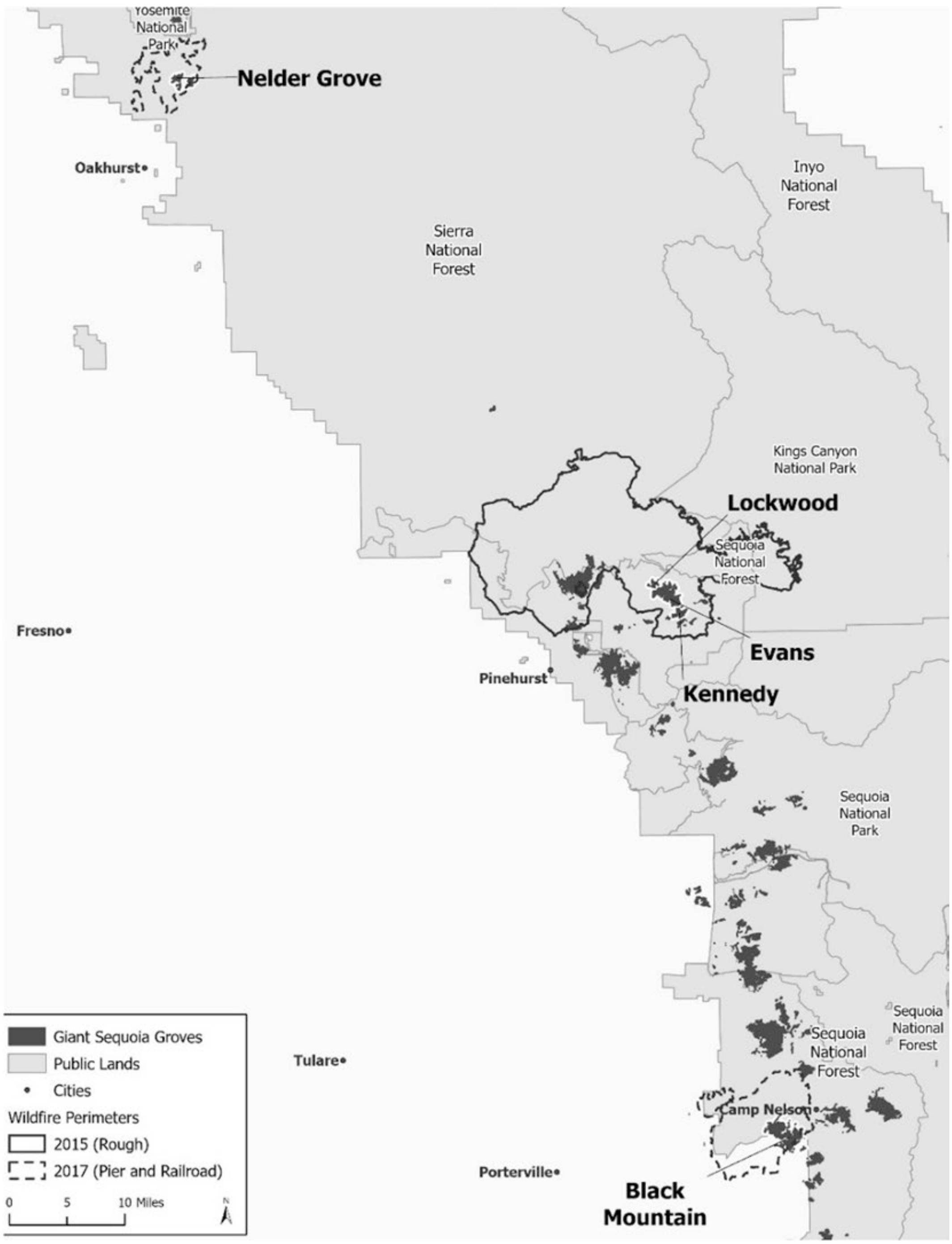

Fig. 1. Map of study area.

younger, understory trees after a low-severity prescribed burn (Stephens and Finney, 2002). Stephens and Finney (2002) found that trees 15–100 cm diameter at breast height (DBH) tended to survive until crown scorch exceeded 90–95%, but it is unclear how this translates to larger legacy trees, particularly under recent warming climate trends.

Given the combination of their exceptional adaptations to survive fire – tall crowns and overall height, thick bark – and the potential for large sequoia to withstand high levels of crown damage as documented in smaller trees (Stephens and Finney, 2002), we expected that though some large sequoias would be killed in high severity areas, most would survive. Following the dramatic rise in area of giant sequoia groves burned at high severity in recent years, understanding these mortality patterns and drivers will be critical for future management of both burned and unburned groves. To address these foundational questions, we asked:

(1) What are the mortality rates and fire effects for large sequoias in high and moderate severity areas?
(2) What individual tree characteristics and topographic variables are associated with mortality for all three fires?
(3) What first order fire effects best predict mortality by three years postfire at Black Mountain Grove, and how does this compare with existing models?

2. Methods

2.1. Study area

We conducted field surveys in high and moderate severity burn areas in groves that burned in three different wildfires. In the Giant Sequoia National Monument (GSNM) we surveyed the Evans, Lockwood and Kennedy Groves that burned in the 2015 Rough Fire (hereafter: Rough Fire Groves); other groves burned in this wildfire but we excluded them because they did not contain old growth, did not burn at high or moderate severity or were inaccessible by road. We also surveyed Black Mountain Grove (BLMO) in GSNM which burned in the 2017 Pier Fire, and Nelder Grove (NELD) in the Sierra National Forest that burned in the 2017 Railroad Fire (Fig. 1, Table 1). In addition to giant sequoias, all of the groves include components of ponderosa pine, white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.), incense cedar (*Calocedrus decurrens* (Torr.) Florin) and sugar pine (*Pinus lambertiana* Douglas) with the specific species mixtures varying by elevation (Table 1), aspect and management history. The climate is Mediterranean with hot, dry summers and cool, moist winters, where mean annual precipitation ranged from 960 to 1,179 mm. Using weather station data from two weather stations near study sites on the Sierra and Sequoia National Forests (i.e., Southern Yosemite and Grant Grove) the 30-year mean annual minimum temperature of the coldest month near NELD ranges from −6.2–0.9° C (December) and near BLMO and the Rough Fire Groves was −6.5 – 1.2° C (February); mean maximum temperature of the hottest month (July) ranged from 23.3 to 30.6° C near NELD and 21.3–27.7° C near BLMO and the Rough Fire Groves. All of these groves have had a history of some logging (Stephenson, 1996), but we excluded areas where large, legacy trees had been removed. In several of the groves there was also logging of all species other than giant sequoia (i.e., “whitewoods”) as recently as the 1980 s, but this more recent logging did not occur in our study areas. The presence of old skid trails and general forest stature in some of our stands suggests that some logging of whitewoods may also have occurred well before the 1980 s, but records of this work were unavailable (George Powell, USFS District Silviculturist, personal communication). All of the areas sampled have experienced fire exclusion since at least ∼ 1900; the most recent documented fires in any of our sampling areas was in 1938, and those fires covered relatively small areas (NELD has no documented fire history after the onset of fire exclusion).

2.2. Study design and data collection

For all fires we used classified burn severity maps of the Composite Burn Index (CBI) generated from the Relativized differenced Normalized Burn Ratio (RdNBR) to delineate high and moderate severity areas (Miller and Thode, 2007). RdNBR uses differences in greenness and wetness between pre- and postfire images to estimate severity via CBI, which is then binned into four classes (low, moderate, high and undetected change) based on field-validated thresholds. We used the best assessment as determined by the USFS in the Region 5 burn severity database which uses thresholds in Miller and Thode (2007) (https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=stelprd3805100), which for NELD and BLMO were immediate postfire assessments and for Rough Fire Groves was the extended assessment (estimated one-year postfire). For observations on total area burned within groves and by severity class, we used a recent grove boundary dataset (Appendix 1 in Stephenson and Brigham, 2021); we used this spatial dataset, even though it is in draft form because observations by managers and our own surveys showed that it is a dramatic improvement over prior boundary estimates. We buffered all high- and moderate-severity patches by 15 m in BLMO; in NELD and Rough Fire Groves, the survey areas were not buffered due to logistical constraints. For all study areas, we limited our surveys to patches that were accessible by road/day hike. In BLMO 87% of the 792-hectare grove burned; 181 ha were classified as high or moderate severity and we surveyed 65 ha of mostly high/moderate severity (with some unburned/low severity that was captured within the 15 m buffer). In NELD 82% of the 153-hectare grove burned; 33 ha were classified as high or moderate severity which we fully surveyed. In the Rough Fire Groves, 93% of the 1,480 ha of giant sequoia grove area burned (spread across 15 distinct groves), with 628 ha burned at high or moderate severity. The majority of the grove area burned in the Rough Fire was substantially logged at the turn of the 19th century and we only surveyed groves with large legacy trees that were also accessible by road/day hike. Field sampling in the Rough Fire Groves was further limited by a reduced field season due to USFS forest-wide closures for fire risk and hazardous air quality due to smoke, resulting in ∼ 60 ha of moderate and high severity areas surveyed.

For all study sites we surveyed the selected areas and documented all

Table 1
Summary information on fires and groves surveyed. Because the data was collected at different times postfire at each of our study sites, not all sites were analyzed for each research question; we indicate which sites were used to answer individual research questions with an “X”.

	Rough Fire Groves (Evans, Lockwood, Kennedy Groves)	Black Mountain Grove (BLMO)	Nelder Grove (NELD)
Fire year and name	2015 Rough Fire	2017 Pier Fire	2017 Railroad Fire
US Forest Service Management Unit	Giant Sequoia National Monument	Giant Sequoia National Monument	Sierra National Forest
Year(s) surveyed	2020	2018, 2019, 2020*	2018/2019/2020*
Elevation (m) surveyed	1,784–2,266	1,528–1,974	1,540–1,886
Research questions:			
(Q1) Mortality rates	X	X	X
(Q2) Topographic/tree characteristic drivers	X	X	X
(Q3) Delayed mortality		X	

* At BLMO, trees were tracked each year for three years. At NELD, each tree was visited at least once between 2018 and 2020.

large giant sequoias, defined as ≥ 1.2 m DBH (1.37 m above ground). Crews did not consistently record trees that had complete structural failure after the fire and were fully down on the ground, but based on field notes we suspect this left out only two downed trees. Where they did record downed large sequoias, it was not always possible to determine if the tree died from fire injury and then fell, or if the crown was still alive and the structural failure killed the tree. At each tree we minimally recorded live/dead status (where we only classified trees with no visible green foliage as dead), DBH, height and height to pre-fire live crown (HLC). We did not include any trees that were dead before the fire (which we determined by the stage of bark and branch decay) in any analyses. Due to extremely large tree sizes, the tendency for sequoias to form substantial buttresses, and presence of fire scars or "catfaces" (i.e., areas of fire-killed cambium at a tree's based that forms a cavity of exposed wood bordered by woundwood (Dieterich and Swetnam, 1984), see Fig. 2a), the reported DBHs likely contain some error (Sillett et al., 2015). Crews also made ocular estimates of pre-fire crown vigor and assigned one of three qualitative classes that described the fullness of the crown relative to a hypothetical full crown. Very sparse crowns (<25% of a full crown) were classified as low vigor, crowns with more contiguous live branches (25–75%) pre-fire were classified as moderate vigor and mostly full crowns (>75%) were classified as high vigor. We also recorded evidence of epicormic sprouting and presence of a fire scar (Fig. 2a).

Preliminary analysis indicated that taller HLC was generally linked with increased mortality, which was counterintuitive since lower HLC is generally associated with fire-caused mortality, due to increase continuity between ladder fuels and the tree crown. HLCs are also correlated with crown ratio, a measure of the percent of a tree's total height that has crown foliage, where taller HLC is linked with lower crown ratios (i.e., a smaller crown overall). We explored correlations between crown ratio and a qualitative measure for crown vigor that we recorded at NELD and BLMO and found that they were strongly related. Given that all of our sample trees had relatively high HLC because of their exceptional size, crown ratio is likely more relevant for understanding mortality probability as it related to photosynthetic capacity and overall vigor. Therefore, for all relevant models we tested crown ratio instead of HLC when developing the mortality models.

We collected first order fire effects at NELD and BLMO because we visited them in the first few years postfire whereas Rough Fire Groves was visited five years postfire, making assessment of first order fire effects difficult. These first order fire effects included: percent crown volume scorch and torch, crown scorch and torch height and maximum bark char height (m), where crown scorch is the portion of the crown that has browned needles and crown torch is the portion of the crown that was completely consumed (Varner et al., 2021). Because anecdotal evidence suggests that basal injury could be a primary driver (Nate Stephenson, personal communication), we also experimented with ways to measure it on these thick-barked trees, including recording the percent of the circumference of the tree with bark loss at least 5 cm deep and average loss depth.

At BLMO only, we tracked the 205 sample trees annually from 2018 (one-year postfire) through 2020 to assess delayed mortality. In NELD we visited all of the trees in the high and moderate severity areas at least once during 2018–2020 and so we report on overall mortality rates, first order fire effects and the topographic and tree characteristics that are linked with mortality, but do not use these data to predict delayed mortality (Question 3).

We used ArcMap version 10.8.1 (ESRI, 2011) to derive elevation, slope and aspect from digital elevation models downloaded from USGS (https://www.usgs.gov/core-science-systems/national-geospatial-program/national-map). We also classified each tree by its landscape management unit (LMU; https://www.ice.ucdavis.edu/project/landscape_management_unit_lmu_tool.html).

2.3. Statistical analyses

For research question 1, we report only summary statistics of mortality because the differences in when the data was collected limited our ability to pool all of the data for subsequent modelling. To test probability of mortality by topographic and tree characteristics (Q2), we used a generalized linear mixed model with a binomial family and logit link,

Fig. 2. (a) Image of a large fire scar in a giant sequoia; person shown for scale. (b) Three large giant sequoias (316–357 cm DBH) killed in the 2017 Pier Fire in Black Mountain Grove (BLMO), Giant Sequoia National Monument. Photos by K. Shive.

where the fire area was the random effect. Because there is some guidance suggesting that random effects should only be used if they have ≥ five levels (Bolker et al., 2009) we also explored a model with fire as a fixed effect, which had p-values and standard errors were similar to the random effect model. We therefore report the model with fire as a random effect since the fire variable fits the definition of a random effect (i.e., quantify variation across sampled populations). To test the probability of mortality at three years postfire based on first order fire effects at BLMO only (Q3), we used a generalized linear model with a binomial distribution.

To build each model, we explored univariate models for all candidate variables and considered any variable that was significant at $p > 0.1$ in the univariate models as a candidate for the multivariate models (Hosmer and Lemeshow, 2000). For correlated variables, we selected the variable from the univariate model that had the lowest AIC. Finally, we combined the resulting group of variables into a comprehensive model, dropping variables that became insignificant at $p < 0.05$ when included with other variables and that also did not improve model performance as indicated by Akaike Information Criterion (AIC). All data were analyzed in R (R Core Team, 2021).

3. Results

3.1. What are the mortality rates and fire effects for large sequoias in high and moderate severity areas?

Of the 458 large sequoias in the ~ 160 ha we surveyed in moderate and high severity across the three fire areas (BLMO, NELD, Rough Fire Groves), 41% (186) were dead by 2020;130 of these were in areas classified as high severity (Table 2, Fig. 2b). The average mortality rate across the three sites was 84% for high severity and 28% for moderate severity. At least five of the dead sequoias had complete structural failure and were on the forest floor. There were nine trees that were still partially standing but had significantly broken boles that removed portions of the tree crown, five of which were dead.

NELD is the smallest of the groves sampled and it also has a near-complete census of all large sequoias across the grove, so we estimated the impact of this fire on the entire grove population. There are roughly 95 documented large giant sequoias throughout the entire grove (including areas beyond our survey areas); 43% of them died in this one fire.

Tree sizes ranged from 124 to 950 cm in diameter (median: 287 cm) and 22–87 m in height (median: 63 m) (Fig. 3). In NELD and the Rough Fire Groves, the DBH of dead giant sequoias were generally smaller than live trees, but the pattern was reversed for BLMO. Dead trees were generally shorter at BLMO and the Rough Fire Groves but the trend was the opposite at NELD (though this fire had the smallest sample size). When the study sites were combined, median heights were similar between live and dead trees, but median DBH was slightly larger for dead trees.

First order fire effects varied considerably within fire areas, but overall tended toward more severe effects in NELD because BLMO included more moderate severity areas (Fig. 4; Rough Fire Groves are excluded here because they were recorded five years postfire, see methods). Crown torching > 90% occurred on trees ranging from 51 to 78 m tall, most of which were from NELD. Bark char height and relative bark char height followed a similar trend. Based on a subsample of 246 trees at BLMO and NELD, 36% showed some epicormic growth, which occurred on trees with a median of 30% crown damage and a maximum of 98%. Of the trees that were still alive in 2020, 11 had ≤ 10% green canopy remaining and also showed signs of postfire crown dieback, suggesting they may be in decline.

3.2. What individual tree characteristics and topographic variables are associated with mortality for all three fires?

Of the 459 trees surveyed across the three study sites, 443 had complete data for inclusion in model development for this research question. We did not test crown scorch or torch in this model because one fire was measured five years postfire, when those first order fire effects are difficult to measure. The best predictors of tree mortality included estimated pre-fire crown ratio, presence of a fire scar and elevation; all three were highly significant when included together in the combined model ($p < 0.001$ for all; Fig. 5). The probability of mortality was 2.4 times larger for trees with a fire scar. Of the 260 trees that had a fire scar, 47% were dead; of the 183 without a fire scar, only 30% were dead. There was a significant difference in elevation between live (mean (S.E.): 1,815 (±9m)) and dead (mean (S.E.): 1,789 (±11 m)) trees; this was also true for crown ratio, but the difference between means was very small (mean (S.E.): live 0.65 (±0.1); dead 0.61± (0.1)).

We also examined slope, aspect (eastness and northness), LMU, height and DBH in the univariate models; only eastness was significant at the 0.1 screening threshold ($p = 0.096$) but it was not significant when included in the multivariate model.

3.3. What first order fire effects best predict mortality within three years at Black Mountain grove (BLMO), and how does this compare with existing models?

Of the 204 large sequoias surveyed at BLMO where we tracked trees through time, 52 (25%) were dead one-year postfire with a total of 71 (35%) dead by year three. Of the 19 that were live in 2018 but dead by 2020, all but one had crown damage > 90%. An additional seven trees had < 10% green canopy with signs of fading crowns at the last sampling in 2020), suggesting that more delayed mortality may yet occur. Two of the dead trees had fallen postfire and crown damage was difficult to

Table 2
Number and mortality levels of large giant sequoias (>1.2 m DBH) surveyed, by severity class (high, moderate) across three wildfires. Mortality for BLMO includes delayed mortality through three years postfire.

Groves Surveyed	Total no. trees surveyed	*Remote sensing-classified burn severity*											
		Unchanged			**Low**			**Moderate**			**High**		
		Live trees (#)	*Dead trees (#)*	*Mortality rate (%)*	*Live trees (#)*	*Dead trees (#)*	*Mortality rate (%)*	*Live trees (#)*	*Dead trees (#)*	*Mortality rate (%)*	*Live trees (#)*	*Dead trees (#)*	*Mortality rate (%)*
Black Mountain (BLMO)	204	2	0	0%	37	5	12%	80	25	24%	14	41	75%
Nelder (NELD)	55	2	1	33%	6	2	25%	6	5	45%	0	33	100%
Evans, Lockwood, Kennedy (Rough Fire Groves)	199	0	0	NA	2	0	0%	106	17	14%	18	56	76%

Note: Trees in unchanged and low severity were generally adjacent to moderate and high severity; in BLMO this was a result of buffering the high/moderate areas by 15 m and in the other study sites it was likely due to positional error in the field.

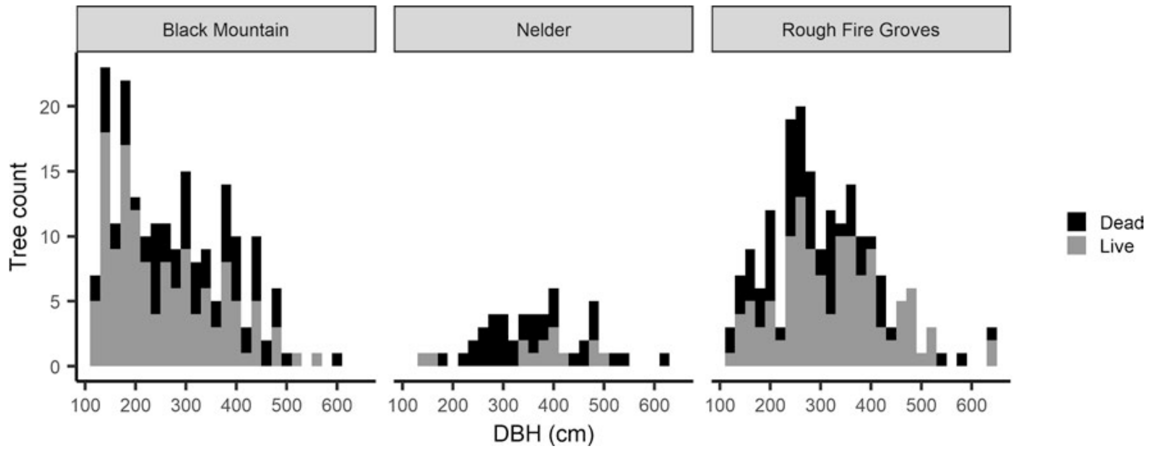

Fig. 3. The range of DBH for sampled trees by study site and final live/dead status. The trees shown in the histogram range from 120 to 632 cm; two trees that were recorded as 830 cm and 950 cm from the Rough Fire Groves are not included to improve figure readability, and because these outliers may be to the result of measurement error.

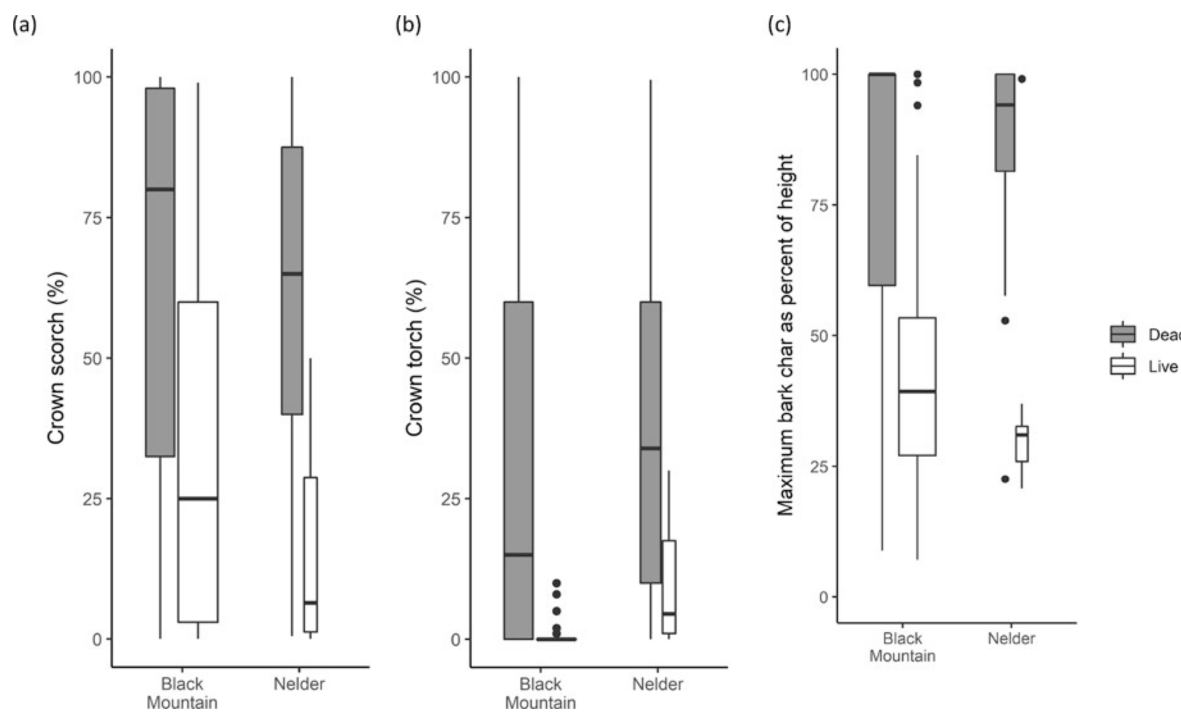

Fig. 4. Range of observed crown scorch (a), crown torch (b) and maximum bark char height as a percent of total height (c) by study site and live/dead status. Boxplot width is scaled by sample size, where boxes denote first and third quartiles, lines the median, and whiskers the 1.5 inter-quartile range. Dots are outliers.

assess, so these trees were excluded from model development, leaving 202 trees in the dataset.

First order fire effects variables were significant in univariate models (crown torch, crown scorch, total crown damage, maximum bark char height, relative bark char height). The bark char variables were correlated with crown torch and total crown damage variables and so they were not explored in the multivariate models. DBH was also significant in a univariate model, where increasing DBH was associated with increasing mortality ($p < 0.001$). DBH was not significant in a model with the inclusion of fire scar, likely because trees with fire scars tended to be larger trees at BLMO. Fire scar area was also significant in a univariate model, but the presence/absence of a fire scar performed better in a univariate model in terms of AIC (258.0 and 237.0 respectively). Finally, crown ratio and height were significant in a univariate model, but when included in a multivariate model with fire scar and the crown damage variables, they were not significant, and their inclusion did not improve model performance with AIC. Average depth of basal scarring and the percent of the circumference that had > 5 cm of the bark burned away were not significant in the univariate models.

The best multivariate model predicting mortality at three years postfire in BLMO (Pier Fire) included percent crown scorch ($p < 0.001$), percent crown torch ($p = 0.017$) and presence of a fire scar ($p = 0.011$; AIC: 69.5; Table 3). Fig. 4 highlights that many trees at BLMO survived fairly high levels of crown scorching, but no trees with more than ~ 10% crown torch survived. However, those levels of crown torch were nearly always associated with high crown scorch, which makes it somewhat difficult to tease out the role of crown torch and total crown damage. Given our relatively small dataset, concerns about overfitting the model, and the objective of developing the simplest predictive model possible for management applications, we also explored a model with fire scar

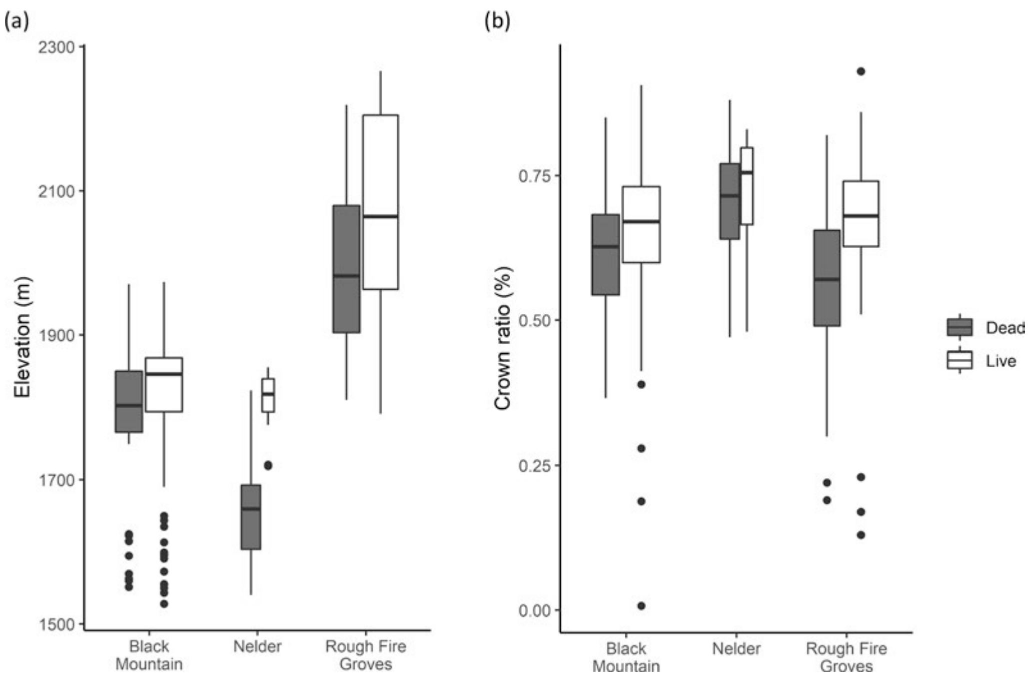

Fig. 5. Live and dead large sequoias per study area, by (a) elevation and (b) estimated pre-fire crown ratio. Boxplot widths are scaled to sample size, where boxes denote first and third quartiles, lines the median, and whiskers the 1.5 inter-quartile range. Dots are outliers.

Table 3
Parameters for BLMO delayed mortality models. β_0 is the model intercept, β_1, β_2 and β_3 are coefficients for the corresponding x_1, x_2 and x_3 variables.

Model	*Parameters*							**Model AIC**
	β_0	β_1	x_1	β_2	x_2	β_3	x_3	
Null	−0.6562							261.4
Crown damage (%)	−25.1787	0.2818	Crown damage					55.0
Crown damage (%) + fire scar	−26.4363	0.2810	Crown damage	2.2841	Fire scar			48.8
Scorch (%) + torch (%)	−24.9955	0.2722	Scorch (%)	0.5166	Torch (%)			44.7
Scorch (%) + torch (%) + fire scar	−25.5916	0.2741	Scorch (%)	0.5283	Torch (%)	2.3167	Fire scar	40.0

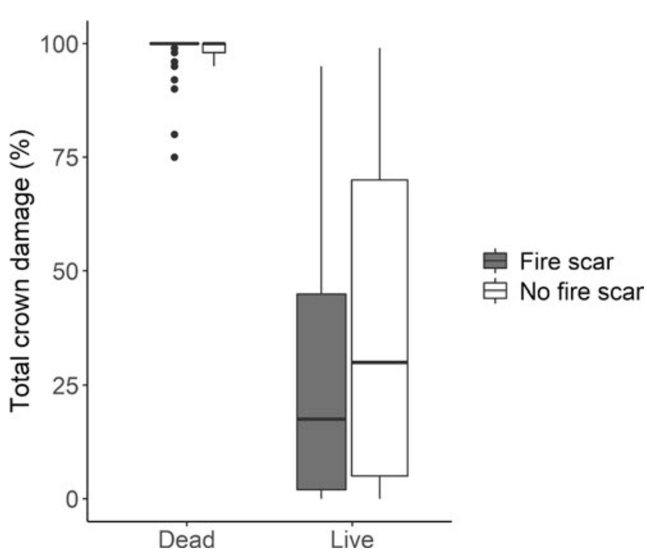

Fig. 6. Percent crown damage by presence/absence of a fire scar. Boxplot width is scaled by sample size, where boxes denote first and third quartiles, lines the median, and whiskers the 1.5 inter-quartile range.

presence that included total crown damage rather than the separate variables of scorch and torch. In this model, both crown damage ($p < 0.001$; Fig. 6) and the presence of a fire scar ($p = 0.007$) were significant. When compared with the model that included scorch and torch separately, it had a higher AIC (82.3) but nearly equal classification accuracy (Table 4). There was significantly higher crown damage in trees that eventually died (97.0 ± 1.5%) versus surviving live (33.3 ± 2.8%) trees (Fig. 6).

The fitted probabilities suggest that large giant sequoias with a fire scar can sustain up to ~ 85% crown damage before probability of mortality exceeds 50% and trees without a fire scar can sustain up to ~ 95% crown damage before reaching that same threshold; the curves generally show rapid increases in probability of mortality above ~ 80% (Fig. 7).

We also compared the accuracy of our two best multivariate models with the accuracy of that created by Stephens and Finney (2002) for smaller sequoias (<100 cm DBH), which included only crown scorch, and the model used in FOFEM which included allometric estimates of bark thickness and crown damage as predictors (Table 4). The crown damage + fire scar model and crown scorch + crown torch + fire scar model performed similarly using a mortality threshold of 0.5 (Table 4). Overall, our models performed substantially better than either existing model, with a total accuracy of 96%, compared to 74% for the Stephens and Finney (2002) model and 76% for the FOFEM model (Table 4). The lower total accuracy was driven by the two existing models' poor performance in classifying the number of observed dead trees (i.e., sensitivity = 28% and 38%) in favor of high performance in classifying the

Table 4
Accuracy assessment of our two best multivariate models, the model from Stephens and Finney (2002) and FOFEM (Keane and Lutes 2020), based on a predicted probability of mortality threshold of 0.5.

Modelled mortality	Observed Dead	Observed Live	*Positive Predictive Value (%)*[*]	*Negative Predictive Value (%)*[**]	*Total Accuracy (%)*[+]
Models from this paper:					
Total crown damage (%)			*91*	*98*	*96*
Predicted live	2	126			
Predicted dead	67	7			
Total crown damage (%) + fire scar			*92*	*98*	*96*
Predicted live	2	127			
Predicted dead	67	6			
Crown scorch (%) + crown torch (%)			*94*	*98*	*97*
Predicted live	3	129			
Predicted dead	66	4			
Crown scorch (%) + crown torch (%) + fire scar			*93*	*98*	*97*
Predicted live	2	128			
Predicted dead	67	5			
Stephens and Finney (2002): (crown scorch (%))			*91*	*98*	*74*
Predicted live	51	131			
Predicted dead	20	2			
FOFEM: (bark thickness + crown damage (%))			*87*	*75*	*76*
Predicted live	44	129			
Predicted dead	27	4			

[*] Positive predictive value = dead trees predicted to die divided by total predicted dead trees.
[**] Negative predictive value = live trees predicted to survive divided by total predicted live trees.
[+] Total accuracy = correctly classified live and dead trees divided by total trees.

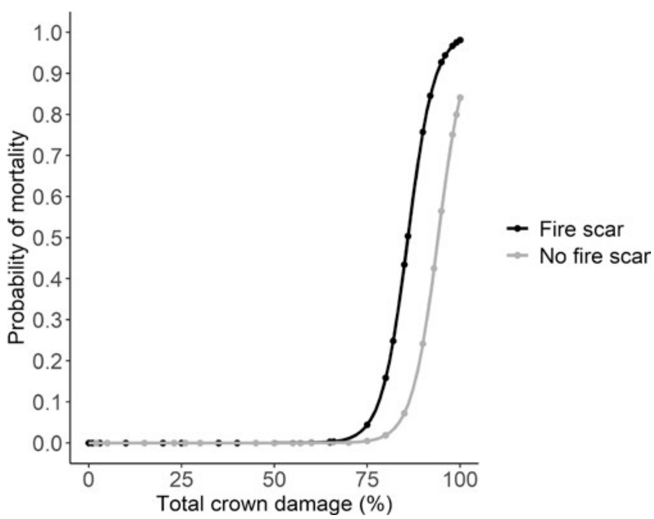

Fig. 7. Total crown damage by fitted probability of mortality by postfire year three at BLMO, by presence/absence of a fire scar.

number of observed live trees (i.e., specificity = 95% and 95%). Although neither of the existing models were developed with data from large giant sequoias, both had fairly high positive predicted values (i.e., the trees predicted to die did actually die). The Stephens and Finney (2002) model had equivalently high negative predictive value as our model at 98%, reflecting the model's ability to correctly classify predicted surviving trees. In contrast, the FOFEM model had a lower negative predictive value of 75%, meaning that of the total number of trees the model predicted to survive, 25% ended up dying postfire.

4. Discussion

Our surveys are the first to show that even the largest among the quintessentially fire-adapted giant sequoias are vulnerable to recent increases in fire severity. Within areas designated as high severity in remotely-sensed severity maps, we observed 75% (BLMO), 76% (Rough Fire Groves) and 100% (NELD) mortality of large, legacy giant sequoia trees (>1.2 m DBH). In NELD, the 100% mortality came from a single high severity patch which burned during an extreme downdraft. Outside of such an extreme event, mortality rates at BLMO and Rough Area Groves are on the low end of the > 75% tree mortality threshold (Monitoring Trends in Burn Severity, 2022), and much lower than the > 95% tree canopy mortality that has been associated with this CBI class (though our mortality rates are calculated on density, not canopy cover; Miller et al., 2009a). Mortality rates in areas designated as moderate severity areas were considerably lower at 14–45%. Collectively, we interpret these data to suggest that large, legacy giant sequoia trees are overall more likely to survive than their non-sequoia neighbors, but that within areas classified as high severity, mortality rates are still very high, particularly under extreme fire weather events.

Across the three fire footprints, the biggest topographic predictor of mortality was decreasing elevation within each of the fires. This was at least partly because there was more area burned at high severity at lower elevations, where burning conditions were warmer and where there also may have been greater drought-related tree mortality in the surrounding forest (Wayman and Safford, 2021; Young et al., 2017). We also hypothesize that more moisture at higher elevations may have also influenced tree health, moderating the amount of fire damage incurred (Agee et al., 2002) and subsequent resistance to fire-caused injury (Meyer et al., 2019). Crown ratio, an indicator of photosynthetic capacity and tree vigor, was also an important predictor of mortality, which is not surprising given its importance for photosynthesis and the substantial amount of variation in giant sequoia crowns. Repeated basal injuries and crown scorching from frequent fires can lead to very sparse crowns with little photosynthetic material (Hartesveldt et al., 1975). For a tree with a sparse crown prefire, 50% crown loss is likely to have a bigger impact on tree health than the same percentage on a tree with a robust crown. Sparse crowns also suggest that the tree may have been in decline prior to the fire from the standpoint of ability to acquire carbon and transport water and nutrients. Antecedent reductions in tree vigor has been linked with reduced resilience to fire in other western conifers (van Mantgem et al., 2018).

Fire scar presence was important in both the landscape scale model that included all three fires and the delayed mortality model in BLMO, likely for several reasons. First, when fire gets into a fire scar, the exposed wood facilitates flame movement up the bole of the tree, which is more likely to result in crown damage or combustion of a tree's heartwood. It also means that there is less healthy cambium to transport nutrients and potentially damage to water-conducting sapwood (Rundel, 1973). Bark tissues surrounding the fire scar are likely thinner than elsewhere around the tree, and duff accumulation at the base of a fire scar also increases the likelihood of the fire scar igniting, potentially leading to greater cambium damage in subsequent fires (Hood, 2010). In addition, in much smaller ponderosa pine saplings, Partelli-Feltrin et al. (2020) found that the wound wood around fire scars can increase vulnerability to cavitation (Partelli-Feltrin et al., 2021), which could also be a factor for sequoia though more research is needed on this topic (Hood, 2021). In contrast to our findings, Lambert and Stohlgren (1988) and Haase and Sackett (1998) found no effect of fire scar presence on giant sequoia mortality in prescribed burned groves, but prescription burns were generally characterized as low intensity surface fires that were presumably less intense than the high to moderate severity burned areas examined in this study (Haase and Sackett, 1998; Lambert and Stohlgren, 1988). One study of an endemic conifer (*Athrotaxis cupressoides* D. Don) on the island of Tasmania also found that trees with prior fire scars were more likely to die in a wildfire (Bowman et al., 2019).

Despite fire scars creating vulnerability in trees during subsequent fire, this variable is not included in FOFEM to predict postfire tree mortality (Keane and Lutes, 2020). Our models which include fire scar presence, performed substantially better than the current model used in FOFEM, which relies on crown damage and bark thickness. Because giant sequoia grow exceptionally thick bark, trees > 1.2 m DBH may have already met a minimum threshold for cambium protection outside of fire scar wounds, making estimates of increased thickness with increasing DBH less important. We acknowledge that our model was not evaluated with independent data, so it is not surprising that it performed better than the Stephens and Finney (2002) and FOFEM models. However, our findings are a meaningful improvement because the inclusion of fire scar presence improves model performance and adds valuable postfire mortality data that is sorely lacking for giant sequoia (Cansler et al., 2020a, 2020b).

More broadly, the importance of crown damage in predicting delayed mortality in giant sequoia is consistent with many other studies on delayed mortality, which have found varying combinations of crown scorch, crown torch and total crown damage to be the most important predictors (Fowler et al., 2010; Fowler and Sieg, 2004; Hood et al., 2018; Shearman et al., 2019; Sieg et al., 2006). Our findings for these large giant sequoias are similar to those observed in smaller giant sequoias by Stephens and Finney (2002), which suggested that giant sequoias can survive with up to 90–95% crown loss. This trend is likely one of the reasons that the species can be so long-lived, particularly relative to other species that are more likely to die at lower amounts of crown damage, such as white fir (Grayson et al., 2017).

Other studies looking at delayed tree mortality have also documented the importance of cambium damage (Hood et al., 2018; Shearman et al., 2019). We suspect this is important in our study as well, but to inspect the cambium the bark needs to be physically removed, which would be extremely labor intensive with such thick-barked trees and potentially cause harm to surviving individuals. In addition, anecdotal reports suggest that severe basal scarring may be an important driver of fire-related giant sequoia mortality in Sequoia and Kings-Canyon National Parks (Nate Stephenson, personal communication), but we found this attribute difficult to quantify. We attempted to measure the average depth of basal scarring into the bark, as well as the percent of the circumference that had > 5 cm of the bark burned away at the base. Neither of these variables were significant predictors, but we suspect that is because our measurement approach did not capture the extent of basal damage, not because basal scarring is inconsequential. We recommend future research develop accurate quantification methodology for basal scarring and its physiological effects on large giant sequoia.

While this study has clarified patterns related to delayed mortality, our most important findings are likely the most basic – the extent of increasing fire impacts to highly valued trees with a limited distribution. Roughly 20% of all legacy giant sequoia trees were logged during the last century, reducing the extent of old individuals even before the Anthropocene began. Since systematic burn severity mapping efforts in the U.S. began in 1984, only ~ 1 ha burned in high severity within a giant sequoia grove between 1984 and 2014, but 279 ha of high severity burned in these three fires between 2015 and 2017 (USDA Forest Service, 2018). This is alarming not only in the sharp upward trend, but also in magnitude, since the largest, high severity fires in a multi-millennia fire history record were estimated at 202 ha, which itself may be an overestimate (Caprio et al., 1994). On our study sites, at least 84% of large giant sequoias (>1.2 m DBH) in high severity areas were killed, which included 71 very large trees (>3.0 m DBH), often called "monarchs" (Cook, 1955), with substantial additional mortality in areas classified as moderate severity via remote sensing. That these three fires we are reporting on here were dwarfed more recently by over 1,400 ha of high severity in the 2020 and 2021 fire seasons should be raising high alarm on the status of ancient, legacy giant sequoia. Using the data presented here, two National Park Service reports have estimated that 13–19% of all large giant sequoias may have been lost in 2020–2021 (Shive et al., 2021; Stephenson and Brigham, 2021), signaling a precipitous decline in the population of the ancient trees that have significant cultural value.

In addition to studying mortality patterns on these more recent fires, future research should investigate impacts to second-growth groves that have also burned (e.g., Converse Basin and others in the Rough Fire footprint), to quantify the effects of recent wildfires on giant sequoias more broadly. Although one study looked at regeneration in burned second growth groves (Meyer and Safford, 2011), our understanding of mature tree survival and fire effects in these stands remains limited. In addition, these recent fires have also burned into areas that had selective logging of conifer species other than giant sequoia (i.e., "whitewoods"), presenting an opportunity to evaluate how a range of stand structures influenced fire behavior and the subsequent fire effects on large sequoias.

4.1. Management implications

Groves that burn at high enough intensity to cause mortality of old, large giant sequoia would have taken millennia to recover their old-growth stature even under historical climate scenarios; under modern climate conditions, their recovery trajectory is highly uncertain. The recent trends in wildfire activity suggest that managers have a narrowing window of opportunity to protect the remaining legacy trees from severe fire via ecological restoration (Agee and Skinner, 2005; Prichard et al., 2010; Ritchie et al., 2007; Safford et al., 2012; Stephenson, 1996). At the end of the 2021 fire season, roughly 65% of the range of giant sequoia has burned in a wildfire since 2015; of the remaining grove area, some have received beneficial fire, but there are also several groves that have not had fire in them for over a hundred years. Currently, the fuel loads in these groves are likely to facilitate intense fire behavior with resultant high severity burns unless fuel loads are reduced through restoration treatments such as prescribed fire and mechanical thinning (York et al., 2013).

In addition to the needed restoration in unburned groves, recent fires in giant sequoia have also presented an opportunity. Areas within groves that burned at lower severity and that have high survival of large giant sequoias may have received a "fuel treatment" (Prichard et al., 2021). Between 2015 and 2021, roughly 5,500 ha of giant sequoia have been classified as having low or moderate severity fire effects. The resulting fuels conditions within those hectares will vary tremendously, depending on how much fuel was consumed and how much "new" dead fuel was created by the first fire (Eskelson and Monleon, 2018). Where fuel loads are not within the range of desired conditions for fire resilience, they should be a priority for early re-treatment with prescribed fire. Where postfire fuels conditions are desirable, particularly where the fire was a “second entry” (for example, where a recent fire reburned a prescribed fire), managers could have up to 10–15 years to plan and amass the necessary resources to implement the next treatment. There may also be an opportunity in these areas to use managed wildfire (i.e., wildfires managed to support natural resource objectives) where possible, since low severity burned areas that reburn within one to two decades in this region and fuel type tend to reburn at lower severity (Collins et al., 2009; van Wagtendonk, 2012).

Many stakeholder collaboratives are forming around the dire problem of restoring Sierran forests at landscape-scales, well beyond the scale of giant sequoia groves (North et al., 2021). Unfortunately, the reality is that extensive, landscape-scale restoration is still many years away given our current workforce, funding, and regulatory compliance needs (Collins et al., 2010). If large-scale restoration is the end goal, prioritizing initial restoration efforts on specific forest stands that are highly valued for habitat, cultural, recreation or ecosystem service values, such as giant sequoia groves, will be critical during this time of rapid change. Studies have repeatedly shown that restoration to reduce fuels can reduce fire severity where they are implemented (Fulé et al., 2012; Lydersen et al., 2017; Pollet and Omi, 2002), enabling a wildfire to burn in ways that retains functioning, resilient forests. Given that giant sequoias have a limited distribution across the Sierra Nevada, serve as major carbon stores and are highly valued culturally, it is increasingly important to prioritize sequoia groves for restoration and continued future management.

CRediT authorship contribution statement

Kristen L. Shive: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Amarina Wuenschel:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Linnea J. Hardlund:** Conceptualization, Data curation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Sonia Morris:** Visualization. **Marc D. Meyer:** Conceptualization, Writing – original draft, Writing – review & editing. **Sharon M. Hood:** Methodology, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Kristen Shive reports financial support was provided by Save the Redwoods League.

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