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Interaction between mountain pine beetle-caused tree mortality and fire behavior in subalpine whitebark pine forests, eastern Sierra Nevada, CA; Retrospective observations

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A B S T R A C T

The 1351 ha Walker Fire burned in late August 2015 on the eastern Sierra Nevada, California escarpment from sagebrush steppe and pinyon pine woodlands (2150 m) through mid-elevation forests into subalpine whitebark pine (WBP; 3310 m). Fuels were particularly dry due not only to the season but as a result of a record multi-year drought (2012–2015). The fire burned into stands heavily impacted by a mountain pine beetle outbreak (MPB) during a prior drought (2007–2010). Using plot data, we report 100% mortality due to fire of understory vegetation and trees in pinyon pine, aspen, white fir, and lodgepole pine forest types. Fire-caused tree mortality was lower in Jeffrey pine forests (80%), although 100% of the understory was killed by the fire. For WBP plots in areas that had not been affected by MPB, 100% of understory and tree layers also burned. Where the fire burned through plots within the former MPB-outbreak area, 2 of 15 plots had 100% understory vegetation and trees burned by the fire, while the remaining 13 had varying levels of survivorship. In those plots, pines dead from prior beetle-kill as well as live trees remained unburned, as did understory vegetation. Whereas such "gray-stage" stands have been found to reduce fire severity in other regions and forest types, the observed reduction of surface fire was unexpected. In that fires in the subalpine WBP zone and bark beetle-fire interactions have not been studied in California, these preliminary observations suggest that subalpine forests are vulnerable to fire where continuous fuels exist below them. However, in xeric, Mediterranean landscapes, MPB outbreaks in WBP may reduce subsequent burn severity in unexpected ways. These findings may be important given current concerns for WBP's rangewide vulnerability.

1. Introduction

Interest in disturbance interactions has heightened in recent years, partly as a result of climate effects and also due to growing awareness of the potential for mega-disturbances that might result (Millar and Stephenson, 2015). In western North American forests, drivers such as hotter drought (Allen et al., 2015), wildfire (Stephens et al., 2014), and bark beetles (Bentz et al., 2009) have directly catalyzed massive mortality in many species. When these disturbances combine, resulting outcomes often are unexpectedly severe, pushing systems toward ecological thresholds (Allen et al., 2015; Bentz et al., 2010; Anderegg et al., 2015).

Mountain pine beetle (MPB, *Dendroctonus ponderosae*), native to western North America and hosted by many pine species, has been a focus of intense research and management attention in recent decades (Negrón and Fettig, 2014) due to widespread mortality it has caused (Raffa et al., 2008; Bentz et al., 2009; Kolb et al., 2016). The conditioning effects of climate change, especially hotter droughts, in promoting extensive MPB outbreaks is widely documented (Bentz et al., 2010). Given changing regimes of MPB outbreaks and forest fires (Raffa et al., 2008; Westerling et al., 2006; Vose et al., 2018), an important question for western pine forests is: do MPB outbreaks affect behavior of subsequent wildfires, and in particular, do they change (increase) area burned and fire severity?

Simard et al. (2011) described two types of disturbance interactions and related them to MPB and wildfire. *Linked disturbances* occur when one disturbance event alters the extent, severity, or probability of occurrence of a subsequent one in an additive way; *compound disturbances* occur when two events in time have unexpected synergistic effects. Considerable research has tackled the problem of MPB and wildfire interactions, with mixed findings. Whereas models predict that MPB-induced tree mortality increases flammability of forests by changing

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canopy and forest floor fuels, observed effects are not clear-cut (Hicke et al., 2012; Hart et al., 2015). In some cases, predisposition of forests by MPB resulted in subsequent fires that were more severe and covered more area than in undisturbed forests (Lynch et al., 2006), and in other situations no interactions were found (Hicke et al., 2012; Hart et al., 2015). Simard et al. (2011) report that MPB outbreaks can actually reduce the probability of active crown fire by thinning pine canopies. They found that the nature of the interaction depends on—and changes with—the stage of forest response following MPB attack ("green", "red", or "gray" phase, corresponding to increasing time since attack).

Most studies on fire-MPB interactions have investigated effects in lodgepole pine (*Pinus contorta*) and ponderosa pine (*P. ponderosa*) forests, MPB's primary hosts, and in mid-montane zones that have optimal climatic conditions for MPB. In recent warmer decades, MPB has moved aggressively into higher-elevation subalpine forests, with outbreaks increasing in the past several decades in the five-needled pines, especially whitebark pine (WBP; *P. albicaulis*; Gibson et al., 2008; Kolb et al., 2016). Interactions of drought, MPB, and the exotic fungal disease, white pine blister rust (caused by *Cronartium ribicola)*, which causes extensive mortality in WBP, have been a key focus of research and conservation attention (Keane et al., 2017). The impacts of combined disturbances on WBP mortality have been severe enough that the species is under consideration for federal endangerment status in the United States and has been listed as endangered in Canada.

Most studies on WBP have been in Rocky Mountain ecosystems, where disturbances from blister rust, MPB, and fire have been most extensive and severe (Keane et al., 2017). WBP forests in California, where climates are drier and warmer, and where stands have more open woodland structure, have experienced far fewer fires and MPB outbreaks than elsewhere in the species' range (Kliejunas and Dunlap, 2007; Gibson et al., 2008). This situation is changing, however, and as of the 2007–2010 drought, higher detection of MPB-caused mortality was observed in California, with highest incidence in the north and decreasing southward in the Sierra Nevada (Millar et al., 2012; Nesmith et al., 2019). Trends in fire in subalpine pine forests in the Sierra Nevada are unclear, although potential increases may be occurring (Miller et al., 2009; Hanson and Odion, 2014).

The Walker Fire of 2015 burned into subalpine WBP forests in the eastern Sierra Nevada, California, including into stands that experienced a severe MPB outbreak during 2007–2010 (Millar et al., 2012). We took advantage of existing data to make retrospective observations on the interaction of prior MPB outbreak and fire effects, asking the following questions: What was the extent of tree mortality caused by the Walker Fire as it moved upslope through pinyon woodland, montane conifer, and into subalpine forests? How did the fire behave when it encountered stands of tree mortality caused by prior MPB attack? Based on our observations, we further consider what significance this might have for whitebark pine stand persistence and regeneration in situations that resemble those of the Walker Fire.

2. The Walker Fire, setting, and mountain pine beetle history

The human-caused Walker Fire burned on the eastern slopes of the Sierra Nevada, California, extending from the base of the escarpment at 2150 m to cliffs and scree under Mt Gibbs at 3310 m (Fig. 1). The fire started near the east end of Walker Lake, Mono County, CA on the evening of August 14, 2015, about 6 km south of the town of Lee Vining, and burned rapidly north, northwest, northeast, and upslope. Although the fire mostly burned the broad, open east/southeast-facing slopes of the main escarpment, it also burned over the top of the south ridge of Gibbs Canyon into the canyon on northwest-facing slopes. The fire was contained on August 31, 2015, by which time it had covered 1531 ha and burned with high severity through the range of vegetation communities on the escarpment. From low to high elevation these included Great Basin sagebrush steppe (*Artemisia tridentata*); pinyon pine woodland (*Pinus monophylla;* Fig. 2a); mountain mahogany woodland (*Cercocarpus betuloides*); trembling aspen forests (*Populus tremuloides;* Fig. 2b); mixed-conifer montane forests of Jeffrey pine (*P. jeffreyi*; Fig. 2c), lodgepole pine (Fig. 2d), western white pine (*P. monticola*), and/or white fir (*Abies concolor*); and subalpine whitebark pine forests (Fig. 3a) mixed with lodgepole pine and occasional limber pine (*P. flexilis*) at lower elevations. About 200 ha of WBP forests burned within the Walker Fire. At its uppermost (western) reaches, the fire burned into stunted WBP stands on steep slopes where it stopped on its own (Fig. 3b), as it did to the north in Gibbs Canyon, where it ran into rockfields at the base of the ridge (Fig. 4a). Suppression efforts contained the other active sides. In most of the burn area, understory vegetation was completely killed by the fire (Fig. 4b).

The only record of prior fire within the Walker Fire perimeter was a small fire in Jeffrey pine forests at mid-elevations that occurred ~50 years ago. Jeffrey pine had been re-planted after the old fire, which burned in the Walker Fire. Other than that, and a few dirt tracks near the edges of fire, no known management or resource manipulation has taken place historically within the Walker Fire area.

The Walker Fire occurred during a particularly warm and dry summer. The eastern Sierra Nevada lies in a semi-arid climate zone as a result of rain-shadow effects of the Sierra crest and Pacific-dominated storms. Although Mediterranean climates of California regularly bring extended summer droughts, enhancing fire risk, August of 2015 was near the end of an extreme multi-year drought. 2012–2015 was the driest 3-yr period in the past 1200 years (Griffin and Anchukaitis, 2014), and the winter of 2014–2015 experienced its lowest snowpack on record for the Sierra Nevada. For the winter of 2014/2015, water content of snow (SWE) for the Sierra Nevada on April 1, 2015 was 5% of the historic average (CDWR, 2015; Belmecheri et al., 2016). At Tioga Pass (2987 m), 22 km west of the Walker Fire at the Sierra crest, average SWE measured over 85 years is 66.3 cm; for 2015 it was 3.8 cm (CCSS, 2018).

Temperatures that year were also unusually warm, especially during winter: whereas average temperature for Dec-Jan-Feb at Mammoth Lakes, CA (2404 m and 30 km south of the fire) is −2.2 C, average temperature for the winter of 2014–2015 was 2.2 C (US Climate Data, 2019). Mean daily maximum temperature for the 17 days before the Walker Fire was contained, as recorded at the Virginia Ridge SNOTEL site (2880 m and 20 km north) was 22.6 °C (range 19–25 °C; WRCC, 2019). Mean wind speed during the fire period for the time of day of highest winds (1600 hrs), measured at the Mammoth-Yosemite Airport (2175 m and 40 km south) was 24 km/h (range, 13–35 km/hr), and from the west, including WSW and SNW (MesoWest, 2019).

Subalpine forests of the Sierra Nevada, as throughout much of western North America, had experienced in years prior to the Walker Fire variable levels of mortality as a result of mountain pine beetle outbreaks. Another multi-year drought (2007–2010), which resulted in significant cumulative water deficit for Sierran forests, as well as unusually high minimum temperatures (Millar et al., 2012), was implicated in the outbreaks. Of 72,514 ha aerially surveyed for mortality by the U.S. Forest Service across the Sierra Nevada (USFS, 2011), 4.5% of the area was affected by MPB-caused mortality, with higher mortality in the northern Sierra and decreasing amounts southward (Millar et al., 2012).

In the central eastern Sierra Nevada, the outbreak remained at endemic levels, with widely scattered areas of severe attack. Millar et al. (2012) studied interactions of MPB-caused mortality and drought in six locally impacted WBP regions; Gibbs Canyon, including forests within the subsequent Walker Fire, was the northernmost study site. These forests were mostly small diameter (mean, 25 cm), middle-aged (< 200 yrs), and dense stands (mean basal area, 55.1 m^2/ha) of WBP. Mortality of trees ≥12 cm diameter over the six regions averaged 70% within plots; for the Gibbs Canyon stands it was 82% (Fig. 5a). Many small WBPs survived within the outbreak stands, such that mortality over all stems within plots for the six regions was 29% and 30% for Gibbs Canyon (Fig. 5b). Environmental contexts of the stands were consistent

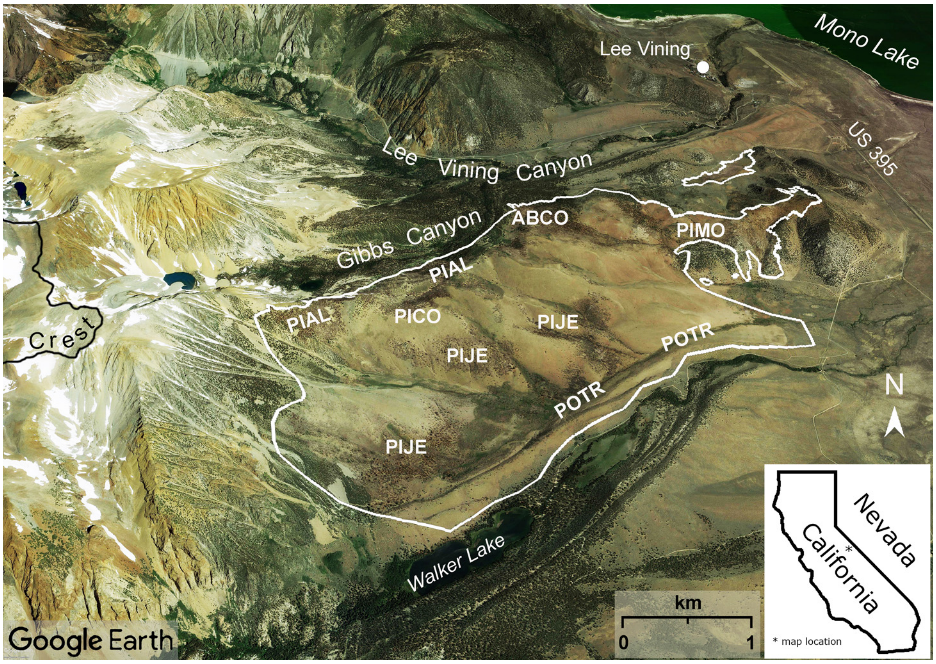

Fig. 1. Map of the Walker Fire (white outline), Mono County, eastern Sierra Nevada, California. The fire started on August 14, 2015 at the base of the slope near Walker Lake, and burned upslope to the north, northwest, and northeast, from sagebrush steppe and pinyon pine woodlands to whitebark pine forests at the upper reaches. General areas of forest types are given as: POTR, *Populus tremuloides*; PIMO, *Pinus monophylla*; PIJE, *P. jeffreyi*, PICO, *P. contorta*; PIAL, *P. albicaulis*, and ABCO, *Abies concolor*. Black line at the middle left of the image is the hydrologic crest of the Sierra Nevada near Mt. Gibbs. Base image, Google Earth Pro, vs. 7.3.1, August 11, 2017, accessed March 12, 2019.

across the six sites: Stands were located at the eastern edges of the Sierran escarpment, in low-elevation portions of WBP's distribution in this region (mean elevation 2993 m), aspects were dominantly northerly, and slopes averaged 12° (Millar et al., 2012).

3. Methods

To estimate the extent of fire damage across forest zones within the Walker Fire, we stratified the burn area by forest type, and randomly assigned plots within these. Forest types (by dominant species) were aspen; pinyon pine; Jeffrey pine; white fir; lodgepole pine; and WBP. Areas within the burn area that did not contain trees (shrubland or grassland) were excluded. For non-WBP forest types, we sampled plots roughly in proportion to their cover in the fire area (Table 1). Generalized forest zones were drawn within the burn area in Google Earth Pro (vs. 7.3.1), and pins were placed randomly as candidate plot centers within the zones. Coordinates were found in the field, which became the centers of 15 m radius circular plots unless no trees were within the plot. In that case, a random azimuth was chosen and another plot center was attempted 30 m distant. A small number of plots had unusually high density of tree stems and 7.5 m radius plots were used in those cases.

As the primary focus of the study was the effect of fire in WBP, we increased density of plots in that forest type relative to non-WBP forest (Fig. 6). Using information from our prior study, and corroborating with Google Earth historic imagery, we selected 15 plots within

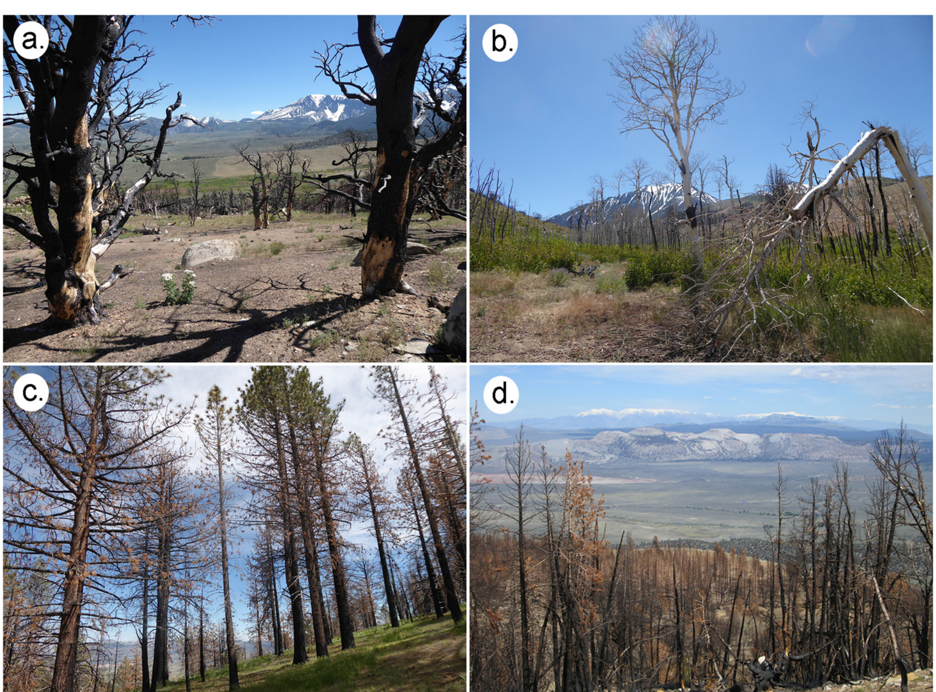

Fig. 2. Typical conditions in burned forests of the Walker Fire below the whitebark pine zone. (a) Pinyon pine woodland; (b) Trembling aspen forests; (c) Jeffrey pine forests; (d) Lodgepole pine forests (with whitebark pine on slopes in foreground). All photos taken June 2017, except (d), which was taken May 2016. Green vegetation on the ground is post-fire regrowth in all photos. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

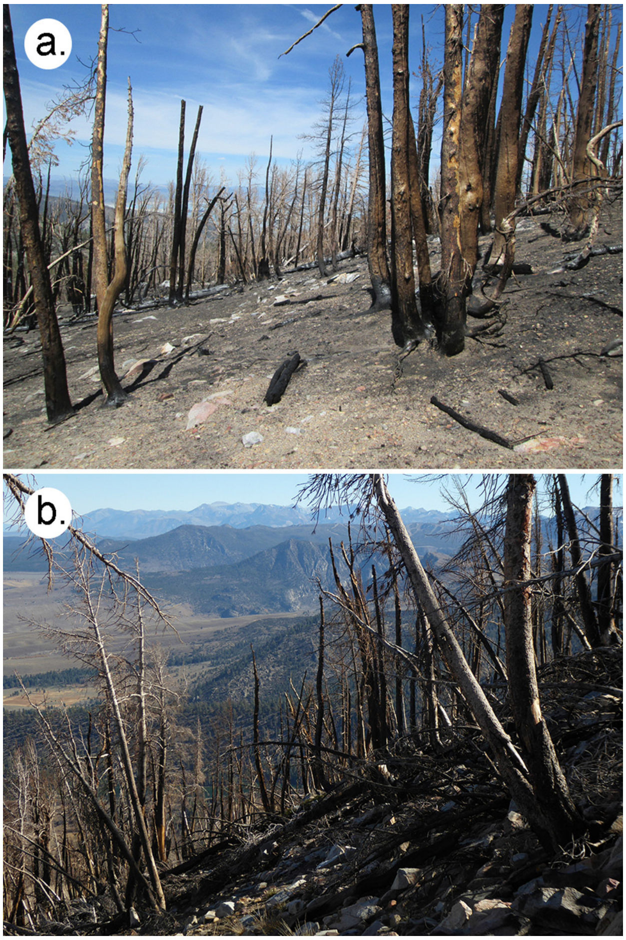

Fig. 3. Severely burned whitebark pine in forests that had not experienced prior mountain pine beetle attack. (a) Typical conditions in upright forests (photo, May 2016); (b) Stunted pines at highest elevation near the top of the burn area (photo, October 2017). Green vegetation on the ground is post-fire regrowth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

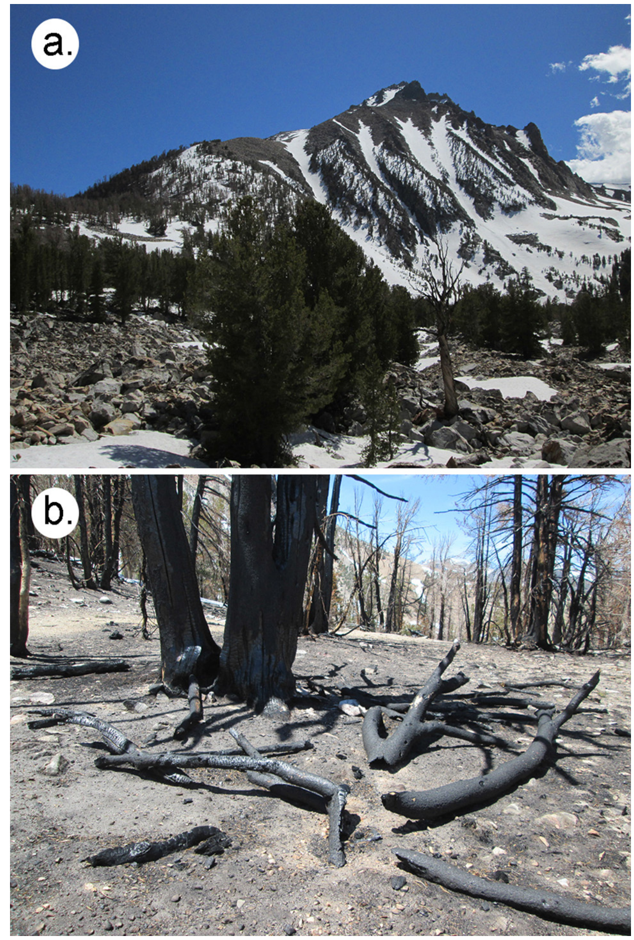

Fig. 4. (a) Rocky substrate in Gibbs Canyon that served to break the fire's northward spread; (b) Severely burned ground and soils typical of the whitebark pine conditions post-fire.

locations that we had noted as being heavily affected by bark beetles (Table 1). For the remaining WBP area, we used our notes and Google Earth to distribute a relatively equal number of candidate plots (22) to represent the elevation and aspect diversity of WBP. We confirmed using historical imagery that these plots locations were not within the areas of bark beetle mortality.

For each plot elevation, aspect, and slope were noted. Within plots all trees with diameters ≥10 cm at 1.3 m stem height were tallied by species. Diameters at 1.3 m were measured and trees were scored as alive or dead, and, if dead, likely cause of death (burned or other) was recorded. For surviving burned trees, scorch heights were noted, and where entire trees were burned at the plot level, the fire was assumed to have crowned. An ocular estimate of percent cover of surviving (live) pre-fire understory in the plot was made (Shimwell, 1972). No observations were made on post-fire regeneration.

4. Results

The 66 survey plots ranged from 2249 to 3242 m, slopes ranged from 0 to 40°, and all aspects were represented, with north, east, and southeast most common (Table 1). Thirty-seven plots sampled WBP forests, including two in the high-elevation stunted forests. For the five non-WBP forest types, the Walker Fire killed all understory and all trees in sampled plots except in Jeffrey pine type (Table 2). For Jeffrey pine plots, although 100% of the understory burned, a mean of 20% of the trees survived the fire, despite that stems were scorched as much as about 25% the tree height. Other than Jeffrey pine, total death of trees by the fire was unrelated to species, diameters, or basal area, which ranged widely by species and plot (Table 2).

Fire effects in the WBP plots (n = 37) differed from those in plots of the other species (Table 3). For WBP plots outside areas of pre-fire MPB attack (n = 22), 100% understory and 100% trees were killed by the fire (Fig. 3). The 15 plots within the area of pre-fire MPB attack experienced considerable escape from burning, despite that crown fire occurred in the stands near them (Fig. 7a). Although two prior-MPB plots were 100% burned (understory and all WBP), the remaining 13 plots had low levels of understory burn (mean, 14.4%) and retained live trees (mean 25.7% survivorship; Table 3), including pre-fire WBP saplings, woody shrubs, forbs, and graminoids (Fig. 7b). On average within these plots 12.9% of trees were dead due to fire and 61% died in prior years due to MPB (i.e., these dead trees showed no evidence of burn, or were burned only on their lower stems). Variation in mean stem diameters, stem densities, and basal areas among the MBP plots for dead and live trees was high (Table 3).

5. Discussion

Fires in subalpine forests of California have historically been infrequent and, unlike lower elevation zones, generally unaffected by 20th century fire exclusion (Van Wagtendonk et al., 2018). For this reason, we considered it instructive to describe the conditions of the Walker Fire, which burned into and killed subalpine forests. Confirming

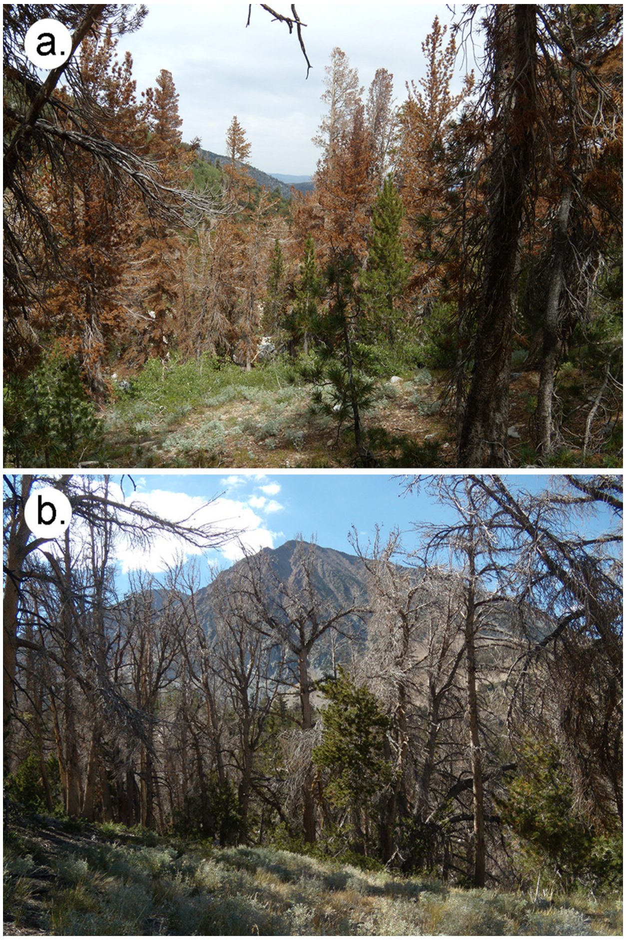

Fig. 5. Pre-fire conditions in whitebark pine forests affected by mountain pine beetle (MPB) outbreak, Gibbs Canyon. (a) "Red stage" pines during the MPB outbreak stand near what would become the edge of the Walker Fire (photo, August 2009); (b) "Gray stage" pines (photo, September 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

casual observation, our data indicate that 100% mortality of vegetation (tree and understory) occurred in pinyon pine, aspen, lodgepole pine, and white fir-dominated forest plots. Jeffrey pine forest types were the only mid-slope forests that were not entirely killed, although surface fires affected them widely (100% understory burned). Subalpine WBP plots that were undisturbed by prior MPB attack were 100% killed by the fire, as was surface vegetation. Despite that winds were moderate and from the west, it seems likely that the drought-stricken forests, late summer conditions including low humidity and high temperatures, and the uninterrupted steep gradient of the eastern Sierran escarpment, allowed the fire to burn severely upslope through all lower elevation vegetation types. Thus conditioned, the fire was able to continue into dense, low-canopied WBP forests it encountered, burning as an active crown fire through the main WBP stands and into the uppermost stunted WBP stands near treeline. This corroborates observations that subalpine WBP forests can be vulnerable to fire when they are in contact with flammable lower-elevation forests that provide continuous fuels adjacent to them (Jenkins, 2011).

Unexpected were the interactions of the fire with prior MPB-attacked stands of WBP. During the 2007–2010 drought, MPB killed scattered stands of WBP and mixed WBP/lodgepole pine on the south ridgetop of Gibbs Canyon and north-aspect slopes of the canyon (Millar et al., 2012). In some of these areas we found that the fire did not enter the stands, despite that severe crown and surface burn typified conditions surrounding the fire-free stands. These former MPB affected plots appeared much as they did before the fire. This included mature dead (unburned) pines with needles mostly dropped and bark dehiscing (MPB, "gray stage"); live mature and seedling-to-pole-sized pines; and live understory. The extent of fire exclusion in former MPB plots varied from 0% where all vegetation and trees burned, through intermediate levels, to 100%. Most beetle-affected plots retained significant levels of surviving trees and understory vegetation. This was in stark contrast to WBP plots that had not experienced MPB outbreaks where 100% of the overstory and understory burned.

Considerable research effort has been put into understanding the interaction of prior bark beetle and subsequent fire behavior in diverse locations and forest types. Whereas studies range in conclusions from no or minimal interactions (Hart et al., 2015; Andrus et al., 2016) to prior MPB tree mortality worsening fire vulnerability and severity (Lynch et al., 2006), a number of studies have concluded that the type of interaction depends on the time since bark beetle attack as well as environmental conditions (Simard et al., 2011; Harvey et al., 2014a; Harvey et al., 2014b; Jenkins et al., 2014; Meigs et al., 2016). In brief, summarizing this sequence of fire behavior relative to prior MPB outbreak from Simard et al. (2011), during the "red stage" (1–2 yrs post-outbreak, large trees killed, canopy needles dry), surface temperatures increase as crowns thin, and dry crowns with needles intact increase the likelihood of torching and active crown fires. At 3–5 yrs post- outbreak, the "gray stage" (dead needles fall, surface vegetation increases), with reduced canopy fuels, decreases crown fire susceptibility although surface fires can increase. In old attacks (10–40 yrs post-outbreak, understory vegetation accumulates, snags fall, tree regeneration increases), surface fires increase, as do torching and crowning due to increase in ladder fuels and dense mid-canopy layers. Harvey et al. (2014a) further refine the MPB-outbreak effect on subsequent fire in relation to whether the fire is moderate or severe. In Rocky Mountain lodgepole pine forests, they found fire severity during the red stage mostly unaffected by prior MPB except during extreme burning conditions. Similarly, in the gray stage, they found that surface fire severity increased only under extreme burn conditions. Many variants of these

Table 1
Walker Fire study plot characteristics: species, elevation, aspect, slope, and prior bark-beetle beetle status.

Forest type[a]	Other species in plot[a]	Plots (n)	Plots with bark beetle[b] (n)	Elevation (m)		Aspect (octant)	Slope (°)	
				Mean	Range		Mean	Range
Aspen-POTR	PIJE	6	0	2347	2249–2499	N, NE, E, SE	9	3–30
Pinyon pine-PIMO	PIJE, CELE	8	0	2438	2336–2513	E, S, SW, W, NW	30	15–40
Jeffrey pine-PIJE	PIMO, CELE	11	0	2430	2366–2506	NE, E, S	17	5–28
White fir-ABCO	–	2	0	2599	2572–2626	E	33	31–35
Lodgepole pine-PICO	–	2	0	2792	2784–2801	NE, E	6	0–12
Whitebark pine-PIAL	CELE, PICO, PIFL, PIMN, POTR	37	15	2935	2804–3242	N, E, E, SE, NW	10	0–35

[a] Forest type, dominant species in plot; Other species in plot: ABCO, *Abies concolor*; CELE, *Cercocarpus ledifolius*; PIAL, *Pinus albicaulis*; PICO, *P. contorta*; PIJE, *P. jeffreyi*; PIFL, *P. flexilis*; PIMN, *P. monticola*; PIMO, *P. monticola*; POTR, *Populus tremuloides*.
[b] Number of plots affected by pre-fire mountain pine beetle mortality.

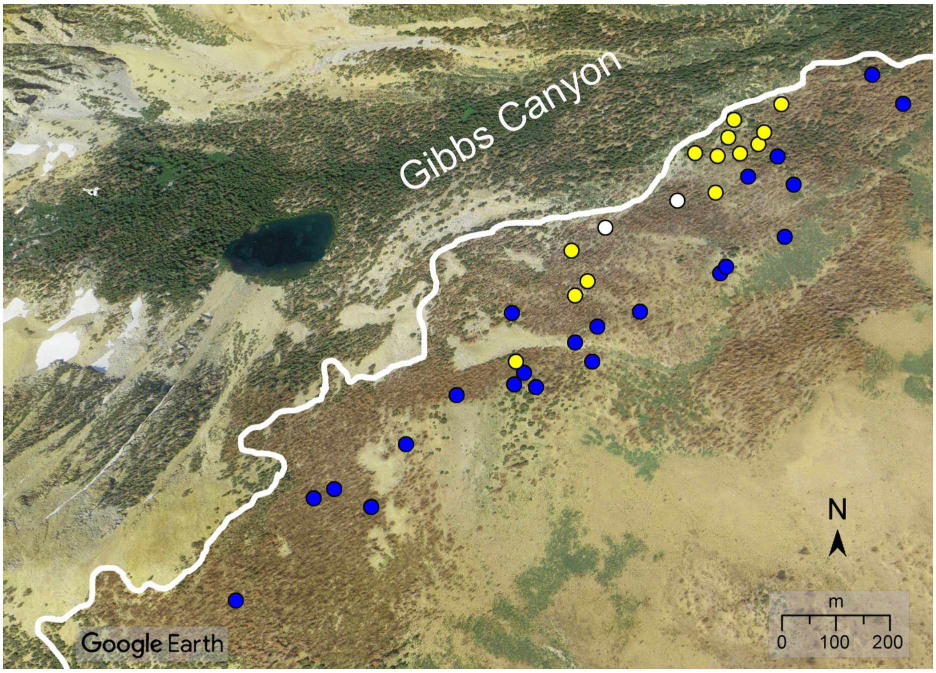

Fig. 6. Map of the northwest portion of the Walker Fire showing the WPB stands on the Gibbs Canyon south ridge. Dots are WBP plot locations; blue, non-MPB plots; yellow, MPB plots where fire mortality was < < 100%; white dots, MPB plots where fire mortality was 100%. Base image, Google Earth Pro, vs. 7.3.1, August 11, 2017, accessed May 1, 2019. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

patterns occur, depending on topography, micro-climate and weather, and forest type (Simard et al., 2011; Harvey et al., 2014a; Jenkins et al., 2014).

Little of this prior research on interactions with bark-beetle cycle and fire has investigated effects on WBP forests or on subalpine forests in general in the Pacific cordillera, including California. Small admixture of WBP was included in some Rocky Mountain studies but the dominant lodgepole pine element defined the ecological conditions for those ecosystems (Harvey et al., 2014a). Jenkins (2011) focused directly on WBP, with conditions relevant to Rocky Mountain climates, topographies, and forest species mixes and structure. He drew attention to the important surface and canopy variables, affected by prior MPB outbreak, for subsequent fire behavior. These included the pine fuel zone (circle of fuels below the drip line of affected trees); non-pine fuel matrix; crown width (width of individual tree crowns); inter-crown distance (distance between crowns of neighboring trees), crown base height (height of lowest live crown); and canopy bulk density. As these characteristics change during the bark-beetle rotation cycle in WBP, Jenkins (2011) proposed similar changes as in other species in subsequent fire related to forest structure, fuels accumulation, understory development, and location of fuels (crown or ground).

The Jenkin's (2011) study has useful implications for WBP forests that burned in the Walker Fire. Although we do not have quantitative measures, the local WBP forests (stands unaffected and affected by MPB) were relatively dense, mostly with low crown width, dense crowns, and low inter-crown distances (high canopy cover), suggesting high canopy bulk densities. These characteristics, combined with weather and climate conditions (multi-year drought/late summer), topography (steep, uninterrupted), and continuous extent of dense lower-elevation non-WBP forests, support expectations of active crown fire continuing into the WBP zone. Further, for the MPB-affected WBP stands, their gray-stage condition (4–5 yrs post-outbreak) meant needles had dropped and the already thin bark was sloughing off, thus reducing canopy fuels. The exclusion of crowning in these MPB-affected stands could, thus, be expected, even though surrounding burn conditions were severe (conclusions as in Harvey et al., 2014a). Moderate wind speed was also a characteristic defining crown-fire reduction in gray-stage forests of lodgepole pine in the Yellowstone region (Simard et al., 2011).

Unexpected were the reduction and exclusion of surface fires in some Walker Fire MPB affected plots, and survival of understory vegetation including pine regeneration. In that conditions of these high, dry eastern Sierra Nevada subalpine forests have not been previously studied, this fire provided a new situation to examine beetle-fire interactions, where possibly the low biomass of surface fuels, as well as the reduction of crown fire in these environments, helped to retard fire spread. Likely key to the fire exclusion and reduction in these plots were the combined conditions of north aspect, downslope path of fire, lower understory vegetation cover, and location near the edge of fire run-out. These might have had the effect of slowing the rate of spread of the fire, and contributing to mosaic intensity. Unexplained, however, is the presence of 100% surface/crown burned conditions surrounding the fire-escape plots, which contradicts an interpretation of lessening fire intensity. Only at the edge of the fire where these MPB stands also occur

Table 2
Burn statistics, basal area, diameters, and stem densities for plots in non-whitebark pine forest types. All dead trees were fully burned and assumed to have been killed by the fire.

Forest type	Understory burned (%)	Live trees/Plot (%)		Dead trees/Plot (%)		Basal area/Plot (m^2/ha)		Diameter, (cm)	Stem density (stems/ha)
		Mean	Std dev, range	Mean	Std dev, range	Mean	Std dev, range	Mean, std dev	Mean, std dev
Aspen	100	0	–	100	–	36.3	36 (4–78)	16.1, 11	920.1, 481
Pinyon Pine	100	0	–	100	–	14.8	19 (3–64)	18.7, 9	366.0, 219
Jeffrey Pine	100	20	38 (0–100)	80	38 (0–100)	29.1	16 (7–58)	31.8, 19	232.9, 88
White Fir	100	0	–	100	–	22.4	11 (10–42)	30.1, 15	127.4, 70
Lodgepole Pine	100	0	–	100	–	18.7	11 (7–30)	17.5, 9	474.2, 149

Table 3
Burn statistics, basal area, diameters, and stem densities for plots in whitebark pine forest type. Mortality is indicated by whether the tree was fully burned or unburned but dead from prior mountain pine beetle.

Plot type	Understory burned (%)		Live trees/Plot (%)		Dead trees/Plot (%)				Basal area/Plot (m^2/ha)		Diameter (cm)	Stem density (stems/ha)
	Mean	Std dev, range	Mean	Std dev, range	Dead, Burned		Dead, Unburned, Bark Beetles		Mean	Std dev, range		
					Mean	Std dev, range	Mean	Std dev, range			Mean, std dev	Mean, std dev
All Plots (n = 37)	76.1	41 (0–100)	9.3	15 (0–43)	69.4	42 (0–100)	21.6	31 (0–88)	30.4	23 (8–110)	18.9, 8	911.7, 581
No Prior Bark Beetle (n = 22)	100	–	0	–	100	–	–	–	29	23 (9–81)	18.9, 8	925.3, 575
Prior Bark Beetle (n = 15)	25.9	12 (0–100)	22.9	12 (0–43)	24.5	23 (0–100)	53.2	24 (0–88)	32.4	20 (9–110)	18.9, 8	891.8, 589
Prior Bark Beetle excluding 2 fully burned plots (n = 13)	14.4	11 (0–100)	25.7	11 (0–43	12.9	7 (0–21)	61	15 (39–88)	30.6	27 (3–110)	18.8, 2	692.1, 155

Fig. 7. Whitebark pine stands within the Walker Fire that experienced mountain pine beetle (MPB) mortality prior to 2011. (a) Condition of fire-escape stands, with unburned dead trees from MPB attack and live understory, including young lodgepole and whitebark pines; (b) Typical understory vegetation in fire-escape MPB stands.

does it seem likely to explain the fire being at low intensity and burning in a mosaic pattern. To the extent the Walker Fire conditions accurately indicate fire interactions with former MPB outbreak, they suggest a compound-type disturbance interaction where prior MPB activity suppressed fire behavior (Simard et al., 2011).

Our study presents simple retrospective observations, fortuitous due to prior study of the same forests during an MPB outbreak (2007–2012). A number of uncertainties and assumptions could bias our conclusions. While we document major structure from plot data, we did not quantitatively assess surface or crown fuel conditions, or develop quantitative measures of crown height, crown distances, etc. We assume the Walker Fire burned as an active crown fire into the locations of the former WBP-affected stands, and we assume the conditions of these stands contributed to fire reduction in the crowns and surface fuels. The distribution of plots in the WBP beetle-affected stands may have been imbalanced so as to favor stands where fire was excluded (in addition to random assignment, we used stand locations from our prior study), giving more weight to fire exclusion rather than burning than would be warranted. In that the observed effects were unexpected and because WBP/subalpine forests have not been studied for beetle-fire interactions in typical dry Great Basin conditions, we believe it is valuable to describe the effects observed from this fire and to encourage further study in the California WBP region.

6. Conclusions

The 1531 ha Walker Fire burned on the eastern Sierra Nevada escarpment in late August 2015 near the end of an extreme multi-year drought. It was unusual for California in that it burned as an active crown fire into and through high-elevation WBP forests. Plot data from the forests below the subalpine zone, including pinyon pine, trembling aspen, Jeffrey pine, lodgepole pine, and white fir forest types, indicated that for all but the Jeffrey pine stands the fire killed all understory and tree vegetation as it moved upslope. Jeffrey pines survived in low percentages (20%) where crown heights were high above the ground, in which case the fire burned as a surface fire. Prior outbreak by MPB (2007–2010) in the area of the fire had been studied by Millar et al. (2012), wherein stands with up to 80% mortality were reported. In 13 of 15 post-fire WBP plots located within the former MPB-outbreak area, fire was excluded at moderate to complete levels. In those plots, many dead trees from prior beetle-kill were unburned, as was understory vegetation, including pine regeneration, as well as pole-sized and mature pines. The lack of crown fire corroborates prior studies that found reduced fire severity due to lower fine fuels in the crowns of "gray-stage" stands. The reduction or lack of surface fire in these stands, however, was unexpected and not readily explained. A slow fire, moving downslope on cooler north aspects with low winds, may have stalled altogether due to lack of crown fuels and low understory cover when it met stands of former mortality.

In that fire in the California WBP subalpine zone has been little documented or studied, and interactions of former MPB outbreaks and fire not studied at all for this region, we present these preliminary observations to encourage further study. Should the interactions we observed occur in future fires, the implications for WBP persistence and management planning differ from those studied in other regions. Former MPB-attacked stands, with surviving live pines and understory vegetation, could provide regeneration sources scattered in otherwise severely burned zones. The legacy of these trees as seed sources could become increasingly important under changing conditions of climate change (Young et al., 2019) Moreover, as we have shown for WBP and limber pine in this area (Millar et al., 2007, 2012), surviving trees in the MPB outbreak appear to be genetically better suited to the current climate, thus post-fire regeneration from these stands should result in better adapted forests, a result that appears to be more widespread (Six et al., 2018). Conservation assessments for WBP following MPB outbreak such as in the eastern Sierra would evaluate these stands as having higher potential for persistence and regeneration than assumed from conclusions in other regions. Given concerns for WBP's rangewide vulnerability, this information may provide important information for assessments of its status and conservation.

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References

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6 (129), 1–55. https://doi.org/10.1890/ES15-00203.1.

Anderegg, W.R., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist 208, 674–683. https://doi.org/10.1111/nph.13477.

Andrus, R.A., Veblen, T.T., Harvey, B.J., Hart, S.J., 2016. Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. Ecol. Appl. 26, 700–711. https://doi.org/10.1890/15-1121.

Belmecheri, S., Babst, F., Wahl, E.R., Stahle, D.W., Trouet, V., 2016. Multi-century evaluation of Sierra Nevada snowpack. Nat. Clim. Change 6, 2–3.

Bentz, B., Logan, J., MacMahon, J., Allen, C.D., Ayres, M., Berg, E., Carroll, A., Hansen, M., Hicke, J., Joyce, L., Macfarlane, W., 2009. Bark beetle outbreaks in western North America: CAUSES and consequences. In: Bark Beetle Symposium, Snowbird, Utah, November 2005. UT, University of Utah Press, Salt Lake City, pp. 1–42.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60, 602–613. https://doi.org/10.1525/bio.2010.60.8.6.

CCSS (California Department of Water Resources). California Cooperative Snow Survey, Accessed November 12, 2018. < https://cdec.water.ca.gov/snow/ > .

CDWR (California Department of Water Resources), 2015. Sierra Nevada snowpack is virtually gone; water content now only 5 percent of historic average, lowest since 1950. Accessed October 10, 2018,. http://www.water.ca.gov/news/newsreleases/2015/040115snowsurvey.pdf.

Gibson, K., Skov, K., Kegley, S., Jorgensen, C., Smith, S., Witcosky, J., 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges, US Department of Agriculture Forest Service, Northern Region, Missoula, Montana. R1-08-020, pp. 1–32.

Griffin, D., Anchukaitis, K.J., 2014. How unusual is the 2012–2014 California drought? Geophys. Res. Lett. 41, 9017–9023. https://doi.org/10.1002/2014GL062433.

Hanson, C.T., Odion, D.C., 2014. Is fire severity increasing in the Sierra Nevada, California, USA? Int. J. Wildland Fire 23, 1–8. https://doi.org/10.1071/WF13016.

Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc. Natl. Acad. Sci. 112, 4375–4380. https://doi.org/10.1073/pnas.1424037112.

Harvey, B.J., Donato, D.C., Turner, M.G., 2014a. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc. Natl. Acad. Sci. 111, 15120–15125. https://doi.org/10.1073/pnas.1411346111.

Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2014b. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol. Appl. 24, 1608–1625. https://doi.org/10.1890/13-1851.1.

Hicke, J.A., Johnson, M.C., Hayes, J.L., Preisler, H.K., 2012. Effects of bark beetle-caused tree mortality on wildfire. For. Ecol. Manage. 271, 81–90. https://doi.org/10.1016/j.foreco.2012.02.005.

Jenkins, M.J., 2011. Fuel and fire behavior in high-elevation five-needle pines affected by mountain pine beetle. In: Keane, R.E. (ED.), Proc. The future of high-elevation five-needle white pines in western North America, Gen. Tech. Rep. RMRS, USDA Forest Service. Rocky Mountain Research Station, Missoula, MT, pp. 1–15.

Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., Bentz, B.J., 2014. Interactions among the mountain pine beetle, fires, and fuels. Forest Sci. 60, 489–501. https://doi.org/10.5849/forsci.13-017.

Keane, R.E., Holsinger, L.M., Mahalovich, M.F., Tomback, D.F., 2017. Restoring whitebark pine ecosystems in the face of climate change, Gen. Tech. Rep. RMRS-GTR-361. Fort Collins, CO, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 123 p.

Kliejunas, J., Dunlap, J., 2007. Status of whitebark pine and other high-elevation five-needle pines with emphasis on Pacific Coast ecosystems: what are the issues and concerns? Perspective from California. In: Goheen, E.M., Sniezko, R.A. (Eds.), Proceedings of the Conference: Whitebark Pine: A Pacific Coast Perspective, pp. 27–37, doi: 10.1.1.180.6922&rep=rep1&type=pdf.

Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., Weed, A.S., 2016. Observed and anticipated impacts of drought on forests insects and diseases in the United States. For. Ecol. Manage. 380, 321–334. https://doi.org/10.1016/j.foreco.2016.04.051.

Lynch, H.J., Renkin, R.A., Crabtree, R.L., Moorcroft, P.R., 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9, 1318–1327. https://doi.org/10.1007/s10021-006-0173-3.

Meigs, G.W., Zald, H.S., Campbell, J.L., Keeton, W.S., Kennedy, R.E., 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environ. Res. Lett. 11, 045008. https://orcid.org/0000-0001-5942-691X.

MesoWest, 2019. Historical wind data accessed March 12, 2019. < https://mesowest.utah.edu/ > .

Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826. https://doi.org/10.1126/science.aaa9933.

Millar, C.I., Westfall, R.D., Delany, D.L., 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Can. J. Forest Res. 37, 2508–2520. https://doi.org/10.1139/X07-097.

Millar, C.I., Westfall, R.D., Delany, D.L., Bokach, M.J., Flint, A.L., Flint, L.E., 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. Can. J. For. Res. 42, 749–765. https://doi.org/10.1139/x2012-031.

Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12, 16–32. https://doi.org/10.1007/s10021-008-9201-9.

Negrón, J.F., Fettig, C.J., 2014. Mountain pine beetle, a major disturbance agent in US western coniferous forests: a synthesis of the state of knowledge. Forest Sci. 60, 409–413. https://doi.org/10.5849/forsci.13-169.

Nesmith, J., Wright, M., Jules, E., McKinney, S., 2019. Whitebark and foxtail pine in Yosemite, Sequoia, and Kings Canyon National Parks: initial assessment of stand structure and condition. Forests 10, 35. https://doi.org/10.3390/f10010035.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517. https://doi.org/10.1641/B580607.

Shimwell, D.W., 1972. The Description and Classification of Vegetation. University of Washington Press, pp. 322.

Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81, 3–24. https://doi.org/10.1890/10-1176.1.

Six, D.L., Vergobbi, C., Cutter, M., 2018. Are survivors different? Genetic-based selection of trees by mountain pine beetle during a climate change-driven outbreak in a high-elevation pine forest. Front. Plant Sci. 9, 1–11. https://doi.org/10.3389/fpls.2018.00993.

Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G., Van Wagtendonk, J.W., 2014. Temperate and boreal forest mega-fires: characteristics and challenges. Front. Ecol. Environ. 12, 15–122. https://doi.org/10.1890/120332.

US Climate Data, Accessed February 15, 2019. < https://www.usclimatedata.com/climate/california/united-states/3174 > .

USFS (USDA Forest Service), 2011. U.S. Forest Service Pacific Southwest Regional Forest Health Monitoring Aerial Detection Survey Data. Accessed Nov. 12, 2012. < http://www.fs.fed.us/r5/spf/fhp/fhm/aerial/ > .

Van Wagtendonk, J.W., Fites-Kaufman, J., Safford, H.D., North, M.P., Collins, B.M., 2018. Sierra Nevada bioregion. In: Van Wagtendonk, J.W., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites-Kaufman, J. (Eds.), Fire in California ecosystems, second ed. University of California Press, Berkeley, CA, pp. 251–280.

Vose, J.M., Peterson, D.L., Domke, G.M., Fettig, C.J., Joyce, L.A., Keane, R.E., Luce, C.H., Prestemon, J.P., Band, L.E., Clark, J.S., Cooley, N.E., D'Amato, A., Halofsky, J.E., 2018. Forests. In Reidmiller, D.R., Avery, C.W., Easterling, D.R., Kunkel, K.E., Lewis, K.L.M., Maycock, T.K., Stewart, B.C. (Eds.), Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II, U.S. Global Change Research Program, pp. 223–258.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834.

WRCC (Western Regional Climate Center), 2019. Historical temperature data accessed March 3, 2019. < https://wrcc.dri.edu/ > .

Young, D.J.N., Werner, C.M., Welch, K.R., Young, T.P., Safford, H.D., Latimer, A.M., 2019. Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion. Ecology 100 (2), e02571. https://doi.org/10.1002/ecy.2571.