

Mortality, structure, and regeneration in whitebark pine stands impacted by mountain pine beetle in the southern Sierra Nevada

Marc D. Meyer, Beverly Bulaon, Martin MacKenzie, and Hugh D. Safford

Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) is vulnerable to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) attack throughout western North America, but beetle outbreaks in the southwestern portion of the range (i.e., Sierra Nevada) have been spatially limited until recently. We examined patterns of mortality, structure, and regeneration in whitebark pine stands impacted by mountain pine beetle in the southern Sierra Nevada. Mortality was greatest in medium to large diameter (>10–20 cm dbh) trees, resulting in declines in mean and maximum tree diameter and tree size class diversity following an outbreak. Severity of beetle attack was positively related to mean tree diameter and density. Density of young (<3 years old) whitebark pine seedling clusters was positively related to severity of beetle attack on mature stands. All sites showed a stable production of whitebark pine regeneration within at least the past 30–40 years, with a pulse of new seedlings in the past 3 years in beetle-impacted stands. Our results show that mountain pine beetle outbreaks in the southern Sierra Nevada result in substantial changes in whitebark pine stand structure and suggest low resistance but high resilience to initial attack, especially in the absence of white pine blister rust.

Key words: whitebark pine, mountain pine beetle, Sierra Nevada, resistance, resilience.

Résumé : Le pin à écorce blanche (*Pinus albicaulis* Engelm.) est vulnérable à l'attaque du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins) à travers l'ouest de l'Amérique du Nord, mais jusqu'à maintenant les épidémies se sont peu répandues dans le sud-ouest de la Sierra Nevada. Nous avons étudié les patrons de mortalité, la structure et la régénération dans les peuplements de pin à écorce blanche touchés par le dendroctone du pin ponderosa dans la Sierra Nevada méridionale. La mortalité était plus élevée chez les arbres de diamètre intermédiaire à gros (dhp >10–20 cm), entraînant une diminution du diamètre moyen et maximum des arbres et de la diversité des classes d'âge des arbres à la suite d'une épidémie. La sévérité de l'attaque du dendroctone était positivement reliée au diamètre moyen des arbres et à la densité. La densité des groupes de jeunes (<3 ans) semis de pin à écorce blanche était positivement reliée à la sévérité de l'attaque des peuplements matures par le dendroctone. Toutes les stations avaient une production stable de régénération de pin à écorce blanche depuis au moins les 30 à 40 dernières années avec une recrudescence de nouveaux semis au cours des trois dernières années dans les peuplements attaqués par le dendroctone. Nos résultats montrent que les épidémies du dendroctone du pin ponderosa dans la Sierra Nevada méridionale entraînent des changements substantiels dans la structure des peuplements de pin à écorce blanche et indiquent qu'il y a une faible résistance mais une grande résilience à l'attaque initiale, particulièrement en l'absence de rouille vésiculeuse du pin blanc. [Traduit par la Rédaction]

Mots-clés : pin à écorce blanche, dendroctone du pin ponderosa, Sierra Nevada, résistance, résilience.

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is one of several five-needled pines limited to high-elevation mountain ranges in the western United States (Arno and Hoff 1990; McCaughey and Schmidt 2001). This keystone species is vital to the sustainability of high-elevation montane ecosystems, providing ground stabilization for snowpack, overstory cover for delicate subalpine vegetation, essential wildlife habitat and forage, microclimate refugia for understory species, and other ecosystem functions and services (Tomback et al. 2001b). Despite its critical importance, whitebark pine populations are highly vulnerable to climate change, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, and white pine blister rust (*Cronartium ribicola* J.C. Fisch.)

throughout much of the species' geographic range (Keane et al. 2012). Recent impacts resulting from these combined stressors have substantially reduced populations of whitebark pine in many parts of its range (Gibson et al. 2008; Schwandt et al. 2010; Keane et al. 2012), including some portions of the Sierra Nevada (Maloney et al. 2012; Millar et al. 2012).

Whitebark pine communities are particularly prone to mountain pine beetle outbreaks, which can vary substantially across the broad geographic and environmental distribution of whitebark pine (Gibson et al. 2008). For instance, several factors at different spatial scales may influence the susceptibility of whitebark pine forests to mountain pine beetle attack. At the tree level, tree diameter, basal area, and the number of stems in a tree cluster

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are important predictors of individual tree attack (Perkins and Roberts 2003). Similarly, basal area and stand density are important predictors of beetle attack at the stand scale (Perkins and Roberts 2003; Simard et al. 2012). At the landscape scale, whitebark pine mortality resulting from mountain pine beetle activity may be associated with lower elevations, more northerly aspects, and warmer and drier climates (Millar et al. 2012). In contrast, lower density and less productive stands located in areas of lower climatic water deficit appear to be less likely to experience large-scale, beetle-induced mortality. In all of these studies, attacked stands experience significant declines in tree density, basal area, and mean tree diameter, indicating low resistance (i.e., capacity of an ecosystem to withstand displacement after disturbance) and high susceptibility (i.e., likelihood of disturbance based on ecosystem characteristics) to beetle attack, especially in regions experiencing elevated temperatures (Bentz et al. 2010; Jewett et al. 2011).

Despite their high susceptibility and low resistance to mountain pine beetle attack, whitebark pine stands often exhibit high resilience (i.e., speed of recovery following disturbance) to mountain pine beetle impacts, especially in the absence of other stressors such as white pine blister rust. Many whitebark pine stands continue to dominate a site following mountain pine beetle attack, because small size classes (e.g., saplings) survive beetle attack and contribute to successional replacement in the absence of shade-tolerant competitors (i.e., “climax whitebark pine” stands; Arno and Hoff 1990; Keane 2001). Whitebark pine regeneration also increases in response to beetle-induced tree canopy mortality when sufficient seed sources are available (Larson and Kipfmüller 2010). However, white pine blister rust may affect these seed sources by reducing the number of current and future seed-bearing trees (Fiedler and McKinney 2014), diminishing host fecundity (Maloney et al. 2012), or reducing the likelihood of seed dispersal by Clark’s Nutcracker (*Nucifraga columbiana* (A. Wilson, 1811)), a primary dispersal agent of whitebark pine (McKinney and Tomback 2007). These and other impacts (e.g., competition from shade-tolerant trees) may inhibit or delay the reestablishment of whitebark pine in many high-elevation landscapes (Keane et al. 2012).

The southern Sierra Nevada represents the southernmost extent of the whitebark pine geographic range (McCaughy and Schmidt 2001) and is unique in several respects. Whitebark pine populations in this region have been relatively unaffected by mountain pine beetle compared with more northerly regions (Gibson et al. 2008). The occurrence of white pine blister rust on high-elevation white pines is also relatively low in the southern Sierra Nevada (e.g., this pathogen is currently undetected in the southeastern Sierra Nevada), possibly due to the relatively drier conditions in this region that may limit white pine blister rust incidence and spread (Maloney 2011; Dunlap 2012). Population genetic structure suggests that whitebark pine populations in the region are characterized by a high degree of genetic divergence from other populations in the species’ geographic range and may be considered one of only a few contemporary climate refugia (Richardson et al. 2002). Climate models show lower projected future climate vulnerability in whitebark pine populations of the southern Sierra Nevada compared with other parts of the range (Warwell et al. 2007), suggesting that the region may be a future climate refugium for whitebark pine and other high-elevation white pine species (e.g., foxtail pine, *Pinus balfouriana* Balf.). Additionally, successional dynamics of Sierra Nevada whitebark pine stands are poorly understood compared with other regions of North America (i.e., Northern Rockies, Northern and Central Cascades, British Columbia) where the regional pool of tree species is significantly different (e.g., subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is absent from the Sierra Nevada; Fryer 2002; Keane et al. 2012), underscoring the need for more information from the Sierra Nevada.

Our goal was to examine patterns of tree mortality, forest structure, and tree regeneration in whitebark pine stands experiencing mountain pine beetle outbreaks in the southern Sierra Nevada. This included an evaluation of potential explanatory variables influencing individual tree mortality and severity of mountain pine beetle attack and regeneration response in whitebark pine stands. We were especially interested in examining these patterns and potential factors to evaluate whether whitebark pine stands exhibited initial signs of resistance (i.e., retention of dominant structures and canopy cover) and resilience (i.e., regeneration response, retention of small-diameter stems) to mountain pine beetle attack.

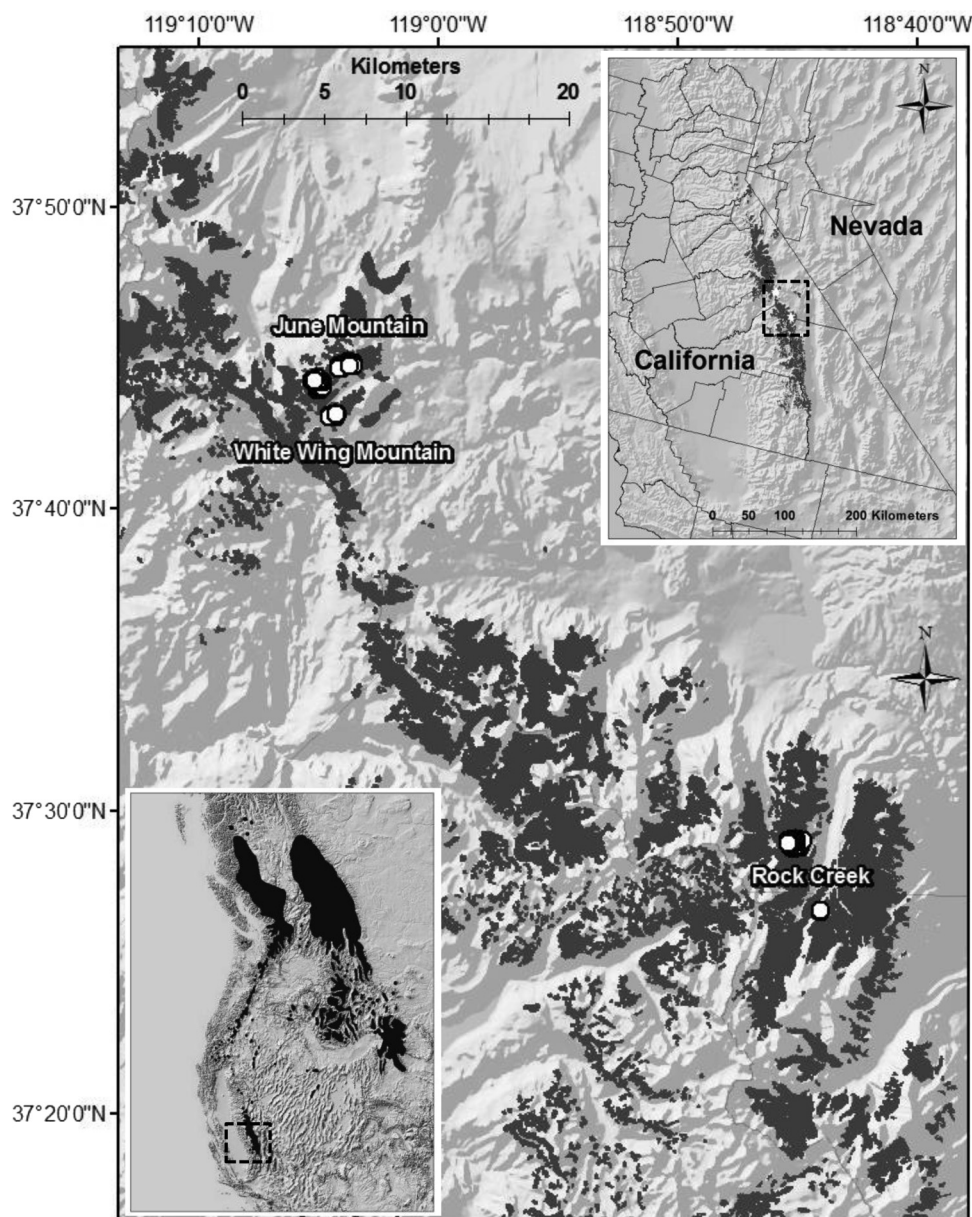
Methods

Study area and plot selection

Our study area was centered on the Inyo National Forest in the southeastern Sierra Nevada of California, which extends from central Mono County to northwestern Inyo County (Fig. 1). Whitebark pine is commonly a dominant or codominant subalpine conifer throughout this region, especially at elevations exceeding 3000 m. At lower elevations (2800–3200 m) within this zone, subalpine forests can be dominated by upright stands of whitebark pine, occurring with other subalpine conifers such as Sierra lodgepole pine (*Pinus contorta* var. *murrayana* (Balf.) Engelm.), red fir (*Abies magnifica* A. Murray), western white pine (*Pinus monticola* Douglas ex D. Don), mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), limber pine (*Pinus flexilis* E. James), southern foxtail pine (*Pinus balfouriana* var. *austrina* (Bruijn & J. Mastrog.) Silba), and Sierra juniper (*Juniperus grandis* R.P. Adams) (Meyer 2013). Patches of quaking aspen (*Populus tremuloides* Michx.) also occur within some subalpine stands in the region. Above this zone, whitebark pine may occur as monotypic, krummholz vegetation, especially on harsh and exposed sites near treeline (~3500 m in the region). We focused our study in areas that (i) contained recent (≤7 years) evidence of mountain pine beetle activity that exceeded 100 ha in size and (ii) were dominated by stands of whitebark pine (≥50% of tree basal area or density). We identified areas with recent mountain pine beetle activity in whitebark pine stands using a combination of geospatial data (i.e., aerial surveys of insect and disease activity (USDA Forest Service 2011)) and extensive field reconnaissance of the study area. We identified three study sites based on our criteria (proceeding north to south): June Mountain, White Wing Mountain, and Rock Creek and Hilton Creek (collectively “Rock Creek”) (Fig. 1). Study sites at June Mountain and White Wing Mountain were located on excessively drained, cryic soils derived from pumice, whereas Rock Creek sites were located on well-drained, cryic soils derived from granodiorite (Table 1).

We surveyed whitebark pine stands in our study area in July through September of 2011 to 2013. We established a total of 72 circular plots (12.61 m radius; 0.05 ha) on a systematic 100 m grid throughout the three study sites: June Mountain (30 plots), White Wing Mountain (10 plots), and Rock Creek (32 plots). We selected whitebark pine stands exhibiting evidence of extensive mountain pine beetle attack (e.g., pitch tubes, beetle galleries) and recent tree mortality. We also selected several neighboring undisturbed sites lacking evidence of recent beetle related mortality (“controls”) at June Mountain (9 plots) and Rock Creek (8 plots); we did not detect whitebark pine stands unaffected by mountain pine beetles at White Wing Mountain. We located most control sites at June Mountain on south-facing aspects (Table 1), because these were the only locations at this site that contained whitebark pine stands lacking extensive mountain pine beetle attack. Within each 0.05 ha plot, we recorded site attributes (e.g., slope, aspect, geographic coordinates), vegetation cover (ocular estimates of live and dead canopy cover, live shrub and herb cover, dominant understory species), ground cover (e.g., bare ground and litter cover), and stand variables (e.g., live and dead basal area, snag density

Fig. 1. Map of study locations in the southern Sierra Nevada, California. Plot locations (white points with black outline) include June Mountain (northern site; mortality and control plots), White Wing Mountain (north-central site; mortality plots only), and Rock Creek (southern site; mortality and control plots). The shaded area represents the potential distribution of whitebark pine (source: USDA Forest Service Region 5 spatial stratification for whitebark pine (Slaton et al. 2014)). The range-wide distribution of whitebark pine in western North America is displayed on the inset map in the lower left corner.



that excludes recent beetle-related mortality ≤ 7 years since inventory). Within each plot, we also recorded the attributes of all trees ≥ 7.6 cm diameter at breast height (dbh, 1.37 m), including species, status (live or dead), dbh, number of stems per cluster (defined as ≤ 1 m of the base of a neighboring stem), percent live crown, presence of small (dbh, < 7.6 cm) “horizontal” stems arising from a cluster (i.e., often an underground branch extending horizontally from a central point that occasionally develops roots by asexual reproduction or “layering”), beetle attack severity, years since beetle attack, cone abundance rating (0, 0 cones; 1, 1–10 cones; 2, 11–100 cones; 3, > 100 cones), and the evidence of other insects and pathogens (e.g., white pine blister rust). We estimated beetle attack severity for each tree based on the rating system developed by the Greater Yellowstone Whitebark Pine Monitoring Work Group (2007): 0, no evidence of attack; 1, few pitch tubes; 2, mod-

erate number of pitch tubes with limited spatial extent on bole; 3, many pitch tubes spread throughout bole. We identified small, horizontal whitebark pine stems based on their immediate proximity to tree clusters (distance, < 1 m), basal stem angle (directed more or less horizontally toward tree cluster), or evidence of physical underground connection to neighboring tree clusters. We noted twig beetle (*Pityophthorus boycei* Swaine) sign based on the presence of dying needles, pitch tubes, and brood chambers on terminal branches and stems. Within each 0.05 ha plot, we also recorded attributes of all seedlings (height, < 1.37 m) and saplings (height, ≥ 1.37 m; dbh, < 7.6 cm), including species, status (live or dead), height, estimated age (based on whorl counts and bud scars), number of stems per cluster (defined as ≤ 10 cm of the base of a neighboring seedling or sapling stem), and evidence of insects or pathogens. We also estimated seedling age of whitebark pine

Table 1. Sample size and environmental characteristics of whitebark pine stands at three study sites in the southern Sierra Nevada.

Variable	Study site		
	June Mountain	White Wing Mountain	Rock Creek
No. of mortality plots	21	10	24
No. of control plots	9	0	8
Elevation (m)	3089	3051	3160
Slope (%)	27	25	12
Aspect: mortality/control	NE/S	NW	NE/NE
Annual precipitation (mm)	768	936	606
Minimum temperature (°C)	−3.7	−3.6	−3.4
Mean temperature (°C)	3.7	3.0	2.7
Maximum temperature (°C)	11.1	9.7	9.2
Available water capacity (mm)	2.78	2.78	3.30
Soil parent material	Pumice weathered from andesite	Pumice weathered from andesite	Colluvium derived from granodiorite
Rock cover (%)	15.4	19.8	12.0
Bare ground cover (%)	6.6	9.7	4.1

Note: Mean values are presented for all environmental variables. “Mortality” plots are whitebark pine stands experiencing recent mountain pine beetle associated mortality and “control” plots are relatively unaffected by mountain pine beetle attack. For aspect, the predominant slope aspect includes the following: NW, north or west; NE, north or east; S, south. Climate variables (precipitation and temperature) are based on PRISM (2016) 30 year averages (1981–2010). Available water capacity estimated for 0–50 cm soil depth.

based on growth ring counts from a sample of 16 seedlings located at all three sites. We extracted increment cores from eight randomly selected mature (dbh, >20 cm) whitebark pine trees from mortality plots at each site and estimated tree age for all samples using standard tree-ring techniques (Maeglin 1979).

Analysis

We used logistic regression to examine the relationship between tree diameter and the number of stems per cluster to the status (live, dead) of whitebark pine trees. To reduce model overfitting, we only included significant ($P < 0.05$) predictors in our logistic regression analyses and tested for multicollinearity by examining correlations between independent factors in our model. We used a sensitivity analysis of each factor to evaluate the performance of the reduced logistic regression model and assess model accuracy in successfully predicting tree status. We used a χ^2 test to examine the association between beetle attack severity and tree status. We used Kruskal–Wallis tests to examine for the effect of mountain pine beetle activity (mortality versus control plots) on changes in forest structural variables (mean tree diameter, maximum tree diameter, tree size class diversity) between pre- and post-attack periods. We estimated pre-attack conditions in these structural variables by including all recently dead trees (≤ 7 years since inventory) in addition to live trees in our calculations, whereas post-attack conditions included live trees only. We calculated size class diversity as the number of live tree diameter classes (5 cm increments) present within a plot both before and after the attack.

We calculated beetle attack severity at the plot level as the average attack severity rating for all live and dead trees in each plot. We calculated the density of young (<3 years old) whitebark pine seedling clusters per plot to provide an estimate of recent tree regeneration response to recent mountain pine beetle attack. We used multiple regression with a forward stepwise procedure (included in the model if $P = 0.10$) to select independent predictors (pre-attack basal area, whitebark pine tree density, and mean whitebark pine tree diameter) of beetle attack severity at the plot level. We used linear regressions to examine the relationships between beetle attack severity (independent predictor) and percent decrease in whitebark pine density, total basal area, live canopy cover (all species), and the density of young whitebark pine seedling clusters (dependent variables). We used Spearman's rank correlation to examine the association between whitebark

pine tree diameter and cone production (ordinal variable) for all cone-bearing trees. We also used Pearson's correlation to examine the association between whitebark pine seedling ages estimated from whorl and growth ring counts. All variables were evaluated for normality, homoscedasticity, and independence of residuals. We log transformed the density of young whitebark pine seedling clusters to meet the parametric assumptions of our linear regression model. We tested for serial correlation using a Durbin–Watson statistic and multicollinearity by examining correlations between independent factors and calculating the variance inflation factor for each significant factor (Statsoft, Pittsburg, Pennsylvania). Unless otherwise noted, we conducted all statistics with Statistica 6.1 (StatSoft Inc., Tulsa, Oklahoma) or JMP 12 (SAS Institute Inc., Cary, North Carolina) and an α level of 0.05.

Results

Tree mortality and stand structure

We inventoried a total of 3767 trees and 7415 seedlings and saplings. Nearly all plots (96%) were dominated by whitebark pine, and the remainder was dominated by a mixture of whitebark pine and lodgepole pine. Across all sites, $92\% \pm 15\%$ (mean \pm standard deviation (SD)) of all measured trees (live and dead stems) were identified as whitebark pine (Table 2). Other tree species included lodgepole pine (7.3% of trees), red fir (0.9% of trees), quaking aspen (0.2% of trees), mountain hemlock (<0.1% of trees), and Sierra juniper (<0.1% of trees). At June Mountain, we located 94% of mortality plots on north- and east-facing aspects but located 89% of control plots on south-facing slopes. Aspects at White Wing Mountain and Rock Creek (both mortality and control plots) were entirely north, west, or east facing (Table 1). Most plots with evidence of recent mountain pine beetle attack occurred within 4 years prior to sampling. Whitebark pine mortality was considerable and consistent across mortality sites, resulting in 80%–85% loss in basal area, 60%–65% loss in whitebark pine tree densities (dbh, ≥ 7.6 cm), and 70%–80% loss in live canopy cover in mortality plots (Table 2). Overall, pre-attack biomass (i.e., live and dead basal area, tree densities, or canopy cover) was generally lower at Rock Creek compared with June Mountain and White Wing Mountain (Table 2). The estimated mean (\pm SD) age of larger whitebark pine trees (dbh, 20–50 cm) was 162 ± 36 years at Rock Creek ($N = 7$), 123 ± 37 years at June Mountain ($N = 8$), and 146 ± 21 years at White Wing Mountain ($N = 8$).

Table 2. Mean (\pm standard deviation) values of stand variables in mortality and control whitebark pine plots in the southern Sierra Nevada.

Variable	June Mountain		White Wing Mountain	Rock Creek	
	Mortality plots	Control plots		Mortality plots	Control plots
Years since pine beetle attack	3.3 (0.6)	—	3.8 (0.3)	2.6 (0.4)	—
Beetle attack severity	1.45 (0.68)	0.02 (0.05)	1.73 (0.42)	1.74 (0.41)	0 (0)
Live tree basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	8.5 (8.4)	41.6 (20.5)	9.6 (9.9)	6.1 (7.3)	39.7 (10.6)
Dead tree basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	41.2 (19.7)	0.1 (0.2)	41.4 (14.3)	30.7 (17.6)	0.1 (0.2)
Basal area loss (%)	82.9	0.2	81.2	83.4	0.3
Live tree density ($\text{number} \cdot \text{ha}^{-1}$)	342 (220)	1120 (526)	457 (369)	269 (168)	603 (201)
Dead tree density ($\text{number} \cdot \text{ha}^{-1}$)	573 (350)	9 (21)	830 (277)	414 (219)	38 (20)
Tree density loss (%)	62.6	0.8	64.5	60.6	5.9
Percent <i>P. albicaulis</i>	86 (22)	95 (9)	85 (14)	97 (6)	92 (10)
Mean live dbh (cm)	13.8 (2.9)	18.8 (2.8)	14.2 (4.7)	14.6 (3.5)	24.8 (2.9)
Maximum live dbh (cm)	19.9 (6.0)	39.6 (11.6)	22.4 (18.4)	22.4 (5.5)	59.6 (16.9)
Size class diversity	4.9 (1.5)	7.3 (0.8)	5.0 (1.4)	3.8 (1.1)	10.0 (1.2)
Live canopy cover (%)	12 (9)	41 (19)	10 (11)	5 (6)	32 (11)
Dead canopy cover (%)	30 (11)	<1 (2)	37 (13)	19 (11)	<1 (2)
Canopy cover loss (%)	71	1	79	79	3
Shrub cover (%)	0.2 (0.3)	25.1 (20.4)	0.6 (0.9)	7.0 (15.6)	0.2 (0.3)
Herb cover (%)	10 (11)	8 (8)	3 (5)	14 (13)	2 (2)
<i>P. albicaulis</i> trees with cones (%)	18.7 (17.3)	34.2 (36.2)	6.8 (8.1)	21.0 (13.1)	31.0 (8.9)
<i>P. albicaulis</i> seedling density ($\text{number} \cdot \text{ha}^{-1}$)	4716 (3081)	433 (565)	2951 (2984)	1083 (813)	440 (734)
<i>P. albicaulis</i> sapling density ($\text{number} \cdot \text{ha}^{-1}$)	329 (318)	59 (96)	190 (193)	267 (221)	236 (191)
Snag density ($\text{number} \cdot \text{ha}^{-1}$)	61 (93)	20 (60)	16 (35)	39 (58)	28 (21)

Note: The beetle attack severity is an index that is calculated as the average attack severity rating of individual trees (range, 0–3) within a stand. Tree density includes all stems ≥ 7.6 cm diameter at breast height (dbh); sapling density includes all stems 0.1–7.5 cm dbh; seedling density includes all stems < 1.37 m in height. The percent *P. albicaulis* is the percentage of live and dead trees that are *P. albicaulis*. Estimation of mean and maximum dbh includes post-attack live trees only. Size class diversity is the number of diameter classes of live trees in 5 cm increments following the beetle attack. The percent of *P. albicaulis* trees with cones is based on percentage of live *P. albicaulis* with cones observed in 2012 (June Mountain and White Wing Mountain) or 2011 and 2013 (Rock Creek; percentage averaged across years). Snag density does not include dead trees resulting from recent (≤ 7 years) mountain pine beetle attack.

Survival probability of individual whitebark pine trees in mortality plots was negatively related to tree diameter ($\chi^2 = 630.682$, $P < 0.001$, $\beta_1 = -0.26 \pm 0.01$ standard error (SE)) but not the number of neighboring stems per cluster ($\chi^2 = 0.009$, $P = 0.923$). The greatest tree mortality was observed in trees > 10 –20 cm dbh (Fig. 2). The selected logistic regression model correctly classified 84% and 82% of live and dead whitebark pine trees, respectively. Survival of lodgepole pine trees in mortality sites was also negatively related to tree diameter ($\chi^2 = 36.414$, $P < 0.001$, $\beta_1 = -0.07 \pm 0.01$ SE), and the greatest mortality was observed in trees > 20 –40 cm dbh (Fig. 2). The logistic regression model correctly classified 80% and 61% of live and dead lodgepole pine trees, respectively. Whitebark pine tree status (live or dead) was contingent on the beetle attack severity ($\chi^2 = 2854.622$, $\text{df} = 3$, $P < 0.001$), with 91% of all dead trees exhibiting the highest attack rating and 94% of all live trees with no sign of beetle activity.

Stand structure was significantly altered by mountain pine beetle activity in mortality plots compared with control plots, including greater post-attack reductions in mean diameter (whitebark pine only: $H_{[1,72]} = 37.517$, $P < 0.001$), maximum diameter (whitebark pine only: $H_{[1,72]} = 36.407$, $P < 0.001$), and tree size class diversity (all species: $H_{[1,72]} = 39.373$, $P < 0.001$) in mortality plots than in control plots (Fig. 3). Approximately 72% of whitebark pine clusters in mortality plots retained small (dbh, < 7.6 cm) and horizontal live stems despite severe mountain pine beetle impacts to larger stems in these clusters. Percent reduction in whitebark pine tree density ($F_{[1,70]} = 675.41$, $R^2 = 0.905$, $\beta_1 = 0.95$, $P < 0.001$; Fig. 4), basal area ($F_{[1,70]} = 217.29$, $R^2 = 0.753$, $\beta_1 = 0.87$, $P < 0.001$), and live canopy cover ($F_{[1,70]} = 211.85$, $R^2 = 0.748$, $\beta_1 = 0.87$, $P < 0.001$) were positively related to severity of mountain pine beetle attack across all sites. The severity of mountain pine beetle attack on whitebark pine was positively related to stand structure variables ($F_{[2,51]} = 23.486$, $R^2 = 0.459$, $P < 0.001$), including pre-attack mean tree diameter ($\beta_1 = 0.75$, $R = 0.692$, $P < 0.001$) and pre-attack white-

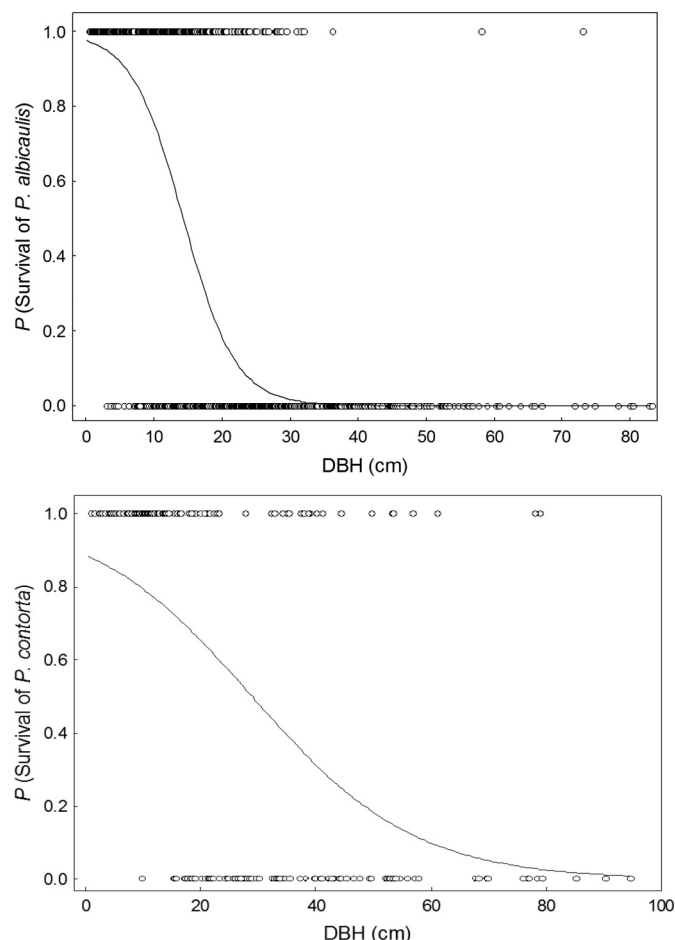
bark pine tree density ($\beta_1 = 0.25$, $R = 0.302$, $P = 0.028$) across all sites.

Twig beetle was recorded in 26% of live trees across all sites. Most of these observations were recorded from Rock Creek, with 88% of all live whitebark pine trees in mortality and control plots exhibiting twig beetle sign. Approximately 6% of live trees exhibited twig beetle sign at June Mountain, and there was no evidence of twig beetle in plots from White Wing Mountain. At Rock Creek, the percentage of live whitebark pine trees with evidence of twig beetle activity was greater in mortality plots (median, 100%) than in control plots (median, 85%; $Z = 2.615$, $P = 0.009$). Live whitebark pine trees with twig beetle had slightly less live crown (median, 80%) than uninfected trees (median, 90%; $Z = 4.403$, $P < 0.001$). We did not detect signs or symptoms of white pine blister rust at any of our study sites.

Tree reproduction and regeneration

The percentage of live whitebark pine trees producing cones was generally higher in control plots than in mortality plots across sites (Table 2). There was a positive correlation between tree diameter and cone production ($r = 0.760$, $P < 0.001$) in cone-bearing whitebark pine. Density of whitebark pine regeneration tended to be greater in mortality plots across all sites (Table 2). Approximately 88.9% of tree regeneration consisted of whitebark pine in all mortality and control plots across sites. The remainder of tree regeneration consisted of red fir (6.5%), lodgepole pine (4.6%), mountain hemlock ($< 0.01\%$), and Jeffrey pine (*Pinus jeffreyi* Balf.; $< 0.01\%$). Field estimates of whitebark pine seedling age were positively correlated to estimates based on growth ring counts from seedlings ($r = 0.814$, $P < 0.001$; $N = 16$; range, 5–17 years; Fig. 5). All sites showed a relatively stable production of whitebark pine regeneration at least within the past 30–40 years (field-derived age estimates exceeding 17 years are not validated by growth ring counts and considered tentative; Fig. 6), with an apparent pulse of

Fig. 2. Relationship between tree diameter and the probability of whitebark pine (top panel) and lodgepole pine (bottom panel) survival in stands impacted by mountain pine beetle (based on analysis of 2600 and 182 trees, respectively). The model is fit using a logit transformation. The greatest change in the probability of survival occurs at approximately 10–20 cm dbh (whitebark pine) and 20–40 cm dbh (lodgepole pine).



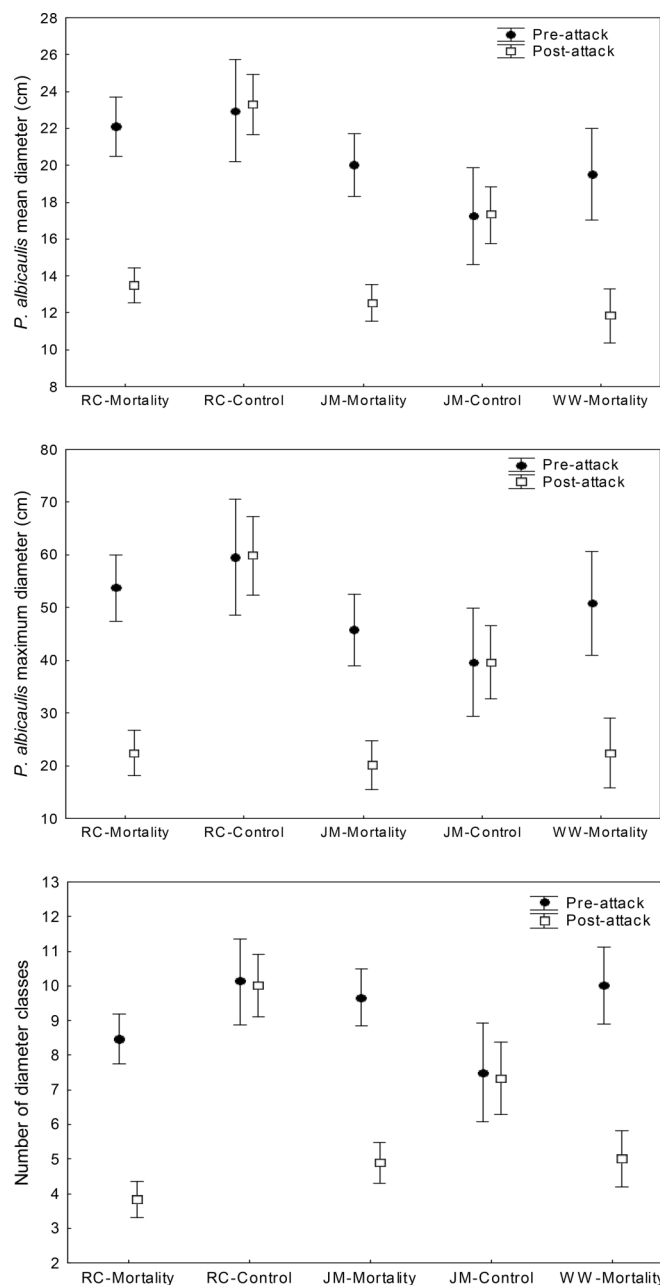
young (<3 years old) seedlings from mortality plots relative to control plots at all locations (Fig. 7). Approximately 8.3% of whitebark pine regeneration across sites had recently died, and an additional 9.6% exhibited signs of declining health (e.g., abnormal pitching, significant needle loss, occurrence of brown felt blight (*Neopeckia coulteri* (Peck) Sacc.). Across all sites, 45% of whitebark pine regeneration occurred in clusters of multiple stems, with most of these ranging from 2 to 4 stems (Fig. 8). The density of young (<3 years old) whitebark pine regeneration clusters was positively related to the severity of mountain pine beetle attack on whitebark pine across sites ($F_{[1,70]} = 31.701$, $R^2 = 0.312$, $\beta_1 = 0.56$, $P < 0.001$).

Discussion

Stand structure, tree mortality, and stand resistance

Mountain pine beetle activity significantly altered the structure of whitebark pine stands in our study by eliminating virtually all larger diameter (≥ 30 cm) trees, shifting the size class distribution to smaller diameters (<15 cm), and reducing size class diversity. These results indicate low resistance of whitebark pine stands to initial mountain pine beetle attack, especially because beetles disproportionately impacted the largest live trees with the highest reproductive potential. The probability of individual tree mor-

Fig. 3. Differences in mean ($\pm 95\%$ confidence interval) tree diameter (*P. albicaulis* only; top panel), maximum tree diameter (*P. albicaulis* only; middle panel), and size class diversity (5 cm increments, including all tree species; bottom panel) between pre-attack and post-attack of the mountain pine beetle in mortality and control plots from Rock Creek (RC), June Mountain (JM), and White Wing Mountain (WW).



tality was strongly associated with tree diameter, consistent with patterns of whitebark pine mortality caused by mountain pine beetle in central Idaho (Perkins and Roberts 2003) and lodgepole pine in the Rocky Mountains (Amman et al. 1977; Berryman 1982). Similarly, the severity of mountain pine beetle attack in whitebark pine stands was positively related to mean tree diameter and tree density at the stand scale, similar to patterns observed in whitebark pine stands from Montana, Idaho, and Oregon (Larson 2011). However, we did not find a relationship between tree mortality probability and the number of trees per cluster, possibly because beetles were insensitive to variation in cluster number,

Fig. 4. Relationship between severity of mountain pine beetle attack and percent decrease in whitebark pine density following attack. See Table 2 for description of the mountain pine beetle attack severity index.

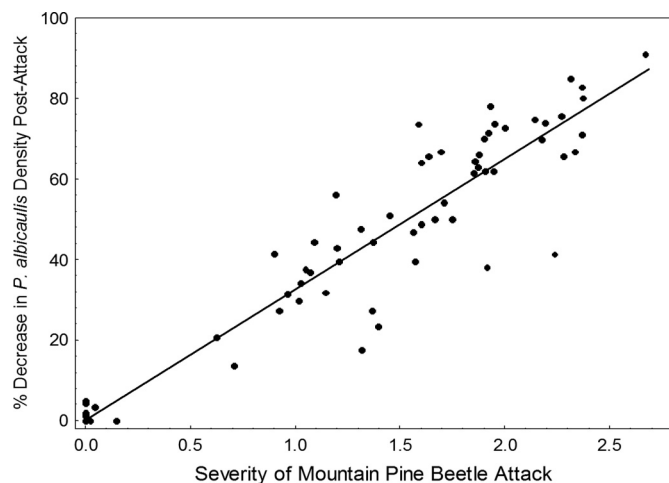
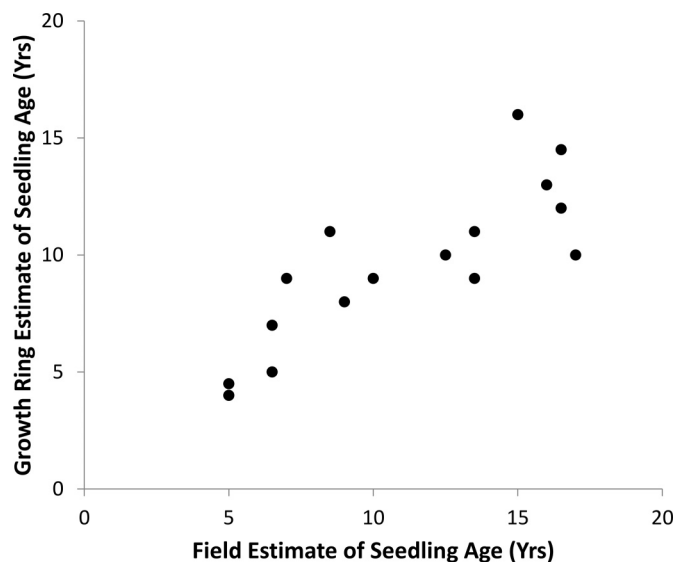


Fig. 5. Relationship between field and growth ring estimates of whitebark pine seedling age.



selecting for host susceptibility at larger spatial scales (e.g., Millar et al. 2012), or such trends were not apparent over the relatively short duration of our study. The pattern of greater mountain pine beetle activity and tree mortality in denser stands with larger trees is well documented in whitebark pine and lodgepole pine stands throughout many parts of western North America (e.g., Amman et al. 1977; Perkins and Roberts 2003; Millar et al. 2012; Simard et al. 2012).

On average, the threshold diameters below which most whitebark pine trees survived or avoided attack was approximately 15 cm in our study, which is similar to the threshold values from whitebark pine in central Idaho (18 cm; Perkins and Roberts 2003) and lodgepole pine in the Rocky Mountains (20 cm; Amman et al. 1977). However, we observed a higher (~30 cm) and weaker (decreased slope) threshold diameter for lodgepole pine compared with whitebark pine in our study, suggesting that mountain pine beetle preferred smaller whitebark pine to relatively larger lodgepole pine in our study. This apparent preference for whitebark pine may be a consequence of its relatively greater nutritional value (i.e., greater phloem thickness and concentration of carbo-

Fig. 6. Field-estimated age class distribution of whitebark pine regeneration at all study sites. High mortality and control plots are pooled for June Mountain and Rock Creek.

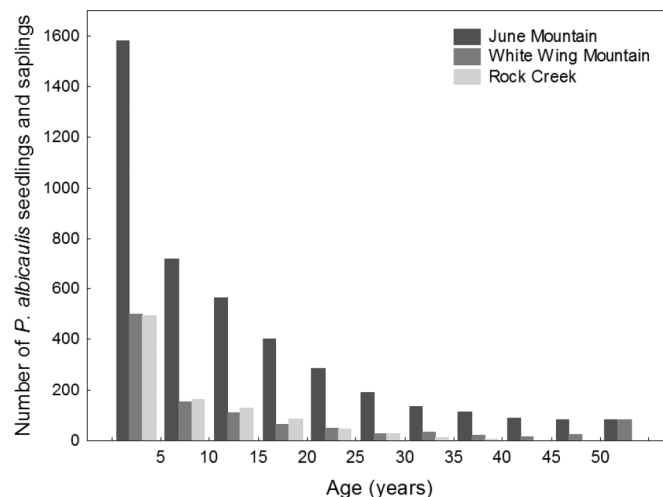
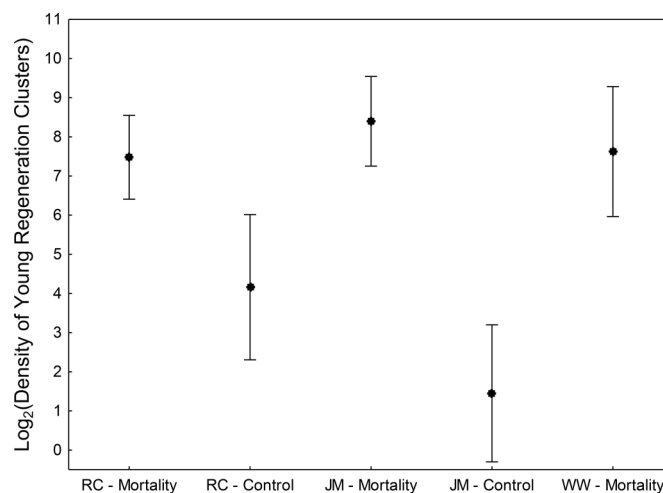


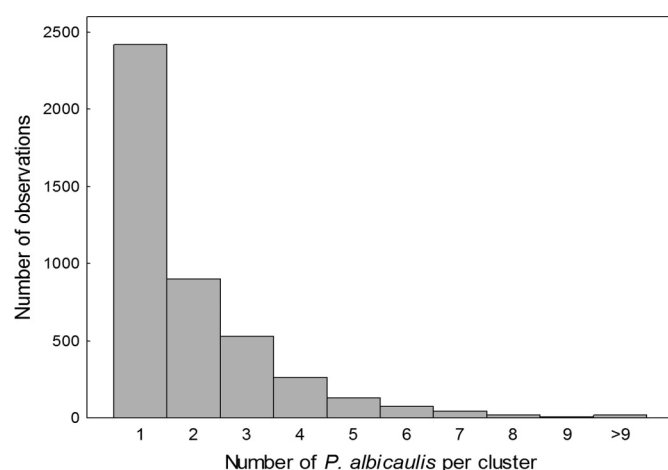
Fig. 7. Mean ($\pm 95\%$ confidence interval) density of young (<3 years of growth) *P. albicaulis* seedling clusters (\log_2 transformed) among study sites (mortality and control plots). RC, Rock Creek; JM, June Mountain; WW, White Wing Mountain.



hydrates; Lahr and Sala 2014) and lower plant defense capacity (less resin production and lower concentrations of toxic monoterpenes and pheromonal inhibitors; Raffa et al. 2013) than lodgepole pine. The difference in nutritional quality is apparent even when comparing smaller diameter whitebark pine with larger diameter lodgepole pine from the same area (Lahr and Sala 2014).

Several environmental variables also may have influenced pre- and post-attack structural patterns of whitebark pine stands in our study. First, differences in aspect between mortality (more north facing) and control (more south facing) plots at June Mountain may have accentuated the stand structural differences attributed to beetle attack in our study. However, we suspect this topographic influence was relatively minor for several reasons, including (i) the overall difference in pre-attack stand variables (e.g., live and dead basal area) was relatively slight (<20% of their total value) between mortality and control plots at June Mountain, (ii) these differences in stand variables were inconsistent (e.g., greater basal area in mortality plots, but greater tree densities in control plots, and no difference in canopy cover between plots), and (iii) pre- and post-attack stand structural patterns at Rock Creek (where there was no confounding influence of aspect on

Fig. 8. The number of live *P. albicaulis* seedlings and saplings per cluster. Data pooled from all study sites.



mortality versus control plots) were broadly similar to June Mountain with only minor exceptions (e.g., shrub cover). Second, the tendency for greater pre-attack stand biomass (e.g., live and dead basal area and canopy cover) at more northern sites (i.e., June Mountain and White Wing Mountain) compared with Rock Creek may be partially attributed to differences in soils or climate among these sites (Table 1). For example, the relatively lower annual precipitation at Rock Creek may have limited stand biomass in these whitebark pine stands compared with northern sites. However, the presence of granodiorite-derived soils at Rock Creek (with higher available soil water content than pumice soils at northern sites) may support larger whitebark pine trees and greater size class diversity pre-attack than northern sites (Table 2). These environmental associations are speculative but underscore the potential importance of local climate and soil conditions in structuring whitebark pine stands in western North America (Larson and Kipfmüller 2010) and the Sierra Nevada (Maloney 2014; Millar et al. 2012).

Tree regeneration and stand resilience

New whitebark pine regeneration was positively related to the severity of attack, suggesting the recruitment or survival of whitebark pine seedlings may increase in response to stand impacts by mountain pine beetle, especially the reduction of live tree densities and overstory canopy cover. Whitebark pine regeneration was also positively associated with tree canopy mortality caused by mountain pine beetle in southwest Montana, central Idaho, and Oregon (Larson and Kipfmüller 2010). Increased light availability was also associated with enhanced whitebark pine seedling establishment, survival, and growth within burned stands in central Idaho (Perkins 2015). In the northern Sierra Nevada, the density of whitebark pine seedlings was positively related to increased light availability (i.e., canopy openness) and nearby seed source from cone bearing trees based on a multivariate analysis (Maloney 2014). The positive regeneration response to mountain pine beetle attack suggests that whitebark pine stands in the southern Sierra Nevada may be resilient to initial beetle impacts in the absence of white pine blister rust. This resilience is also reinforced by several stand features noted in our study, including the presence of an advanced regeneration class consisting of many age classes and cohorts, and numerous small diameter whitebark pine trees that survive initial attack, including a large proportion of small horizontal stems in tree clusters. These combined features suggest that whitebark pine stands in the Sierra Nevada may be highly resilient to the initial impacts of mountain pine beetle attack. Our results support the general conclusion that whitebark pine communities may be highly resilient to mountain pine beetle out-

breaks in areas lacking significant white pine blister rust impacts (Larson and Kipfmüller 2012). However, in the Sierra Nevada, it is not clear whether this resilience will be maintained over time in the face of warming regional climate trends (Safford et al. 2012), probable future beetle attacks, episodic drought, and the potential arrival of additional insects and pathogens that may target smaller diameter trees and the regeneration class (e.g., white pine blister rust). For example, the unexpected impacts of *P. boycei* at the Rock Creek site were concerning, because this widespread species is generally uncommon and cryptic in montane forest ecosystems of western North America and previously undetected in high-elevation white pines (Wood 1982). As an exception, Ciesla et al. (2010) noted recent outbreaks of *P. boycei* in Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) from Colorado. These combined observations emphasize the importance of anticipating surprises with rapidly changing climate conditions (Millar et al. 2007), especially when historic information (i.e., historic range of variation) in insect disturbance regimes is lacking (e.g., Meyer 2013).

Management recommendations

Our results and existing published research provide several management recommendations for whitebark pine stands in the southern Sierra Nevada. First, low survival of larger diameter (dbh, >15 cm) whitebark pine trees to mountain pine beetle attack indicates that there are limited management options for retaining these larger structures following the onset of severe mountain pine beetle outbreaks. Rather, greater management attention could be placed on smaller stem retention and regeneration class enhancement of whitebark pine for the long-term persistence of this keystone species in subalpine landscapes of the Sierra Nevada. This could include the protection of existing regeneration microsites during mechanical operations (e.g., flagging of whitebark pine regeneration patches during “hazard tree” removal) or use of wildland fire to promote new whitebark pine seedlings in areas lacking a regeneration class, especially in dense and overstocked whitebark pine stands that are susceptible to mountain pine beetle attack (Keane et al. 2012). Second, the relatively high density of whitebark pine regeneration representing multiple age cohorts observed in most beetle impacted stands (e.g., June Mountain and White Wing Mountain) suggests that passive restoration methods, coupled with long-term monitoring, may be sufficient to sustain these resilient whitebark pine stands in the immediate future. Additionally, whitebark pine stands selected for restoration treatment and regeneration enhancement would ideally delay treatments for at least 4 years following mountain pine beetle attack to determine if natural regeneration is sufficient for potential stand replacement (i.e., passive restoration approach). This delay is to allow sufficient time for whitebark pine seeds to germinate and grow in response to increased resource availability such as soil moisture (Tomback et al. 2001a). However, stands lacking whitebark pine regeneration following this period could be targeted for ecological restoration treatments (e.g., use of wildland fire; Perkins 2015) using prioritization criteria and approaches similar to those developed in other regions (e.g., Aubry et al. 2008; Keane et al. 2012; Schwandt et al. 2010).

The resilience of whitebark pine stands in the southern Sierra Nevada is largely contingent on the maintenance of size class diversity and continued low occurrence (or absence) of white pine blister rust from this region, especially in the drier eastern side of the Sierra Nevada crest (Maloney 2011; Dunlap 2012). Ecological restoration treatments that promote a diversity of size classes may reduce the impacts of large-scale stressors (e.g., mountain pine beetle, uncharacteristically large and severe wildfires, prolonged drought) to whitebark pine stands even if white pine blister rust spreads through the region (Aubry et al. 2008; Schoettle and Sniezko 2007; Keane and Parsons 2010). Although increased warming and drying trends could impact whitebark pine popula-

tions in areas of greater climate vulnerability (e.g., Millar et al. 2012), these climate trends could also inhibit or reverse the spread of white pine blister rust in the region, as climate conditions are important controls over white pine blister rust distribution in California (Maloney 2011). Ultimately, the success of management actions will benefit from the development of a regional, inter-agency whitebark pine restoration and monitoring strategy (Schwandt et al. 2010; Keane et al. 2012), which is currently lacking for the Sierra Nevada.

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