Are High Elevation Pines Equally Vulnerable to Climate Change-induced Mountain Pine Beetle Attack?

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Mountain pine beetle (*Dendroctonus ponderosae)* (MPB), a native insect to western North America, caused extensive tree mortality in pine ecosystems during a recent warm and dry period. More than 24 million acres were affected, including in the relatively low elevation lodgepole (*Pinus contorta*) and ponderosa (*P. ponderosa*) pines, and the high-elevation whitebark (*P. albicauli*s) and limber (*P. flexilis*) pines.

High-elevation pines are hypothesized to be more susceptible to MPB than low elevation pines due to cold, unfavorable temperatures and potentially minimal long-term contact, resulting in less evolved defensive strategies against insect attack (Raffa et al. 2013). Tree-ring and written records indicate that MPB-caused mortality of whitebark pine has been a consistent occurrence throughout the 20th century, with a particularly large pulse in the late 1920s and early 1930s (Perkins and Swetnam 1996).

Warm summer temperatures fueled MPB population growth during this 'dust bowl' period until a record cold event in 1933 caused extensive MPB mortality and halted outbreaks. By contrast, both warm summers and warm winters recently coincided (Fig. 1) to allow sustained MPB population growth, resulting in extensive and severe MPB-caused mortality in whitebark pine ecosystems (Buotte et al. 2016).

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Pines have the capacity for both permanently expressed constitutive defenses and stimulated induced defenses in response to attack, and trees with greater concentration and responses are considered more resistant.

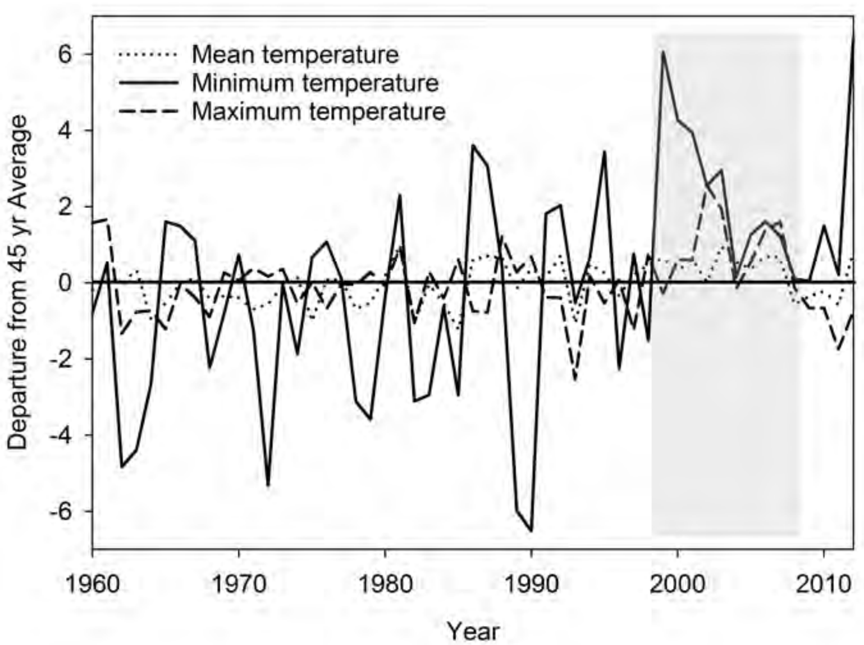

Figure 1. Temperature change from 1960 to 2012 in pine habitats across the western US showing that both summer (maximum) and winter (minimum) temperatures were above average during the period of extensive MPB-caused pine mortality in the 2000s.

Bentz et al. (2015) found no differences in constitutive defenses between lodgepole and whitebark pines growing in mixed stands, although induced defenses in lodgepole pine were found to be greater (Raffa et al. 2013).

Furthermore, more unsuccessful attacks were observed on lodgepole pine at these study sites, suggesting a greater capacity to defend against attack relative to whitebark pine. The number of mass attacked trees of each species did not differ, however, and the defenses of both species were apparently overwhelmed by the large MPB populations.

Although data from additional sites will be necessary to fully understand defense strategies in these species, the extensive mortality in whitebark pine is troubling given the significant ecological roles they play and their advanced age until reproduction. Moreover, other high-elevation pines may be equally vulnerable to climate change-induced outbreaks of MPB.

Great Basin (GB) bristlecone pine (*P. longaeva*) and its close relatives foxtail pine (*P. baulforianae*) and Rocky Mountain (RM) bristlecone pine (*P. aristata*) are high elevation species in the bristlecone or Balfourianae group that have the longest lifespans of all Pinus. GB bristlecone pine is considered the oldest living non-clonal organism worldwide with ages exceeding 5000 years, and foxtail and RM bristlecone pines can exceed 2400 years in age. All three species can grow in mixed stands with the ubiquitous limber pine, which is a known host to MPB.

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Low levels of MPB-caused mortality have been documented in RM bristlecone and foxtail pines, but not GB bristlecone pine despite high levels of MPB-caused limber pine mortality in the same stands (Bentz et al. 2016) (Fig. 2).

The lack of attacks on GB bristlecone pine and low level of attacks on foxtail pine can be at least partially explained by the high levels of constitutive phloem resin concentration found in these species, relative to co-occurring limber pine. GB bristlecone had double the concentration of total resin compounds found in foxtail pine, and more than eight times the concentration found in limber pine (Bentz et al. 2016).

GB bristlecone and foxtail pines also had significantly greater wood density than limber pine. Moreover, of the thousands of GB bristlecone pines examined, only a few showed signs of MPB parent galleries and in all cases no egg hatch was observed. Is GB bristlecone pine less attractive to MPB, in addition to being potentially more defended, than co-occurring limber pine?

Attraction of mountain pine beetle to GB bristlecone pine

To evaluate potential attraction of MPB to GB bristlecone pine, we used attack boxes attached to living pairs of GB bristlecone and limber pine (Fig. 3). Sets of ten live, unmated female MPB were placed in the boxes which were sealed to each tree.

After 48 hours, MPB activity was recorded as 1) in the exit jar (farthest from the bole), 2) in the attack box, 3) on the tree bark, but not boring and 4) attacking the tree (boring with frass) (Fig. 3). We conducted 36 paired tests at three sites using 720 MPB.

Based on ordinal logistic regression of the data, MPB were over two times more likely to be in a lower attack category

Figure 2. Live GB bristlecone pine surrounded by MPB-caused limber pine mortality in the Snake Mountains, NV.

(i.e., farther from the tree) on GB bristlecone pine than on limber pine. These results suggest that MPB has a low preference for GB bristlecone pine and that it is potentially repellent.

Mountain pine beetle reproduction in GB bristlecone pine

If MPB were to be successful in overcoming the defenses of GB bristlecone pine, could offspring be produced? To answer this question we manually infested MPB into freshly cut bolts of paired GB bristlecone and limber pine trees harvested from two sites.

Sixteen infested bolts of each tree species were placed in incubators at 22.5^{0}C. To evaluate the first steps in the MPB reproduction process, mating and laying eggs, four infested bolts of each species were peeled after 26 days and the number of viable eggs counted. The remaining 12 bolts of each species were left in incubators for brood to complete development and emerged brood adults were collected daily for 100 days (Fig. 4).

Although MPB laid viable eggs in both limber and GB bristlecone pine, there were dramatic differences between the species in brood adult emergence (Fig. 4).

Parent beetles in limber pine produced an average of 30.9 adult offspring per parent pair, yet in GB bristlecone pine only 0.4 adult offspring per parent pair, on average, were produced. Several factors could explain the poor reproduction in GB bristlecone compared to limber pine, including high levels of phloem resin concentration in GB bristlecone as documented from field sampling, in addition to the presence of multiple resin compounds found in GB bristlecone (Bentz et al. 2016) that have previously shown to be toxic or repellent to insects.

Summary

A recent pulse of warm and dry conditions in the western US resulted in extensive MPB-caused tree mortality. MPB equally mass-attacked lodgepole and whitebark pine growing in the same stands, yet few or no mass attacks were observed on foxtail and GB bristlecone

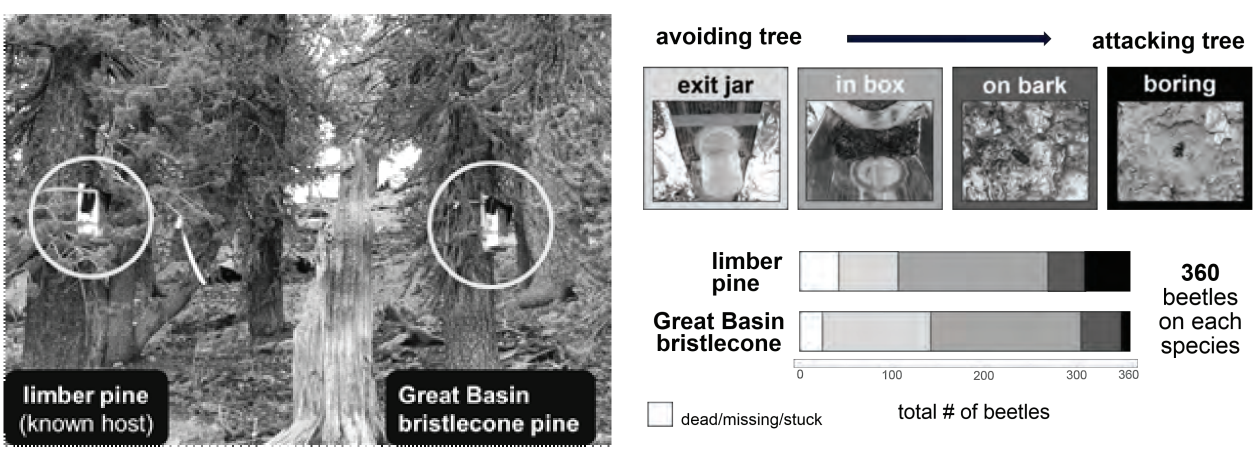

Figure 3. Attack boxes on paired trees. Ten live beetles were placed in each box for 48 hours, then activity recorded.

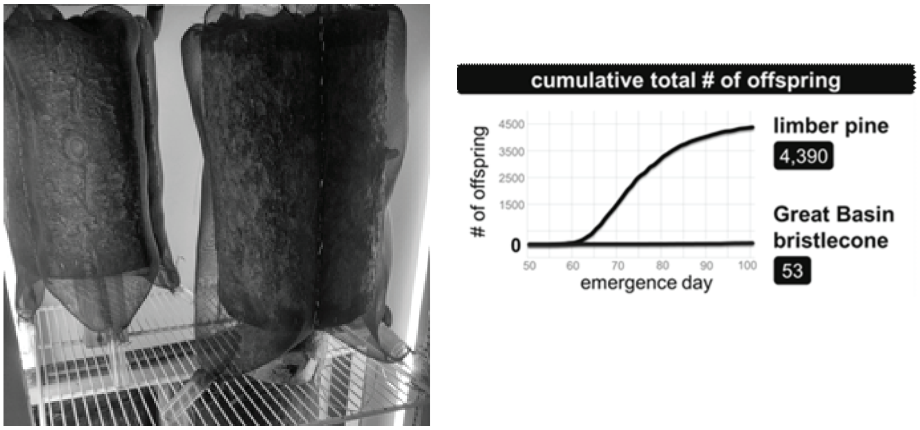

Figure 4. MPB brood produced from an equal number of manually infested bolts of GB bristlecone and limber pines.

pine when they were growing in the same stands with MPB-attacked limber pine.

Although high-elevation pines are hypothesized to be more susceptible to MPB due to historically unfavorable thermal conditions and a subsequent lack of evolved defenses, GB bristlecone and foxtail pines respectively have over eight times and over four times the concentration of total constitutive resin compounds found in co-occurring limber pine, in addition to having higher wood density and toxic compounds not found in limber pine.

Moreover, in our attack box study MPB were more likely to avoid GB bristlecone pine than limber pine, and produced few offspring in GB bristlecone pine when manually forced into cut bolts of each species. Although our results may imply that GB bristlecone and foxtail pines have a more long-term and evolved relationship with MPB than other pine species, the fact that limber pine has been a long-term and common associate with GB bristlecone pine suggests that other factors may also influence tree vulnerability.

The high resin concentration and wood density found in GB bristlecone and foxtail pine contribute to their ability to grow in harsh habitats and to attain very old ages, and these traits may have been co-opted for use in defense against MPB attacks (Bentz et al. 2016).

Tree longevity may also serve to maintain evolutionary signals of past traits that confer resistance to attack.
Predicting climate change-induced MPB-caused mortality is complex due to a need to understand the intricacies of MPB adaptation to temperature, in addition to factors that influence pine susceptibility, including evolved histories.

To fully understand future vulnerability of pines to MPB, standardized data is needed on relative defense strategies, including resin quality and quantity and structural mechanisms, among and within pine species that have varying longevity and that grow in multiple environments across the range of MPB.

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References

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