Mountain Pine Beetle and Great Basin Bristlecone Pine: A Complicated Story

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During the 1990s through 2010 bark beetle-caused tree mortality was a hot news topic in the western United States (US). An estimated > 5 Mha were affected by multiple bark beetle species. A large proportion of the total tree mortality, however, was attributable to a single species, the mountain pine beetle (MPB, *Dendroctonus ponderosae* Coleoptera: Curculionidae, Scolytinae). MPB has a large current distribution (Baja California Norte through the western United States and into British Columbia and Alberta, Canada), is polyphagous on most *Pinus* species within its range, and true to its name has adapted to mountain climates. Recorded hosts to MPB include multiple five-needle high-elevation pines (*Pinus albicaulis, P. aristata, P. flexilis, P. strobiformis, P. balfouriana*), and most other pines when they are growing at moderate to high elevations in the western US (*P. contorta ssp. murrayana and latifolia, P. edulis, P. lambertiana, P. monophylla, P. monticola, P. ponderosa*) (Furniss and Carolin 1977, Wood, 1982). Notably missing from this list is the iconic Great Basin (GB) bristlecone pine (*P. longaeva*). Does this suggest that GB bristlecone pine is not a suitable host to MPB? If yes, are both MPB oviposition preference and larval performance deterred in GB bristlecone pine? Conversely, if GB bristlecone pine is a suitable MPB host, why are infestations rare and undocumented? I provide an overview of the current knowledge of the intriguing relationship between MPB and GB bristlecone pine.

Background

GB bristlecone pine is a keystone species that typically grows on abiotically stressed sites at high elevations in the Great Basin. It has the longest lifespan of any non-clonal organism world-wide, and the oldest recorded living tree, Methuselah, is estimated to be 4851 yrs. In 2013 aerial surveyors (USFS, Forest Health Protection, Aerial Detection Surveys) observed MPB activity in high-elevation stands of mixed GB bristlecone and limber (*P. flexilis*) pines in the Snake Range, Nevada. From the air it was unclear if both tree species were being attacked and killed by MPB. A preliminary survey suggested that only limber pine was being affected. Given the lack of written records of MPB infestations in GB bristlecone pine, however, surveys were conducted across the range of GB bristlecone in 2014, focusing on stands where GB bristlecone co-occurred with limber pine and where aerial surveys detected MPB activity. Across the 10 mountain ranges surveyed, no GB bristlecone that were killed by MPB were observed, despite relatively high MPB-attacked limber pine in the same stands (Fig. 1; Bentz et al. 2017). In the few cases where MPB attacks were observed on GB bristlecone pine, egg and larval galleries were apparently aborted and wood borers were abundant. The closely related foxtail pine (*P. balfouriana*) was also surveyed, and a few trees in the southern Sierra Nevada population were found to be attacked and killed by MPB, although in much lower numbers than co-occurring limber pine. In a separate study that included no-choice field tests

Figure 1. MPB-caused limber pine mortality in mixed limber and GB bristlecone pine stands in the Pequop Mountains, NV. Photo, Matt Hansen, 2014.

where female MPBs were confined to exposed areas of tree boles, extremely few beetles bored into GB bristlecone pine, relative to limber pine (Eidson et al. 2017).

These observations suggested that GB bristlecone in particular, but also foxtail pine, have a level of resistance against, and are not preferred hosts of MPB, relative to limber pine. Tree resistance to bark beetles is a function of traits that have evolved to decrease behavioral preferences for oviposition (i.e., attack and egg laying), and negatively affect fecundity and brood growth and survival. Investment in defense traits, including carbon-based phloem secondary metabolites (e.g., terpenes) and axial resin ducts, are known traits that can significantly deter bark beetle attacks (Hood and Sala 2015). Trees with greater defenses are considered to have an evolutionary relationship with, and be more defended against, bark beetles (Franceschi et al. 2005). Phloem terpenes, axial resin ducts and structural defenses of co-occurring GB bristlecone and limber pines, and foxtail and limber pines, were investigated to evaluate if defense traits could explain the observed lack of MPB preference for GB bristlecone and foxtail pine. We found that GB bristlecone averaged almost eight times and foxtail almost four times greater terpene defenses than co-occurring limber pine (Fig. 2). GB bristlecone also had a greater number of axial resin ducts, relative to growth area, and higher sapwood and heartwood density than limber pine (Bentz et al. 2017). The GB bristlecone and foxtail pines we sampled, therefore, tended to invest more in secondary metabolites and defense structures than limber, potentially playing a role in MPBs reduced preference for these species. Slow growing trees in resource poor environments are hypothesized to invest a greater proportion of carbon into secondary defense metabolites than growth (Coley et al. 1985, Mattson and Herms 1992), and our finding that the slow growing GB bristlecone pine had the highest levels of carbon-based defenses supports this hypothesis. The comparatively high levels of constitutive defense traits in GB bristlecone pine may also be the result of previous evolutionary pressure from phloem-feeding herbivores.

In addition to deterring bark beetle preference for tree attacks, resinous defenses can influence brood development and survival. The preference-performance hypothesis predicts that female insects are choosy mothers and they assess plant suitability for their offspring and preferentially oviposit on host plants that will support optimal offspring performance (Jaenike 1978). To assess if MPB choosiness was associated with poor offspring performance, male and female MPB adults were manually infested into freshly cut logs of GB bristlecone and limber pines in the laboratory. Although MPB oviposited viable eggs that hatched in both GB bristlecone and limber pine logs, only 0.4 surviving offspring were produced per parent adult in GB bristlecone pine compared to 30.9 offspring in limber pine

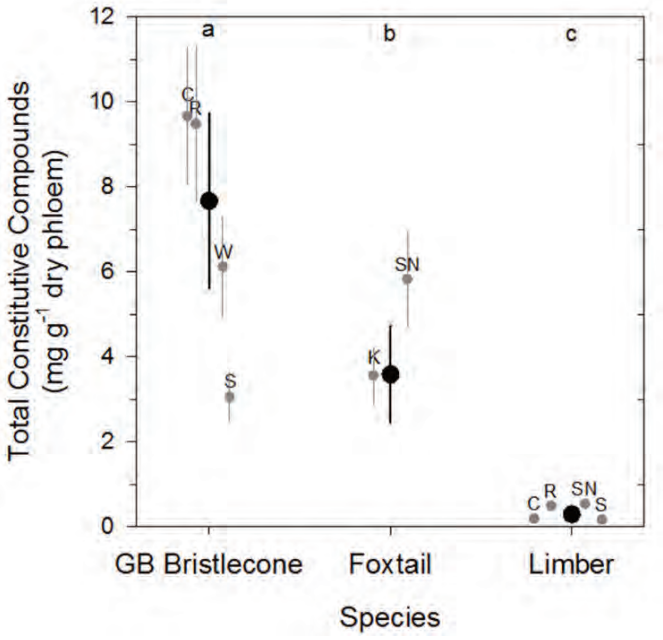

Figure 2. Across multiple sites, total terpene defense compounds in GB bristlecone pines were 8 times greater, and foxtail pines 4 times greater, than co-occurring limber pines (Bentz et al. 2017). C = Cedar, R = Ruby, W = White, S = Spring, SN = Sierra Nevada, and K = Klamath ranges.

(Fig. 3; Eidson et al. 2018). The high offspring mortality in GB bristlecone pine is unique among pine species. All other pine species tested, including several high-elevation species and species from outside the current MPB range, were found to be highly suitable (e.g., Amman 1982, Langor et al. 1990, Esch et al. 2016, Rosenberger et al. 2017). These results support the preference-performance hypothesis and suggest that if attacked, GB bristlecone pine may be a population sink for MPB. Low preference for and low performance in GB bristlecone pine also

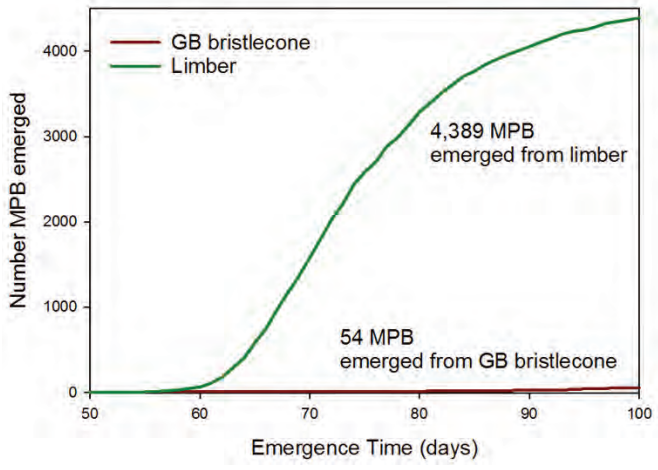

Figure 3. In a laboratory study, MPB brood survival was extremely low in GB bristlecone compared to limber pine (Eidson et al. 2018).

implies a potentially long evolutionary history between GB bristlecone pine and MPB.

GB bristlecone pine can grow in isolated areas with poor soils, but also form extensive stands. In both cases GB bristlecone pine can grow either mixed with or in close proximity to other *Pinus*, including limber pine, pinyon pines (*P. monophylla*, *P. edulis*) and ponderosa pine (*P. ponderosa*). Pinyon pines are known hosts for MPB, but pinyon ips (PI) (*Ips confusus*) is their main bark beetle predator. PI was responsible for large swaths of dead pinyons during the 2001-2003 drought in the southwest US. Although GB bristlecone pine is not listed as a PI host, in 2017 we observed several relatively young GB bristlecone pine that were attacked and killed by PI in the Wah Wah range, Utah. Preliminary data from emergence cages on the attacked trees in the Wah Wah stand suggest that PI brood production in GB bristlecone pine was low, similar to our laboratory observations for MPB brood survival in GB bristlecone pine. PI was found infesting pinyon pine and MPB and western pine beetle (*D. brevicomis*) were infesting ponderosa pine growing downslope from GB bristlecone pine in the Wah Wahs. Yet, MPB infestation of GB bristlecone pine was not observed.

Returning to the question initially posited, based on a lack of MPB-GB bristlecone pine infestations in written records, "*Is GB bristlecone pine not a suitable host for MPB? If yes, are both MPB oviposition preference and larval performance deterred in GB bristlecone pine?*" Based on the field surveys and study observations, GB bristlecone pine appears to not be a suitable host for MPB. Extremely few offspring emerged from GB bristlecone pine in the laboratory and of the few trees observed attacked in the field, egg and larval galleries ended abruptly and there were no apparent adult emergence holes. MPB preference for, and performance in, GB bristlecone pine were both low, hypothetically due to the high levels of resinous defenses and apparent toxicity to developing MPB brood. There are several factors that could explain the observed patterns.

Potential Factors Influencing the GB Bristlecone Pine and MPB Relationship

Long-term evolutionary relationship Long-term contact and evolutionary history between specific plant and herbivorous insect species are expected to increase plant allocation to secondary metabolic defenses (Herms & Mattson, 1992). Some bark beetle species, including MPB, have evolved counter-adaptations to tolerate and even benefit from tree defense allocations. MPB has evolved to use terpene defense compounds as synergists in aggregation pheromones that facillitate mass attacks on trees (Franceschi et al. 2005). This 'Red Queen arms-race' between MPB and *Pinus* has undoubtedly been battled throughout evolutionary time. Extant tree species within *Pinus* and beetle species within *Dendroctonus* both have Eastern Eurasia as the likely center of origin (Eckert and Hall 2006, Godefroid et al. 2019). For *Pinus*, inter-continental migrations between Eurasia and North America, through the Beringia Land Bridge, were concentrated in the late Cretaceous and Tertiary (Eckert and Hall 2006). The first inter-continental vicariance event for *Dendroctonus*, also across the Beringia Land Bridge, is estimated to have occurred later, during the early Miocene (Godefroid et al. 2019). Community reorganization and diversification during the Quaternary followed in both *Pinus* (Millar 1998, Godbout et al. 2008) and *Dendroctonus* (Godefroid et al. 2019). The *Pinus* subsection Balfourianae, which includes GB bristlecone and foxtail pine, were concentrated in Great Basin, western US refugia during the early Tertiary with population expansions and shrinkages during glacial and interglacial waves of the Quaternary (Wells 1983, Millar 1998). Downward GB bristlecone pine movement during the last full glacial, to as low as 1900 m elevation, likely occurred prior to a retreat upward to the sky island mountain ranges inhabited today. Glacial patterns within the western US that influenced GB bristlecone pine also played a role in *Dendroctonus* diversification, which is ongoing. MPB is considered to be in the early stages of speciation wherein infertile F_1 offspring are produced when populations from either side of the Great Basin are mated (Bracewell et al. 2017, Dowle et al. 2017). Although glacial and interglacial range shifts may have decoupled GB bristlecone pine and its insect predators, the long-lived and non-senescent GB bristlecone pine likely retained evolutionary signals of past selection (Hamrick 1979).

Exaptation Another plausible explanation for MPBs lack of preference for, and limited brood survival in, GB bristlecone pine is evolution by exaptation. Traits including high resin production and wood density may have been originally adapted for the maintenance of extreme longevity, and were then co-opted as exaptive defense traits against phloem feeders. Large amounts of resin and high wood density, as found in GB bristlecone pine, can limit wood decay and provide structural integrity to support living cambium, thereby also conferring longevity and survival in marginal habitats (LaMarche 1969). Evolution by exaptation has been shown to be important in the origin of new defense traits (Armbruster et al. 1997), and may have played a role in the evolutionary trait outcome that allows GB bristlecone defense against phloem-feeding bark beetles and toxicity to their brood.

New Developments

During the summer of 2019 recently dead GB bristlecone pine mortality was observed by Connie Millar and colleagues across several ranges on the western edge of the species distribution

(see more in the story starting at page 70). This is in contrast to our own surveys in the Fishlake and Dixie National Forests, and the Spring, White, and Ruby mountain ranges where we observed no MPB-caused GB bristlecone pine mortality during surveys and sampling in 2019. One of the ranges with observed recent GB bristlecone pine mortality is the Panamint Range, located in Death Valley National Park. Telescope Peak, the highest in the Park was observed in 2019 by Millar to have high levels of tree mortality. A one day trip to Telescope Peak revealed interesting factors regarding recent GB bristlecone pine mortality. Pinyon pines at the base of the peak were found infested with MPB, as well as extensive MPB-caused limber pine mortality that occurred over the past 5-6 years, along the extent of slopes to where limber pine and GB bristlecone pine mixed. GB bristlecone pine mortality was extensive on the slopes where it mixed with limber and minimal on slopes with relatively pure GB bristlecone pine. The few GB bristlecone pines we examined showed signs of MPB attack in 2018, but without apparent adult emergence. MPB larval brood galleries stopped abruptly before completing the lifecycle to the adult stage. My colleagues and I hypothesize that MPB populations built up to very high levels in a single year (2018) in the pinyon and limber pines, spilling over to GB bristlecone pine. Low brood performance in GB bristlecone pine is expected based on previous field observations and laboratory studies, and our preliminary hypothesis is that GB bristlecone pine was a population sink for MPB.

Next steps are to survey stands with recent GB bristlecone pine mortality and evaluate potential biotic (e.g., insects) and abiotic (e.g., drought and temperature) factors influencing tree mortality. It is unclear why tree mortality is occurring in some, but not other GB bristlecone pine stands, and if the tree mortality is historically novel. Our goals include to evaluate if GB bristlecone pine is a population sink for MPB and PI, potential roles for climate and tree age, and if having MPB/PI *Pinus* hosts in spatial proximity increases the probability of bark beetle attacks on GB bristlecone pine. Additional data will provide insight to the ongoing evolutionary arms race between GB bristlecone pine and insect predators. As the Red Queen suggested to Alice, it takes all the running you can do to keep in the same place.

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