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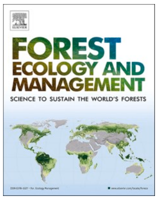

Great Basin bristlecone pine mortality: Causal factors and management implications☆

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ABSTRACT

High-elevation five-needle pines are foundational species and iconic components of subalpine forests across western North America. Because they often grow at environmental extremes, high-elevation pines are vulnerable to changing climate conditions. In addition to the direct effects of recent climatic changes, these species are increasingly threatened by biotic disturbances that thrive in the warming and drying conditions now occurring at higher elevations. Among the high-elevation pines, Great Basin bristlecone pine (*Pinus longaeva*) is revered for its extreme longevity and has been considered an icon of stability during periods of change. Life history strategies of Great Basin bristlecone pine that contribute to its longevity include physiological traits that enhance survival in harsh and dry habitats, and defensive traits that make it less vulnerable than other high-elevation pines to tree-killing bark beetles. Recent increases in growing degree days with no associated increase in precipitation is causing temperature-amplified tree drought stress, while warming temperatures positively influence bark beetle population growth. We report on preliminary investigations into recent and unexpected Great Basin bristlecone pine mortality at two sites, including the potential roles of weather-induced stress and bark beetles. At both sites climatic water deficit (CWD), a cumulative measure of moisture stress, and mean annual temperature increased during the 2010 decade and CWD was the highest in 2020 relative to any time during the past 40 years. Although Great Basin bristlecone pine mortality has not previously been attributed to bark beetles, we observed recent (i.e., 2013 to 2020) bark beetle-attacked trees at both sites, coincident with the timing of increasing temperature and CWD. Few adult beetles were produced, however, and our results support previous research that Great Basin bristlecone pine is a population sink for bark beetles. Because bark beetles are likely not self-sustaining in Great Basin bristlecone pine, bark beetle-caused mortality of this iconic species will most likely occur when it grows mixed with or near other pine species that support bark beetle population growth. We found *Ips confusus* and *Dendroctonus ponderosae* attacking Great Basin bristlecone pine in areas where their host trees, *P. monophylla* and *P. flexilis*, were also growing. These results suggest that the presence of these infested conifers likely contributed to Great Basin bristlecone pine mortality. We highlight several factors that may be used for prioritizing future research and monitoring to facilitate development of management strategies for protecting this iconic species.

1. Introduction

High-elevation five-needle pines are among the longest-lived trees globally (Piovesan and Biondi, 2021), and in western North America they inhabit the highest elevations of mountain ranges where they serve as foundational species (Tomback et al., 2011). This group includes whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*P. flexilis* James), foxtail pine (*P. balfouriana* Grev. & Balf.), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey), Rocky Mountain bristlecone pine (*P. aristata* Engelm.) and southwestern white pine (*P. strobiformis* Engelm.). Because these pines often grow in habitats near the edge of their environmental limits, they are exceptionally vulnerable to changing climatic regimes both directly and via climate-mediated effects on biotic disturbance agents. Changing environmental conditions are increasingly threatening vast areas of temperate forests, including at high elevations, as hotter droughts drive emerging megadisturbances and associated tree mortality (Allen et al., 2015, Millar and Stephenson, 2015). Extreme water limitation in conifers causes hydraulic failure via stomatal closure and

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subsequent carbon starvation which can directly cause tree death (McDowell et al., 2008). Water stress also compromises quantitative and qualitative tree defenses against insect herbivores including bark beetles (Anderegg et al., 2015, Arango-Velez et al., 2016, Kolb et al., 2019). Warming temperatures that favor bark beetle survival and population growth (Bentz and Jönsson, 2015) and decreasing precipitation that stresses trees are drivers of bark beetle-caused tree mortality globally (Young et al., 2017, Stephenson et al., 2019, Fettig et al., 2019, Huang et al., 2020, Koontz et al., 2021), including in western United States (US) high-elevation pine habitats (Buotte et al., 2017, Millar et al., 2007, 2012). Predicting high-elevation pine sustainability in a changing climate requires not only knowledge of the direct effects of changing temperature and precipitation regimes on pine growth and regeneration (Millar et al., 2015; Bucholz et al. 2020, Smithers et al. 2021), but also an understanding of the dynamic and integrated effects of biotic mortality agents (Meddens et al., 2015, Trugman et al., 2021).

1.1. Bark beetles and high-elevation pines

A diversity of native bark beetles (Coleoptera: Curculionidae, Scolytinae) attack and reproduce in high-elevation pines (Furniss and Carolin, 1977, Wood, 1982) including species within the genera *Pityopthorus*, *Pityogenes*, and *Polygraphus* that typically do not kill trees, and *Ips,* which can be tree-killers particularly when trees are stressed. For example, the pinyon ips (*Ips confusus* Leconte) was responsible for widespread pinyon pine mortality during a 2000–2004 drought in the southwest US that stressed trees (Kleinman et al., 2012), but beetle populations subsided as wetter conditions returned (Raffa et al., 2008). The most notable bark beetle species associated with high-elevation pines is the tree-killer mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins. Unlike *Ips*, pheromone-mediated mass attacks allow MPB to be self-amplifying and attack and kill trees even when stressing conditions subside (Boone et al., 2011). About one half of the pine species found in the western US are recorded hosts to MPB, including a majority of high-elevation pine species (Wood 1982, Furniss and Carolin, 1977). Pollen and macrofossils from lake sediments and evidence from tree rings document the antiquity of the relationship between MPB and multiple high-elevation pines (Perkins and Swetnam, 1996; Brunelle et al., 2008, Bentz et al., 2011; Kipfmueller et al., 2002). MPB is an ectotherm with life history traits that are thermally regulated and have evolved for the harsh climates in montane environments, as highlighted in its common name. Appropriately acclimated cold hardening allows larvae to survive extreme cold (Bentz and Mullins, 1999, Rosenberger et al., 2017), and developmental traits regulate timing to avoid cold intolerant lifestages during winter (Bentz et al., 1991, Bentz and Hansen, 2017, Bleiker and Smith, 2019). These same developmental traits enable synchronous adult emergence which, in concert with a powerful aggregation pheromone, facilitates mass attacks on trees that serve to overwhelm tree defenses (Logan and Bentz, 1999).

MPB’s evolved traits allow flexibility in lifecycle timing, which can promote population persistence at the widely ranging elevations where its pine hosts grow. At cool, high-elevation sites a high proportion of MPB can take two years to complete a lifecycle compared to a single-year lifecycle at low elevation and warm sites. It is not uncommon, however, for both lifecycle types to occur at a single high-elevation site depending on the weather for a particular year (Bentz et al., 2014). In the historically coldest regions of the western US, recent warming at high elevations has increased the proportion of MPB that can complete a generation in a single year and reduced cold-induced larval mortality (Weed et al., 2015, Buotte et al., 2017). Increased MPB survival and faster lifecycle completion at high elevations have contributed to recent MPB-caused mortality of whitebark pine, limber pine, and Rocky Mountain bristlecone pine (Gibson et al., 2008, Millar et al., 2007, 2012, Cleaver et al., 2015, Buotte et al., 2017, Bentz et al., 2021). MPB-caused mortality of other high-elevation pine species, however, appears to be rare or isolated to a few trees within a stand.

MPB attacks have been observed on foxtail pine, although significantly fewer than on other pines growing in the same stand (Bentz et al., 2017, Nesmith et al., 2019, Dudney et al., 2020). Similarly, in the introgression hybrid zone of southwestern white and limber pines in Arizona (Menon et al., 2018) isolated attacks and successful MPB reproduction occurs (McManis et al., 2018, Soderberg et al., 2021), although large scale MPB outbreaks in these forests have not been recorded. In an extensive survey across the range of another high-elevation pine species, Great Basin bristlecone pine, no successful MPB attacks were found despite extensive MPB-caused mortality in co-occurring limber pine (Bentz et al., 2017). In the few cases where MPB attacks were observed on Great Basin bristlecone pine, there was no evidence of larval mining or brood adult emergence. Further, in a field test where female MPBs were confined to exposed areas of tree boles of one species at a time, few beetles bored into Great Basin bristlecone relative to limber pine (Eidson et al., 2017). MPB was also observed to orient toward volatile organic compounds from limber pine, and away from Great Basin bristlecone pine volatile compounds (Gray et al., 2015). Perhaps most importantly, in a laboratory experiment a mean of 0.4 surviving offspring were produced per female in Great Basin bristlecone pine compared to 30.9 offspring in limber pine (Eidson et al., 2018). Other high-elevation pines that have been studied in the same manner (i.e., manually infesting male and female MPBs into harvested bolts of live trees) were shown to be highly suitable for offspring production (Amman, 1982, Langor et al., 1990, Esch et al., 2016). These results collectively suggest that Great Basin bristlecone pine is not attractive to MPB, and if attacked could be a population sink due to low offspring survival. In fact, we know of no records documenting a bark beetle species that can successfully reproduce in Great Basin bristlecone pine.

1.2. Great Basin bristlecone pine ecology and importance

Great Basin bristlecone pine grows in disjunct populations scattered across high mountain ranges of eastern California, Nevada, and western Utah. The highest-elevation tree species in these ranges, Great Basin bristlecone pine co-occurs primarily with limber pine, although at some locations Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and white fir (*Abies concolor* (Gordon) Lindley ex Hildebrand) are present. Singleleaf pinyon pine (*P. monophylla* Torr. & Frém.), ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), and Douglas-fir (*Pseudotsuga menziesii* var. glauca (Mirbel) Franco) overlap Great Basin bristlecone pine at the lower elevation of its habitat, varying by location. Among Nevada populations, the lowest recorded observation is 1944 m and the highest is 3546 m (Charlet, 1996), although Millar (unpublished 2021) recently observed a 1.5 m recruit on Sheep Mountain, White Mountains, CA at 3611 m. The southernmost occurrence of Great Basin bristlecone pine was recorded as Potosi Mountain in the Spring Mountains, Nevada, although this occurrence has not been documented in decades and a recent search failed to find the species there (David Charlet, pers. comm. 26 August 2021). Great Basin bristlecone pine is strongly associated with carbonate substrates, on which it is a superior competitor to other tree and shrub species. It is not, however, a carbonate obligate, as it occasionally grows on granitic, volcanic, and metamorphic substrates.

Among the high-elevation pines, Great Basin bristlecone pine is arguably the best known, famous for its scientific importance due to its longevity. Individual trees more than four millennia old are found across its range, and at least one tree was dated at over 5,000 yrs (Salzer and Baisan, 2013). Individual tree longevity is ascribed to its cold and arid climate (slowing growth and limiting wood decomposition), sparse stand structure (limiting fire), long needle retention, and strip-bark or sectored architecture. Strip-bark, or partial cambial mortality, is a result of cambial death along a tree’s vertical axis, wherein branches are directly connected to particular roots and vertical segments are independent from other portions of the stem (Schauer et al., 2001). Stripbarking allows a tree to reduce its aboveground living biomass to a level that can be supported by the available root capacity. Individual longevity of trees and preservation of solid deadwood across its landscape have allowed development of a tree-ring chronology for Great Basin bristlecone pine that extends, with one short gap, to the late Pleistocene, nearly 11,000 yrs ago and in one stand a continuous chronology of 8848 yrs was developed (Salzer et al., 2019). These long chronologies provide some of the most reliable and long-term annually-dated climate records available globally, and were used by the Intergovernmental Panel on Climate Change reports (IPCC, 2001) to compare relative temperatures of the modern era to prehistoric climate. Annual dating of Great Basin bristlecone pine chronologies was also extremely important for enabling calibration of the radiocarbon curve (Suess, 1967), critical to the work of many scientific disciplines. As the dominant subalpine and treeline-forming species of the Great Basin, Great Basin bristlecone pine supports diverse and unique vegetation communities and provides critical habitat for high-elevation animal species throughout the bioregion.

Despite the ubiquity of recent drought- and bark beetle-caused conifer mortality in the western US, large-scale mortality events in Great Basin bristlecone pine have been rare. As described above, this species has significant defenses against bark beetles (Bentz et al., 2017, Eidson et al., 2018) and is hypothesized to be less susceptible to long-term drought events given lower sensitivity to water availability than other pines including limber pine (Smithers et al., 2021). Recently observed mortality events (Millar et al., 2019) provided a rare opportunity to explore potential causal factors of mortality in this iconic species. We describe a preliminary investigation into mortality at two sites that, based on prior research, is unexpected for Great Basin bristlecone pine. Our preliminary observations document the unexpected and isolated mortality providing a basis for future research, and perhaps most importantly, to alert managers to the vital need for monitoring and preventive actions in Great Basin bristlecone pine stands. Our observations highlight potential emerging threats to this species as climate continues to change and relay the need for targeted research.

2. Methods

2.1. Study sites and sampling

Two sites with recently observed Great Basin bristlecone pine mortality were investigated, the Wah Wah Mountains in west-central UT, and the Panamint Range in eastern CA (Fig. 1). The Wah Wah site is within the Lawson Cove drainage at elevations ranging from 2200 to 2718 m. Utah juniper (*Juniperus osteosperma* Torr.) and singleleaf pinyon pine dominate the lower elevations, and isolated, mixed stands of Great Basin bristlecone pine, ponderosa pine, and white fir occupy the higher elevations (Kitchen, 2012). The population in the Panamint Range occurs on summits surrounding and including Telescope Peak, the highest peak (3366 m) in Death Valley National Park. This population is one of the southernmost occurrences of the species. Singleleaf pinyon pine occurs at the lowest elevations (~2400 m), transitioning to pure limber pine, and extensive stands of mixed limber pine and Great Basin bristlecone pine above ~ 3100 m. The GLORIA alpine plant monitoring

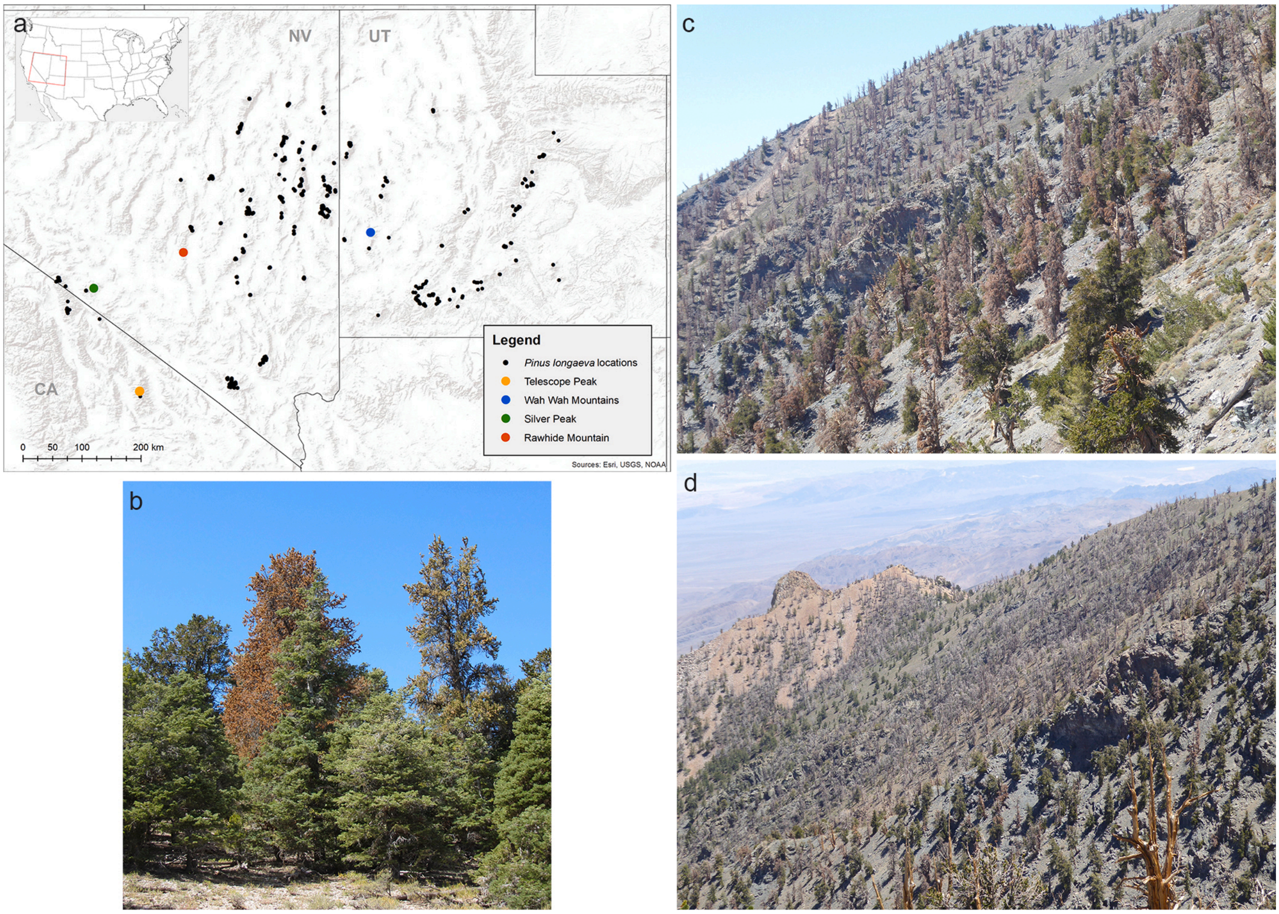

Fig. 1. a) Geographic locations of field-verified Great Basin bristlecone pine habitats, highlighting locations with recently observed Great Basin bristlecone pine mortality; locations from Bentz et al. (2017), Eidson et al. (2017, 2018), Charlet (1996; pers. comm.) and Burchfield (2021). We note that the Potosi site included in Burchfield (2021) was not included. b) Great Basin bristlecone pine mortality at the Wah Wah Mountains site (photo credit B. Bentz). c, d) limber pine and Great Basin bristlecone pine mortality at the Telescope Peak site (photo credits C. Millar).

project identified 43 plant species across the elevational gradient (GLORIA Great Basin: https://www.gloriagreatbasin.org/).

2.2. Wah Wah Mountains, UT

Following up on a report of recent Great Basin bristlecone pine mortality (S. Kitchen, pers. comm), the Wah Wah site was initially visited 18 August 2017. Our initial goal was to identify agents of mortality in the stand. In an informal survey of the area recent bark beetle attacks in several singleleaf pinyon pines were observed at the lower elevations, and one recently dead and several small DBH (diameter at breast height) currently attacked (i.e., orange and red needles) Great Basin bristlecone pine at the upper elevations. Several dead and large diameter Great Basin bristlecone pine with fire scars were found, in addition to two bark beetle-attacked ponderosa pine. For each recently dead or currently attacked tree, identification of the attacking bark beetle species was made by removing bark and visually inspecting the egg and larval galleries. Additionally, live and dead adult beetles were returned to the Rocky Mountain Research Station (RMRS) laboratory in Logan, UT, and bark beetle species were identified (J. LaBonte, J. Vlach, Oregon Department of Agriculture, pers. comm.).

On 23 October 2017 the site was revisited and seven total emergence cages were attached on multiple bole aspects of four smaller diameter Great Basin bristlecone pine currently infested with bark beetle larvae. Emergence cages were made of 30 × 61 cm pliable mesh and were stapled to the tree boles with a tube attached at the bottom to collect any insects that emerged from beneath the bark (Supplemental Fig. 1). DBH was recorded for each tree. The site was visited again on 6 June 2018 and all emergence cages emptied. Insects in sample tubes were placed in vials with 95% ethanol, and the mesh cages were removed from all trees. All samples were returned to the RMRS laboratory in Logan, UT, and bark beetle species were identified (J. LaBonte, J. Vlach, Oregon Department of Agriculture, pers. comm.).

2.3. Panamint Range, Telescope Peak, CA

Telescope Peak was first visited on 9 July 2019, at which time widespread and previously undocumented mortality was observed in all sizes of Great Basin bristlecone pine and limber pine. Mortality occurred on at least the south, east, and north slopes of Telescope Peak and multiple slopes of the unnamed peak to the south, as observed from the summit of Telescope Peak. Based on needle color, a mix of new and recent death of trees of both species were estimated. On 9 September 2019 an informal survey was conducted to further investigate the cause of tree mortality. The upper slopes are extremely steep and scree covered (see Fig. 1), making access to trees off the trail difficult. Both Great Basin bristlecone pines and limber pines that were accessible from the trail and that also had red needles were sampled. Red needles are an indication that the trees were dying and potentially under attack by bark beetles. The outer bark was removed and returned to the RMRS laboratory in Logan, UT. Bark beetle attacks were confirmed, and the site was revisited on 16–17 October 2020 to further assess causal factors in death of both tree species and to evaluate if bark beetle brood (i.e., offspring) were successfully produced in each tree species. Recently dead limber pine (N = 9) and Great Basin bristlecone pine (N = 22) were sampled at multiple aspects and elevations along the trail to Telescope Peak (Supplemental Fig. 2). Because it is known that limber pine is a successful host for MPB, but previous research found no evidence of MPB success in Great Basin bristlecone pine, additional Great Basin bristlecone pines were sampled. DBH of each tree was measured and its GPS location recorded. A 15 × 15 cm area of outer bark was removed from two bole aspects of each tree at DBH, with the exception of 7 trees where only one bole aspect was accessible due to the steep, loose terrain.

2.4. Bark beetle identification and measuring brood success

Identification of bark beetle species was determined by gallery patterns under the bark and adult beetles when available. In the case of MPB, brood success was determined by examining the spatial placement of holes that extended through the outer bark of each sample. Holes on the outer bark could be made by 1) attacking parent adults, 2) emerging brood adults, or 3) ventilation holes made by parents within galleries during egg laying (Fig. 2). We refer to beetles that attack a tree as parent adults and offspring that subsequently emerge from a tree as brood adults. Following tree attack, parent adults mate and bore an egg gallery vertically through the phloem where females lay eggs on each side of the gallery. A parent adult hole (i.e., the initial entry hole) is therefore positioned at the bottom of the egg gallery. Ventilation holes made by the parent adults are found along the egg gallery. Following egg hatch, larvae mine horizontally proceeding through at least four instars prior to chewing a chamber for pupation during the last larval instar (i.e., pupal chamber). Metamorphoses to pupae and then pre-emergent brood adults occurs in these chambers. Brood adults continue their maturation in these chambers prior to emergence from the host tree. Successful MPB brood adult emergence was quantified by counting the number of holes on the outer bark that originated from a pupal chamber. For each MPB bark sample, the number of pupal chambers with emergence holes and the total egg gallery length within the sample area were measured. The first is a measure of successful brood adult offspring emergence, and the second is a relative indicator of MPB attack density on the tree. Mixed model analyses (SAS v 9, PROC GLIMMIX) were used to evaluate differences between the tree species in two response variables, number of brood adult emergence holes and egg gallery length. A lognormal error distribution was used given the positive skewness in the data, with tree included as a random effect. We also tested for the fixed effects of tree bole aspect and DBH on both response variables.

Visual cues of needle color and retention during our visits to Telescope Peak confirmed that Great Basin bristlecone pine and limber pine mortality occurred at least in 2017, 2018, and 2019. To estimate the year when tree mortality first occurred on the slopes of Telescope Peak and surrounding unnamed peaks, we acquired NAIP (National Agriculture Imagery Program) imagery (https://gis.apfo.usda.gov/arcgis/rest/services) for the years 2012, 2014, 2016 and 2018.

2.5. Tree ages

At the Wah Wah site, increment cores were collected on 19 May 2021 from the five small-diameter Great Basin bristlecone pines that had been attacked by bark beetles and were dead at the time of coring. These trees contained live bark beetle larvae in 2017 and four of the trees had been caged to identify the attacking species. At Telescope Peak we collected increment cores from the stems of 18 recently dead Great Basin bristlecone pines on 12 June 2021. These trees were different than those sampled for bark beetle identification and reproductive capacity, and were located off the Telescope Peak trail at three elevations (3236 m, 3180 m, 3140 m) (Supplemental Fig. 2). The two groups at the highest elevation were on the east aspect of Telescope Peak and the lower elevation group was on the west aspect. At both sites, we used standard dendrochronological methods (Holmes, 1999), Cook and Kairukstis, 1990), and cores were extracted at 0.5 m height. In the lab, cores were mounted on grooved wood molding, sanded, and the rings were counted under a dissecting scope. Presence of blue stain caused by bark beetle fungal mutualists (e.g., MPB mutualists *Grosmannia clavigera* and *Ophiostoma montium*) (Bleiker and Six, 2014) was recorded for each core. In cases where the pith was not reached, and/or rot occurred on the inner stem, the number of mature rings was estimated from the mean number of rings/cm beyond the first 5 cm from cores containing the pith (Norton et al., 1987, Duncan 1989). The mean number of rings in the first 5 cm of juvenile/young-tree growth was similarly estimated and added to the mature tree age to obtain final ages for cores without pith.

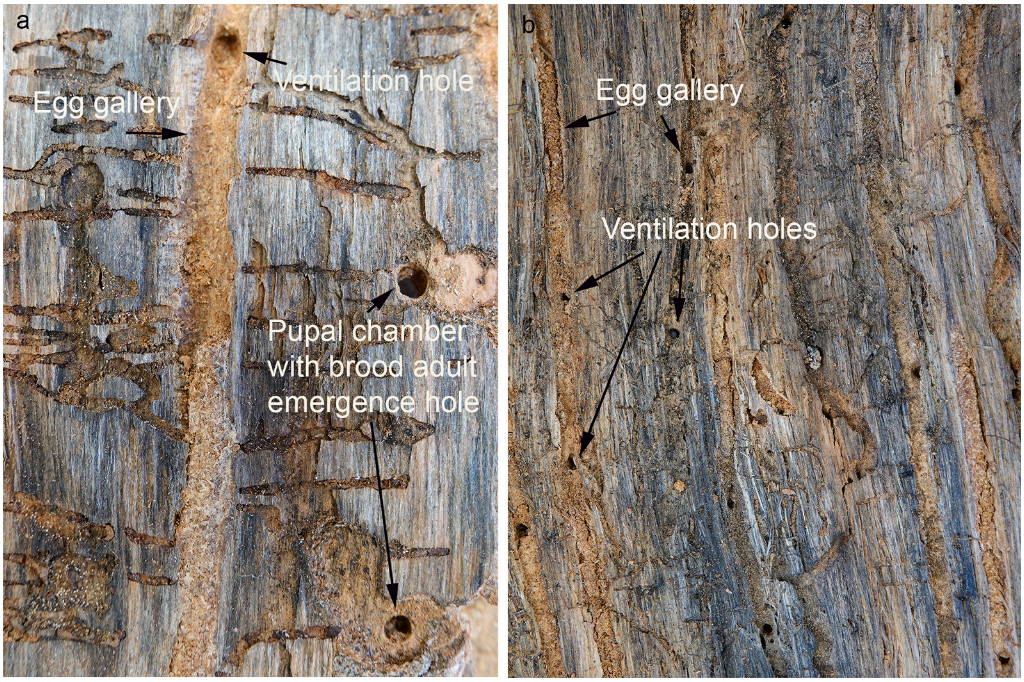

Fig. 2. Mountain pine beetle egg galleries with ventilation holes, larval mining, and pupal chambers with brood adult emergence holes: a) a sample with successful brood adult emergence and b) a sample with no brood adult emergence. Photo credits B. Bentz.

2.6. Climate data

Climate variables were calculated using 30-yr normals (1981–2010) and annual monthly gridded PRISM climate data at 800 m resolution (PRISM Climate Group). Climatic water deficit (CWD), a metric of water stress experienced by plants (Stephenson 1990), was modeled using a Thornthwaite water balance model (Lutz et al., 2010). CWD is a measure of evaporative demand that exceeds available water and is computed as potential evapotranspiration (PET) minus actual evapotranspiration (AET). CWD ranges from zero, when soils are fully saturated, to positive values with no upper limit. Higher values indicate soils depleted of water and water increasingly unavailable to meet transpiration demand. CWD, PET, and AET were calculated using monthly average temperature and summed precipitation, latitude, folded aspect, slope, soil available water storage, and modeled hydrological processes including snow and rain accumulation and snow water storage. Soil available water storage for each site, representing the amount of water that the soil can store in the top 1 m, was acquired from the USDA soil survey gridded SSURGO database (Natural Resources Conservation Service 2013). All values were calculated on a monthly interval using R (R Core Development Team) and equations found in Lutz et al. (2010) and Redmond (2019) using either the 30-yr normals or annual monthly data. CWD, AET and precipitation were summed by month and annually, and temperature metrics were averaged annually.

Climate variables based on the 800 m 30-yr normals were calculated for Great Basin bristlecone pine habitats across the range of the species, including the Telescope Peak and Wah Wah Mountains (Fig. 1). We also highlight two additional sites with recently observed Great Basin bristlecone pine mortality, the Silver Peak Range and Rawhide Mountain within the Hot Creek Range (Millar et al., 2019), although the presence of bark beetles at these sites has not been confirmed. This allowed us to evaluate if sites with recent observed Great Basin bristlecone pine mortality were among the warmest and driest sites within the species range. Annual climate variables were calculated for the Telescope Peak and Wah Wah sites, where bark beetle attacks were observed, using annual monthly gridded 800 m data. Trends in annual precipitation, mean annual temperature, CWD and AET between 1981 and 2020 were estimated using **loess** smoothing, and linear regression (function **lm**) (R Core Development Team) was used to highlight trends during 2010 to 2020, the decade when bark beetle attacks were observed at both sites.

3. Results

3.1. Wah Wah Mountains, UT

In October 2017, bark removal from three singleleaf pinyon pines at the lowest elevation showed that the trees were attacked and killed by a combination of MPB and pinyon ips. In the higher elevation stand one ponderosa pine was currently under attack by western pine beetle (*D. brevicomis* LeConte). Western pine beetle has distinct winding egg galleries, in contrast to vertical egg galleries made by MPB, and the species also differ in that late stage western pine beetle larvae move to the outer bark for the remainder of their development. Just downslope from this tree, bark removal showed that a single ponderosa pine had been killed by MPB, and foliage color and needle retention suggested the attack occurred in 2016. Based on a previous fire history study, this MPB-killed tree was estimated to be the oldest ponderosa pine in the western US (941 years) (Heyerdahl et al., 2011). These observations suggest that both MPB and western pine beetle were active in the stand during 2016 and 2017, but only pinyon ips successfully attacked the Great Basin bristlecone pine. Two large Great Basin bristlecone pines with fire scars had signs of recent MPB egg galleries, but no pupal chambers or emergence holes were observed, suggesting no MPB brood survival in these Great Basin bristlecone pines.

Bark beetle adults successfully attacking the five smaller diameter Great Basin bristlecone pine in the stand were identified as pinyon ips. The egg galleries of pinyon ips are straight and often with a slight J shape, very similar to MPB egg galleries, but the adult beetles are morphologically distinct (Wood 1982). Moreover, unlike MPB, pinyon ips is polygamous and multiple vertical egg galleries can extend from a single mating chamber. Brood adults collected in emergence cages attached to four bark beetle-attacked Great Basin bristlecone pines confirmed that pinyon ips had attacked and reproduced in these trees. We also found adult *Pityokteines ornatus* Swaine in the emergence cage collections. Neither species has previously been reported to attack Great Basin bristlecone pine. Although some pinyon ips adults were found in each of the seven emergence cages attached to four Great Basin bristlecone pine stems, only 22 total pinyon ips adults emerged into the seven cages. Although not a direct comparison, hundreds of MPB adults emerged into two similar size cages on a single tree, including a singleleaf pinyon pine (Bentz et al. 2014), suggesting very low pinyon ips brood production in Great Basin bristlecone pine. Age of the pinyon ips-infested Great Basin bristlecone pine ranged from 144 to 217 yrs, averaging 194 yrs, and DBH ranged from 18 to 35 cm, averaging 27.4 cm (Table 1). Although it is unclear if pinyon ips is associated with a blue-staining fungi, we did not observe blue stain in any of the cores (Table 1). In May 2021, we observed a single small diameter Great Basin bristlecone pine in the stand that was infested by pinyon ips.

3.2. Panamint Range, Telescope Peak, CA

Similar to our findings in the Wah Wah Mountains, galleries beneath the outer bark confirmed that MPB had attacked and killed singleleaf pinyon pine at the lowest elevations on Telescope Peak. At the higher elevations, live MPB larvae were found in Great Basin bristlecone pines and limber pines in September 2019, suggesting that at least some trees had been attacked earlier that year. Sampling of both species was conducted in October 2020, following completion of brood development. At that time, sampled trees of both species were estimated to have been attacked between 2017 and 2019. Based on NAIP imagery of a slope to the east of Telescope Peak, we estimate the trend in recent tree mortality began in 2013 (Supplemental Fig. 2).

In September 2019, our observations from currently attacked trees suggested that many larval galleries in Great Basin bristlecone pine ended with dead early instar larvae (Supplemental Fig. 3). In October 2020, using brood adult emergence holes as an indicator of MPB brood success, we confirmed extensive larval mortality in Great Basin bristlecone pine. The number of bark holes classified as brood adult emergence was significantly less in Great Basin bristlecone pine samples than limber pine ($F_{1,53} = 29.54$, $p < 0.0001$) (Fig. 3). Moreover, only eight of the 22 sampled Great Basin bristlecone pines (36%) showed signs of brood adult emergence, whereas eight of the nine sampled limber pine (89%) had brood adult emergence. This result highlights a significant lack of brood development to the adult stage in Great Basin bristlecone pine. No consistent trend in brood adult emergence by tree bole aspect or DBH was found for either tree species. Total egg gallery length within the sample areas was greater in limber pine (mean = 72.267 ± 45.85, N = 13) than Great Basin bristlecone pine (mean = 51.211 ± 30.85, N = 42), and the difference was marginally significant ($F_{1,52.06} = 3.72$, $p = 0.0578$). Total egg gallery length was a good predictor of brood adult emergence in limber pine ($F_{1,11} = 20.01$, $P = 0.0009$), but not Great Basin bristlecone pine ($F_{1,40} = 0.48$, $p = 0.4943$) (Fig. 3). Overall, Great Basin bristlecone pine (mean DBH = 35.21 ± 15 cm) that we sampled were larger than sampled limber pine (mean DBH = 23.31 ± 10.34 cm) ($F_{1,52.04} = 6.40$, $P = 0.0145$).

Table 1
Age and diameter (DBH) of recent (i.e., within 3 years) dead Great Basin bristlecone pine at the Panamint Range Telescope Peak and Wah Wah Mountains sites. Also shown are the cores of dead trees with evidence of blue-staining in the sapwood caused by bark beetle fungal associates.

Site-tree number	Blue stain	DBH (cm)	Estimated tree age
Telescope-1	Y	46	225
Telescope-2	Y	69	630
Telescope-3	N	36	798
Telescope-4	N	81	864
Telescope-5	Y	76	690
Telescope-6	Y	89	1015
Telescope-7	Y	157	1612
Telescope-8	N	89	1044
Telescope-9	N	56	275
Telescope-10	Y	56	485
Telescope-11	Y	89	438
Telescope-12	N	89	846
Telescope-13	N	64	462
Telescope-14	Y	41	370
Telescope-15	Y	91	918
Telescope-16	Y	69	294
Telescope-17	Y	76	810
Telescope-18	Y	89	788
Wah Wah-1	N	35	205
Wah Wah-2	N	28	209
Wah Wah-3	N	28	194
Wah Wah-4	N	27	217
Wah Wah-5	N	18	144

Based on the core samples extracted from 18 recently killed Great Basin bristlecone pine, ages ranged from 225 yrs to 1612 yrs with a mean of 698 yrs (Table 1). Mean DBH for the cored trees was 75.6 cm, ranging from 41 cm to 157 cm. Evidence of blue staining MPB fungal associates was found in the sapwood of 67% of the cored trees.

Unidentified woodborer larvae and adults of *Pityophthorus confertus* Swaine were found in dead Great Basin bristlecone pine, including trees with no signs of MPB, suggesting they also contributed to tree death. *Pityopthorus confertus* and other *Pityopthorus* species infest multiple *Pinus* species in the western US, including other high-elevation pine species (Wood, 1982), although Great Basin bristlecone pine is a new host record. In October 2020, no new attacked trees of either species were observed in the stands, as could be observed from the Telescope Peak trail.

3.3. Climate

Modeled mean annual temperature across the decades 1981 to 2010 for field-verified Great Basin bristlecone pine habitats (Fig. 1) ranged from slightly below 0 °C to slightly above 8 °C, and cumulative annual precipitation was between ∼ 300 and 900 mm (Fig. 4). Sites with recently observed Great Basin bristlecone mortality due in part to bark beetles, that is, Wah Wah and Telescope Peak, were not the warmest or driest habitats across the Great Basin bristlecone pine range, nor with the highest CWD. Two areas where mortality has been observed but the role of bark beetles has not been confirmed, Rawhide Mountain and Silver Peak, were among the sites with the lowest annual precipitation (Fig. 1). Annual data describing climate and plant water stress metrics (CWD and AET) at the Telescope Peak and Wah Wah sites show increasing trends since 1981 in mean annual temperature and CWD with associated declines in precipitation and AET (Fig. 5). Recent bark beetle attacks were estimated to have occurred between 2013 and 2020 at Telescope Peak and between 2016 and 2020 at the Wah Wah site. When only the last decade (i.e., 2010 to 2020) is considered, linear trends in each variable reveal substantial warming and declining precipitation at both sites, coinciding with the time period of bark beetle-caused mortality.

4. Discussion

Great Basin bristlecone pine is the longest-lived non-clonal organism globally and a foundational species in high-elevation forests of the western US Great Basin where documented mortality events are historically rare. Although found within the range of MPB, a dominant mortality agent of pines across western North America, Great Basin bristlecone pine is attacked less by MPB than co-occurring pine species (Bentz et al., 2017, Eidson et al., 2017). Moreover, very few MPB larvae survived to an adult when reared in Great Basin bristlecone pine phloem in the laboratory (Eidson et al., 2018). These results provided hope that this iconic and important tree species may have evolved traits that repel and provide resistance against bark beetles. We report for the first time unexpected Great Basin bristlecone pine mortality that was associated with two bark beetle species. The story is complicated, however, and our findings suggest that Great Basin bristlecone pine does have traits that

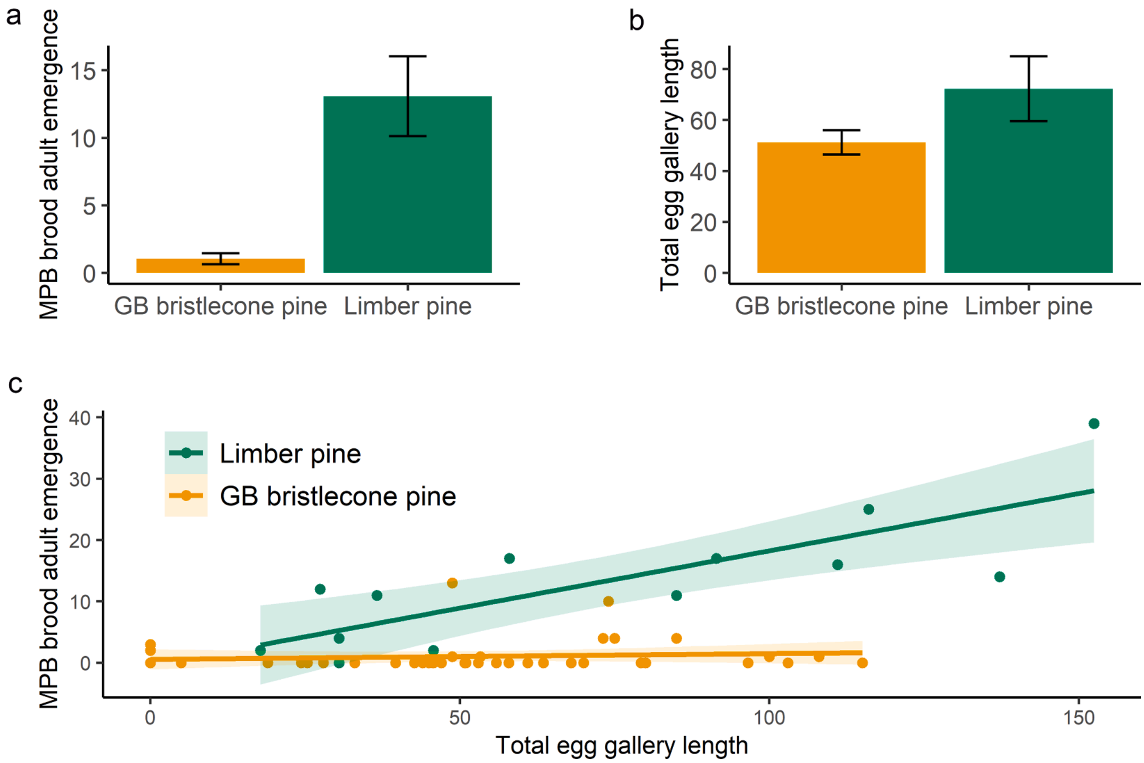

Fig. 3. Mountain pine beetle (MPB) a) brood adult emergence, based on emergence holes that connect to pupal chambers, b) total egg gallery length in Great Basin (GB) bristlecone pine and limber pine, and c) the relationship between egg gallery length and adult emergence in the two species. Data is from bark samples taken on 9 MPB-attacked limber pines and 22 Great Basin bristlecone pines at the Telescope Peak site.

may protect it from extensive bark beetle-caused mortality in locations where it is the solitary or primary pine species. Our findings also suggest that bark beetle-caused Great Basin bristlecone pine mortality likely occurs when it is intermixed with pines that are known hosts to bark beetles, and that hotter droughts likely play a role.

At the Wah Wah site, MPB and western pine beetle were active in the Great Basin bristlecone pine stand, although they were only found attacking and successfully reproducing in ponderosa pine. Surprisingly, pinyon ips was the only species that attacked and successfully reproduced in Great Basin bristlecone pine, although brood production was very low. Great Basin bristlecone pine is a new host tree record for pinyon ips, a species that is typically found attacking stressed pinyon pine and was responsible for large swaths of dead pinyon pines during a 2000–2004 drought in the southwest US (Kleinman et al., 2012). Singleleaf pinyon pines that were infested by pinyon ips at a lower elevation were the likely source for ips adults attacking the relatively young Great Basin bristlecone pine at the higher elevation. Although MPB was also found attacking singleleaf pinyon pine at lower elevations, we only found MPB attacking and successfully reproducing in one ponderosa pine at the upper elevation stand that included Great Basin bristlecone pine. Ponderosa pine is a common host for both MPB and western pine beetle, but not for pinyon ips (Wood, 1982). These results confirm our previous surveys suggesting that the likelihood of MPB attacks on Great Basin bristlecone pine is low when more susceptible pine hosts are available in large enough numbers. Our observations at Telescope Peak, however, suggest there is a threshold MPB population size above which spillover to Great Basin bristlecone pine may occur, particularly during hotter droughts.

At the Telescope Peak site, Great Basin bristlecone pine intermixes with limber pine and although vegetation maps are not available, the occurrence of both species appears extensive (Fig. 1). This differs from the Wah Wah site where limber pine is not found. The Wah Wah site also has a greater diversity of conifer species, including Douglas fir (*Pseudotsugae menziesii* (Mirbel) Franco) and white fir (*Abies concolor* (Gordon) Lindley) (Kitchen, 2012). Great Basin bristlecone pine attacked by bark beetles at the Telescope Peak site were also older and larger than those attacked by pinyon ips at the Wah Wah site. Large numbers of 2018 and 2019 MPB-attacked limber pine were found at multiple elevations along the slopes of Telescope Peak, in addition to MPB-attacked pinyon pine at lower elevations. We also observed MPB-attacked Great Basin bristlecone pines at elevations where limber and Great Basin bristlecone pine co-occurred. <50% of the sampled Great Basin bristlecone pine showed any sign of MPB brood adult emergence, however, and of these the mean number of adult emergence holes was 5.5 holes per sample area per tree. In contrast, 89% of sampled limber showed signs of adult MPB emergence and the average number of holes per sample area was 21.3, four times that of Great Basin bristlecone pine. Moreover, the total length of parent gallery did not differ between the two species yet was only a significant predictor of adult emergence holes in limber pine. These results support a previous laboratory study that showed MPB oviposition and egg hatch were similar between Great Basin bristlecone pine and limber pine, but that larval death occurred prior to pupation within Great Basin bristlecone, resulting in < 1 offspring per parent adult compared to > 30 offspring per adult in limber (Eidson et al., 2018). MPB was likely a major contributor to death of the Great Basin bristlecone pine at Telescope Peak. However, because a high proportion of MPB in Great Basin bristlecone pine died prior to becoming an adult, MPB that pupated in and emerged from limber pines were the likely source of MPB infesting Great Basin bristlecone pine. Great Basin bristlecone pine indeed appears to be a population sink for MPB, relative to co-occurring pine host species.

Despite more than a century of research on bark beetles and tree defense, detailed knowledge of the mechanisms of tree death due to bark beetles is limited. Excavation of vertical egg galleries following attack, however, are considered not sufficient to kill a tree (Krokene, 2015). The likely proximate cause of tree death is a combination of horizontal larval mining and fungal inoculation that eventually starves the roots, reduces photosynthate, and disrupts water transport (Paine et al., 1997). At the

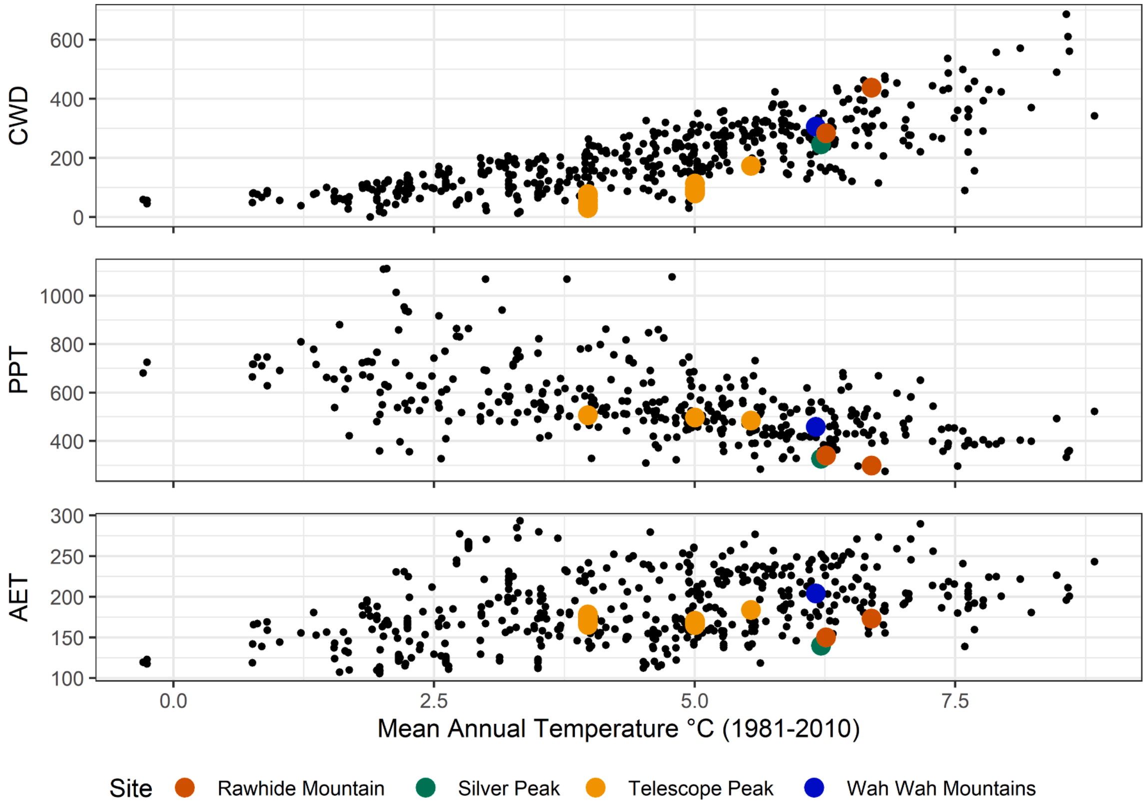

Fig. 4. Biplots showing the bio-climatic niche space of Great Basin bristlecone pine in terms of mean annual temperature and annual cumulative climatic water deficit (CWD), cumulative annual precipitation (PPT), and actual evapotranspiration (AET). Climate data based on PRISM 800 m 1981–2010 normals. Shown within the bio-climatic niche space are the relative positions of trees at the Telescope Peak and Wah Wah Mountains sites where bark beetle-induced mortality was observed, and Silver Peak and Rawhide Mountain (see Fig. 1) where recent Great Basin bristlecone pine mortality was observed, although the role of bark beetles has not been confirmed.

Telescope Peak site we observed larval mining in samples taken from Great Basin bristlecone pine, and estimated that larval death occurred in the second or third of four larval instars (Supplemental Fig. 3), similar to findings in a previous laboratory study (Eidson et al., 2018). Even though few MPB survived to the adult stage, early larval mining was apparently sufficient to cause tree death. In addition to providing nutrients to developing beetle brood (Bleiker and Six, 2014)), fungal associates also contribute to tree death by colonizing and killing tree tissue beyond the areas of beetle mechanical damage. Although blue-staining caused by some fungal symbionts is a characteristic sign of bark beetle attack, tree death likely occurs prior to staining and occlusion of the sapwood by the fungi (Paine et al., 1997). We found no blue stain in the tree cores taken from pinyon ips-infested Great Basin bristlecone pine at the Wah Wah site; the role of blue staining fungal associates in this bark beetle species is unclear. At Telescope Peak, only 67% of the cored, dead trees showed signs of blue stain due to MPB fungal associates. This could indicate that not all cored and dead trees were attacked by MPB, or that fungal growth into the sapwood of MPB attacked trees was minimal due to larval death in an early stage. One promising observation at the Telescope Peak site was the large number of Great Basin bristlecone pine attacked by MPB that retained some proportion of green needles, especially near their bases (Supp Fig. 4). Further surveys will be required to ascertain if mortality eventually occurs, but this observation is encouraging and highlights how the strip-bark or sectored architecture (Schauer et al., 2001) of bristlecone pines may be one of several traits that provide protection from extensive bark beetle-caused mortality.

Pines have evolved numerous morphological and resin chemical traits for defense against bark beetles (Franceschi et al., 2005). Their shared history has been described as an *evolutionary arms race* (Feeny, 1975) as some bark beetle species, including MPB, have evolved the capacity to circumvent host resin defenses for use in locating suitable hosts and attracting conspecifics to overwhelm host defenses (Raffa et al., 2008). Great Basin bristlecone has constitutive (i.e., always present) resin compounds and concentrations that can be up to eight times greater than co-occurring limber pines, in addition to denser sapwood and heartwood and higher relative area and density of resin ducts (Bentz et al., 2017). These defensive traits are hypothesized to protect pines from bark beetle attack (Ferrenberg et al., 2014, Hood et al., 2015, Kichas et al., 2020) and in Great Basin bristlecone pine may play a role in killing larval offspring (Eidson et al., 2018). Considering the antiquity of the MPB and high-elevation pine relationship, Great Basin bristlecone pine may be in an evolutionary period where it is winning the *evolutionary arms race* with bark beetles, although recent climate anomalies may be disrupting this balance.

Extreme drought and excessively warm temperatures that are known to influence bark beetle dynamics (Bentz et al., 2014, Buotte et al., 2017) and predispose pines to bark beetle attack (Kolb et al., 2019, Koontz et al., 2021) are occurring globally. Although Great Basin bristlecone pine was thought to be more resilient to drought, recent observed increases in growing degree days with no associated increase in precipitation is causing temperature-amplified drought stress (Bunn et al., 2018). At the Wah Wah and Telescope Peak sites the years just preceding and during tree attack by bark beetles (2010 to 2020) had increasing mean annual temperature, directly benefiting bark beetle population success, and decreasing annual precipitation, directly stressing trees and reducing capacity for defense. Metrics of plant water stress that incorporate topographic and edaphic factors with local temperature and moisture, AET and CWD, confirm that trees at both sites were the most stressed in 2020 relative to any time during the past 40 years. These climate factors in association with large numbers of MPB brood that

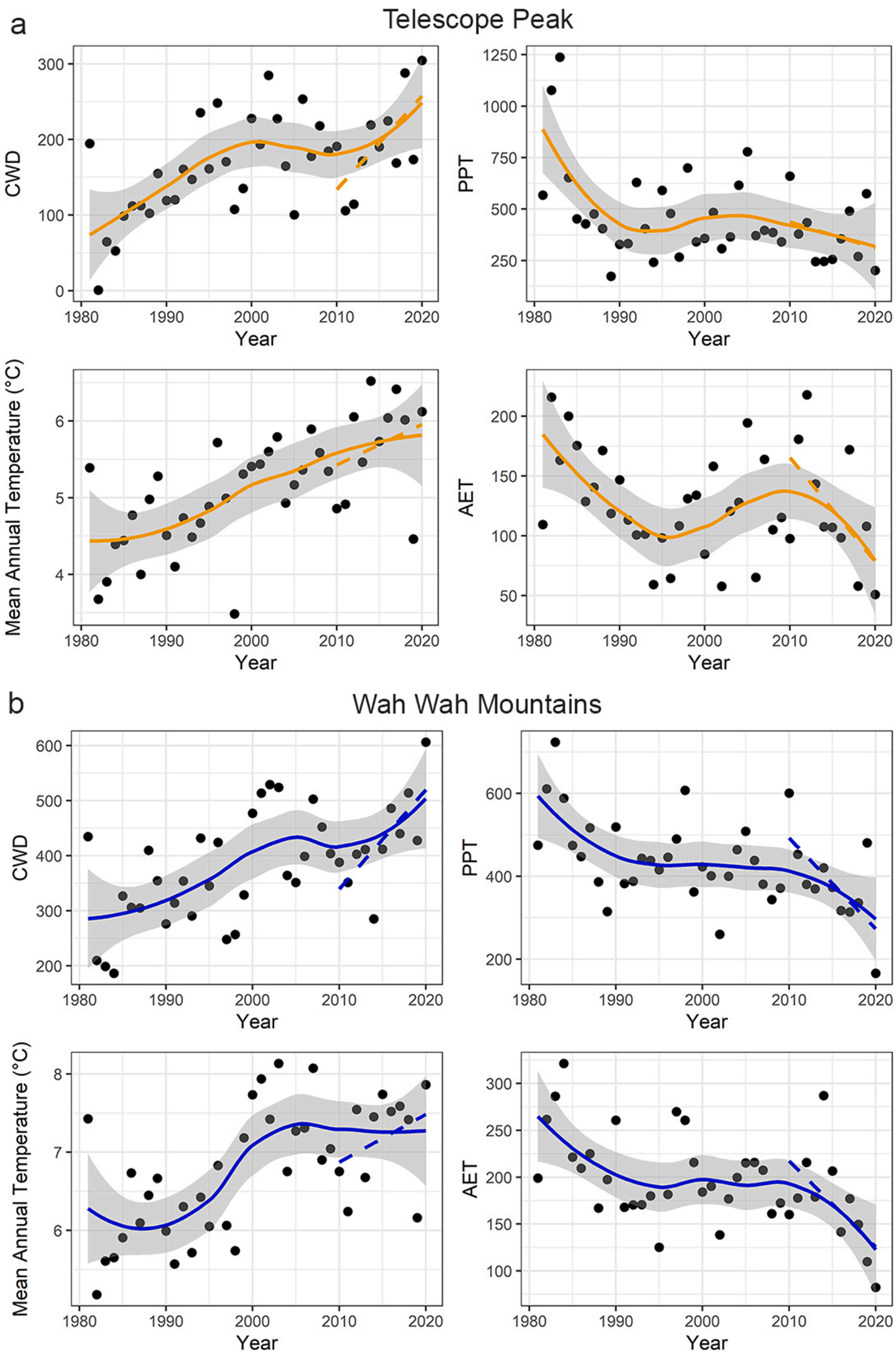

Fig. 5. Climate time series for Great Basin bristlecone pine locations with recent observed mortality at (a) Telescope Peak in Death Valley National Park, California and (b) the Wah Wah Mountains. Annual cumulative climatic water deficit (CWD), annual cumulative precipitation (PPT), mean annual temperature, and actual evapotranspiration (AET) were modeled using PRISM 800 m monthly annuals. Solid line based on loess smoothing between 1981 and 2020 and dashed line is a linear regression across years between 2010 and 2020.

emerged from nearby limber pine at the Telescope Peak site, and pinyon ips at the Wah Wah site, likely contributed to mortality of Great Basin bristlecone pine that ranged in age from 144 to 1612 years. Although Great Basin bristlecone pine has been considered an icon of stability in periods of change, evolved traits that allow it to resist bark beetle-caused mortality may be disrupted by the rapidly changing climate, potentially altering their long-term shared co-evolutionary path (Hamann et al., 2020).

The occurrence of significant bark-beetle mortality on Great Basin bristlecone pines, particularly in the Panamint Range, alerts the scientific and resource management communities to possible continuing effects at those stands, the potential for outbreaks in other populations, and opportunities for management action. The high probability for continued warming and more severe droughts in the western US forecast increasing opportunity for bark beetle population outbreaks at high elevations. At the Wah Wah and Telescope Peak sites, intermix of Great Basin bristlecone pine with susceptible host species puts bristlecone pine at risk of future mortality events. Recent mortality that we observed in the Great Basin bristlecone pine population in the relatively hot, dry Silver Peak Range, although not confirmed from bark beetles, might also experience greater mortality in the future putting this small, relict stand at risk of decline or extirpation. Investigating this mortality is particularly important because singleleaf pinyon pine is present, and as observed at the Wah Wah site, could be a source for pinyon ips that we now know attacks and can kill Great Basin bristlecone pine.

Other Great Basin bristlecone pine populations at climate margins and of potential future risk for bark beetle population outbreaks include the scientifically and culturally significant populations in the White Mountains of California. In addition to the Silver Peak Range, we have observed recent mortality in limber, pinyon, and Great Basin bristlecone pines at Rawhide Mountain, a low elevation site at the southern end of the Hot Creek Range, NV (Millar et al., 2019). This small Great Basin bristlecone pine stand is disjunct from others in the Hot Creek Range and elsewhere and has among the lowest annual precipitation across Great Basin bristlecone pine habitats (Fig. 4). This stand is at risk of decline if a bark beetle outbreak in limber and pinyon pines overwhelmed the Great Basin bristlecone pines there.

These documented recent events prompt coordinated monitoring action throughout the range of Great Basin bristlecone pine, and particularly for small, marginal, and/or valued populations. The millennial-old ages of trees attacked at Telescope Peak warn that the even older trees in the White Mountains and elsewhere, such as Great Basin National Park, could be at risk. As the sole population of Great Basin bristlecone pine in Death Valley National Park, in addition to monitoring, park managers could take actions to protect the population using semiochemical treatments (Seybold et al., 2018) and treatments to reduce loss from wildfire. Rapid suppression of wildfire below or in the stands could help to protect remaining live trees, not only on slopes currently unaffected, but live trees that remain within the severely impacted stands. Park managers could also help to educate the public through interpretive signs and on websites. At these and other valued locations of Great Basin bristlecone pine, especially the ancient stands in the White Mountains, CA, and Great Basin National Park, NV, concerted efforts to collect and archive seed in a conservation bank would provide added protection for the genetically distinct germplasm of Great Basin bristlecone pine. In the most urgent situation to protect a tree or stand (e.g., the Methuselah tree and/or the Methuselah Grove of ancient trees), a highly aggressive defensive strategy would be to manually remove nearby pines that are known hosts to MPB.

5. Conclusion

Recently observed Great Basin bristlecone pine mortality at two sites was likely due to a combination of warming temperatures, declining precipitation, reduced tree defenses, and bark beetle attacks that originated from brood production on co-occurring pine species. Supporting previous studies, Great Basin bristlecone pine appears to be a population sink for MPB. Pinyon ips that likely developed on lower elevation singleleaf pinyon pine was also found attacking Great Basin bristlecone pine, and similar to MPB, brood production was low. Trends in multiple climate variables highlight increasing plant stress at both sites over the previous 40 years, particularly the last decade. We anticipated these sites would be at the climatic extremes of Great Basin bristlecone pine habitats, particularly given that Telescope Peak is at the southern range edge of the species. Based on 30-year climate normals, Telescope Peak and the Wah Wah site are not at the temperature or precipitation extremes of the species habitats. The Silver Peak and Rawhide Mountain sites, however, where recent mortality has been observed but bark beetles have not been confirmed, are among the driest habitats. Due to the isolated nature of Great Basin bristlecone pine stands and historically rare mortality events, mortality across the range of the species is currently unknown. Surveys across the range of Great Basin bristlecone pine are needed to quantify tree mortality, associated stand conditions, climate metrics, and the spatial nature of intermixing of other pine species with Great Basin bristlecone pine at landscape scales. Only then can we fully examine biotic and abiotic factors that are emerging threats to this species in a changing climate.

Our findings highlight two factors that may be used for prioritizing future research and risk monitoring. First, bark beetle populations appear not to be self-sustaining in Great Basin bristlecone pine, and extensive beetle-caused mortality will most likely occur where large stands of pines that are known bark beetle hosts are in the vicinity. Second, habitats undergoing climate-mediated water stress and high temperatures may be more likely to experience tree death, particularly when bark beetle populations are nearby. The possibility of beetle spillover from associated pines to Great Basin bristlecone pine, with resulting mortality, serves as motivation for heightened resource management. Monitoring for bark beetles in areas where susceptible pines mix with Great Basin bristlecone pine, especially in warm, dry edge-of-range sites, should be done annually to provide advance notice of possible attacks on Great Basin bristlecone pine. Further, protecting highly valued as well as already affected populations, such as the Wah Wah Mountains and Telescope Peak stands, from wildfire would help to ensure that remaining live trees in these stands survive and conserve the genetic heritage of these isolated populations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120099.

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