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Rocky Mountain bristlecone pine (*Pinus aristata*) is a confirmed host to mountain pine beetle (*Dendroctonus ponderosae*)

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Abstract.—Mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) is a native bark beetle that reproduces in pine (*Pinus*) species across western North America. High population levels can result in widespread host tree mortality. Over the past 2 decades, MPB has been responsible for pine mortality across millions of forested hectares in the western United States. Although a majority of the pine species found in the western United States are considered hosts to MPB, the host status of Rocky Mountain (RM) bristlecone pine (*Pinus aristata*) is unclear. We surveyed stands across the range of RM bristlecone pine in Colorado, USA, and quantified MPB-caused mortality within the past 10 years in stands where RM bristlecone and at least one other pine species co-occurred. We also evaluated in the field whether successful MPB brood production occurred in RM bristlecone pine. Our results confirm that RM bristlecone pine is susceptible to MPB attack and suitable for MPB reproduction. In mixed-species stands, pine species availability influenced MPB attack occurrence. The proportion of trees experiencing fatal beetle attack within a particular *Pinus* species was best predicted by the basal area proportion of that species in the stand prior to the most recent 10 years of mortality. These results indicate that RM bristlecone pine is vulnerable to ongoing climate change–induced contact with MPB.

Resumen.—El escarabajo del pino de montaña (*Dendroctonus ponderosae* Hopkins) es un escarabajo nativo de la corteza que se reproduce en especies de pino (*Pinus*) en el oeste de América del Norte. Los altos niveles de población pueden resultar en una mortalidad generalizada de árboles hospederos. Durante las últimas 2 décadas, el escarabajo del pino de montaña fue responsable de la mortalidad de pinos en millones de hectáreas boscosas en el oeste de los Estados Unidos. Aunque la mayoría de las especies de pino que se encuentran en el oeste de los Estados Unidos se consideran hospederos del escarabajo, el estado de huésped del pino Bristlecone (*Pinus aristata*) de las Montañas Rocosas no está muy claro. Encuestamos rodales en todo el rango de pino Bristlecone de las Montañas Rocosas en Colorado, Estados Unidos, y cuantificamos la mortalidad causada por el escarabajo de pino en los últimos 10 años en rodales donde coexistieron con el pino Bristlecone y al menos otra especie de pino. También evaluamos en el campo si se produjo una producción exitosa de reproductores de escarabajo de pino de montaña en el pino Bristlecone de las Montañas Rocosas. Nuestros resultados confirman que el pino Bristlecone es susceptible al ataque de los escarabajos y adecuado para su reproducción. En rodales de especies mixtas, la disponibilidad de una especie de pino influyó en la ocurrencia del ataque de escarabajos de pino. La proporción de árboles que experimentaron un ataque mortal de escarabajos dentro de una especie particular de *Pinus* se predijo mejor por la proporción de área basal de esa especie en el rodal antes de los 10 años más recientes de mortalidad. Estos resultados indican que el pino Bristlecone de las Montañas Rocosas es vulnerable al contacto continúo inducido por el cambio climático con el escarabajo del pino de montaña.

Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins; Coleoptera: Curculionidae, Scolytinae) is a native bark beetle that reproduces in the phloem layer of multiple pine (*Pinus*) species across western North America. At endemic population levels, MPB is found infesting suppressed or weakened pines that are co-colonized by other Scolytine beetles (Smith et al. 2011). Given appropriate exogenous stress events (e.g., drought, pathogens) that increase the availability of host trees with low vigor, MPB populations can build and transition to attacking and killing host trees of greater vigor and therefore greater phloem resources (Carroll et al. 2006, Boone et al. 2011). Favorable weather for MPB

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BJB orcid.org/0000-0002-2741-1542

development and survival (Logan and Bentz 1999) and ample host trees of sufficient size (Amman and Cole 1983) can then combine to create a population outbreak, resulting in high percentages of pine mortality across a landscape. In the past few decades, millions of forested hectares in the western United States (U.S.) were killed by this insect (Hicke et al. 2016) during periods of warming winters (Weed et al. 2015) and summers (Bentz et al. 2014), including at higher elevations (Cleaver et al. 2015, Buotte et al. 2016), where thermal conditions for MPB population success have historically fluctuated (Perkins and Swetnam 1996, Bentz et al. 2011). These patterns suggest a potential for future increased climate change–induced contact between MPB and pines at upper elevations.

Of the 21 pine species found in the western United States, about one half are recorded as hosts to MPB, including several species that can grow at higher elevations: whitebark pine (*P. albicaulis* Engelm.), lodgepole pine (*P. contorta* Douglas), limber pine (*P. flexilis* E. James), foxtail pine (*P. balfouriana* Balf.), and southwestern white pine (*P. strobiformis* Engelm.). Wood (1982) and Furniss and Carolin (1977) are considered the most accurate references for observed bark beetle–tree host records. Notably missing from Wood's (1982) list of host trees for MBP are 2 pine species that grow at higher elevations, Great Basin (GB) bristlecone (*P. longaeva* D.K. Bailey) and Rocky Mountain (RM) bristlecone (*P. aristata* Englem.). Furniss and Carolin (1977) list RM bristlecone, but not GB bristlecone pine, as MPB host trees. Recent surveys found only rare MPB attacks on GB bristlecone pine in stands with extensive MPB-infested limber pine (Bentz et al. 2017). Moreover, in no-choice field experiments, MPB bored into limber pine more than it did into GB bristlecone pine (Eidson et al. 2017). Attempts to rear MPB in GB bristlecone pine in the laboratory resulted in below-replacement-level reproduction, whereas brood production in limber pine averaged >30 surviving brood adults per parent female (Eidson et al. 2018). Collectively, these results support the lack of historical records of MPB in GB bristlecone pine and suggest that GB bristlecone is a poor host for MPB, presumably due to high levels of constitutive defenses and volatiles that are unattractive to MPB (Gray et al. 2015, Bentz et al. 2017). However, the status of RM bristlecone pine as a host to MPB remains unclear. Gibson et al. (2008) report RM bristlecone pine mortality due to MPB based only on aerial insect detection surveys; no ground plots were included in cited reports. Klutsch et al. (2011) also mention infestation of RM bristlecone pine by MPB in stands with co-occurring limber pine, but they do not present further details or evidence.

Bristlecone pines (also known as foxtail pines), including GB bristlecone, foxtail, and RM bristlecone, are among the longest-living tree species worldwide (https://en.wikipedia.org/wiki/List_of_oldest_trees; Lanner 2007). They are keystone components of the forests that they inhabit and are of high value to forestland managers, scientists, and the public. Given the ambiguity in written records of the MPB host status of RM bristlecone pine and the apparent lack of MPB preference for its 2 close relatives (GB bristlecone and foxtail), we hypothesized that RM bristlecone pine would be less vulnerable to MPB than co-occurring pines are. Our primary objective was to evaluate the vulnerability of RM bristlecone pine to MPB attack. Specifically, we quantified MPB-caused mortality within the past 10 years in stands where RM bristlecone and at least one other pine species co-occurred, and we then evaluated whether MPB attacked and successfully reproduced in RM bristlecone pine.

METHODS

Potential field survey locations were identified from several key sources. Sources included U.S. Forest Service Forest Inventory and Analysis (FIA) data (USDA Forest Service 2017a); vegetation maps from the *Tree Species Atlas* (Ellenwood et al. 2015) and *Atlas of United States Trees* (Little 1971); and data provided by Dr. Anna Schoettle (personal communication), who maintains a network of permanent plots in high-elevation pine type throughout the Colorado Rocky Mountain Range. We targeted locations with known RM bristlecone pine and at least one other pine species (*P. flexilis*, *P. ponderosa* P. & C. Lawson, *P. contorta*). Using ArcGIS, we overlaid Insect and Disease Survey data (USDA Forest Service 2017b) to identify areas with MPB-caused mortality mapped between 2006 and

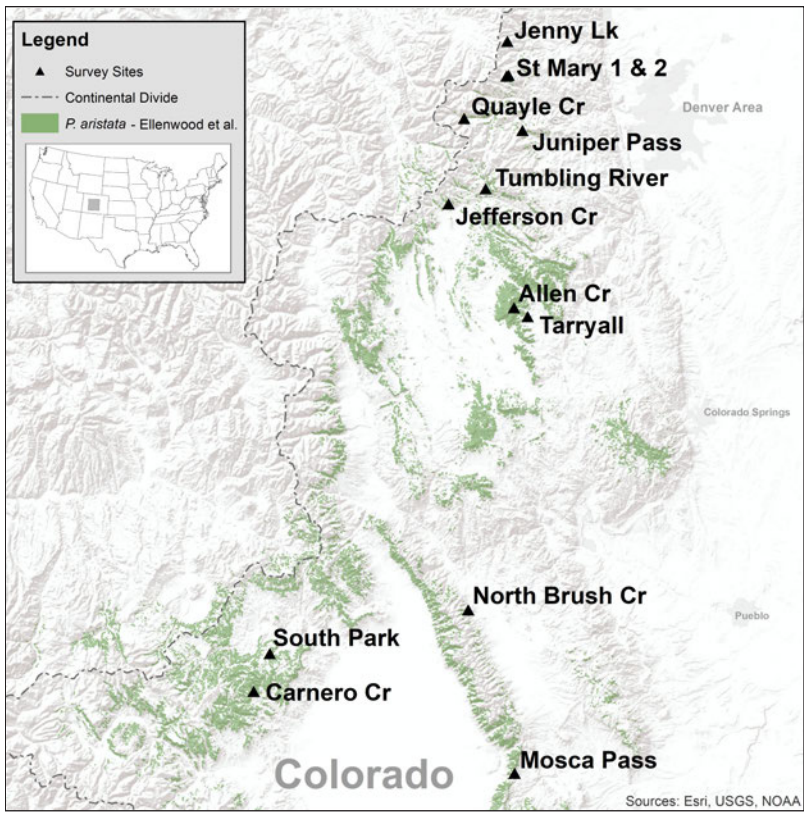

Fig. 1. Locations of 2017 surveys of mixed pine stands with recent mountain pine beetle–caused mortality. All sites were located east of the Continental Divide. Also shown is an estimate of the Rocky Mountain bristlecone pine (*Pinus aristata*) distribution in Colorado, USA, based on Ellenwood et al. (2015). See Table 1 for site information.

2016. To maximize the number of locations sampled, we targeted locations within 3 miles of road access. Potential survey areas were identified throughout the Colorado portion of the RM bristlecone distribution (i.e., mostly on the east side of the Continental Divide, from Cameron Pass in the north to the San Juan and Sangre de Cristo mountains in the south; Fig. 1). The distribution of RM bristlecone extends into northern New Mexico, with an additional isolated population near Flagstaff, Arizona. However, MPB activity has not been recorded in either of these RM bristlecone pine populations.

During the 2017 summer, potential survey locations were visited and evaluated for the presence of RM bristlecone pine and at least one other pine species, in addition to the occurrence of recent MPB-caused mortality (i.e., within 10 years). Thirteen sites met these criteria (Fig. 1), and they were sampled using fixed-radius plots (Table 1). Bentz et al. (2017) used a double sampling scheme of fixed-radius plots to characterize stand conditions and 100% interplot surveys to greatly increase the sampled area of potential MPB-infested GB bristlecone pine. For this study, we discovered that MPB-infested RM bristlecone pine trees are considerably more common than MPB-infested GB bristlecone pines. Rather than a double sampling scheme, we used contiguous 405-m^2 fixed-radius plots extending linearly along a randomly chosen azimuth for as far as MPB-infested pine continued within the location. Live trees of all species were measured for DBH (diameter at breast height; 7.5-cm minimum). Pines were examined for status (live, MPB-killed, or other mortality) and for signs of dwarf mistletoe (*Arceuthobium* spp.) and white pine blister rust caused by the pathogen *Cronartium ribicola* J.C. Fisch. MPB-killed trees were confirmed by the presence of egg galleries typical for MPB (i.e., relatively straight vertical galleries from 30 to 90 cm long

Table 1. Survey site information.

Site	Number of fixed plots	Latitude	Longitude	Elevation (m)
Allen Cr	4	39.1368	−105.566	3013
Carnero Cr	4	37.9314	−106.462	2882
Jefferson Cr	5	39.4345	−105.846	3215
Jenny Lk	4	39.9334	−105.659	3343
Juniper Pass	8	39.6698	−105.578	3345
Mosca Pass	16	37.7412	−105.454	3087
North Brush Cr	9	38.2223	−105.668	3073
Quayle Cr	6	39.6935	−105.807	3045
South Park	11	38.0484	−106.411	2944
St Mary-1	13	39.8294	−105.653	3424
St Mary-2	11	39.8323	−105.645	3285
Tarryall	6	39.1131	−105.512	2870
Tumbling River	7	39.4875	−105.706	3021

Table 2. Stand conditions and metrics of mountain pine beetle (MPB)–killed pines at each survey site (non-pines were a minor component). BA = basal area, DBH = diameter at breast height.

Site	Species	% of total pine	Sum MPB trees	BA live pre-outbreak (m^2/ha)	BA MPB-killed (m^2/ha)	DBH live pre-outbreak (cm)	DBH MPB-killed (cm)
Allen Cr	*P. aristata*	72.4	2	19.05	0.94	21.1	25.0
	P. flexilis	27.6	0	9.84	—	23.9	—
Carnero Cr	*P. aristata*	90.9	2	10.50	1.62	24.0	33.5
	P. contorta	6.1	0	0.32	—	17.9	—
	P. ponderosa	3.0	0	0.38	—	27.9	—
Jefferson Cr	*P. aristata*	81.9	37	21.43	11.67	20.9	27.9
	P. contorta	18.1	11	11.38	5.86	33.0	35.4
Jenny Lk	*P. aristata*	4.0	0	1.25	—	18.9	—
	P. flexilis	96.0	31	28.68	7.54	18.8	21.7
Juniper Pass	*P. aristata*	35.7	1	6.01	0.37	22.5	28.7
	P. contorta	9.8	0	3.45	—	34.0	—
	P. flexilis	54.5	22	20.23	9.05	34.8	39.3
Mosca Pass	*P. aristata*	59.9	24	12.97	3.60	22.8	32.5
	P. flexilis	36.9	10	17.74	2.10	31.6	39.1
	P. ponderosa	3.2	3	1.79	0.94	35.1	47.2
North Brush Cr	*P. aristata*	10.5	0	1.58	—	20.4	—
	P. contorta	32.3	5	5.37	1.04	21.8	30.1
	P. flexilis	50.4	26	11.82	5.96	25.7	30.7
	P. ponderosa	6.8	2	2.19	1.41	28.8	56.0
Quayle Cr	*P. aristata*	19.4	14	6.56	4.13	26.7	28.6
	P. contorta	80.6	17	15.09	3.54	18.3	24.2
South Park	*P. aristata*	88.9	10	10.16	2.34	19.6	34.4
	P. contorta	2.2	0	0.81	—	30.1	—
	P. ponderosa	8.9	3	2.55	1.16	31.7	46.5
St Mary-1	*P. aristata*	92.4	58	52.68	12.65	31.9	33.8
	P. flexilis	7.6	0	1.48	—	18.9	—
St Mary-2	*P. aristata*	48.3	21	12.45	4.62	22.5	32.3
	P. flexilis	51.7	62	34.45	24.79	35.9	45.3
Tarryall	*P. aristata*	70.7	12	10.35	2.65	23.2	25.5
	P. flexilis	24.0	1	4.99	1.07	25.8	57.2
	P. ponderosa	5.3	0	1.35	—	31.8	—
Tumbling River	*P. aristata*	42.7	0	11.23	—	27.0	—
	P. contorta	57.3	5	14.51	1.90	25.7	32.4

and with a short crook near the entrance hole; Fig. 2C). For pines attacked by MPB, year of attack can be reliably estimated up to 3 years postattack by using characters of foliage color and needle retention (Chojnacky et al. 2000). Needle and fine branch retention were used

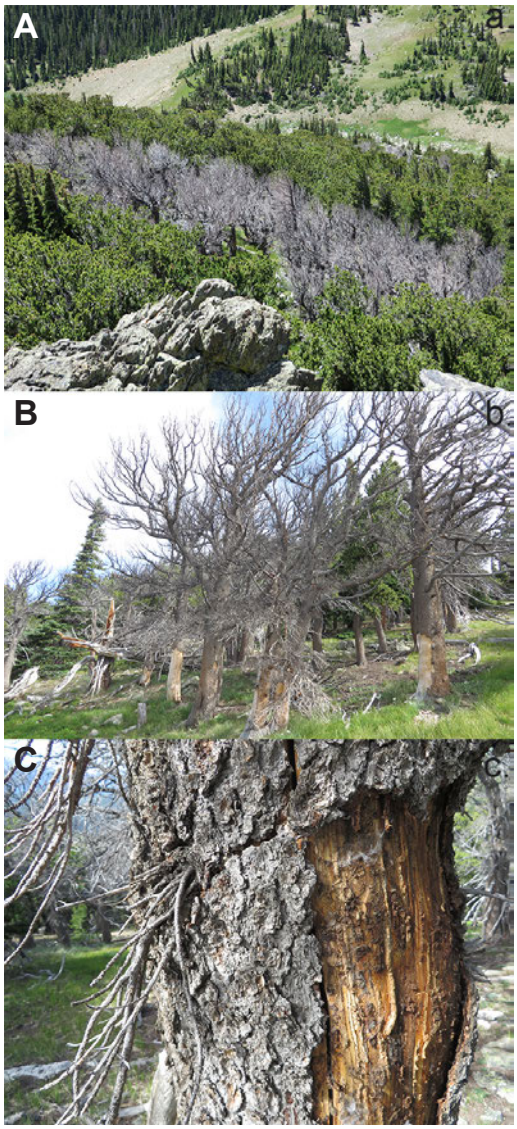

Fig. 2. ***A*** and ***B***, Rocky Mountain bristlecone pine mortality caused by mountain pine beetle at the St. Mary-1 site. ***C***, Mountain pine beetle galleries under the bark of Rocky Mountain bristlecone pine. Emergence holes on trees were confirmed to be associated with mountain pine beetle pupal chambers. Photos were taken in 2017 by E.M. Hansen.

to estimate that observed tree mortality was not more than 10 years before our surveys. For this analysis, we pooled all trees estimated to have been attacked and killed between 2006 and 2016, given that all tree mortality occurred during one beetle outbreak period. Each plot location was georeferenced.

Basal area (BA; m^2/ha) was calculated for live pines and for pines killed by MPB at each site. Live and MPB-killed pines were summed by species to describe total live pines prior to the most recent 10 years of MPB-caused mortality (i.e., pre-outbreak) at the site. General linear mixed models (GLIMMIX, SAS v9) were used to test whether the BA of a particular species at a site pre-outbreak, the total pine BA at a site pre-outbreak, and the mean DBH of pines pre-outbreak influenced the number of trees (by species) that were killed by MPB at a specific site. A beta error distribution was used, with site included as a random factor.

RESULTS AND DISCUSSION

Surveyed stands contained a mix of pine species, with RM bristlecone pine constituting 4% to 92% of all pines at each site (Table 2). No signs of white pine blister rust or dwarf mistletoe were observed on RM bristlecone pine within our plots. Based on galleries beneath the bark of dead trees, MPB was confirmed as the causal agent of death in all pine species surveyed (Fig. 2). Emergence holes leading to pupal chambers on attacked trees also confirmed that MPB reproduced successfully in RM bristlecone pine. Although we made no attempt to quantify MPB brood production, we found that RM bristlecone appears to be notably more vulnerable than its close relative GB bristlecone. We readily found exit holes originating from pupal chambers on RM bristlecone pine, whereas Bentz et al. (2017) found "no evidence of egg hatch, larval mining, pupal chambers or brood adult emergence" on 4 GB bristlecone pines with at least one MPB parent gallery. GB bristlecone pine was also found to be a poor host for MPB reproduction in the laboratory (Eidson et al. 2018). High levels and composition of terpene constitutive defenses in GB bristlecone and foxtail pines (relative to limber pine) were hypothesized to play a role in the trees' defense against MPB attack and reproduction (Bentz et al. 2017). However, other than a general survey of monoterpenes in western North American pines (Smith 2000), there is no published information on terpene defenses of RM bristlecone pine for comparison.

RM bristlecone pine habitat extends to upper montane and alpine tree line communi-

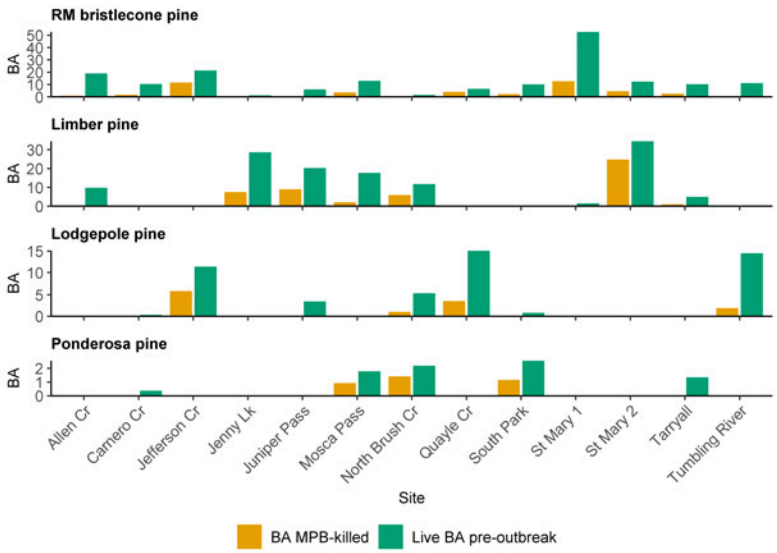

Fig. 3. Basal area (BA; m^2/ha) killed by mountain pine beetle (MPB) and live BA pre-outbreak for each species and survey site. See Table 1 and Fig. 1 for site information and number of plots at each site used in calculating BA. Note the differences in *y*-axis scales among species.

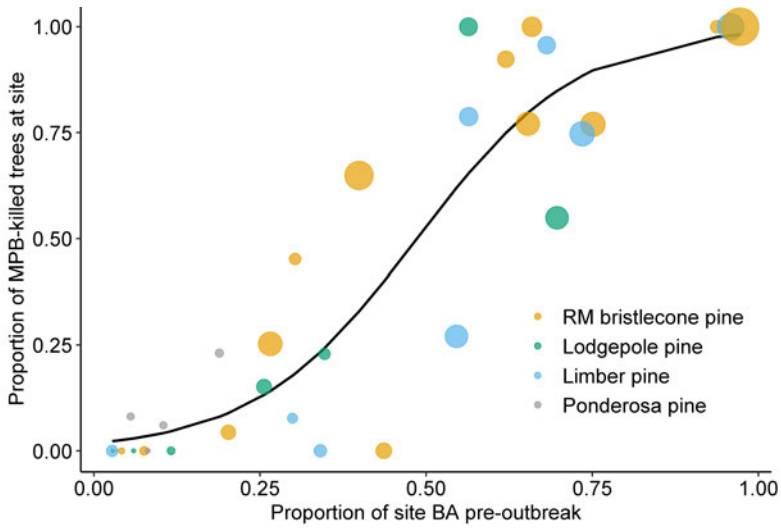

Fig. 4. The proportion of a pine species killed by mountain pine beetle (MPB) over a 10-year period (2006 to 2016) was best predicted by the proportion basal area (BA; m^2/ha) of that species in the stand pre-outbreak. Shown is the linear mixed model (SAS v 9.4, GLIMMIX) regression prediction (solid line) for all species. The size of a point is relative to the number of trees of that species at a site (see Table 1).

ties, but as found in our surveys, it also occurs at lower elevations intermixed with ponderosa pine (Bailey 1970; Tables 1, 2). The highest elevation site in our study, St. Mary-1, contained the greatest amount of RM bristlecone pine (92%), and it was also the site with the greatest amount of RM bristlecone pine BA that was killed by MPB. Although the St. Mary-2 site contained relatively equal amounts of RM bristlecone and limber pine, the greatest MPB-caused mortality at this site occurred in limber pine (Table 2, Fig. 3). Overall, the

proportion of each MPB-killed pine species at a site was correlated with host species availability. The proportion of a MPB-killed pine species over the 10-year period was best predicted by the proportion BA of that species in the stand pre-outbreak ($F_{1,15} = 41.64$, $P < 0.0001$) (Fig. 4). Site mean DBH ($P = 0.6265$), sum of pine BA ($P = 0.9909$), and species ($P = 0.3856$) were not significant in predicting BA killed by MPB.

We found that MPB attacks occurred most often on the predominant pine species in a stand. This finding is similar to attack patterns found in mixed stands of hosts with known vulnerability to MPB, including whitebark and lodgepole pine in Wyoming (Bentz et al. 2015) and lodgepole and ponderosa pine in Colorado (West et al. 2014). However, our results contrast with survey results from stands of mixed GB bristlecone and limber pine, and mixed foxtail and limber pine. MPB attacks in these surveys were extensive on limber pine, low on foxtail pine, and rare on GB bristlecone pine, regardless of the proportions of each species in the stand (Bentz et al. 2017). Ambiguity in the written records of MPB attacks on RM bristlecone pine could be due to a lack of historical surveys in this species, because of its low economic value. Given that we observed successful MPB attacks on RM bristlecone pine in our surveys, it is likely that MPB-attacked RM bristlecone pine historically occurred during periods of thermal suitability, similar to patterns found in whitebark pine (Perkins and Swetnam 1996). However, differing attack and host preference patterns among bristlecone species observed in this and recent studies (Bentz et al. 2017, Eidson et al. 2017) suggest potential differences among species within the bristlecone group in their vulnerability and suitability to MPB.

Our survey results confirm that RM bristlecone pine is susceptible to MPB attack and is also suitable for MBP reproduction, differing from its close relative GB bristlecone. As climate change increases the probability of MPB population success at upper elevations, data on defense compounds of RM bristlecone pine (relative to co-occurring pines) will provide critical information for further evaluating the fate of this pine. Understanding causal agents of tree mortality, particularly agents such as MPB with the capacity for widespread impacts, is important for gene conservation and protection of keystone species in upper tree line alpine communities.

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