Ecological Applications, 31(3), 2021, e02274
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Alpine treeline ecotones are potential refugia for a montane pine species threatened by bark beetle outbreaks

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Citation: Maher, C. T., C. I. Millar, D. L. R. Affleck, R. E. Keane, A. Sala, C. Tobalske, A. J. Larson, and C. R. Nelson. 2021. Alpine treeline ecotones are potential refugia for a montane pine species threatened by bark beetle outbreaks. Ecological Applications 31(3):e02274. 10.1002/eap.2274

Abstract. Warming-induced mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks have caused extensive mortality of whitebark pine (*Pinus albicaulis*; WBP) throughout the species' range. In the highest mountains where WBP occur, they cross alpine treeline ecotones (ATEs) where growth forms transition from trees to shrub-like krummholz, some of which survived recent MPB outbreaks. This observation motivated the hypothesis that ATEs are refugia for WBP because krummholz growth forms escape MPB attack and have the potential to produce viable seed. To test this hypothesis, we surveyed WBP mortality along transects from the ATE edge (locally highest krummholz WBP) downslope into the forest and, to distinguish if survival mechanisms are unique to ATEs, across other forest ecotones (OFEs) from the edge of WBP occurrence into the forest. We replicated this design at 10 randomly selected sites in the U.S. Northern Rocky Mountains. We also surveyed reproduction in a subset of ATE sites. Mortality was nearly absent in upper ATEs (mean ± SE percent dead across all sites of 0.03% ± 0.03% 0–100 m from the edge and 14.1% ± 1.7% 100–500 m from the edge) but was above 20% along OFEs (21.4 ± 5.2% 0–100 m and 32.4 ± 2.7% 100–500 m from the edge). We observed lower reproduction in upper ATEs (16 ± 9.9 cones/ha and 12.9 ± 5.3 viable seeds/cone 0–100 m from the edge) compared to forests below (317.1 ± 64.4 cones/ha and 32.5 ± 2.5 viable seeds/cone 100–500 m from the edge). Uniquely high WBP survival supports the hypothesis that ATEs serve as refugia because krummholz growth forms escape MPB attack. However, low reproduction suggests ATE refugia function over longer time periods. Beyond our WBP system, we propose that plant populations in marginal environments are candidate refugia if distinct phenotypes result in reduced disturbance impacts.

Key words: boundary; climate change refugia; edge; mountain pine beetle; Pinus albicaulis*; tree mortality; whitebark pine.*

Introduction

The identification of refugia for forest species and ecosystems vulnerable to direct and indirect effects of climate change is an important aspect of conservation planning (Keppel et al. 2012, Lawler et al. 2015, Morelli et al. 2016). Indeed, widespread tree mortality is occurring globally as forest ecosystems react to the impacts of climate change (van Mantgem et al. 2009, Allen et al. 2010, Millar and Stephenson 2015). However, common approaches for identifying refugia assume direct effects of climate change on tree species (e.g., thermal tolerances), rather than indirect effects of altered biotic interactions or disturbance regimes (Keppel et al. 2012, Michalak et al. 2020). One result of discounting indirect effects is that areas identified as climate change refugia may still leave species vulnerable to the negative effects of altered biotic interactions (as noted in marine ecosystems by Kavousi 2019). Because the proximate causes of recent tree mortality are often outbreaks of phytophagous insects, a biotic interaction altered by increasing drought stress and warmer temperatures (Anderegg et al. 2015; Stephens et al. 2018), a deeper understanding of tree population responses to these disturbances is crucial to successful identification of refugia.

Manuscript received 9 September 2020; accepted 5 October 2020. Corresponding Editor: Jill S. Baron.

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In western North America, recent outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB), triggered by warming, have caused widespread tree mortality (Raffa et al. 2013, Creeden et al. 2014). One species experiencing declines is whitebark pine (*Pinus albicaulis* Engelm.; WBP), a common, and often dominant, species forming alpine treelines throughout its range in western North America (Arno 1984). In fact, severe mortality in WBP (Macfarlane et al. 2013, Jules et al. 2016, Meyer et al. 2016) due to the combined effects of MPB outbreaks and white pine blister rust (WPBR; caused by the exotic fungus *Cronartium ribicola* J.C. Fisch. ex Rabenh) has led to the species being categorized as "warranting listing as an endangered species" in the United States. (USFWS 2011), listed as endangered in Canada (COSEWIC 2010), and on the IUCN Red List (Mahalovich and Stritch 2013). Because temperature directly affects MPB population and outbreak dynamics, high-elevation WBP forests have become more suitable for MPB as climates warm (Bentz et al. 1991, Logan and Powell 2001, Hicke et al. 2006). Increasing temperatures and recent MPB outbreaks have led to projections that the bioclimatic niche of WBP may shrink to less than 30% of its current extent in the Greater Yellowstone Ecosystem (GYE; Chang et al. 2014). However, much remains unknown about how WBP populations will respond to these impacts.

The upper elevation boundaries of WBP forests, alpine treeline ecotones (ATEs), typically contain shrub-like krummholz growth forms (Arno 1984). These ATEs are characterized by gradients from forests with tall trees, the timberline, to areas with dispersed short-stature trees, the treeline, sensu stricto, and finally to the tree species limit at the upper edge of the ecotone, the krummholz zone (Griggs 1946, Körner and Paulsen 2004). In WBP populations impacted by MPB outbreaks, these ATE habitats are hypothesized to serve as refugia: in their extensive aerial survey of MPB-caused WBP mortality in the GYE, Logan et al. (2010) and Macfarlane et al. (2013) observed that mortality gradients often corresponded with growth form gradients at treeline: live WBP krummholz in ATEs persisted above forests with extensive mortality. Macfarlane et al. (2013) hypothesized that "long-term survival of the species likely resides in the [krummholz] growth form found throughout the ecosystem near treeline, because it is too small for beetles to attack…" Thus far, however, no tree- or population-level studies have verified these observations nor tested the proposed mechanisms of this hypothesis, but survivors at treeline are visible in some locations (Fig. 1).

Refugia for WBP from MPB outbreaks is plausible in ATEs for two principal reasons. First, krummholz growth forms of WBP appear to be a phenotypic expression due to the harsh treeline environment: krummholz populations are not genetically distinct, as was previously speculated (Clausen 1965), from the tree populations below them (Rogers et al. 1999). Instead, the genetic structure of WBP populations in the ATE is consistent with the scatter-hoarding behavior of Clark's Nutcrackers (*Nucifraga columbiana* Wilson), the primary dispersal agent of WBP (Hutchins and Lanner 1982, Tomback 1982). Thus, krummholz or their offspring would likely grow as trees in a milder environment. Second, MPBs have long been known to prefer trees with diameters greater than 10–15 cm (Cole and Amman 1969). The small stems and contorted shapes of krummholz and other treeline growth forms may indeed underpin the mechanisms that could maintain WBP refugia from MPB in ATE habitats.

Despite the plausibility of the ATE refugia hypothesis, there are alternate mechanisms that could explain a pattern of low WBP mortality above the treeline. For instance, ATEs may share with other forest ecotones (OFEs) key attributes that affect MPB spread and impacts. Changes in structure near forest boundaries are known to modulate effects of herbivores (i.e., "edge effects"), the direction of the effect depending on behavioral patterns of the herbivore (Cadenasso and Pickett 2000). For example, interruption of pheromone signals by wind may occur to some degree at all forest boundaries: pheromone plumes are diluted by circulation (Thistle et al. 2004). Because the krummholz growth form is unique to ATEs, an examination of MPB impacts across OFEs should provide a first approximation of whether the mechanisms of survival are related to growth form or are due to more general edge effects discussed above.

Aside from understanding survival mechanisms in a potential refugium, the reproductive capacity of surviving individuals is needed to discern if a population is a "holdover" or a "stepping stone" (sensu Hannah et al. 2014), the latter permitting dispersal into new or previously occupied environments. Treeline growth forms of trees have generally been observed to have low reproductive output due to severe growing conditions (Tranquillini 1979, Körner 2012). Although these observations suggest that ATE populations of WBP may be population sinks, there is genetic evidence that reproduction and regeneration occur within these marginal habitats (Rogers et al. 1999). Additionally, seeds from ATEs may reach far away locations due to the long distance dispersal ability of Clark's Nutcrackers (Lorenz et al. 2011).

Lastly, the refugial status of ATE populations of WBP must be understood in the context of the status of survivors in the subalpine forests below ATEs. Forest trees that survived MPB attack are also likely to be important contributors to future populations. The MPB preference for larger diameter WBP (Perkins and Roberts 2003) should allow seedlings, saplings, and small trees to survive within attacked stands, though these survivors might be undetectable in aerial surveys. If small-diameter WBPs are abundant in MPB-attacked stands, these "prey size refugia" (a concept important in marine food webs; e.g., Baskett 2006) might allow for population

FIG. 1. Surviving whitebark pines near treeline (dark green band) with extensive mortality (gray trees) in the subalpine forest below. Tobacco Root Mountains, Montana, USA. Photo credit: C. T. Maher.

recovery between outbreaks apart from ATE refugia. A ground-based understanding of the patterns of WBP survivors of widespread MPB outbreaks is crucial, therefore, for predicting the future status of these ecologically important forests.

The importance of biotic interactions on the viability of climate change refugia has been noted in the literature but this aspect of refugia remains largely unexplored for tree species. Furthermore, an examination of the potential for refugia in marginal habitats, perhaps maintained by consequential changes in plant phenotype, carries important implications for how plant populations may resist altered biotic interactions or disturbances due to climate change. In this research, we identify possible refugia from climate change effects for a montane tree species with a focus on understanding the disturbance-related mechanisms and demographic attributes that generate and maintain the refugia. The specific goals of this research were to verify that WBP populations in the ATE did survive recent MPB outbreaks, to distinguish between plausible mechanisms of survival in the ATE, to assess the relative reproductive contributions in ATE, and to examine overall survival in post-MPB outbreak WBP forests in the U.S. Northern Rocky Mountains. Three questions guided our study. (1) Are mortality rates of WBP in upper ATEs lower than in subalpine forest interiors and how does this mortality gradient differ from OFEs? (2) What is the current reproductive output (number of cones and viable seed) of krummholz WBP in treeline habitats relative to subalpine forests? (3) What is the overall post-outbreak survival status of WBP populations in the U.S. Northern Rocky Mountains?

METHODS

Field site selection

Upper subalpine forests in the U.S. Northern Rocky Mountains typically consist of mixed-species stands of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt., lodgepole pine (*Pinus contorta* Dougl.), Englemann spruce (*Picea englemannii* Parry ex Engelm.), occasionally limber pine (*Pinus flexilis* James), and WBP, which often forms nearly monotypic stands at the highest elevations near treeline (Pfister et al. 1977, Arno and Hoff 1989). We used GIS layers of MPB-caused forest mortality, alpine vegetation type, and WBP occurrence to create a sampling frame of possible field site locations using ArcMap (ESRI 2010). Maps of MPB-caused mortality in the U.S. states of Idaho, Montana, and Wyoming were obtained from the USDA Forest Service's Forest Health Protection aerial Insect and Disease Surveys (IDS; Forest Health Protection 2014). IDS data tend to underestimate the magnitude of beetle-caused mortality because surveys are not flown everywhere in every year and surveys are biased toward recording only recent mortality (1–2 yr post-outbreak), as only trees with red needles are easily detected (Meddens et al. 2012, Macfarlane et al. 2013). We used a detailed 2008 aerial survey focused specifically on MPB-caused mortality of WBP in the Greater Yellowstone Ecosystem that addressed many limitations of IDS data in that region (Macfarlane et al. 2013). We then filtered all mortality data to include only polygons where MPB-caused mortality was observed in WBP and where these areas overlapped with or were adjacent to alpine vegetation recorded in USGS GAP land cover layers (U.S. Geological Survey Gap Analysis

Program [GAP] 2011). Additionally, we noticed gaps in IDS coverage within the range of WBP (range map from the Whitebark Pine Ecosystem Foundation 2014; Fig. 2a), but where MPB-caused mortality and treelines were apparent from stock ESRI World Imagery satellite photographs (ESRI 2015). These areas included parts of the Selway-Bitterroot, Anaconda-Pintler, and Scapegoat designated wilderness areas, and the Flint Creek Range, East Pioneer Mountains, and Highland Mountains in Montana. We included these areas in the sampling area by visually identifying the elevation of the upper edge (highest krummholz) of the ATE in ArcMap using satellite imagery and digital elevation models. We then defined contour lines that were ~200–300 m in elevation below these upper edges. All land area above these contours was added to the sampling area.

After potential sampling areas had been identified, we used stock ESRI World Imagery satellite photos to manually verify that the resulting polygons were in ATE habitats (high mountain areas with alpine vegetation and apparent growth form changes or forest density gradients typical of treeline), contained WBP (distinctive crown shape is visible), and contained evidence of recent MPB-caused mortality in the subalpine forests (red or grey standing trees). The final sampling frame was a ~7,480-km^2 map area shown as the collection of blue polygons in Fig. 2b.

We selected field sampling locations within the sampling frame by randomly placing 10 sampling points using the random point tool in ArcGIS (n = 10; Fig. 2b). WBP treeline sites in our study region are mainly located in remote settings. Our sample size was constrained to 10 because field sampling locations were determined independent of accessibility concerns to ensure an unbiased sample. We accessed field sites through a combination of unimproved 4x4 roads, ATV trails, and multiday backpacking trips. All sampling points landed within national forest lands administered by USDA Forest Service. Three of the 10 landed in federally designated wilderness areas. At each sampling point, we initiated two transects: one at the nearest ATE edge and one at the nearest OFE edge. We defined ecotone “edges” as the last WBP directly bordering the alpine or other non-forest vegetation; Fig. 2c). Thus ATE edges were the highest elevation “outpost” krummholz (i.e., the local WBP species limit, sensu Körner and Paulsen 2004) that was visible from satellite imagery. The area above the ATEs comprised alpine communities of low herbaceous vegetation, graminoids, and rock (typically talus or scree). We defined OFEs as WBP forest boundaries with non-forest openings that could be formed by avalanche paths, forest–meadow interfaces, geologic and topographic features, or other forest margins that are not associated with elevation-related boundaries. Non-forest areas beyond OFE edges were at least 150 m across and included montane shrublands, meadow communities, talus fields, etc. ATE transects were oriented downslope perpendicular to the contour to capture the elevational transition from krummholz into subalpine forest. OFE transects were oriented perpendicular to the WBP edge extending into the forest, regardless of the contour. All transects were 50 m wide and 500 m long (map distances). Transects were divided along their length into twenty contiguous 50 m by 25 m rectangular plots (the unit of analysis). After transects were positioned on the landscape, transect plot outlines were ported to a GPS device to guide sampling in the field.

Field sampling

Within each of the ATE and OFE transect plots (n = 20 plots each) at our 10 sites, we tallied WBP by status (live or dead) and by growth form (upright trees or krummholz plants). Trees were defined as any WBP stems that were at least 3 m tall (regardless of stem diameter). Fused stems were considered separate if their junction was below 1.4 m from the ground. Krummholz were defined as WBP with crowns that were 1 m or more across and at least as wide in any horizontal dimension as they were tall but were less than 3 m tall. Shorter upright stems and smaller krummholz were considered saplings or seedlings and were not counted in mortality surveys. We made this distinction to avoid assigning the krummholz growth form to young individuals that might become trees. We later used these classifications to calculate the proportion of tree-form WBP in each transect plot (number of WBP trees/(number of WBP trees + WBP krummholz)).

We recorded cause of death for all dead WBP that retained some bark; we assumed that krummholz and trees without bark died long before the most recent MPB outbreaks. MPB was determined as the cause of death by peeling away bark and identifying one or more of the following: j-shaped galleries, pitchout evidence, or frass (according to USDA Forest Service Common Stand Exam criteria; USDA Forest Service 2016). The cause of death in WBP that had evidence of both WPBR (swollen stems, rodent chewing, and excessive pitch bleeding) and MPB attack was assumed to be MPB: although WPBR infection may increase the likelihood of MPB attack in some cases (Bockino and Tinker 2012), the larvae of tree-killing beetles like MPB feed on living phloem; thus, a tree with signs of MPB attack was most likely killed by the attack, not by WPBR before the attack. Cause of death was recorded as “other” if MPB evidence was absent. Field sampling was completed in July–October 2015 and July–October 2016. We estimated pre-outbreak density of WBP as the sum of both live and dead individuals (krummholz and trees) in each transect plot. We were unable to sample three plots along the OFE transect at the Lemhi site because they were located on a cliff.

At the Gravelly site, we selected an additional, separate ATE transect (n = 1) to characterize changes in size distributions along an ATEs. This transect was constructed identically to the primary mortality transects.

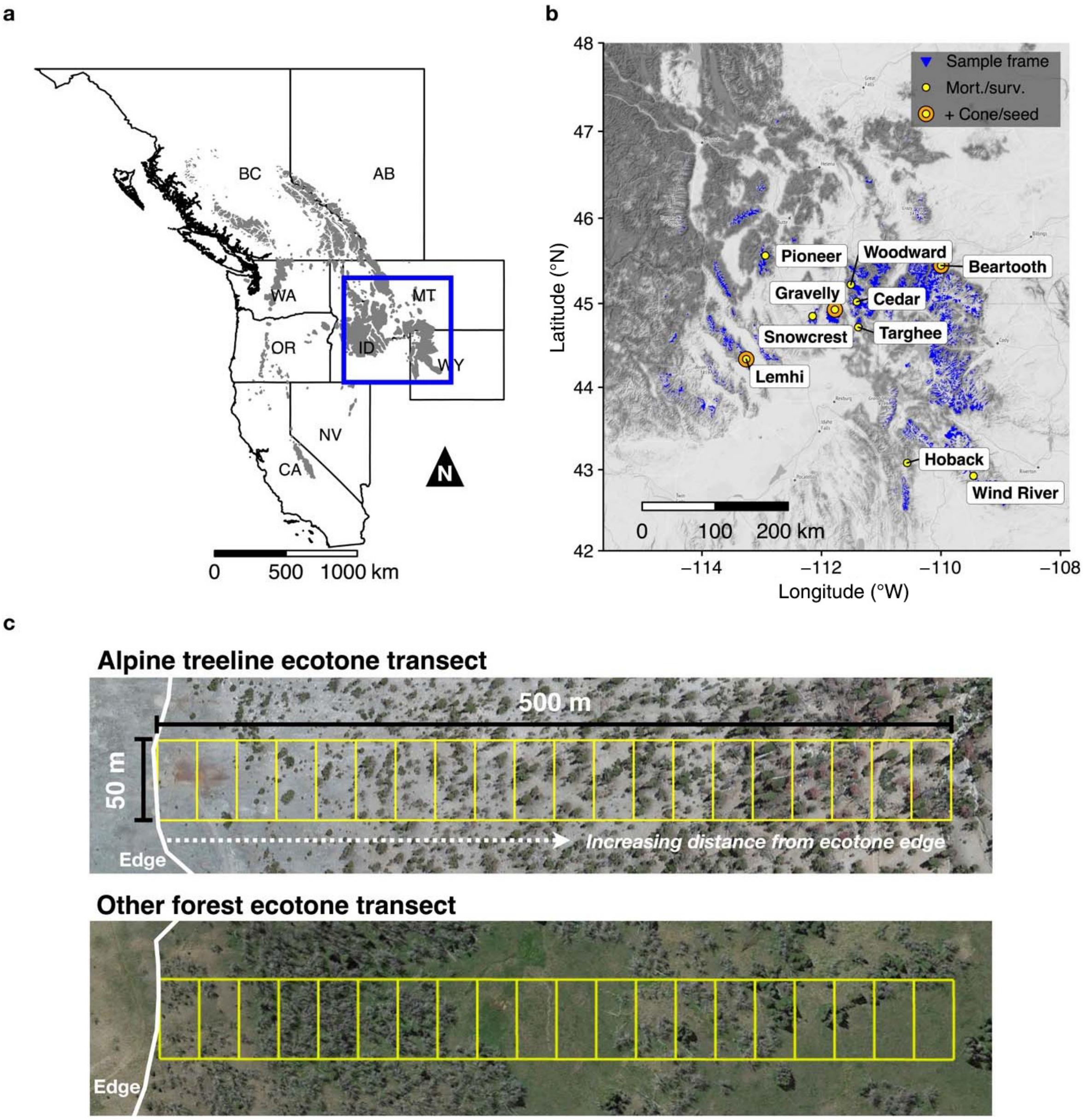

FIG. 2. (a) Location of the study area within western North America (blue rectangle, ~418,000-km^2 map area), and the range of whitebark pine (WBP; gray shading; range map from the Whitebark Pine Ecosystem Foundation 2014). (b) The U.S. Northern Rocky Mountains study area in detail (blue rectangle from (a). Blue polygons represent the sampling frame (~7,480-km^2 map area), areas where there is mountain pine beetle-killed WBP near alpine treeline ecotones (ATEs). Yellow circles are randomly selected mortality/survival survey field sites (n = 10). Orange circles represent sites where we also sampled cone and seed production along an ATE (n = 3). At each site, we surveyed the status of WBPs along one ATE and one other forest ecotone (OFE) to assess whether ATE habitats were refugia from mountain pine beetle outbreaks. Size distribution was measured along one ATE at the Gravelly site. (c) Satellite photos (Google Earth) of the Lemhi and Gravelly sites, illustrating sampling design and location of mortality/survival transects with respect to ATE edges and OFE edges, respectively. Heavy white lines represent the ecotone edges, the boundaries of WBP occurrence. Yellow grids represent transects, with 20 50 × 25 m rectangular plots representing increasing distance from the edge. Both ATE and OFE transects were oriented ± perpendicular to edges. ATE transects had downslope orientations. OFE transect orientation was independent of topography. OFEs were formed by meadows, talus slopes, avalanche paths, etc. All transects were 50 m wide by 500 m long (map distances).

We conducted a more intensive tally where we classified all WBP of all sizes by height (individuals < 3 m tall; i.e., saplings, seedlings, or krummholz) or diameter at breast height (dbh; >3 m tall; i.e., upright trees) classes as well as status (live or dead). We used a collapsible PVC pipe marked with measurement increments to classify WBP into six height classes (0–15, 16–46, 47–76, 77–107, 108–137, and 137–300 cm) and 11 dbh classes (10 cm classes from <10 to >100 cm). We later grouped smaller WBP (<3 m tall) into the <10 cm dbh size class.

We characterized the reproductive contributions of WBP populations along ATEs at a subset of three sites (Appendix S1: Table S1). To increase sampling density within these sites, we established one or two additional (peripheral to original mortality transects) ATE transects (all 50 × 500 m) by choosing the nearest treelines from the original sampling points (two or three cone count transects at each of three sites; $n = 7$ transects total). Transects were oriented downslope, using the methods described above, then divided into 10 50 × 50 m plots. In each plot of each transect, we counted the number of maturing (second year) seed cones visible from the ground on all cone-bearing WBP using binoculars. We also collected cones to estimate the percent viable seed for all cone-bearing WBP that were safe to climb or had cone-bearing branches that were accessible from the ground (1–7 cones per WBP). We caged maturing seed cones along four of the seven cone-count transects (all three sites represented; Appendix S1: Table S1) in July 2016 to protect them from seed predators and then collected the cones in September–October 2016. Not all transect plots containing cone-bearing WBP had trees that were safe to climb at each site, but all 50 × 50 m transect plots were represented with at least one cone-bearing WBP across all transects and sites. The number of cones collected varied both within and across sites. Viability of seeds from each cone was estimated using x-ray images (Berdeen et al. 2007). A seed was considered viable if an embryo was visible. X-rays were performed at the USDA Forest Service Nursery in Coeur d'Alene, Idaho.

Analyses

To answer our first question concerning differences in mortality rates along ATEs vs. OFEs and subalpine forest interiors, we constructed a negative binomial generalized linear model predicting the number of MPB-killed WBP in each transect plot (25 × 50 m) as a function of first- and second-order orthogonal polynomials of distance from ecotone edge (Fig. 2c; the centroid distance of each transect plot from the edge), ecotone type, and the interactions between each polynomial term with ecotone type (distance × ecotone type, distance^2 × ecotone type). The polynomial term was added to accommodate nonlinearities: in our exploratory data analysis, MPB-caused mortality appeared to have nonlinear or curvilinear relationships with distance from edge, but the relationships varied depending on ecotone type. Site was included as a random effect to account for between-site variability in MPB-caused mortality (e.g., due to differences in MPB attack pressure and pre-outbreak stand density). We specifically accounted for effects of variation in pre-outbreak WBP density on the number of MPB-killed pines by including the natural log of the total number of WBP (live + dead) as an offset term in our model. The data were not overdispersed relative to our model (Pearson's $\chi^2 = 0.89$). We then tested the null hypotheses that the number of MPB-killed WBP was equivalent for different values or levels of each predictor term in the model using a type-II Wald chi-square analysis of deviance test. Transect plots that contained no WBP trees or krummholz (live or dead) were removed from the data set (30 of 397 total transect plots across all 10 sites) prior to analyses to avoid the influence of these false zeros in the interpretation of effects.

To assess the reproductive contribution of WBP in upper ATE habitats relative to subalpine forests, we modeled the relationship between cone count in each large transect plot (50 × 50 m) and distance from edge with a negative binomial generalized linear mixed model, with site (Beartooth, Gravelly, or Lemhi) as a random effect. Distance was rescaled and centered for this analysis. We tested the null hypothesis that cone count was equivalent between distances using a type-II Wald Chi-square analysis of deviance test. Seed counts were too low in some transect plots across sites (i.e., some transect positions were represented at just one site due to inability to safely install cages on some WBP) to allow meaningful analysis of seed viability or density as a function of distance. We give a descriptive interpretation of these data instead. All analyses were performed in the R environment (R Core Team 2020).

To determine the overall post-outbreak survival status of WBP populations across all sites and transects, we tested for differences in density of post-outbreak living and MPB-killed WBP across whole transects (transects within sites as the unit of analysis) using nonparametric two-sample Wilcoxon signed rank tests with status (live vs. MPB-killed) as the grouping factor. We performed this test for all transects combined (ATE and OFE), for just ATE transects, and for just OFE transects to assess the effect of transect type on differences in density.

Data and analysis scripts for this study are available at Mendeley Data (see *Data Availability*).

RESULTS

MPB-killed WBP were almost non-existent in upper ATEs, with mortality becoming more common with increased distance from the edge (i.e., downslope into the subalpine forest; Fig. 3). Specifically, we observed only one krummholz at one site (overall mean ± SE of 0.03% ± 0.03% of stems across all sites) that had been killed by MPB within 100 m from ATE edges, and 14.1% ± 1.7% dead between 100 and 500 m. MPB-killed WBP also showed an increasing trend with distance from edge in OFEs. In contrast with ATEs, however, mortality in OFEs reached the ecotone edge and was higher overall than in ATEs: we observed 21.4% ± 5.2% MPB-killed within 100 m from OFE

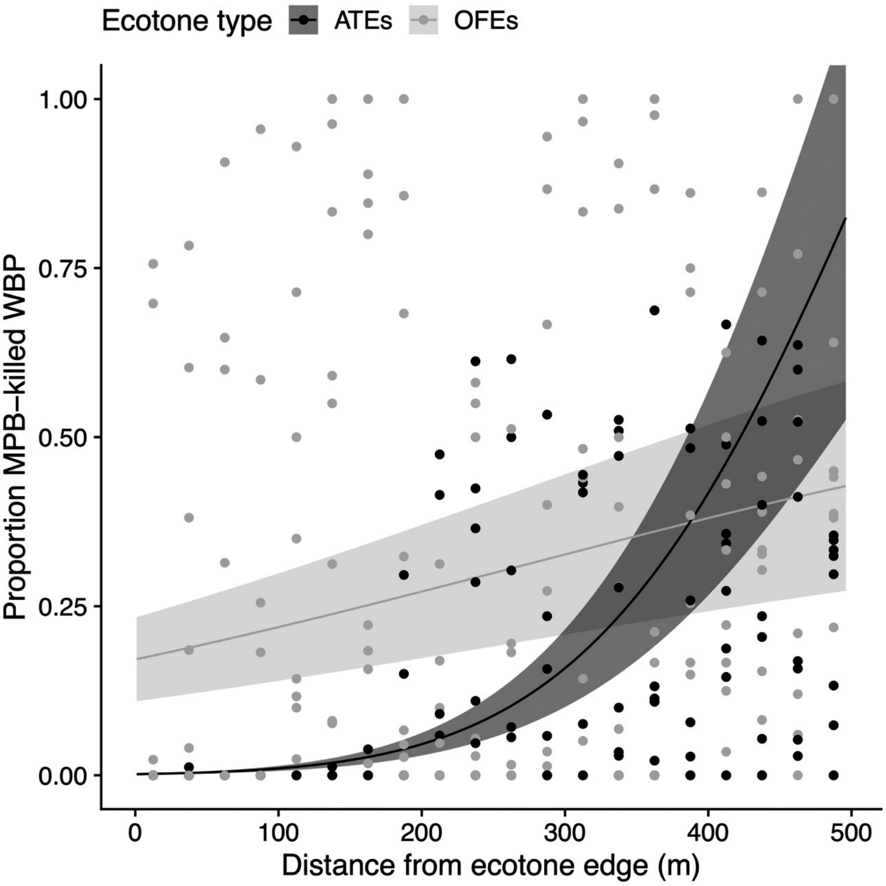

FIG. 3. Proportion of mountain pine beetle (MBP)-killed whitebark pine (WBP) along alpine treeline ecotones (ATEs; black points and line) and other forest ecotones (OFEs; gray points and line; $n = 10$ sites). Only WBP > 3 m tall (trees) and at least 1 m wide × 1 m tall (krummholz) were considered in this analysis. Smaller WBP were considered seedlings or saplings and were excluded. Lines are mean predicted counts of MPB-killed WBP from a negative binomial mixed model shown with 95% confidence intervals (reflecting variation in site-specific trends), divided by the median total WBP (live + dead) of all transect plots to reflect the results as a proportion. The model predicts the number of MPB-killed WBP in each transect plot as a function of first and second- order orthogonal polynomials of distance from ecotone edge, ecotone type, and the interactions between each polynomial term with ecotone type (distance × ecotone type, distance^2 × ecotone type). Site was included as a random effect and we added the log of total WBP as an offset term to control for differences in density among transect plots and sites. The data was not overdispersed relative to the negative binomial model (Pearson's $\chi^2 = 0.89$).

edges and 32.4% ± 2.7% between 100 and 500 m, although some sites had high mortality near OFE edges (75–100%; Fig. 3). These patterns were reflected by a significant interactive effect on total MPB-killed WBP between distance from edge and ecotone type ($\chi^2 = 45.5$, df = 2, $P < 0.0001$, Table 1).

The pattern in size distributions we observed along the additional Gravelly ATE transect mirrored that of our general findings: there was a clear pattern of increasing mortality with distance from the edge (Fig. 4). This mortality pattern was only apparent in WBP > 10 cm DBH, however, coinciding with a sharp increase in density of trees this size at ~200 m from the edge. Most of these trees >10 cm DBH were dead, and they represented the majority of the mortality. Most WBP ≤ 10 cm DBH were surviving throughout the ecotone, these included some small trees (>3 m tall) and seedlings/saplings of any size.

Upper ATE habitats had lower reproductive output than did the subalpine forests below them (in 2016; Fig. 5). The upper ATE typically had lower cone density (mean ± SE; within 100 m from ATE edge: 16.0 ± 9.9 cones/ha) than did lower elevations (100–500 m from ATE edge: 317.1 ± 64.4 cones/ha), although overall cone density varied greatly among sites (85–502 cones/ha). These findings were reflected in a highly significant effect of distance from edge on cone count ($\chi^2 = 29.1$, df = 1, $P < 0.0001$). The data were not overdispersed relative to our model (Pearson's $\chi^2 = 0.93$). Cone production per cone-bearing WBP varied greatly at all elevations. Although sample sizes were low at high elevations, we found no evidence that the

TABLE 1. Analysis of deviance table of predictors of the proportion of mountain-pine-beetle (MPB)-killed whitebark pine in transect plots from a polynomial negative binomial generalized linear model.

Predictor	χ^2	df	*P*
poly(dist,2)	49.2	2	<0.001
ecotone type	19.2	1	<0.001
poly(dist,2) × ecotone type	45.5	2	<0.001

Notes: Poly(dist,2) refers to first- and second-order orthogonal polynomial terms of distance from ecotone edge along transects. Ecotone type is the alpine treeline ecotone (ATE) or other forest ecotone (OFE). Site is the 10 field sampling sites (Fig. 2). The last term is an interaction term between distance and ecotone type.

number of cones per cone-bearing WBP were different than at lower elevations (within 100 m from ATE edge: 6.1 ± 2.1 cones/bearing WBP; 100–500 m from ATE edge: 8.4 ± 0.9 cone/bearing WBP). However, cones at high elevations contained fewer viable seeds than those at lower elevations (within 100 m from ATE edge: 12.9 ± 5.3 seeds/cone; 100–500 m from ATE edge: 32.5 ± 2.5 seeds/cone; Fig. 5).

We found an overall higher density of living (mean ± 1 SE; 286.3 ± 72.0 WBP/ha) versus MPB-killed (62.4 ± 16.4 WBP/ha) WBP on a whole-transect basis across our study region when including both ecotone types (two-sample Wilcoxon signed rank test, $P = 0.002$; Fig. 6). This overall effect was driven mainly by differences in live vs. MPB-killed density in ATEs (273.2 ± 73.2 vs. 40.4 ± 8.4 WBP/ha; $P = 0.002$); there was no significant difference in OFEs (299.4 ± 128.3 vs. 84.4 ± 31.0 WBP/ha; $P = 0.2$). Two sites, Beartooth and Pioneer, had much higher densities of living than dead WBP (both ecotone types combined; by 346.2 ± 89.0 and 1146.8 ± 241.6 WBP/ha, respectively). A repeat of the test with those sites removed from the data verified that the overall differences were still significant ($P = 0.02$; Table 2).

DISCUSSION

Identification of refugia and an understanding of the mechanisms that maintain them are important aspects of conservation in an era of rapid climate change (Millar

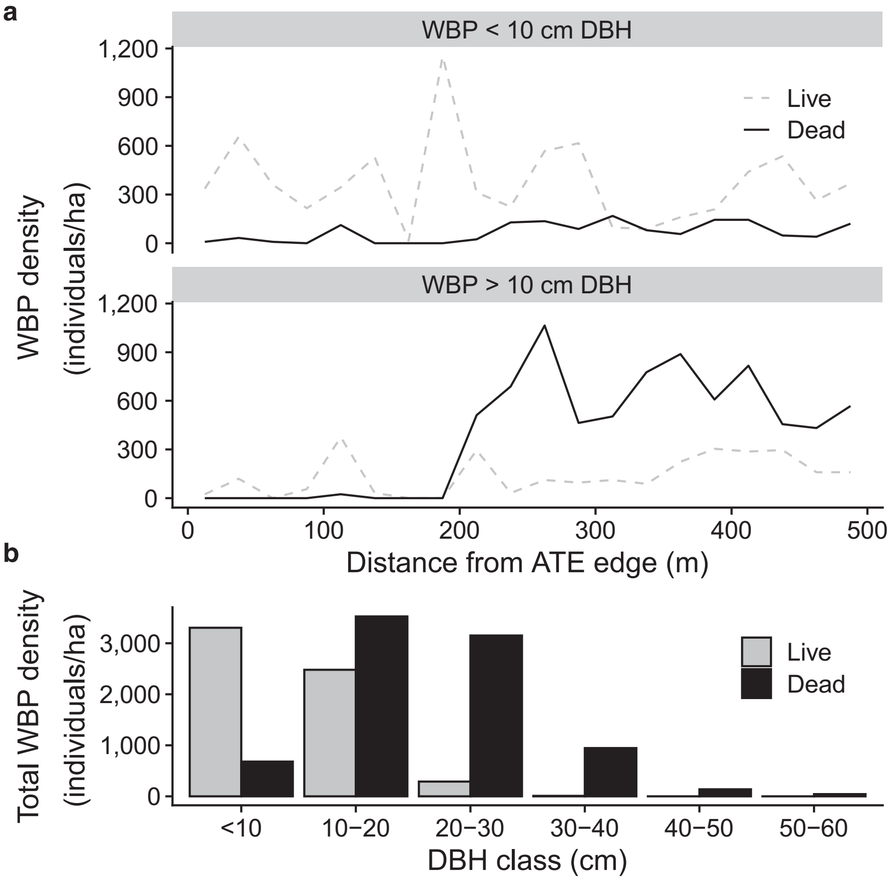

FIG. 4. (a) Density (number of individuals/ha) of live (dashed gray lines) and dead (solid black lines) whitebark pine (WBP) in two size classes (top plot: krummholz, small trees, saplings, and seedlings < 10cm dbh; bottom plot: trees or krummholz ≥ 10 cm dbh) along a single intensively sampled alpine treeline transect at the Gravelly site ($n = 1$). (b) Diameter distribution by dbh class of live (gray shading) and dead (black shading) whitebark pine along the same transect.

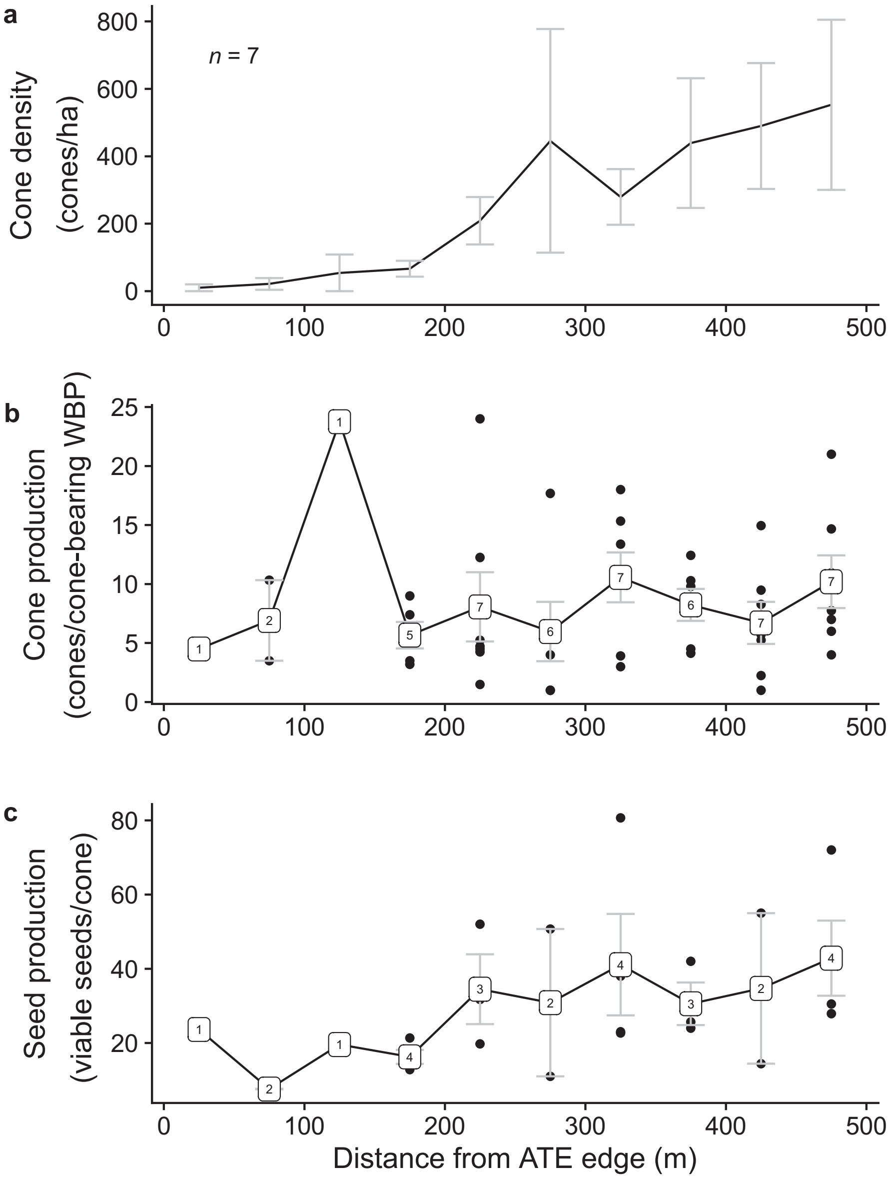

FIG. 5. (a) Cone density, (b) cone production (number of cones produced by each cone-bearing WBP), and (c) viable seed production (number of viable seeds per cone) for WBP along alpine treeline ecotones (ATEs) at three sites in the U.S. northern Rocky Mountains (Lemhi, Gravelly, and Beartooth). Values are mean ± SE. Numbers in boxes indicate sample size (number of transects plots containing cone-bearing trees or where cones were sampled for seed viability analysis) at each distance. Points show estimates for all plots containing cone-bearing WBP (b) or where cones were sampled (c). Error bars are absent when there was only one sample.

et al. 2007, Keppel et al. 2012, Morelli et al. 2016). Our findings suggest that populations of krummholz and other stunted treeline growth forms may serve as refugia for WBP, especially in areas with high pressure from MPB. Stunted WBP near the upper edge of ATEs persisted through the most recent climate-related MPB outbreaks despite mortality in the forests below. This pattern was clearly strongest in ATEs, which also have unique growth form transitions not found along OFEs. These results support the hypothesis that krummholz and other small treeline WBP escape MPB because of characteristics of their growth forms. Our finding of viable seed production in ATEs, although lower than in forests below, supports the idea that surviving WBP in ATE habitats can be functional “stepping stone” refugia (Hannah et al. 2014). Additionally, in our random sample of subalpine forests of the U.S. Northern Rocky Mountains, we found that many more WBP survived recent MPB outbreaks than were killed. This unexpected finding, given concern for the future of WBP and high mortality in some areas, suggests that at least some WBP forest populations within this landscape may

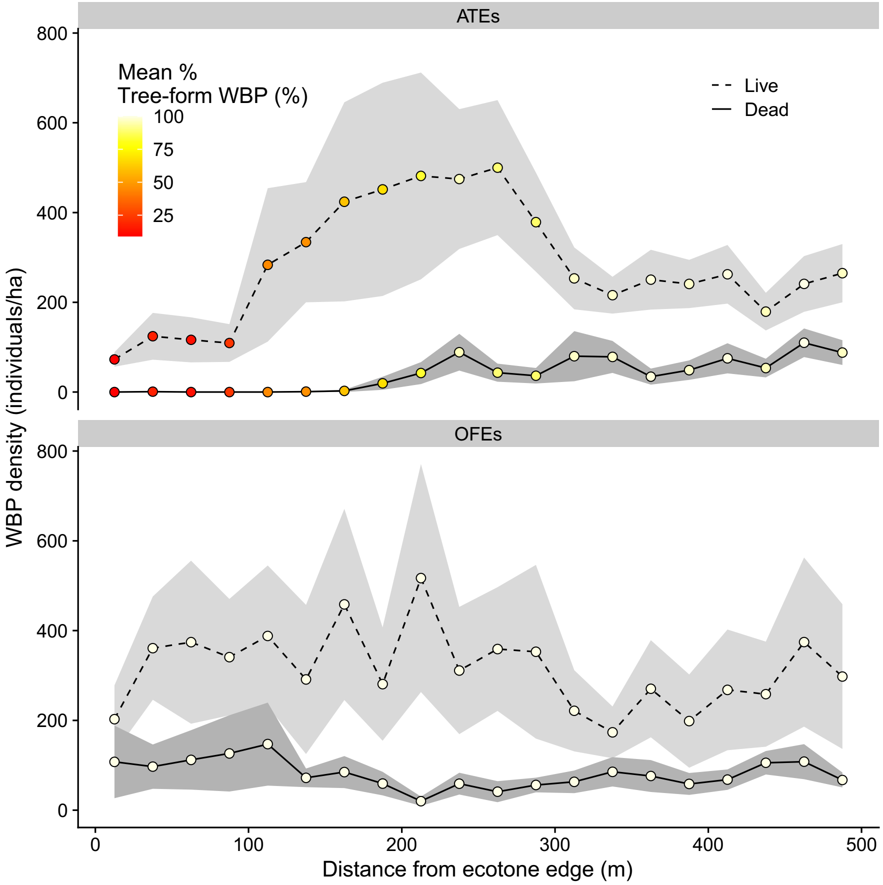

FIG. 6. Mean density of living (dashed black lines) and mountain-pine-beetle-killed (solid black lines) whitebark pine (WBP) along alpine treeline ecotones (ATEs; top plot) and other forest ecotones (OFEs; bottom plot) at $n = 10$ sites. These data exclude seedlings and saplings. Symbol color represents the mean percentage of tree-form (>3 m tall) whitebark pine (in contrast with krummholz growth forms; at least 1 m wide and 1 m tall and as wide or wider than tall) at each transect position: white represents 100% tree-form (0% krummholz) and red 0% tree-form (100% krummholz). Gray bands represent ± SE.

remain stable in the short term, despite the widespread MPB impacts throughout the region.

Several possible mechanisms could enable WBP in the upper ATE to escape MPB attack. Stems of WBP in ATE habitats (i.e., stunted trees and krummholz) are known to have smaller diameters, and at lower densities, than in the subalpine forest (as we have shown; also Clausen 1965). Proximally, the causes of MPB preference for large stems appear to be related to dispersal and detection. Smaller-diameter pines that are located near trees that the beetles emerge from can be attacked, by presenting a larger target than distant small trees (Mitchell and Preisler 1991, Perkins and Roberts 2003). Small stems combined with greater distance from large emergence trees (i.e., low host density) may make WBP in ATEs less detectable to MPBs. Additionally, krummholz stems are typically prostrate in stature and are often covered in a mat of dense foliage. These attributes may make krummholz individuals less likely to be attacked by MPB because typical visual cues related to vertical bare stems are disrupted (Shepherd 1966, Strom et al. 1999, Campbell and Borden 2006*a*, *b*) or from physical blockage of the stem. Another potential mechanism of escape from MPB attack is the dilution of pheromone signals (or of beetle flight) by wind (Thistle et al. 2004). Although all forest edges are likely windier than forest interiors, ATE edges are likely even windier than their lower elevation counterparts. Conversely, upslope winds might facilitate transport of beetles to habitats above treeline.

Besides escaping MPB attack altogether, it is also plausible that WBP in the upper ATE can survive attack. Lower temperatures in the ATE should reduce beetle brood success (Dooley et al. 2014), which could increase the chances of WBP survival after attack. Temperatures generally decrease with increasing elevation (due to adiabatic lapse rates; Barry 2008) and MPB developmental rates and population dynamics are sensitive to temperature (Bentz et al. 1991, Logan and Powell 2001, Hicke et al. 2006), as is the case for most insects. Unfortunately, we do not have fine-scale temperature data along our treeline transects during the outbreaks (~2001–2009;

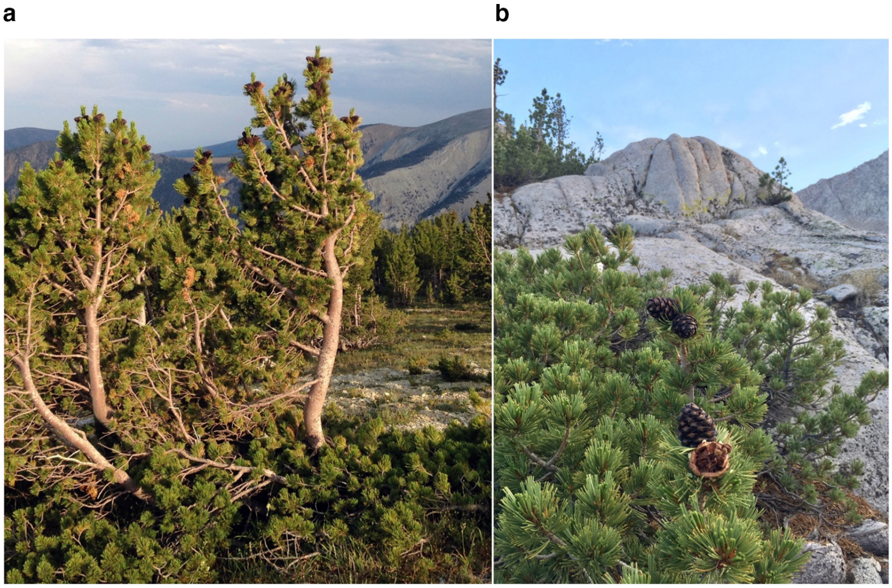

Fig. 7. Cone production in whitebark pines near treeline. (a) Abundant 2018 cone crop on small-diameter and krummholz in the Pioneer Mountains, Montana, USA. (b) Current year (2020) and previous year cones on krummholz in the Sierra Nevada Mountains, California, USA. Photo credits: C. T. Maher.

Creeden et al. 2014) and cannot directly evaluate whether temperatures were low enough to inhibit larvae development. It is also conceivable that growth form could play a role in enhancing post-attack survival. If phloem thickness is lower in krummholz (not measured in this study), for example, this could also reduce MPB brood success (Amman 1972, Lahr and Sala 2014). However, we observed that krummholz mortality from MPB was exceedingly rare; we found only one dead krummholz with signs of MPB attack across the 10 field sites (834 total krummholz counted). We reason this likely indicates krummholz were never attacked: we would expect reduced MPB brood success to reduce relative mortality of krummholz compared to trees, not to drive it to zero. However, we were not able to directly examine live WBP for signs of attack, and thus cannot eliminate this possibility. An improved understanding of beetle dispersal, attack density, and larval growth in treeline environments, e.g., through further observation, beetle trapping, or manipulative experiments, is required to further distinguish the mechanisms of WBP survival in ATEs.

Even if WBP in the ATE can currently survive MPB outbreaks, these environments will likely not remain static indefinitely: some treelines have been observed to shift upward in elevation (Harsch et al. 2009). Many krummholz ATEs, however, have been found to be changing little or not at all (Harsch et al. 2009, Harsch and Bader 2011). Still, elevational shifts and changes in growth form at krummholz treelines have been documented (e.g., LaMarche and Mooney 1972, Hessl and Baker 1997). It is therefore conceivable that contemporary krummholz may eventually become trees, possibly exposing them to MPB attack. However, the development of an individual WBP changing growth form from krummholz to a larger tree that is vulnerable to MPB may take several decades or more. For example, Millar et al. (2004) observed a mean age of 37 yr in vertical branches (the potential *beginnings* of trees) emerging from WBP krummholz. The development time may be sufficient to allow local increases in reproduction and establishment of a new krummholz refugia zone upslope (where such terrain is available) before a worst-case scenario with heavy mortality in these “new” trees. Additionally, climate change refugia need not be static, instead acting as “slow lanes” that reduce the pace of change such that a species can maintain populations in the foreseeable future (Morelli et al. 2020).

The periodic nature of mast seeding in WBP (Crone et al. 2011) and the longevity of some krummholz suggests that occasional mast seeding events may allow reproductive contributions from ATE habitats over long time spans. Populations of long-lived species can have low apparent fecundity yet still maintain positive population growth due to low mortality rates (Barber 2013). In the year that we sampled (2016), overall reproductive output was lower in treeline habitats than in the subalpine forest. Nonetheless, our results indicate that viable seed production does occur in these habitats, consistent with general observations that reproduction does occur at treelines, albeit typically in lower quantity than at lower elevations due to the resource costs of reproduction (Körner 2012, Sala et al. 2012). Although anecdotal, we observed an abundant cone crops at two disparate treeline sites in August 2018 in the Pioneer Mountains, Montana, and in July 2020 in the Sierra

TABLE 2. Whole-transect results from both ecotone types at each field sample site.

Site and ecotone type	Proportion of WBP: Tree form	Proportion of WBP: Killed by MPB	Pre-outbreak WBP density (no./ha)
Beartooth			
ATE	0.43 ± 0.11	0.04 ± 0.02	319 ± 67.7
OFE	1.00 ± 0.00	0.05 ± 0.02	453 ± 51.2
Cedar			
ATE	0.71 ± 0.10	0.16 ± 0.04	365 ± 89.1
OFE	1.00 ± 0.00	0.27 ± 0.07	139 ± 21.6
Gravelly			
ATE	0.66 ± 0.10	0.14 ± 0.05	344 ± 75.9
OFE	1.00 ± 0.00	0.85 ± 0.04	368 ± 78.9
Hoback			
ATE	0.71 ± 0.12	0.17 ± 0.06	143 ± 53.2
OFE	1.00 ± 0.00	0.74 ± 0.06	148 ± 24.5
Lemhi			
ATE	0.64 ± 0.09	0.02 ± 0.02	242 ± 37.5
OFE	1.00 ± 0.00	0.03 ± 0.02	285 ± 54.8
Pioneer			
ATE	0.83 ± 0.08	0.03 ± 0.02	949 ± 156.6
OFE	1.00 ± 0.00	0.01 ± 0.01	1411 ± 105.4
Snowcrest			
ATE	0.67 ± 0.10	0.24 ± 0.06	168 ± 31.5
OFE	1.00 ± 0.00	0.46 ± 0.04	362 ± 38.3
Targhee			
ATE	0.93 ± 0.03	0.08 ± 0.04	149 ± 18.5
OFE	1.00 ± 0.00	0.21 ± 0.05	309 ± 36.3
Wind River			
ATE	0.80 ± 0.11	0.11 ± 0.05	298 ± 58.4
OFE	1.00 ± 0.00	0.20 ± 0.04	406 ± 38.1
Woodward			
ATE	0.80 ± 0.08	0.17 ± 0.05	284 ± 41.8
OFE	1.00 ± 0.00	0.34 ± 0.08	109 ± 28.6

Notes: Values are means ± SE. Ecotone type is alpine treeline ecotone (ATE) or other forest ecotone (OFE). Data columns are proportion of tree-form whitebark pine (WBP), proportion of WBP killed by mountain pine beetle (MPB), and pre-MPB-outbreak density of WBP (number/ha) across transects (n = 20 plots per transect). Proportion tree-form is relative to krummholz growth forms. WBP density includes WBP > 3 m tall (trees) and at least 1 m wide × 1 m tall (krummholz).

Nevada mountains, California, USA (Fig. 7). It is possible that if ATEs were the only source of WBP seed, Clark’s Nutcrackers could consume the majority of these sparse seeds, rather than leaving them to germinate in former caches. Yet WBP krummholz can be extremely long lived: individuals over 1,700 yr old, much older than the oldest known WBP tree (1,267 yr; Perkins and Swetnam 1996), have been found in the Sierra Nevada mountains, California, USA, persisting via branch-layering despite multiple losses of the older stems (King and Graumlich 1998). Furthermore, there is direct genetic evidence of krummholz-origin seed establishment within krummholz mats (Rogers et al. 1999). Thus, over longer time periods, there may be many opportunities for ATE habitats to contribute to WBP populations elsewhere.

Although treeline habitats may serve as “disturbance refugia” (Krawchuk et al. 2020) for WBP populations from MPB outbreaks, these habitats are not immune to fire (Cansler et al. 2018) and other disturbances. Cansler et al. (2016) found some treeline communities are now being burned by wildfires. Thus as climates warm, fire risk to treeline WBP may also increase (Millar and Delany 2019). Smaller-diameter WBP are especially vulnerable to mortality from fire (e.g., Keane and Parsons 2010) but fire poses a potential threat to whole populations because of low fire tolerance in WBP. In contrast with early hypotheses about fire resistance and dependence (e.g., Arno 1986), WBP of all sizes are likely to die from any amount of bole scorch (Hood et al. 2008). On the other hand, post-MPB outbreak WBP stands may be *less* susceptible to fire than their intact living counterparts due to reductions in fine canopy fuels, although this effect appears to be mediated by time since MPB outbreak (Jenkins 2011, Millar and Delany 2019).

WBP of all sizes and ages are also vulnerable to white pine blister rust (WPBR) infections (Tomback et al. 1995), although several studies indicate the population effects of this disease are smaller than those of MPB.

Although we did not quantify WPBR infections in our study, the disease has been documented in krummholz (Resler and Tomback 2008). However, a 12-yr demographic analysis of WBP populations in Crater Lake National Park, Oregon, USA, found that MPB, not WPBR, lowered population growth rates, despite a nearly 45% WPBR infection rate by the end of the study (Jules et al. 2016). Maloney et al. (2012) similarly found that WBP populations in the Lake Tahoe Basin, California, USA were stable due to high survivorship despite a 35% (range 1–65%) mean WPBR infection rate. Although demographic effects of WPBR may be greater elsewhere, like the Crown of the Continent ecosystem (northwest Montana, USA into the Canadian provinces of British Colombia and Alberta) with ~80% of WBP infected (Smith et al. 2013), they indicate that MPB outbreaks can present a more acute and severe threat to WBP populations than WPBR. However, these studies documented increasing infection rates, suggesting that WPBR could become a more important factor.

Surviving WBP below treeline may have short-term positive effects on populations, given their greater abundance and reproductive potential than treeline WBP. Although we could not document size distributions across our study area, we did observe that survivors in the most heavily impacted forests were more often smaller diameter saplings (all WBP ≥ 9 m tall were counted as trees). Our single size transect also reflected this pattern (Fig. 4). Previous studies used basal area to infer massive WBP population declines after MPB outbreaks (e.g., Kegley et al. 2011, Goeking and Izlar 2018). Basal area, however, is a misleading indicator of demographic processes, because basal area will decline exponentially with the loss of a few large trees even with survival of large numbers of smaller trees. Counter to the intuitive focus on large trees, Jules et al. (2016) found that growth rates of WBP populations were most sensitive to numbers of WBP in the 0.01–10 cm DBH size class, which had the highest survivorship in their study stands.

Beyond this WBP–MPB system, our study suggests the possibility that refugia for plant populations may exist in marginal habitats where the environment induces phenotypic changes to plants that also affect the species' susceptibility to phytophagous insects. There are other examples from the literature that further indicate this possibility. For example, Piper and Fajardo (2014) reported a sharp elevation boundary in defoliation of southern beech (*Nothofagus pumilio* (Poepp. & Endl.) Krasser) in Chilean Patagonia caused by caterpillars of the moth *Ormiscodes amphimone* Fabricius, which they attributed to an elevation-related thermal threshold of that particular caterpillar. Earlier experimental work by Garibaldi et al. (2011) revealed that smaller leaves in *N. pumilio* associated with increasing elevation was an important mechanism in reducing folivore damage. Thus, phenotypic plasticity, e.g., a species' ability to assume different growth forms depending on the environment, may be a crucial factor. Evolutionary theory predicts that phenotpyic plasticity may have important adaptive significance for species success in marginal environments (Chevin and Lande 2011). For example, a pattern of reduced bark beetle-caused mortality near white spruce (*Picea glauca*) treelines was observed at some sites in the Yukon Territory, Canada, although the most impacted site had mortality through the treeline ecotone (Mazzocato 2015). Although white spruce does form krummholz (e.g., Caccianiga and Payette 2006), it does not often form extensive dense krummholz patches as in WBP and generally exhibits less variation in growth form (C. Maher, *personal observation*). Patterns like the one we observed are clearly not universal to treelines, rather they may be species specific. Identifying marginal habitats as refugia require both an identification of a pattern of survival, but also an understanding of the mechanisms that produce the pattern, as we attempted in this study.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS FOR WHITEBARK PINE

ATE habitats afford potential climate change refugia for WBP from MPB attacks. The krummholz and stunted trees that exist in these high mountain populations are a mechanism by which WBP could remain in a landscape over long time scales as climate change causes fluctuations in disturbance regimes. Furthermore, MPB-impacted forests with surviving WBP may retain populations, due in part to the growth potential of small-diameter individuals. These populations are likely to persist because insect outbreaks tend to be episodic, i.e., the degree of mortality pressure on tree populations might not be constant into the future, allowing some recovery between outbreaks. It further suggests that there may not be a need for management intervention in some locations, and that some management actions may be especially harmful, e.g., the use of prescribed fire where survivors are smaller trees, saplings, and seedlings. While uncertainty remains about the future of survivors in subalpine forests below the treeline, WBP in ATEs may allow for population persistence and may eventually contribute to population recovery in other habitats.

Our findings suggest that ATE habitats should be considered valuable attributes of management units containing WBP. While many common management actions (e.g., silviculture or fuels treatments) might not be applicable directly in ATE habitats, planting WPBR-resistant seedlings or directly sowing seeds is possible (Keane 2018), if appropriate given the sensitivity of these environments or their status as federally designated Wilderness (Tomback 2014). Given that planting WPBR-resistant seedlings is projected to have benefits over centuries, not decades (Keane et al. 2017), it makes sense to ensure that resistant genotypes are represented in treeline environments where WBP also have the best chance of surviving future MPB outbreaks. Additionally, because treelines are an important front of climate change, promoting and maintaining already MPB-resistant ATE populations of WBP that are also resistant to WPBR will be an important aspect of ensuring the species' success into the future.

Acknowledgments

Funding for this research was provided by grants from the Montana Institute on Ecosystems, the Whitebark Pine Ecosystem Foundation, and the Associated Students of the University of Montana as well as the NIFA McIntire-Stennis Cooperative Forestry Program [project accession no. 225109] from the USDA National Institute of Food and Agriculture. We thank David Foushee and Kevin Egan at the USDA Forest Service Coeur d'Alene Nursery for seed x-rays and for providing guidance on identifying viable seed from x-ray imagery. Wally Macfarlane generously shared GIS data on mountain pine beetle impacts in WBP forests of the Greater Yellowstone Ecosystem. We thank Cullen Weisbrod, Jesse Bunker, Alyssa Hands, Haley Wiggins, Michael Fazekas, and Danica Born-Ropp for their help field sampling. We thank two anonymous reviewers for insightful comments. The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2274/full

DATA AVAILABILITY

Data are available from Mendeley Data (Maher 2020): http://dx.doi.org/10.17632/j2zhdc8rtz.1