

Cal Poly Humboldt

Digital Commons @ Cal Poly Humboldt

H5II Conference

Conference Proceedings

Alpine Treeline Ecotones are Potential Refugia for a Montane Pine Species Threatened by Bark Beetle Outbreaks

Colin T. Maher

Constance I. Millar

David L.R. Affleck

Robert E. Keane

Anna Sala

See next page for additional authors

Follow this and additional works at: <https://digitalcommons.humboldt.edu/h5ii>

Authors

Colin T. Maher, Constance I. Millar, David L.R. Affleck, Robert E. Keane, Anna Sala, Claudine Tobalske, Andrew J. Larson, and Cara R. Nelson



Alpine Treeline Ecotones are Potential Refugia for a Montane Pine Species Threatened by Bark Beetle Outbreaks

Colin T. Maher, <cmbistlecone@gmail.com>, WA Franke College of Forestry and Conservation, The University of Montana; **Constance I. Millar**, <connie.millar@usda.gov>, Pacific Southwest Research Station, USDA Forest Service; **David L.R. Affleck**, <david.affleck@umontana.edu>, WA Franke College of Forestry and Conservation, The University of Montana; **Robert E. Keane**, <robert.e.keane@usda.gov>, Rocky Mountain Research Station, Missoula Fire Science Laboratory, USDA Forest Service; **Anna Sala**, <asala@mso.umt.edu>, Division of Biological Sciences, The University of Montana; **Claudine Tobalske**, <claudine.tobalske@mso.umt.edu>, Spatial Analysis Lab, Montana Natural Heritage Program, The University of Montana; **Andrew J. Larson**, <a.larson@umontana.edu>, WA Franke College of Forestry and Conservation, The University of Montana; **Cara R. Nelson**, <cara.nelson@umontana.edu>, WA Franke College of Forestry and Conservation, The University of Montana.

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 high mountains, WBP cross alpine treeline ecotones (ATEs) where growth forms transition from trees to shrub-like krummholz—some of which survived recent outbreaks. This observation motivated the hypothesis that ATEs are refugia for WBP because krummholz escape MPB attack and can reproduce. 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 random sites in the US Northern Rocky Mountains. We also surveyed reproduction at 3 ATE sites. Mortality was nearly absent in upper ATEs (mean \pm 1 s.e. % dead across all sites of $0.03 \pm 0.03\%$ 0-100 m from the edge and $14.1 \pm 1.7\%$ 100-500 m from the edge) but was above 20% along OFEs ($21.4 \pm 5.2\%$ 0-100 m and $32.4 \pm 2.7\%$ 100-500 m). We observed lower reproduction in upper ATEs (16 ± 9.9 cones-ha⁻¹ and 12.9 ± 5.3 viable seeds-cone⁻¹ 0-100 m) versus forests below (317.1 ± 64.4 cones-ha⁻¹ and 32.5 ± 2.5 viable seeds-cone⁻¹ 100-500 m). Uniquely high survival of krummholz and small trees in the ATE indicate they escaped MPB attack, supporting the refugia hypothesis. However, low reproduction suggests ATE refugia function over longer time periods.

Keywords: boundary, climate change refugia, edge, mountain pine beetle, *Pinus albicaulis*, tree mortality, whitebark pine

INTRODUCTION

The upper elevation boundaries of whitebark pine (*Pinus albicaulis* Emgelm.; hereafter 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 to areas with dispersed short-stature trees 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 mountain pine beetle (MPB) outbreaks, ATE habitats are hypothesized to serve as refugia: Logan et al. (2010) and Macfarlane et al. (2013) observed that live WBP krummholz in ATEs persisted above forests with extensive MPB-caused mortality (figure 1). 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...”

Refugia for WBP from MPB outbreaks is plausible in ATEs for two principal reasons. First, krummholz WBP are not genetically distinct from tree WBP (Rogers et al. 1999). Thus, krummholz or their offspring would likely grow as trees in a milder environment. Second, MPBs are 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 underpin mechanisms that could maintain WBP refugia from MPB in ATE habitats.

Despite the plausibility of the ATE refugia hypothesis, there are alternate explanations for a pattern of low WBP mortality above 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”), depending on the herbivore’s behavior (Cadenasso and Pickett 2000). Interruption of MPB pheromone signals by wind may occur at all forest boundaries—pheromone plumes are diluted by circulation (Thistle et al. 2004). Because krummholz 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.

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 that 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, and to examine overall survival in post-MPB outbreak WBP forests in the U.S. Northern Rocky Mountains. We asked:

- (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 overall post-outbreak survival status of WBP populations in the US Northern Rocky Mountains?

METHODS

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). We used a detailed 2008 aerial survey focused specifically on MPB-caused mortality of WBP in the Greater Yellowstone Ecosystem (Macfarlane et al., 2013) and Maps of MPB-caused mortality in the US states of Idaho, Montana, and Wyoming from the USDA Forest Service’s Forest Health Protection aerial Insect and Disease Surveys (IDS; Forest Health Protection, 2014). We filtered 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 in USGS GAP land cover (US Geological Survey Gap Analysis Program (GAP) 2011). The final sampling frame was a ~7,480 km² area.

We selected field sampling locations within the sampling frame by randomly placing 10 points in ArcGIS ($n = 10$). Near 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 bordering the alpine or other non-forest vegetation). ATE edges were the highest elevation ‘outpost’ krummholz visible from satellite imagery. We defined OFEs as WBP forest boundaries with non-forest openings formed by avalanche paths, forest-meadow interfaces, geologic and topographic features, or other forest margins not associated with elevation-related boundaries. ATE transects were oriented downslope following the elevational transition from krummholz to forest. OFE transects were oriented perpendicular to the WBP edge extending into the forest, regardless of slope direction. All transects were 50 m wide and 500 m long. Transects were divided into twenty contiguous 50 m by 25 m rectangular plots (the unit of analysis). Transect plot outlines were ported to a GPS device to guide 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 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 across and at least as wide as they were tall but were < 3 m tall. We used these classifications to calculate the proportion of tree-form WBP in each transect plot (n WBP trees / (n WBP trees + WBP krummholz)). We recorded cause of death for all dead WBP that retained bark—we assumed

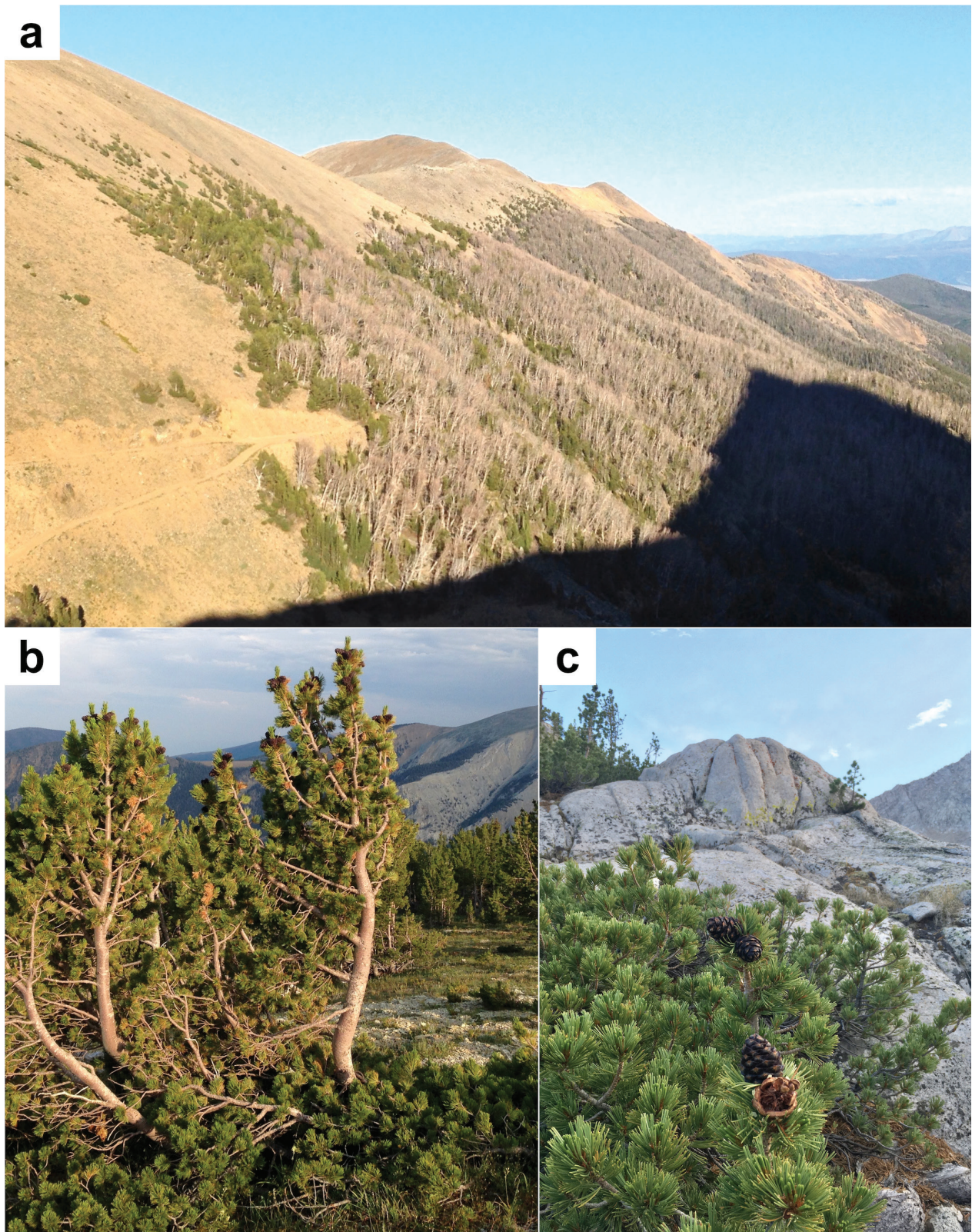


Figure 1. Survival and cone production in whitebark pine near treelines. a) Surviving whitebark pines near treeline (green band at upper edge of forest) with extensive mortality in the subalpine forest below (grey trees). Tobacco Root Mountains, Montana, U.S.A. b) Abundant 2018 cone crop on small-diameter and krummholz whitebark in the Pioneer Mountains, Montana, USA. c) 2020 current year and previous year cones on krummholz whitebark in the Sierra Nevada Mountains, California, USA. Photo credits: C. T. Maher. (Maher et al. 2021)

that WBP 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). 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.

Analyses and further methods are described in Maher et al. (2021).

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 sub-alpine forest; figure 2). Specifically, we observed only one krummholz at one site (overall mean \pm 1 s.e. 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 100–500 m. In contrast with ATEs, mortality in OFEs extended to the ecotone edge and was higher overall than in ATEs: we observed 21.4 ± 5.2 % MPB-killed within 100 m from OFE edges and 32.4 ± 2.7 % between 100–500 m, although some sites had higher mortality near OFE edges (75–100 %). These patterns were reflected by a significant interactive effect on total MPB-killed WBP between distance from edge and ecotone type ($\chi^2 = 45.5$, $df = 2$, $P < 0.0001$).

We found an overall higher density of living (mean \pm 1 s.e.; 286.3 ± 72.0 WBP·ha⁻¹) versus MPB-killed (62.4 ± 16.4 WBP·ha⁻¹) WBP on a whole transect basis across our study region when including both ecotone types (two-sample Wilcoxon signed rank test, $P = 0.002$; figure 2). 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⁻¹; $P = 0.002$); there was no significant difference in OFEs (299.4 ± 128.3 vs 84.4 ± 31.0 WBP·ha⁻¹; $P = 0.2$).

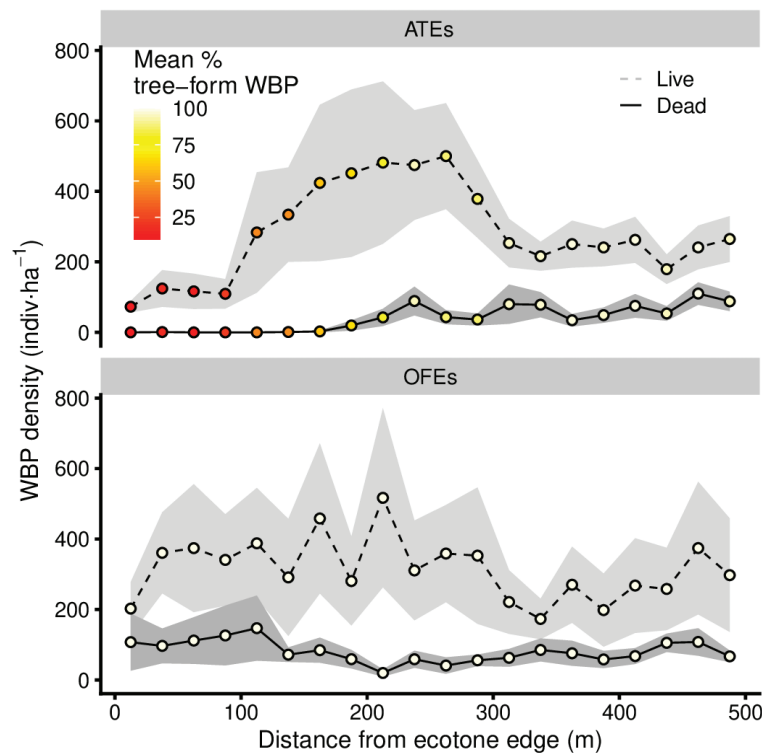


Figure 2. Mean density of living (dashed black lines) and mountain pine beetle-killed (solid black lines) whitebark pine (WBP) along alpine treeline ecotones (ATEs; top plot) and other forest ecotones (OFEs; bottom plot) at $n = 10$ sites. This data excludes seedlings and saplings. Symbol color represents 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). Grey bands represent \pm 1 standard error of the mean. (Maher et al. 2021)

CONCLUSIONS & 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 could persist because insect outbreaks tend to be episodic—i.e., the pressure on tree populations might not be constant into the future, allowing some recovery between outbreaks. Further, there may not be a need for management intervention in some locations, and some management actions may be 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 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.

ACKNOWLEDGEMENTS

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.

REFERENCES

- Arno, SF. 1984. *Timberline: Mountain and Arctic Forest Frontiers*. Seattle, WA, USA: Mountaineers Books.
- Cadenasso ML, and STA Pickett . 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *J Ecol.* 88(1):31–44. doi.org/10.1046/j.1365-2745.2000.00423.x.
- Cole, W. E., and GD Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. Research Note INT-95. USDA Forest Service Intermountain Range and Experiment Station, Ogden, Utah, USA.
- ESRI (Environmental Systems Resource Institute). 2010. ArcGIS. ESRI, Redlands, California, USA.
- Forest Health Protection. 2014. Insect and disease detection survey database (IDS). Digital Data. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team. <http://foresthealth.fs.usda.gov/ids>.
- Griggs, RF. 1946. The timberlines of Northern America and their Interpretation. *Ecology.* 27(4):275–289. doi.org/10.2307/1933539.
- Keane, RE. 2018. Managing wildfire for whitebark pine ecosystem restoration in western North America. *Forests.* 9(10):648. doi.org/10.3390/f9100648.
- Keane, RE, LM Holsinger, MF Mahalovich, and D F Tomback. 2017. Restoring whitebark pine ecosystems in the face of climate change. General Technical Report RMRS-GTR-36. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. doi.org/10.2737/RMRS-GTR-361.

Körner C, and J Paulsen. 2004. A world-wide study of high altitude treeline temperatures. *J Biogeogr.* 31(5):713–732. doi.org/10.1111/j.1365-2699.2003.01043.x.

Logan JA, WW MacFarlane, and L Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecol Appl.* 20(4):895–902. doi.org/10.1890/09-0655.1.

Macfarlane WW, JA Logan, and WR Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. *Ecol Appl.* 23(2):421–437. doi.org/10.1890/11-1982.1.

Maher CT, CI Millar, DLR Affleck, RE Keane, A Sala, C Tobalske, AJ Larson, and CR Nelson. 2021. Alpine treeline ecotones are potential refugia for a montane pine species threatened by bark beetle outbreaks. *Ecol Appl.* 31(3):e02274. doi.org/10.1002/eap.2274.

Rogers, DL, CI Millar, and RD Westfall. 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): associations with watershed and growth form. *Evolution* 53:74–90. doi.org/10.1111/j.1558-5646.1999.tb05334.x.

Thistle, HW, H Peterson H, G Allwine B Lamb, T Strand, EH Holsten, and PJ Shea. 2004. Surrogate pheromone plumes in three forest trunk spaces: Composite statistics and case studies. *For Sci.* 50(5):610–625. doi.org/10.1093/forestscience/50.5.610.

Tomback DF. 2014. The Wilderness Act and whitebark pine. *Nutcracker Notes.* 27(Winter/Spring 2014-2015):1–2. whitebarkfound.org/wp-content/uploads/2015/01/Nutcracker-Notes-27.pdf.

US Geological Survey Gap Analysis Program (GAP). 2011. National land cover, Version 2. www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap/science/land-cover-data-download?qt-science_center_objects=0#qt-science_center_objects.

USDA Forest Service. 2016. Region one vegetation classification, mapping, inventory and analysis report: common stand exam and inventory and monitoring field guide. Rep 16-5 v60. www.fs.fed.us/nrm/fsveg/index.shtml.